

A new phylogeny for basal Trechnotheria and Cladotheria and affinities of South American endemic Late Cretaceous mammals

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Abstract The endemic South American mammals Meridiolestida, considered previously as dryolestoid cladotherians, are found to be non-cladotherian trechnotherians related to spalacotheriid symmetrodontans based on a parsimony analysis of 137 morphological characters among 44 taxa. Spalacotheriidae is the sister taxon to Meridiolestida, and the latter clade is derived from a primitive spalacolestine that migrated to South America from North America at the beginning of the Late Cretaceous. Meridiolestida survived until the early Paleocene (*Peligrotherium*) and early Miocene (*Necrolestes*) in South America, and their extinction is probably linked to the increasing competition with metatherian and eutherian tribosphenic mammals. The clade Meridiolestida

plus Spalacotheriidae is the sister taxon to Cladotheria and forms a new clade Alethinotheria. Alethinotheria and its sister taxon Zhangheotheria, new clade (Zhangheotheriidae plus basal taxa), comprise Trechnotheria. Cladotheria is divided into Zatheria (plus stem taxa, including *Amphitherium*) and Dryolestida, including Dryolestidae and a paraphyletic array of basal dryolestidans (formerly classified as “Paurodontidae”). The South American *Vincelestes* and *Groebertherium* are basal dryolestidans.

Keywords Mammalia · Trechnotheria · Cladotheria · Meridiolestida · Late Cretaceous · South America

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Introduction

According to the current view of mammalian evolution in the Mesozoic, there occurred three major diversifications before the origin of modern tribosphenic mammals: basal trechnotherians, including “acute-angled” symmetrodontans (or spalacotheroids); basal cladotherians, including dryolestoids with an initial talonid; and basal zatherians with more elaborated and basined talonid (McKenna 1975; Luo et al. 2002; Kielan-Jaworowska et al. 2004; Luo 2007a, b). The main arena of evolution of these groups was confined to the northern continents of Laurasia. Mammalian evolution on the southern, Gondwanan continents in the Mesozoic was quite different from this mainstream. One group, the australosphenidans, achieved a tribosphenic or nearly tribosphenic dentition independently from the Laurasian tribosphenic mammals (Rich et al. 1997, 1999, 2001; Flynn et al. 1999; Luo et al. 2001a, 2002; Rauhut et al. 2002; Kielan-Jaworowska et al. 2004; Martin and Rauhut 2005; Rougier et al. 2007b). In Africa and South America, these unusual mammals existed in the Jurassic, and they are known from the Early Cretaceous of Australia. According to Averianov and

Lopatin (2011), australosphenidans belong to two different radiations: the South American (and possibly African) Jurassic tribosphenids represent a diversification of more basal mammals with the postdentary bones not yet detached from the dentary (Henosphenida), whereas the Australian tribosphenic mammals originated from a more derived stock with fully detached postdentary bones (Ausktribosphenida). For unknown reasons, the Jurassic tribosphenic mammals (henosphenids) did not persist to the Cretaceous in South America. This vacuum was filled by peculiar mammals known until recently by only a few isolated teeth. One group was the enigmatic allotherian-like Gondwanatheria (Gurovich and Beck 2009 and references therein), which is not considered here. The other Cretaceous South American mammals were members of the Laurasian pretribosphenic radiation and apparently originated from North America. Initially, they were classified as symmetrodontans and dryolestoidans (Bonaparte 1986, 1990, 2002), but subsequently, the majority or all of them were referred to Dryolestoida (see review in Rougier et al. 2011).

The recently discovered two partial skulls of *Cronopio dentiacutus* from the Cenomanian Candeleros Formation of Argentina represent the best and oldest specimens of these enigmatic mammals (Rougier et al. 2011). The phylogenetic analysis provided by Rougier et al. (2011) links the South American *Groebertherium* with the Laurasian dryolestids, whereas the other South American dryolestoids are united into the monophyletic Meridiolestida within Dryolestoida. This corroborates the current view that all these enigmatic South American taxa are dryolestoids. However, there are several problems with this interpretation. Among these taxa, *Groebertherium* is clearly a dryolestid-like taxon with initial talonid and possibly a reduced distal root on the lower molars; it also has a wear pattern similar to that in other dryolestids (Crompton et al. 1994; Schultz and Martin 2010). The other taxa do not show distinct dryolestoid characters. The distal root of their lower molars is not reduced compared with the mesial root. The roots are somewhat mesiodistally compressed in cross section, as in spalacotheroids, and not oval, as in dryolestoids. Often, there are prominent mesial and distal cingulids on the lower molars, as in spalacotheroids, but a distinct talonid characteristic for dryolestoids is not developed. The lower premolars of Meridiolestida, attributed previously to the triconodontan genus *Austrotriconodon* Bonaparte (1986) (see Rougier et al. 2011), are of symmetrodontan design, with well-developed mesial and distal cingulid cusps and a distinct cusp c between the main cusp and the distal cingulid cusp, whereas in dryolestids, the lower premolars are quite different, without a mesial cingulid cusp or cusp c. The dentary of *Cronopio* lacks the angular process so characteristic for dryolestoids, and in general, appearance is similar to the dentary of zhangheotheriids and spalacotheroids (Simpson 1928; Hu et al. 1997; Rougier et al. 2003a; Ji et al.

2009). Rougier et al. (2011) reported the presence of a small angular process for *Cronopio*, but this interpretation of the poorly preserved distal part of the dentary is problematical; as evident from the published illustrations, the angular process is likely totally lacking in this taxon. In all Meridiolestida, Meckel's groove is lacking, as in spalacolestine symmetrodontans, while in Dryolestida, it is pronounced. The unique masseteric process of *Cronopio* corresponds to the masseteric shelf in the spalacolestine symmetrodontans *Heishanlestes* and *Spalacolestes* from the Late Cretaceous of Asia and North America (Cifelli and Madsen 1999; Hu et al. 2005). Rougier et al. (2011), based on their phylogenetic hypothesis, consider that this process is not homologous in these taxa. Actually, the homology of these structures has not been tested because no spalacolestine was included in that analysis. According to the alternative phylogenetic hypothesis presented here, these structures are homologues and related to a uniquely transformed masticatory musculature of these taxa connected with predominant jaw rotation during mastication.

One of the shortcomings of the analysis that places Meridiolestida within Dryolestoida is the lack of some relevant taxa of spalacotheroids, which may be crucial to assess the phylogenetic position of Meridiolestida. As the authors noted themselves (Rougier et al. 2011), the tree topology has been recovered by utilizing a set of additive characters; if all characters are treated as non-additive in that analysis, the Meridiolestida and the Dryolestida appear as successive sister groups of the stem therians, as in our analysis (see below). This suggests that Meridiolestida has evolved from spalacotheriid symmetrodontans rather than dryolestoidans, which is in agreement with the above-mentioned characters.

In the more recent paper by Rougier et al. (2012), Meridiolestida is no longer linked to Dryolestidae. The Dryolestoida in classic sense (Dryolestidae + Paurodontidae) is found to be polyphyletic: Paurodontidae is a sister taxon to Meridiolestida, and this clade is sister to the tribosphenic mammals.

In this paper, we present a new phylogenetic analysis of basal trechnotherian and cladotherian mammals utilizing a novel set of characters and a wider range of taxa. It is based on our taxonomic revision of the Laurasian Dryolestida and South American taxa and suggests that Meridiolestida was part of the symmetrodontan radiation of Mesozoic mammals.

Institutional abbreviations

BMNH, Natural History Museum, London, Great Britain; MACN-RN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Colección Río Negro, Buenos Aires, Argentina; MG, Museo Geológico, Lisbon, Portugal (some specimens temporarily housed in the Steinmann-

Institut für Geologie, Mineralogie und Paläontologie of the Universität Bonn, Germany); PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow; PM TGU, Paleontological Museum of Tomsk State University, Tomsk; STIPB, Steinmann-Institut für Geologie, Mineralogie und Paläontologie of the Universität Bonn, Germany; USNM, United States National Museum, Washington DC, USA; YPM, Yale Peabody Museum, Yale University, New Haven, USA.

