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

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As one of the earliest-known mammaliaforms, *Haramiyavia clemenseni* 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 postdental 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 contemporaneous mammaliaforms suggest that dietary diversification is a major factor in the earliest mammaliaform evolution.

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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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).
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 discernable 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
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.C7.P7.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).
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 cingular cusp(s) of multituberculates (5).

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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).

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); Mammaliaforms (node b); haramiyidans (node 1 or 2, alternative positions); Eleutherodontida (node c). The rescored datasets and analyses are presented in SI Appendix.
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. 2C 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 inclinations are more vertically inclined near the bases of cusps A2 and B2 but become horizontally inclined 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 cuspsules 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. 2G–I, blue) from the median furrow distal to the saddle (Fig. 2G–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. 2G–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. 2F–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 orhtal 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 buccal–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 cinematic simulation using Oclusal 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 orhtal 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. 2B–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. 2B–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 buccal–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 (MCZ7/0/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 “collisions”) 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 a height differential similar to that in Thomasia and the referred specimen (MCZ10/95G) of Haramiyavia. The ultimate molars (m3 and M3) are orthal to 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 mammaliforms and some pro-mammaliforma cynodonts show a pattern of successive loss of 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 (body mass in grams) = 2.9677 x Ln (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).

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 haramiyid–multituberculate clade (18) or the haramiyid–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 mammaliform 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 haramiyids. Removing haramiyids from the putative haramiyid–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 haramiyid–multituberculate clade, if upheld, would have another implication for vertebrate macroevolution. Fossils of Haramiyavia, Thomasia, and their putative theropid 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. 4D), and later again survived the mass extinction at the end of the Cretaceous. On the contrary, our current analyses conclude that haramiyids are a stem clade by its new dental and mandibular features. This conclusion is consistent with a macroevolutionary scenario that major mammalian clades split after the end of Triassic extinction, not before it (Fig. 4B). The mammaliform 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 large 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 temporals 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 (34, 35), according to some recent phylogenies (47, 48). Consistent with this anatomy, their molars exhibit minimal orthal occlusal wear but a greater range of wear by palinal movement (34, 35), according to some recent phylogenies (47, 48). Moreover, haramiyids with their multicusped and multirow teeth, which are adapted to omnivorous/herbivorous feedings, are distinctive from contemporary marsupiomiids and Sinocodonid with triconodont-like teeth (11, 28) and keunotheriids 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 mammalian evolution through the paleoecological changes in the Late Triassic to Early Jurassic continental ecosystems (44).

We posit that teeth with multiple cusp rows evolved iteratively, each time with distinctive skeletal muscular 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 multicusped teeth, which are adapted to omnivorous/herbivorous feedings, are distinctive from contemporary marsupiomiids and Sinocodonid with triconodont-like teeth (11, 28) and keunotheriids 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 mammalian evolution through the paleoecological changes in the Late Triassic to Early Jurassic continental ecosystems (44).

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