# The Miocene mammal *Necrolestes* demonstrates the survival of a Mesozoic nontherian lineage into the late Cenozoic of South America

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Edited by Richard L. Cifelli, University of Oklahoma, Norman, OK, and accepted by the Editorial Board October 18, 2012 (received for review July 27, 2012)

**The early Miocene mammal *Necrolestes patagonensis* from Patagonia, Argentina, was described in 1891 as the only known extinct placental "insectivore" from South America (SA). Since then, and despite the discovery of additional well-preserved material, the systematic status of *Necrolestes* has remained in flux, with earlier studies leaning toward placental affinities and more recent ones endorsing either therian or specifically metatherian relationships. We have further prepared the best-preserved specimens of *Necrolestes* and compared them with newly discovered nontribosphenic Mesozoic mammals from Argentina; based on this, we conclude that *Necrolestes* is related neither to marsupials nor placentals but is a late-surviving member of the recently recognized nontherian clade Meridiolestida, which is currently known only from SA. This conclusion is supported by a morphological phylogenetic analysis that includes a broad sampling of therian and nontherian taxa and that places *Necrolestes* within Meridiolestida. Thus, *Necrolestes* is a remnant of the highly endemic Mesozoic fauna of nontribosphenic mammals in SA and extends the known record of meridiolestidans by almost 45 million years. Together with other likely relictual mammals from earlier in the Cenozoic of SA and Antarctica, *Necrolestes* demonstrates the ecological diversity of mammals and the mosaic pattern of fauna replacement in SA during the Cenozoic. In contrast to northern continents, the Cenozoic faunal history of SA was characterized by a long period of interaction between endemic mammalian lineages of Mesozoic origin and metatherian and eutherian lineages that probably dispersed to SA during the latest Cretaceous or earliest Paleocene.**

anatomy | paleontology | vertebrate | fossorial

Patterson (1) believed that the 16-My-old (2) *Necrolestes* from the early Miocene of Patagonia is "a form represented by such excellent material...actually among the better known fossil mammals—should reveal enough...to permit at least its infraclass affinities to be firmly known." Nevertheless, the relationships of this taxon have remained enigmatic, with proposed affinities including African golden moles (3, 4), palaeanodonts (5), and borhyaenoid metatherians (1). Our interest in *Necrolestes* was raised by the recent publications by Asher et al. (6) and Ladevèze et al. (7), the former coming to no firm taxonomic conclusion other than that *Necrolestes* is a therian and the latter supporting metatherian affinities. Goin et al. (8) described a new species of *Necrolestes*, *N. mirabilis*, based mostly on a fragmentary jaw that included a tooth in eruption, which represents the first evidence of tooth replacement in this taxon; this material unambiguously demonstrates that the dental formula of *Necrolestes* includes three molars, two fully molarized premolars, and one nonmolariform premolar, in contrast to the four molars and three nonmolariform premolars seen in most metatherians. Goin et al. (8) concluded that *Necrolestes* exhibits some similarities with eutherians but has no features that unequivocally support metatherian affinities; they even considered possible affinities with extinct lineages of Theria not referable to either Metatheria or Eutheria, but did not discuss the evidence for this interpretation, nor did they identify the specific therian lineages they considered to be potential relatives of *Necrolestes*. Starting in 2007, we oversaw additional preparation of *Necrolestes* specimens that comprise the best-preserved material currently available, including skulls, jaws, and some isolated postcranial bones; as a result, many phylogenetically significant features have been revealed for the first time. At the same time, parallel research conducted on nontherian mammals from the Mesozoic of Patagonia (e.g., ref. 9), in particular, the first meridiolestidan cranial remains (10), revealed striking similarities with *Necrolestes* and brought to mind the inspired comment by Van Valen (11): "It is even conceivable that the enigmatic Miocene genus *Necrolestes*, usually thought to be a marsupial, is a late surviving Gondwantherian pantothere." We focus here on the evidence supporting the conclusion that *Necrolestes* is a nontherian and reinterpret this taxon within the context of the fast growing sample of nontherian mammals from the Mesozoic and Cenozoic of South America (SA).

## Systematic Paleontology

We follow a crown-group definition of Theria here, namely that it comprises the last common ancestor of placentals and marsupials and all of its descendants. Similarly, we restrict Marsupialia and Placentalia to their respective crown-groups and use Metatheria to refer to Marsupialia plus all fossil taxa closer to Marsupialia than to Placentalia and Eutheria to refer to Placentalia plus all fossil taxa closer to Placentalia than to Marsupialia.

The number and morphology of the dentition of *Necrolestes* are well known (4, 6). However, the homologies of the postcanine teeth have been difficult to assess until recently. The discovery that the two more mesial molariforms in *Necrolestes* are in fact premolars (8) leads to a reinterpretation of the tooth formula that renders metatherian affinities unlikely (8). The dentition in *Necrolestes* [I5/i4, C1/c1, P3/p3, M3/m3 (incisors, canines, premolars, molars)] is relatively simple (Fig. 1; Figs. S1 and S2), with robust upper and lower incisors, double-rooted canines, and a tricuspid first premolar followed by two fully molarized premolars. The cusps of the three lower molars form an acute triangle, without any traces of talonid or cingula, whereas the three upper molars are dominated by two major cusps but are otherwise similar to the lower molars in occlusal outline. Surprisingly,

Author contributions: G.W.R. designed research; G.W.R., J.R.W., R.M.D.B., and S.A. performed research; G.W.R., J.R.W., R.M.D.B., and S.A. analyzed data; and G.W.R., J.R.W., and R.M.D.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. R.L.C. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1212997109/-/DCSupplemental.

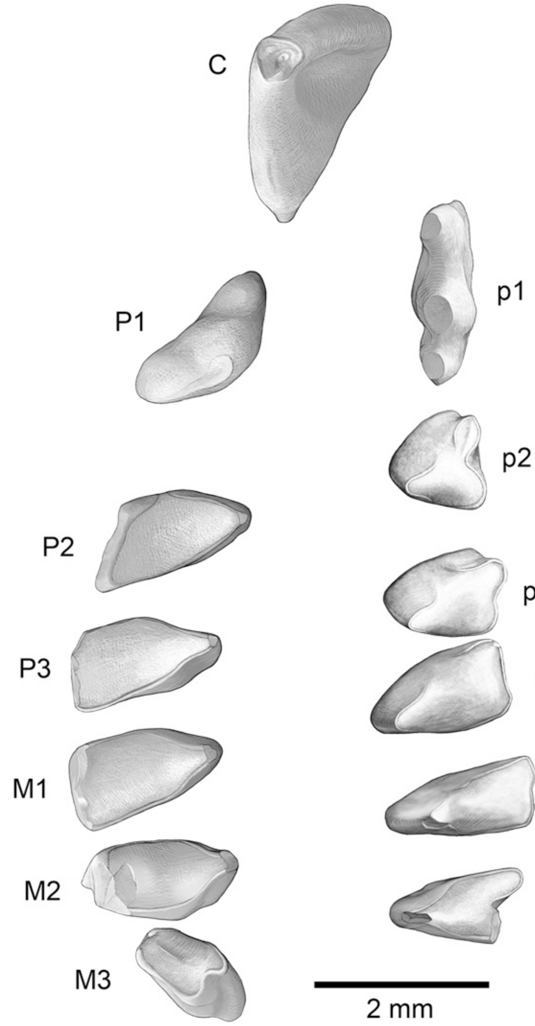


**Fig. 1.** Composite illustration of the partial upper and lower dentitions (occlusal view, lingual toward the midline) of *N. patagonensis* from the early Miocene of Argentina, ∼16 MYA (2), based on YPM PU 15384 and 15699. C, upper canine; P/p, premolar; M/m, molar; YPM PU, Yale Peabody Museum Princeton Collection.

the first upper and lower premolars are double rooted and the following five molariform elements are single rooted, a condition shared only with the recently described meridiolestidan mammal *Cronopio* (10), a nontherian from the early Late Cretaceous of Argentina (Fig. S1). Taken at face value, the molar cusp and overall dental morphology of *Necrolestes* can be homologized a priori with that of zalambdodont placentals or some dentally specialized metatherians (both of which represent modifications from an ancestrally tribosphenic molar pattern) or, alternatively, a variety of nontherian, pretribosphenic forms, including symmetrodonts, dryolestoids, and meridiolestidans. However, the specific hypothesis of cusp homology would differ depending on the taxon used in the comparison: in the absence of other evidence, the major lingual cusp of the upper molars in *Necrolestes* could be interpreted as homologous with either the paracone (e.g., dryolestoids, meridiolestidans, and most zalambdodont placentals) or the metacone [e.g., the zalambdodont marsupial *Notoryctes* (12)], with Asher et al. (6) preferring the latter interpretation.

With the exception of the root pattern in the premolars and molars shared with *Cronopio*, no other dental feature of *Necrolestes* is unequivocally synapomorphic with a single taxon or clade, rendering it difficult to choose between these alternative interpretations when the dental evidence is considered in isolation. Interpretation of the dental morphology of *Necrolestes*, therefore, depends on a broader comparative framework. Newly revealed features of the cranial morphology of *Necrolestes* are described below and indicate that *Necrolestes* is not a member of Theria; instead, the proper and necessary comparative sampling must focus on nontherian mammals, in particular the nontribosphenic dryolestoids and meridiolestidans: Class Mammalia Linnaeus, 1758; Clade Cladotheria McKenna, 1975; Order Meridiolestida Rougier et al., 2011; *Necrolestes patagonensis* Ameghino, 1891 (Figs. 1–3 and 4*C*).

**Revised Diagnosis.** The revised diagnosis is based primarily on restudy of three specimens originally collected more than 100 y ago by the Princeton Patagonian Expeditions (4): Yale Peabody Museum Princeton Collection (YPM PU) 15065, 15384, and 15699. Meridiolestidan shares the following with *Cronopio*: presence of a double-rooted anterior premolar followed by single-rooted molars; a long, relatively horizontal condylar process; an angular process with some medial inflection (but that is nevertheless not shelf-like, unlike the medially inflected angular process independently acquired by metatherians); a long rostrum; and a

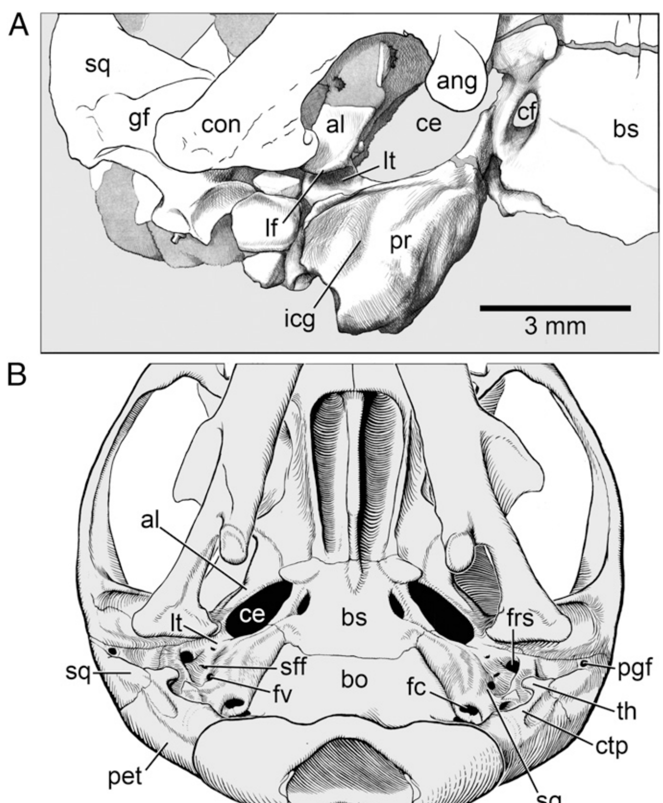


**Fig. 2.** Basicranium of *N. patagonensis* in ventral view. (*A*) Ventral view of YPM PU 15699 showing partial right petrosal and lower jaw in articulation; missing is the basioccipital and posterior parts of the petrosal and squamosal, as well as a portion of the lateral braincase sidewall. (*B*) Reconstruction of the basicranium and lower jaw based on YPM PU 15065, 15384, and 15699 (Fig. S3). al, anterior lamina of petrosal; ang, angular process; bo, basioccipital; bs, basisphenoid; ce, cavum epiptericum; cf, carotid foramen; con, condylar process; ctp, caudal tympanic process of petrosal; fc, fenestra cochleae; frs, foramen for ramus superior; fv, fenestra vestibuli; gf, glenoid fossa; icg, internal carotid groove; lf, lateral flange; lt, lateral trough; pet, petrosal; pgf, postglenoid foramen; pr, promontorium of petrosal; sff, secondary facial foramen; sg, stapedial artery groove; sq, squamosal; th, tympanohyal.

