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Phylogenetic placement of *Adalatherium hui* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar: implications for allotherian relationships

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RH: HOFFMANN ET AL.—PHYLOGENY OF *ADALATHERIUM HUI*

ABSTRACT—The phylogenetic position of Gondwanatheria within Mammaliaformes has historically been controversial. The well-preserved skeleton of *Adalatherium hui* from the Late Cretaceous of Madagascar offers a unique opportunity to address this issue, based on morphological data from the whole skeleton. Gondwanatheria were, until recently, known only from fragmentary dental and mandibular material, as well as a single cranium. The holotype of *A. hui* provides the first postcranial skeleton for gondwanatherians and substantially increases the amount of character data available to score. We sampled 530 characters and 84 cynodonts (including 34 taxa historically affiliated with Allotheria) to test the phylogenetic relationships of Gondwanatheria and Allotheria using parsimony, undated Bayesian, and tip-dated Bayesian methods. We tested three lower dental formulae for *Adalatherium*, because its postcanines are distinctly different from those of other mammaliaforms and cannot readily be homologized with any known dental pattern. In all analyses, *Adalatherium* is recovered within Gondwanatheria, most frequently outside of Sudamericidae or Ferugliotheriidae, which is congruent with establishment of the family Adalatheriidae. The different dental coding schemes do not greatly impact the position of *Adalatherium*, although there are differences in character optimization. In all analyses, Gondwanatheria are placed within Allotheria, either as sister to Multituberculata, nested within Multituberculata, as sister to *Cifelliodon* (and Euharamiyida), or in a polytomy with other allotherians. The composition of Allotheria varies in our analyses. The haramiyidans *Haramiyavia* and *Thomasia* are placed outside of Allotheria in the parsimony and tip-dated Bayesian analyses, but in a polytomy with other allotherians in the undated Bayesian analyses.

INTRODUCTION

The Late Cretaceous to Paleogene Gondwanatheria are one of the least well known early mammaliaform clades from the southern hemisphere, and currently include ten valid, monotypic genera: *Ferugliotherium* [=*Vucetichia*], *Trapalcotherium*, *Gondwanatherium*, *Sudamerica*, *Bharattherium* [=*Dakshina*], *Lavanify*, *Vintana*, *Galulatherium*, *Greniodon*, and *Adalatherium*. With the exception of the most recently described taxa, *Vintana* (Krause et al., 2014) and *Adalatherium* (Krause et al., 2020), gondwanatherians are known only from fragmentary dental and gnathic remains. Based on the very limited morphological information available, the phylogenetic position of Gondwanatheria within Mammaliaformes has historically been controversial, and has included a proposed close relationship to (1) the placental clade Xenarthra (Scillato-Yané and Pascual, 1985; Bonaparte, 1986a, 1986b, 1986c, 1987, 1988, 2017; Bonaparte and Pascual, 1987; Mones, 1987) or (2) members of Allotheria, which have at various times been considered to include Multituberculata, Haramiyida (sensu Butler, 2000), and Euharamiyida (e.g., Krause et al., 1992, 2014, 2020; Bonaparte et al., 1993; Krause, 1993; Krause and Bonaparte, 1993; Kielan-Jaworowska and Bonaparte, 1996; Gurovich, 2006; Pascual and Ortiz-Jaureguizar, 2007; Gurovich and Beck, 2009; Rougier et al., 2009; Rougier, Gaetano et al., 2011; Bi et al., 2014). Pascual et al. (1999) concluded that Gondwanatheria could not be assigned with certainty to any mammalian clade and simply referred to them as Mammalia incertae sedis, an opinion followed in the compendium on Mesozoic mammals by Kielan-Jaworowska et al. (2004). It should be noted that Kielan-Jaworowska et al. (2004) used a stem-based definition of Mammalia that includes Mammaliaformes. It is likely that Pascual et al. (1999) were also referring to Mammaliaformes rather than crown Mammalia when they assigned Gondwanatheria to ‘Mammalia incertae sedis.’ For completeness, it bears mentioning that *Vintana*, as a representative of Gondwanatheria, has been found to lie outside of Allotheria in some recent analyses (Han et al., 2017; Wang et al., 2019). Finally, relationships between gondwanatherians and the bizarre Cenozoic *Groeberia* and *Patagonia* have also been proposed (Chimento et al., 2014) but the analysis and results were criticized by Beck (2017). Zimicz and Goin (2020) provided a more detailed critique of Chimento et al.’s (2014) conclusion to assign *Groeberia* to Gondwanatheria, but did not discuss *Patagonia*. We consider the putative gondwanatherian relationships of *Groeberia* refuted and those of *Patagonia* unsubstantiated and unlikely; as such, they will not be discussed further in this paper.

The first formal phylogenetic analysis to include Gondwanatheria was conducted by Gurovich and Beck (2009), who placed the gondwanatherians *Sudamerica*, *Gondwanatherium*, and *Ferugliotherium* in a polytomy with ‘plagiaulacidan’ and cimolodontan multituberculates within Allotheria, with the haramiyidans *Thomasia* and *Haramiyavia* placed outside of Mammaliaformes. Based on a greatly expanded sample of multituberculates and gondwanatherians (including the first cranium of a gondwanatherian, that of *Vintana*), Krause et al. (2014) recovered Allotheria, including Multituberculata, Gondwanatheria, *Haramiyavia*, *Thomasia*, and *Arboroharamiya*, within Mammalia. Although Multituberculata, Gondwanatheria, and Euharamiyida (including *Arboroharamiya*) were still recovered within Mammalia in a parsimony analysis by Krause et al. (2020), the haramiyidans *Haramiyavia* and *Thomasia* were placed outside of Mammaliaformes.

The composition and position of Allotheria have gained attention in recent years because of the implications for the timing of the origin of Mammalia (sensu Rowe, 1988). Contrasting hypotheses have either (1) placed Allotheria, including the Late Triassic-to-Jurassic

Haramiyavia and *Thomasia*, within Mammalia (e.g., Yuan et al., 2013; Zheng et al., 2013; Bi et al., 2014; Krause et al., 2014; Han et al., 2017; Wang et al., 2019), implying that Mammalia originated by the Late Triassic, or (2) placed Multituberculata within Mammalia but *Haramiyavia* and *Thomasia* outside of Mammalia (e.g., Zhou et al., 2013; Close et al., 2015; Luo et al., 2015, 2017; Huttenlocker et al., 2018), compatible with an origin of mammals some 40 million years later, in the latest Early Jurassic, and potentially a relatively "explosive" diversification (Cifelli and Davis, 2013:161). Supporting a possible close relationship among Gondwanatheria, Multituberculata, and Haramiyida are the presence of postcanines with numerous cusps that are arranged longitudinally in multiple rows, enlarged incisors, and, typically, loss of canines. The discovery of a nearly complete and well-preserved skeleton of the gondwanatherian *Adalatherium hui* (UA 9030) from the Late Cretaceous of Madagascar (Krause et al., 2020) provides a unique opportunity to explore phylogenetic relationships of purported allotherian taxa based on morphological data from the whole skeleton.

Here, we test the phylogenetic relationships of the most complete gondwanatherian, *Adalatherium* and, more broadly, the composition and relationships of Allotheria, using the matrix of Krause et al. (2020). In addition to the parsimony analysis presented in Krause et al. (2020), we (1) employ different coding schemes to test for uncertainty in homologizing the lower dentition of *Adalatherium*, (2) constrain relationships within Multituberculata to match the current consensus view, and (3) analyze the data set using both undated and tip-dated Bayesian methods. Tip-dated Bayesian inference has only recently been applied to paleontological data sets (e.g., Beck and Lee, 2014; Lee et al., 2014; Close et al., 2015; Bapst et al., 2016; Matzke and Wright, 2016; Turner et al., 2017; Lee and Yates, 2018; Sterli et al., 2018; Beck and Taglioretti, 2019; King and Beck, 2019), but including stratigraphic information could be particularly informative in the case of Allotheria because the fossil record of potential allotherian taxa extends from the Late Triassic to the Eocene. Theoretically, including fossil dates might more realistically constrain relationships of taxa from very disparate time periods, and may help distinguish synapomorphies from cases of homoplasy (Lee and Yates, 2018). At the very least, the topologies that result from undated and tip-dated Bayesian analyses of the same data set can differ markedly, and so it is appropriate to investigate both of these approaches (Lee and Yates, 2018; Beck and Taglioretti, 2019; King and Beck, 2019).

Detailed information on the discovery, preservation, and geological context of UA 9030, the holotype and only known specimen of *Adalatherium hui*, can be found in Krause, Groenke, et al. (this volume), and detailed morphological description and comparisons of the cranium, inner ear, lower jaw, dentition, and postcranial skeleton are presented in various other chapters of the same volume (Krause and Hoffmann, this volume).

Institutional Abbreviations—**UA**, Université d'Antananarivo, Antananarivo, Madagascar.

Anatomical Abbreviations—**c**, lower canine; **C**, upper canine; **i**, lower incisor; **I**, upper incisor; **m**, lower molar; **M**, upper molar; **p**, lower premolar; **P**, upper premolar; **pc**, lower postcanine; **PC**, upper postcanine.

Methodological Abbreviations—**ACCTRAN**, accelerated transformation; **CI**, ensemble consistency index; **ESS**, effective sample size; **IGR**, independent gamma rates; **MCC**, maximum clade credibility tree; **MCMC**, Markov Chain Monte Carlo; **Mk**, Markov k; **MPT**, most parsimonious tree; **PAUP**, Phylogenetic Analysis Using PAUP*; **PP**, Bayesian posterior probability; **RAS**, random addition sequence; **RI**, ensemble retention index; **TNT**, Tree Analysis using New Technology; **TBR**, tree bisection and reconnection branch swapping.

MATERIALS AND METHODS

Morphological Characters

The matrix of 84 taxa and 530 characters used here to test the phylogenetic relationships of *Adalatherium* is a modified version of the data set developed by Hoffmann (2016) and subsequently revised by Krause et al. (2020). Characters for this matrix have been culled from various references including Rougier et al. (1997, 1998, 2007), Hopson and Kitching (2001), Luo et al. (2002, 2007, 2011, 2015, 2017), Hu (2006), Wible et al. (2009), Liu and Olson (2010), Rougier, Apesteguía, et al. (2011), O'Leary et al. (2013), 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), and Huttenlocker et al. (2018). Characters specifically intended to resolve relationships among multituberculates were obtained from Simmons (1993), Rougier et al. (1997), Kielan-Jaworowska and Hurum (1997, 2001), Gurovich and Beck (2009), Yuan et al. (2013), and Krause et al. (2014). The character matrix was initially compiled in Mesquite 3.6 (Maddison and Maddison, 2019) and later transferred to MorphoBank to allow simultaneous scoring by authors. The data matrix is available as a NEXUS file in the Supplementary Data section (Supplementary Data 1) or on MorphoBank under Project 3637. In addition, a character list containing further notes and explanations is included in the Supplementary Data section. This list includes references to corresponding character numbers of Krause et al. (2014; indicated as K###), Huttenlocker et al. (2018; H###), and Han et al. (2017; HAN###). A total of 22 characters were newly developed for the matrix implemented by Krause et al. (2020; chars. 16, 27, 43, 44, 47, 48, 50, 61, 64, 71, 72, 73, 131, 140, 146, 219, 221, 222, 223, 224, 291, 424) and are indicated as

(NEW) in the character list. Changes to characters are indicated by "~". These changes include minor adjustments in wording, and/or a different ordering of character states. Explanations for substantial changes are presented in red font in the character list.

Taxa and Sources

A total of 84 extinct and extant cynodonts are included in the character-taxon matrix. This matrix focuses particularly on those taxa that are represented by well-preserved specimens, namely those that are known from more than dental or gnathic remains. Taxa that have been affiliated with Allotheria in previous studies and that are most germane to this analysis of gondwanatherian relationships are represented in the matrix regardless of their completeness. These include, in particular, the gondwanatherians *Ferugliotherium*, *Trapalcotherium*, *Gondwanatherium*, *Sudamerica*, *Bharattherium*, *Lavanify*, *Galulatherium*, and *Greniodon*, and the haramiyidans *Haramiyavia* and *Thomasia*, all of which are represented by rather fragmentary material (isolated teeth and/or partial dentaries). Most of the scorings are based on first-hand observation of original specimens, casts, 3D prints, or Computed Tomography data. A full list of taxa and specimens is provided in the Supplementary Data. Those taxa that one or more of the authors have personally observed are listed with specimen numbers. Literature references were used to supplement direct observations and to score taxa that we were not able to study in person.

Genus-level terminal units were used for most taxa, with two exceptions. The multituberculates *Bolodon* and *Plagiaulax* were grouped into a single terminal taxon, Plagiaulacidae, in an effort to maximize available complementary dental and mandibular morphology for scoring this group. The multiple species within *Bolodon* are known from upper and lower dentitions, whereas *Plagiaulax* is known solely from dentaries and lower dentitions

(Simpson, 1928; Kielan-Jaworowska et al., 2004). Secondly, relationships within a number of Late Jurassic multituberculates from the Guimarota coal mine in Portugal are uncertain and many taxa were intentionally over-split to distinguish between upper and lower dentitions (Hahn and Hahn, 2006). We therefore combined scorings for the best-represented genera — *Kuehneodon*, *Paulchoffatia*, *Meketichoffatia*, and *Pseudobolodon* — into one terminal taxon, Guimarota Paulchoffatiidae, in this study.

Here we use the following phylogenetic definitions to describe relevant higher-level clades. We follow Rowe's (1987, 1988) definition of Mammaliaformes as the last common ancestor of Morganucodontidae and Mammalia and all of its descendants, and restrict the term Mammalia to the descendants of the last common ancestor of monotremes and therians. We follow Sereno's (2006) definition of Allotheria as the most inclusive clade including *Taeniolabis taoensis* but not *Mus musculus* or *Ornithorhynchus anatinus*; and Simmons's (1993) definition of Multituberculata as the last common ancestor of *Paulchoffatia* and Cimolodonta. A phylogenetic definition of Gondwanatheria is currently lacking. For the purpose of discussing Gondwanatheria in this paper and as a working hypothesis, we refer to Gondwanatheria as the most inclusive clade including *Gondwanatherium* but not *Taeniolabis*, *Cifelliodon*, or *Shenshou*. A more explicit definition is at this point difficult to establish because of the uncertain placement of taxa potentially associated with Gondwanatheria in our analyses. As a working hypothesis, we refer to Sudamericidae as the last common ancestor of *Vintana* and *Sudamerica* and all of its descendants. We do, however, caution that resolution within Gondwanatheria and at the base of Sudamericidae is poor and that the topology varies among our analyses. More complete fossil material will be necessary to stabilize relationships within Gondwanatheria and to establish meaningful and reliable definitions of these clades.

