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LOWER JAW MORPHOLOGY OF *ADALATHERIUM HUI* (MAMMALIA, GONDWANATHERIA) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT—The lower jaw of the holotype of *Adalatherium hui*, from the Late Cretaceous of Madagascar, is the most complete yet known for a gondwanatherian mammal. It reveals for the first time the morphology of the character-rich ascending ramus of the dentary in a gondwanatherian. Each half of the lower jaw is composed of only one bone, the dentary, which is short and deep and houses only five teeth: an enlarged, procumbent incisor and four postcanine teeth. In comparable parts of its anatomy, the dentary of *Adalatherium* is strikingly similar to that of *Sudamerica* but differs slightly from that of *Galulatherium* (conformation anterior to first postcanine, mental foramen position), the only two other gondwanatherians represented by complete horizontal rami. Among other Mesozoic mammaliaform taxa, the dentary of *Adalatherium* is most similar to those of the largely Laurasian group Multituberculata, most notably in absence of postdentary trough and Meckelian sulcus; presence of short, deep dentary with sizable diastema and articulating with squamosal via mediolaterally narrow condyle that continues onto posterior surface (i.e., no distinct peduncle); possession of much reduced dentition; absence of angular process; possession of large pterygoid fossa and pterygoid shelf, ventral surface of which is flat; absence of coronoid bone; and possession of unfused mandibular symphysis. Most of these features are clearly derived and stand in stark contrast to the much more plesiomorphic morphology exhibited by the lower jaw of the haramiyaviid *Haramiyavia*. The lower jaws of euharamiyidans, although derived in their own right, are also relatively plesiomorphic.

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INTRODUCTION

The lower jaw of *Adalatherium hui*, from the Late Cretaceous of Madagascar, is the most complete for any known member of the Gondwanatheria and is the first gondwanatherian specimen to reveal the morphology of the ascending ramus of the dentary. As such, it provides new insights into the morphology of the gondwanatherian lower jaw and the putative relationships of gondwanatherians with multituberculates, euharamiyidans, and *Haramiyavia*. The lower jaw described, illustrated, and analyzed in this report is part of the holotype and only known specimen of *A. hui*, UA (Université d'Antananarivo) 9030, a well-preserved and nearly complete cranium, lower jaw, and postcranial skeleton discovered in the Anembalemba Member of the Maevarano Formation in the Mahajanga Basin of northwestern Madagascar (see Krause, Groenke, et al., 2020; Krause, Hoffmann, et al., 2020).

The primary objectives of this article are to (1) illustrate and describe in detail the morphology of the lower jaw of *Adalatherium* and (2) make detailed comparisons with the lower jaws of other Mesozoic mammaliaforms, with special emphasis on those of other gondwanatherians, multituberculates, euharamiyidans,

and *Haramiyavia*, all considered, at one time or another, to be members of the Allotheria.

Institutional Abbreviations—**DMNS**, Denver Museum of Nature & Science, Denver, Colorado, U.S.A.; **MACN-RN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Colección Río Negro, Buenos Aires, Argentina; **MLP**, Facultad de Ciencias Naturales y Museo, Universidad Nacional de la Plata, La Plata, Argentina; **MPEF**, Museo Paleontológico ‘Egidio Feruglio,’ Trelew, Argentina; **NMT**, National Museums of Tanzania, Dar Es Salaam, Tanzania; **RRBP**, Rukwa Rift Basin Project, Tanzania Antiquities Unit, Dar es Salaam, Tanzania; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

Anatomical Abbreviations—**c**, mandibular condyle; **cp**, coronoid process; **i**, lower incisor; **maf**, mandibular foramen; **masf**, masseteric fossa; **mc**, mandibular canal; **mf**, mental foramen; **mn**, mandibular notch; **PC**, upper postcanine tooth; **pc**, lower postcanine tooth; **pfs**, pterygoid fossa; **pfv**, pterygoid fovea; **ps**, pterygoid shelf; **s**, symphysis.

MATERIALS AND METHODS

Specimen

The lower jaw of UA 9030 is composed of left and right dentaries, both of which are essentially complete but suffered some

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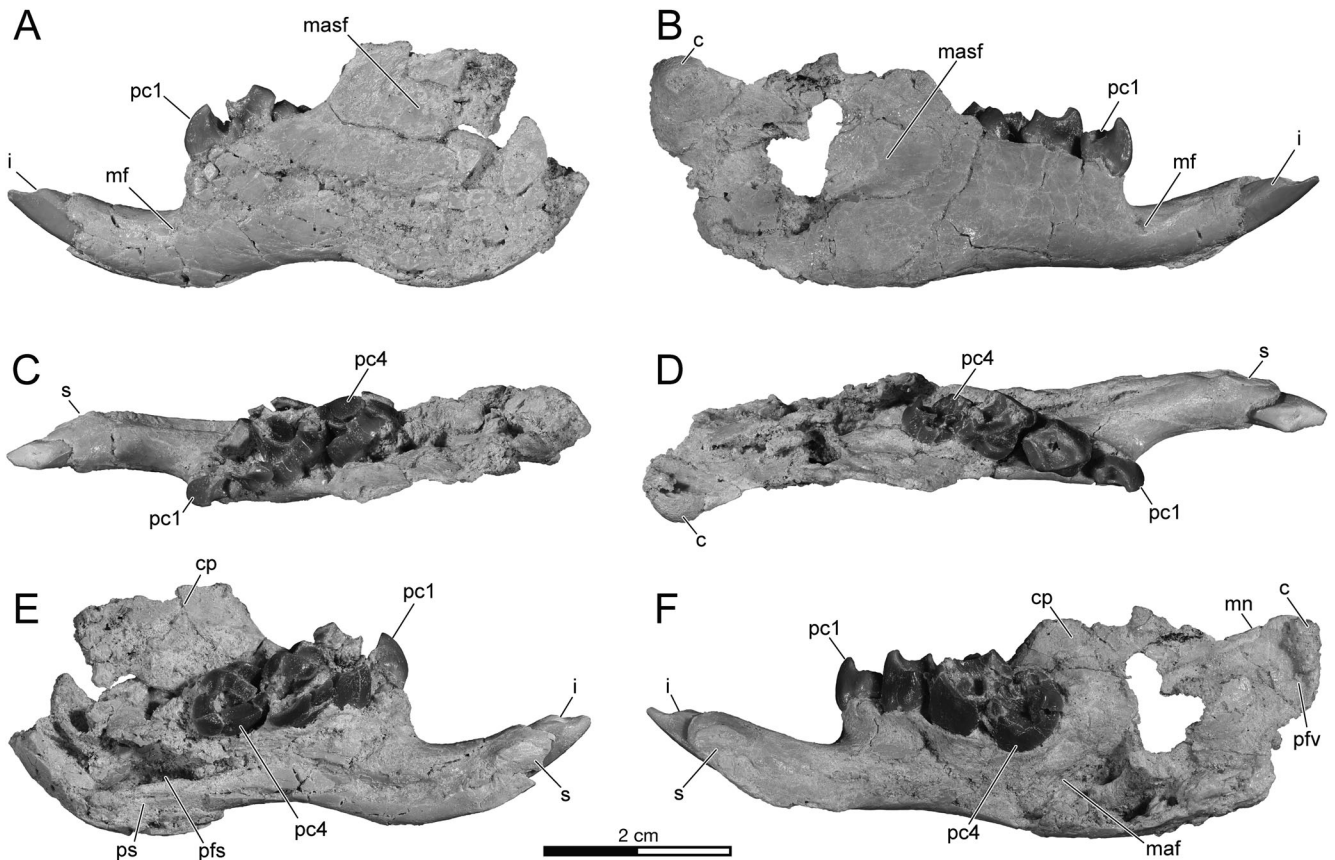


FIGURE 1. Lower jaw of *Adalatherium hui* (UA 9030). **A, C, E**, left dentary in **A**, lateral, **C**, dorsal (occlusal), and **E**, medial views. **B, D, F**, right dentary in **B**, lateral, **D**, dorsal (occlusal), and **F**, medial views. **Abbreviations:** **c**, mandibular condyle; **cp**, coronoid process; **i**, lower incisor; **maf**, mandibular foramen; **masf**, masseteric fossa; **mf**, mental foramen; **mn**, mandibular notch; **pc**, lower postcanine tooth; **pfs**, pterygoid fossa; **pfv**, pterygoid fovea; **ps**, pterygoid shelf; **s**, symphysis.

postmortem breakage and deformation, the thin coronoid process being the most incomplete and damaged region on both sides (Fig. 1). The condyle of the left dentary is not preserved, but that of the right side is almost complete. The lateral surface of the dentary is better preserved (less fractured) on the right side than on the left, except for the coronoid process (the base of which is more complete on the left) and a region near the center of the ascending process (i.e., near the center of the masseteric fossa), which is missing. Despite the breakage and deformation, the preserved parts of the two bones complement one another, allowing examination and description of the morphology of almost the entire dentary. As preserved, the left dentary is shorter and deeper than the right one, the latter of which appears to have been elongated, perhaps through dorsoventral compression upon or after burial. Conversely, the height of the left dentary appears to be slightly exaggerated owing to displaced, roughly horizontal fractures. The reconstructed dentary illustrated in Figure 2 attempts to compensate for what is perceived to be the exaggerated depth of the left dentary and the exaggerated length of the right dentary.

Mechanical Preparation

The dentaries of UA 9030 were mechanically prepared in the Vertebrate Fossil Preparation Laboratory of Stony Brook University by V. Heisey. Ms. Heisey isolated the dentaries from the cranium, with which they were in articulation but not tight

occlusion (see Krause, Groenke, et al., 2020:fig. 2; Krause, Hoffmann, et al., 2020:fig. 1, ED fig. 1).

Computed Tomography

The lower jaws were scanned via micro-computed tomography (μ CT) at Avonix Imaging in Plymouth, Minnesota, U.S.A. Scanning was performed on a Nikon Metrology MCT225 industrial μ CT scanner (225 kV microfocus reflection target X-ray tube; PerkinElmer XRD 1621 AN3 ES detector panel). Raw scan data were converted to 16-bit TIFF stacks using VG Studio Max (Volume Graphics) for study. Both dentaries (along with the left PC5) were scanned together (kV = 160; μ A = 58; 1,808 slices; voxel size = 0.0453 mm $\times$ 0.0453 mm $\times$ 0.0453 mm).

Digital Preparation and Visualization

The μ CT-scan data were processed and visualized using two different software programs: (1) Avizo (Visualization Sciences Group) Label Field, Surface Editor, Isosurface, and Volume Rendering modules; and (2) Dragonfly (Object Research Systems) Image Segmentation and 3D Visualization tools (ROI Tools and ROI Painter of the Segment Tools panel). Supplementary videos of both dentaries were created by J. Groenke (Ohio University) using the Animation Producer in Avizo and exported as TIFF file stacks that were compiled in Adobe Premiere Pro (Creative Cloud edition); these videos are presented as Videos S5–S8 in Krause, Hoffmann, et al. (2020).