Characters

We used 137 characters for the phylogenetical analysis, some of which are new and others are compiled and mostly modified from the literature (Simpson 1928, 1929; Prothero 1981; Martin 1999; Luo and Wible 2005; Li and Luo 2006; Rougier et al. 2007a, 2011, 2012 and others). The list of characters is presented in the [Supplementary Information](#). The complete morphological data set is available at Morphobank (www.morphobank.org; Project 876). In this section, we discuss the interpretation of the postcanine dental formula in Meridiolestida, which affects coding of some characters.

In *Cronopio*, the postcanine dental formula originally has been interpreted as P1–4 M1–3 with two-rooted premolars and single-rooted molars (Rougier et al. 2011). This interpretation implies that the ultimate premolars, P4 and p4, have a molariform shape. No rationale was given for this interpretation, except for the difference in root number, a character which was never used to distinguish between premolars and molars, at least in Mesozoic mammals. Evidently, this interpretation was influenced by the fact that in some meridiolestids (*Coloniatherium* and *Peligrotherium*), a replacement in the first molariform locus occurs based on differences in tooth wear (Páez Arango 2005; Rougier et al. 2009b). However, replacement in the first molariform locus has been observed in some symmetrodontans: *Zhangheotherium*, *Maotherium*, and *Kiyatherium* (Luo et al. 2001b; Luo and Ji 2005; Rougier et al. 2003a; Lopatin et al. 2010a). It is thus a semantic issue to call this first molariform tooth a premolar or a molar. The replacement criterion, in spite of its appealing simplicity, could be misleading in assessing the tooth homology. By this criterion, the first premolar (P1 and p1) in the majority of eutherians should be called a molar because it is never replaced (Luckett 1993; Archibald and Averianov 2012). According to our hypothesis, the first molariform tooth of symmetrodontans, in spite of its replacement in some taxa, is homologous to the first molar of cladotherians. The loss of replacement in this locus is considered as an important synapomorphy of Cladotheria. The Meridiolestida, retaining this primitive trait, belongs to a more basal level of mammal radiation. Subsequently, the first molariform tooth of Meridiolestida, traditionally designated

as the ultimate premolar (Páez Arango 2008; Rougier et al. 2009b, 2011), is considered here the first molar.

Another controversial question concerns the interpretation of isolated upper molariform teeth from the Campanian Los Alamos Formation of Argentina, considered previously as distinct taxa of symmetrodontans, *Barberenia* and *Quirogatherium* (Bonaparte 1990). Later, these teeth were reinterpreted as deciduous premolars of *Brandonia* and *Mesungulatum*, respectively, which are known from the same formation (Martin 1999; Averianov 2002; Kielan-Jaworowska et al. 2004). Rougier et al. (2011, p. 98), based on newly discovered specimens of *Cronopio*, thought that the dental morphotype of *Barberenia* and *Quirogatherium* “represents just the penultimate premolar position of other taxa” of Meridiolestida. However, the morphology of the teeth in question is actually quite different from that of the ultimate premolars of *Cronopio* or *Coloniatherium* (Rougier et al. 2011, Fig. S3). They have a high lingual paracone and a vast labial basin separated by a median ridge. In *Cronopio*, the ultimate premolar has a much smaller basin which is distal to the main cusp, and in *Coloniatherium*, this basin is strongly reduced, and the main cusp has a central position on the crown (Rougier et al. 2011, Fig. S3B, D). Another argument that these teeth are permanent rather than deciduous is based on the observation that “the frequency of these teeth in the collection from Los Alamos [Formation] is too high to regard them as shed deciduous teeth” (Rougier et al. 2011, p. 48 of [Supplementary Information](#)). This argument is based on an a priori assumption that Mesozoic mammals were similar in biology to modern mammals of similar size which replace teeth during the first year of their life. However, this assumption seems improbable. Mesozoic mammals likely had a longer and a slower growth and may have replaced their dentition much later in ontogenesis. In more derived Late Cretaceous eutherian mammals (Zhelestidae), the milk teeth certainly worked for a long period, and often, they are worn down to the root, suggesting that the first tooth generation played an important role during the first years of life (Archibald and Averianov 2012). In addition, milk teeth of zhelestids are quite common in the localities. The milk teeth usually come to the fossil record with dead mammals; the shed teeth are often swallowed by the animals and therefore may have been completely digested. With the mortality curve typical for small mammals, in which the majority of individuals die early in life and that can be assumed for the taxa considered here, even a small delay in tooth replacement would produce a much higher percentage of dead animals with milk teeth still in place. The great similarity of the *Barberenia*–*Quirogatherium* dental morphotype with the milk premolars of dryolestids and stem zatherians (Martin 1997, 1999, 2002) supports their interpretation as deciduous teeth.

Finally, we have to discuss the homology of the principal cusps of the upper tribosphenic molars which may affect coding of some characters. According to the tritubercular theory of Cope–Osborn (summarized in Gregory 1934), the lingual cusp of the tribosphenic molar, the protocone, is homologous to the single cusp of reptilian teeth. In triconodontans, it was supplemented by two additional longitudinally aligned cusps, paracone (anterior) and metacone (posterior). In symmetrodontans, the cusps became triangulated, so paracone and metacone shifted to a position labial of the protocone. This long-standing theory was revised by Patterson (1956), who concluded that the lingual cusp of symmetrodontans and “pantotherians” (dryolestidans) is actually a paracone and the tribosphenic protocone is a neomorph cusp that was developed from the lingual cingulum of *Peramus*-like mammals (see also Mills 1964, 1967; Butler 1972, 1978). Crompton (1971; see also Fox 1975) further modified Patterson's (1956) ideas. He concluded that also the tribosphenic metacone is a neomorph cusp, not homologous to the “metacone” (=cusp C) of *Kuehneotherium* (this cusp is greatly reduced or lost in symmetrodontans and dryolestidans). The tribosphenic metacone was developed in relation to development of the hypoconid on the lower molars (Crompton considered the distal cingulid cusp d of *Kuehneotherium* homologous to the hypoconulid of the tribosphenic dentition). However, a more recent study suggests that the tribosphenic metacone is actually homologous to cusp C of *Kuehneotherium* (Davis 2011). The interpretation of the single lingual cusp as a paracone or a metacone may affect the phylogenetic position of the zalambdodont mammal *Necrolestes*. Eutherians enhance the prevallum/postvallid shear, while metatherians focus on the postvallum/prevallid shear (Crompton 1971; Fox 1975), and thus, in the former, the paracone is larger than the metacone, while in the latter, the relative size of these cusps is reversed. In taxa with zalambdodont dentition, one of these cusps is reduced, and it is not surprising that in zalambdodont eutherians the single remaining cusp is the paracone, while in zalambdodont metatherians, it is the metacone (see review in Asher and Sánchez-Villagra 2005). In dryolestidans, the main shear plane is the prevallum/postvallid, as in eutherians (Schultz and Martin 2010), and therefore, the metacone is reduced or lost in Dryolestida. Asher et al. (2007) concluded that the single lingual cusp of the upper molars of *Necrolestes* is a metacone based on the observed occlusal relationships with the lower molar structures. In our analysis, there are eight characters related to the paracone or metacone (characters 39–43, 45, 46, and 49). For all of these characters, the situation in *Necrolestes* is coded as unknown (“?”), and thus, the issue of homology of its lingual cusp has no effect on the resulting cladogram. Interpretation of this cusp as a metacone is highly unlikely based on the topology of the cladogram: the metacone was completely lost in Spalacolestinae, the sister group of Meridiolestida.

Taxa

Amphilestidae—Amphilestids with triconodont dentition having three principal, aligned cusps and with detached postdentary bones were likely the initial group for the radiation of the clade containing modern therian mammals (Mills 1971; Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2007a; Averianov and Lopatin 2011), and thus, they are chosen here for the outgroup. Two amphilestid taxa have been included in the analysis, *Phascolotherium bucklandi* (Broderip 1828) and *Amphilestes broderipi* (Owen 1845), both from the Middle Jurassic (Bathonian) Sharps Hill Formation of England. The first taxon is set as outgroup in the analysis. Coding is based on specimens or casts in the BMNH collection.

