

# Mandibular and dental characteristics of Late Triassic mammaliaform *Haramiyavia* and their ramifications for basal mammal evolution

Zhe-Xi Luo<sup>a</sup>, Stephen M. Gatesy<sup>b</sup>, Farish A. Jenkins Jr.<sup>c,d,1</sup>, William W. Amaral<sup>c,d,2</sup>, and Neil H. Shubin<sup>a,3</sup>

<sup>a</sup>Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637; <sup>b</sup>Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912; <sup>c</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138; and <sup>d</sup>Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138

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As one of the earliest-known mammaliaforms, *Haramiyavia clemmensei* from the Rhaetic (Late Triassic) of East Greenland has held an important place in understanding the timing of the earliest radiation of the group. Reanalysis of the type specimen using high-resolution computed tomography (CT) has revealed new details, such as the presence of the dentary condyle of the mammalian jaw hinge and the postdentary trough for mandibular attachment of the middle ear—a transitional condition of the predecessors to crown Mammalia. Our tests of competing phylogenetic hypotheses with these new data show that Late Triassic haramiyids are a separate clade from multituberculate mammals and are excluded from the Mammalia. Consequently, hypotheses of a Late Triassic diversification of the Mammalia that depend on multituberculate affinities of haramiyids are rejected. Scanning electron microscopy study of tooth-wear facets and kinematic functional simulation of occlusion with virtual 3D models from CT scans confirm that *Haramiyavia* had a major orthal occlusion with the tallest lingual cusp of the lower molars occluding into the lingual embrasure of the upper molars, followed by a short palinal movement along the cusp rows alternating between upper and lower molars. This movement differs from the minimal orthal but extensive palinal occlusal movement of multituberculate mammals, which previously were regarded as relatives of haramiyids. The disparity of tooth morphology and the diversity of dental functions of haramiyids and their contemporary mammaliaforms suggest that dietary diversification is a major factor in the earliest mammaliaform evolution.

mammaliaform | haramiyid | occlusion | Rhaetic

**H**aramiyids are among the first mammaliaforms to appear during the Late Triassic in the evolutionary transition from pre-mammalian cynodonts. Their fossils have a cosmopolitan distribution during the Late Triassic to the Jurassic (1–8), tentatively with the youngest record in the Late Cretaceous of India (9). Most of these occurrences are of isolated teeth. For this reason, *Haramiyavia clemmensei* (1) holds a special place in mammaliaform phylogeny: It is the best-preserved Late Triassic haramiyid with intact molars, nearly complete mandibles, and also postcranial skeletal elements (Figs. 1 and 2 and *SI Appendix*, Figs. S1–S4) (1). By its stratigraphic provenance from the Tait Bjerg Beds of the Fleming Fjord Formation, East Greenland (Norian–Rhaetic Age) (7), *Haramiyavia* is also the oldest known haramiyid (5, 7). Haramiyids, morganucodonts, and kuehneotheriids are the three earliest mammaliaform groups that are distinctive from each other in dental morphology and masticatory functions (10–12).

Haramiyids are characterized by their complex molars with longitudinal rows of multiple cusps. The cusp rows occlude alternately between the upper and lower molars. Primarily because of similarities in molar morphology, haramiyids are considered to be related to poorly known therapsid relatives of the Late Triassic (5, 13) and leutherodontids of the Middle to Late Jurassic (14–17). Collectively haramiyids and leutherodontids are referred to as “haramiyidans” (10, 14, 15, 18, 19). Recent discoveries of diverse

leutherodontids or leutherodontid-related forms with skeletons from the Tiaojishan Formation (Middle to Late Jurassic) of China (18–20) have greatly augmented the fossil record of haramiyidans, ranking them among the most diverse mammaliaform clades of the Late Triassic and Jurassic.

Historically, it has been a contentious issue whether haramiyidans (later expanded to include therapsid relatives and leutherodontids) are closely related to the more derived multituberculates from the Middle Jurassic to Eocene (13) or represent a stem clade of mammaliaforms excluded from crown mammals (21, 22). The conflicting placement of haramiyidans was attributable in part to the uncertainties in interpreting the isolated teeth of most Late Triassic haramiyids (21, 22). More recent phylogenetic disagreements have resulted from different interpretations of mandibular characters in *Haramiyavia* (17–20, 23–25), which has not been fully described (figure 2 in ref. 1).

Here we present a detailed study of the mandibles and teeth of *Haramiyavia* from the exhaustive documentation during initial fossil preparation (Fig. 1 and *SI Appendix*, Figs. S1–S4), from scanning electron microscopy (SEM) images, and from computed tomography (CT) scans and 3D image analyses of the two fossil slabs with mandibles (MCZ7/95A and B), plus a referred

## Significance

The origins and earliest evolution of mammals can be deciphered by studying Late Triassic fossil relatives of modern mammals. The computed tomography study of *Haramiyavia* from the Late Triassic has revealed new information about the skull evolution and dental function in the forerunners of mammals. *Haramiyavia* had a unique way of chewing. Its teeth of multiple cusp-rows were adapted to omnivory or herbivory and are distinctive from the teeth of other early mammal relatives that are presumed to be insectivorous. On the mammal family tree *Haramiyavia* occupies a position crucial for dating the initial appearance of the major mammalian groups. Our reanalysis affirms that the earliest diversification of mammals occurred in the Jurassic.