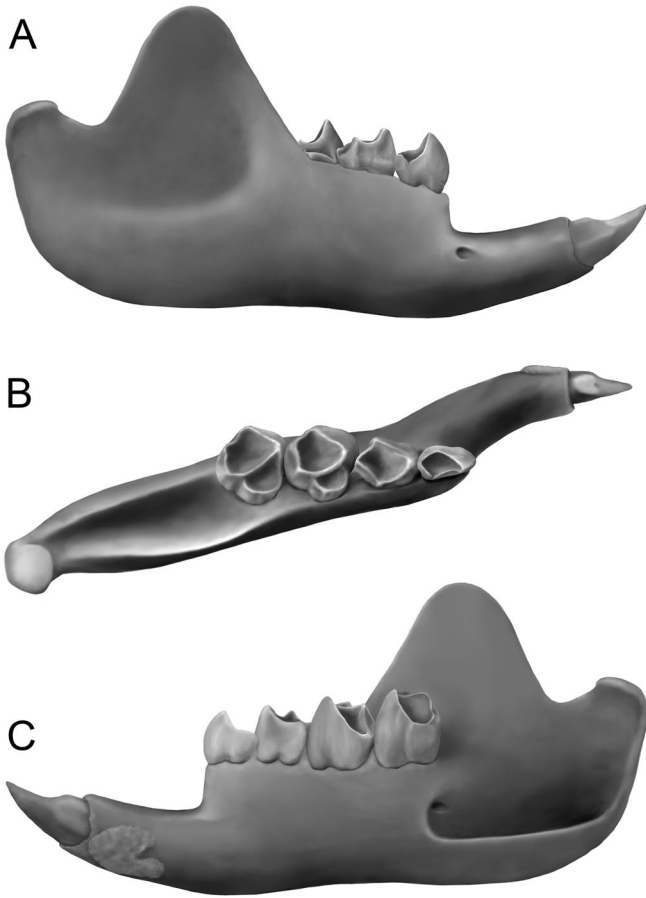


FIGURE 2. Reconstruction of right dentary of *Adalatherium hui* based on preserved, complementary morphology of both left and right dentaries of UA 9030 in **A**, lateral, **B**, dorsal (occlusal), and **C**, medial views.

Measurement

Linear measurements of ≤ 10 mm reported here were taken with an ocular micrometer inserted into one of the two eyepieces of a Nikon SMZ1500 stereomicroscope; the micrometer was calibrated before each measurement session with a 10 mm graticule slide. Measurements of >10 mm were taken with Mitutoyo CD-8" CSX calipers.

DESCRIPTION

Each half of the lower jaw of *Adalatherium* has only one bone, the dentary, which, along with the teeth it housed, is reconstructed in Figure 2. Each dentary is composed of a horizontal ramus (or body) anteriorly, consisting of a base ventrally and an alveolar process dorsally, and an ascending ramus (or simply ramus) posteriorly. The horizontal ramus can be loosely divided into anterior and posterior parts based on angulation relative to the sagittal plane, the anterior part containing most of the incisor except the end of the root (and the diastema) lying in an anteromedial-posterolateral plane in dorsal (or ventral) view and the posterior part containing the postcanine teeth lying in a nearly sagittal plane. Seen in lateral (or medial) view, the ventral edge of the anterior part of the horizontal ramus is convex and the dorsal margin is concave,

essentially matching the curvature of the incisor alveolus. The ventral convexity, coupled with the concave ventral border of the posterior half of the horizontal ramus (ventral to the postcanine teeth) and the convex ventral border of the ascending ramus, results in a sinuous outline to the ventral border of the dentary. This sinuosity is present on both sides but is more pronounced on the left (Fig. 1A, C, E, F). It is unknown which side best represents the degree of sinuosity in life; therefore, Figure 2A, C portray an intermediate condition. The convex ventral border of the ascending ramus continues posterodorsally such that the posteroventral border of the dentary forms a smooth arc that reaches the posteroventral base of the condyle; there is no trace of an angular process.

The anterior part of the horizontal ramus is oriented from anterodorsal to posteroventral in side view and, posterior to the symphysis, is essentially elliptical in cross-section, with the longitudinal axis of the ellipse oriented from dorsolateral to ventromedial (Fig. 3B). This portion of the horizontal ramus is essentially composed of a thin-walled, gently curved tube of bone that surrounds the anterior three-fifths of the incisor alveolus and therefore includes the long diastema that extends posteriorly to the first postcanine tooth, pc1 (12.8 mm on left, 12.0 mm on right; measured from dorsal margin of incisor alveolus to mesial margin of pc1 alveolus). In dorsal or ventral view, the lateral surface of the anterior part of the horizontal ramus forms an angle of 160° – 165° (more precise measurement is impossible) to the lateral surface of the rest of the dentary, which thus results in a distinct, rounded convexity at the transition between the anterior and posterior parts of the horizontal ramus (Figs. 1C, D, 2B). As such, the anterior part of the horizontal ramus extends in an anteromedial-to-posterolateral direction, whereas the more posterior part of the dentary (including the posterior part of the horizontal ramus and the ascending ramus, which lie essentially in the same plane) is more anteroposteriorly oriented (i.e., more closely approximating the sagittal plane). Also, in dorsal or ventral view, the medial surface of the anterior part of the horizontal ramus forms an angle of 25° – 30° (more precise measurement is impossible) relative to the midline (as indicated by the flat plane of the mandibular symphysis). This results in an included angle between the medial surfaces of the left and right anterior parts of the horizontal rami of approximately 55° .

A single mental foramen is located on the lateral surface of the dentary near the posterior end of the diastema, at a level just anterior to where the horizontal ramus becomes much deeper as it rises dorsally to house the roots of pc1 (Figs. 1A, B, 2A, 3C). The foramen lies closer to the dorsal than to the ventral edge of the dentary. It is roughly circular in outline (although slightly taller than wide), about 1 mm in maximum diameter, and opens anterolaterally. The μ CT scans allow tracing of the mandibular canal from the mental foramen posteromedially toward the root of the incisor (Fig. 3D). The continuation of the mandibular canal farther posteriorly into the horizontal ramus proved difficult to follow because of deformation and fracturing of the dentary's bony interior.

Also included in the anterior part of the horizontal ramus is the symphyseal facet medially, which forms a low and slightly roughened surface (Figs. 1C–F, 2B, C). The left and right dentaries are not fused at the symphysis and almost undoubtedly were not fused in life, even though there is evidence from the dentition (Krause, Hu, et al., 2020) and postcranial skeleton (Hoffmann, Hu, et al., 2020) that the individual represented by UA 9030 is a subadult (Krause, Hoffmann, et al., 2020). The symphyseal facets on both the left and right dentaries are comma-shaped, each with a big head anteriorly and an elongate, narrowing tail extending posteroventrally from the ventral portion of the head. On the left dentary, there appears to be a short tail dorsally as well, but it is simply a ridge that did not directly contact the opposing symphyseal facet. Measured along and perpendicular

to their longitudinal axes, and including the ventral tails, the symphyseal facets are 9.7 mm (left) and 12.9 mm (right) long and 5.4 mm (both left and right) high, respectively. Posterior to the head and dorsal to the tail of each symphyseal facet, there is a concavity. The concavity is roughly ovoid in shape, anteroposteriorly longer than dorsoventrally tall. Posterior to this ovoid concavity is the beginning of a shallow longitudinal depression that roughly parallels the root of the lower incisor and extends posteriorly onto the posterior part of the horizontal ramus. As preserved, this curvilinear depression (concave dorsally, convex ventrally) is asymmetrical on the left and right dentaries; that on the left side suffered less postmortem deformation but it is clearly deformed on both sides, to the extent that portions of the incisor are revealed. Indeed, these depressions appear to be largely or completely a feature on both sides that is the result of mediolateral compression. That this is the case is further confirmed by the fact that the distal portions of the lower incisors are also severely deformed on their medial aspects (Fig. 3C–E).

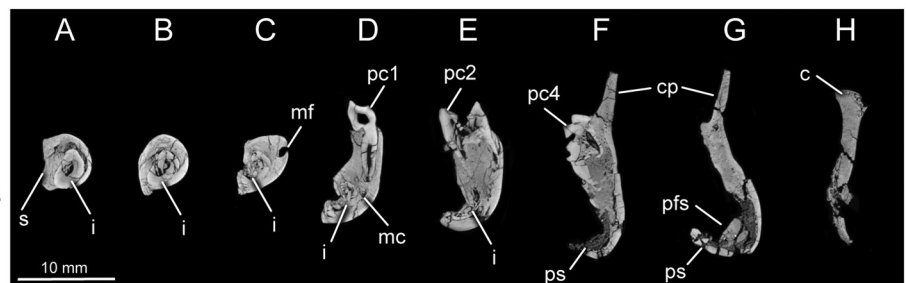
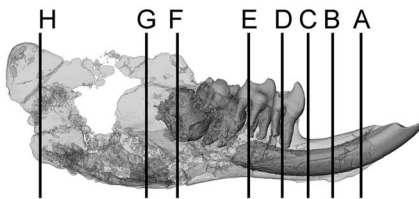
The anterior border of the posterior part of the horizontal ramus is marked by the nearly vertical margin of bone anterior to the mesial root of pc1. This posterior part (~23 mm on left, ~25.5 mm on right; measured as the anteroposterior length of the postcanine tooth row) of the horizontal ramus is dorsoventrally much taller (~15.2 mm on left [which appears exaggerated because of displaced fractures], ~12.9 mm on right; measured ventral to pc2 on lateral side) than the anterior part and contains alveoli for the roots of the four postcanine teeth in its dorsal portion and the posterior two-fifths of the incisor alveolus in its ventral portion (Figs. 3, 4). Indeed, the alveolus of the incisor extends far posteriorly, reaching the level of pc3 and therefore occupying most of the ventral portion of the horizontal ramus; its total length is nearly half of the entire length of the dentary. The alveoli for the roots of the two mesial-most postcanine teeth (pc1 and pc2) are long, extending ventrally almost as far as the dorsal margin of the incisor alveolus and terminating slightly dorsolateral to it (Figs. 3, 4).

In dorsal view, the long axis of the postcanine tooth row is not in alignment with the anterior part of the horizontal ramus; it is instead more nearly parallel to the sagittal plane (Figs. 1C, D, 2B). The medial view of the dentary reveals twisting along the occlusal plane of the postcanine tooth row, from pc1 to pc4; this torsion extends in a mesiolaterodorsal-to-distomedioventral direction such that whereas the occlusal surface of pc1 faces dorsally, that of pc4 faces slightly dorsomedially (see Krause, Hu, et al., 2020). Postmortem deformation, particularly the mediolateral compression ventral to pc3 and pc4, and the fact that these two teeth had not yet fully erupted, probably somewhat exaggerates the twisting of the tooth rows on both dentaries; it is unlikely that these more distal postcanine teeth faced as far medially in life as they do in the preserved dentaries.