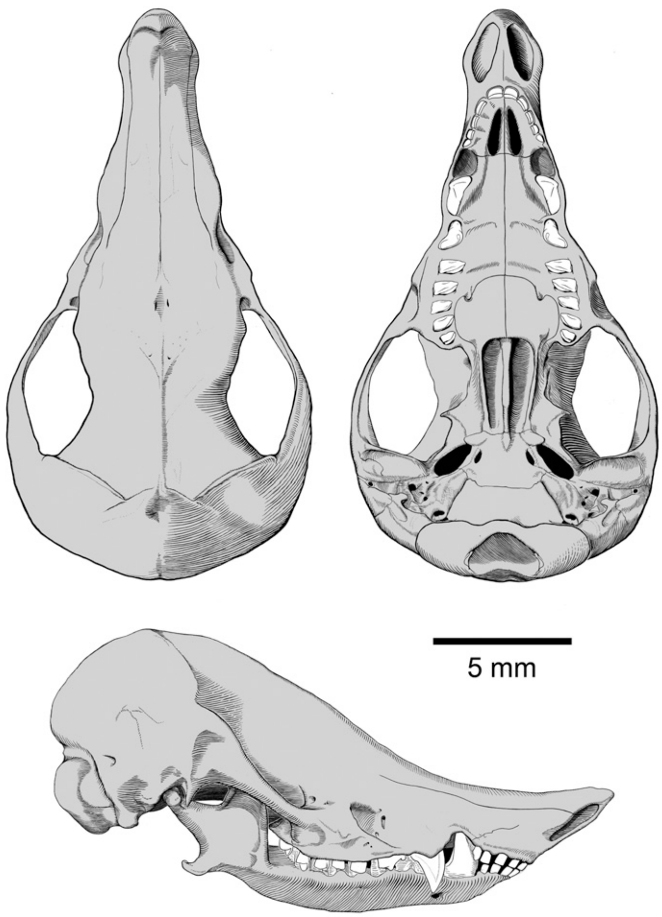


**Fig. 3.** Reconstruction of the skull of *N. patagonensis* in dorsal, ventral, and lateral views.

globular braincase (Fig. 3; Fig. S2). It shares with *Leonardus* the presence of two molarized premolars and the complete absence of talonids or other accessory cusps. *Necrolestes*, *Cronopio*, and *Leonardus* share a curved postcanine dental arcade that narrows posteriorly (Figs. 1 and 3; Fig. S1). *Necrolestes* and *Cronopio* share very tall molar crowns, no recognizable distinction between molar crowns and roots, and enamel extending deep into the molar alveoli (hypsodonty). *Necrolestes* differs from other meridiolestidans by the presence of massive subtriangular canines, a simple tricuspid (triangular) molar pattern, the presence of a characteristic upturned rostrum, and a prenasal process of the premaxilla (Figs. 1 and 3; Fig. S2).

**Anatomical Information.** The mammalian basicranium, the petrosal bone in particular, has been an important source of characters in phylogenetic analyses of extinct and extant mammals, providing features that help distinguish many higher-level clades (13, 14). The YPM PU cranial material is generally well preserved, but individual boundaries of some bones are hard to determine because they are obliterated by sutural fusion and/or masked by fractures and artifacts. Aspects of the external and internal morphology of the basicranium of the specimens of *Necrolestes* studied here were described previously (6, 7), before our repreparation. Our repreparation revealed a few partial sutures and several features hitherto unrecognized—in particular, new structures in the middle-ear region, basicranium, and sidewall of the braincase. We uncovered morphologies that are unknown in therians and are broadly considered plesiomorphic for a variety of nontherian mammals, including the living monotremes and the extinct dryolestoids and meridiolestidans, which we discuss here.

The YPM PU sample includes six petrosals and two partial skulls (Fig. 2*A*); together, these specimens allow us to make a robust reconstruction of the basicranium (Fig. 2*B*; Fig. S3). Anterolateral to the promontorium (cochlear housing) of YPM PU 15699 is a concave shelf, the lateral trough, the long axis of which is obliquely oriented (Fig. 2*A*). Forming a prominent exterior wall to the lateral trough and extending anteromedially is a thin ridge, the lateral flange. Dorsal to and seamlessly continuous with the lateral flange is the sidewall of the braincase, here formed by the anterior lamina of the petrosal. The full extent of the anterior lamina is unknown, but it is far more extensive than in any known therian. Between the promontorium, lateral trough, anterior lamina, and basisphenoid is a large, oval gap, the ventral opening of the cavum epiptericum (Fig. 2*A*). This gap probably served as the foramen for the mandibular division of the trigeminal nerve, as in the platypus *Ornithorhynchus* (15, 16). The petrosals also attest to the presence of a transpromontorial internal carotid artery (Fig. 2), a shallow notching of the rim of the fenestra vestibuli (oval window) indicating the presence of a stapedial artery (Fig. 2*B*), an opening for the ramus superior of the stapedial artery (Fig. 2*B*), and a large posttemporal canal. As reconstructed by us, the stapedial system of *Necrolestes* would be similar to that predicted to be primitive for therians, with a dominant arteria diploëtica magna in the posttemporal canal supplying the orbit and basicranium (14, 17, 18).

The shape of the fenestra vestibuli, usually reported as the stapedial ratio (19), has been shown to be more elliptical in placentals than in marsupials and essentially round in monotremes and archaic nontherian lineages. Ladevèze et al. (7) reported

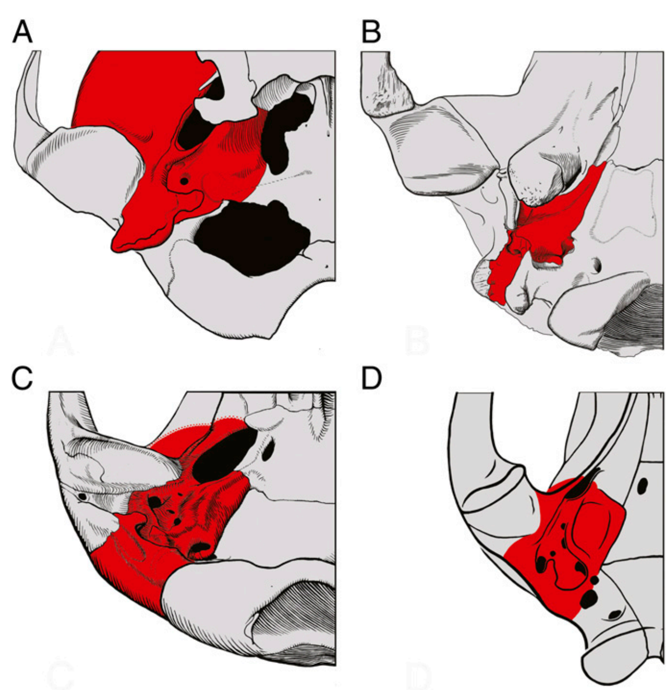


**Fig. 4.** Right basicrania in ventral view. (*A*) *Ornithorhynchus anatinus*, based on CM 50815. (*B*) *Didelphis virginiana*, based on CM 39794. (*C*) *Necrolestes patagonensis*, as reconstructed here. (*D*) *Cronopio dentiacutus*, based on MPCA 453. Petrosal contribution to basicranium and extension into the braincase sidewall are colored red. In *C* and *D*, the extent of the petrosal contribution to the sidewall is uncertain beyond the colored portion. In *B*, the North American opossum exhibits the general therian pattern with no petrosal contribution to the sidewall. CM, Carnegie Museum of Natural History; MPCA, Museo Paleontológico Carlos Ameghino.

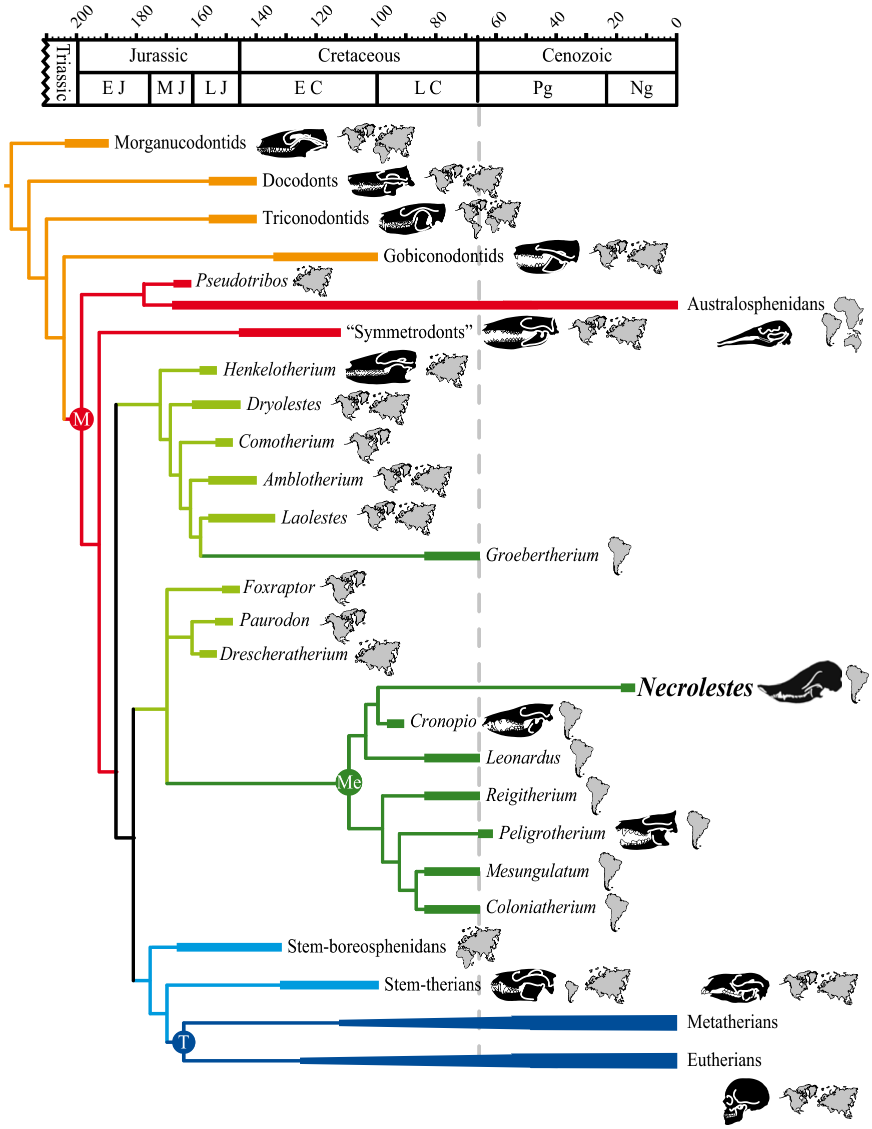


**Fig. 5.** Simplified phylogenetic tree showing *Necrolestes* as a member of the Meridiolestida, a group widely represented in SA. Some of the archaic Mesozoic lineages survived into the Cenozoic only in SA, Antactica, and Australia. This tree is the strict consensus of 36 equally most parsimonious trees (length = 1,154), resulting from parsimony analysis performed with WINCLADA/Asado Version 1.7 on a matrix of 58 taxa and 317 characters. Branch representation and resultant geologic ranges are based on the 58 taxa included in the analysis and are not intended to represent the full fossil record of the high-level groups represented by those taxa. For full consensus tree with Bremer support (Fig. S5), data matrix (Dataset S1), and character list see *SI Text*. Templeton tests provide strong support for *Necrolestes* as a nontherian mammal (*SI Text*). Dark green represents SA meridiolestidans and dryolestoids. Letters at the nodes indicate high-level clades: M, Mammalia; Me, Meridiolestida; T, Theria.

a stapedial ratio of 1.5 for *Necrolestes*, which is similar to many marsupials. However, the specimen that they studied, YPM PU 15384, has a poorly preserved fenestra vestibuli. In contrast, the fenestra vestibuli is completely preserved on the left petrosal of YPM PU 15699 and is nearly circular (Fig. S4). The cochlear duct of *Necrolestes*, with its low coiling [just over 360° (7)], resembles other nontherian mammals, such as the meridiolestidans *Coloniatherium* [close to 360° (20)] and *Peligrotherium* (21), and represents the presumed basal condition for therians (22).