Tinodon—*Tinodon bellus* Marsh 1879a (= *T. lepidus* Marsh 1879a) is an “obtuse-angled” symmetrodontan represented by dentary fragments from the Upper Jurassic (Kimmeridgian–Tithonian) Morrison Formation of WY, USA (Simpson 1929). Isolated symmetrodontan teeth from the Morrison Formation in UT, USA (Engelmann and Callison 1998) possibly do not belong to *Tinodon*. “*Tinodon*” *micron* Ensom and Sigogneau-Russell 2000, known by isolated lower and upper molars from the Lower Cretaceous (Berriasian) Lulworth Formation (Purbeck Limestone Group) of England is excluded from this genus (Lopatin et al. 2005; Averianov and Lopatin 2008). Coding of *Tinodon* is based on direct observations of specimens in the USNM and YPM collections. The maxillary and upper molar characters of *Tinodon* are coded after YPM 13639, the holotype of *Eurylambda aequicrurius* Simpson 1925. An isolated upper molar USNM 2846 (Rougier et al. 2003b) apparently does not belong to *Tinodon* (Averianov and Lopatin 2008).

Yermakia—*Yermakia domitor* Lopatin et al. 2005 is based on dentary fragments and isolated lower and upper molars from the Lower Cretaceous (?Barremian–Aptian) Itat Formation of West Siberia, Russia (Lopatin et al. 2005; Averianov and Lopatin 2008). An edentulous dentary fragment PM TGU 16/7-22, referred originally to *Yermakia* (Lopatin et al. 2005, Fig. 2, pl. 10, Fig. 2), may actually belong to an amphidontid triconodontan *Acinacodus tagaricus* Lopatin et al. 2010b, known from the same locality and was not used for coding. The coding of *Yermakia* is based on other specimens in the PM TGU and PIN collections, positively identified as such based on resemblance to the type material.

Gobiotheriodon—*Gobiotheriodon infinitus* (Trofimov 1980) is known from two dentary fragments with incomplete dentition and several isolated lower molars from the Early Cretaceous Höövör locality in Mongolia (Trofimov 1980; Averianov 2002; Lopatin et al. 2005). Studied specimens are housed in the PIN collection.

Kiyatherium—*Kiyatherium cardiogens* Maschenko et al. 2002 is known from the same Itat Formation as *Yermakia*, but from a different locality where *Yermakia* is not present (Lopatin et al. 2010b). The coding of *Kiyatherium* is based on specimens from the PM TGU collection.

Zhangheotherium—*Zhangheotherium quiquecuspidens* Hu et al. 1997 has been described from the Lower Cretaceous (Barremian) Yixian Formation of Liaoning Province, China (Hu et al. 1997, 1998; Luo and Ji 2005). It is represented by two rather complete but flattened skeletons of different ontogenetic age from two different localities. For one of these localities, there is a radiometric date suggesting a middle Barremian age (Wang et al. 2001). The coding of this taxon is based on Hu et al. (1997, 1998) and Luo and Ji (2005).

Maotherium—Two complete skeletons from different localities within the Yixian Formation of Liaoning Province, China are referred to different species, *Maotherium sinense* Rougier et al. 2003a and *M. asiaticum* Ji et al. 2009 (species name spelling has been corrected by Lopatin et al. 2010a). For one of these sites, there is a radiometric date of middle Barremian age (Ji et al. 2009). Both species are coded separately after Rougier et al. (2003a) and Ji et al. (2009).

Spalacotherium—The type species of the genus, *S. tricuspidens* Owen 1854 (= *Peralestes longirostris* Owen 1871) is represented by several maxillary and dentary fragments from the Lulworth Formation of England (Owen 1871; Simpson 1928). Four other named species of *Spalacotherium* from the Early Cretaceous of England and Portugal are known by less complete materials and do not differ significantly from the type species (Clemens and Lees 1971; Krebs 1985; Ensom and Sigogneau-Russell 2000; Gill 2004). *Spalacotherium* is coded here based on the studied materials of the type species in the BMNH collection.

Spalacolestes—The single species of this genus, *S. cretulablatta* Cifelli and Madsen 1999 is represented by abundant isolated teeth and some dentary fragments in the Albian-Cenomanian Cedar Mountain Formation, UT, USA (Cifelli and Madsen 1999). This taxon is coded based on the published information and casts in the ZIN collection.

Dryolestes—*Dryolestes* Marsh 1878 (= *Herpetairus* Marsh 1879b) is represented by two species, *D. priscus* Marsh 1878 from the Morrison Formation of WY, USA, and *D. leiriensis* Martin 1999, from the Guimarota beds (Kimmeridgian) of Portugal. The coding is based on Martin (1999) and specimens housed in the YPM, USNM, and MG collections.

Laolestes—*Laolestes* Simpson 1927 (= *Melanodon* Simpson 1927) includes three species. The type species, *L. eminens*

Simpson 1927 is known by maxillary and dentary fragments from the Morrison Formation of WY, USA (Simpson 1929). Two European species, *L. hodsoni* Clemens and Lees 1971 from the Lower Cretaceous (Valanginian) Wadhurst Formation of England, and *L. andresi* Martin 1999 from Porto Pinheiro (Berriasian) of Portugal, are based on isolated teeth. The coding of *Laolestes* is based on specimens of the type species housed in the YPM and USNM collections.

Krebsotherium—*Krebsotherium lusitanicum* Martin 1999 is represented by maxillae and dentaries from the Guimarota beds of Portugal. The coding of this species is based on Martin (1999) and original materials in the MG collection.

Guimarotodus—*Guimarotodus inflatus* Martin 1999 is represented only by dentary fragments with dentition from the Guimarota beds of Portugal. The coding of this species is based on Martin (1999) and on the specimens in the MG collection.

Amblotherium—*Amblotherium* Owen 1871 (= *Kepolestes* Simpson 1927; = *Miccylyotyrans* Simpson 1927) is the third dryolestid genus known from both North America and Europe. The American species, *A. gracile* Marsh 1879c (= *A. debile* Simpson 1927; = *Miccylyotyrans minimus* Simpson 1927) from the Morrison Formation, is represented by abundant lower and single upper jaw fragments with dentition. *A. pusillum* (Owen 1866) is known from upper and lower jaw fragments from the Lulworth Formation of England (Simpson 1928). The second British species, *A. nanum* (Owen 1871), referred to this genus by Simpson (1928) and all subsequent authors, is considered here to be generically distinct (see *Achyrodon*). The type species for *Amblotherium* was designated as *Stylodon pusillus* Owen 1866 in Simpson (1928) and as *Amblotherium soricinum* Owen 1871 in Simpson (1929); the latter assignment was repeated in Kielan-Jaworowska et al. (2004). *Stylodon pusillus* is a senior subjective synonym of *Amblotherium soricinum* and is the correct type species for *Amblotherium*; the species should be referred to as *Amblotherium pusillum* (Owen 1866). *Amblotherium* is the only dryolestid from the Lulworth Formation with upper and lower dentitions found in association (Simpson 1928). Coding of *Amblotherium* is based on the specimens in the BMNH, YPM, and USNM collections.

Achyrodon—*Achyrodon nanus* Owen 1871 comes from the same locality as *A. pusillum* and differs from the latter by somewhat smaller size, double-rooted lower canine, a p2 that is smaller than p1, molar talonids without shelf-like labial extension, and upper molars without cusps along the metacrista. The species was formerly referred to *Amblotherium*, but Simpson (1928, p. 136) thought that it could be generically different from *A. pusillum*. Generic

distinction of this species is supported by the current phylogenetic analysis (see below).

Phascolestes—The single species, *Phascolestes mustelulus* (Owen 1871) (= *Peraspalax talpoides* Owen 1871, syn. nov.; = *Kurtodon pusillus* (Osborn 1888), syn. nov.) is known from dentary and maxillary fragments with dentition from the Lulworth Formation of England. Simpson (1928, pp. 140, 141) previously noted a possible synonymy of *Peraspalax* and *Phascolestes* and their possible association with the upper dentition of *Kurtodon*. Sigogneau-Russell and Kielan-Jaworowska (2002, p. 249) also suggested that *Kurtodon* is a possible synonym of *Peraspalax*. However, Kielan-Jaworowska et al. (2004, p. 382) synonymized *Kurtodon* with *Amblotherium*. *Kurtodon* is clearly distinct from the latter by larger size and presence of a median ridge on the upper molars. *Phascolestes* was conditionally proposed by Owen (1871) as a subgenus of *Perales* (a symmetrodontan), and according to the ICZN Article 15.1, this name is available as published before 1960. Another taxonomic problem with *Phascolestes* is that this name appeared with the species epithet *longirostris*, the type species of *Perales* Owen 1871 (= *Spalacotherium* Owen 1854). Simpson (1928, p. 143) fixed *Amblotherium mustelula* Owen 1871 as the type species for *Phascolestes* (ICZN Article 67.2.2; corrected to *mustelulus* in Kielan-Jaworowska et al. 2004, p. 387). *Phascolestes* is chosen here as the senior subjective synonym by the principle of the first reviser (ICZN Article 24.2) because its type species is represented by more complete specimens. The coding of this species is based on specimens from the BMNH collection.