The ascending ramus of the dentary (~27 mm long anteroposteriorly; measurable only on the right side, from distal margin of pc4 to posterior margin of condyle) overlaps with the posterior part of the horizontal ramus in that the anterior edge of the coronoid process arises lateral to pc3, rather than posterior to the tooth row as in many other mammaliaforms. The ascending ramus bears four main parts: (1) the coronoid process dorsally, (2) the pterygoid fossa and associated pterygoid fovea medially, (3) the masseteric fossa laterally, and (4) the mandibular condyle posteriorly. Each is described below.

The basal portion of the coronoid process is preserved, more so on the left than on the right dentary, but the apex of the process is broken away and missing on both sides. In dorsal view, the coronoid process is thin, its anterior edge being only slightly thickened mediolaterally (i.e., a distinct coronoid crest is not developed). In lateral view, the base of the anterior edge of the coronoid process obscures the distoventral portion of pc3 and all of pc4. The posterior edge of the coronoid process is broken away on both sides, but, based on the natural, unbroken edge of bone anterior to the mandibular condyle on the right dentary, it clearly ended well anterior to the condyle, thus resulting in a prominent mandibular notch. The anterior edge of the process is inclined

Right dentary



Left dentary

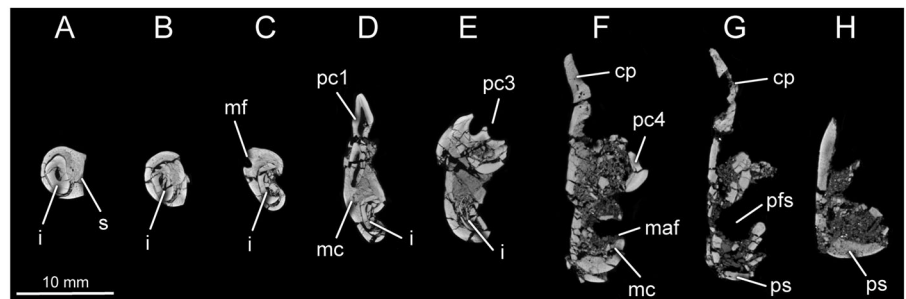
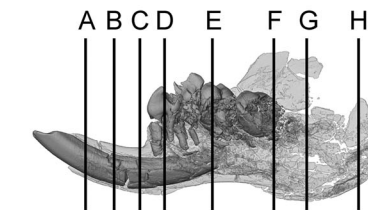


FIGURE 3. Serial transverse (coronal) sections through right (top) and left (bottom) dentaries of *Adalatherium hui* (UA 9030) obtained via μ CT scanning. Position of each transverse slice (A–H) along longitudinal axis of each dentary indicated in three-dimensional μ CT reconstructions at left. Individual slices numbered according to respective positions along anteroposterior axis passing through transversely resampled μ CT data set as follows (transverse slices; right dentary/left dentary): A, 1,535/1,610; B, 1,430/1,534; C, 1,337/1,427; D, 1,262/1,362; E, 1,130/1,179; F, 384/931; G, 754/814; H, 288/609. Total number of slices = 1,995. **Abbreviations:** c, mandibular condyle; cp, coronoid process; i, lower incisor; maf, mandibular foramen; mc, mandibular canal; mf, mental foramen; pc, lower postcanine tooth; pfs, pterygoid fossa; ps, pterygoid shelf; s, symphysis.

posterodorsally and forms an obtuse angle (as preserved, $\sim 145^\circ$ on the left dentary and $\sim 140^\circ$ on the right) relative to the alveolar edge of the dentary lateral to the postcanine teeth. There is no evidence of a fossa or scar for a separate coronoid bone on the medial side of the ascending ramus posterior to the tooth row.

The pterygoid fossa on the dentary is a very deep, large, and anteroposteriorly elongate pocket on the medial side of the ascending ramus (Figs. 1E, 2B, C). The base of the pterygoid fossa is formed by a wide, robust, curved pterygoid shelf (variously called a ridge or crest in early mammals [Kielan-Jaworowska et al., 2004], but in *Adalatherium* it is truly a broad, shelf-like structure) that, in cross-section, extends medially from the base of the vertical part of the ascending ramus and then dorsally. Its ventral surface is mediolaterally flat. The pocket-like fossa is widest and deepest in its middle portion, posterior to the tooth row, and diminishes in width and depth toward both ends. Deformation on the medial aspect of the left dentary precludes a clear determination of the boundaries of the pterygoid fossa. An obliquely oriented (posterodorsal to anteroventral), low, rounded ridge ventral to mid-length of pc4 on the right dentary, however, suggests that the fossa did not extend anterior to this point. Similarly, a horizontally oriented, low, rounded ridge, directly posterior to pc4 on the right dentary, suggests that the pterygoid fossa did not extend dorsal to the level of the tooth row. Although the anterior and dorsal boundaries of the pterygoid fossa are not well defined, the ventral aspect of the fossa is clearly bounded by the broad and prominent pterygoid shelf, which formed a mediolaterally broad and deep pocket for insertion of the ventral portions of what must have been a massive, mediolaterally thick medial pterygoid muscle. The dorsomedial edges of the shelf are chipped and broken in places, with various pieces displaced laterally toward or into the pterygoid fossa (especially on the right side), but the portions that are preserved intact (primarily on the left dentary) indicate that the fossa was about 5.5 mm wide at its widest (measured from the medial wall of the ascending ramus to the lateral border of the shelf). Furthermore, although breakage precludes a definitive assessment, complementary preservation on the left and right sides indicates that the pterygoid shelf continued posteriorly and then posterodorsally in a smooth arc to extend up toward

the mandibular condyle, decreasing in mediolateral breadth as it does so but forming the posteroventral boundary of the pterygoid fossa (as well as, more dorsally, the posterior boundary of the pterygoid fovea). In lateral view, the posteroventral region of the ascending ramus is rounded (convex posteroventrally); therefore, as stated above, there is no angular process (Fig. 1A, B). In medial view, the thickening of the condyle (preserved only on the right side) produces a prominent depression, the pterygoid fovea, just ventral to the condyle on the medial aspect of the ascending ramus (Fig. 1F), for insertion of the lateral pterygoid muscle. The fovea is well delimited posterodorsally by the oblique crest marking the boundary of the articular surface of the condyle, but its anterior and ventral limits are not conspicuous, merging onto the relatively flat medial surface of the condylar process.

Despite a concerted attempt at visualization and digital segmentation of μ CT scans, a continuous mandibular canal could not be identified with confidence because of deformation (mediolateral compression) and fracturing of the dentary. Nonetheless, we see evidence in μ CT sections for the ventral margin of the mandibular foramen inside the pterygoid fossa, in the form of a rounded edge posteroventral to pc4 (Fig. 3F). For scoring purposes in our phylogenetic analyses (Hoffmann, Beck, et al., 2020; Krause, Hoffmann, et al., 2020), we tentatively ascribe this position to the foramen. Unfortunately, deformation of the horizontal ramus precludes following this opening into the mandibular canal. Although the bone on the medial side of the ascending ramus and the posterior part of the horizontal ramus is broken and deformed, there is no evidence of any slit-like groove for the attachment of bony or soft tissues on either dentary anterior to the pterygoid fossa; we tentatively conclude that a Meckelian sulcus (= groove) was absent. As described above, there is a shallowly depressed, linear feature extending anteriorly from the ascending ramus onto the horizontal ramus, but this is wider and more consistently parallel-sided than the Meckelian sulci seen in any other mammaliaforms (e.g., Kielan-Jaworowska et al., 2004; Maier and Ruf, 2015; Luo et al., 2016, and references therein), even those considered to have relatively wide sulci (e.g., *Fruitafossor* [Luo and Wible, 2005:fig. 1b]; *Acinodus* [Lopatin et al., 2010a:fig. 1b]; *Kiyatherium* [Lopatin et al., 2010b:pl. 11,

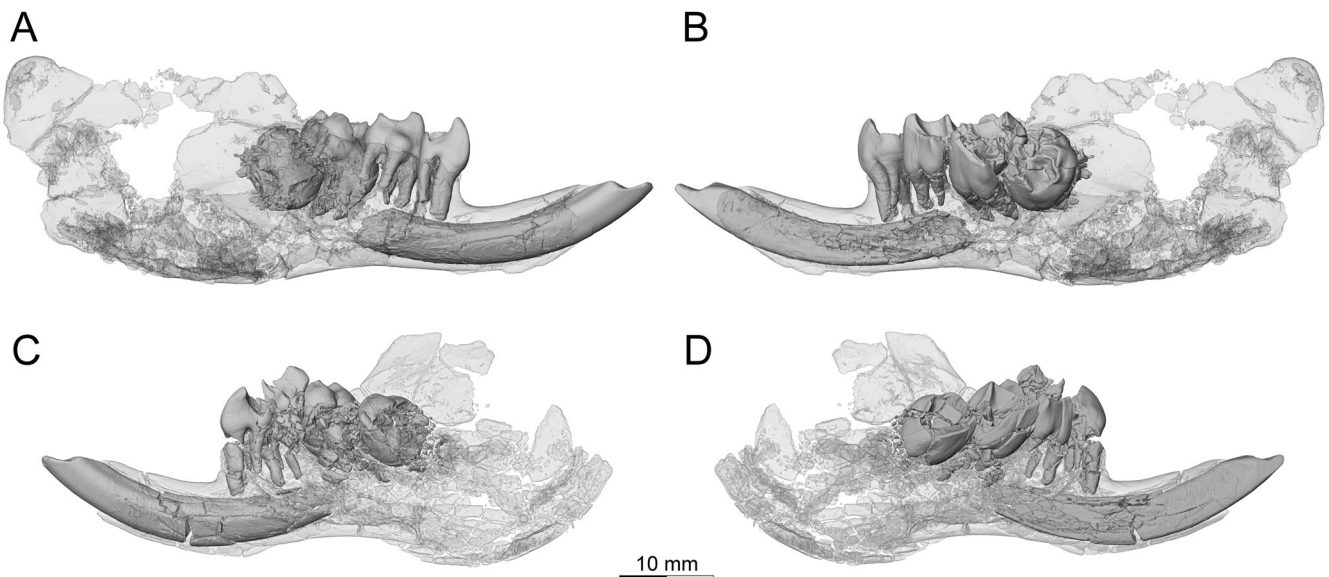


FIGURE 4. Composite μ CT images of lower jaws of *Adalatherium hui* (UA 9030), with jaw material rendered somewhat transparent so as to reveal relationship of tooth root structure to morphology of dentary. **A, B**, right dentary in **A**, lateral and **B**, medial views. **C, D**, left dentary in **C**, lateral and **D**, medial views.

fig. 3c]; *Liaconodon* [Meng et al., 2011:figs. 2c, S5a]; *Spinolestes* [Martin et al., 2015:supplementary video 2]; *Ausktribosphenos* [Rich et al., 2016:fig. 16]). Furthermore, this depression has no sharp edges and does not narrow and terminate anteriorly, as is typical of Meckelian sulci in Mesozoic mammaliaforms (e.g., Luo, 2011:figs. 4–6; Luo et al., 2016:figs. 6.3–6.5, 2017:fig. 3, ED fig. 9), although there is considerable variation both between specimens and ontogenetically (e.g., Meng et al., 2011; Lopatin and Averianov, 2015:fig. 10). Also, cross-sections of the jaw show that the interior was indeed compressed, as further demonstrated by the fact that the medial side of the distal end of the incisor is displaced laterally (Fig. 3D, E). That this is the case is further supported by the fact that the longitudinal depressions are expressed differently on the left and right sides, suggesting that they are not natural (Fig. 1E, F). We therefore regard these long, broad, shallow depressions to be the result of mediolateral compression and that they do not represent original structure. Similarly, there is no definitive evidence of a postdentary trough extending anteriorly from the posteroventral margin of the medial aspect of the ascending ramus. Instead, the pterygoid shelf continues uninterrupted posterodorsally from the ventral margin of the ascending ramus up to the condyle, thus suggesting that there was no space for posterior entrance of a postdentary trough (i.e., this region of the dentary is ‘rimmed off’).