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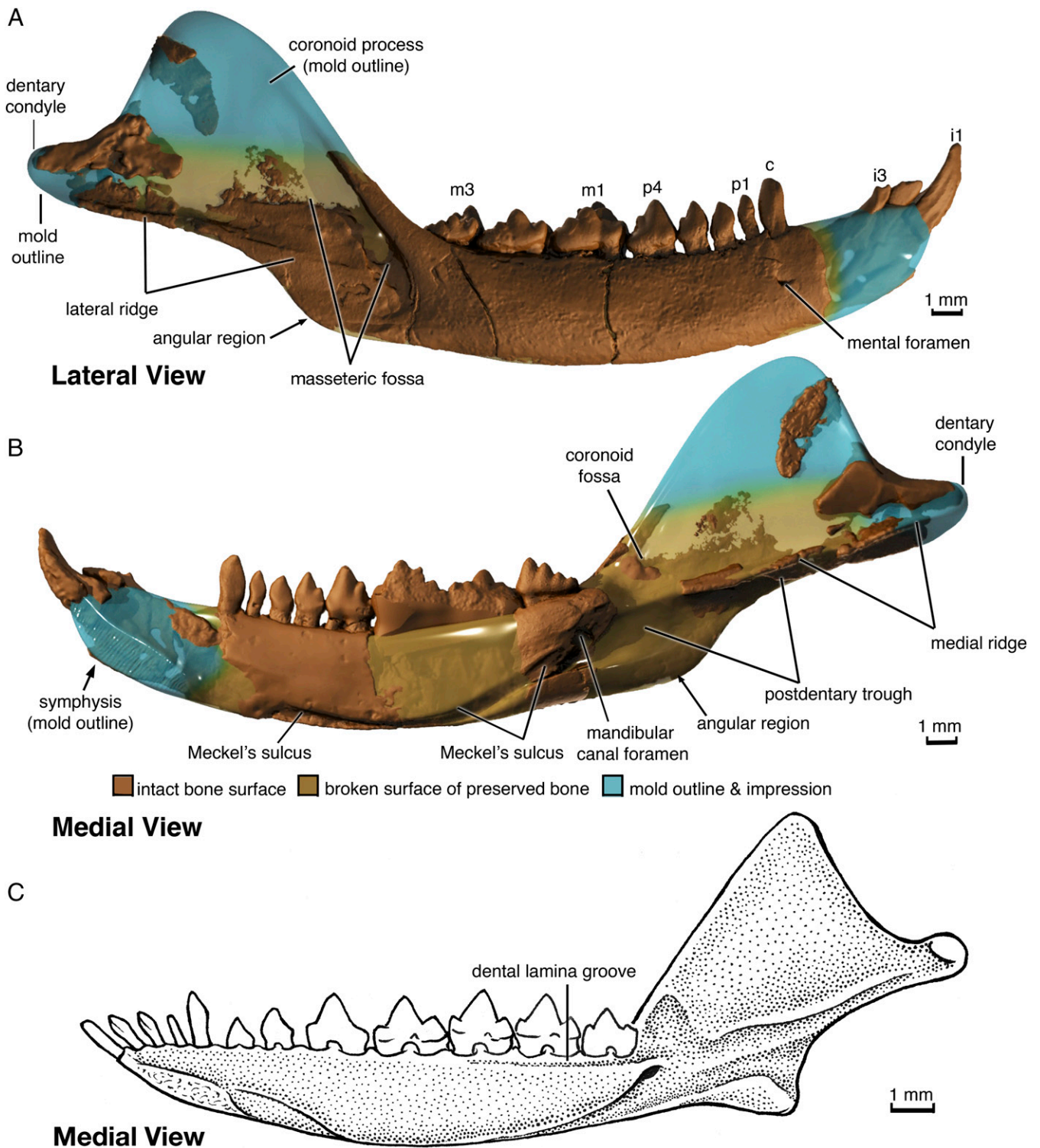
Data deposition: The data reported in this paper have been deposited in [Morphobank.org](http://Morphobank.org) (accession no. Project 2292).

<sup>1</sup>Deceased November 11, 2012.

<sup>2</sup>Deceased March 20, 2015.

<sup>3</sup>To whom correspondence should be addressed. Email: [nshubin@uchicago.edu](mailto:nshubin@uchicago.edu).

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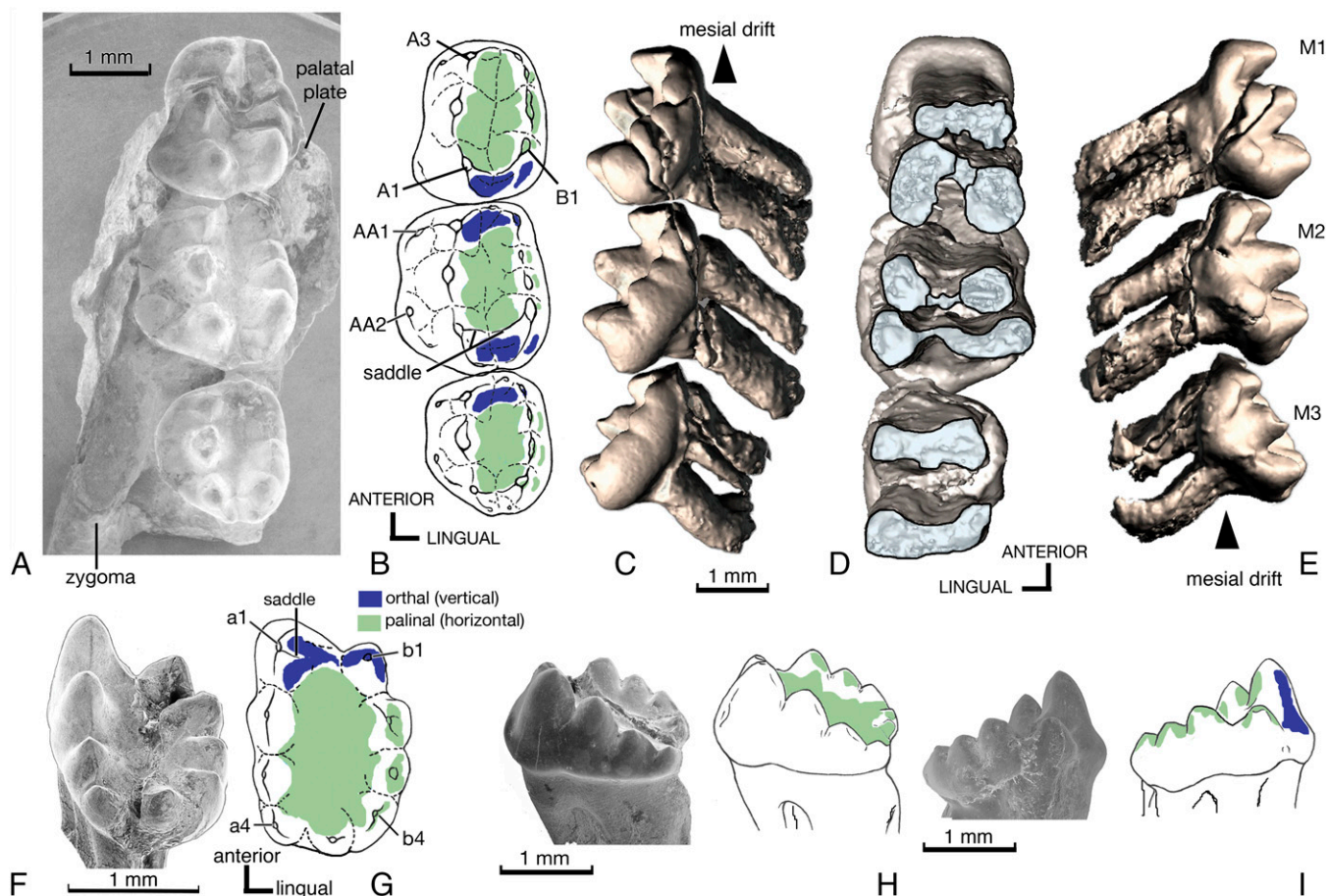