Assumptions Concerning Tooth Homologies

We follow tooth homology assumptions laid out in the Supplementary Information sections of Krause et al. (2014, 2020). Here we review those assumptions most relevant to scorings of *Adalatherium*. In general, we provisionally assume, in the absence of contradictory information, that incisors and molars are lost from the distal ends of tooth series (Ziegler, 1971; Luckett, 1993). The mesial and distal upper incisors (I) in *Adalatherium* are therefore scored as I1 and I2, respectively. However, derived multituberculates and some euharamiyidans do not appear to follow this pattern. Whereas basal multituberculates have three upper incisors, identified by most authors as I1, I2, and I3 (e.g., Clemens and Kielan-Jaworowska, 1979; Simmons, 1993; Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004), more derived multituberculates (cimolodontans) have lost I1, leaving only I2 and I3. Similarly, although there is some controversy concerning upper incisor homologies, at least one euharamiyidan, *Xianshou*, appears to retain a reduced I1 along with an enlarged I2, whereas others (e.g., *Arboroharamiya*, *Maiopatagium*, *Shenshou*, and *Vilevolodon*; Mao et al., 2019) have lost the mesial upper incisor and retain only a single, large upper incisor, identified as I2 (Bi et al., 2014; Han et al., 2017; Luo et al., 2017; Meng et al., 2017; Mao et al., 2019).

We further follow the AToL Mammal Tree of Life coding strategy (O’Leary et al., 2013) that premolars are lost from the middle (p3/P3) of the series, and then mesially (p1/P1 or p2/P2). The penultimate and ultimate premolars are thus identified as p4/P4 and p5/P5, respectively. We extended this assumption to multituberculates, euharamiyidans, and *Haramiyavia* (Jenkins et al., 1997; Kielan-Jaworowska et al., 2004; Luo et al., 2015; Bi et al., 2014).

If not explicitly stated otherwise, we scored molar characters based on the first or second positions (m1/m2 and M1/M2). Referring to a specific molar position is particularly problematic in basal cynodonts, as premolars and molars cannot be clearly distinguished based on either morphological criteria or replacement pattern (e.g., Crompton, 1963; Crompton and Jenkins, 1979; Gow, 1980, 1985; Luo et al., 2004; Martinelli and Bonaparte, 2011; Abdala et al., 2013). We therefore scored most premolar or molar characters referring to a specific premolar/molar position as inapplicable for *Thrinaxodon*, *Probainognathus*, *Cynognathus*, *Diademodon*, *Exaeretodon*, *Pachygenelus*, *Brasilodon*, and *Riograndia*. However, we scored molar characters for tritylodontids, in order to test relationships among multi-rowed teeth of tritylodontids, multituberculates, haramiyidans, euharamiyidans, and gondwanatherians.

As in the phylogenetic data set employed by Krause et al. (2020), we scored *Sudamerica* and *Galulatherium* as having one lower incisor, no canines, no lower premolars, and four lower molars, and *Vintana* as having two upper incisors, no canines, one upper premolar and four upper molars. The dental formula is unknown for *Bharattherium*, *Ferugliotherium*, *Gondwanatherium*, *Greniodon*, *Lavanify*, and *Trapalcotherium*. The morphology of the postcanines in *Adalatherium* is distinctly different from that of any other mammaliaform and cannot readily be homologized with any known dental pattern (Krause, Hu, et al., this volume). For scoring purposes, it is, however, necessary to make assumptions regarding the positional homology of the postcanines of *Adalatherium*. A morphological discontinuity is present in the upper dentition of *Adalatherium*: the mesial-most upper postcanine (PC1 in Krause, Hu, et al., this volume) is small, two-rooted, and peg-like and identified here as the ultimate premolar (P5), whereas the following four postcanines (PC2–PC5 in Krause, Hu, et al., this volume) differ from P5 in being much larger, having more than two roots, and displaying a complex cusp pattern. Thus, for scoring purposes, we identify the posterior upper postcanines as upper molars (M1–M4) in all analyses. Establishing homologies for the lower postcanines is more difficult (Krause, Hu, et al., this volume) and, as such, we scored *Adalatherium* assuming three different lower dental formulae. First, '*Adalatherium* 1004' was scored as having no lower premolars and four molars, similar to the lower dental formula of *Sudamerica* and *Galulatherium*. In addition to specifically testing affiliations with *Sudamerica* and *Galulatherium*, this formula was chosen because it mirrors the number of molars in the upper jaw. Second, '*Adalatherium* 1013' was scored as having one lower premolar and three molars. In support of this interpretation, a slight disruption in morphological gradient is visible between pc1 and pc2–pc4: pc1 is smaller and has two roots, compared to the numerous roots seen in more distal postcanines. In addition, pc1 has fewer cusps and lacks the mesiobuccal basin that is at least incipiently developed as a bulge on pc2 and fully developed on pc3 and pc4. '*Adalatherium* 1013' is the coding scheme assumed by Krause et al. (2020). Third, '*Adalatherium* 1022' was scored as having two premolars and two molars. The last two postcanines, pc3 and pc4, have a well-developed, rimmed, mesiobuccal basin, that is absent in pc1 and only incipiently developed in pc2. This dental formula assumes that *Adalatherium* has the same number of lower molars as multituberculates, namely two. However, we must note that a lower dental formula of two premolars and two molars stands in strong contrast to the upper dental formula of one premolar and four molars presumed here for *Adalatherium*. In mammaliaforms, the number of upper and lower molars are usually in better agreement, which might render this dental formula less likely than '*Adalatherium* 1004' or '*Adalatherium* 1013'.

Data Sets

Separate analyses were conducted for the three different lower dental formulae of *Adalatherium*: '*Adalatherium* 1004' (i1 c0 p0 m4), '*Adalatherium* 1013' (i1 c0 p1 m3) and '*Adalatherium* 1022' (i1 c0 p2 m2), abbreviated in the following sections as 1004, 1013, and 1022, respectively. In addition, for some parsimony analyses, we constrained nodes within multituberculates to reflect the current consensus view of their relationships by forcing the Jurassic paulchoffatiids and *Rugosodon* to be at the base of Multituberculata, and *Taeniolabis* and *Lambdopsalis* to be sister to Djadochtatherioidea (see "Multituberculata" for more detailed review). The constrained tree is presented separately in the Supplementary Data 2). Combinations of these different coding strategies led to a total of six parsimony analyses (Table 1). Given the time required to run the Bayesian analyses, we performed undated and tip-dated Bayesian analyses without topological constraints. In addition, relationships among multituberculates in the Bayesian analyses were in better accord with currently accepted relationships even when unconstrained. In the following section, the analyses will be listed as 1004, 1004_constraint, 1004_undated, 1004_dated; 1013, 1013_constraint, 1013_undated, 1013_dated; and 1022, 1022_constraint, 1022_undated, and 1022_dated, thus referring to the dental coding schemes used for *Adalatherium* (1004, 1013, and 1022), whether or not nodes within multituberculates were constrained (_constraint or blank), and type of analysis (blank or _constraint for parsimony, _undated for undated Bayesian, and _dated for tip-dated Bayesian) .

Phylogenetic Methods

Parsimony Analyses—The maximum parsimony analyses were performed in Tree Analysis using New Technology software package (TNT) version 1.1 (Goloboff et al., 2008). A traditional search algorithm (heuristic tree search) was conducted performing 10,000 replicates of Wagner trees using random addition sequence (RAS), followed by tree bisection and reconnection (TBR) branch swapping, holding 10 trees per replicate. The shortest trees obtained through this analysis were subjected to a final round of TBR branch swapping. Trees were rooted along the branch leading to *Thrinaxodon*. All characters were treated as equally weighted and unordered. Nelson strict consensus trees were calculated in TNT. Support for each node was assessed using Bremer values (also known as decay indices; Bremer, 1994). Bremer support was calculated for each node in TNT by retaining all trees suboptimal up to 10 steps longer than the shortest trees. README files for an exemplar analysis (1013) can be found in Supplementary Data 3. Ensemble consistency index (CI) and retention index (RI) values were calculated in Phylogenetic Analysis Using PAUP* 4.0a (PAUP) (Swofford, 2003). All most parsimonious trees (MPTs), as well as the strict consensus trees, are provided in Supplementary Data 4–10. Character optimization for the parsimony analyses was performed in PAUP* using the accelerated transformation (ACCTRAN) optimization criterion. Only unambiguous apomorphies are listed in Table 2; complete apomorphy lists for each analysis are provided in Supplementary Data 11–16. These lists, which are also excerpted below in the text, include autapomorphies in addition to synapomorphies.

Undated Bayesian Analyses—Undated Bayesian phylogenetic analyses of the 1004, 1013, and 1022 data sets were performed in MrBayes 3.2.7a (Ronquist et al., 2012) using the CIPRES Scientific Gateway web portal (Miller et al., 2010), and are herein referred to as 1004_undated, 1013_undated, and 1022_undated. We used Lewis' (2001) Markov (Mk) model for morphological data, with the assumption that only variable characters were scored (i.e., the Mk*v* variant), and an eight category lognormal distribution to model rate heterogeneity between characters (Harrison and Larson, 2015). Analyses were run for 10 million Markov Chain Monte

Carlo (MCMC) generations, sampling every 5000 generations. Four runs were performed simultaneously, with four MCMC chains, three of which were heated (temp = 0.1, which is the MrBayes default). Visual inspection of parameter values in Tracer 1.6 (Rambaut et al., 2014) indicated that stationarity and convergence between chains were achieved within 1 million generations (i.e., the first 10%) in the analyses of all three data sets; with this burn-in period excluded, effective sample size (ESS) was >200 for all parameters, indicating sufficient sampling. The post-burn-in trees were summarized in MrBayes using 50% majority-rule consensus trees (using the 'contype=halfcompat' command) and 50% majority-rule consensus but retaining all compatible clades that occurred in <50% of the trees (using the 'contype=allcompat' command). Maximum Clade Credibility (MCC) trees were also produced using TreeAnnotator v2.3.0 in the BEAST2 package (Bouckaert et al., 2019), using 'Common Ancestor' node heights, after first combining the post-burn-in trees from all four runs into a single file, using the perl script BurnTrees (available here: https://github.com/nylander/Burntrees). Clade support was estimated using Bayesian posterior probabilities (PPs), with values between 0 and 0.25 considered 'very weakly supported,' between 0.26 and 0.50 'weakly supported,' between 0.51 and 0.75 'moderately supported,' and between 0.76 and 1.00 'strongly supported.' README files for the analyses can be found in Supplementary Data 3. Halfcompat, allcompat, and MCC trees are provided in Supplementary Data 17–19. Character optimization for the undated Bayesian analyses was performed on the MCC trees in PAUP* using the accelerated transformation optimization criterion, similarly to the parsimony analyses. Only unambiguous synapomorphies are listed in Table 3; complete synapomorphy lists for each analysis are provided in Supplementary Data 20–22.

Tip-dated Bayesian Analyses—Tip-dated Bayesian analyses used the same Mkv model plus eight category lognormal distribution employed in the undated analyses. An Independent Gamma Rates (IGR) clock model was used, assuming a normally distributed clock rate prior with a mean of 0.001 and standard deviation of 0.01, and an exponential prior on the variance of the gamma distribution of the IGR model with a value of 10 (the MrBayes default). The position of the root was specified by enforcing monophyly of all taxa except *Thrinaxodon*. Ages of taxa were specified as either uniform distributions between maximum and minimum bounds, or (for those taxa where the age was very tightly constrained) as fixed-point estimates. The age of the root was constrained as a uniform distribution with a minimum age of 259.1 million years and maximum age of 272.9 million years, which corresponds to the middle Permian (Guadalupian). A fossilized birth-death prior was specified on the branch lengths (‘clock:fossilization’), with diversity sampling and an assumed sampling fraction of 0.003 (four extant mammalian genera out of a total of approximately 1,258 currently recognized). We used the MrBayes default priors on speciation rate (exponential prior with a value of 10), and extinction and fossilization rates (in both cases, a “flat” beta prior with a mean and variance of 1). MCMC analyses were run for 10 million generations, with the same settings as for the undated analyses, and Tracer was again used to identify an appropriate burn-in period, which varied between 1 and 4 million generations (10 and 20%), depending on the analysis. In each analysis, ESS values were >100 for all parameters, and >200 for most parameters, after exclusion of the burn-in period. As in the undated analyses, post-burn-in trees for each tip-dated analysis were summarized using 50% majority-rule consensus and 50% majority-rule consensus but retaining all compatible clades. After combining the post-burn-in trees using BurnTrees, MCC trees were again produced using TreeAnnotator v2.3.0, but with ‘Median’ node heights specified, as some of the post-burn-in trees included sampled ancestors. Posterior probability values between 0 and 0.25 will be considered ‘very weakly supported,’ between 0.26 and 0.50 ‘weakly supported,’ between 0.51 and 0.75 ‘moderately supported,’ and between 0.76 and 1.00 ‘strongly supported.’ README files for the analyses can be found in Supplementary Data 3. Halfcompat, allcompat and MCC trees are provided in Supplementary Data 23–25. Character optimization for the undated Bayesian analyses was performed on the MCC trees in PAUP* using the accelerated transformation optimization criterion. Only unambiguous synapomorphies are listed in Table 3; complete synapomorphy lists for each analysis are provided in Supplementary Data 26–28.

RESULTS

Parsimony Analyses

The number of most parsimonious trees (MPTs), tree length, ensemble consistency index (CI), and ensemble retention index (RI) for each analysis are listed in Table 1. Simplified cladograms of the unconstrained (Fig. 1A, B) and constrained (Fig. 1C, D) parsimony analyses are shown in Figure 1. The strict consensus topologies are identical for the unconstrained 1013 and 1022 analyses, and for the constrained 1013_constraint and 1004_constraint analyses; as such, only the topologies for 1013 are shown in Figure 1A and C, respectively. The MPTs (Supplementary Data 4–9), strict consensus trees (Supplementary Data 10), and synapomorphy lists (Supplementary Data 11–16) for each parsimony analysis can be found in the Supplementary Data section. In all six parsimony analyses, *Adalatherium* falls within Gondwanatheria (Fig. 1). The topology within the gondwanatherian clade is identical in all three unconstrained analyses, but constraining nodes among multituberculates affected relationships within Gondwanatheria. In all but the 1022_constraint analysis, Gondwanatheria are recovered as sister to Multituberculata, and Gondwanatheria + Multituberculata are placed as sister to Euharamiyida within Allotheria. In all six analyses, *Haramiyavia* and *Thomasia* are not supported as members of Allotheria, but are instead placed as sister to Tritylodontidae + *Megaconus*, outside of Mammaliaformes.