Crusafontia—*Crusafontia cuencana* Henkel and Krebs 1969 is known from dentary fragments with teeth and isolated upper and lower teeth from the Barremian Uña and Galve localities of Spain (Henkel and Krebs 1969; Krebs 1985; Martin 1998; Cuenca-Bescós et al. 2011). The coding of *Crusafontia* is based on Henkel and Krebs (1969) and specimens from the STIPB collection.

Euthlastus—*Euthlastus cordiformis* Simpson 1927 is represented by a poorly preserved maxillary fragment with four molars from Quarry 9 of the Morrison Formation in WY, USA (Simpson 1929). Engelmann and Callison (1998, Fig. 2) referred to this species a well-preserved upper molar from Dinosaur National Monument in UT, USA. This is one of the smallest cladotherians in the Morrison fauna, and there are no lower dentitions clearly associated with it. Engelmann and Callison 1998 noted an undescribed skull from the Morrison Formation which may belong to this species. At present, *Euthlastus* is universally considered as a “paurodontid” (Martin 1999; Kielan-Jaworowska et al. 2004 and references therein). *Euthlastus* is coded based on the cited above literature.

Tathiodon—*Tathiodon agilis* (Simpson 1927) (= *Comotherium richi* Prothero 1981) is a poorly known cladotherian from Quarry 9 of the Morrison Formation in WY, USA (Simpson 1929; Prothero 1981). The dentary fragment, holotype of *T. agilis*, bears two molariform teeth, likely dp4 and m1. The upper dentition is known from a maxillary fragment with three molars (holotype of *C. richi*) and isolated upper molar (AMNH collection). The coding is based on the specimens from the AMNH collection.

Paurodon—*Paurodon valens* Marsh 1887 (= *Pelicipsis dubius* Simpson 1927) is represented by dentary and maxillary fragments from Quarry 9 and a nearby locality of the Morrison Formation in WY, USA. The coding is based on the specimens in the USNM and AMNH collections.

Henkelotherium—*Henkelotherium guimarotae* Krebs 1991 is represented by a rather complete skeleton from the Guimarota beds (Kimmeridgian) of Portugal (Krebs 1991). Coding is based on Krebs (1991) and holotype specimen in the MG collection.

Drescheratherium—*Drescheratherium acutum* Krebs 1998 is known from two maxillary fragments with teeth from the same locality as *Henkelotherium* (Krebs 1998). Coding is based on Krebs (1998) and specimens in the MG collection.

Amphitherium—*Amphitherium prevostii* (Meyer, 1832) (= *A. rixoni* Butler and Clemens 2001) is based on several dentary fragments with lower teeth from the Middle Jurassic (Bathonian) Sharps Hill Formation of England (material reviewed in Butler and Clemens 2001). Freeman (1979) referred to ?*Amphitherium* sp. an isolated lower molar from the Forest Marble Formation of England, but most likely, this specimen belongs to *Palaeoxonodon ooliticus* (see below). The coding is based on specimens and casts in the BMNH collection.

Palaeoxonodon—*Palaeoxonodon ooliticus* Freeman 1976 (= *P. freemani* Sigogneau-Russell 2003) is represented by abundant isolated upper and lower molars from the Middle Jurassic (Bathonian) Forest Marble Formation of England (Freeman 1976, 1979; Sigogneau-Russell 2003). Coding is based on Freeman (1976, 1979) and Sigogneau-Russell (2003).

Amphibetulimus—*Amphibetulimus krasnolutsii* Lopatin and Averianov 2007a is known from the holotype dentary fragment with one molar and several undescribed dentary fragments from the Middle Jurassic (Bathonian) Itat Formation of West Siberia, Russia (Lopatin and Averianov 2007a), housed in PIN collection. The coding is based on specimens in the PIN collection.

Nanolestes—There are three species of *Nanolestes*: *N. drescheri* Martin 2002 (type species) from the Guimarota beds (Kimmeridgian) of Portugal, *N. krusati* Martin 2002 from Porto Pinheiro (Berriasian) in Portugal, and *N. mackennai* Martin et al. 2010 from the Late Jurassic (Oxfordian) Qigu Formation in Xinjiang, China (Krusat 1969; Martin 2002; Martin et al. 2010). Isolated upper and lower molars are known for all three species, and premolars, dentary fragments, and a single maxillary fragment of the type species. The coding is based on the type species (see Martin 2002 and specimens in the MG collection); the other species do not show variation in the coded character states.

Arguimus—*Arguimus khosbajari* Dashzeveg 1979 (= *Arguitherium cromptoni* Dashzeveg 1994) is represented by several dentary fragments with partially preserved dentitions from the Early Cretaceous Höövör locality in Mongolia (species revised in Lopatin and Averianov 2006b). The coding is based on PIN specimens and published illustrations.

Mozomus—*Mozomus shikamai* Li et al. 2005 is known from a single dentary fragment with seven teeth, interpreted as two premolars and m1-5 (see Averianov et al. 2010a), from the Early Cretaceous (Aptian) Shihai Formation of Liaoning, China (Li et al. 2005). The coding is based on the published photograph (Li et al. 2005, Fig. 2). The published drawing of this specimen (Li et al. 2005, Fig. 3) is not accurate as the supporting needle and glue were depicted as part of dentary in labial view.

Peramus—*Peramus tenuirostris* Owen 1871 comes from the Lulworth Formation of England where it is represented by one maxillary and several dentary fragments with teeth (Simpson 1928; Clemens and Mills 1971). The coding is based on specimens in the BMNH collection, including several previously unrecognized dentary fragments.

Vincelestes—*Vincelestes neuquenianus* Bonaparte 1986 is one of the best known Early Cretaceous mammals, represented by several skulls and postcranial elements from the Hauterivian-Barremian La Amarga Formation of Argentina. The cranial anatomy is described in a series of publications (Bonaparte and Rougier 1987; Rougier et al. 1992; Macrini et al. 2007), but dentition and postcranial elements of this taxon are still undescribed. The coding of *Vincelestes* in most cases is repeated from the coding in Rougier et al. (2011, 2012) data matrices, except the character states describing this taxon as having a functional protocone and basined talonid. The only published detailed picture of the *Vincelestes* dentition (Sigogneau-Russell 1999, Fig. 7) suggests that this taxon has a lingual cingulum at the upper molars but not a functional protocone and the talonid is single cusped and not basined.

Some additional characters were coded after cited publications and images in the Digital Morphology Library of the University of Texas at Austin (http://digimorph.org/specimens/Vincelestes_neuquenianus/).

Kielantherium—*Kielantherium gobiense* Dashzeveg 1975 is a basal tribosphenic mammal from the Early Cretaceous Höövör locality in Mongolia known from two dentary fragments and two isolated molars (Dashzeveg 1975; Dashzeveg and Kielan-Jaworowska 1984; Lopatin and Averianov 2006a, 2007b). The coding is based on PIN specimens and published illustrations of other specimens.

Prokennalestes—This is one of the earliest known eutherian mammals represented by abundant dentitions, jaw fragments, and isolated petrosals from the Aptian-Albian Höövör locality in the Gobi Desert, Mongolia. These materials are referred to two species, *P. trofimovi* Kielan-Jaworowska and Dashzeveg 1989 and *P. minor* Kielan-Jaworowska and Dashzeveg 1989. The coding of *Prokennalestes* is based on publications (Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992; Wible et al. 2001) and numerous additional unpublished specimens in the PIN collection.