The masseteric fossa on the lateral aspect of the left dentary is difficult to discern because of numerous fractures and deformation, although there is faint evidence of an anterodorsal boundary on the coronoid process. The fossa on the right side is much better preserved, as a curvilinear feature (Figs. 1B, 2A). The rounded anterior-most extent of the fossa lies opposite the approximate mid-length of pc4. The anterodorsal margin extends posterodorsally from this anterior apex onto the coronoid process more clearly on the right dentary than on the left. The anteroventral margin extends posteroventrally as a low, rounded ridge, but it is quite high on the dentary. As it continues posteriorly, it becomes more difficult to discern but it does not appear to descend any farther ventrally than 8.5–9 mm above the ventral margin of the ascending process. Breakage on both dentaries precludes a definitive assessment of whether or not a masseteric foramen (= labial mandibular foramen; see discussion in ‘Comparisons’ below) is present, but there is no trace of it, either on the surface or leading into a canal (as examined on μ CT scans), on the parts that are preserved; we therefore scored it as absent (Hoffmann, Beck, et al., 2020; Krause, Hoffmann, et al., 2020).

The mandibular condyle is almost completely preserved on the right dentary, missing only a few chips from around its periphery (particularly anteromedially) (Fig. 1B), but it is entirely missing on the left. The condyle is positioned at a level above the dorsal alveolar margin of the postcanine tooth row and projects posterodorsally (but primarily dorsally). In lateral view, there is no distinct peduncle, or neck, supporting the condyle anteroventrally. Also, in lateral view, a relatively long, curved, unbroken edge anterior to the condyle indicates the presence of a large mandibular notch, between the condyle and the posterior margin of the coronoid process (reconstructed in Fig. 2A, C). The condyle is mediolaterally broad relative to the process from which it arises, but still narrow, approximately equal in length and width in dorsal view. It is difficult to distinguish the limits of the articular surface itself, in particular how far it might have extended beyond the dorsal surface onto the posterior aspect, as in many multituberculates [see ‘Comparisons’]). In side view, the dorsal aspect of the articular surface is gently convex. A small lateral portion of the mandibular condyle is broken, but the bone surface adjacent to the condyle is almost flat, suggesting that the condyle protruded only slightly laterally.

COMPARISONS

The dentary of *Adalatherium* is the most complete for any known gondwanatherian and the first to preserve the character-rich ascending process. As such, we take this opportunity to make detailed comparisons of the dentary of *Adalatherium* with those of other Mesozoic mammaliaforms, with emphasis on gondwanatherians, multituberculates, euharamiyidans, and *Haramiyavia* because all four taxa are known from lower jaw material and, at one time or another, have been considered to be members of the subclass Allotheria. The basic morphological shape and structure of the dentary of *Adalatherium* is depicted relative to those of a broad range of mostly Mesozoic mammaliaform taxa in Figure 5. The following comparisons are based, in large part, on characters employed in recent phylogenetic analyses of Mesozoic mammaliaforms (e.g., Luo et al., 2001a, 2001b, 2002, 2003, 2007a, 2007b, 2011, 2015, 2017; Ji et al., 2002, 2009; Luo and Wible, 2005; Rougier et al., 2011, 2012; Yuan et al., 2013; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014, 2018; Krause et al., 2014; Han et al., 2017; Huttenlocker et al., 2018; Hoffmann, Beck, et al., 2020; Krause, Hoffmann, et al., 2020). This is not ideal but is done of necessity because many of the early multituberculates, euharamiyidans, and other Mesozoic mammaliaforms, particularly those from China, have only been published in brief reports and have not been described and illustrated in detail.

We also take this opportunity to reevaluate some mandibular characters, including how they are coded and, in a few cases, how they are scored for certain mammaliaform taxa. These reevaluations are generally restricted to the section below comparing the dentary of *Adalatherium* with those of multituberculates.

Masseteric Foramen—For clarity, we deem it necessary to deal with a terminological issue related to the masseteric foramen. Following the *Nomina Anatomica Veterinaria* (Gasse et al., 2017), the opening into and passageway within the mammalian dentary, transmitting the inferior alveolar nerve, artery, and vein, are the mandibular foramen and mandibular canal, respectively. There appears to be general agreement concerning these terms in the literature on mammaliaforms. However, an accessory conduit connecting to the mandibular canal from the masseteric fossa is found in some extant marsupials and monotremes, as well as in some Mesozoic mammaliaforms, and has led to some terminological confusion. Such a connection is normally absent in domestic animals, and it is not considered in the *Nomina Anatomica Veterinaria*.

This accessory conduit was most extensively described in some diprotodontian marsupials by Abbie (1939). These forms have a broad opening in the ventral or anteroventral recesses of their deep masseteric fossae. Dissection by Abbie revealed the occupants of this conduit to be a specialized part of the masseter muscle as well as a muscular branch of the inferior alveolar artery. Abbie (1939) named the opening in the masseteric fossa and conduit to the mandibular canal the ‘masseteric foramen’ and ‘masseteric canal,’ respectively. The name for the former was taken from Osgood (1921:pl. XX, fig. 2) for a similarly situated, inconstant, tiny opening in the extant shrew opossum *Caenolestes*, but with the contents unknown.

Another occurrence of a similarly positioned accessory conduit, but of more moderate dimensions, is in the platypus *Ornithorhynchus anatinus* (see Davis, 2012:fig. 3i). Zeller (1989:70) described a small opening in the anteroventral recesses of the deep masseteric fossa (his mandibular fossa) connecting to the mandibular canal but did not name the opening. Archer et al. (1993) described this same opening in the Miocene platypus *Obdurodon dicksoni* and named it the ‘mandibular fenestra,’ a term that has not been used subsequently (except for nonhomologous structures in, for example, archosaurs [e.g., Nesbitt and Hone, 2010] and early-branching synapsids [e.g., Huttenlocker,

2009]). Musser and Archer (1998) left the platypus masseteric fossa/mandibular canal connector unnamed but noted its resemblance to the masseteric canal of kangaroos.

Another occurrence, a small labial foramen behind the base of the coronoid process connecting to the mandibular canal, was reported in the Early Cretaceous aegialodontid *Kielantherium gobiensis* by Dashzeveg and Kielan-Jaworowska (1984). These authors did not name the foramen but noted its positional similarity to Abbie's (1939) large foramen in diprotodontians. Dashzeveg and Kielan-Jaworowska (1984) suggested that the foramen in *K. gobiensis* was too small to transmit slips of the masseter muscle and doubted any homology with the marsupial condition. In 1989, Kielan-Jaworowska and Dashzeveg coined the term 'labial mandibular foramen' for this opening in the Early Cretaceous eutherian *Prokennalestes trofimovi* (Kielan-Jaworowska and Dashzeveg, 1989). Since 1989, a labial mandibular foramen has been reported in numerous Mesozoic mammaliaforms (e.g., triconodontids [Cifelli et al., 1998]; some pretribosphenic mammals [Lopatin and Averianov, 2006]; some metatherians [Cifelli and Muizon, 1997]) and, after being first employed by Rougier et al. (1998:char. 70), has been used repeatedly as a character in phylogenetic analyses.

Rougier et al. (2001) and Davis (2012) explicitly accepted the homologies of the masseteric foramen of Abbie (1939) and the labial mandibular foramen of Kielan-Jaworowska and Dashzeveg (1989), preferring the former term over the latter. Rougier et al. (2007b, 2011, 2012) also employed 'masseteric foramen' in their character lists and were the first to score it in, for example, *Obdurodon*, *Ornithorhynchus*, and *Prokennalestes* as the same structure. We concur, as we did in Krause et al. (2014), that 'masseteric foramen,' in addition to having precedence, is a more appropriate descriptive term, in part because referring to a labial mandibular foramen implies that there is a lingual mandibular foramen as counterpart.

Although the masseteric foramen (=labial mandibular foramen) has been widely used in phylogenetic analyses of Mesozoic mammaliaforms, the scores for many taxa have varied. For example, the Early Cretaceous eutherian *Montanalestes* was initially reported by Cifelli (1999) as lacking the labial mandibular foramen and scored as such by Ji et al. (2002) and Luo et al. (2003). Based on their examination of *Montanalestes*, Wible et al. (2004) changed this condition to 'present,' which has been followed by most subsequent authors (but not, for example, Rougier et al., 2007b, 2011, 2012). Cifelli and Davis (2015:fig. 7) have recently published μ CT images documenting the presence of this opening and its connection to the mandibular canal in *Montanalestes*. As another example, the incidence of the masseteric foramen in the Late Jurassic zatherian *Peramus* has been scored as unknown (e.g., Rougier et al., 1998, 2004), absent (e.g., Rougier et al., 2007b, 2011, 2012), and present (e.g., Ji et al., 2002; Wible et al., 2009; Rougier et al., 2015). The presence of a well-developed masseteric foramen in *Peramus* and other peramurids (as well as eutriconodontans) has been subsequently documented from μ CT scans by Davis (2012). These are only a few examples (e.g., another is listed below in 'Comparisons' on gobiconodontids), and we therefore caution our colleagues to not rely on the scores for this structure in published taxon-character matrices.