**Fig. 1.** (A and B) Composite reconstruction of *Haramiyavia clemmenseni* right mandible in lateral (A) and medial (B) views. Dark red: original bone with intact periosteal surface; brown: broken surface of preserved bone or remnant of bone; light blue: morphologies preserved in mold outlines or clear impression. (C) *Morganucodon* mandible in medial view.

specimen of upper molars in a maxilla (MCZ10/G95) (Figs. 2 and 3, *SI Appendix*, Figs. S5–S8 and Tables S2 and S3, and *Movie S1*). These new data are informative for testing alternative mammaliaform phylogenies (Fig. 4 and *SI Appendix*) and are useful for reconstructing evolutionary patterns of feeding function in the earliest mammaliaforms.

### Mandibular Features

All mandibular characteristics of *Haramiyavia* are documented by the paired stereo photographs of the original fossil slabs and by CT scans (Fig. 1, *SI Appendix*, Figs. S1–S4, and *Movie S1*). The dentary condyle is relatively small, posteriorly directed, and continuous with the lateral ridge in the masseteric fossa (Fig. 1

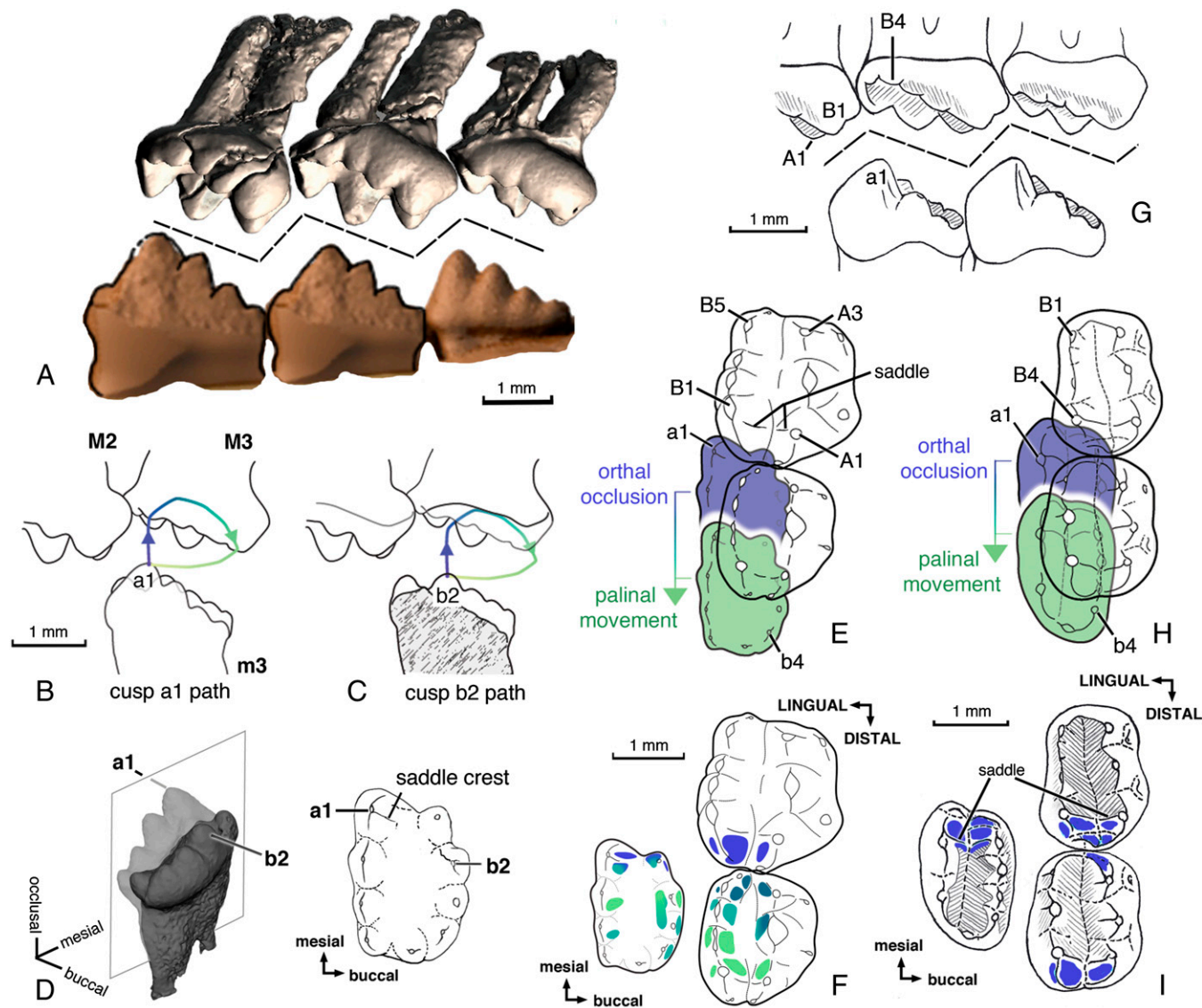


**Fig. 2.** Molar features of *Haramiyavia*. (A) Right M1–M3 in occlusal view (medio-lateral orientation by the zygomatic root and the palate). (B) Occlusal facets of upper molars. (C) Lingual view of M1–M3. (D) Root structures of upper molars (M1 and M2 show three partially divided anterior roots connected by dentine and two posterior roots connected by dentine; M3 has two anterior and two posterior roots connected respectively by dentine). These roots have separate root canals. (E) Buccal view of M1–M3. All roots are bent posteriorly, suggesting that crowns shifted mesially, relative to the roots, during the tooth eruption, also known as mesial drift of teeth (arrowhead), typical of successive eruption of multirooted postcanines. (F) SEM photograph of lower m3 in a posterior occlusal view. (G) Approximate extent of wear facets by orthal occlusion (a1 cusp in embrasure of upper molars) (blue) and palinal movement of b2–b4 cusps sliding across the median furrow of upper molars (green). (H) Lingual view of m3. There are no wear facets on lingual side of cusps a1–a4. (I) Buccal view of m3 showing wear facets on the buccal sides of cusps b1–b4 and on apices.