To sum up, this evidence shows that the basicranium and braincase of *Necrolestes* lack therian synapomorphies and are constructed on a generalized nontherian pattern (Fig. 4). As in monotremes (Fig. 4*A*) and extinct nontherian mammals (Fig. 4*D*), *Necrolestes* (Fig. 4*C*) has a large anterior lamina, lateral flange, and lateral trough, and the ventral opening of the cavum epiptericum is large. In therians (Fig. 4*B*), the cavum epiptericum is more extensively floored (13); the anterior lamina/lateral trough are only vestigial (if present at all) in some metatherians and eutherians of the Cretaceous and wholly absent in placentals and marsupials (23). A full stapedial system is present in *Necrolestes*, including parental and tributary branches such as the arteria diploëtica magna and ramus superior. By contrast, no known fossil or extant metatherian exhibits any evidence of a groove for the stapedial artery on the petrosal (24). The fenestra vestibuli is round in *Necrolestes*, unlike the more elliptical shape seen in placentals and marsupials, and the petrosal in general is at the level of the glenoid fossa, as in most nontherian mammals (25). As a result, we conclude that *Necrolestes* is a nontherian mammal, and hence the most appropriate comparisons for evaluating the dental morphology of *Necrolestes* are with those nontherian mammals having triangulated molar cusps. Of these, the most likely candidates are meridiolestidans from SA, particularly given the unique pattern of postcanine root number shared by *Necrolestes* and the meridiolestidan *Cronopio*.

## Phylogenetic Analysis

In light of the foregoing discussion, we included *Necrolestes* in a modified and expanded version of the most recent phylogenetic analysis on dryolestoids and other nontherian mammals (10). Our analysis recovers 36 trees with a length of 1,154 steps; a simplified strict consensus of these is shown in Fig. 5. *Necrolestes* is a member of an SA clade of Cretaceous and Paleocene nontherians, Meridiolestida (10). The closest relatives of *Necrolestes* are the Late Cretaceous *Cronopio* and *Leonardus*. These three taxa have very compressed triangular teeth (Fig. S1); *Necrolestes* and *Cronopio* are the only mammals of which we are aware with double-rooted premolars and single-rooted molars. The tooth count of *Necrolestes* appears to resemble more closely that of *Leonardus* than of *Cronopio*, given that *Leonardus* also probably had fully molarized premolars (9, 10). In this regard, *Cronopio* from the early Late Cretaceous, in which only the last premolar is fully molarized, shows the primitive condition relative to *Necrolestes* and *Leonardus*.

The most notable result of this analysis is that *Necrolestes* is recovered as a late survivor of a mostly Mesozoic radiation of nontherian mammals, having survived the end Cretaceous extinction event by nearly 50 million years and extending the known record of Meridiolestida by 45 million years. The pronounced discontinuity between the Late Cretaceous and Paleocene mammalian faunas of the northern continents (26, 27) does not seem to have been the case in SA. In the middle Paleocene of the Hansen Formation of Patagonia are survivors of three Mesozoic lineages that are coeval with early members of the eutherian and metatherian lineages that would go on to dominate the later Cenozoic mammalian faunas of SA. These archaic lineages are the australosphenidan monotremes, represented by *Monotrematum sudamericanum* (28); the gondawanatherians, represented by *Sudamerica ameghinoi* (29); and the meridiolestidans, represented by *Peligrotherium tropicalis* (21, 30). More recently, the survival of the gondwanatherians into the Cenozoic has been documented in the Eocene of Antarctica (31), Peru (32), and Argentina (33). The gondwanatherian material is fragmentary and difficult to interpret, but sufficient to suggest that archaic mammalian lineages survived into the mid-Paleogene as minority components amid the highly diverse eutherian and metatherian radiations in SA and Antarctica. The ghost lineage implied by the inclusion of *Necrolestes* among meridiolestidans predicts their presence in the Eocene faunas of SA (and possibly Antarctica). It is striking that the inferred insectivorous and fossorial habits of *Necrolestes*, perhaps akin to African golden moles (1, 3, 4), have no close analog among any other Cenozoic SA mammal, suggesting that these numerically rare forms exploited marginal niches outside the ecological diversity of the SA therians. This is reminiscent of the equally relictual modern monotremes, which occupy a highly specialized ecological niche and have done so at least since the early Miocene (34), if not earlier (35).

The increasing number of Mesozoic lineages now known to have survived into the Cenozoic of SA, Australia, and most likely also in Antarctica demonstrates the integration of the nontherian mammalian faunas of the Late Cretaceous (10, 36, 37) into the eutherian and metatherian faunas that made their first appearance in the fossil record of SA during the Paleocene. These therians, which presumably reached SA as the result of dispersal from North America, radiated widely over the course of the Cenozoic. For most of the Cenozoic, SA lacked connections with other major landmasses, leading Simpson (38) to recognize the diversity of SA Cenozoic mammals as the product of "splendid isolation." A few members of that remarkable faunal succession, *Necrolestes* among them, had long roots extending into the Mesozoic, integrating two separate radiation events of the Late Cretaceous and early-mid Cenozoic (39). A more complex picture of the origin and development of the Cenozoic SA mammalian fauna is starting to emerge, showing integration of faunal elements from different biogeographic events: surviving members of Mesozoic nontherian mammalian lineages, metatherian and eutherian lineages that presumably dispersed to SA in the latest Cretaceous or early Paleocene, and platyrrhine primates and caviomorph rodents that dispersed to SA in the mid-Cenozoic are all members of the mid-Cenozoic faunas of Patagonia. However, to date, some members of the groups represented in the older Jurassic and Early Cretaceous strata of SA, such as australosphenidans (represented by Paleocene monotremes), persisted into the Cenozoic, whereas others, such as triconodonts, apparently did not (40). Based on current evidence, there appears to be a larger faunal break for SA mammals between the Jurassic and the Late Cretaceous than across the Cretaceous/Paleogene (K/Pg) boundary.

*Necrolestes* is a member of the early Miocene Santacrucian fauna, one of the best-known Cenozoic faunas from SA. If the well-preserved specimens of *Necrolestes*, collected before the beginning of the 20th century, can elude systematic identification for so long, we can be certain that plenty of surprises are to be found in the less well-known strata of the Cenozoic of SA.

**ACKNOWLEDGMENTS.** We thank Walter Joyce, Marilyn Fox, and Christopher Norris (Yale Peabody Museum) for access to specimens and Alejandro Kramarz (Museo Argentino de Ciencias Naturales). Paul Bowden and Michelle Spaulding (Carnegie Museum of Natural History) completed Figs. 1–4 and assisted with Fig. 5 and the supplemental figures, respectively. Funding for this project was provided by National Science Foundation Grants Division of Environmental Biology (DEB) 0946430, DEB 1068089 (to G.W.R.), and Assembling the Tree of Life (AToL) 0629959 (to G.W.R. and J.R.W.), the R.K. Mellon North American Mammal Research Institute (J.R.W.), ARC Discovery Early Career Researcher Award DE120100957 (to R.M.D.B.), and the Jurassic Foundation (S.A.).

1. Patterson B (1958) Affinities of the Patagonian fossil mammal *Necrolestes*. *Breviora Mus Comp Zool* 94:1–14.
2. Vizcaíno SF, et al. (2010) A baseline paleoecological study for the Santa Cruz Formation (late-early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeogr Palaeoclimatol Palaeoecol* 292(3–4):507–519.
3. Ameghino F (1891) Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correciones [New remains of fossil mammals discovered by Carlos Ameghino in the lower Eocene of southern Patagonia. New species, additions and corrections]. *Rev Arg Hist Nat* 1:289–328. Spanish.
4. Scott WB (1905) Paleontology. Part II. Insectivora and Glires. *Reports of the Princeton University Expeditions to Patagonia 1896–1899* 5:365–383.
5. Saban R (1954) Phylogénie des insectivores [Phylogeny of the insectivores]. *Bull Mus Natl d'Hist Nat. Ser 2* 26:419–432. French.
6. Asher RJ, Horovitz I, Martin T, Sánchez-Villagra M (2007) Neither a rodent nor a platypus: a reexamination of *Necrolestes patagonensis* Ameghino. *Am Mus Novit* 3546:1–40.
7. Ladevèze S, Asher RJ, Sánchez-Villagra MR (2008) Petrosal anatomy in the fossil mammal *Necrolestes*: evidence for metatherian affinities and comparisons with the extant marsupial mole. *J Anat* 213(6):686–697.
8. Goin FJ, et al. (2007) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, edad-mamífero Colhuehuapense). Part I: Introducción, Didelphimorphia y Sparassodonta [The South American early Neogene Metatheria (early Miocene, Colhuehuapian mammal age). Part I: Introduction, Didelphimorphia and Sparassodonta]. *Ameghiniana* 44:29–71. Spanish.
9. Chornogubsky L (2011) New remains of the dryolestoid mammal *Leonardus cuspidatus* from the Los Alamitos Formation (Late Cretaceous, Argentina). *Paläontol Z* 85(3):343–350.
10. Rougier GW, Apesteguía S, Gaetano LC (2011) Highly specialized mammalian skulls from the Late Cretaceous of South America. *Nature* 479(7371):98–102.
11. Van Valen L (1988) Faunas of a southern world. *Nature* 333(6152):113.
12. Archer M, et al. (2011) Australia's first fossil marsupial mole (Notoryctemorphia) resolves controversies about their evolution and palaeoenvironmental origins. *Proc R Soc B* 278(1711):1498–1506.
13. MacPhee RDE (1981) Auditory regions of primates and eutherian insectivores: morphology, ontogeny, and character analysis. *Contrib Primatol* 18:1–282.
14. Rougier GW, Wible JR (2006) *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles*, eds Carrano MT, Gaudin TJ, Blob RW, Wible JR (Univ. of Chicago Press, Chicago), pp 269–311.
15. Zeller U (1989) Die Entwicklung und Morphologie des Schädels von *Ornithorhynchus anatinus* (Mammalia: Prototheria: Monotremata) [The development and morphology of the skull of *Ornithorhynchus anatinus* (Mammalia: Prototheria: Monotremata]. *Abh Senckenberg Natur Gesell* 545:1–188. German.
16. Wible JR, Hopson JA (1995) Homologies of the prootic canal in mammals and non-mammalian cynodonts. *J Vertebr Paleontol* 15(2):331–356.