Comparisons with Other Gondwanatherians

Partial dentaries referred to other gondwanatherian taxa have been described for (1) *Sudamerica ameghinoi* (MPEFCH 534) from the early Paleocene of Argentina—dentary fragment preserving the horizontal ramus, containing a single, fragmentary, enlarged incisor, two mesial postcanine teeth, and alveoli for two distal postcanine teeth, but missing all of the ascending ramus (Pascual et al., 1999:fig. 1); (2) *Galulatherium jenkinsi*

(based on NMT 02067, now RRBP 02067) from the Late Cretaceous (recently refined to Turonian–Campanian; Widlansky et al., 2018) of Tanzania—dentary fragment preserving the horizontal ramus, containing a single, fragmentary, enlarged incisor and alveoli and/or poorly preserved crowns of four postcanine teeth, as well as the anterior portion of the ascending ramus (Krause et al., 2003:figs. 3, 4; O'Connor et al., 2019:figs. 1–4, 5a); (3) cf. *Sudamerica ameghinoi* (MLP 95-I-10-5) from the middle Eocene of the Antarctic Peninsula—small dentary fragment consisting of only an anterior part of the horizontal ramus containing a single, fragmentary, enlarged incisor (Goin et al., 2006:fig. 2; see also Reguero et al., 2002, 2013:fig. 5.18); (4) *Ferugliotherium windhauseni* (MACN-RN 975) from the Late Cretaceous (Campanian–Maastrichtian) of Argentina—small dentary fragment consisting of a part of the horizontal ramus containing a buccolingually compressed, blade-like postcanine tooth and the alveolus for a single, enlarged incisor (Kielan-Jaworowska and Bonaparte, 1996:figs. 1, 2); and (5) *Gondwanatherium patagonicum* (MACN-RN 228) from the Late Cretaceous (Campanian–Maastrichtian) of Argentina—anterior dentary fragment containing alveoli, or partial alveoli, for an incisor and three postcanine teeth (Bonaparte, 1990; see also Gurovich, 2001, 2006:fig. 7.4). Whether or not the dentary specimens referred to *F. windhauseni* and *G. patagonicum* are correctly allocated has been controversial (Pascual et al., 1999; Kielan-Jaworowska et al., 2004; Gurovich, 2006; Pascual and Ortiz-Jaureguizar, 2007; Gurovich and Beck, 2009; Rougier et al., 2009; see review in Krause, 2014), but even if they are, they are extremely fragmentary and mostly uninformative with regard to lower jaw morphology. Also, the specimen of cf. *S. ameghinoi* yields no new morphological information that is not already present in *S. ameghinoi*. As such, we restrict our comparisons here to the dentary specimens of *S. ameghinoi* and *Galulatherium jenkinsi*.

Pascual et al. (1999) described the following characteristics as present in the dentary of *Sudamerica* (MPEFCH 534): horizontal ramus short and deep; contains very large and laterally compressed alveolus for a single incisor, whose root passes inferior to postcanine teeth; incisor lies oblique to longitudinal axis of postcanine tooth row; does not contain alveolus for canine; contains alveoli for four postcanine teeth; well-developed diastema between incisor and postcanine teeth; single mental foramen mesial to postcanine teeth and nearer to dorsal than to ventral margin; unfused mandibular symphysis; pterygoid fossa large; coronoid process originates far anteriorly; and inferred palinal lower jaw movement direction. All of these characters also pertain to the dentary of *Adalatherium*, although some minor differences exist (compare Fig. 5A and B). For instance, the horizontal ramus of the dentary of *Adalatherium* is not quite as short and deep (in large part because the diastema is relatively long), the coronoid process does not begin quite as far anteriorly (opposite the third rather than the second postcanine tooth), the ventral margin is slightly concave rather than flat, the incisor root does not extend as far posteriorly ventral to the postcanine teeth (passing ventral to pc3 rather than to all of the postcanines), and the incisor crown is not as erect. Furthermore, the orientation of wear striations in *Adalatherium*, as well as in *Vintana* (Schultz et al., 2014), indicates that the direction of the power stroke of the chewing cycle was not strictly palinal (mesiodistal) but also included a significant mesiolingual-distobuccal component. The sudamericid gondwanatherians *Sudamerica* and *Gondwanatherium*, by contrast, had a more strictly mesiodistal power stroke (Schultz et al., 2014).

The dentary of *Galulatherium* (RRBP 02067), originally described by Krause et al. (2003), was recently redescribed by O'Connor et al. (2019) with the benefit of μ CT scans. The scans reveal a major difference from the initial description by Krause et al. (2003) in that the dentary had only four, not five, postcanine teeth. In this regard, RRBP 02067 therefore resembles the

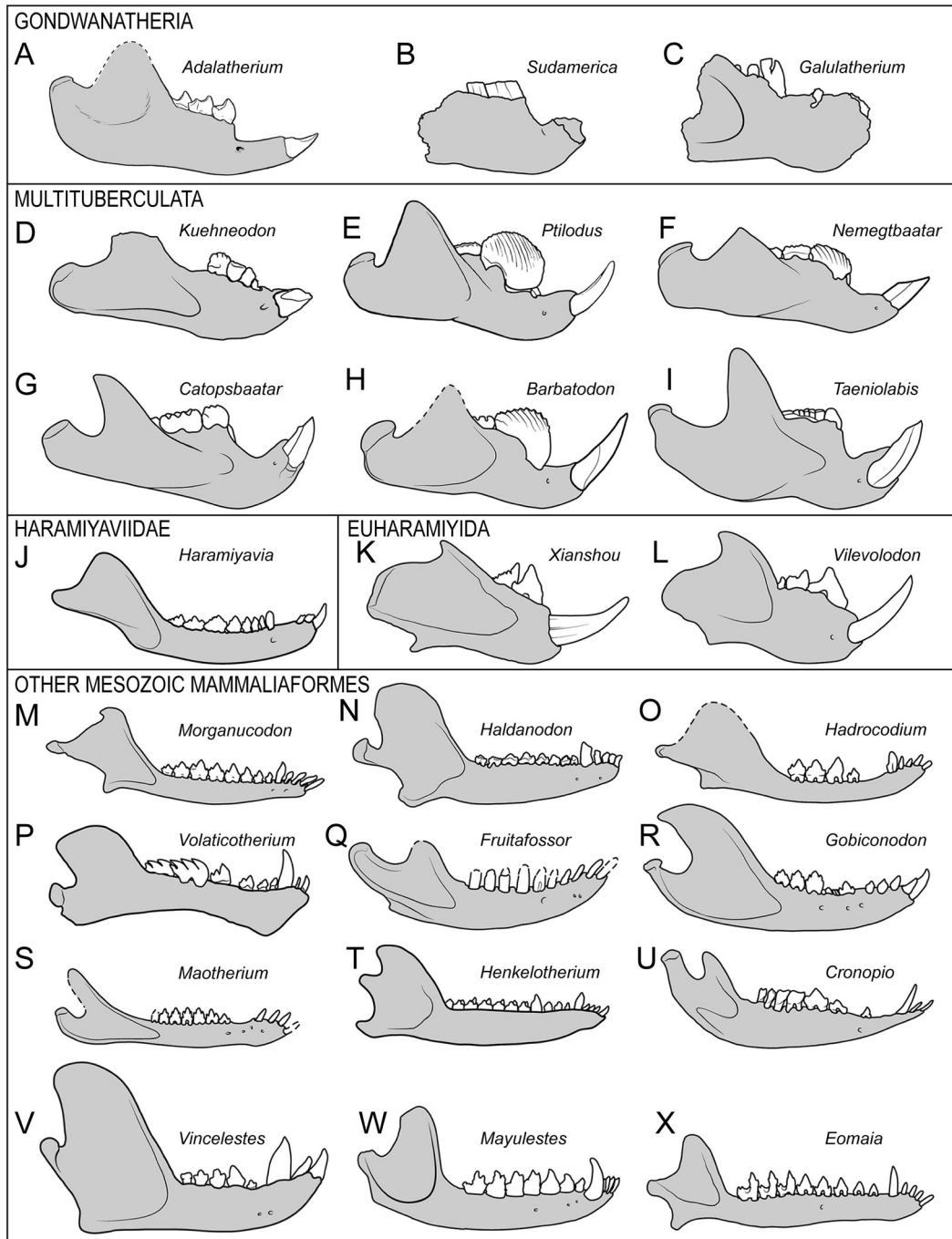


FIGURE 5. Comparison of general morphology of right dentary (lateral view) of the gondwanatherian *Adalatherium* with those of other taxa of Mesozoic mammaliaforms. **A**, *Adalatherium*; **B**, the sudamericid gondwanatherian *Sudamerica* (modified from Pascual et al., 1999:fig. 1a); **C**, the gondwanatherian *Galulatherium* (modified from O'Connor et al., 2019:fig. 1a₁); **D**, the paulchoffatiid multituberculate *Kuehneodon* (modified from Hahn, 1969:fig. 17a); **E**, the ptilodontid multituberculate *Ptilodus* (modified from Krause, 1982:fig. 2c); **F**, the djadochtatheriid multituberculate *Nemegtbaatar* (modified from Kielan-Jaworowska et al., 2004:fig. 8.40d); **G**, the djadochtatheriid multituberculate *Catopsbaatar* (modified from Kielan-Jaworowska et al., 2004:fig. 8.40k); **H**, the kogaionid multituberculate *Barbatodon* (modified from Smith and Codrea, 2015:fig. 2i, o); **I**, the taeniolabidid multituberculate *Taeniolabis* (modified from Kielan-Jaworowska et al., 2004:fig. 8.40c); **J**, the haramiyaviid *Haramiyavia* (modified from Luo et al., 2015:fig. 1a); **K**, the euharamiyidan *Xianshou* (modified from Bi et al., 2014:fig. 2b); **L**, the euharamiyidan *Vilevolodon* (modified from Luo et al., 2017:figs. 1b, 3f, ED fig. 3b); **M**, the morganucodontid morganucodontan *Morganucodon* (modified from Kermack et al., 1973:fig. 7a); **N**, the docodontid docodontan *Haldanodon* (modified from Wible and Rougier, 2017:fig. 32a); **O**, the indeterminate mammaliaform *Hadrocodium* (modified from Luo et al., 2001b:fig. 1a, and Luo et al., 2017:fig. 3i); **P**, the indeterminate mammaliaform *Volaticotherium* (modified from Meng et al., 2006:fig. 1d); **Q**, the indeterminate mammaliaform *Fruitafossor* (modified from Luo and Wible, 2005:fig. 1a); **R**, the eutriconodontan *Gobiconodon* (modified from Jenkins and Schaff, 1988:fig. 1); **S**, the symmetrodontan *Maothierium* (modified from Ji et al., 2009:fig. 2e); **T**, the dryolestoid *Henkelotherium* (modified from Luo, 2007:fig. 2e); **U**, the meridiolestidan dryolestoid *Cronopio* (modified from Rougier et al., 2011:fig. 4c); **V**, the stem therian *Vincelestes* (modified from Hopson and Rougier, 1993:fig. 2a); **W**, the stem marsupial *Mayulestes* (modified from Muizon, 1998:fig. 6c); **X**, the stem placental *Eomaia* (modified from Ji et al., 2002:fig. 2c). Dentaries not to scale; all drawn to same length.

dentaries of both *Sudamerica* and *Adalatherium*. Other similarities among all three forms include the following characteristics (compare Fig. 5A–C): horizontal ramus short and deep, unfused mandibular symphysis, sizable diastema between incisor and postcanines, single mental foramen situated on diastematic portion, coronoid process originating lateral to distal postcanines, incisor lies oblique to postcanine tooth series, and presence of large, laterally compressed, procumbent incisor. The dentary of *Galulatherium* differs from those of *Sudamerica* and *Adalatherium* in a number of ways: the symphysis is larger; the horizontal ramus lacks a pronounced, stepped differential in height between the diastema and the alveolar portion containing the postcanines; the mental foramen is located near mid-height rather than nearer the dorsal margin; the root of the incisor is shorter (extending posteriorly ventral to only the first postcanine tooth); the first postcanine is separated from the second by another diastema; and the postcanines were all enamel-less and ever-growing. The dentary of *Galulatherium* resembles that of *Adalatherium* but not that of *Sudamerica* in possessing a concave rather than straight ventral border of the horizontal ramus.