Adalatherium—In all unconstrained analyses, *Adalatherium* is sister to a clade containing *Galulatherium* + Sudamericidae (here including *Gondwanatherium*, *Greniodon*, *Sudamerica*, *Bharattherium*, *Lavanify*, and *Vintana*) (Fig. 1A, B). In these analyses, *Adalatherium* is characterized by eight unambiguous apomorphies (Table 2), including presence of a septomaxillary foramen (char. 122), internasal vacuity (char. 131), large foramen in lacrimal (char. 146), rostral tympanic process (char. 252), and upper canines (char. 370). By contrast, in the constrained analyses (1013_constraint and 1004_constraint), *Adalatherium* is recovered as sister to *Galulatherium* in a polytomy with sudamericids (Fig. 1C). In these two analyses, *Adalatherium* and *Galulatherium* are united by the absence of transverse lophs (char. 417), absence of synclines or furrows (char. 419), and absence of islets or infundibula (char. 421) on their molars. Relationships within Gondwanatheria collapse in 1022_constraint, with *Adalatherium* placed in a polytomy with non-ferugliotheriid gondwanatherians.

Gondwanatheria—Gondwanatheria are a poorly supported node, with a Bremer value of 1 for all unconstrained analyses (Fig. 1A, B), and a Bremer value of 2 in the 1013_constraint and 1004_constraint analyses (Fig. 1C). In all but one analysis (1022_constraint), presence of a gliriform I1 (char. 359), and enamel covering of I1 restricted to buccal surface (char. 362) optimize as unambiguous synapomorphies of Gondwanatheria. In addition, in the unconstrained 1013 and 1022 analyses, lower molars with three or more roots (char. 459) is resolved as a synapomorphy of Gondwanatheria, whereas in the 1013_constraint and 1004_constraint analyses, lower i1 with restricted enamel (char. 368), presence of synclines or furrows (char. 419), and presence of islets or infundibula on molars (char. 421) are found to be synapomorphies. In all unconstrained analyses, the low-crowned *Ferugliotherium* and *Trapalcotherium* form a monophyletic Ferugliotheriidae (Fig. 1A, B), but Ferugliotheriidae are paraphyletic in the 1013_constraint and 1004_constraint analyses (Fig. 1C). *Ferugliotherium* and *Trapalcotherium* do not cluster with Gondwanatheria in the 1022_constraint analysis, but are instead resolved in a polytomy with multituberculates, the remaining gondwanatherians, euharamiyidans, and *Cifelliodon* (Fig. 1D). Sudamericidae are recovered in all unconstrained analyses, but resolution within the clade is poor. *Vintana*, *Gondwanatherium*, *Sudamerica*, *Greniodon*, and a clade containing *Bharattherium* and *Lavanify* are placed in a polytomy supported by presence of transverse lophs (char. 417), synclines or furrows (char. 419), and islets or infundibula (char. 421) on molars. *Galulatherium* is resolved as sister to Sudamericidae in the unconstrained analyses (Fig. 1A, B), whereas *Galulatherium* and *Adalatherium* are placed in a polytomy with sudamericids in the 1013_constraint and 1004_constraint analyses (Fig. 1C), although the MPTs reveal that *Adalatherium* + *Galulatherium* are always nested within Sudamericidae. The least resolved topology is recovered in the 1022_constraint analysis, with only *Lavanify* and *Bharattherium* forming a clade, and the remaining gondwanatherians (to the exclusion of ferugliotheriids) placed in a polytomy (Fig. 1D).

Multituberculata—The unconstrained parsimony analyses recover a rather unconventional topology for multituberculates relative to other studies, with the Paleogene *Taeniolabis* and *Lambdopsalis* placed at the base of Multituberculata, whereas the Jurassic paulchoffatiids are nested deeply within a monophyletic Plagiaulacida (Fig. 1A, B). This topology is driven partly (1) by the basal position of Euharamiyida within Allotheria, and (2) by similarities between *Adalatherium* and multituberculates that are generally considered derived in most recent studies (e.g., Smith and Codrea, 2015; Xu et al., 2015; Mao et al., 2016; Csiki-Sava et al., 2018; Wang et al., 2019). This combination of factors leads to a topology that optimizes morphological features that are currently considered to be characteristic of derived multituberculates as plesiomorphic for Multituberculata, and morphological features that are currently considered to be plesiomorphic as having evolved deeply nested within Multituberculata. For example, the number of upper premolars is optimized as ‘one’ at the base of Multituberculata and Gondwanatheria (based on the presence of a single upper premolar in *Vintana*, *Adalatherium*, *Taeniolabis*, and *Lambdopsalis*), but paulchoffatiids, eobaatariids, and plagiaulacids all have five upper premolars, which is generally assumed to be the plesiomorphic condition for Multituberculata (e.g., Kielan-Jaworowska et al., 2004). A likely convergent loss of premolars is here optimized as a plesiomorphic multituberculate trait. Similar examples include the shape of the incisors, number of cusps on the incisors, and the number of infraorbital foramina.

We therefore constrained relationships within multituberculates to match those recovered in most recent phylogenetic analyses that focus more specifically on multituberculates (e.g., Smith and Codrea, 2015; Xu et al., 2015; Mao et al., 2016; Csiki-Sava et al., 2018; Wang et al., 2019). Unsurprisingly, there is a rather drastic change in character support between the unconstrained and constrained analyses. In the unconstrained analyses, multituberculates are characterized by 17–19 synapomorphies, compared to 21 in the 1004_constraint and 1013_constraint analyses and 14 in the 1022_constraint analysis, but there are only five synapomorphies in common between the analyses, including reduced jugal (chars. 160, 162); two or more foramina for mandibular division of trigeminal nerve (char. 181); and absence of tabular (char. 292). The Bremer support is higher in the constrained analyses (only considering those nodes that were not constrained), with a value of 6–8 for the Multituberculata node, and 5 for the Djadochtatherioidea node (Fig. 1C, D). Both nodes receive a Bremer value of 3 in the unconstrained analyses. In the unconstrained analyses, the Guimarota paulchoffatiids, *Rugosodon*, Plagiaulacidae, *Sinobaatar*, and *Jeholbaatar* form a monophyletic Plagiaulacida, whereas they are placed successively more basal to cimolodontans in the constrained analyses. Djadochtatherioidea are recovered in all analyses. In the unconstrained 1013 and 1022 analyses, *Ptilodus* is placed in a polytomy with Plagiaulacida and Djadochtatherioidea, but as sister to Djadochtatherioidea in the 1004 analysis (Fig. 1A, B).

Multituberculata + Gondwanatheria—Multituberculata and Gondwanatheria are recovered as sister taxa in all (Fig. 1A–C) but one analysis (1022_constraint, Fig. 1D). Support for the clade is low, with a Bremer value of 1 (Fig. 1). However, the clade is characterized by at least 15 unambiguous synapomorphies in the unconstrained analyses, eight of which are also recovered as synapomorphies in the constrained analyses. These include: presence of parafibula (char. 82), presence of nasal foramina (char. 128), absence of angular process on mandible (char. 325), and medial pterygoid ridge that reaches dentary condyle (char. 332, 333).

Allotheria—In all parsimony analyses, Allotheria include Euharamiyida, Multituberculata, Gondwanatheria, and *Cifelliodon*. *Thomasia* and *Haramiyavia* are recovered outside of Allotheria and Mammaliaformes, as sister to a clade containing *Megaconus* and Tritylodontidae (Fig. 1). The clade comprising *Thomasia*, *Haramiyavia, Megaconus*, and Tritylodontidae has a low Bremer support of 1 and is characterized by five synapomorphies: anteroventral margin of masseteric fossa on mandible forms low crest (char. 336), diastema distal to lower incisors (char. 355), upper postcanines much wider than lower postcanines (char.

415), postcanines with multiple rows (char. 424), and dorsoposterior movement of dentary during power stroke (char. 521). In the unconstrained analyses, the Multituberculata + Gondwanatheria clade is recovered as sister to a monophyletic Euharamiyida, with *Cifelliodon* placed at the base of Allotheria (Fig. 1A, B). A similar typology is recovered in the 1013_constraint and 1004_constraint analyses (Fig. 1C). Basal relationships within Allotheria are unresolved in the 1022_constraint analysis, with Multituberculata, non-ferugliotheriid gondwanatherians, *Ferugliotherium*, *Trapalcotherium*, Euharamiyida, and *Cifelliodon* recovered in a polytomy (Fig. 1D). The Bremer support for the Allotheria node is low in all analyses, with a value of 1. Allotheria are characterized by only seven unambiguous synapomorphies in the unconstrained analyses, and five or two synapomorphies in the constrained analyses. Two of these synapomorphies are common to both the unconstrained and constrained analyses: facial process of premaxilla contacting nasal (char. 117) and essentially flat glenoid (char. 192).

Undated Bayesian Analyses

Simplified cladograms of halfcompat topologies of the undated Bayesian analyses are shown in Figure 2; complete halfcompat, allcompat, and MCC trees (Supplementary Data 17–19), as well as synapomorphy lists (Supplementary Data 20–22) for each analysis, can be found in the Supplementary Data section. The following discussion refers to the halfcompat topology shown in Figure 2. In all undated Bayesian analyses, *Adalatherium* is nested within Gondwanatheria (Fig. 2), which are nested within Multituberculata. Allotheria include euharamiyidans, multituberculates (including gondwanatherians), *Thomasia*, *Haramiyavia*, *Megaconus*, and *Cifelliodon* in the 1022_undated and 1004_undated analyses. Relationships collapse in the 1013_undated analysis: Multituberculata (including Gondwanatheria), euharamiyidans, *Megaconus*, *Haramiyavia* + *Thomasia*, eutriconodontans, and Trechnotheria are placed in a polytomy.

Adalatherium—The different coding schemes do not greatly impact the position of *Adalatherium*. In all undated Bayesian analyses, *Adalatherium* is nested with Gondwanatheria, either in a polytomy with all other gondwanatherians except *Ferugliotherium* and *Trapalcotherium* (1013_undated, 1022_undated; Fig. 2A, B) or as sister to *Galulatherium* (1004_undated; Fig. 2C). A close relationship with *Galulatherium* receives moderate support, with a posterior probability (PP) of 0.58, and the clade is united by a series of molar features: absence of islets or infundibula (char. 417), absence of synclines or furrows (char. 419), and absence of transverse lophs (char. 421). *Adalatherium* is characterized by eight apomorphies in the 1013_undated analysis, and 11 synapomorphies in the 1022_undated analysis (Table 3), including presence of a septomaxillary foramen (char. 122), internasal vacuity (char. 131), foramen for V_1 in lacrimal (char. 146), rostral tympanic process (char. 252), and upper canine (char. 370). Only five apomorphies optimize for *Adalatherium* in the 1004_undated analysis.

Gondwanatheria—Gondwanatheria are recovered in all analyses (Fig. 2) and are moderately supported (PP = 0.63–0.75). Gondwanatheria are characterized by three synapomorphies in the 1022_undated and 1004_undated analyses (Table 3): presence of synclines or furrows on molars (char. 419), presence of transverse lophs on molars (char. 421), and distal aspect of molars closed by cuspules or ridge (char. 463). In all analyses, Gondwanatheria are nested deeply within Multituberculata as sister to *Lambdopsalis* and *Taeniolabis* (Fig. 2). This relationship is moderately supported with PPs of 0.65–0.76. Eleven synapomorphies unite this clade in the 1004_undated and 1022_undated analyses, and 12 in the 1013_undated analysis. Relationships within Gondwanatheria are largely unresolved.

Ferugliotherium and *Trapalcotherium* are placed as sister to the remainder of Gondwanatheria, with *Ferugliotherium* as the first taxon to branch (1022_undated, 1004_undated; Fig. 2B, C), or with *Ferugliotherium* and *Trapalcotherium* placed in a polytomy with a clade comprising all other gondwanatherians (1013_undated; Fig. 2A). Relationships among the remaining gondwanatherians are largely unresolved in the 1013_undated (Fig. 2A) and 1022_undated analyses (Fig. 2B), with the exception that *Bharattherium* and *Lavanify* form a clade in both analyses (PP = 0.84–0.90). *Gondwanatherium*, *Sudamerica*, *Bharattherium* + *Lavanify*, *Vintana*, *Galulatherium*, *Greniodon*, and *Adalatherium* are clustered in a polytomy in these two analyses. In the 1004_undated analysis (Fig. 2C), *Adalatherium* and *Galulatherium* are sister taxa, as are *Bharattherium* and *Lavanify*, with *Vintana*, *Bharattherium*, and *Lavanify* forming a clade that is moderately supported (PP = 0.51) and united by the presence of modified radial enamel (char. 517).

Multituberculata—Relationships within Multituberculata in the undated Bayesian analyses are in better agreement with current hypotheses than they are in the parsimony analyses, with the Jurassic *Rugosodon* and Guimarota Paulchoffatiidae placed at the base of Multituberculata, and Plagiaulacida recovered as paraphyletic but Cimolodonta as monophyletic (Fig. 2). Monophyly of Multituberculata (including Gondwanatheria) is strongly supported in most analyses, with PPs ranging from 0.84–0.96. Between five (1013_undated) and 13 (1022_undated) synapomorphies unite Multituberculata, with reduced jugal (chars. 160, 162) in common among the three different analyses. In contrast to the parsimony analyses, Gondwanatheria are placed within Multituberculata, as sister to *Taeniolabis* and *Lambdopsalis*.

Allotheria—In the 1022_undated and 1004_undated analyses, Allotheria encompass euharamiyidans, multituberculates (including gondwanatherians), *Cifelliodon*, and (in contrast to the parsimony analyses) *Thomasia*, *Haramiyavia*, and *Megaconus* (Fig. 2B, C). The allcompat topologies of these analyses reveal that there is moderate support (PP = 0.50–0.53) for placing *Haramiyavia* and *Thomasia* as sister to the remainder of Allotheria (Supplementary Data 17, 19). Allotheria are only moderately supported in the 1022_undated (PP = 0.53) and 1004_undated (PP = 0.50) analyses, and collapse into a polytomy with several eutriconodontans and trechnotherians in the 1013_undated analysis (Fig. 2A). Allotheria are united by seven synapomorphies in the 1022_undated and 1004_undated analyses (Supplementary Data 20, 22). Basal relationships within Allotheria are largely unresolved in all three undated analyses, with *Megaconus*, *Cifelliodon*, *Thomasia*, *Haramiyavia*, euharamiyidans, and multituberculates placed in a polytomy. In the 1004_undated analysis, Euharamiyida are recovered as a clade that includes *Arboroharamiya*, *Shenshou*, *Qishou*, *Vilevolodon*, and *Xianshou*, but not *Maiopatagium* (Fig. 2C).

Tip-dated Bayesian Analyses

Simplified cladograms of halfcompat topologies of the tip-dated Bayesian analyses are shown in Figure 3; complete halfcompat, allcompat, and MCC trees (Supplementary Data 23–25), as well as synapomorphy lists (Supplementary Data 26–29) for each analysis, can be found in the Supplementary Data section. The following discussion refers to the halfcompat topology shown in Figure 3. In all dated Bayesian analyses, *Adalatherium* is nested within Gondwanatheria (Fig. 3). Gondwanatheria + *Cifelliodon* are sister to euharamiyidans in the 1022_dated and 1013_dated analyses, but are placed in a polytomy with Multituberculata and Euharamiyida in the 1004_dated analysis. Similar to the parsimony analyses, Allotheria include Euharamiyida, Gondwanatheria, Multituberculata, and *Cifelliodon*, whereas *Thomasia*, *Haramiyavia*, and *Megaconus* are recovered outside of Mammaliaformes, in a clade with Tritylodontidae.