17. Wible JR (1987) The eutherian stapedial artery: character analysis and implications for superordinal relationships. *Zool J Linn Soc* 91:107–135.
18. Rougier GW, Wible JR, Hopson JA (1992) Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. *J Vertebr Paleontol* 12(2):188–216.
19. Segall W (1970) Morphological parallelisms of the bulla and auditory ossicles in some insectivores and marsupials. *Fieldiana Zool* 51:169–205.
20. Rougier GW, Forasiepi AM, Hill RV, Novacek MJ (2009) New mammal remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. *Acta Palaeontol Pol* 54(2):195–212.
21. Paéz-Arango N (2008) Dental and craniomandibular anatomy of *Peligrotherium tropicalis*: the evolutionary radiation of South American dryolestoid mammals. MS thesis (Univ. of Louisville, Louisville, KY).
22. Wible JR, Rougier GW, Novacek MJ, Asher RJ (2009) The eutherian mammal *Maelestes gobiensis* from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bull Am Mus Nat Hist* 327:1–123.
23. Wible JR, Rougier GW, McKenna MC, Novacek MJ (2001) Earliest eutherian ear region: a petrosal referred to *Prokennalestes* from the Early Cretaceous of Mongolia. *Am Mus Novit* 3322:1–44.
24. Rougier GW, Wible JR, Novacek MJ (1998) Implications of *Deltatheridium* specimens for early marsupial history. *Nature* 396(6710):459–463.
25. Rougier GW, Wible JR, Hopson JA (1996) Basicranial anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the Late Jurassic of Colorado, and a reappraisal of mammaliaforms interrelationships. *Am Mus Novit* 3183:1–38.
26. Bininda-Emonds ORP, et al. (2007) The delayed rise of present-day mammals. *Nature* 446(7135):507–512.
27. Meredith RW, et al. (2011) Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334(6055):521–524.
28. Pascual R, Goin FJ, Balarino L, Udrizar Sauthier DE (2002) New data on the Paleocene monotreme *Monotrematum sudamericanum*, and the convergent evolution of triangulate molars. *Acta Palaeontol Pol* 47(3):487–492.
29. Pascual R, Goin FJ, Krause DW, Ortíz-Jauregízar E, Carlini AA (1999) The first gnathic remains of *Sudamerica*: implications for gondwanathere relationships. *J Vertebr Paleontol* 19(2):373–382.
30. Bonaparte JF, Van Valen L, Kramarz AG (1993) La fauna local de Punta Peligro, Paleoceno inferior de la Provincia del Chubut, Argentina [The local fauna of Punta Peligro, lower Paleocene of the province of Chubut, Argentina]. *Evol Monogr* 14:1–61. Spanish.
31. Goin FJ, et al. (2006) *Cretaceous-Tertiary High-Latitude Paleoenvironments, James Ross Basin, Antarctica*, eds Francis JE, Pirrie D, Crame JA (Geological Society, London), pp 145–161.
32. Antoine P-O, et al. (2012) Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. *Proc R Soc B* 279(1732): 1319–1326.
33. Goin FJ, et al. (2012) Persistence of a Mesozoic, non-therian mammalian lineage (Gondwanatheria) in the mid-Paleogene of Patagonia. *Naturwissenschaften* 99(6): 449–463.
34. Archer M, Jenkins FA, Jr., Hand SJ, Murray P, Godthelp H (1992) *Platypus and Echidnas*, ed Augee ML (Royal Zoological Society, Mosman, NSW, Australia), pp 15–27.
35. Phillips MJ, Bennett TH, Lee MSY (2009) Molecules, morphology, and ecology indicate a recent, amphibious ancestry for echidnas. *Proc Natl Acad Sci USA* 106(40):17089–17094.
36. Bonaparte JF (1986) Sobre *Mesungulatum houssayi* y nuevos mamíferos cretácicos de Patagonia [On *Mesungulatum houssayi* and new Cretaceous mammals from Patagonia]. *IV Congreso Argentino de Paleontología y Biostratigrafía* 2:48–61. Spanish.
37. Bonaparte JF (1990) New Late Cretaceous mammals from the Los Alamitos Formation, southern Patagonia. *Natl Geogr Res* 6:63–93.
38. Simpson GG (1980) *Splendid Isolation* (Yale Univ. Press, New Haven, CT).
39. Pascual R, Ortíz-Jaureguizar E (2007) The Gondwanan and South American episodes: Two major and unrelated moments in the history of the South American mammals. *J Mamm Evol* 14(2):75–137.
40. Rougier GW, et al. (2010) A review of the Mesozoic mammalian record of South America. *Paleontología y Dinosaurios desde América Latina* [*Paleontology and Dinosaurs from Latin America*], eds Calvo J, Porfiri J, González Riga G, Dos Santos D (Univ. Nacional de Cuyo, Mendoza, Argentina), pp 195–214. Spanish.

# Supporting Information

## Rougier et al. 10.1073/pnas.1212997109

### SI Text

### Comments on Homology Decisions and Character Scope

The dental homologies, particularly among *Necrolestes*, *Cronopio*, and *Leonardus*, are relevant for our results and not entirely trivial. Regarding *Necrolestes*, we follow Goin et al. (1) and regard the postcanine formula as P/p3, M/m3; we believe that the evidence of replacement is conclusive. *Cronopio* is interpreted following Rougier et al. (2), using the abrupt change of morphology (root and crown) as the main criterion to distinguish premolar from molars. *Leonardus* is interpreted as in Rougier et al. (2), which reverses the maxilla from a left (3, 4) to a right. In our view, the additional mandibular material described by Chornogubsky (4) can be interpreted as two molarized premolars (possibly the last and penultimate premolars). The presence of three roots on the more distal element is in agreement with the multiple roots known for the ultimate premolar for several meridiolestidans (2, 5). Presence of two fully molarized premolars would be shared by *Leonardus* and *Necrolestes*. Therefore, our interpretation differs from that offered by Chornogubsky (4) on the side represented by the maxilla of *Leonardus* and by the locus of the lower molariform elements, which were originally described as molars.

The characters in our matrix are craniodental, which minimizes missing data when including the mostly dentally known Mesozoic taxa. There are some postcrania associated with the specimens of *Necrolestes* (6); however, the specimens are very damaged, and the crucial tarsal bones originally described, but not illustrated by Scott (6), are now lost. The astragalus was described as having a neck that would be a condition found in Theria (7) but absent in forms putatively close to them like *Vincelestes* (8); if such was the case, it would support, against our view, therian affinities for *Necrolestes*.

### Testing the Alternative Hypothesis That *Necrolestes* Is a Crown-Therian

We tested the alternative hypothesis that *Necrolestes* is a crown-therian [as suggested by Ladevèze et al. (9), who argued that *Necrolestes* has diagnostic metatherian characters] by reanalyzing our character matrix with a constraint tree in which *Necrolestes* was forced to form a clade with the eight crown-therian taxa included in the matrix, namely *Pappotherium*, *Asiatherium*, *Kokopellia*, *Pucadelphys*, *Didelphis*, *Prokennalestes*, *Erinaceus*, and *Asioryctes*. Reanalysis of the matrix using maximum parsimony with the constraint tree enforced resulted in 24 most parsimonious trees (after collapsing all potentially zero-length branches) of 1,187 steps. This is 33 steps longer than the 36 shortest most parsimonious trees recovered when the matrix was analyzed using maximum parsimony without topological constraints (length = 1,154 steps; Fig. S5). Based on one-tailed Templeton (Wilcoxon signed-ranks) tests, all 24 constrained most parsimonious trees (MPTs) are significantly longer than the 36 unconstrained MPTs, with $P$ values ranging from 0.0006 to 0.0031 (mean $P = 0.0015$).

### Character List

**1. Symphysis Height.**

0. Robust, verticalized
1. Slender, oblique, or approaching horizontal

**2. Position of Posteriormost Mental Foramen.**

0. Below the canine and anterior premolariform region
1. Below the penultimate premolar
2. Below the ultimate premolar
3. Between the ultimate premolar and the first molar

**3. Postdentary Trough.** Behind tooth row:

0. Present
1. Absent

**4. Mandibular Alveolar Border.**

0. Subequal in height to the lingual edge
1. Labial border much lower than lingual

**5. Degree of Development of Meckelian Groove in Adults.**

0. Well developed
1. Weakly developed
2. Vestigial or absent

**6. Curvature of Meckelian Groove in Adults.** Under the tooth row:

0. Parallel to the ventral border of mandible
1. Convengent to the ventral border of mandible

**7. Groove for Replacement Dental Lamina.**

0. Present
1. Absent

**8. Angular Process Presence.**

0. Absent
1. Present

**9. Angular Process Direction.**

0. Small knobby process, not projected
1. Straight process, posteriorly directed
2. Transversely flaring
3. Inflected
4. Downturned

**10. Antero-Posterior Position of Angular Process Relative to Dentary Condyle.**

0. Anterior position, the angular process is below the main body of the coronoid process
1. Posterior position, the angular process is placed at the level of the posterior end of the coronoid process

**11. Vertical Position of Angular Process.**

0. Low, at or near the level of the ventral border of the mandibular horizontal ramus
1. High, at or near the level of the molar alveolar line

**12. Coronoid, or Its Attachment Scar, in Adults.**

0. Present
1. Absent

**13. Medial Fossa on Dentary Angular Process.**

0. Present
1. Absent

**14. Pterygoid Fossa.**

0. Absent
1. Present

**15. Medial Pterygoid Ridge or Shelf Direction.**

0. Directed to angular process
1. Reaching the dentary condyle via a low crest

**16. Pterygoid Shelf.**

0. Absent
1. Present

**17. Ventral Border of Masseteric Fossa.**

0. Absent
1. Present as a low and broad crest
2. Present as a well-defined and thin crest

**18. Position of Mandibular Foramen.**

0. Below or near to the base of the anterior border of the coronoid process
1. Posterior to the anterior edge of the coronoid process

**19. Masseteric Foramen.**

0. Absent
1. Present

**20. Crest of Masseteric Fossa Along Anterior Border of Coronoid Process.**

0. Absent or weakly developed
1. Present as a distinct anterior border

**21. Mylohyoid Process at Level of Anterior Border of Coronoid Process.**

0. Absent
1. Present

**22. Orientation of Dentary Peduncle and Condyle.**

0. Dentary peduncle is posteriorly directed, forms an angle of 40° or less to the alveolar margin
1. Vertically directed dentary peduncle, above 40°
2. Dentary condyle is continuous with the semicircular posterior margin of the dentary

**23. Lower Mandibular Margin/Condylar Peduncle.**

0. Not continuous, interrupted by an angular process or a sharp angle
1. Continuous as a single line in lateral view

**24. Shape and Relative Size of Dentary Articulation.**

0. Small and dorsoventrally compressed
1. Condyle is massive and bulbous, transversely broad in its dorsal aspect
2. Condyle mediolaterally narrow and vertically deep, forming a broad arc in lateral outline, either ovoid or triangular in posterior view

**25. Ventral Border of Dentary Peduncle.**

0. Posteriorly tapering without a condyle
1. Columnar or ridge-like
2. Ventrally flaring
3. Robust and short

**26. Position of Dentary Condyle Relative to Vertical Level of Postcanine Alveoli.**

0. Below or about the same level as the postcanine alveoli
1. Above the level of the postcanine alveoli

**27. Tilting of Coronoid Process of Dentary.** Measured as the angle between the imaginary line of the anterior border of the coronoid process and the horizontal alveolar line of all molars:

0. Coronoid process is strongly reclined forming an obtuse angle
1. Coronoid process less reclined, 135–145°
2. Coronoid process less than vertical, 115–125°
3. Coronoid process is near vertical and the angle is small, 95–105°

**28. Retromolar Space.** At least half the length of the last molar:

0. Absent
1. Present

**29. Alignment of Ultimate Molar to Anterior Margin of Dentary Coronoid Process.**

0. Ultimate functional molar is medial to the coronoid process
1. Ultimate functional molar is in alignment with the anterior margin of coronoid process

**30. Shape of Ventral Edge of Jaw in Area of Angular Process.**

0. Straight
1. Convex
2. Concave

**31. Incisor Replacement.**

0. Alternating and multiple replacement
1. Diphyodont replacement or none

**32. Number of Lower Incisors.**

0. Three or more
1. Two or fewer

**33. Maxillary Incisor.**

0. Present
1. Absent

**34. Staggered Incisor.**

0. Absent
1. Present

**35. Canine Replacement.**

0. Multiple replacements
1. Diphyodont

**36. Canines.**

0. Present and large
1. Present and small
2. Absent

**37. Upper Canine Height.**

0. Long, at least twice the height of tallest postcanine
1. Short, less than twice the height of the tallest postcanine

**38. Long Upper Canine Height.**

0. Relatively short, less than three times the height of the tallest postcanine crown
1. Tall, more than three times the height of tallest postcanine crown

**39. Replacement of Premolariforms.**

0. Multiple replacement
1. One replacement or none

**40. Total Number of Premolars.** Lower premolar preferred; uppers used if no lowers are available:

0. Two or fewer
1. Three premolars
2. Four premolars
3. Five or more

**41. Diastema Separating P1 From P2.** Distance equal or larger than half of the P1:

0. Absent
1. Present

**42. Penultimate Lower Premolar Size.**

0. Small and subequal to other premolars
1. Larger than any other premolar, longer and/or taller
2. Hypertrophied, dominant tooth in the series