Comparisons with Multituberculates

Outside of Gondwanatheria, the lower jaw of *Adalatherium*, like that of *Sudamerica* and *Galulatherium*, is most similar to those of multituberculates, including representative, relatively early-branching forms such as the paulchoffatiids *Rugosodon* (Yuan et al., 2013:figs. 1, 2, S4) and *Kuehneodon* (Hahn, 1969:fig. 17), the plagiaulacid *Plagiaulax* (Simpson, 1928:fig. 9 [bottom]; Ride, 1957:fig. 1), and the eobataarids *Sinobaatar* (Kusuhashi et al., 2009:figs. 3, 6, 8, 9, 13, 16) and *Jeholbaatar* (Wang et al., 2019:fig. 2a, ED fig. 1). These resemblances (which are not necessarily synapomorphies) include absence of postdentary trough (incorrectly scored as reduced in multituberculate taxa by Luo et al. [2017] but corrected to absent in Huttenlocker et al. [2018]); absence of medial ridge overhanging postdentary trough (whether this character state is independent of ‘absence of postdentary trough’ is debatable [e.g., Luo et al., 2002; Rougier et al., 2007a]); absence of postdentary bones (sensu Allin [1975], the articular, prearticular, angular, and surangular) connected to the lower jaw, and therefore full development of dentary-squamosal (temporomandibular) jaw joint; absence of Meckelian sulcus; absence of groove for dental lamina; absence of angular process; presence of flat ventral surface of dentary in angular region; absence of coronoid bone (note that *Kuehneodon*, which retains a ‘vestigial’ coronoid, represents the only known exception among multituberculates [see below]); position of mandibular foramen inside pterygoid fossa, and below level of alveolar plane; absence of splenial bone; presence of large pterygoid fossa and associated mediolaterally wide pterygoid shelf that reaches dentary condyle via low crest (see below for discussion on scoring in multituberculates); distinctive crest/edge of masseteric fossa along anterior border of coronoid process; anterior extension of masseteric fossa onto horizontal ramus of dentary, up to level of last postcanine tooth (most, if not all, multituberculates, however, have an even greater extension anteriorly to below the ultimate premolar/first molar); absence of masseteric foramen; presence of single mental foramen in region of diastema; dentary condyle mediolaterally narrow and vertically deep, forming broad arc in lateral outline, and at or below the level of postcanine alveoli; dentary peduncle generally indistinct (i.e., not gracile, elongate, and with diameter less than condyle in lateral view, although it must be noted that some forms [e.g., *Lambdopsalis*, *Nessovbaatar*] approach this condition); coronoid process with robust base, beginning far anteriorly (lateral to ultimate postcanine tooth), and only moderately reclined (135°–145°); unfused mandibular symphysis; enlarged diastema

between distal incisor and postcanine teeth; and dentary short and deep. In addition, like multituberculates (Krause, 1982; Gambaryan and Kielan-Jaworowska, 1995), *Adalatherium* had a palinially directed power stroke of the chewing cycle, although, like *Vintana* (Schultz et al., 2014), it differed somewhat in also including a significant buccally directed component (Krause, Hu, et al., 2020). Also, the emplacement of the teeth in the dentary of *Adalatherium* is similar to the condition in almost all multituberculates in that the longitudinal axis of the incisor crown and root is oblique to the longitudinal axis of the postcanine tooth row, resulting in a marked external angle between the anterior and posterior parts of the horizontal ramus in dorsal (or ventral) view. Hahn (1971:fig. 1) noted that *Paulchoffatia* appears to be unique among multituberculates in not exhibiting such an obliquity between the incisor and the postcanine tooth row. Finally, the presence of a large, broadly open mandibular notch, between the condyle and the posterior margin of the coronoid process, is reminiscent of the condition typical of mammals, but perhaps most similar to that seen in at least some multituberculates (see, for example, a variety of paulchoffatiids, plagiaulacids, and cimolodontans [Kielan-Jaworowska et al., 2004:figs. 8.29, 8.35c₂, and 8.40, respectively]; Fig. 5D–I).

We take this opportunity to clarify scoring of several mandibular characters in multituberculates. First, it should be noted that the presence and degree of development of the pterygoid shelf (variously referred to as the pterygoideus shelf, the pterygoid crest, or the [medial] pterygoid ridge; see Simpson, 1926; Ride, 1957; Miao, 1988, 1993; Gambaryan and Kielan-Jaworowska, 1995) has had a checkered and confusing history of how it has been scored for multituberculates. Whereas early papers (e.g., Rowe, 1988; Luo et al., 2001a, 2001b) correctly scored it as being present (indeed, Luo et al. [2001b:S48] characterized it as “present, strongly developed and shelf-like”), many later papers (e.g., Luo et al., 2002, 2003, 2007a, 2011; Luo and Wible, 2005; Ji et al., 2009; Yuan et al., 2013; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014) scored the pterygoid shelf as being absent in multituberculates: this later interpretation is clearly incorrect. A well-developed pterygoid shelf has been described explicitly (and illustrated) as being present in a diversity of multituberculates (e.g., *Plagiaulax* [Simpson, 1928:35; Ride, 1957:400]; *Ptilodus* [Wall and Krause, 1992:174]; *Chulsanbaatar*, *Kryptobaatar*, *Nemegtbaatar*, *Sloanbaatar*, *Zofiabaatar* [Gambaryan and Kielan-Jaworowska, 1995]; *Kryptobaatar* [Wible and Rougier, 2000]; *Sinobaatar* [Hu and Wang, 2002:934; Kusuhashi et al., 2009:1266]; *Prochetodon* [Scott, 2004:243]; *Catopsbaatar* [Kielan-Jaworowska et al., 2005:504]; *Neoplagiaulax* [Scott, 2005:1206]; *Liaobaatar* [Kusuhashi et al., 2009:1280]). Indeed, several authors have generalized to state that a pterygoid shelf is characteristic of multituberculates (e.g., Simpson, 1926, 1928; Wall and Krause, 1992; Gambaryan and Kielan-Jaworowska, 1995; Woodburne et al., 2003; Kielan-Jaworowska et al., 2004). Various errors in scoring the pterygoid shelf in multituberculates were corrected by Krause et al. (2014) and then further refined by Luo et al. (2015), but Luo et al. (2017) reverted to the original, incorrect scorings. To summarize, not only is the pterygoid shelf present in all known multituberculates, including relatively primitive forms such as *Rugosodon* and *Sinobaatar*, it is mediolaterally expanded and has a ridge that extends posterodorsally to the dentary condyle; we have scored it as such for all multituberculates in which this region of the dentary can be evaluated (Hoffmann, Beck, et al., 2020; Krause, Hoffmann, et al., 2020).

Second, another character seemingly scored incorrectly for most, and potentially all, multituberculates concerns the ventral surface of the angular region of the dentary (Luo, pers. comm. [2017] confirmed that this refers to the angular region, not the angular process per se, so as to include those taxa that do not have an angular process). This region, in *Adalatherium*, is the same as the ventral surface of the pterygoid shelf. It is scored in

recent character evaluations of multituberculates as not flat (i.e., rounded) (e.g., Luo et al., 2003, 2007a, 2011, 2015, 2017; Luo and Wible, 2005; Ji et al., 2009; Yuan et al., 2013; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014; Han et al., 2017). Although there certainly is considerable subjectivity involved in characterizing this feature (which is why it was not employed by Krause et al., 2014), we believe it to be as flat or flatter in multituberculates than it is in various marsupial taxa that have been scored as flat in many analyses (e.g., *Didelphis*, *Macropus*, *Phascogale*); indeed, we would be inclined, by comparison, to list many of the taxa that have been scored as flat in this feature to be definitively rounded (e.g., *Canis*, *Felis*, *Bradypus*, *Tamandua*, *Dasyurus*, *Chaetophractus*) (D.W.K., pers. observ., DMNS mammalogy collections). The relatively planar nature of this region in multituberculates is strikingly well illustrated for *Kryptobaatar* by Wible and Rougier (2000:figs. 3b, 5, 12, 14, 20, 30) but is also seen in illustrations of a number of other taxa (e.g., *Plagiaulax* [Ride, 1957:fig. 1c]; *Paulchoffatia* [Hahn, 1969:fig. 1c]; *Kuehneodon* [Hahn, 1969:fig. 17]; *Nemegtbaatar* [Gambaryan and Kielan-Jaworowska, 1995:fig. 3a]; *Ectypodus* [Gambaryan and Kielan-Jaworowska, 1995:fig. 4a]; *Catopsbaatar* [Kielan-Jaworowska et al., 2005:fig. 9b5]; *Sinobaatar* [Kusuhashi et al., 2009:fig. 16]; *Barbatodon* [Smith and Codrea, 2015:fig. 2j]). This region of the dentary in *Adalatherium* is as flat as in these multituberculates.