Adalatherium—The different coding schemes do not impact the position of *Adalatherium*. In all dated Bayesian analyses, *Adalatherium* is nested within Gondwanatheria as sister to Sudamericidae (Fig. 3). A sister-group relationship with Sudamericidae is moderately supported (PP = 0.59–0.61), and the clade is united by a dorsally positioned mental foramen on the dentary (char. 320). *Adalatherium* is characterized by eight apomorphies in the 1013_dated and 1022_dated analyses and seven apomorphies in the 1004_dated analysis (Table 3). Apomorphies in common to all dated analyses include: presence of septomaxillary foramen (char. 122), internasal vacuity (char. 131), foramen for V_1 in lacrimal (char. 146), and rostral tympanic process (char. 252).

Gondwanatheria—Gondwanatheria (here excluding the ferugliotheriids *Ferugliotherium* and *Trapalcotherium*) are recovered in all analyses (Fig. 3), and the clade is strongly supported, with a PP of 1. Despite the high PP values, no unambiguous synapomorphies optimize as supporting this clade in 1013_dated and 1004_dated. Interestingly, in all dated Bayesian analyses, Ferugliotheriidae are placed outside of Gondwanatheria and are deeply nested within Multituberculata, as sister to Taeniolabidoidea. Placement of Ferugliotheriidae within Multituberculata is moderately supported with PPs ranging between 0.56 and 0.58. Three synapomorphies unite Ferugliotheriidae with Taeniolabidoidea: presence of three or fewer lower postcanines (char. 377), buccal cingulid on p5 (char. 405), and mesiobuccal exodaenodont lobe on p5 (char. 412). This placement is therefore strongly influenced by the assumption that the dentary fragment containing a laterally compressed ultimate premolar is correctly assigned to *Ferugliotherium* (Kielan-Jaworowska and Bonaparte, 1996). In contrast to the parsimony and undated Bayesian analyses, relationships within Gondwanatheria are resolved in the dated Bayesian analyses (Fig. 3). Sudamericidae are recovered as sister to *Adalatherium* and are strongly supported, with PPs ranging from 0.85–0.89. Presence of islets or infundibula (char. 417), synclines or furrows (char. 419), and transverse lophs (char. 421) on molars unite Sudamericidae. In all dated analyses, Sudamericidae are divided into two clades: *Sudamerica*, *Gondwanatherium*, and *Greniodon* form a South American grouping that is sister to a clade containing the Indo-Madagascan genera *Vintana*, *Bharattherium*, and *Lavanify*. The South American clade is strongly supported, with PPs of 0.83–0.84, but no synapomorphies optimize for this clade. The Indo-Madagascan clade is moderately supported (PPs = 0.52–0.56) and united by a single synapomorphy: modified radial enamel (char. 517). In all dated analyses, *Galulatherium* is recovered at the base of Gondwanatheria as sister to *Adalatherium* + Sudamericidae (Fig. 3). Furthermore, in all analyses, *Cifelliodon* is recovered as sister to Gondwanatheria, although with mixed support (PP = 0.77 and 0.78 in the 1013_dated and 1004_dated analyses, respectively, but 0.9 in the 1022_dated analysis).

Multituberculata—Similar to the undated Bayesian analyses, relationships within Multituberculata are in better agreement with current hypotheses than those found in the parsimony analyses, with the Jurassic Guimarota Paulchoffatiidae and *Rugosodon* placed at the base of Multituberculata, a paraphyletic Plagiaulacida, and a monophyletic Cimolodonta (but which here includes Ferugliotheriidae) (Fig. 3). Multituberculata are strongly supported in most analyses with PPs ranging between 0.88 and 0.99. Twelve (1013_dated, 1022_dated) or eight (1004_dated) synapomorphies unite Multituberculata, with seven synapomorphies in common among the three different analyses, including absence of septomaxilla (char. 119), presence of five upper premolars (char. 381), and M2 lingually offset relative to M1 (char. 514). In contrast to the parsimony analyses and undated Bayesian analyses, the ferugliotheriids *Ferugliotherium* and *Trapalcotherium* are placed within Multituberculata as sister to *Taeniolabis* and *Lambdopsalis* (Fig. 3).

Allotheria—In all dated Bayesian analyses, Allotheria form a clade that includes euharamiyidans, multituberculates, gondwanatherians, and *Cifelliodon*. Similar to the parsimony analyses, and in contrast to the undated Bayesian analyses, *Thomasia* + *Haramiyavia* are sister to Tritylodontidae + *Megaconus* and outside of Mammaliaformes (Fig. 3). The clade comprising *Thomasia*, *Haramiyavia, Megaconus*, and Tritylodontidae is moderately supported (PP 0.69–0.74) and characterized by the same five synapomorphies as in the parsimony analyses.

Allotheria are united by a high number of synapomorphies in the 1004_dated (18), 1013_dated (17), and 1022_dated (17) analyses, with 13 synapomorphies in common between the three analyses. The clade is strongly to moderately supported with PPs of 0.86 (1013_dated), 0.77 (1022_dated), and 0.69 (1004_dated). Relationships at the base of Allotheria are more resolved than in the undated Bayesian analyses. *Cifelliodon* + Gondwanatheria are recovered as sister to Euharamiyida in the 1022_dated analysis (PP = 0.56) and in a polytomy with euharamiyidans in the 1013_dated analysis (PP = 0.64). Five synapomorphies support a sister-group relationship of euharamiyidans and *Cifelliodon* + Gondwanatheria in the 1013_dated and 1022_dated analyses, including scaphoid twice the size of lunate (char. 51), straight dorsal margin of ischium (char. 60), and presence of tabular bone (char. 292). Euharamiyida, including *Arboroharamiya*, *Shenshou*, *Qishou*, *Vilevolodon*, *Xianshou*, and *Maiopatagium*, are recovered as monophyletic in the 1022_dated and 1004_dated analyses, but not in the 1013_dated analysis.

DISCUSSION

Adalatherium

Adalatherium is recovered within Gondwanatheria in all analyses, independent of lower dental formula coding scheme or method of phylogenetic inference. None of the apomorphies are common to all analyses, but presence of septomaxillary foramen (char. 122), internasal vacuity (char. 131), lacrimal foramen on edge of orbit (char. 144.0), foramen for V_1 in lacrimal (char. 146), rostral tympanic process (char. 252), and unique occlusal pattern (char. 520) have been recovered in nine of the 12 analyses. In addition to the apomorphies listed here, Krause et al. (2020:Supplementary Information Part G) and Krause, Groenke, et al. (this volume) provided a complete list of traits that diagnose *Adalatherium*. Several features shared or possibly shared with *Vintana* are discussed below.

The placement of *Adalatherium* within Gondwanatheria varies between different analyses, with *Adalatherium* either being placed as sister to Sudamericidae + *Galulatherium* (all unconstrained parsimony, Fig. 1A, B), sister to Sudamericidae (all tip-dated Bayesian, Fig. 3), sister to *Galulatherium* (1013_constraint, 1004_constraint, Fig. 1C; 1004_undated, Fig. 2C), or in a polytomy with gondwanatherians except for *Ferugliotherium* and *Trapalcotherium* (1022_constraint, Fig. 1D; 1013_undated and 1022_undated, Fig. 2A, B).

Interestingly, a sister-group relationship with the contemporary Madagascan *Vintana* was not recovered in any of the analyses except for the MCC of 1022_undated (Supplementary Data 19), despite the fact that *Adalatherium* and *Vintana* share several cranial and dental traits that are only rarely (or not at all) seen in other Mesozoic mammaliaforms. These include (1) presence of a septomaxilla with large intranarial process (chars. 119, 120); (2) large facial process of lacrimal (char. 142), contacting septomaxilla and excluding frontal and nasal from contact with maxilla (char. 143); (3) secondary bony canal in inner ear that parallels cochlear ganglion canal and likely enclosed vascular network (char. 221); as well as possibly shared features such as (4) thin, single-layered primary osseous lamina in inner ear that lacked habenulae perforatae, with cochlear nerve branches presumably passing along surface of osseous lamina (char. 219); and (5) two large and curved upper incisors (chars. 359, 360; the upper incisors of *Vintana* are not preserved but similarities in alveolar morphology between the two taxa indicate that this feature is shared) (Krause et al., 2020; Hoffmann and Kirk, this volume; Krause, Hoffmann et al., this volume; Krause, Hu et al., this volume). *Vintana* and *Adalatherium* are the only gondwanatherians represented by cranial material, and whether these features are unique to *Vintana* and *Adalatherium* or shared with other gondwanatherians is currently unknown.

Based on the many autapomorphic features of *Adalatherium*, Krause et al. (2020) established a new family within Gondwanatheria: Adalatheriidae. Most tree topologies recovered here are congruent with placing *Adalatherium* into its own family. In all tip-dated Bayesian and unconstrained parsimony analyses, *Adalatherium* is placed outside of both Sudamericidae and Ferugliotheriidae, warranting the recognition of a new family. In all undated Bayesian analyses the relationships within Gondwanatheria are poorly resolved, and *Adalatherium* is placed in a polytomy with various sudamericids. Of these undated analyses, the allcompat and MCC trees place *Adalatherium* within Sudamericidae in the 1004_undated analysis and outside of Sudamericidae in the 1013_undated analysis (Supplementary Data 17, 18). The relationships within Gondwanatheria are likewise unresolved in the 1022_constraint parsimony analysis, with 16 of the MPTs placing *Adalatherium* within Sudamericidae and 24 outside (Supplementary Data 9). In contrast, in all of the 16 MPTs of the 1004_constraint and 1013_constraint analyses *Adalatherium* + *Galulatherium* are placed within Sudamericidae (Supplementary Data 5, 7).

Nevertheless, we consider that the establishment of a new family for *Adalatherium* seems justified based on available evidence, but requires further testing via the discovery of more complete skeletal material of other gondwanatherians.

Gondwanatheria

Gondwanatheria, including ferugliotheriids, are recovered in all parsimony analyses (except 1022_constraint; Fig. 1) and all undated Bayesian analyses (Fig. 2). In contrast, in the tip-dated Bayesian analyses, the ferugliotheriids *Ferugliotherium* and *Trapalcotherium* are nested within Multituberculata, as sister to Taeniolabidoidea. The character support for Gondwanatheria remains low and inconsistent across analyses, ranging between zero synapomorphies (dated Bayesian) to five synapomorphies (constrained parsimony). Most commonly, Gondwanatheria are supported by two unambiguous dental synapomorphies: (1) presence of furrows/synclines on molars (char. 419) and (2) presence of transverse lophs on molars (char. 421), both of which were also recovered as gondwanatherian synapomorphies in Krause et al. (2014). In addition, presence of a first upper gliriform incisor (char. 359), and enamel restricted to buccal surface of first upper incisor (char. 362) optimize as gondwanatherian synapomorphies in most parsimony analyses. On balance, and as a working hypothesis, we consider Gondwanatheria to include Sudamericidae (*Bharattherium*, *Gondwanatherium*, *Greniodon*, *Lavanify*, *Sudamerica*, and *Vintana*), Adalatheriidae (*Adalatherium*), and *Galulatherium* as Gondwanatheria incertae sedis. We consider it uncertain whether Ferugliotheriidae are members of Gondwanatheria.

The position of Ferugliotheriidae is contentious, and affiliations with Multituberculata have been suggested multiple times. Bonaparte (1986a) originally described *Ferugliotherium* based on an isolated molar, and tentatively placed the newly established family Ferugliotheriidae within Multituberculata. Bonaparte (1990) and Krause et al. (1992) reaffirmed the placement of *Ferugliotherium* within Multituberculata based on additional specimens. Later, Krause and Bonaparte (1993) proposed close ties between Ferugliotheriidae and Sudamericidae based on molar wear patterns, incisor morphology, enamel microstructure, and inferred jaw motion and placed both families within the superfamily Gondwanatherioidea, within the order Multituberculata. Particularly relevant for the placement of Ferugliotheriidae is a partial dentary with a blade-like ultimate lower premolar that was assigned to ?*Ferugliotherium* by Kielan-Jaworowska and Bonaparte (1996). To date, no other gondwanatherian is known to have a blade-like lower premolar. The dentaries of *Sudamerica* and *Galulatherium* suggest the presence of four hypsodont postcanines, which we identified as molars for scoring purposes. Under this assumption, *Sudamerica* and *Galulatherium* completely lack premolars. Alternative interpretations of dental homologies have been presented by Gurovich (2006). Regardless of which dental loci they represent, none of the postcanines is blade-like. *Adalatherium* likewise possesses four lower postcanines of uncertain affinity, but, even if the first or second postcanines are homologized with premolars, none of them is blade-like.

Kielan-Jaworowska et al. (2004, 2007) excluded the dentary fragment with its blade-like premolar from *Ferugliotherium* and assigned it to Multituberculata incertae sedis. Rougier et al. (2009) criticized the reassignment and suggested that the blade-like premolar and a newly published bladed premolar of *Argentodites* both likely belong to ferugliotheriids. Furthermore, Rougier et al. (2009) argued that ferugliotheriids are either multituberculates or closely related to multituberculates. A similar conclusion was reached by Gurovich and Beck (2009), who included the blade-like premolar as part of their scorings for *Ferugliotherium*. *Ferugliotherium* was resolved in a polytomy with Sudamericidae and cimolodontan and ‘plagiaulacidan’ multituberculates in the phylogenetic analysis of Gurovich and Beck (2009), supporting placement of *Ferugliotherium* within, or sister to, Multituberculata. Krause et al. (2014) recovered a paraphyletic Ferugliotheriidae when either scoring *Ferugliotherium* based on molars only (*Ferugliotherium* A) or based on incisor, premolars, and molars (*Ferugliotherium* B). In the parsimony analyses of Krause et al. (2014), *Ferugliotherium* (A or B) was placed at the base of Gondwanatheria outside of Multituberculata, whereas in the undated Bayesian analysis *Ferugliotherium* B was recovered in a polytomy with gondwanatherians, multituberculates, and *Arboroharamiya*, but *Trapalcotherium* was still placed within Gondwanatheria. In other words, inclusion of the bladed premolar did not impact the position of *Ferugliotherium* in the parsimony analyses, whereas the position of *Ferugliotherium* was ambiguous in the undated Bayesian analysis of Krause et al. (2014).