and *SI Appendix, Fig. S1*). The condyle and its lateral ridge are leveled to the molar alveolar line. The preserved bony parts of the condyle were extracted by CT from the two fossil slabs (*SI Appendix, Fig. S1*), and the bony parts on one slab are matched with the complementary outlines in the matrix of the opposite slab (*SI Appendix, Figs. S2–S4 and Table S3*). The masseteric fossa is bound by a low crest on its anterior and ventral margins and does not extend into the body (ramus) of the mandible (Fig. 1 and *SI Appendix, Fig. S1*). The coronoid process is typical of mammaliaforms, with its anterior margin forming a 150° angle to the molar alveolar line. There is a discernible angular region for the insertion of superficial masseter muscle, although there is no distinctive angular process. The medial side of the mandible shows a prominent postdentary trough and its medial ridge (Fig. 1 and *SI Appendix, Figs. S2–S4*). The posterior opening of the mandibular canal (alveolar foramen of ref. 1) is in the anterior part of the trough near the point where the trough continues into Meckel's sulcus (*SI Appendix, Fig. S4*). Meckel's sulcus is wider under m2 and m3 but is narrower under the premolars, maintaining a course parallel to the mandibular margin (Fig. 1). The coronoid fossa, although incomplete, is represented by a small rugose area on the left mandible. A right mandibular segment bearing m3 clearly shows the absence of

the dental lamina groove on the medial side. The mandibular symphysis extends to the level of p2 and is unfused (*SI Appendix, Figs. S2 and S4*). The left mandible has a single mental foramen below the canine, but the right mandible shows two foramina. Thus, the number of foramina is variable (*SI Appendix, Fig. S1*). There is no foramen in the masseteric fossa (Fig. 1).

*Haramiyavia* is distinguishable from premammaliaform cynodonts by its dentary condyle (10, 25–27). *Haramiyavia* lacks the dental lamina groove (*SI Appendix, Fig. S4*) and is more derived than *Sinoconodon* and *Morganucodon* in this regard (11, 28). However, its other mandibular features are typical of mammaliaforms and are plesiomorphic for mammals. Although the middle ear bones themselves are not preserved, we infer from the postdentary trough and its related structures that *Haramiyavia* had a mandibular middle ear (*sensu ref. 29*). These structures have vis-à-vis correspondence to the middle ear in other mammaliaforms and include the medial ridge supporting the surangular, the angular concavity (also a part of the trough) accommodating the reflected lamina of the angular, and the wide sulcus hypothesized to house the Meckel's cartilage, as seen in *Sinoconodon* (25), *Morganucodon* (13), and docodonts (30). Other plesiomorphies include the absence of the pterygoid fossa defined by an



**Fig. 3.** Molar occlusion of haramiyavids. (A) In *Haramiyavia* the upper and lower molars form an *en echelon* pattern, a series of parallel and step-like occlusal surfaces in lingual and buccal views (based on 3D scaled models from CT scans of MCZ7/G95 and MCZ10/G95). (B–E) In *Haramiyavia* are shown the occlusal paths of cusps a1–a4 of the lingual row (B), cusps b2–b4 of the buccal row (shown with the lingual half of the tooth cut away) (C), and tooth orientation and the cut-away plane (D). During the orthal occlusion phase, the tallest lingual cusp a1 occludes into the embrasure of the preceding and the opposing upper molars (B and E), and the tallest buccal cusp b2 occludes into the upper furrow and behind the A1–B1 saddle of the upper molar (C). During the palinal occlusion phase, cusps b1–b4 of the buccal row slide posteriorly in the upper furrow, and in the upper row cusps B5–B1 slide in the lower furrow (lower molars with blue and green shading, superpositioned by flipped upper molar in clear outlines) (E). (F) Extent of wear on molars during the orthal phase (blue) and the palinal movement (green) produced by OFA simulation (Movie S1). (G–I) In *Thomasia*, reconstruction of upper and lower molar series on the basis of wear surfaces and tooth crown morphology (revised from refs. 2, 3, and 10). (G) The *en echelon* occlusal surfaces in lingual view. (H) Orthal occlusion (blue) is followed by palinal occlusal movement (green). (I) Occlusal wear facets of molars. Facets worn by orthal occlusion are shown in blue, and facets worn by palinal occlusion are shown in gray hatching. Cusp and facet designations are after refs 3 and 6.