Third, among multituberculates, the presence of a coronoid bone has been scored as polymorphic (present/absent) for ‘plagiaulacids’ (e.g., Luo et al., 2001b, 2002, 2003, 2007a, 2011; Luo and Wible, 2005; Zheng et al., 2013) and for plagiaulacids (e.g., Yuan et al., 2013; Zhou et al., 2013; Bi et al., 2014; Luo et al., 2017). Luo et al. (2002:49) explicitly and correctly stated the following with regard to the distribution of this character in primitive multituberculates: “(0/1 polymorphic) ‘plagiaulacids’ (present [0] for *Kuehneodon*, Hahn 1977a, but absent [1] in other ‘plagiaulacids’).” Bi et al. (2014) modified this character to include three states (0, present and significant; 1, vestigial; and 2, absent) but still scored plagiaulacids as 1/2. The presence of a coronoid bone was indeed noted in the paulchoffatiid *Kuehneodon* by Hahn (1977), but, to our knowledge, its presence has not been noted for any other ‘plagiaulacidan’ (or any other multituberculate) taxon more recently. As such, it is correct to score this character as polymorphic for ‘plagiaulacids,’ a presumably paraphyletic clustering of taxa that includes paulchoffatiids such as *Kuehneodon*, but not for plagiaulacids, which includes only *Plagiaulax* and *Bolodon* (sensu Kielan-Jaworowska et al., 2004).

Fourth, multituberculates are characterized as not having ‘exoflection’ (also occasionally referred to as efflection) of the angular process of the dentary (character 11 of, for example, Luo et al., 2007b, 2015, 2017; Yuan et al., 2013; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014; Meng et al., 2015; Han et al., 2017). There are two issues here: (1) multituberculates do not have an angular process, so, technically, they should be scored as ? for this character, as it is currently described in the literature (‘exoflection of the angular process of mandible’); and (2) if this character is referring to the angular region, which it appears to be, and not to the angular process per se, most multituberculates, including relatively primitive forms such as *Paulchoffatia* (see Hahn, 1969:fig. 1c) and *Kuehneodon* (Hahn, 1969:fig. 17a), should indeed be characterized as not possessing exoflection of this region. However, some plagiaulacids (e.g., *Plagiaulax*; see Ride, 1957:fig. 1a, c, e) do. As a result, plagiaulacids should be scored as having this characteristic but ‘plagiaulacids’ should be scored as polymorphic.

In a few respects, the dentary of *Adalatherium* resembles more closely those of derived multituberculates (i.e., cimolodontans; Fig. 5E–I) than those of earlier-branching forms (Fig. 5D). Such similarities are especially evident in taeniolabidids such as *Catopsalis* (Middleton, 1982:pl. 1, figs. 1, 2) and *Taeniolabis* (Granger and Simpson, 1929:fig. 4; Simmons, 1987:fig. 4),

kogaionids such as *Barbatodon* (Smith and Codrea, 2015:fig. 2), and djadochtatheriids such as *Djadochtatherium*, *Catopsbaatar*, and *Mangasbaatar* (Kielan-Jaworowska and Hurum, 1997:fig. 12; Rougier et al., 2016:figs. 23, 31). Perhaps the most significant similarity is that in cimolodontans, the dentary condyle is directed more dorsally than posteriorly (Fig. 5D–I; Kielan-Jaworowska et al., 2004:fig. 8.40).

Comparisons with Euharamiyidans

The higher taxonomy of several described genera from the Middle–Late Jurassic of China—*Arboroharamiya* (Zheng et al., 2013; Meng et al., 2014, 2016; Han et al., 2017), *Shenshou* (Bi et al., 2014), *Xianshou* (Bi et al., 2014), *Maiopatagium* (Meng et al., 2017), *Vilevolodon* (Luo et al., 2017), and *Qishou* (Mao and Meng, 2019a)—is complex and changing rapidly. For the purposes of comparison here, they will be collectively referred to as members of the clade Euharamiyida. The lower jaw is known for all but one of these genera, *Maiopatagium* (Meng et al., 2017). *Megaconus* (Zhou et al., 2013), also from the Middle–Late Jurassic of China, although represented by lower jaw material, is not considered here (following Krause et al. [2014], Han et al. [2017], and Wang et al. [2019]) because of unresolved and contentious interpretations of both its morphology, including that of the lower jaw, and its taxonomic/systematic status (Bi et al., 2014; Meng, 2014; Meng et al., 2014; Zhou et al., 2014; Debuysschere, 2016; Mao and Meng, 2019a). *Megaconus* has been regarded an eleutherodontid eleutherodontidan haramiyidan by Zhou et al. (2013); an allotherian but possibly a stem mammal by Bi et al. (2014); either “a stem mammal or a multituberculate” by Meng (2014:530); a possible multituberculate by Meng et al. (2014); an unspecified haramiyidan by Meng et al. (2017); a non-eleutherodontidan euharamiyidan haramiyidan by Luo et al. (2017); and a non-eleutherodontid eleutherodontidan haramiyidan by Huttenlocker et al. (2018). Our phylogenetic analyses recovered *Megaconus* as the sister taxon of Tritylodontidae or in a polytomy with other allotherians (Hoffmann, Beck, et al., 2020; Krause, Hoffmann, et al., 2020). A detailed description and reanalysis of this taxon appears warranted.

The lower jaws of euharamiyidans are similar to one another and differ from that of *Adalatherium* in the following features: horizontal ramus mediolaterally narrow (consistent with mediolaterally narrow teeth); mandibular condyle mediolaterally narrow (longer than wide in dorsal view), posteriorly directed, and situated below level of postcanine alveoli; presence of angular process; rounded ventral surface of angular region (it is relatively flat in *Adalatherium*); presence of vestigial coronoid bone (condition unknown in *Vilevolodon*); presence of well-defined anterodorsal crest of masseteric fossa; mental foramen positioned below p4, well posterior to diastema (this is contrary to Luo et al. [2017] who scored *Arboroharamiya*, *Xianshou*, *Vilevolodon*, and *Shenshou* as possessing the posterior-most mental foramen in the canine and anterior premolar region; this was seemingly corrected by Han et al. [2017:supplementary information p. 37], but their discussion leaves it unclear as to whether the mental foramen lies below p4 or below the junction of p4 and m1; however, the illustrations of *Arboroharamiya allinopsoni* [Han et al., 2017:fig. 2a] and *Shenshou* [Han et al., 2017:left figure on p. 37 of supplementary information] appear to show it directly below p4). It must also be noted that the dentary of *Qishou* appears to have two mental foramina, both of them positioned anterior to p4 (Mao and Meng, 2019a:fig. 2h). Another difference appears to be that the mandibular notch descends to a level below the condyle in *Adalatherium* but does not do so in euharamiyidans; unfortunately, not all of the mandibular notch is preserved in UA 9030, nor is the coronoid process. As such, we also cannot conclusively determine the conformation of the coronoid process in *Adalatherium* to determine whether it is

pointed, recurved (apex directed posterodorsally), and with a thick, rounded anterodorsal edge as it appears to be in all euharamiyidans discovered to date. As best shown in the lower jaw of *Qishou* (Mao and Meng, 2019a:fig. 2e), the postcanine tooth row is aligned with the longitudinal axis of the lower incisor rather than lying oblique to it as in *Adalatherium*. Finally, following the interpretation of euharamiyidan lower jaw morphology in Han et al. (2017), Mao and Meng (2019a), and Wang et al. (2019), *Adalatherium* is considered to be similar to euharamiyidans in lacking a postdentary trough. Luo et al. (2017) reported the trough to be present and reduced in euharamiyidans, but this view has been challenged, at least for *Qishou* (Mao and Meng, 2019a).

The lower jaws of euharamiyidans and *Adalatherium* are similar in exhibiting the following features: absence of fully developed postdentary trough; absence of separate scars for surangular/prearticular; Meckelian sulcus reduced or absent (scored as reduced by Luo et al. [2017] in euharamiyidans and absent by Han et al. [2017] in *Arboroharamiya*, *Shenshou*, and *Xianshou*; Mao and Meng [2019a] stated that it is also absent in *Qishou*—it is absent in *Adalatherium*); dentary short and deep, with sizable diastema between distal incisor and postcanine teeth; absence of groove for dental lamina; mandibular foramen located in pterygoid fossa, below alveolar plane; absence of concavity for reflected lamina of angular bone; absence of splenial; possession of condyle/glenoid articulation of dentary/squamosal (postdentary complex not involved in craniomandibular joint); absence of gracile and elongate dentary peduncle; presence of medially expanded pterygoid fossa with associated pterygoid shelf (in *Adalatherium*, the shelf is medio-laterally broader and reaches the dentary condyle via a low crest); presence of low anterodorsal and anteroventral crests of masseteric fossa (there is some disagreement on the degree of development of the anteroventral crest between Luo et al. [2015; low and broad] and Luo et al. [2017; well defined and thin]; Han et al. [2017] regarded it as a low and broad crest); absence of masseteric foramen; ultimate postcanine medial to coronoid process, which has a robust base and is reclined at approximately 135°–145°; unfused mandibular symphysis; and palinal direction of power stroke of chewing cycle, although that of *Adalatherium* has a buccal component that is not present in euharamiyidans (Mao and Meng, 2019b).

Some clarification appears to be in order regarding how the anteroventral extension of the masseteric fossa is characterized for euharamiyidans. The fossa extends anteriorly to a position below or nearly below p4 in *Arboroharamiya* (Zheng et al., 2013:figs. 2b, S2; Meng et al., 2014:fig. 2a), *Xianshou* (Bi et al., 2014:fig. 2b; although the photographs in ED figs. 5b and 6a suggest that it might not extend quite as far anteriorly in *X. linglong*, where it appears to extend anteriorly only as far as below m1, as in *X. songae*), and *Qishou* (Mao and Meng, 2019a:fig. 2b, g). The precise anteroventral limit of the masseteric fossa in *Shenshou* is difficult to discern based on the available photographs, but it was characterized as extending to below p4 for all euharamiyidans known at the time, including *Shenshou*, by Bi et al. (2014). The anterior border of the masseteric fossa in the more recently described *Vilevolodon* is depicted as being posterior to m2 and scored as having no anteroventral extension onto the horizontal ramus (Luo et al., 2017:fig. 1b, character 23). Furthermore, Luo et al. (2017:supplementary information p. 7) stated that “All eleutherodontids for which mandibles are known... lack the anterior extension of the masseteric fossa into the mandibular body” and scored them as such. As noted by Han et al. (2017) and Mao and Meng (2019a), this appears to be an error; indeed, ED figs. 2 and 3 in Luo et al. (2017) ostensibly depict the masseteric fossa of *Vilevolodon* farther forward on the right dentary, and extending anteriorly to below the first molar, if not farther, on the left dentary.