Cronopio—*Cronopio dentiacutus* Rougier, Apesteguia and Gaetano, 2011 is based on two incomplete skulls from the Cenomanian Candeleros Formation of Argentina (Rougier et al. 2011). The coding is based on the information published in the above cited paper, with an alternative interpretation of its dental formula (see section “Characters” above).

Groebertherium—*Groebertherium stipanicici* Bonaparte 1986 (= *G. novasi* Bonaparte 1986; = *Brandonia intermedia* Bonaparte 1990, syn. nov.) has been based originally on isolated upper and lower molariform teeth from the Campanian Los Alamos Formation of Argentina (Bonaparte 1986; Fig. 1a). The species is also reported from the Campanian Allen Formation of Argentina (Rougier et al. 2009a). Rougier et al. (2009a, p. 229), synonymizing *G. stipanicici* and *G. novasi*, have chosen “the type of *G. novasi* (MACN-RN 19) as the neotype of *G. stipanicici*” and declared that the “two species become objective synonyms.” However, a subjective change of the holotype does not make taxa objective synonyms. The designation of a neotype for *G. stipanicici* by Rougier et al. (2009a) is not congruent with the criteria of ICZN Article 75 and is not followed here.

Brandonia intermedia Bonaparte 1990 is based on isolated upper molariform teeth from the Los Alamos Formation that are narrower labiolingually and have a longer anterior cingulum compared with the teeth of *Groebertherium*. These teeth are considered here as more anterior molariform teeth of *Groebertherium*.

The coding of *Groebertherium* is based on casts and published specimens from the Los Alamos Formation.

Leonardus—*Leonardus cuspidatus* Bonaparte 1990 (= *Barberenia araujoae* Bonaparte 1990, syn. nov.; = *Casamiquelia rionegrina* Bonaparte 1990, syn. nov.) is known by the holotype maxilla (MACN-RN 172) containing four molariform teeth and a referred dentary fragment with two molariform teeth from the Los Alamos Formation (Bonaparte 1990; Chornogubsky 2011; Fig. 1b). Here, we accept the original interpretation of the holotype maxilla as a left bone (Bonaparte 1990; Chornogubsky 2011 contra Páez Arango 2008). The holotype of *Casamiquelia rionegrina* Bonaparte 1990 (MACN-RN 163; Fig. 1b), interpreted as a right upper molariform tooth, may represent the left ultimate molariform tooth of *Leonardus* (missing on MACN-RN 172). Two other teeth referred to *Casamiquelia* (MACN-RN 1032 and 1033; Bonaparte 2002, Figs. 2 and 3) may be as well the last molariforms of *Leonardus*.

Bonaparte (1990, Fig. 8) referred a dentary fragment (MACN-RN 170) with two molariform teeth interpreted as m3 and m5 to *Barberenia araujoae*. However, as evident from the published figure and casts, the two teeth are preserved in dentary fragments which have no contact. It is more likely that “m5” is a tooth placed more anterior than “m3.” The morphology of the former tooth agrees with the description of p2 in *Coloniatherium* (Rougier et al. 2009b). The other tooth may be the first molariform tooth. By size and general appearance, it is similar to the lower molars of *Leonardus*, and MACN-RN 170 is referred here to that taxon (Fig. 1b).

A lower molariform tooth with mesiodistally compressed roots from the Allen Formation referred to cf. *Brandonia* sp. (Rougier et al. 2009a, Fig. 6) could be a first molariform of a taxon similar to *Leonardus*. It differs from the specimen from the Los Alamos Formation by a postcingulid with a talonid-like extension. A possible ultimate upper premolar from the Allen Formation, the holotype of *Barberenia allenensis* Rougier et al. 2009a (Rougier et al. 2009a, Fig. 7), may also belong to a *Leonardus*-like taxon.

The upper molariform teeth of *Barberenia araujoae* Bonaparte 1990 from the Los Alamos Formation have been considered as upper permanent premolars of *Groebertherium* or *Brandonia* (Bonaparte 2002; Pascual and Ortiz-Jaureguizar 2007; Rougier et al. 2011). Here, these teeth are interpreted as upper deciduous premolars (see above). They are more referable to *Leonardus cuspidatus* based on size (Fig. 1b).

The coding of *Leonardus* is based on casts and published specimens from the Los Alamos Formation.

Reigitherium—*Reigitherium bunodontum* Bonaparte 1990 is a poorly known taxon based on the holotype lower molar

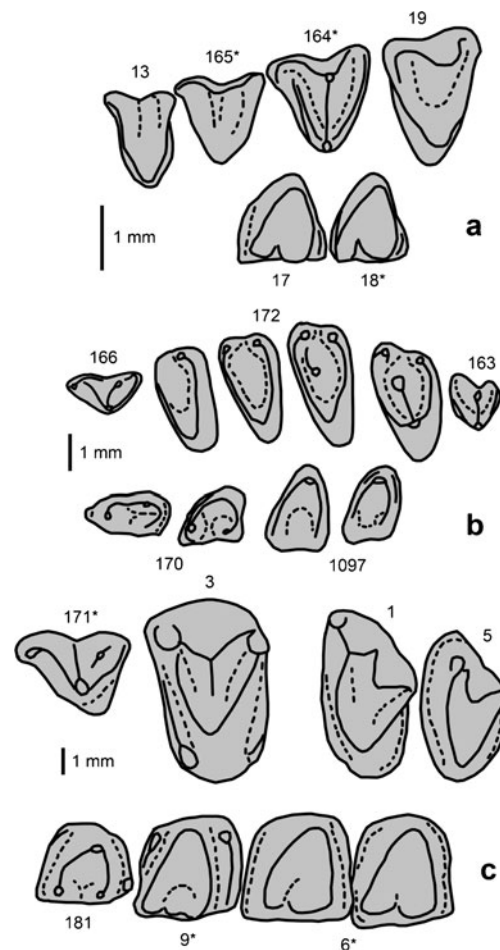
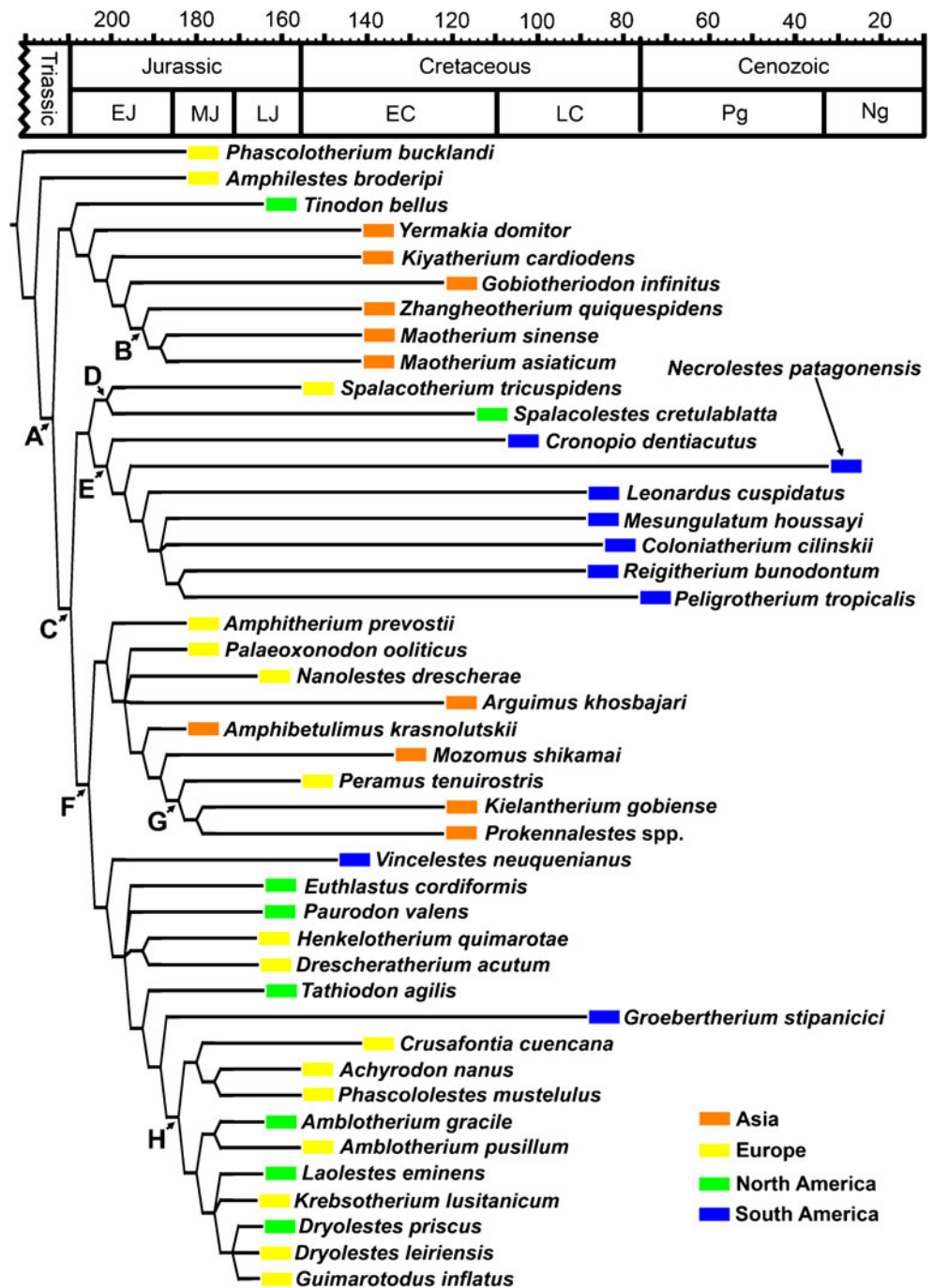