**43. Penultimate Lower Premolar—Paraconid (Cusp b).**

0. Much smaller than metaconid (cusp c) of the same tooth, or absent
1. Well developed as an important cusp of trigonid

**44. Last Lower Premolar—Symmetry of Main Cusp a (Protoconid).**

0. Asymmetrical, anterior edge of cusp a is more convex in outline than the posterior edge
1. Symmetrical, anterior and posterior cutting edges are equal or subequal in length

**45. Last Lower Premolar—Anterior Cusp b (Paraconid).**

0. Present, at least subequal to cusp c, or posterior cingular cusp of the same tooth
1. Small, much smaller than cusp c or posterior cingular cusp of the same tooth, or vestigial to absent

**46. Last Lower Premolar—Arrangement of Principal Cusp a, Cusp b (if Present), and Cusp c.**

0. Aligned straight or at a slight angle
1. Distinctive triangulation

**47. Last Lower Premolar—Distinct Distal Cingulid Cusp d.**

0. Absent
1. Posterior cingular cusp present
2. Present as part of a continuous distal cingulid

**48. Last Lower Premolar Outline.**

0. Laterally compressed, crown outline longer than wide
1. Transversely wide, crown outline subequal or wider than long

**49. Last Lower Premolar Size.**

0. Small and subequal to other premolars
1. Large tooth, taller than or subequal to first molar
2. Hypertrophied, much larger than any molar

**50. Labial Cingulid of Last Lower Premolar.**

0. Absent or vestigial
1. Present along more than half of the crown length

**51. Lower Premolars Lingual Cingulid.**

0. Absent or vestigial
1. Present

**52. Relative Height of Primary Cusp a to c of Last Lower Premolar.** Measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusps:

0. Posterior cusp c is absent or very small
1. Posterior cusp c is distinctive but less than 30% of primary cusp a
2. Posterior cusp c and primary cusp a are equal or subequal in height (c is 40–100% of a)

**53. Last Upper Premolar—Functional Protocone.**

0. Absent
1. Present

**54. Last Upper Premolar—Parastylar Hook.**

0. Present
1. Absent or very small

**55. Number of Molars or Molariform Postcanines.** Lowers preferred, uppers used if no lowers are known:

0. Two molars
1. Three molars
2. Four to five molars
3. Six or more

**56. Alignment of Main Cusps of Posterior Lower Molars.** m3 or more posterior teeth considered if present:

0. Simple longitudinal row
1. Obtuse angle (>95)
2. Acute angle (<90)

**57. Alignment of Main Cusps of Anterior Lower Molar (m1).**

0. Single longitudinal row
1. Acute angle
2. Obtuse angle

**58. Development of Postprotocrista on Upper Molars for Double Rank Postvallum Shear.** For molars with reversed triangulation of molar cusps:

0. Postprotocrista is short and does not extend labially beyond metacone
1. Postprotocrista is long and extends labially beyond metacone

**59. Precise Opposition of Upper and Lower Molars.** Either one-to-one, or occluding at the opposing embrasure or talonid:

0. Absence of precise opposition of upper and lower molars
1. Present (either one-to-one or occluding at the opposing embrasure or talonid)

**60. Relationships Between Cusps of Opposing Upper and Lower Molars.**

0. Absent
1. Present, lower primary cusp a occludes in the groove between upper cusp a and b
2. Present, lower main cusp a occludes in front of upper cusp b and into the embrasure between the opposing and preceding upper teeth
3. Present, part of the talonid occluding with the lingual face (or any part) of the upper molar
4. Lower multicuspate rows alternately occlude between the upper multicuspate rows

**61. Relative Height of Primary Cusp a (Protoconid) to Cusp c (Metaconid) of Anterior Lower Molars.** Measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusp, on m1:

0. Posterior cusp c is less than 40% of the primary cusp a (protoconid)
1. Posterior cusp c is more than 40% of cusp a

**62. Relative Size/Height of Cusp b (Paraconid) to Cusp c (Metaconid).** Based on m2 when possible:

0. c taller than b
1. b and c subequal in height
2. b taller than c

**63. Relative Elevation of Bases of Paraconid (Cusp b) and Metaconid (Cusp c).**

0. Almost or at the same level
1. Base of the paraconid higher than base of the metaconid
2. Base of metaconid higher than base of the paraconid

**64. Cristid Obliqua.**

0. Absent
1. Present

**65. Cristid Obliqua Orientation.**

0. Oriented to or lingual to the metaconid-protoconid notch
1. Hypertrophied and directed to posterior part of the metaconid
2. Short and pointed anteriorly between the metaconid-protoconid notch and the protoconid

**66. Lower Molar—Pre-Entocristid on Talonid Heel.**

0. Talonid lacks medial and longitudinal crest
1. Pre-entoconid cristid of talonid in alignment with the metaconid or with the postmetacristid if the latter is present
2. Pre-entocristid crest is offset from the metaconid and it is lingual to the base of the metaconid

**67. Labial Curvature of Primary Cusp a of Lower Molars (at Base Level) Relative to Curvature of Cusps b and c.**

0. Cusps a, b, and c have the same degree of bulging
1. Cusp a is far more bulging than cusps b and c

**68. Labial Curvature of Main Cusps a, b, and c at Level of Cusp Valley of Penultimate and Ultimate Upper Molars.**

0. Cusp a, b, and c have about the same degree of curvature
1. Cusp a is slightly concave (or far less convex than either cusp b or c)

**69. Labiolingual Compression of Primary Functional Cusps of Lower Molars.** At the level of the cusp base but above the cingulid:

0. Absent
1. Present

**70. Posterior Lingual Cingulid of Lower Molars.**

0. Absent or weak
1. Distinctive
2. Strongly developed, crenulated with distinctive cuspules

**71. Cingular Cuspule e on Lower Molars.**

0. Present
1. Absent

**72. Cingular Cuspule f on Lower Molars.**

0. Absent
1. Present

**73. Mesial Transverse Cingulid.**

0. Absent
1. Present as a continuous shelf below the trigonid without occlusal function
2. Present, having occlusal contact with the upper molar

**74. Cingulid Shelf Wrapping Around Anterointernal Corner of Lower Molar to Extend to Lingual Side of Trigonid Below Paraconid.**

0. Absent
1. Present, weakly developed restricted to the mesial aspect of the paraconid base
2. Present, strongly developed, running along most of the lingual base of the paraconid

**75. Postcingulid.**

0. Absent
1. Present, oblique, and connected to hypoconulid
2. Present, horizontal above the gum level

**76. Interlocking Mechanism Between Two Adjacent Lower Molars.**

0. Absent
1. Present, posterior cingular cuspule d of the preceding molar fits in between cingular cuspules e and f of the succeeding molar or flat surfaces of mesial cingula or cusp b
2. Present, posterior cingular cuspule d fits between cingular cuspule e and cusp b of the succeeding molar
3. Present, posterior cingular cuspule d of the preceding molar fits into and embayment or vertical groove of the anterior aspect of cusp b the succeeding molar

**77. Size Ratio of Posterior Molars.** Lower molar preferred when available:

0. Last three postcanines forming a series of posteriorly decreasing size
1. Penultimate molar is the largest of molars
2. Ultimate molar is the largest of molars

**78. Orientation of Paracristid Relative to Longitudinal Axis of Molars.**

0. Longitudinal orientation
1. Oblique
2. Nearly transverse

**79. Paraconid Presence on Lower Molars.**

0. Present
1. Absent

**80. Mesiolingual Surface of Paraconid on Lower Molars.**

0. Rounded
1. Forming a keel

**81. Procumbent Paraconid on Lower Molars.**

0. Absent
1. Present, projected as a conical cusp beyond crown base

**82. Proximity Between Paraconid and Metaconid.**

0. Bases widely separated
1. Bases approaching each other becoming confluent
2. Single cusp (amphyconid)

**83. Molar Trigonid/Talonid Width Ratio.**

0. Narrow or absent (talonid <40% of trigonid)
1. Wide (talonid is 40–70% of the trigonid)
2. Talonid is equal or wider than trigonid (above 70% of the width of the trigonid)

**84. Lower Molar Hypoflexid.**

0. Absent or shallow
1. Deep (but less than 50% of the talonid width)
2. Very deep (>60% of the talonid width)

**85. Talonid Basin.**

0. Absent
1. Present

**86. Morphology of Rear Portion of Molariform.**

0. Single cusp (d), cingulum or absent
1. Present as an incipient heel
2. Present as a heel (with at least one functional cusp)
3. Present as a transverse V-shaped basin with two major cusps
4. Rimmed with three major cusps

**87. Hypoconulid (=Cusp d).**

0. Hypoconulid at the cingulid level
1. Hypoconulid elevated above the cingulid level

**88. Hypoconid.**

0. Absent
1. Present

**89. Hypoconulid Orientation.**

0. Cusp tip erect or procumbent
1. Cusp tip recumbent (reclined posteriorly)

**90. Entoconid.**

0. Absent
1. Present but far from hypoconulid, at least equal to one cusp length
2. Present and twinned with hypoconulid

**91. Height of Entoconid Compared With Other Talonid Cusps.**

0. Lower than the hypoconulid (or even vestigial)
1. Subequal height to the hypoconulid

**92. Alignment of Paraconid, Metaconid, and Entoconid.**

0. Cusps not aligned
1. Cusps aligned

**93. Aspect Radio in Occlusal View (Length vs. Width) of Functional Talonid Basin at Cingulid Level.**

0. Longer than wide
1. Length equals width
2. Wider than long

**94. Elevation of Talonid.**

0. Hypoconulid/protoconid height ratio less than 20% (hypoconulid = cusp d)
1. Hypoconulid/protoconid height ratio between 25% and 35%
2. Hypoconulid/protoconid height ratio between 40% and 50%
3. Hypoconulid/protoconid height ratio: 50% or higher

**95. Width of Upper Molar Stylar Shelf.**

0. Present and broad
1. Present and narrow
2. Absent

**96. Labial Cingulum of Upper Molars.**

0. Absent or weak
1. Distinctive cingulum, straight
2. Distinctive cingulum with strong ectoflexus (but without hypertrophied stylar cusps)
3. Wide cingulum with distinctive ectoflexus, plus individualized and hypertrophied stylar cusps
4. Cingulum with distinctive and even-sized multiple cuspules

**97. Upper Molars With Functional Lingual Protocone That Grinds Against Basin on Lowers.**

0. Absent
1. Present

**98. Trigon Basin.** Protocone must be present:

0. Absent
1. Present, the labial slope of the protocone determines a basin against the lingual slope of the paracone/metacone

**99. Transverse Width of Protocone on Upper Molars.** Protocone must be present:

0. Narrow (distance from the protocone apex to paracone apex <0.60 of total tooth width)
1. Strongly transverse (distance from the protocone apex >0.60 of total width)

**100. Anteroposterior Development of Lingual Region on Upper Molars.** Protocone must be present:

0. Narrow (anteroposterior distance medial to the paracone and metacone <0.30 of total tooth length)
1. Moderate development (distance between position of conules = 0.31–0.50 of total tooth length)
2. Long (distance between conules >0.51 of total tooth length)

**101. Conules on Upper Molars.**

0. Absent
1. Present but weak and without cristae
2. Conules distinctive, with cristae

**102. Relative Height and Size of Paracone (Cusp b) and Metacone of Upper Molars.**

0. Paracone higher and larger than metacone
1. Metacone is higher and larger than paracone

**103. Centrocrista Between Paracone and Metacone of Upper Molars.** Consider only for tribosphenic forms:

0. Straight
1. V-shaped, with labially directed postparacista and premetacrista

**104. Upper Molars Cuspule e.**

0. Present
1. Absent

**105. Upper Molar Interlock.**

0. Absent
1. Tongue-in-groove interlock

**106. Central Crest (Medianergrat) in Triangular Upper Molariforms.**

0. Absent
1. Present

**107. Outline of m1.**

0. Oval-shaped
1. Laterally compressed
2. Oblong with slight labial bulge
3. Oblong with strong labial bulge
4. Triangular or tear-drop shaped
5. Rectangular or slightly rhomboidal