Comparisons with *Haramiyavia*

Employing taxonomy consistent with our most recent phylogenetic analysis (Hoffmann, Beck, et al., 2020; Krause, Hoffmann, et al., 2020), the only haramiyidan represented by lower jaw material is the haramiyaviid *Haramiyavia*, from the Late Triassic of Greenland (Jenkins et al., 1997; Butler, 2000; Luo et al., 2015). The lower jaw of *Haramiyavia* (see Jenkins et al., 1997; Luo et al., 2015) differs radically from those of both *Adalatherium* and euharamiyidans in a host of features, most of them clearly plesiomorphic: presence of alveoli for many more teeth (11 as opposed to only four [euharamiyidans] or five [*Adalatherium*]); retention of fully developed postdentary trough; presence of well-developed Meckelian sulcus that extends anteriorly onto horizontal ramus of dentary; presence of mandibular foramen in postdentary trough or posterior part of Meckelian sulcus; presence of concavity for reflected lamina of angular bone; dentary long and shallow, without sizable diastema between distal incisor and postcanine teeth (instead, a diastema exists between the distal incisor and the canine); presence of well-developed coronoid bone (absent in *Adalatherium*; vestigial in euharamiyidans); absence of well-developed pterygoid fossa and associated pterygoid shelf; absence of ventral border of masseteric fossa; absence of anteroventral extension of masseteric fossa onto horizontal ramus; coronoid process not overlapping lateral aspect of postcanine teeth; ventral border of dentary convex (rather than slightly concave); and lower jaw movement relatively orthal in direction during power stroke of chewing cycle. *Adalatherium* differs from both *Haramiyavia* and euharamiyidans in having a dorsally, rather than posteriorly, directed mandibular condyle.

Similarities between the dentaries of *Adalatherium* and *Haramiyavia* include absence of groove for dental lamina (regarded as clearly absent in *Haramiyavia* by Luo et al. [2015] but scored as unknown by Han et al. [2017]); mediolaterally wide horizontal ramus (in contrast to euharamiyidans); absence of angular process (although *Haramiyavia* is characterized as possessing an ‘angular region’); position of mandibular foramen below alveolar plane; absence of masseteric foramen; position of posterior-most mental foramen in anterior part of dentary; condyle/glenoid articulation of dentary and squamosal (note that Luo et al. [2015] likely mis-scored this character; see Han et al. [2017]); dentary condyle above alveolar plane; anterodorsal crest of masseteric fossa absent or weak; coronoid process with robust base; degree of tilting of coronoid process (note that this appears to have been incorrectly measured by Luo et al. [2015: fig. 1a, b]); and unfused mandibular symphysis. In general, *Haramiyavia* seems to retain a more plesiomorphic mammaliaform dentary morphology than that of *Adalatherium*.

Comparisons with Other Mesozoic Mammaliaformes

The general shape and structure of the lower jaw of *Adalatherium* differs considerably from that of most other Mesozoic mammaliaforms across a broad spectrum of taxonomic and ecomorphological types (Luo, 2007). Indeed, the dentary of *Adalatherium* appears to be derived relative to most Mesozoic forms (Fig. 5M–X), other than multituberculates (Fig. 5D–I) and, to a lesser extent, euharamiyidans (Fig. 5K, L). Outside of these forms, perhaps the closest similarities are with gobiconodontid eutriconodontans.

Comparison with Gobiconodontids—The dentary of *Adalatherium* bears some similarities to those of eutriconodontans, and particularly to gobiconodontids such as *Gobiconodon* (Fig. 5R), *Repenomamus*, and *Spinolestes*, especially with regard to the morphology of the ascending process. These similarities include the absence of a postdentary trough and postdentary bones (articular, prearticular, angular, surangular), therefore indicative of a fully load-bearing dentary-squamosal jaw joint;

absence of the splenial; absence of a groove for the dental lamina; presence of an enlarged pterygoid fossa and associated pterygoid shelf; and presence of an unfused mandibular symphysis. Furthermore, the ventral margin of the ascending process in *Adalatherium* and the gobiconodontids is similar in lacking an angular process and in rising in a smooth arc through a somewhat indistinct peduncular region to reach the dentary condyle, which faces posterodorsally. Also, the ventral surface of the angular region in gobiconodontids, like that of *Adalatherium*, appears rather flat (e.g., Jenkins and Schaff, 1988:figs. 4, 5; Meng et al., 2003:figs. 1, 2), contrary to how it is typically scored, even in recent analyses (e.g., Martin et al., 2015; Han et al., 2017; Luo et al., 2017).

Despite these similarities, the lower jaws of gobiconodontids differ fundamentally from that of *Adalatherium* in that their dentaries are much longer and shallower, bear more teeth, and lack a sizable diastema. They also differ in retaining a Meckelian sulcus (and ossified Meckel's cartilage; Wang et al., 2001; Meng et al., 2003; Martin et al., 2015); in possessing a massive, bulbous, and transversely broad (e.g., Jenkins and Schaff, 1988:fig. 9) rather than a relatively gracile, mediolaterally narrow, and vertically deep dentary condyle; in having a large, deep masseteric fossa that extends ventrally to near the ventral margin of the dentary, resulting in a well-defined and thin ventral crest (by contrast, the ventral border of the masseteric fossa in *Adalatherium* is relatively far dorsal in position and marked by only a low, rounded edge); and in possessing multiple mental foramina, the posterior-most of which is much farther posteriorly located (below the penultimate premolar) than the single mental foramen in *Adalatherium*.

Whether or not the coronoid bone was present in all or some gobiconodontids is somewhat unclear from the literature. For example, Jenkins and Schaff (1988:4) stated that there “appears to be a faint, triangular facet for a coronoid bone (fide H.-D. Sues)” in *Gobiconodon ostromi*, and the presence of a coronoid bone or attachment scar in *Gobiconodon* is scored in recent papers as present by Rougier et al. (2001, 2007a, 2007b, 2011, 2012), Ji et al. (2002, 2009), Luo et al. (2002, 2003, 2007a, 2007b, 2011), Luo and Wible (2005), Hu (2006), Zheng et al. (2013), Zhou et al. (2013), and Martin et al. (2015); absent by Krause et al. (2014); and vestigial or absent by Bi et al. (2014), Luo et al. (2015, 2017), and Han et al. (2017). Lopatin and Averianov (2015) and Kusuhashi et al. (2016) explicitly stated that there is no trace of a coronoid bone in either *G. haizhouensis* or *G. hoburensis*, respectively, and none appears evident in illustrations of *G. borissiakii* either (e.g., Lopatin and Averianov, 2015:fig. 15b). In light of this recent evidence, it would appear appropriate to score *Gobiconodon* as polymorphic (vestigial/absent) for this feature. Similarly, *Repenomamus* is consistently scored as lacking any trace of a coronoid bone (Hu, 2006; Luo et al., 2007a, 2007b, 2015, 2017; Ji et al., 2009; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014; Martin et al., 2015:cynodont/mammaliaform data set; Han et al., 2017), with the exception of Martin et al. (2015:eutriconodontan data set), in which it is scored as present. Finally, *Spinolestes* is scored in one data set (cynodont/mammaliaform data set) by Martin et al. (2015) as absent for this character but as unscorable in another (eutriconodontan data set) in the same paper, whereas Luo et al. (2017) scored it as being present and significant. These examples simply underscore the need for detailed description and illustration of phylogenetically important forms such as these.

Similarly, whether a masseteric foramen (= labial mandibular foramen) is present, absent, or polymorphic in gobiconodontids is also unclear from the literature. For instance, Rougier et al. (2001:fig. 4) noted and illustrated its presence in *Gobiconodon*, sp. indet., consistent with scoring in Luo et al. (2003), Rougier et al. (2007a, 2007b, 2011, 2012), and Gaetano and Rougier (2011). By contrast, a number of papers (e.g., Ji et al., 2002,

2009; Luo and Wible, 2005; Luo et al., 2007a, 2007b, 2015, 2017; Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014; Han et al., 2017) scored the masseteric foramen as absent in *Gobiconodon*, and Kusuhashi et al. (2016) explicitly stated that it is not present in *G. haizhouensis*. Lopatin and Averianov (2015) also stated that there are no foramina in the masseteric fossa of *G. hoburensis*, and, indeed, none are apparent in their illustrations (e.g., figs. 13b, 15c) of *G. borissiakii*. It appears from this brief literature survey that *Gobiconodon*, and gobiconodontids in general, following Krause et al. (2014), should be scored as polymorphic for this character.

CONCLUSIONS

The dentary in the holotype and only known specimen of *Adalatherium* (UA 9030) is the most complete yet known for a gondwanatherian. Lacking any clear evidence for either a Meckelian sulcus or a postdentary trough, we conclude that the middle ear ossicles of *Adalatherium* were completely separated from the dentary, attached only to the cranium, and functioned as strictly auditory structures. A distinct autapomorphy of *Adalatherium* appears to be the dorsal position of the masseteric fossa. To our knowledge, no Mesozoic mammaliaform, including multituberculates and euharamiyidans, exhibits such a dorsally placed masseteric fossa. That said, the dentary of the recently described euharamiyidan *Vilevolodon* (Luo et al., 2017:ED fig. 3b) seems to exhibit a substantial region of the dentary ventral to the masseteric fossa, but clearly not as much as in *Adalatherium*.

Although minor differences exist, the horizontal ramus of the dentary of *Adalatherium* is fundamentally identical in structure to that of *Sudamerica*, which was previously the best-known gondwanatherian in terms of mandibular morphology. The mandibular morphology of *Adalatherium* (and Gondwanatheria in general) is highly derived relative to that of most other Mesozoic mammaliaforms and is most similar to that of multituberculates. In fact, the dentaries of *Adalatherium* and multituberculates are constructed on a remarkably similar bauplan, with, for example, a short and deep horizontal ramus, a large diastema between the incisor and postcanines, a coronoid process lateral to the ultimate postcanine, an anterior extension of the masseteric fossa onto the horizontal ramus, and a large pterygoid fossa. Multituberculata are a group that has long formed the core of Marsh's (1880:239) order Allotheria (“*Plagiaulax*, the allied genus *Ctenacodon*, and possibly one or two other genera”). Marsh's (1880) Allotheria was elevated to the rank of subclass by Simpson (1928) and has, at one time or another, in addition to multituberculates, included tritylodontids (now considered non-mammaliaform cynodonts), haramiyids, haramiyavids, eleutherodontids, arboroharamiyids, theroteinids, and gondwanatherians (see reviews in Butler, 2000; Kielan-Jaworowska et al., 2004; Martin, 2018), not all of which are represented by mandibular material.

Among those allotherians, or erstwhile allotherians, represented by mandibular material (multituberculates, haramiyavids, euharamiyidans, and gondwanatherians), the dentary of *Adalatherium* is also similar to those of euharamiyidans in an array of features, second only to those of multituberculates. The only known representative of the Haramiyavidae, *Haramiyavia*, exhibits a mandibular morphology that is exceedingly plesiomorphic relative to that of euharamiyidans, which, in turn, is plesiomorphic relative to those of multituberculates and gondwanatherians (as represented by *Adalatherium*, *Sudamerica*, and *Galulatherium*) in most respects.

Among Mesozoic mammaliaforms that are clearly not allotherians, the dentary of *Adalatherium* bears some similarities to those of gobiconodontids, particularly in the morphology of their ascending processes, but *Adalatherium* is only distantly related to gobiconodontids and any resemblances are therefore superficial.

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