Fig. 1 Interpretation of mostly isolated teeth from the Campanian Los Alamos Formation, Argentina (upper teeth are left, lower teeth are right, and anterior side is to the left; reversed images are marked by asterisk; numbers at teeth correspond to the specimens numbers in MACN-RN collection). **a** *Groebertherium stipanicici* Bonaparte 1986: possible M 1 (MACN-RN 13, holotype), upper anterior molars (MACN-RN 165 and 164), upper posterior molar (MACN-RN 19, holotype of *Groebertherium novasi* Bonaparte 1986), and lower molars (MACN-RN 17 and 18); **b** *Leonardus cuspidatus* Bonaparte 1990: DPX, possible upper ultimate deciduous premolar (MACN-RN 166, holotype of *Barberenia araujoae* Bonaparte 1990), upper molars (MACN-RN 172), upper ultimate molar (MACN-RN 163, holotype of *Casamiquelia rionegrina* Bonaparte 1990), lower penultimate premolar and possible m1 (MACN-RN 170, holotype), and lower molars (MACN-RN 1097); **c** *Mesungulatum housayi* Bonaparte and Soria 1985: DPX, possible upper ultimate deciduous premolar (MACN-RN 171, holotype of *Quirogatherium major* Bonaparte 1990), upper anterior molar (MACN-RN 3), upper penultimate molar (MACN-RN 1, holotype), upper ultimate molar (MACN-RN 5), possible m1 (MACN-RN 181), lower anterior molar (MACN-RN 9), and lower posterior molars (MACN-RN 6). Drawings are based on published illustrations (Bonaparte 1986, 1992, 2002; Chornogubsky 2011) and casts

from the Los Alamos Formation and referred dentary fragment with a premolar and two molars from the Campanian La Colonia Formation of Argentina (Bonaparte 1990; Pascual et al. 2000). The coding is based on the literature and casts from the STIPB collection. Also, some character

Fig. 2 Strict consensus tree of five most parsimonious trees produced by TNT ratchet algorithm using the data set presented in Supplementary Information. The following monophyletic groups can be recognized: Trechnotheria **A.** Zhangheotheriidae **B.** Alethinotheria **C.** Spalacotheriidae **D.** Meridiolestida **E.** Cladotheria **F.** Zatheria **G.** and Dryolestidae **H.** *EC* Early Cretaceous, *EJ* Early Jurassic, *LC* Late Cretaceous, *LJ* Late Jurassic, *MJ* Middle Jurassic, *Ng* Neogene, *Pg* Paleogene



states for this taxon are repeated from the data matrix in Rougier et al. (2011, 2012).

Mesungulatum—*Mesungulatum houssayi* Bonaparte and Soria 1985 (= *Quirogatherium major* Bonaparte 1990) is known from isolated upper and lower molariform teeth and one dentary fragment with two molars from the Los Alamitos Formation (Bonaparte 1986, 1990; Fig. 1c). A similar species, *M. lamarquensis* Rougier et al. 2009a, is represented by isolated upper and lower teeth from the Allen Formation (Rougier et al. 2009a).

The holotype of *Quirogatherium major* Bonaparte 1990, originally described as an upper molar of a symmetrodontan mammal (Bonaparte 1990), is considered here the ultimate deciduous premolar of *Mesungulatum* (Fig. 1c). Rougier et al. (2011) interpreted this tooth as a permanent premolar, which is too small to belong to *Mesungulatum*. It is indeed too small for the ultimate permanent premolar of *Mesungulatum* but seems to be of the right size for a deciduous premolar.

The coding of *Mesungulatum* is based on casts and published specimens from the Los Alamitos Formation.

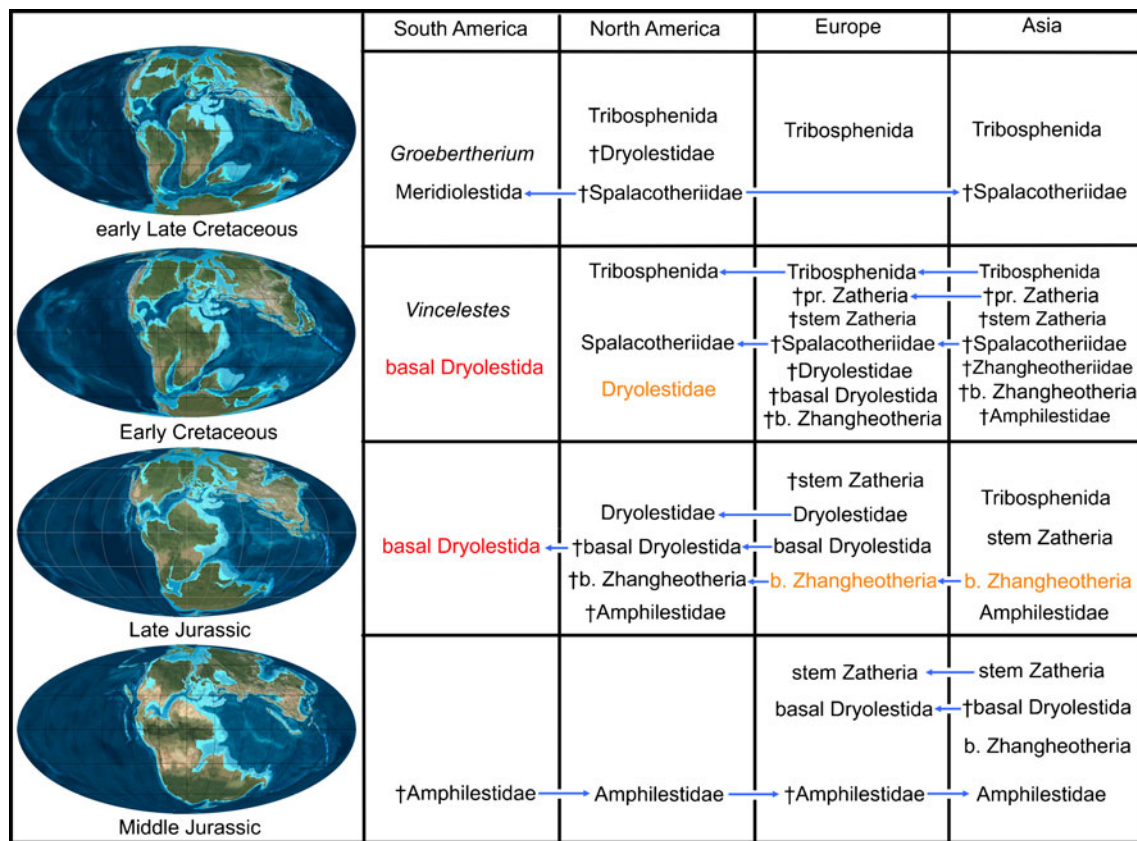


Fig. 3 Pattern of dispersals (designated by blue horizontal arrows) of Amphilestidae and Trechnotheria reconstructed from the phylogenetic hypothesis present here. The taxa in orange are currently unknown by fossils for the considered time interval and continent, but their presence is implied by presence in the previous and subsequent time intervals or

adjacent continents. The presence of basal Dryolestida (in red) in the Late Jurassic and Early Cretaceous is hypothetically reconstructed. The locally or globally extinct taxa are marked by dagger. *b.* basal, *pr.* pretribosphenic. The paleogeographic maps are from Ron Blakey, Colorado Plateau Geosystems, Inc. (<http://cpgeosystems.com/paleomaps.html>)

Coloniatherium—*Coloniatherium cilinskii* Rougier et al. 2009b is represented by abundant isolated teeth, jaw fragments, and petrosals from the Campanian-Maastrichtian La Colonia Formation of Argentina; only a few specimens from this collection have been described so far (Rougier et al. 2009b). The coding is based on the information published in Rougier et al. (2009b).