**108. Crown Length/Width Ratio Among Lower Molariforms.**

0. Crown longer than wide
1. Crown length/width subequal
2. Crown wider than long

**109. Shape of Lingual Margin in Lower Molars.**

0. Notched
1. Flat

**110. Aspect Ratio of M1.**

0. Laterally compressed
1. Oval-shaped or spindle-shaped
2. Triangular outline
3. Dumbbell-shaped
4. Rectangular or nearly so

**111. Crown Height Difference Between Buccal and Lingual Sides in Lower Molariforms.**

0. Buccal and lingual sides of similar height
1. Buccal side much taller than lingual side

**112. Functional Development of Occlusal Facets on Individual Molar Cusps.**

0. Absent for lifetime
1. Absent at eruption but development later by extensive wearing of the crown
2. Wear facet develops on a morphology approximately present upon eruption

**113. Topographic Relationships of Wear Facets to Main Cusps.**

0. Lower cusps a and c support two different wear facet (1 and 4) that contact the upper main cusp a
1. Lower cusps a and c support a single wear facet (4) that contacts the upper primary cusp b

**114. Development and Orientation of Prevallum/Postvallid Shearing.**

0. Absent
1. Present and obtuse
2. Present, hypertrophied, and transverse

**115. Upper Molar—Development of Facet 1 and Preprotocrista (or Paracrista) on Upper Molars.**

0. Facet 1 (prevallum crest) is short, and does not extend to the stylocone area
1. Wear facet 1 extends beyond into the hook-like area near the stylocone
2. Long preprotocrista (below the paracone-stylocone crest) is added to the prevallum shear and extends labially beyond paracone

**116. Differentiation of Wear Facet 3 and Wear Facet 4.**

0. Absent
1. Present
2. Facet hypertrophied on the flanks of the strongly V-shaped talonid

**117. Orientation of Wear Facet 4.**

0. Present and oblique to long axis of the tooth
1. Present and forming a more transverse angle to long axis of the tooth

**118. Wear Pattern on Talonid.**

0. Absent
1. Present

**119. Direction of Jaw Movement During Occlusion.**

0. Dorsomedial movement
1. Dorsomedial movement with a significant medial component
2. Dorsoposterior movement

**120. Metacristid (Protocristid) Orientation on Posterior Molariforms.**

0. Parallel to lower jaw axis
1. Oblique
2. Transverse

**121. Bifid Metaconid.**

0. Absent
1. Present

**122. Bifid Metastyle.**

0. Absent
1. Present

**123. Distal Metacristid.**

0. Present
1. Absent

**124. Superficial Features on Occluding Surface of Wear Facets 5 and 6 in Talonid for Basined Talonid.**

0. Smooth surface on the talonid (or on cusp d)
1. Multiple ridges within talonid basin

**125. Position of Stylocone in Posterior Molariforms.**

0. Along buccal edge
1. Separated

**126. Stylocone Relationship in Triangular Teeth.**

0. Stylocone connected to paracrista or mesial to its end
1. Stylocone distal to labial ending of paracrista
2. Stylocone detached of preparacrista occupying central position on crown

**127. Stylocone Size in Triangular Teeth.**

0. Absent
1. Small stylar cusp
2. Prominent cusp subequal or larger than paracone

**128. Parastylar Hook in Upper Molars.**

0. Absent or poorly developed
1. Present

**129. Paracone Orientation.**

0. Erect
1. Recumbent
2. Procumbent

**130. Metacone.**

0. Present
1. Absent

**131. Paracone-Metacone Labiolingually Aligned.** Consider only in subtriangular upper teeth:

0. Absent, the metacone is labial to paracone
1. Present, the metacone is aproximately aligned mesiodistally with the paracone

**132. Accessory Cusps on Bucal Side of Upper Molars.**

0. Absent
1. Present

**133. Deep Ectoflexus on Upper Molars.**

0. Present only on penultimate/ultimate molar
1. On penultimate and preceding molar
2. Strongly reduced to absent

**134. Lower Molariform Roots.**

0. Incipient or incomplete separation
1. Root divided

**135. Number of Lower Molariform Roots.**

0. One
1. Two
2. Three or more

**136. Size of Lower Molar Roots.**

0. Subequal
1. Posterior molar root much smaller
2. Single root (posterior root absent)
3. Anterior root smaller

**137. Lower Molar Root Cross Section.** m2 considered when available:

0. Circular/subcircular
1. Anteroposteriorly compressed

**138. Replacement of at Least Some Functional Molariforms.**

0. Present
1. Absent

**139. Procumbent and Enlargement of Anteriormost Lower Incisor.**

0. Absent
1. Present, both procumbent and enlarged more than 50% the second.

**140. Trigon Major Axis Orientation.** As indicated by the distal wall of the trigonid:

0. Labially
1. Mesially
2. Sharply distal

**141. Lingual Cingulum/Trigon on Paracone.** Trigon and/or protocone are considered elaborations of the cingulum:

0. Absent
1. Present

**142. Precingulum.**

0. Narrow and closely attached to crown, to absent
1. Developed forming a lingual cusp

**143. Postcingulum.**

0. Narrow and closely oppresed to crown, to absent
1. Developed forming a lingual cusp

**144. Cingula Pre- and Postcingula/Cingulid Height.**

0. Absent or little differentiated
1. Close to crown base
2. Elevated reaching occlusal surface

**145. Prehypoconulid Crest.** A crest connecting the metaconid with the hypoconulid along the lingual edge of the tooth:

0. Absent
1. Present

**146. Number of Upper Molariform Roots.**

0. One
1. Two
2. Three
3. More than three

**147. Position of Lingual Upper Root.**

0. Under paracone
1. Under protocone or trigon

**148. Supernumerary Roots on Penultimate Upper Premolar.**

0. Absent
1. Present

**149. Supernumerary Roots on Penultimate Lower Premolar.**

0. Absent
1. Present

**150. Supernumerary Roots on Ultimate Lower Premolar.**

0. Absent
1. Present

**151. Supernumerary Roots on Ultimate Upper Premolar.**

0. Absent
1. Present

**152. Penultimate Lower Premolar Distal Root.**

0. Subequal to mesial root
1. Large elongated root, more than 50% of crown length

**153. Lower Molar Contact.**

0. Lower molars contact each other somewhere along the mesial and distal edges of the crown
1. Lower molars do not contact each other being separated by interdental spaces

**154. Upper Molar Contact.**

0. Upper molars extensively contact each other
1. Upper molars do not contact each other, or barely do so

**155. Enamel Prism Shape.**

0. Prisms absent
1. Arc
2. Enclosed

**156. Enamel Prism Seams.**

0. Present
1. Absent

**157. Enamel Prism Packing.**

0. Hexagonal
1. Erratic
2. In rows

**158. Fusion of Atlas Neural Arch and Intercentrum in Adults.**

0. Unfused
1. Fused

**159. Atlas Ribs in Adults.**

0. Present
1. Absent

**160. Fusion of Dens to Axis.**

0. Unfused
1. Fused

**161. Rib of Axis in Adults.**

0. Free ribs present
1. Ribs fuse to become transverse process

**162. Postaxial Cervical Ribs in Adult.**

0. Free ribs present
1. Free ribs absent

**163. Thoracic Vertebrae.**

0. 13 thoracic vertebrae
1. 15 or more thoracic vertebrae

**164. Lumbar Ribs.**

0. Unfused to vertebrae
1. Synostosed to vertebrae to form transverse processes

**165. Interclavicle in Adults.**

0. Present
1. Absent

**166. Contact Relationships in Adults Between Interclavicle and Sternal Manubrium.**

0. Posterior end of interclavicle abuts anterior border of manubrium
1. Interclavicle broadly overlaps the ventral side of the manubrium
2. Complete fusion of the embryonic membranous and endochondral elements

**167. Cranial Margin of Interclavicle.**

0. Anterior border is emarginated or flat
1. With a median process (assuming interclavicle is fused to the sternal manubrium in living therians)

**168. Claviculo-Sternal Apparatus Joint.**

0. Immobile
1. Mobile

**169. Acromioclavicular Joint.**

0. Extensive articulation
1. Limited articulation

**170. Curvature of Clavicle.**

0. Boomerang-shaped
1. Slightly curved

**171. Scapula—Supraspinous Fossa.**

0. Absent
1. Weakly developed, present only along a part of the scapula
2. Fully developed and present along the entire dorsal border of scapula

**172. Scapula—Acromion Process.**

0. Short, (even with or behind the glenoid)
1. Hook-like and extending below the glenoid

**173. Scapula—Fossa or Process for Teres Major Muscle.**

0. Absent
1. Present

**174. Procoracoid.**

0. Present as a free element
1. Fused to the sternal apparatus in adult

**175. Procoracoid Foramen.**

0. Present
1. Absent

**176. Coracoid.**

0. Large, with posterior process
1. Small, without posterior process

**177. Manubrium Size Relative to Succeeding Sternebrae.**

0. Large
1. Small

**178. Orientation of Glenoid Relative to Plane or Axis of Scapula.**

0. Nearly parallel to the long axis and facing posterolaterally
1. Oblique and facing more posteriorly
2. Perpendicular to the main plane of the scapular plate

**179. Shape and Curvature of Glenoid.**

0. Saddle-shaped, oval, and elongated
1. Uniformly concave and more rounded in outline

**180. Medial Surface of Scapula.**

0. Concave
1. Flat

**181. Humeral Head.**

0. Subspherical, weakly inflected
1. Spherical and strongly inflected

**182. Intertubercular Groove Separating Deltopectoral Crest From Lesser Tubercle.**

0. Shallow and broad
1. Narrow and deep

**183. Size of Lesser Tubercle of Humerus.**

0. Wider than the greater tubercle
1. Subequal to narrower than the greater tubercle

**184. Torsion Between Proximal and Distal Ends of Humerus.**

0. Strong (>30)
1. Moderate (30–15)
2. Weak (<15)

**185. Ventral Extension of Deltopectoral Crest or Position of Deltoid Tuberosity.**

0. Not extending beyond the midpoint of the humeral shaft
1. Extending ventrally (distally) past the midpoint of the shaft

**186. Ulnar Articulation on Distal Humerus.**

0. Bulbous ulnar condyle
1. Incomplete trochlea with vestigial ulnar condyle in anterior view.
2. Trochlea has extending to the anteroventral side

**187. Radial Articulation on Distal Humerus.**

0. Distinct and rounded condyle separated from the ulnar articulation in the anteroventral view of the humerus
1. Radial articulation forms a rounded condyle anteriorly but its posterior surface is nearly cylindrical
2. Capitulum, radial articulating structure forms a continuous synovial surface with the ulnar trochlea

**188. Entepicondyle and Ectepicondyle of Humerus.**

0. Robust
1. Weak

**189. Rectangular Shelf for Supinator Ridge Extended From Ectepicondyle.**

0. Absent
1. Present

**190. Styloid Process of Radius.**

0. Weak
1. Strong

**191. Enlargement of Scaphoid with a Distomedial Projection.**

0. Absent
1. Present

**192. Size and Shape of Hamate (Unciform) in Wrist.**

0. Anteroposteriorly compressed (wider than longer in dorsal view)
1. Mediolaterally compressed (longer than wide)

**193. Acetabular Dorsal Emargination.**

0. Emarginated
1. With a complete rim

**194. Sutures of Ilium, Ischium, and Pubis Within Acetabulum in Adults.**

0. Unfused
1. Fused

**195. Ischiatic Tuberosity.**

0. Dorsal margin with a small or absent ischiatic tuberosity
1. Dorsal margin concave and ischiatic tubercle hypertrophied