In our analyses, which included the bladed premolar for *Ferugliotherium*, Ferugliotheriidae are either monophyletic and placed at the base of Gondwanatheria (all unconstrained parsimony analyses), paraphyletic and placed at the base of Gondwanatheria (1013_constraint, 1004_constraint, all undated Bayesian analyses), monophyletic and placed within Multituberculata (all dated Bayesian analyses), or possibly paraphyletic and placed in a polytomy with other allotherians (1022_constraint). Placement of the enigmatic ferugliotheriids will likely not be fully resolved until more complete specimens (in particular, with associated premolars and molars) are found and included in phylogenetic analyses.

The composition of Sudamericidae is ambiguous based on the analyses presented here. Sudamericidae was first established by Scillato-Yané and Pascual (1984) to include *Sudamerica*, based on a single hypsodont molar. Subsequently, the South American *Gondwanatherium*, Madagascan *Lavanify* and *Vintana*, and Indian *Bharattherium* were referred to Sudamericidae (Krause and Bonaparte, 1993; Krause et al., 1997, 2014; Prasad et al., 2007; Wilson et al., 2007). In addition, Krause et al. (2014) recovered *Greniodon* and *Galulatherium* (at the time referred to as "unnamed Tanzanian taxon") in a polytomy with the other sudamericids described to date and included them within the family. As a working hypothesis, we are here referring to the last common ancestor of *Vintana* and *Sudamerica* and their descendants as Sudamericidae. Using this definition, the unconstrained parsimony and tip-dated Bayesian analyses recovered Sudamericidae to include *Gondwanatherium*, *Greniodon*, *Sudamerica*, *Vintana*, *Lavanify*, and *Bharattherium*. In the better resolved tip-dated Bayesian analyses, Sudamericidae are divided into a monophyletic South American clade of *Gondwanatherium*, *Sudamerica*, and *Greniodon*, and an Indo-Madagascan grouping of *Vintana*, *Lavanify*, and *Bharattherium*. In contrast, most sudamericids are placed in a polytomy in the parsimony analyses (but with *Bharattherium* and *Lavanify* as sister taxa).

Most of our analyses favor placement of *Greniodon* within Sudamericidae. Goin et al. (2012) originally did not assign *Greniodon* to either Sudamericidae or Ferugliotheriidae, but it was placed in a polytomy with all other sudamericids and included in Sudamericidae by Krause et al. (2014). Our tip-dated Bayesian and unconstrained parsimony analyses support placement of *Greniodon* within Sudamericidae, whereas *Greniodon* is excluded from sudamericids in the tree topology of the 1004_constraint and 1013_constraint analyses. Furthermore, most of our analyses favor exclusion of *Galulatherium* from Sudamericidae. *Galulatherium* was recovered in a polytomy with other sudamericids in Krause et al. (2014), and tentatively assigned to Sudamericidae by Krause et al. (2014) and O'Connor et al. (2019). The latter ultimately concluded (p. 81) that "the support values for Sudamericidae are low and, largely for that reason, we prefer to conservatively refer to *Galulatherium* as ?Gondwanatheria due to the fact that gondwanatherians as a group remain poorly known." In our tip-dated Bayesian analyses, *Galulatherium* is recovered as sister to *Adalatherium* + Sudamericidae, and in the unconstrained parsimony analyses as sister to Sudamericidae. In contrast, *Galulatherium* is placed within Sudamericidae in all MPTs of the 1004_constraint and 1013_constraint parsimony analyses. A grouping of Indo-Madagascan taxa (*Vintana*, *Lavanify,* and *Bharattherium*) within Sudamericidae was recovered in the Bayesian analyses of Krause et al. (2014:figs. S2, S4), and is also recovered in all of our tip-dated Bayesian analyses and one undated Bayesian analysis (1004), whereas a sister-group relationship between *Bharattherium* and *Lavanify* is recovered in all analyses.

In contrast to the unconstraint parsimony and tip-dated Bayesian analyses, in the undated Bayesian and 1022_constraint parsimony analyses, non-ferugliotheriid gondwanatherians are recovered in a polytomy, which ultimately leaves the composition of Sudamericidae ambiguous. As such, even though we tentatively identified Sudamericidae as the clade containing *Vintana* and *Sudamerica*, we want to caution that relationships within Gondwanatheria vary or are unresolved in our analyses. More stable and repeatedly recovered topologies are necessary to establish a robust phylogenetic definition of Sudamericidae.

Gondwanatheria are placed as sister to Multituberculata (unconstrained parsimony, 1013_constraint, 1004_constraint), nested within Multituberculata (undated Bayesian), as sister to *Cifelliodon* and closely related to Euharamiyida (dated Bayesian), or are unresolved in a polytomy with other allotherians (1022_constraint). Close affiliations between Gondwanatheria and Multituberculata have been frequently proposed, often with gondwanatherians (as a family or suborder) nested within Multituberculata (e.g., Krause et al., 1992; Krause and Bonaparte, 1993; Kielan-Jaworowska and Bonaparte, 1996; Gurovich and Beck, 2009). Pascual et al. (1999) challenged the placement of gondwanatherians within Multituberculata, based on the dentary of *Sudamerica* with four hypsodont molars, and regarded Gondwanatheria as Mammalia incertae sedis (likely the clade that we here refer to as Mammaliaformes), a conclusion that was also accepted by Kielan-Jaworowska et al. (2004). Pascual and Ortiz-Jaureguizar (2007) later proposed that Gondwanatheria are sister to Multituberculata within Allotheria.

Phylogenetic analyses including Gondwanatheria are rare (Gurovich and Beck, 2009; Krause et al., 2014; Hoffmann, 2016) and often limited to the inclusion of *Vintana* (Luo et al., 2015; Han et al., 2017; Huttenlocker et al., 2018; King and Beck, 2019; Wang et al., 2019; Zhou et al., 2019). Gurovich and Beck (2009) recovered the gondwanatherians *Ferugliotherium* and *Sudamerica* + *Gondwanatheria* in a polytomy with "plagiaulacidan" and cimolodontan multituberculates. As a result, Gurovich and Beck (2009) included Gondwanatheria and Multituberculata within Allotheria, but could not resolve whether Gondwanatheria are nested within Multituberculata or are sister to the latter. Krause et al. (2014:figs. S2) recovered Gondwanatheria as nested within Multituberculata in their undated Bayesian analysis (similar to our undated Bayesian analyses), but as sister to *Arboroharamiya* (the only euharamiyidan included by Krause et al., 2014:figs. 3, S1, S3), in their parsimony analyses. The latter result is reminiscent of the topology recovered in our dated Bayesian analyses. Several more recent Mesozoic mammaliaform matrices have included the cranium of *Vintana* as the sole representative of Gondwanatheria. In Huttenlocker et al. (2018), *Vintana* was resolved as sister to *Cifelliodon* + *Hahnodon* within Euharamiyida (referred to as 'Eleutherodontida'), which fell outside of Mammalia. A similar topology was also recovered in the parsimony analysis of Zhou et al. (2019) and in the tip-dated Bayesian analysis of King and Beck (2019). A close relationship with *Cifelliodon* is also recovered in our tip-dated Bayesian analyses, with *Cifelliodon* placed as sister to Gondwanatheria. In contrast, *Vintana* was placed outside of Allotheria, as sister to Trechnotheria, in the Bayesian and parsimony analyses of Han et al. (2017:ED fig. 8) and the parsimony analyses of Wang et al. (2019), whereas *Vintana* was recovered as sister to Haramiyida (including Euharamiyida) in the Bayesian analysis of Wang et al. (2019).

Multituberculata

Multituberculata are recovered as monophyletic in all analyses, either as sister to Gondwanatheria (all parsimony analyses, with the exception of the 1022_constraint analysis), sister to all other allotherians (tip-dated Bayesian), or in a polytomy with other allotherians but with Gondwanatheria nested within Multituberculata (undated Bayesian). Multituberculata are strongly supported with high Bremer values (>3), high posterior probabilities (> 0.84), and 5–21 synapomorphies depending on the type of analyses. Surprisingly, the unconstrained parsimony analyses led to a rather unconventional tree topology for multituberculates, with the Paleogene Taeniolabidoidea placed as the most basal taxon and the Late Jurassic Paulchoffatiidae deeply nested within Multituberculata.

Although relationships within multituberculates have been historically difficult to sort, more recent phylogenetic analyses have recovered relatively well-resolved tree topologies that are largely congruent. Initial parsimony analyses by Simmons (1993; 49 taxa and 67 cranial and dental characters), Rougier et al. (1997; 50 taxa and 67 cranial and dental characters), and Kielan-Jaworowska and Hurum (2001; 32 taxa and 62 cranial, mandibular, and dental characters) produced strict consensus trees that were not well resolved and "did not provide meaningful results" (Kielan-Jaworowska and Hurum, 2001:390). More recent phylogenetic treatments of multituberculates, focusing on cranial, mandibular, and dental characters, have been more successful in resolving relationships. These include Yuan et al. (2013; 41 taxa and 102 characters), Xu et al. (2015; 43 taxa and 102 characters), Mao et al. (2016; 43 taxa and 102 characters), Csiki-Sava et al. (2018; 46 taxa and 107 characters), Wang et al. (2019; 51 taxa and 130 characters) focusing on multituberculate relationships in general, and Rougier et al. (2016; 17 taxa and 44 characters) and Wible et al. (2019; 18 taxa and 74 characters) focusing on relationships within Cimolodonta specifically. In all of these recent analyses, the Guimarota paulchoffatiids and *Rugosodon* are placed at the base of Multituberculata, with a paraphyletic Plagiaulacida and a monophyletic Cimolodonta (including Taeniolabidoidea, *Ptilodus*, and Djadochtatherioidea) deeply nested within multituberculates.

Not only are the multituberculate relationships within our unconstrained parsimony analyses contrary to the current consensus view, but the recurrent recovery of a monophyletic Plagiaulacida (including the Guimarota Paulchoffatiidae, Plagiaulacidae, *Rugosodon*, *Jeholbaatar*, and *Sinobaatar*) is noteworthy. In addition to the recent multituberculate matrices listed above, paraphyly of Plagiaulacida was recovered by Simmons (1993) and was also suggested by Kielan-Jaworowska and Hurum (2001). In many earlier analyses of mammaliaform relationships (e.g., Luo et al., 2002, 2007; Rougier et al., 2007; Gurovich and Beck, 2009), 'plagiaulacidans' were grouped and scored as a single taxonomic unit and, as such, the monophyly or paraphyly of this group could not be tested within a broader sample of mammaliaforms. In more recent studies, 'plagiaulacidans' have been split into the paulchoffatiid *Kuehneodon*, *Rugosodon*, plagiaulacids, and the eobaatarid *Sinobaatar*, and these taxa have been successively placed at the base of Multituberculata (e.g., Yuan et al., 2013; Zhou et al., 2013; Bi et al., 2014; Krause et al., 2014; Han et al., 2017; Huttenlocker et al., 2018; as well as in our

Bayesian analyses). It should be noted that, similar to the result recovered in the unconstrained parsimony analyses of this study, Plagiaulacida (including *Sinobaatar*, plagiaulacids, *Kuehneodon* and *Rugosodon*), were also recovered as monophyletic by Luo et al. (2015:fig. 4).

We believe that the unusual topology recovered in our parsimony analysis is driven by derived features that are shared by Taeniolabidoidea and *Adalatherium* but that are almost certainly homoplastic between the two. Because of the current weight of evidence (including our undated and tip-dated Bayesian analyses) that this topology is incorrect, we conducted additional parsimony analyses constraining relationships within Multituberculata to match the current consensus view. The effect of this on the support of Multituberculata was drastic. Multituberculata have a Bremer value of 8 and 6 in the constrained analyses but only 3 in the unconstrained. As noted above, the Bayesian analyses recovered relationships within Multituberculata that are in better agreement with the current consensus view, except for the placement of Gondwanatheria (undated Bayesian) or Ferugliotheriidae (tip-dated Bayesian) as sister to Taeniolabidoidea.

Allotheria

The composition of Allotheria differs between our parsimony and dated Bayesian analyses on the one hand, and the undated Bayesian analyses on the other. In the parsimony and dated Bayesian analyses, *Haramiyavia*, *Thomasia*, and *Megaconus* are placed outside of Allotheria and Mammaliaformes, and grouped with Tritylodontidae. In the undated Bayesian analyses, these three taxa are placed in a polytomy with other allotherians.

The composition of Allotheria has been contentious ever since it was established by Marsh (1880), and such remains the case in recent analyses (Fig. 4). Initially, Marsh (1880:239) only included the two Late Jurassic multituberculates *Plagiaulax* and *Ctenacodon* within Allotheria, which he considered to be characterized by (1) low number of teeth, (2) absence of canines, (3) premolar and molar teeth "specialized," (4) angle of lower jaw distinctly inflected, and (5) absence of mylohyoid groove. At various points, tritylodontids were included in Multituberculata or Allotheria (e.g., Cope, 1884; Broom, 1914; Simpson, 1929), but Simpson (1945) raised Allotheria to a subclass with a single order Multituberculata, and excluded Tritylodontidae from Multituberculata and Allotheria, as had previously been suggested by, for example, Seeley (1894) and Watson (1942). Hahn (1973) first included the suborder Haramiyoidea within Multituberculata, which was tentatively accepted by Lillegraven et al. (1979). Hahn et al. (1989) later raised Haramiyoidea to ordinal status, as Haramiyida, and included it with Multituberculata and Theroteinida in Allotheria. With the description of *Haramiyavia*, Jenkins et al. (1997) questioned the affiliation between Haramiyida and Multituberculata, and excluded Haramiyida from Allotheria. Butler and MacIntyre (1994) and Butler (2000) regarded Haramiyida (including *Theroteinus*, *Haramiyavia*, *Thomasia*, *Allostaffia*, and *Eleutherodon*) as sister to Multituberculata and assigned them to Allotheria, a conclusion followed by Kielan-Jaworowska et al. (2004). Pascual and Ortiz-Jaureguizar (2007) suggested that Gondwanatheria be placed within Allotheria as sister to Multituberculata, which was subsequently supported by Gurovich and Beck (2009) and Krause et al. (2014, 2020).

In recent years, seven taxa that are particularly relevant to understanding the composition and phylogenetic relationships of Allotheria have been described, all of them based on fairly complete specimens from China. These include *Megaconus* (Zhou et al., 2013), *Arboroharamiya* (Zheng et al., 2013; Meng et al., 2014; Han et al., 2017), *Shenshou* (Bi et al., 2014), *Xianshou* (Bi et al., 2014), *Vilevolodon* (Luo et al., 2017), *Maiopatagium* (Meng et al., 2017), and *Qishou*

(Mao and Meng, 2019). In various analyses, combinations of these taxa have either been placed within Allotheria as part of Euharamiyida (as sister to Multituberculata), or outside of Mammalia and separate from Multituberculata as members of Haramiyida, Euharamiyida, Eleutherodonta, Eleutherodontida, or Eleutherodontidae (see Fig. 4 and more detailed discussion on 'Haramiyida, Euharamiyida, and Eleutherodonta' below).