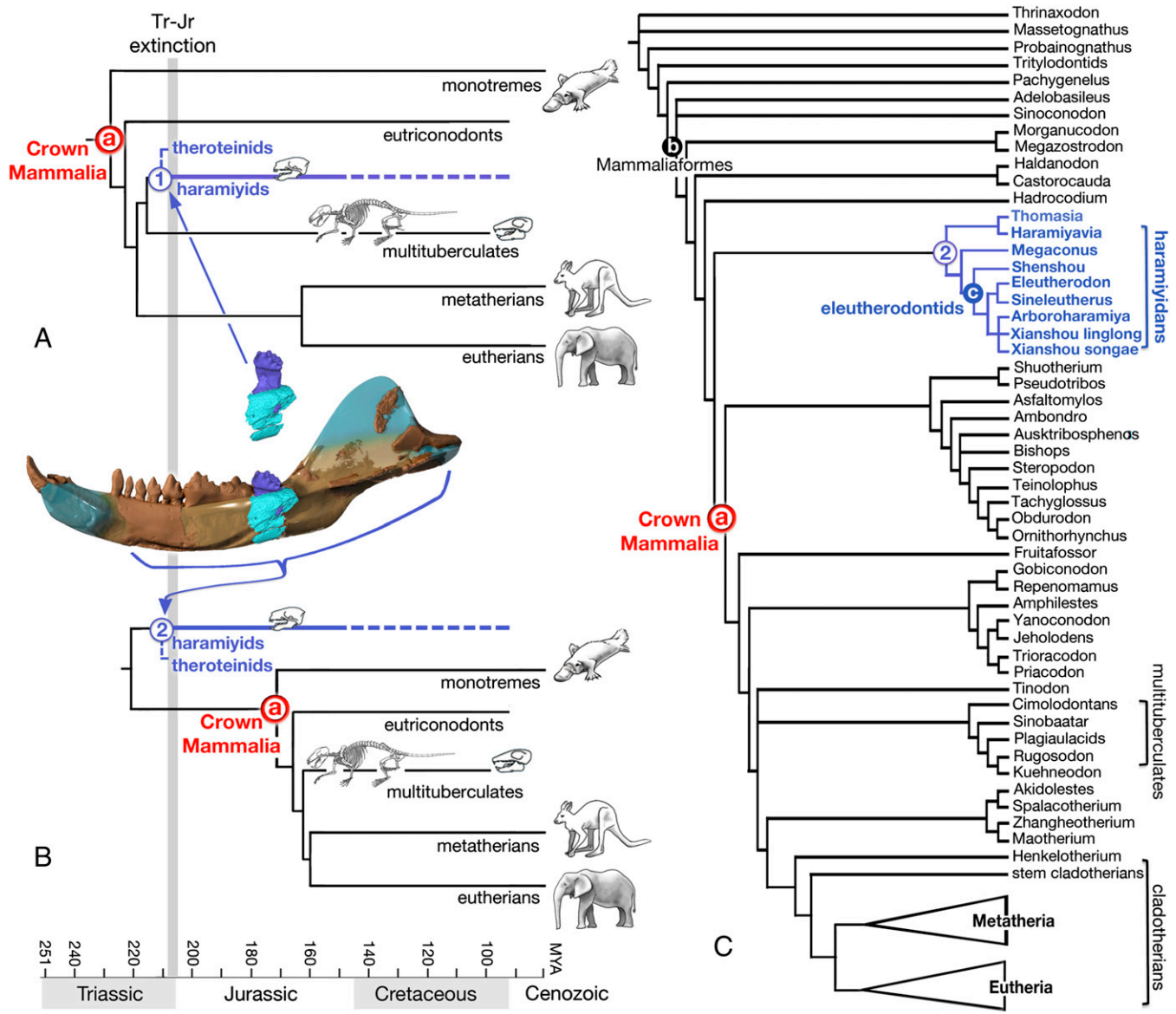
arcuate margin and an anterior location of the posterior mandibular foramen (Fig. 1).

The first report on *Haramiyavia* (1) illustrated only a small segment of the well-preserved mandibles (that under m3) in medial view (SI Appendix, Fig. S4). The mandibular features labeled in that figure (figure 2 in ref. 1) were questioned by Averianov et al. (17). Bi and colleagues (18) further argued that “Logically, a mandibular middle ear cannot be assumed in *Haramiyavia*” (supporting information p. 19 in ref. 18). As a result, most mandibular features of *Haramiyavia* were excluded from two recent phylogenetic estimates (18, 23). We note that Averianov et al. (17) and Bi and colleagues (18) did not examine these

preserved features in the original fossil material of *Haramiyavia* before disregarding these features.

### Dentition

The dentition of *Haramiyavia* is emended here as I4.C?.P?.M3/i3.c1.p4.m3. Our CT examination identified three lower incisors, not four as previously reconstructed (1). The lower p1 is present on the left mandible, but it was shed, and its alveolus was already plugged by bone on the right (SI Appendix, Fig. S1). The loss of anterior premolar(s) with age without replacement is typical of stem mammaliaforms (28) and also occurred in eutriconodont mammals (31).



**Fig. 4.** Hypotheses concerning the phylogenetic relationship of *Haramiyavia* and timing estimates of the basal diversification of crown mammals. (A) *Haramiyavia* is a close relative of multituberculates, both nested in the crown Mammalia. This hypothesis (haramiyidan node position 1) was based on a misinterpretation of a previous illustration of a fragment of the mandible (17, 18). (B) *Haramiyavia* is a stem mammaliaform, as determined by incorporating the features preserved on both mandibles into phylogenetic estimates (haramiyidan node position 2). (C) Placement of *Haramiyavia* and other haramiyidans among mammaliaforms according to this study. Many mandibular features were treated as unknown by studies favoring a Late Triassic diversification of mammals (18, 23). A more complete sampling of informative features revealed by this study now has overturned the previous placement. Clades: crown Mammalia (node a); Mammaliaformes (node b); haramiyidans (node 1 or 2, alternative positions); Eleutherodontida (node c). The rescored datasets and analyses are presented in *SI Appendix*.

The three lower incisors are procumbent and show a size gradient from the largest, i1, to the smallest, i3, with i1 being more than twice as wide and long as i2. All lower incisors have a heel on the lingual cingulid, and their root tips are closed (*Movie S1*). i1 has three buccal ridges along its length and a median lingual ridge. Upper incisors are single-rooted and have a lanceolate outline, a slightly concave lingual surface, and a convex buccal surface (*SI Appendix*, Fig. S1). The upper incisors lack the heel or circular cusp(s) of multituberculates (5). Lower premolars p2–p4 are double-rooted. Lower m3 has partially divided multiple roots (*SI Appendix*, Fig. S6). Each of the two smaller anterior roots has a separate root canal. The larger posterior root contains two root canals, which can be seen in CT serial sections. These partially divided multiple roots are similar to those of the Middle–Late Jurassic haramiyidans (18–20).