**196. Head of Femur Is Inflected and Set off From Shaft by a Neck.**

0. Neck absent, head oriented dorsally
1. Neck present and head inflected medially

**197. Fovea for Acetabular Ligament on Femoral Head.**

0. Absent
1. Present

**198. Greater Trochanter.**

0. Directed dorsolaterally
1. Directed dorsally

**199. Orientation of Lesser Trochanter.**

0. On the medial side of the shaft
1. On the ventromedial or ventral side of the shaft

**200. Size of Lesser Trochanter.**

0. Large
1. Small

**201. Patellar Groove of Femur.**

0. Absent
1. Shallow and weakly developed
2. Well developed

**202. Proximolateral Tubercle or Tuberosity of Tibia.**

0. Large and hook-like
1. Indistinct

**203. Distal Tibial Malleolus.**

0. Weak
1. Distinct

**204. Fibula Contacting Distal End of Femur.**

0. Present
1. Absent

**205. Distal Fibular Styloid Process.**

0. Weak or absent
1. Distinct

**206. Fibula Contacting the Calcaneus.**

0. Extensive contact
1. Reduced
2. Mortise and tenon contact of fibula to the ankle

**207. Superposition of Astragalus Over Calcaneus.**

0. Little or absent
1. Weakly developed
2. Present

**208. Orientation of Sustentacular Facet of Calcaneus With Regard to Horizontal Plane of Astragalus.**

0. Nearly vertical
1. Oblique (<70) to nearly horizontal

**209. Astragalar Neck.**

0. Absent
1. Weakly developed
2. Present

**210. Astragalar Trochlea.**

0. Absent
1. Present

**211. Calcaneal Tubercle.**

0. Short, without terminal swelling
1. Elongated with distal swelling

**212. Peroneal Process and Groove of Calcaneus.**

0. Forming laterally directed shelf, and without a distinct process
1. Weakly developed with shallow groove on the lateral side of process
2. With a distinct peroneal process

**213. Contact of the Cuboid on Calcaneus.**

0. On the anterior end of the calcaneus, the cuboid is aligned with the long axis of the calcaneous
1. On the anteromedial aspect of the calcaneous, the cuboid is skewed to the medial side of the long axis of the calcaneous

**214. Relationships of Proximal End of Metatarsal V to Cuboid.**

0. Metatarsal V is offset from the cuboid
1. Metatarsal V is far offset from the cuboid, so that it contacts the calcaneous
2. Metatarsal V is aligned with the cuboid

**215. Angle of Metatarsal III to Calcaneus.**

0. Metatarsal III is aligned with (or parallel to) an imaginary line through the long axis of the calcaneous
1. Metatarsal III is oriented oblique to an imaginary line through the long axis of the calcaneous

**216. Sesamoid Bones in Flexor Tendons.**

0. Absent
1. Present and unpaired
2. Present and paired

**217. Tarsal Spur.**

0. Absent
1. Present

**218. Sharp Constriction of Rostrum in Front of Molariform-Premolar Boundary.**

0. Present
1. Absent

**219. External Size of Cranial Moiety of Squamosal.**

0. Narrow
1. Broad

**220. Participation of Cranial Moiety of Squamosal in Braincase.**

0. Does not participate in the endocranial wall of the braincase
1. Participates in the endocranial wall of the braincase

**221. Neck Between Glenoid and Cranial Moiety of Squamosal.**

0. Absent
1. Present

**222. External Auditory Meatus.**

0. Present as the postcraniomandibular joint sulcus
1. Absent
2. Present as a groove on the squamosal, or a notch

**223. Position of Craniomandibular Joint.**

0. Posterior or lateral to the level to the fenestra vestibuli
1. Anterior to the level of the fenestra vestibuli

**224. Orientation of Glenoid Fossa.**

0. On the inner side of the zygoma and facing ventromedially
1. On the platform of the zygoma and facing ventrally

**225. Postglenoid Process.**

0. Absent
1. Present as a distinctive process

**226. Postglenoid Foramen Within Squamosal Bone.**

0. Absent
1. Present

**227. Basisphenoid Wing on Ventral Aspect of Skull.**

0. Present, overlapping part of or the whole cochlear housing
1. Absent

**228. Relationship of Pars Cochlearis to Lateral Lappet of Basioccipital.**

0. Pars cochlearis is entirely covered by basioccipital
1. Pars cochlearis partially covered by basioccipital
2. Pars cochlearis fully exposed as promontorium

**229. Medial Flat Facet of Promontorium of Pars Cochlearis.**

0. Flat
1. Inflated and convex

**230. Ventral Outline and Morphology of Promontorium.**

0. Triangular, with steep and slightly concave lateral wall
1. Elongated and cylindrical petrosal cochlear housing
2. Bulbous and oval-shaped promontorium

**231. Cochlea.**

0. Short and uncoiled
1. Elongated and partly coiled
2. Elongate and coiled to about 360° or more

**232. Morphology of Internal Acoustic Meatus.**

0. The floor is ossified and the meatus is a deep tube
1. Present as a shallow depression
2. Present and the floor is developed as the cribriform foramina for auditory nerve

**233. Primary Bony Lamina Within Cochlear Canal.**

0. Absent
1. Present

**234. Secondary Bony Lamina for Basilar Membrane Within Cochlear Canal.**

0. Absent
1. Present

**235. Crista Interfenestralis.**

0. Horizontal and extending to base of the paroccipital process
1. Vertical, delimiting the back of the promontorium

**236. Postpromontorial Tympanic Recess.**

0. Absent
1. Present

**237. Caudal Tympanic Process of Petrosal.**

0. Absent
1. Present as a continuous crest
2. Caudal tympanic process notched

**238. Prootic Canal.**

0. Present
1. Absent

**239. Prootic Canal Confluence With Pterygoparoccipital Foramen.**

0. Prootic canal present, and its tympanic aperture is a distinct separate foramen
1. Prootic canal present, and its tympanic aperture is confluent with the pterygoparoccipital foramen

**240. Lateral Trough Floor Anterior to Tympanic Aperture of Prootic Canal and/or Primary Facial Foramen.**

0. Open lateral trough but no bony floor
1. Present as a bony shelf
2. Lateral trough absent

**241. Enclosure of Geniculate Ganglion by Bony Floor of Petrosal.**

0. Absent
1. Present

**242. Anteroventral Opening of Cavum Epiptericum.**

0. Fully open ventrally
1. Partially enclosed by petrosal or lateral flange
2. Enclosed by both the alisphenoid and the petrosal

**243. Anterior Lamina of Petrosal and Ascending Process of Alisphenoid and Their Relationships to Exit of Mandibular Branch (V3) of Trigeminal Nerve.**

0. V3 foramen placed at the suture of the alisphenoid ascending process and the anterior lamina of petrosal
1. V3 placed within the enlarged anterior lamina of the petrosal
2. Double trigeminal foramina within the anterior lamina in addition to the trigeminal foramen at the anterior lamina border with alisphenoid
3. V3 within the ascending process of the alisphenoid

**244. Quadrate Ramus of Alisphenoid.**

0. Forming a rod overlapping with the anterior part of the lateral flange
1. Present but not extending back too far, mostly laminar process in the vicinity of the oval foramen
2. Absent

**245. Orientation of Anterior Part of Lateral Flange.**

0. Horizontal shelf
1. Ventrally directed
2. Vestigial or absent

**246. Vascular Foramen in Posterior Part of Lateral Flange Anterior to Pterygoparoccipital Foramen.**

0. Present
1. Absent

**247. Relationship of Petrosal Lateral Flange to Crista Parotica.**

0. Widely separated
1. Narrowly separated
2. Continuous bone formed by petrosal

**248. Morphology of Pterygoparoccipital Foramen.** That is, ramus superior foramen:

0. Laterally open notch
1. Foramen enclosed by the petrosal or squamosal or both

**249. Position of Pterygoparoccipital Foramen Relative to Fenestra Vestibuli.**

0. Foramen posterior or lateral to the level of the fenestra vestibuli
1. Foramen anterior to the level of the fenestra vestibuli

**250. Bifurcation of Paroccipital Process of Petrosal.**

0. Absent
1. Present

**251. Posterior Paroccipital Process of Petrosal.**

0. No ventral projection below the level of its surrounding structures
1. Projecting below the surrounding structures

**252. Morphological Differentiation of Anterior Paroccipital Region.**

0. Anterior paroccipital region is indistinct from surrounding structures
1. Anterior paroccipital region is bulbous and distinctive from the surrounding structures
2. Anterior paroccipital region has a distinct crista parotica

**253. Epitympanic Recess Lateral to Crista Parotica.**

0. Absent
1. Present

**254. Relationship of Squamosal on Paraoccipital Process of Petrosal.**

0. Squamosal covers the entire paroccipital region
1. No squamosal cover on anterior paroccipital region
2. Squamosal covering a part of the paroccipital region, but not on the crista parotica (the squamosal wall and the crista parotica are separated by the epitympanic recess)

**255. Medial Process of Squamosal Reaching Toward Foramen Ovale.**

0. Absent
1. Present

**256. Stapedial Artery Sulcus on Pars Cochlearis of Petrosal.**

0. Absent
1. Present

**257. Transpomontorial Sulcus for Internal Carotid Artery on Pars Cochlearis.**

0. Absent
1. Present

**258. Bullar Process of Alisphenoid.**

0. Absent
1. Present

**259. Hypotympanic Recess in Junction of Alisphenoid, Squamosal, and Petrosal.**

0. Absent
1. Present

**260. Separation of Fenestra Cochleae from Jugular Foramen.**

0. Fenestra cochleae and jugular foramen within the same depression
1. Separate

**261. Channel of Perilymphatic Duct.**

0. Open channel and sulcus
1. Channel partially or fully enclosed

**262. Tensor Tympani Fossa.**

0. Indistinct or very shallow
1. Deep recess on lateral trough anterior to hiatus Fallopii

**263. Stapedial Muscle Fossa.**

0. Absent
1. Present and in alignment with the crista interfenestralis
2. Present and lateral to the crista interfenestralis

**264. Hypoglossal Foramen.**

0. Indistinct, either confluent with the jugular foramen or sharing a depression with the jugular foramen
1. Separated from the jugular foramen

**265. Shape of Incudo-Mallear Contact.**

0. Trochlear surface on the incus
1. Trough or saddle-shaped contact on the incus
2. Flat surface

**266. Incus (Quadrate) Neck.**

0. Absent
1. Present

**267. Stapedial Process of Incus (Quadrate).**

0. Absent
1. Present

**268. Dorsal Plate (=Crus Breve) of Incus (Quadrate).**

0. Broad plate
1. Pointed triangle
2. Reduced

**269. Incus—Angle of the Crus Breve to Crus Longum.**

0. Alignment or obtuse angle between stapedial process (crus longum) and the dorsal plate (crus breve)
1. Perpendicular
2. Acute angle between the crus breve and crus longum

**270. Primary Suspension of Incus (Quadrate) on Basicranium.**

0. By squamosal and quadratojugal
1. By squamosal only
2. By petrosal (either by the preserved direct contact of incus, or by the inference from the presence of a well-defined crista parotica)

**271. Quadratojugal Notch in Squamosal.**

0. Present as an independent element in adult
1. Absent

**272. Morphology of Stapes.**

0. Columniform-macroperforate
1. Columelliform-imperforate (or microperforate)
2. Bicrurate-perforate

**273. Bony Secondary Palate.**

0. Ending anterior to the posterior end of the tooth row
1. Level with the posterior end of the tooth row
2. Extending posterior to the tooth row

**274. Relationship of Maxilla to Subtemporal Margin of Orbit.**

0. Participating in the rounded subtemporal margin of the orbit
1. Forming a well-defined edge along the subtemporal margin

**275. Pterygopalatine Ridge.**

0. Present
1. Absent

**276. Transverse Process of pterygoid.**

0. Present and massive
1. Present as the hamulus
2. Greatly reduced or absent

**277. Palatal Width Anterior to Basisphenoid.**

0. Very narrow anterior to the basisphenoid
1. Intermediate width anterior to the basisphenoid
2. Palatal width is as broad at the basisphenoid as the internal choanae

**278. Vault of Nasopharyngeal Passage Near Pterygoid-Basisphenoid Junction.**

0. Roof of the pharynx is V-shaped in transverse section, narrowing toward the basisphenoid
1. Roof of the pharynx is U-shaped in transverse section

**279. Complete Ossification of Orbital Floor.**

0. Absent
1. Present

**280. Pattern of Orbital Mosaic as Exposed Externally.**

0. Alisphenoid contacts the frontal and parietal
1. Petrosal anterior lamina contacts the orbitosphenoid thereby separating the alisphenoid from the front and the parietal

**281. Outline of Facial Part of Lacrimal.**

0. Large, triangular, and pointed anteriorly
1. Small and rectangular or crescentic
2. Excluded from the facial (and preorbital) part of the skull