At the heart of the discussion is how Allotheria are defined. Luo et al. (2002) and Kielan-Jaworowska et al. (2004) defined Allotheria as Multituberculata and Haramiyida, but the inclusion of Haramiyida within Allotheria has been questioned before (e.g., Jenkins et al., 1997). Indeed, the mandible of *Haramiyavia* lacks most of the characteristic features of Allotheria originally listed by Marsh (1880), such as low number of teeth, "specialized" premolars, absence of canines, and a distinctly inflected angle of the lower jaw. Sereno (2006) defined Allotheria as the most inclusive clade containing *Taeniolabis* but not *Ornithorhynchus* or *Mus*. Following this phylogenetic definition and trees resulting from our analysis, Allotheria includes Multituberculata, Gondwanatheria, *Cifelliodon*, and Euharamiyida (*Shenshou*, *Xianshou*, *Arboroharamiya*, *Vilevolodon*, *Maiopatagium*, and *Qishou*) but, in most of our analyses, not *Haramiyavia*, *Thomasia*, or *Megaconus*. *Haramiyavia* and *Thomasia* form a clade in all of our analyses, which we here confirm to be part of Haramiyida.

Haramiyida, Euharamiyida, and Eleutherodonta

Our analyses recover a monophyletic Haramiyida, represented by the haramiyaviid *Haramiyavia* and the haramiyid *Thomasia*, as sister to Tritylodontidae + *Megaconus* outside of Mammaliaformes (parsimony, tip-dated Bayesian), or in a polytomy with other allotherians within Mammalia (undated Bayesian). Haramiyida, which was elevated to the rank of order by

Hahn et al. (1989), originally included *Thomasia* and *Haramiya* (later synonymized with *Thomasia* by Butler and MacIntyre, 1994), based on isolated teeth from the Late Triassic of Europe (Butler and MacIntyre, 1994 and references therein). Butler (2000) revised Haramiyida and included (1) *Thomasia*; (2) *Theroteinus*, based on isolated teeth from the Late Triassic of Europe (originally assigned to Haramiyidae by Sigogneau-Russell et al. [1986], but placed into the order Theroteinida by Hahn et al. [1989]); (3) *Eleutherodon*, based on an isolated tooth from the Middle Jurassic of Europe (originally referred to Eleutherodontida and placed in Allotheria by Kermack et al. [1998]); (4) questionably, *Allostaffia*, based on an isolated tooth from the Late Jurassic of Africa (Heinrich, 1999, 2004); and (5) *Haramiyavia*, based on teeth, mandibular, premaxillary, maxillary, and postcranial elements from the Late Triassic of Greenland (Jenkins et al., 1997). Additional isolated teeth have since been added to *Allostaffia* (Heinrich, 2001) and *Eleutherodon* (Butler and Hooker, 2005). Subsequently, but before 2013, several other taxa currently known only from isolated teeth have been referred to Haramiyida, in some cases tentatively; these include *Sineleutherus* from the Middle Jurassic of Russia and China, *Kirtlingtonia* and *Millsodon* from the Middle Jurassic of the U.K., *Avashishta* from the Late Cretaceous of India, *Hahnodon* and *Denisodon* from the Early Cretaceous of Morocco, and *Mojo* from the Late Triassic of Belgium (Butler and Hooker, 2005; Maisch et al., 2005; Anantharaman et al., 2006; Martin et al., 2010; Averianov et al., 2011; Bi et al., 2014; Huttenlocker et al., 2018). Most of these studies have placed Haramiyida within Allotheria and within Mammalia, although several phylogenetic analyses have previously recovered *Haramiyavia* in a more basal position outside of Mammaliaformes (e.g., Luo et al., 2002; Rougier et al., 2007; Gurovich and Beck, 2009).

Since 2013, fairly complete mammaliaform specimens from the Middle to Late Jurassic of China have been described and variously placed within Haramiyida, Eleutherodonta, Eleutherodontida, Eleutherodontidae, or the newly erected Euharamiyida (Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014; Han et al., 2017; Luo et al., 2017; Meng et al., 2017; Mao and Meng, 2019). The taxonomy of the Chinese forms is in flux and is only briefly outlined here (see also Fig. 4). Zhou et al. (2013; see Fig. 4A) described *Megaconus* and placed it within Mammaliaformes (order Haramiyida, suborder Eleutherodontida, family Eleutherodontidae) but outside of Mammalia. Based on the topology presented by Zhou et al. (2013), Haramiyida includes *Thomasia*, *Haramiyavia*, and the eleutherodontid eleutherodontidans *Megaconus*, *Sineleutherus*, and *Eleutherodon*. Zheng et al. (2013; see Fig. 4B) placed their new genus *Arboroharamiya* in the hierarchy of Mammalia, Allotheria, Haramiyida, and Arboroharamiyidae. Based on the tree topology recovered in Zheng et al. (2013:fig.4), Haramiyida are either paraphyletic, or Multituberculata should be considered a subclade of Haramiyida. Zheng et al. (2013:S13) favored the former interpretation and stated “ that ‘Haramiyida’ should be regarded as a paraphyletic group of those allotherians that are not multituberculates (Butler, 2000).” Similarly, Krause et al. (2014; see Fig. 4C) recovered Allotheria to include the paraphyletic haramiyidans *Thomasia* and *Haramiyavia*, Multituberculata, *Arboroharamiya*, and, in addition to the taxa considered by Zheng et al. (2013), Gondwanatheria.

Bi et al. (2014; see Fig. 4D) erected a new clade, Euharamiyida, of unspecified rank, to accommodate the families Arboroharamiyidae (containing *Arboroharamiya*), Eleutherodontidae (containing *Eleutherodon*, *Sineleutherus*, and *Xianshou*), and the genera *Shenshou* (family indet.) and *Millsodon* (family indet.). In Bi et al.’s (2014) revised diagnosis, Allotheria (which they placed within Mammalia) included *Haramiyavia*, *Thomasia*, *Allostaffia*, Theroteinida (containing the monotypic genus *Theroteinus*), Euharamiyida (new clade), Multituberculata, and

Megaconus. Although Bi et al. (2014:582, fig. 4) referred to Allotheria as "Multituberculata and Haramiyida," their tree either rendered Haramiyida paraphyletic or implied that Multituberculata and Euharamiyida should be considered members of Haramiyida. Luo et al. (2015), in their revised description of the mandible and dentition of *Haramiyavia*, placed Haramiyida, which according to them includes *Thomasia*, *Haramiyavia*, *Megaconus*, and Eleutherodontida (*Shenshou*, *Eleutherodon*, *Sineleutherus*, *Arboroharamiya*, *Xianshou*), outside of Mammalia and separate from Multituberculata. Although *Megaconus* was originally described as an eleutherodontid (Zhou et al., 2013), Luo et al. (2015:fig. 4C; see also Fig. 4E) placed it as sister to Eleutherodontida. This was later reaffirmed by Luo et al. (2017; see Fig. 4F), who resolved *Megaconus* as sister to Eleutherodonta, but within Euharamiyida.

More recently, Meng et al. (2017) described *Maiopatagium* and placed it in the order Eleutherodontida, but outside of the family Eleutherodontidae. With the description of *Vilevolodon*, Luo et al. (2017) recognized Euharamiyida as including Eleutherodonta (rank unspecified, but note different spelling [not Eleutherodontida] from Kermack et al. [1998], Zhou et al. [2013], Luo et al. 2015], and Meng et al. [2017]). Luo et al. (2017) proposed that Eleutherodontidae includes *Eleutherodon*, *Sineleutherus*, *Arboroharamiya*, *Xianshou*, and *Vilevolodon*, with *Shenshou* and *Maiopatagium* falling outside of Eleutherodontidae but within "the eleutherodontidan clade or eleutherodonts" (Luo et al., 2017:S19). Similar to Luo et al. (2015), Haramiyida was placed outside of Mammalia and separate from Multituberculata in Luo et al. (2017).

Huttenlocker et al. (2018; see Fig. 4G) described the cranium of the Early Cretaceous *Cifelliodon* and placed it within a descending hierarchy of Mammaliaformes, Haramiyida, family Hahnodontidae. Based on the topology recovered in Huttenlocker et al. (2018:fig. 4), Haramiyida are positioned outside of Mammalia, separate from Multituberculata, and include *Haramiyavia* and *Thomasia* as sister to Eleutherodontida. In Huttenlocker et al. (2018), Eleutherodontida included *Megaconus* (although *Megaconus* had been excluded from Eleutherodontida by Luo et al. [2017]), *Vintana*, Hahnodontidae, and Eleutherodontidae. In addition to *Eleutherodon*, *Sineleutherus*, *Arboroharamiya*, *Xianshou*, and *Vilevolodon*, Huttenlocker et al. (2018) also assigned *Millsodon*, *Maiopatagium*, and *Shenshou* to Eleutherodontidae (although *Maiopatagium* and *Shenshou* had been excluded from Eleutherodontidae by Luo et al. [2017]). Lastly, Mao and Meng (2019) assigned two of the paratypes of *Shenshou lui* to a new genus and species, *Qishou jizantang*, and to *Qishou* sp. within the subclass Allotheria, order 'Haramiyida', suborder Euharamiyida, and new family Shenshouidae (along with *S. lui*). Mao and Meng (2019) did not provide a tree topology but, assuming a similar topology to that of Han et al. (2017) or Wang et al. (2019) (see Fig. 4H), then Haramiyida would either be paraphyletic (as suggested by the quotation marks used by Mao and Meng [2019]) or monophyletic and (as suggested by the suborder rank) include Euharamiyida and therefore also Multituberculata. In sum, the composition and position of Eleutherodonta, Eleutherodontida, Eleutherodontidae, and Haramiyida is unresolved and varies among different authors.

Based on our tree topologies, there is support for a monophyletic Haramiyida (here only comprising the haramiyaviid *Haramiyavia* and the haramiyid *Thomasia*), separate from *Cifelliodon*, *Maiopatagium*, *Vilevolodon*, *Shenshou*, *Qishou*, *Arboroharamiya*, and *Xianshou* (variously referred to as Eleutherodonta, Eleutherodontida, Eleutherodontidae, and Euharamiyida), and also separate from Multituberculata. Whether Haramiyida are placed outside of Mammaliaformes or within Mammalia is ambiguous in our analyses. As such, for communication purposes, here and throughout various chapters in this volume, we restrict the term Haramiyida to *Thomasia* and *Haramiyavia*, and tentatively still include them in our discussion of Mammaliaformes for the purpose of comparison and until their position is fully resolved and more stable. In addition, we employ the term Euharamiyida to refer to the clade including *Arboroharamiya*, *Maiopatagium*, *Qishou*, *Shenshou*, *Vilevolodon*, and *Xianshou*. In our analysis, we did not include the isolated teeth of the eleutherodontids *Eleutherodon*, *Sineleutherus*, and *Millsodon*. All have been referred to Haramiyida (Kermack et al., 1998; Martin et al., 2010) but have been recovered deeply nested within Euharamiyida by various authors (Bi et al., 2014; Han et al., 2017; Wang et al., 2019; referred to as Eleutherodontida by Luo et al., 2015, 2017; Huttenlocker et al., 2018). If the poorly known eleutherodontids *Eleutherodon*, *Sineleutherus*, and *Millsodon* are confirmed to be members of Euharamiyida, and if a separate position of *Haramiyavia* and *Thomasia* outside of Mammaliaformes is maintained in future analyses, then Eleutherodontidae should be removed from Haramiyida and placed within Allotheria.

Other Nodes of Interest

Eutriconodonta—Eutriconodonta are recovered as monophyletic and sister to Mammalia in all parsimony analyses, as paraphyletic and nested within Mammalia in the undated Bayesian analyses, and as monophyletic but in a polytomy with other mammaliaforms (including Monotremata) in the dated Bayesian analyses. Historically, Eutriconodonta are most commonly recovered as a clade within Mammalia (e.g., Hu et al., 2005; Luo et al., 2007; Zhou et al., 2013; Bi et al., 2014; Krause et al., 2014; Martin et al., 2015; Han et al., 2017; Wang et al., 2019; Zhou et al., 2019). However, exceptions exist; Luo et al. (2017) and Huttenlocker et al. (2018), for example, recovered a paraphyletic Eutriconodonta within Mammalia, and Luo et al.

(2015) found Eutriconodonta to fall outside of Mammalia. Our data matrix, although broadly encompassing early mammaliaforms, is not intended to resolve relationships of eutriconodontans; it neither extensively samples eutriconodontan taxa, nor includes a range of specific eutriconodontan characters such as, for example, those in Martin et al. (2015). As such, here and in the remainder of this volume, we assume that Eutriconodonta are monophyletic and fall within Mammalia, as in most published studies.

Theria—All of our analyses place *Eomaia*, *Juramaia*, *Sinodelphys*, and *Ambolestes* outside of Theria. Sampling at the base of Theria is relatively limited in our matrix, as a greater focus was placed on allotherian taxa. A recent analysis by Bi et al. (2018) designed to test relationships at the base of Theria, placed all four taxa (including *Sinodelphys*, which was originally assigned to Metatheria by Luo et al. [2003]) within Eutheria. Although not without criticism (e.g., Averianov and Lopatin, [2014] questioned the placement of *Juramaia* within Eutheria, and O'Leary et al. [2013], with a very limited sampling of Cretaceous therians, placed *Eomaia* outside Theria), most phylogenetic analyses of early mammaliaforms recover *Eomaia* and *Juramaia* within Eutheria (e.g., Luo et al., 2011, 2015, 2017; Huttenlocker et al., 2018; King and Beck, 2019; Zhou et al., 2019; Mao et al., 2020). Our matrix is not designed to test relationships of therians and, as such, we refrain from revising these taxa and throughout this memoir refer to *Eomaia*, *Juramaia*, *Sinodelphys*, and *Ambolestes* as therians or eutherians.

CONCLUSIONS

In all of our analyses, *Adalatherium* is placed within Gondwanatheria and is most frequently recovered outside of Sudamericidae and Ferugliotheriidae (with the latter family usually found to be a member of the gondwanatherian clade). This is congruent with establishment of the family Adalatheriidae, with the genus *Adalatherium* as its sole member, as proposed by Krause et al. (2020). The effect of the different coding schemes for the dental formula of *Adalatherium* has relatively little effect on its phylogenetic position in our analyses. In only two instances did the placements of *Adalatherium* differ within the same tree inference method (1022_constraint parsimony, 1004_undated Bayesian). Although the tree topologies are largely similar within the same tree inference method, character optimizations and support values for the nodes change between the different coding schemes. Tree inference method has a much greater effect on overall tree topology and placement of *Adalatherium* than do the different coding schemes for its dental formula.