Upper molars have partially divided multiple roots in two root-rows (Fig. 2). Two to three smaller roots in the anterior root-row are connected by dentine; each root has a separate root canal. The two to three larger posterior roots are connected into the posterior root-row; each posterior root has a root canal (Fig. 2). The roots are bent posteriorly from the crown–root junction, indicating that the molar crowns shifted anteriorly relative to the anchored roots, an eruption pattern known as “mesial drift” in extant mammals (*sensu* ref. 32; also see ref. 33). The lower teeth in *Haramiyavia* show no mesial drift. More pronounced mesial drift of both upper and lower toothrows is well documented in tritylodontids, a cynodont group that also has multiple roots of postcanines (33, 34), and also evolved convergently in several marsupials and placentals (32).

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## Molar Occlusion

The upper molars (Fig. 2 and *SI Appendix*, Fig. S5) have two main cusp rows separated by a fusiform median furrow, which is also known as a “basin” because it is closed anteriorly by a crest (on M1) or a cusp B5 (in M2 and M3) (1, 2). The buccal shelf is absent on M1 but is present on M2 and M3. The buccal accessory cusps (AA1–AA3) are variable and have no occlusal contact with the lower molars (Fig. 2 and *SI Appendix*, Fig. S5). Adjacent upper molars are interlocked by cusp B5 of the succeeding molar fitting into a distal cingular notch of the preceding molar (Fig. 2B). Upper molars are in a straight alignment, without a lingual offset of the ultimate upper molar, as seen in multituberculates (1).

Upper molars are set in an *en echelon* (step-like) pattern, as first noted by Jenkins et al. (p. 171 in ref. 1). Each molar crown is much taller from the crown–root junction on the distal end than on the mesial end along both the lingual and buccal sides (Fig. 2 C and D). As the crowns are leveled to the maxillary alveolar line, cusp rows and occluding basins and furrows form a pronounced zigzag contour along the molar series (Fig. 3). Cusps B1 and A1 are the highest points, and the embrasures of adjacent molars are the lowest points of this zigzag contour.

Cusps of lingual row B show mesially (anteriorly) decreasing heights, from the tallest cusp, B1, to the lowest, B4. Cusps of buccal row A also show mesially decreasing cusp heights, with A1 being the tallest. The tallest cusps, B1 (lingual row) and A1 (buccal row), have an elevated transverse saddle (2, 6), which partially divides the distal basin from the mesial furrow. The distal basin is oriented posteroventrally, whereas the mesial furrow is oriented anteroventrally, both sloping away from the saddle. The wear surfaces are more vertically inclined in the distal basin, as seen on cusp A1 posterior to the saddle (facet 1 of ref. 3) (Fig. 2, blue). Anterior to the saddle, the striations are more vertically inclined near the bases of cusps A2 and B2 but become horizontal in most of the mesial furrow (facets 3 and 4) (Fig. 2, green).

Prominent wear of upper molars is visible on the lingual cusp in row B, on their lingual aspect (facet 6), on the apices of B2–B4, and along the furrow side of the cusp row (facet 4) (*SI Appendix*, Fig. S5). Cusps A1–A3 of the buccal row show wear in the median furrow and abrasion on the A2 apex but no sign of wear or contact on their buccal sides (*SI Appendix*, Fig. S5). The buccal shelf and its accessory cusps have no sign of contact with the lower teeth (*SI Appendix*, Fig. S5).

On the lower molars, cusp a1 is the tallest of the lingual row and of the entire tooth. Cusp b2 is the tallest of the buccal cusp row (although still much lower than a1). Cusps a1 and b2 have an elevated oblique saddle that separates the mesial basin (Fig. 2 G–I, blue) from the median furrow distal to the saddle (Fig. 2 G–I, green). The most visible wear is on the buccal cusp row (b2–b4) with abrasion on the apices of cusps, along the furrow side (facet 4), and on the buccal side (facet 6) (Fig. 2 and *SI Appendix*, Figs. S6 and S7). On lower m3, the lingual aspect of the lingual cusp row has no wear striations or any apical wear on cusps a1–a5 (Fig. 2 and *SI Appendix*, Fig. S6).

On m3, the mesial basin anterior to the saddle shows more inclined striations [Fig. 2 G–I, blue, also known as “facet 1” (3)]. The furrow posterior to the saddle shows more vertically inclined wear striations at the bases of cusps a2 and b2 (and also on the posterior aspect of a1) but more horizontal striations along much of the furrow [Fig. 2 F–I, green; also known as “facets 3 and 4” (3)].

The associated tooth-bearing mandibles and maxillary of *Haramiyavia* offer a crucial anatomical context for orienting the isolated teeth of other haramiyids (5, 6, 10). Nonetheless there have been divergent interpretations of dental occlusion. Jenkins et al. (1) noted that the *en echelon* pattern precludes a lower molar from sliding across more than one upper molar and reconstructed only orthal occlusion without palinal movement.

Subsequently, Butler (2) agreed with the interpretation that *Haramiyavia* had orthal movement and one-to-one upper–lower relationship. However, Butler (figure 3, p. 323 in ref. 2) suggested that, after the initial orthal occlusion, there was also a palinal movement about one third of the upper tooth length, similar to the palinal movement of lower teeth in cynodont group of traversodontids (35), although not to the same extent as in multituberculates (2).

Zheng et al. (20) and Meng et al. (36) offered an entirely novel interpretation of haramiyid occlusion. Based on their analysis of the isolated teeth of newly discovered *Arboroharamiya* (20) (*SI Appendix*, Fig. S8), they argued that the bucco–lingual alignment of opposing molars would be for the lingual cusp row of the lower molar to fit into the median furrow of the uppers for *Haramiyavia* and other haramiyids. This alignment of the opposing molars differs by an entire cusp row from the reconstructions for *Haramiyavia* by Jenkins et al. (1) and for all haramiyids by other studies (2, 6). These alternative interpretations can now be tested by SEM studies on wear facets, by manipulation of scaled 3D models from CT scans (*SI Appendix*, *Methods*), and by kinematic simulation using Occlusal Fingerprint Analyzer (OFA) software (*SI Appendix*, *Methods*) (37, 38).

We note that the distal basin of the upper molar and the mesial basin of the lower molar have vertically inclined striations (*SI Appendix*, Figs. S5 and S6). On m3, there also are some inclined striations at the bases of cusps a1 and a2 (*SI Appendix*, Fig. S6). However, most of the furrow of m3 shows the more horizontal striations, and both sides of b2–b4 of the buccal cusp row show a mixture of horizontal and less inclined striations.