Peligrotherium—*Peligrotherium tropicalis* Bonaparte, Van Valen and Kramartz, 1993, the Cenozoic survivor of Meridiolestida, is known by reasonably complete materials, including one skull, from the early Paleocene Salamanca Formation of Argentina (Bonaparte et al. 1993; Gelfo and Pascual 2001; Páez Arango 2008). The coding is based on the above cited publications.

Necrolestes—*Necrolestes patagonensis* Ameghino 1891 is a bizarre mammal from the early Miocene Santa Cruz beds of Argentina which phylogenetic relationships were enigmatic for a long time and which was recently found to be a member of Meridiolestida (see Rougier et al. 2012;

Chimento et al. *in press* and references therein). The coding of *Necrolestes* followed that in Rougier et al. (2012).

Parsimony analysis

The characters used for the phylogenetic analysis are taken mostly from the data matrices provided by Rougier et al. (2011, 2012), which includes 304 and 317 characters, respectively. The latter matrices include a wide range of groups (cynodonts, stem mammals, docodontans, eutriconodontans, hennosferids, ausktribosphenids, monotremes, symmetrodontans, dryolestidans, meridiolestidans, stem zatherians, eutherians, and metatherians). The majority of these groups is represented by a few key taxa. We are focusing on the interrelationships of basal trechnotherians and cladotherians, and our data matrix includes almost every known taxon from these groups but a lower number of characters. We did not include those characters from the Rougier et al. (2011, 2012) data matrices which do not vary within our sample of terminal taxa, but we added some new

characters (see [Supplementary Information](#) for the full list of characters).

The data matrix consisting of 44 taxa and 137 characters has been analyzed by a tree-search maximum parsimony ratchet algorithm using the program NONA version 2.0 (Goloboff 1999; 1000 repetitions) and TNT version 1.1 (Goloboff et al. 2003) run with Winclada version 1.00.08 interface (Nixon 1999). All characters are phylogenetically informative and non-additive. The NONA analysis produced 13 most parsimonious trees with a length of 415 steps, a consistency index of 0.42, and a retention index of 0.76. The TNT analysis produced five most parsimonious trees with the same tree length and the same indices. Both strict consensus trees are present in the [Supplementary Information](#).

Although the TNT strict consensus tree is based on fewer most parsimonious trees, it is less resolved compared to the NONA strict consensus tree. The latter differs by two nodes (*Mesungulatum* + *Coloniatherium* and *Dryolestes priscus* + *D. leiriensis*) that collapsed in the TNT consensus tree. The strict consensus of the TNT trees is accepted here as the current phylogenetic hypothesis (Fig. 2). The bootstrap values (10,000 replications) were calculated in NONA, and the Bremer support values were found by TNT (see [Supplementary Information](#)). The analysis reveals the following most important monophyletic groups (Fig. 2).

Trechnotheria. This clade was proposed by McKenna (1975) as sister taxon to Kuehneotheria and originally included Symmetrodonta and Cladotheria. Luo et al. (2002) defined Trechnotheria as a node-based taxon including the most common ancestor of *Zhangheotherium* (considered as spalacotheriid at that time) and crown Theria. Here, Trechnotheria is defined as a node-based taxon including *Zhangheotherium quiquecuspidens* Hu et al. 1997, *Mus musculus* Linnaeus 1758, their most recent common ancestor, and all of their descendants.

Zhangheotheria, new clade (Zhangheotheriidae + basal zhangheotheriids). A stem-based taxon comprising all taxa that are closer to *Maothierium asiaticum* Ji et al. 2009 than to *Spalacotherium tricuspidens* Owen 1854. This clade includes “obtuse-angled” symmetrodontans (basal zhangheotherians or paraphyletic “Tinodontidae”) and “acute-angled” zhangheotheriids.

Alethinotheria, new clade (from Greek ἀλήθεια, the truth, and θηρίον, wild beast) is a node-based taxon including *Spalacotherium tricuspidens* Owen 1854, *Mus musculus* Linnaeus 1758, their most recent common ancestor, and all of their descendants. This is the best supported clade in the analysis (bootstrap 95 %, Bremer 6).

Meridiolestida + Spalacotheriidae. A stem-based taxon comprising all taxa that are closer to *Peligrotherium tropicalis* Bonaparte, Van Valen and Kramartz, 1993 than to *Dryolestes priscus* Marsh 1878 or *Peramus tenuirostris* Owen 1871.

Cladotheria. The sister taxon to the previous clade established originally to encompass Dryolestoida and Zatheria (McKenna 1975; Prothero 1981). The clade was defined as a node-based taxon including “the common ancestor of dryolestids and living therians, plus all its descendants” (Luo et al. 2002, p. 28). Here, Cladotheria is defined as a stem-based taxon comprising all taxa that are closer to *Mus musculus* Linnaeus 1758 than to *Spalacotherium tricuspidens* Owen 1854.

Zatheria + stem zatherians. A stem-based taxon comprising all taxa that are closer to *Mus musculus* Linnaeus 1758 than to *Dryolestes priscus* Marsh 1878. This clade is similar in content with Prototribosphenida, a node-based taxon including the common ancestor of *Vincelestes* and living therians (Rougier et al. 1996; Luo et al. 2002). However, in our analysis, *Vincelestes* appears as a basal dryolestidan rather than pretribosphenic taxon.

Zatheria. The clade including Peramura and Tribosphenida (McKenna 1975). More specifically, it was defined as the node-based taxon comprising “the common ancestor of *Peramus* and living marsupials and placentals, plus all of its descendants” (Luo et al. 2002). A more formal definition for this clade would be the node-based taxon including *Mus musculus* Linnaeus 1758, *Peramus tenuirostris* Owen 1871, their most recent common ancestor, and all of their descendants. The clade can be diagnosed by the presence of a lingual cingulum (or protocone) on the upper molars, a metacone and paracone that are positioned approximately at the same level, and a cusp-like metacone comparable in size to the paracone. The lower dental characters related to the development of a multicusped and basined talonid were steadily developed in stem zatherians and possibly were not directly correlated with the development of the protocone on the upper molars.

Dryolestida (Dryolestidae + basal dryolestidans). McKenna (1975) and Prothero (1981) used Dryolestoida Butler 1939 for a taxon incorporating *Amphitherium*, Paurodontidae, and Dryolestidae. This phylogenetic grouping is not supported by our analysis, where *Amphitherium* is a stem zatherian. “Paurodontidae” is paraphyletic relative to Dryolestidae. We use the name Dryolestida Prothero 1981 for the clade consisting of Dryolestidae and basal dryolestidans. This clade is defined as a stem-based taxon comprising all taxa that are closer to *Dryolestes priscus* Marsh 1878 than to *Peramus tenuirostris* Owen 1871.

Henkelotheriidae. Henkelotheriidae Krebs 1991 was proposed for *Henkelotherium*, *Pelicipsis*, and *Tathiodon* (Krebs 1991). Krebs (1991) considered *Pelicipsis* and *Tathiodon*, representing the upper and lower dentitions, respectively, of one taxon (see also Martin 1999). Later, *Drescheratherium* was added to the Henkelotheriidae (Krebs 1998). Our analysis confirms grouping of *Henkelotherium* and *Drescheratherium* for which Henkelotheriidae is a valid name. *Pelicipsis* is considered here as a synonym of *Paurodon*, and both

Paurodon and *Tathiodon* are basal dryolestidans according to the present analysis, which explains their similarity with Henkelotheriidae. There is no clade containing *Paurodon* excluding Dryolestidae, and therefore, the long-held concept of “Paurodontia” Marsh 1887 is not valid.