Gondwanatheria are recovered in all analyses, but whether the ferugliotheriids *Ferugliotherium* and *Trapalcotherium* are members of Gondwanatheria is unclear. In the tip-dated Bayesian analyses, Ferugliotheriidae are recovered as monophyletic within Multituberculata. Close affinities between the two groups have been proposed before. In particular, the potential presence of a blade-like lower premolar in *Ferugliotherium* seems to be driving ties between Ferugliotheriidae and Multituberculata. A bladed lower premolar is commonly found in multituberculates but appears to be lacking in other gondwanatherians that can be confidently assessed for this feature.

Gondwanatheria are placed within Allotheria in all of our analyses, either as sister to Multituberculata, sister to *Cifelliodon* and closely related to Euharamiyida, nested within Multituberculata, or in a polytomy with other allotherians. Some of these proposed relationships appear more plausible than others. The undated Bayesian topology, with Gondwanatheria nested within Multituberculata as sister to Taeniolabidoidea, implies a perplexing paleogeographic history and radical character transformations. The implied reacquisition of plesiomorphic mammaliaform features (e.g., presence of a septomaxilla, presence of intranarial process, large lacrimal, large jugal) in the gondwanatherians *Vintana* and *Adalatherium*, which are absent in multituberculates, means that we consider the topology recovered in the undated Bayesian analyses unlikely.

The results of the parsimony and tip-dated Bayesian analyses seem more plausible from a paleogeographic and morphological standpoint. Topologies recovered therein suggest an origin of Gondwanatheria by the Middle Jurassic, a time at which Gondwana was still largely intact and which might explain the broad distribution of gondwanatherians across the southern hemisphere. Regardless of the ultimate relationship of Gondwanatheria to either Euharamiyida (tip-dated Bayesian) or Multituberculata (parsimony), our tree topologies suggest a temporally long, unsampled branch (or ghost lineage) leading to Gondwanatheria. This indicates that much of the temporal (and morphological) diversity is yet to be discovered for Gondwanatheria. The currently known distribution of gondwanatherians in South America, Africa, Madagascar, India, and the Antarctic Peninsula can be interpreted either as the result of dispersal from an ancestral portion of Gondwana or vicariance. Given that a mid-Jurassic record for the group is supported by our analyses, it is possible that we are currently sampling endemic products in individual Gondwanan landmasses that were derived from a previously pan-Gondwanan and possibly morphologically more uniform population.

The parsimony topology linking Gondwanatheria and Multituberculata can be seen as the traditional view of gondwanatherian relationships, with Ferugliotheriidae as the basal member of Gondwanatheria that retained a brachydont and relatively generalized molar dentition. In contrast, our tip-dated Bayesian analyses nest ferugliotheriids inside Multituberculata and recover a Euharamiyida and Gondwanatheria + *Cifelliodon* sister-group relationship, which collectively implies that the molar similarities traditionally recognized between Ferugliotheriidae and Sudamericidae (e.g., Krause and Bonaparte, 1993) are homoplastic.

The composition of Allotheria varies in our analyses. In all parsimony and tip-dated Bayesian analyses, *Haramiyavia* and *Thomasia* are placed outside of Mammaliaformes, whereas they are recovered in a polytomy with other allotherians in the undated Bayesian analyses. Based on the more frequent placement of *Haramiyavia* and *Thomasia* outside of Mammaliaformes, we tentatively conclude that *Haramiyavia* and *Thomasia* should be removed from Allotheria, and we consider that Haramiyida should be defined to include only *Haramiyavia* and *Thomasia* (possible affiliations with *Theroteinus*, *Allostaffia*, *Kirtlingtonia*, *Mojo*, and *Avashishta* still need to be tested in a phylogenetic framework). Unfortunately, other taxa associated with Haramiyida by Butler (2000), including *Allostaffia*, *Eleutherodon*, and *Theroteinus*, as well as the subsequently described *Sineleutherus*, *Millsodon*, *Kirtlingtonia*, *Mojo*, and *Avashishta* (Hahn et al., 1987; Butler and Hooker, 2005; Maish et al., 2005; Anantharaman et al., 2006; Martin et al., 2010; Averianov et al., 2011), are only known from isolated teeth. Although dental similarities exist between the eleutherodontids *Eleutherodon*, *Sineleutherus*, and *Millsodon* and the euharamiyidans *Shenshou*, *Qishou*, *Xianshou*, *Arboroharamiya*, *Maiopatagium*, and *Vilevolodon*, the mandibular morphology of the euharamiyidans is distinctly different from at least *Haramiyavia*, and more similar to those of multituberculates and gondwanatherians. The mandibular morphology for the eleutherodontids *Eleutherodon*, *Sineleutherus*, and *Millsodon* (and, for that matter, any of the purported haramiyidans published before 2013) is unknown and whether it is more similar to those of *Haramiyavia* or euharamiyidans will likely greatly assist in determining their phylogenetic placement. We tentatively conclude that Allotheria encompasses

Multituberculata, Gondwanatheria, Euharamiyida, and Hahnodontidae, but more complete specimens are needed to truly assess the relationships among *Allostaffia*, *Eleutherodon*, *Theroteinus*, *Thomasia*, *Sineleutherus*, *Millsodon*, and *Kirtlingtonia* with Haramiyida or Allotheria.

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FIGURE CAPTIONS

FIGURE 1. Simplified tree topology of strict consensus trees for parsimony analyses using three different coding schemes for *Adalatherium* based on lower dental formulae (1013, 1022, 1004) with nodes within multituberculates either unconstrained (**A**, **B**) or constrained (**C**, **D**). **A**, simplified strict consensus tree of 16 most parsimonious trees (MPTs) from unconstrained analysis using coding scheme 1013 (tree topology but not Bremer support identical to 1022); **B**, simplified strict consensus tree of eight MPTs from unconstrained analysis using coding scheme 1004; **C**, simplified strict consensus tree of 16 MPTs from constrained analysis using coding scheme 1013 (tree topology but not Bremer support identical to 1004_constraint); **D**, simplified strict consensus tree of 40 MPTs from constrained analysis using coding scheme 1022. Bremer values for selected nodes indicated next to node. *Adalatherium* highlighted in yellow, gondwanatherians in green shades (ferugliotheriids in dark green, *Galulatherium* in teal, sudamericids in light green), multituberculates in light blue, euharamiyidans in dark blue, haramiyidans in purple. [planned for page width, color]

FIGURE 2. Simplified tree topology of 'halfcompat' (50% majority rule) trees for undated Bayesian analyses using three different coding schemes for *Adalatherium* based on lower dental formulae (1013, 1022, 1004). **A**, simplified halfcompat tree of 1013_undated; **B**, simplified halfcompat tree of 1022_undated; and **C**, simplified halfcompat tree of 1004_undated. Posterior probabilities for selected nodes indicated next to node. *Adalatherium* highlighted in yellow, gondwanatherians in green shades (ferugliotheriids – dark, *Galulatherium* – medium, sudamericids – light), multituberculates in light blue, euharamiyidans in dark blue, haramiyidans

in purple. [planned for page width, color]

FIGURE 3. Simplified tree topology of ‘halfcompat’ (50% majority rule) trees for tip-dated Bayesian analyses using three different coding schemes for *Adalatherium* based on lower dental formulae (1013, 1022, 1004). **A**, simplified halfcompat tree of 1013_dated; **B**, simplified halfcompat tree of 1022_dated; and **C**, simplified halfcompat tree of 1004_dated. Posterior probabilities for selected nodes indicated next to node. *Adalatherium* highlighted in yellow, gondwanatherians in green shades (ferugliotheriids in dark green, *Galulatherium* in teal, sudamericids in light green), multituberculates in light blue, euharamiyidans in dark blue, haramiyidans in purple. [planned for page width, color]

FIGURE 4. Simplified tree topology of mammaliaform relationships based on **A**, Zhou et al. (2013); **B**, Zheng et al. (2013); **C**, Krause et al. (2014); **D**, Bi et al. (2014); **E**, Luo et al. (2015); **F**, Luo et al. (2017); **G**, Huttenlocker et al. (2018); and **H**, Han et al. (2017). *Millsodon*, *Allostaffia*, Theroteinida were not included in the analysis of Bi et al. (2014:Supplementary Information), but the authors assigned *Millsodon* to Euharamiyida, and *Allostaffia* and Theroteinida to Allotheria. *Megaconus* was included in one of three analyses by Bi et al. (2014:Supplementary Information) and was assigned to Allotheria, contrary to its placement in their analyses. These taxa are not included in part **D**. Eutriconodonta are not monophyletic in **F** and **G** and are therefore labeled as ‘eutriconodonts.’ [planned for page width, grayscale]

TABLE 1. Metrics of six parsimony analyses of systematic position of *Adalatherium*.

	Parsimony			
	TL	MPT	CI	RI
1004	2306	8	0.3027	0.7017
1004_const	2316	16	0.3014	0.6999
1013	2315	16	0.3015	0.7001
1013_const	2321	16	0.3007	0.6990
1022	2316	16	0.3014	0.7000
1022_const	2403	40	0.2905	0.6839

TL, Tree Length; **MPT**, number of most parsimonious trees; **CI**, consistency index; **RI**, retention index.

TABLE 2. List of unambiguous synapomorphies for *Adalatherium*, Gondwanatheria, and Multituberculata + Gondwanatheria, for six parsimony analyses.

Adalatherium

1013	**1013cons**	**1022**	**1022cons**	**1004**	**1004cons**
122/0	337/0	122/0	337/0	122/0	337/0
131/1	338/1	131/1	338/1	131/1	338/1
144/0	380/4	144/0		144/0	416/0
146/1	413/3	146/1		146/1	459/1&2
252/1	416/0	252/1		252/1	520/5
337/0	459/2	337/0		337/0	
338/1	520/5	338/1		338/1	
370/0		370/0		370/0	

Gondwanatheria

1013	**1013cons**	**1022**	**1022cons**	**1004**	**1004cons**
359/1	359/1	359/1	/	359/1	359/1
362/1	362/1	362/1		362/1	362/1
459/2	368/1	459/2			368/1
	419/1				419/1
	421/1				421/1

Multituberculata + Gondwanatheria

1013	**1013cons**	**1022**	**1022cons**	**1004**	**1004cons**
45/1	59/1	45/1	/	45/1	59/1
59/1	82/1	59/1		59/1	82/1
68/1	86/1	68/1		68/1	86/1
82/1	128/1	82/1		82/1	128/1
86/1	325/0	86/1		86/1	325/0
128/1	332/1	128/1		128/1	332/1
325/0	333/1	325/0		325/0	333/1
332/1	379/1	332/1		332/1	379/1
333/1		333/1		333/1	399/2
360/1		360/1		360/1	
379/1		379/1		379/1	
381/4		381/4		381/4	
384/2		384/2		384/2	
415/1		415/1		397/2	
468/1		468/1		415/1	
				468/1	

TABLE 3. List of unambiguous synapomorphies for *Adalatherium*, Gondwanatheria, and Gondwanatheria + Taeniolabidoidea (undated only) and clade containing Gondwanatheria, *Cifelliodon*, Euharamiyida (tip-dated only), for undated and tip-dated Bayesian analyses.

Adalatherium

1013_undat	1022_undat	1004_undat	1013_dated	1022_dated	1004_dated
122/0	122/0	337/0	122/0	122/0	122/0
131/1	131/1	338/1	131/1	131/1	131/1
144/0	144/0	416/0	144/0	144/0	144/0
146/1	146/1	459/1&2	146/1	146/1	146/1
252/1	252/1	520/5	252/1	252/1	252/1
337/0	370/0		413/3	337/0	459/1&2
338/1	416/0		459/2	338/1	520/5
370/0	417/0		520/5	459/2	
	419/0				
	421/0				
	520/5				

Gondwanatheria

1013_undat	1022_undat	1004_undat	1013_dated	1022_dated	1004_dated
459/2	419/1	419/1	/	117/0	/
	421/1	421/1		142/0	
	463/1	463/1		143/1	

				378/4	

Gondwanatheria + Taeniolabidoidea			Gondwanatheria + Euharamiyida		
1013_undat	**1022_undat**	**1004_undat**	**1013_dated**	**1022_dated**	**1004_dated**
38/1	38/1	38/1	51/1	51/1	51/1
129/2	129/2	129/2	60/1	60/1	60/1
150/0	150/0	150/0	206/0	206/0	106/1
165/2	165/2	165/2	292/0	292/0	200/0
227/0	227/0	227/0	459/0	459/0	206/0
307/1	307/1	307/1			225/1
346/1	346/1	346/1			284/1
380/4	381/4	381/4			292/0
381/4	387/0	387/0			459/0
387/0	405/0	405/0			
405/0	412/0	412/0			
412/0					