The vertical (or strongly inclined) striations of the distal basin of the upper molar, the mesial basin of the lower molar, and those close to the lower saddle crest are evidence of orthal occlusion. As a lower molar moved vertically, the tallest lingual cusp, a1 of the lower molar, fit into the embrasure of the opposing upper molars. Concurrently, the lower cusps b2–b4 occluded vertically into the upper furrow (Fig. 2 B–H: orthal occlusion, blue).

The more horizontal striations in the furrow and the mixture of horizontal and less inclined striations along both sides of b2–b4 of the buccal cusp row were produced by palinal movement. Buccal cusps b2–b4 of the lower slid posteriorly along the upper furrow between the lingual row B2–B4 and the buccal row A1–A3. Concurrently, lingual cusps a1–a4 of the lower slid posteriorly past the lingual side of upper lingual cusps (Fig. 2 B–H: palinal movement, green). Therefore, wear patterns documented by SEM corroborate the occlusal contact reconstructed by manipulation of 3D scale models. Within a single occlusal cycle, orthal movement occurs first, followed by a subsequent palinal phase of slightly more than one third of the upper tooth length (*Movie S1*) (2).

We now can demonstrate that the only possible configuration of the bucco–lingual alignment of cusp rows for *Haramiyavia* (*SI Appendix*, Fig. S8) (ref. 36 vs. other studies) is for the buccal row (b2–b4) of the lower m3 to occlude the median furrow of the upper M3 and for the lingual cusp row (B1–B4) of the upper to occlude the median furrow of the lower, as originally established (1, 2). The putative alignment in which lingual cusps a1–a4 of the lower molar fit into the median furrow of the upper molar (36) would result in a mismatch of upper and lower contact surfaces for *Haramiyavia*. Meng and colleagues did not have access to the material that shows the significant height difference of cusp a1 from other lower molar cusps (*SI Appendix*, Fig. S6), the shallow depth of the occluding furrow, and the elevated saddle of the upper molars (*SI Appendix*, Fig. S8). If the lower lingual row a1–a4 were to be placed in the median furrow of the upper molar, the tallest cusp a1 would be the only possible contact point between the two teeth. If upper cusps A1–A3 were to be aligned with the median furrow of the lower molar (36), the apices of A1–A3 would not be tall enough to contact any part of the lower molar at

all (*SI Appendix*, Fig. S8). The buccal aspect of the upper molar and the lingual aspect of the lower molar have no wear striations or facets, as predicted by the cusp row alignment proposed by Meng and colleagues (36).

### 3D Occlusal Tooth Models and OFA

Using 3D models printed from CT scans, we found that rescaling the referred and larger upper molars (MCZ10/G95) to 83% made the best match to the lower teeth (MCZ7/G95). More details are given in *SI Appendix*. Using the OFA kinematic simulation tool (37, 38), we further tested the orthal and palinal occlusal movements (2) and the alternative bucco–lingual cusp row alignments (ref. 36 vs. other studies) for the goodness of fit of the molar contact surfaces (*Movie S1*).

OFA analysis demonstrates that for the orthal phase of occlusion, the best fit is for the tallest cusp a1 of the lower lingual row to occlude into the lingual embrasure of the adjacent upper molars as the lower buccal cusp b1 simultaneously contacts the distal occlusal basin of the preceding upper molar (Fig. 3B, blue arrow and *Movie S1*). For the palinal phase of occlusion, the best fit is for the buccal cusps b2–b4 of the lower molar to slide through the median furrow of the upper (Fig. 3C, green arrow and *Movie S1*). These best fits of the upper–lower contacts resulted in a distribution of tooth contacts (OFA “collision”) very similar to the wear facets directly observed by SEM of the teeth (Fig. 2F). Thus, the occlusal relationship proposed from wear facets (Fig. 2) is corroborated independently by kinematic analysis (*Movie S1*). On the contrary, the bucco–lingual row alignment suggested by Meng and colleagues (36) would result in minimal contact by the apex of lower cusp a1 to the entire opposing upper tooth, an obvious mismatch (*SI Appendix*, Fig. S8).

### Comparison with Other Haramiyids

Tooth wear surfaces and striations of *Haramiyavia* are similar to those of *Thomasia* (2, 3, 6, 39). *Thomasia* shows an upper crown height differential similar to that in *Haramiyavia*: a taller distal end, a shorter mesial end, and a cusp row height gradient with the distal cusp B1 being the tallest (Fig. 2G) (3, 6). Thus, it was proposed that *Thomasia* has a similar *en echelon* arrangement for the occlusal surfaces of upper molars (2, 39). Therefore, the orthal–palinal occlusal movement (2) is likely applicable to haramiyids as a whole. For further comparisons, see Figs. 2 and 3 and *SI Appendix*, Fig. S7.

### Dental Age and Body Size

We estimate by dental eruption stage that the type specimen (MCZ7/95) and the referred specimen (MCZ10/95G) of *Haramiyavia clemmenseni* are adult. The ultimate molars (m3 and M3) are fully erupted and have sustained wear from chewing (*SI Appendix*, Figs. S5 and S6). Our CT scanning detected no dental laminae or erupting teeth inside the jaws, indicating the individual was an adult. Several mammaliaforms and some pre-mammaliaform cynodonts show a pattern of successive loss of the anterior postcanines with advancing age (28, 40). This loss creates and/or enlarges a postcanine diastema in older individuals. The lower right premolar p1 already has been shed, and its alveolus is plugged (*SI Appendix*, Fig. S1), consistent with an interpretation that aging had already started in the *Haramiyavia* type specimen, although the initiation of this pattern is different between the two mandibles.