Dryolestidae. Dryolestidae Marsh, 1879b is an apomorphy-based taxon including all members of the Dryolestida which have unequal roots at the lower molars. Other synapomorphies for this clade are unilateral hypsodonty of the lower molars and unequal height of the alveolar borders of the dentary from labial and lingual sides. Most dryolestids and *Tathiodon* also lack a precingulid. *Tathiodon* and *Groebertherium* are found to be the successive sister taxa of the Dryolestidae. But *Tathiodon* and *Groebertherium* have equal roots at the lower molars, and thus, they are not included in the Dryolestidae. Among Dryolestidae, there are three groups of taxa more derived than *Groebertherium*:

1. *Crusafontia* + (*Achyrodon* + *Phascolestes*). This group is diagnosed by four unambiguous synapomorphies. The grouping of *Achyrodon* and *Phascolestes* is also diagnosed by three unambiguous synapomorphies. This clade, comprising Early Cretaceous taxa, is endemic to Europe. Kurtodontinae Osborn 1888 is a valid family group name for this clade. The remaining taxa could be classified within the subfamily Dryolestinae Marsh, 1879.
2. *Amblotherium* (*A. gracile* + *A. pusillum*). The genus is diagnosed by three unambiguous synapomorphies.
3. Remaining genera of Dryolestidae, diagnosed by five unambiguous synapomorphies.

Discussion

The phylogenetic hypothesis presented here (Fig. 2) implies the biogeographic scenario outlined below (see also Fig. 3). The Late Triassic–Early Jurassic mammal faunas were dominated by stem mammals, non-multituberculate allotherians, and kuehneotheriids. The Middle Jurassic witnessed the second major mammalian diversification which gave rise to multituberculates, docodontans, eutriconodontans, and trechnotherians, the groups that dominated mammalian evolution during the remaining Mesozoic (Kielan-Jaworowska et al. 2004; Luo 2007a, b). The growing evidence from the Middle Jurassic mammal fossils in Asia suggests that this diversification was rooted on that continent (Averianov et al. 2010b; Martin and Averianov 2010; Martin et al. 2010 and unpublished materials).

The currently oldest record of Amphilestidae, the likely sister taxon for the Trechnotheria, is known from late Early Jurassic of South America (Gaetano and Rougier 2012). Several amphilestid-like taxa are known also from strata of similar age (Pliensbachian) in North America (Montellano

et al. 2008). In both Europe and Asia, amphilestids are known in the Middle Jurassic (Bathonian) (Kielan-Jaworowska et al. 2004; Martin and Averianov 2010). In South America and Europe, amphilestids became locally extinct. In North America and Asia, they persisted up to the Late Jurassic and Early Cretaceous, respectively. Trechnotherians originated from an amphilestid-like stock most likely in Asia.

Basal zhangheotherians (“Tinodontidae” in previous usage) were the first trechnotherians. Their Middle Jurassic records in Asia are poor for the moment and represented by a single molar fragment (Martin and Averianov 2010). In the Late Jurassic of Asia, this group is currently unknown. But its diversification in the Early Cretaceous of Asia suggests that that continent was its place of origin. Their putative Late Jurassic representatives spread through Europe to North America where they were never dominant (*Tinodon* is one of the rarest mammals in the Morrison fauna; Simpson 1929). It is not clear if the European Early Cretaceous “tinodontids” (Ensom and Sigogneau-Russell 2000) were autochthonous or spread from Asia or North America.

The next trechnotherian branch, Spalacotheriidae, was most common and diverse in the Early Cretaceous of East Asia, its most probable place of origin (Averianov 2002; Tsubamoto et al. 2004; Sweetman 2008). In the Early Cretaceous, spalacotheriids dispersed to Europe and North America. In Europe and Asia, this group became locally extinct in the Early Cretaceous. But in North America, its more derived clade (Spalacolestinae) underwent a secondary diversification and persisted until the late Santonian (Fox 1976; Kielan-Jaworowska et al. 2004). In the beginning of the Late Cretaceous (Turonian), this group reinvaded for a short time the coastal plains of Asia (Averianov and Archibald 2003; Archibald and Averianov 2005). Somewhat earlier (Cenomanian or latest Early Cretaceous), Spalacolestinae dispersed to South America, where, in isolation, their descendants (Meridiolestida) underwent a new adaptive radiation.

After branching off of the spalacotheriids and their derivatives, trechnotherians split into two major branches, Zatheria (plus stem representatives) and Dryolestida. The oldest dryolestidans are known from the Middle Jurassic of both Asia and Europe (Freeman 1979; Lopatin and Averianov 2006c; Martin and Averianov 2010), with Asia likely as the place of their origin. Notably, in Asia, dryolestidans are not known after the Middle Jurassic. They vanished from that continent apparently because of competition with more derived pretribosphenic and tribosphenic mammals. In the Late Jurassic, basal dryolestidans (“Paurodontidae”) and dryolestids spread from Europe to North America, where the latter group was dominant in mammal faunas. Possibly in the Late Jurassic, basal dryolestidans reached South America, where they gave rise to *Vincelestes* in the Early Cretaceous. *Vincelestes* previously was universally considered as a

pretribosphenic mammal (see Macrini et al. 2007 and references therein). However, it has no functional protocone and basined multicusped talonid, and dentally, this taxon is very similar to *Paurodon*. In our analysis, it is a basal member of Dryolestida (Fig. 2). Pretribosphenic mammals never have been recorded in North America, and the presence of *Vincelestes* in South America would be difficult to explain, if considered as a pretribosphenic mammal. The stock of basal dryolestidans persisted in South America through the Late Cretaceous, where this group is represented by the Campanian *Groebertherium*, a non-dryolestid dryolestoidan (“paurodontid” in former usage).

The oldest stem zatherians (“Amphitheriidae”) are known from the Middle Jurassic of Europe and Asia (Kielan-Jaworowska et al. 2004; Lopatin and Averianov 2007a; Martin and Averianov 2010). In both continents, this group is known up to the Early Cretaceous. The pretribosphenic zatherians (“Peramuridae”) are known from the Early Cretaceous of Asia and Europe. In Asia, they apparently have an older origin, as in this continent tribosphenic mammals are known since the Middle or, more conservatively, Late Jurassic (Luo et al. 2011). Interestingly, neither stem zatherians nor pretribosphenic zatherians were found in North America, which reflects their real absence in North American faunas. Tribosphenic mammals invaded North America somewhere in the late Early Cretaceous.

Our biogeographic scenario implies that trechontherians and the clades included therein subsequently originated in Asia and spread mostly in one direction, from East to West. The migration was delayed in the Late Jurassic of North America and Europe, which gave opportunity for the modest diversification of dryolestidans. The first two waves arrived in time to reach South America before isolation of that continent, where they persisted (*Vincelestes* and *Groebertherium*, derivatives of basal dryolestidans) or even underwent a secondary radiation (Meridiolestida, derivatives of Spalacotheriidae) in the Cretaceous. The decline of meridiolestids in South America was likely caused by competition with metatherian and eutherian tribosphenic mammals, which arrived on that continent shortly before the K-T boundary. Only one highly specialized meridiolestidan taxon (*Necrolestes*) persisted till the early Miocene.

One of the unexpected features of the craniodental morphology of *Cronopio* is a combination of highly specialized characters with very primitive ones (Rougier et al. 2011). One of the specializations of Meridiolestida is the coiling of the cochlea that occurred independently from therian mammals. In *Peligrotherium*, the cochlea is coiled to nearly 360° (Páez Arango 2005, p. 203), and in *Coloniatherium*, it has at least one and half turns (Rougier et al. 2009b, p. 203). Rougier et al. (2011, character 223) coded *Reigitherium* as having the cochlea coiled to about 360°, but no information supporting this coding was provided. In *Cronopio*, the extent of cochlea

coiling is unknown (Rougier et al. 2011). In the dryolestidans *Vincelestes*, *Henkelotherium*, and *Dryolestes*, the cochlea is coiled up to 270° (Ruf et al. 2009; Luo et al. 2012).

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