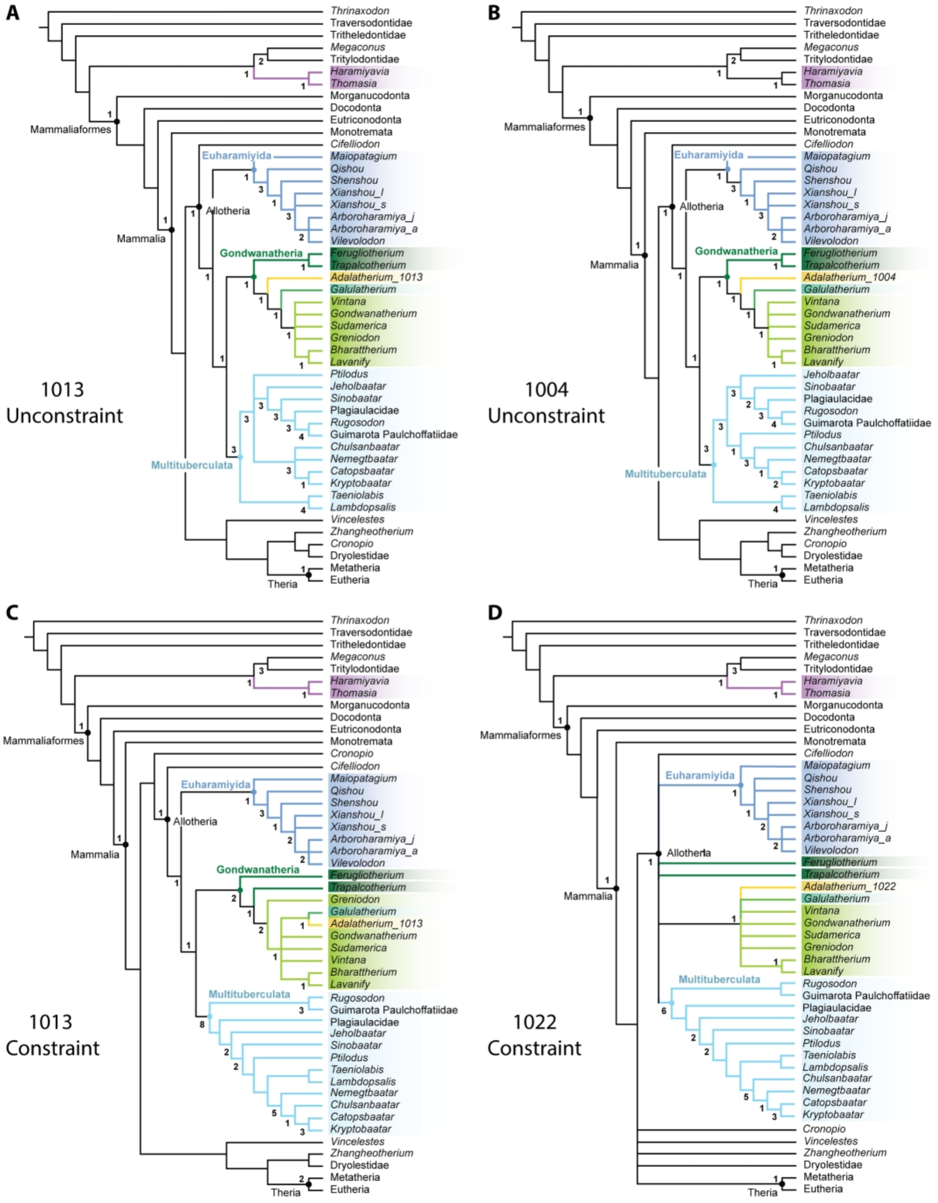

FIGURE 1. Simplified tree topology of strict consensus trees for parsimony analyses using three different coding schemes for Adalatherium based on lower dental formulae (1013, 1022, 1004) with nodes within multituberculates either unconstrained (A, B) or constrained (C, D). A, simplified strict consensus tree of 16 most parsimonious trees (MPTs) from unconstrained analysis using coding scheme 1013 (tree topology but not Bremer support identical to 1022); B, simplified strict consensus tree of eight MPTs from unconstrained analysis using coding scheme 1004; C, simplified strict consensus tree of 16 MPTs from constrained analysis using coding scheme 1013 (tree topology but not Bremer support identical to 1004_constraint); D, simplified strict consensus tree of 40 MPTs from constrained analysis using coding scheme 1022. Bremer values for selected nodes indicated next to node. Adalatherium highlighted in yellow, gondwanatherians in green shades (ferugliotheriids in dark green, Galulatherium in teal, sudamericids in light green), multituberculates in light blue, euharamiyidans in dark blue, haramiyidans in purple. [planned for page width, color]

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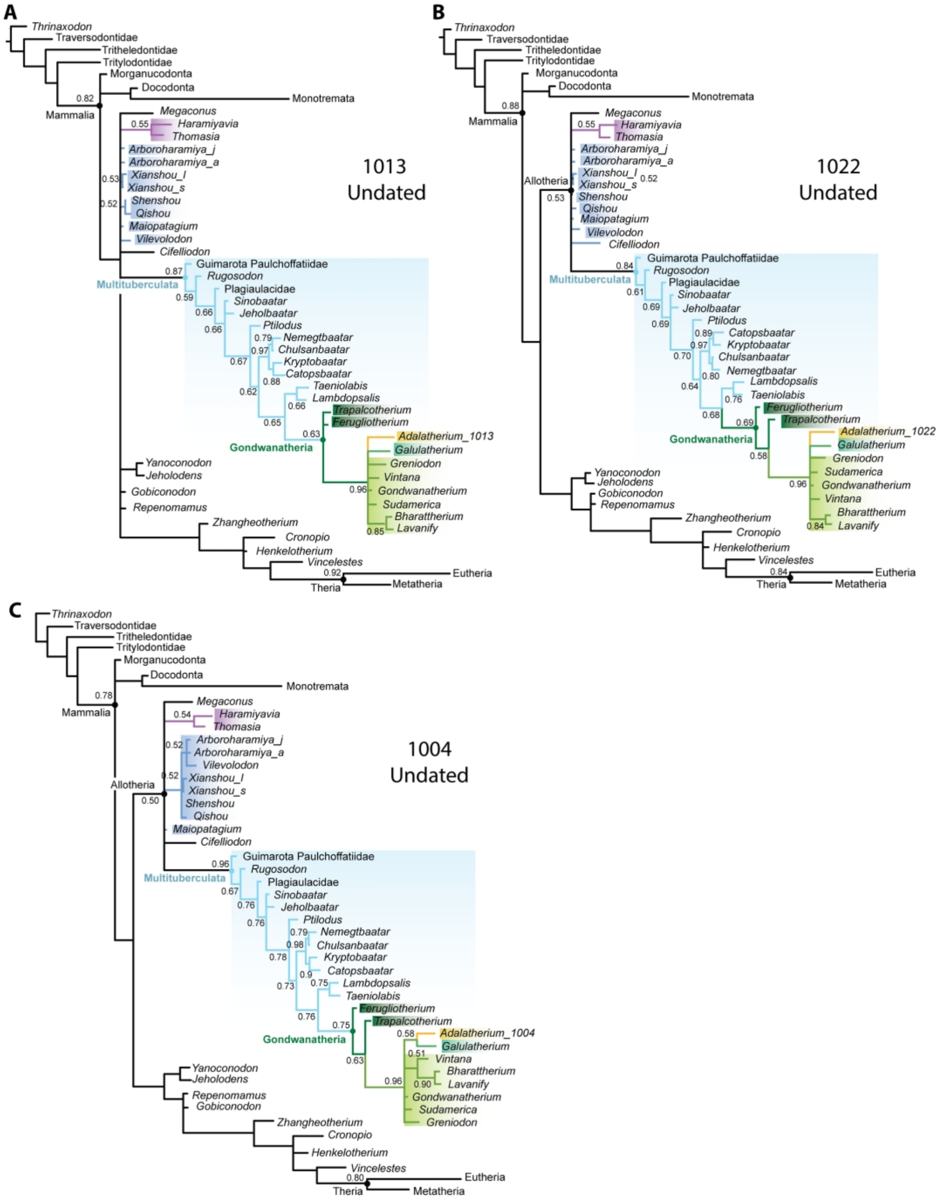

FIGURE 2. Simplified tree topology of 'halfcompat' (50% majority rule) trees for undated Bayesian analyses using three different coding schemes for Adalatherium based on lower dental formulae (1013, 1022, 1004). A, simplified halfcompat tree of 1013_undated; B, simplified halfcompat tree of 1022_undated; and C, simplified halfcompat tree of 1004_undated. Posterior probabilities for selected nodes indicated next to node. Adalatherium highlighted in yellow, gondwanatherians in green shades (ferugliotheriids – dark, Galulatherium – medium, sudamericids – light), multituberculates in light blue, euharamiyidans in dark blue, haramiyidans in purple. [planned for page width, color]

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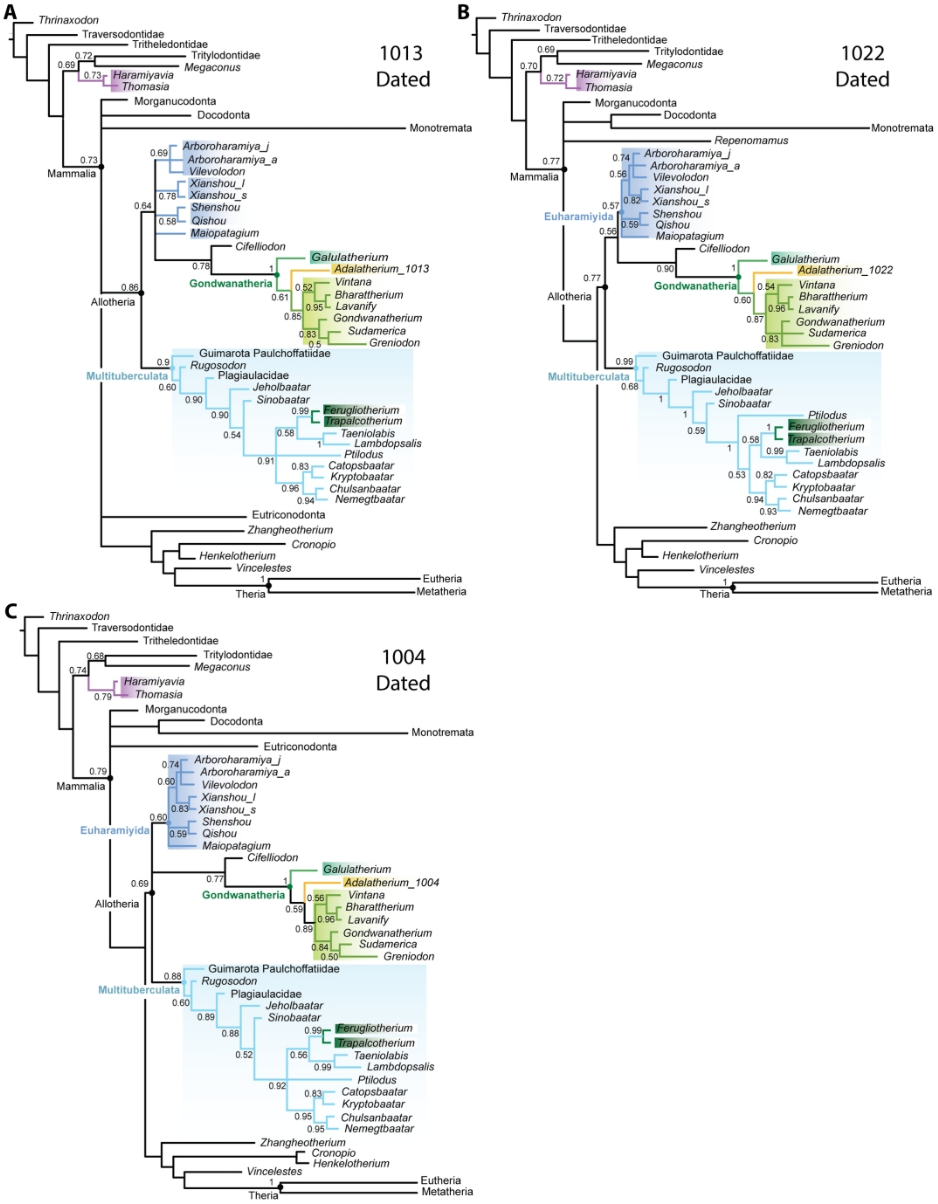

FIGURE 3. Simplified tree topology of 'halfcompat' (50% majority rule) trees for tip-dated Bayesian analyses using three different coding schemes for Adalatherium based on lower dental formulae (1013, 1022, 1004). A, simplified halfcompat tree of 1013_dated; B, simplified halfcompat tree of 1022_dated; and C, simplified halfcompat tree of 1004_dated. Posterior probabilities for selected nodes indicated next to node. Adalatherium highlighted in yellow, gondwanatherians in green shades (ferugliotheriids in dark green, Galulatherium in teal, sudamericids in light green), multituberculates in light blue, euharamiyidans in dark blue, haramiyidans in purple. [planned for page width, color]

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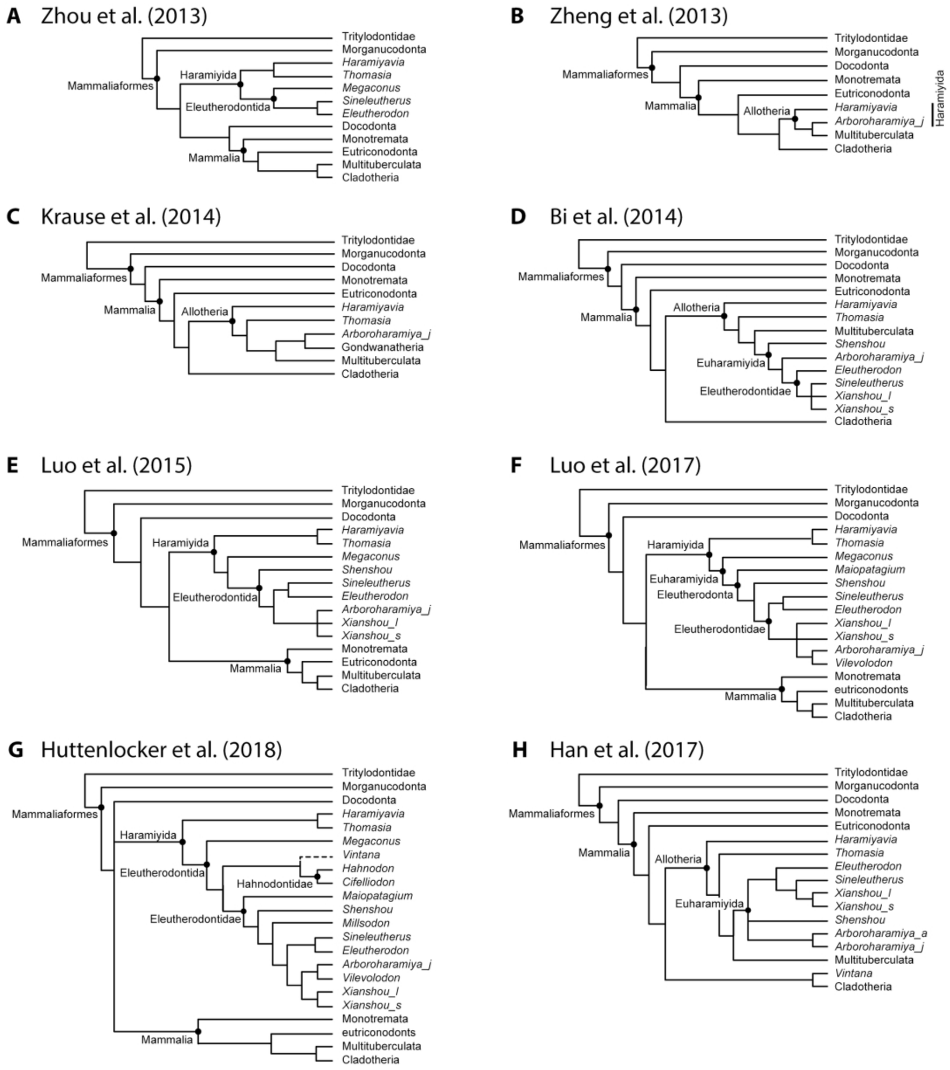

FIGURE 4. Simplified tree topology of mammaliaform relationships based on A, Zhou et al. (2013); B, Zheng et al. (2013); C, Krause et al. (2014); D, Bi et al. (2014); E, Luo et al. (2015); F, Luo et al. (2017); G, Huttenlocker et al. (2018); and H, Han et al. (2017). Millsodon, Allostaffia, Theroteinida were not included in the analysis of Bi et al. (2014:Supplementary Information), but the authors assigned Millsodon to Euharamiyida, and Allostaffia and Theroteinida to Allotheria. Megaconus was included in one of three analyses by Bi et al. (2014:Supplementary Information) and was assigned to Allotheria, contrary to its placement in their analyses. These taxa are not included in part D. Eutriconodonta are not monophyletic in F and G and are therefore labeled as 'eutriconodonts.' [planned for page width, grayscale]

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