We estimate that the body mass of *Haramiyavia* ranged from 50 to 70 g. The right mandible is 27 mm long as measured on the slabs. The reconstructed mandible is 28 mm long, based on complementary parts from the right and the left (Fig. 1 and *Movie S1*). Body mass of the type specimen ranges from 61 to 68 g by regression to mandibular length [ $\ln(\text{body mass in grams}) = 2.9677 \times \ln(\text{jaw length in millimeters}) - 5.6712$ ] from a dataset of some placental insectivores and marsupials (41). The humeral length

is 17 mm (*SI Appendix*, Figs. S2 and S3). The body mass of *Haramiyavia* is estimated to be 47 g by a regression to humeral length ( $\log_{10} \text{body mass} = 2.8626 \times \log_{10} \text{humerus length} - 1.8476$ ) based on a dataset of extant mammals (42).

### Phylogenetic Analyses and Implications

Since the discovery of haramiyids more than 100 years ago, their phylogenetic position has always been controversial (Fig. 4). Traditional studies assumed that haramiyids were associated with multituberculates, and the latter were universally regarded as members of Mammalia (2, 5, 18) (Fig. 4A). A recent variant of this hypothesis is that haramiyids are closely related to the gondwanatherian–multituberculate clade (23). Including Late Triassic haramiyids in a clade with the geologically younger multituberculates would help extend the minimal age of their common ancestor, the basis for recent arguments in favor of a Late Triassic diversification of crown Mammalia (18, 23) (Fig. 4A).

However, a competing hypothesis postulates that haramiyids are a stem lineage separate from Mammalia (1, 19, 21, 22). This hypothesis is supported by the newly documented mandibular and dental characteristics of *Haramiyavia* (Fig. 4B). Our study revealed 37 new mandibular features of *Haramiyavia*. Most of these features were treated as unknown or inapplicable in two recent studies supporting the haramiyidan–multituberculate clade (18) or the haramiyidan–gondwanatherian–multituberculate clade (23). When these features are added into the matrices of these studies, our analyses of the improved datasets show that haramiyids (including *Haramiyavia*) are a mammaliaform clade outside crown Mammalia, separated from multituberculates (Fig. 4B) and from the gondwanatherian–multituberculate clade (*SI Appendix*). The clade of gondwanatherians and multituberculates (23) is relatively robust to the character changes in haramiyidans. Removing haramiyids from the putative haramiyidan–multituberculate clade, which is the sole basis for the Late Triassic diversification of Mammalia, cancels the fossil date for the Late Triassic origin and basal diversification of Mammalia (Fig. 4 and *SI Appendix*) (21, 22, 24).

### Discussion

The hypothesis of the haramiyidan–multituberculate clade, if upheld, would have another implication for vertebrate macroevolution. Fossils of *Haramiyavia*, *Thomasia*, and their putative theroteinid relatives are older than the end of Triassic extinction (7, 13), and they predate the major paleoecological transition from the Late Triassic to Early Jurassic (43, 44). A corollary of this hypothesis is that main crown mammalian clades would have split before the Triassic–Jurassic ecosystem transition, survived the mass extinction at the end of the Triassic (Fig. 4A), and later again survived the mass extinction at the end of the Cretaceous. On the contrary, our current analyses conclude that haramiyidans are a stem clade by its new dental and mandibular features. This conclusion is more consistent with a macroevolutionary scenario that major mammalian clades split after the end of Triassic extinction, not before it (Fig. 4B). The mammaliaform diversification occurred mostly during the paleoecological revolution during the Triassic–Jurassic ecosystem transition (44), not before it.

*Haramiyavia* of the Triassic and multituberculates of the Jurassic and Cretaceous also are different in many mandibular structures: *Haramiyavia* has a postdentary trough, indicating a plesiomorphic mandibular middle ear. It has a small, posteriorly directed dentary condyle, a larger coronoid process, and a masseteric fossa that is limited to the angular region. Also it lacks a pterygoid fossa. In contrast, multituberculates show none of these plesiomorphic features. Instead they are characterized by a rounded, dorsally directed dentary condyle (45), a masseteric fossa extending anteriorly into mandibular body, and a distinctive pterygoid fossa. These phylogenetically derived features also have significant functions in the jaws of multituberculates.

The small coronoid process of multituberculates provided less area of insertion for the temporalis muscle and likely less orthal biting force. However, their masseteric fossa has a prominent anterior extension for a larger masseter muscle and the backward power stroke of the jaw (45). Consistent with this anatomy, their molars exhibit minimal orthal occlusal wear but a greater range of wear by palinal movement (2). By comparison, *Haramiyavia* has a relatively large coronoid process (a mammaliaform plesiomorphy; see Fig. 1) with a more sizable insertion area for the temporalis muscle that is more effective in vertical biting. This characteristic is consistent with major wear by orthal occlusion as constrained by *en echelon* tooth surfaces. However, *Haramiyavia* lacks an anterior extension of the masseteric fossa and likely had a less developed masseteric muscle than can be inferred for multituberculates. We hypothesize that it has a shorter posterior power stroke powered by the masseter, as also evidenced by the limited extent of palinal wear on teeth (Fig. 2 and Movie S1).

Molariform teeth with longitudinal cusp rows in alternate upper-lower occlusion are a major feeding adaptation for a herbivorous diet or for an omnivorous diet with a major plant component (46, 47). In the cynodont–mammal phylogeny, this adaptation occurred first in traversodontids with both orthal and palinal occlusal movements (35) and then in tritylodontids with predominantly palinal movement (34, 35), according to some recent phylogenies (47, 48). It evolved again in multituberculates and rodents, two mammal clades that had spectacular radiations and evolutionary success. However, the rodent-like teeth in multituberculates occlude by a backward (palinal) power stroke of the jaw, whereas the teeth of rodents occlude by a forward power stroke of the jaw (49, 50). Thus, their dental functions are likely convergent.

We posit that teeth with multiple cusp rows evolved iteratively, each time with distinctive skeletomuscular functions of the mandible and also different occlusal structures of teeth. Molars of haramiyids represent such an iterative and convergent evolution. Moreover, haramiyids with their multirow and multicusp teeth, which are adapted to omnivorous/herbivorous feedings, are distinctive from contemporary morganucodonts and *Sinoconodon* with triconodont-like teeth (11, 28) and kuehneotheriids with a triangular cusp pattern, both of which are adapted to insectivorous feeding (12). These disparate dental patterns of the earliest mammaliaforms suggest that dietary diversification was a major factor in the earliest mammaliaform evolution through the paleoecological changes in the Late Triassic to Early Jurassic continental ecosystems (44).

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