**282. Pila Antotica.**

0. Present
1. Absent (in adult)

**283. Fronto-Parietal Suture on Alisphenoid.**

0. Dorsal plate of alisphenoid contacting the frontal by the anterior corner
1. Dorsal plate of alisphenoid has more extensive contact to the frontal (~50% of its dorsal border)

**284. Jugal on Zygoma.**

0. Anterior part of the jugal extends on the facial part of the maxilla and forming a part of the anterior orbit
1. Anterior part of jugal does not reach the facial part of the maxilla and is excluded from the anterior part of the orbit

**285. Maximum Vertical Depth of Zygomatic Arch Relative to Length of Skull.**

0. Between 10% and 20%
1. Between 5% and 7%

**286. Posterior Opening of Posttemporal Canal.**

0. At the junction of the petrosal, squamosal, and tabular
1. Between the petrosal and the squamosal

**287. Anterior Ascending Vascular Channel for Arteria Diploëtica Magna in Temporal Region.**

0. Open groove
1. Partially enclosed in a canal
2. Completely enclosed in a canal or endocranial

**288. Nuchal (Lambdoidal) Crest.**

0. Crest overhanging the concave or straight dorsal part of the occipital plate
1. Weak crest with convex dorsal part of the occipital plate

**289. Sagittal Crest.**

0. Prominently developed
1. Weakly developed
2. Absent

**290. Tabular Bone.**

0. Present
1. Absent

**291. Shape of Occipital Condyle.**

0. Bulbous
1. Ovoid
2. Subcylindrical

**292. Occiput Slope.**

0. Occiput slopes posterodorsally, or vertically from the occipital condyles
1. Occiput slopes anterodorsally from the occipital condyles

**293. Foramina on Dorsal Surface of Nasal.**

0. Absent
1. Present

**294. Septomaxilla.**

0. Present and with a ventromedial shelf
1. Present and without the septomaxillary shelf
2. Absent

**295. Premaxillary Internarial Process.**

0. Present
1. Absent

**296. Facial Part of Premaxilla Borders on Nasal.**

0. Absent
1. Present

**297. Ossified Ethmoidal Cribriform Plate of Nasal Cavity.**

0. Absent
1. Present

**298. Posterior Excavation of Nasal Cavity Into Bony Sphenoid Complex.**

0. Absent
1. Present, confluent with the nasal cavity
2. Present and partitioned from the nasal cavity

**299. External Bulging of Braincase in Parietal Region.**

0. Absent
1. Expanded, the parietal part of the cranial vault is wider than the frontal part, but expansion does not extend to the lambdoidal region
2. Greatly expanded, expansion of cranial vault extends to lambdoidal region

**300. Interparietal.**

0. Present as a separate element in adult
1. Absent

**301. Bony Tentorium Septum.**

0. Present
1. Absent

**302. Overall Size of Vermis.**

0. Small
1. Enlarged

**303. Lateral Cerebellar Hemisphere (Excluding Paraflocculus).**

0. Absent
1. Present

**304. Lateral Extension of Paraflocculus.**

0. Less than 30% of total cerebellar width
1. More than 30% of the cerebellar width

**305. External Division on Endocast Between Olfactory Lobe and Cerebral Hemisphere (Circular Sulcus).**

0. Absent
1. Present

**306. Anterior Expansion of Cerebral Hemisphere.**

0. Absent
1. Developed

**307. Expansion of Posterior Cerebral Hemisphere.**

0. Absent
1. Present

**308. Interprismatic Matrix.**

0. On all sides, widely separated prisms
1. Distinct inter-row sheets
2. Prisms "shoulder to shoulder," little interprismatic matrix

**309. Outer Aprismatic Zone.**

0. Present
1. Absent

**310. Lacrimal Foramen Number.**

0. One
1. Two
2. None

**311. Lacrimal Foramen Position.**

0. Within orbit
1. On face

**312. Preglenoid Process.**

0. Absent
1. Present

**313. Anterior Lamina of Petrosal.**

0. Absent
1. Present

### 314. Anterior Lamina of Petrosal Contribution to Braincase Wall.

0. Large (present)
1. Small (absent)

### 315. Curved Ridge Connecting Caudal Tympanic Process and Crista Interfenestralis.

0. Absent
1. Present

### 316. "Tympanic Process" of Kielan-Jaworowska.

0. Absent
1. Present

### 317. Fenestra Vestibuli.

0. Round (stapedial ratio <1.6)
1. Oval (stapedial ratio >1.6)


1. Goin FJ, et al. (2007) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, edad-mamífero Colhuehuapense). Part I: Introducción, Didelphimorphia y Sparassodonta [The South American early Neogene Metatheria (early Miocene, Colhuehuapian mammal age). Part I: Introduction, Didelphimorphia and Sparassodonta]. *Ameghiniana* 44:29–71. Spanish.
2. Rougier GW, Apesteguía S, Gaetano LC (2011) Highly specialized mammalian skulls from the Late Cretaceous of South America. *Nature* 479(7371):98–102.
3. Bonaparte JF (1990) New Late Cretaceous mammals from the Los Alamitos Formation, southern Patagonia. *Natl Geogr Res* 6:63–93.
4. Chornogubsky L (2011) New remains of the dryolestoid mammal *Leonardus cuspidatus* from the Los Alamitos Formation (Late Cretaceous, Argentina). *Paläontol Z* 85(3):343–350.
5. Rougier GW, Forasiepi AM, Hill RV, Novacek MJ (2009) New mammal remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. *Acta Palaeontol Pol* 54(2):195–212.
6. Scott WB (1905) Paleontology. Part II. Insectivora and Glires. *Rep Princeton Univ Expedition to Patagonia 1896–1899* 5:365–383.
7. Szalay F (1994) *Evolutionary History of the Marsupials and an Analysis of Osteological Characters* (Cambridge Univ. Press, Cambridge, UK).
8. Rougier GW (1993) *Vincelestes neuquenianus* Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina [*Vincelestes neuquenianus* Bonaparte (Mammalia, Theria a primitive mammal from the Lower Cretaceous of the Neuquen Basin]. PhD thesis (Univ. of Buenos Aires, Buenos Aires, Argentina). Spanish.
9. Ladevèze S, Asher RJ, Sánchez-Villagra MR (2008) Petrosal anatomy in the fossil mammal *Necrolestes*: evidence for metatherian affinities and comparisons with the extant marsupial mole. *J Anat* 213(6):686–697.


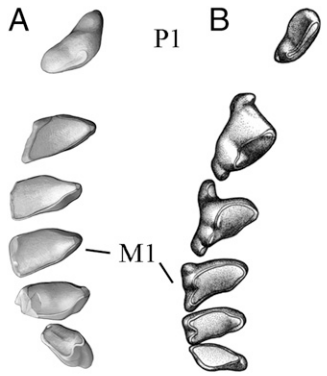


**Fig. S1.** Occlusal view (lingual to the right, mesial toward the top) of the upper dentition of *Necrolestes patagonensis* (*A*) and *Cronopio dentiacutus* (*B*). Not to scale. *Cronopio* shows primitive features lost in the younger and more derived *Necrolestes*, such as defined parastyles and less molarized posterior premolars. P1, first premolar; M1, first molar.

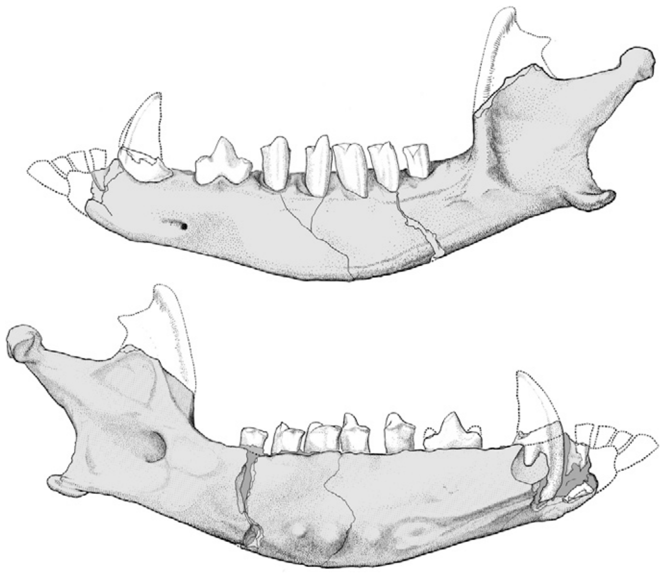

**Fig. S2.** Reconstructed left lower jaw of *Necrolestes patagonensis*, based mostly on YPM PU 15384 supplemented by specimen YPM PU 15699. *Upper* is lateral view and *Lower* is medial view. The incisors are staggered, a condition widespread in basal metatherians (1), but not common outside Theria. Note the bulges along the ventral edge of the jaw in medial view indicating the extreme length of the crowns inside the alveoli. A thin groove leading toward the symphysis in medial view could represent the anterior extent of a thin Meckel's cartilage.


1. Hershkovitz P (1995) The staggered marsupial third lower incisor: hallmark of cohort Didelphimorphia, and description of a new genus and species with staggered i3 from the Albian (Lower Cretaceous) of Texas. *Bonn Zool Beitr* 45(3–4):153–169.


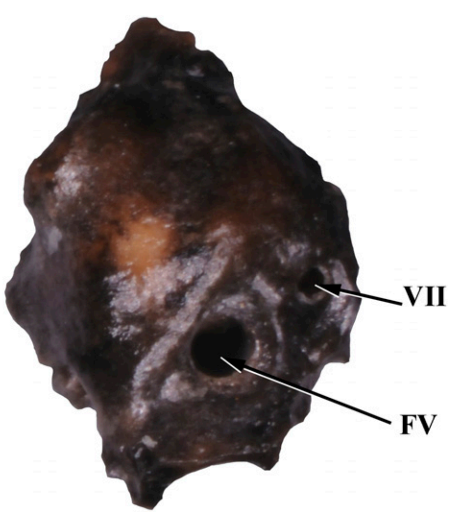


**Fig. S3.** Ventral view of the left petrosal of *Necrolestes patagonensis*, YPM PU 15699, showing the subcircular fenestra vestibuli. VII, facial foramen, exit of the VII cranial nerve; Fv, Fenestra vestibuli.

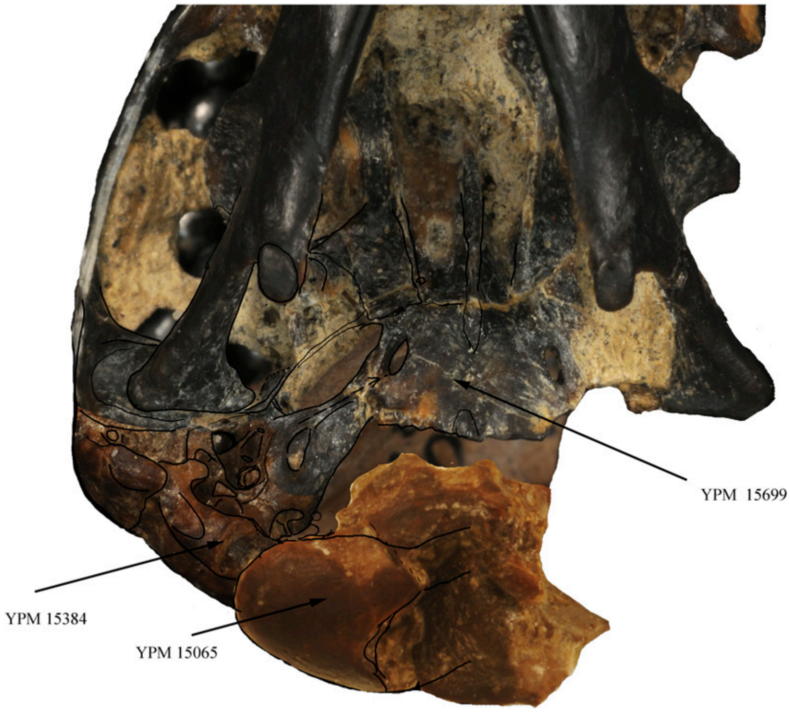


**Fig. S4.** Composite ventral view showing the bases for our reconstruction of the braincase in *Necrolestes patagonensis*.

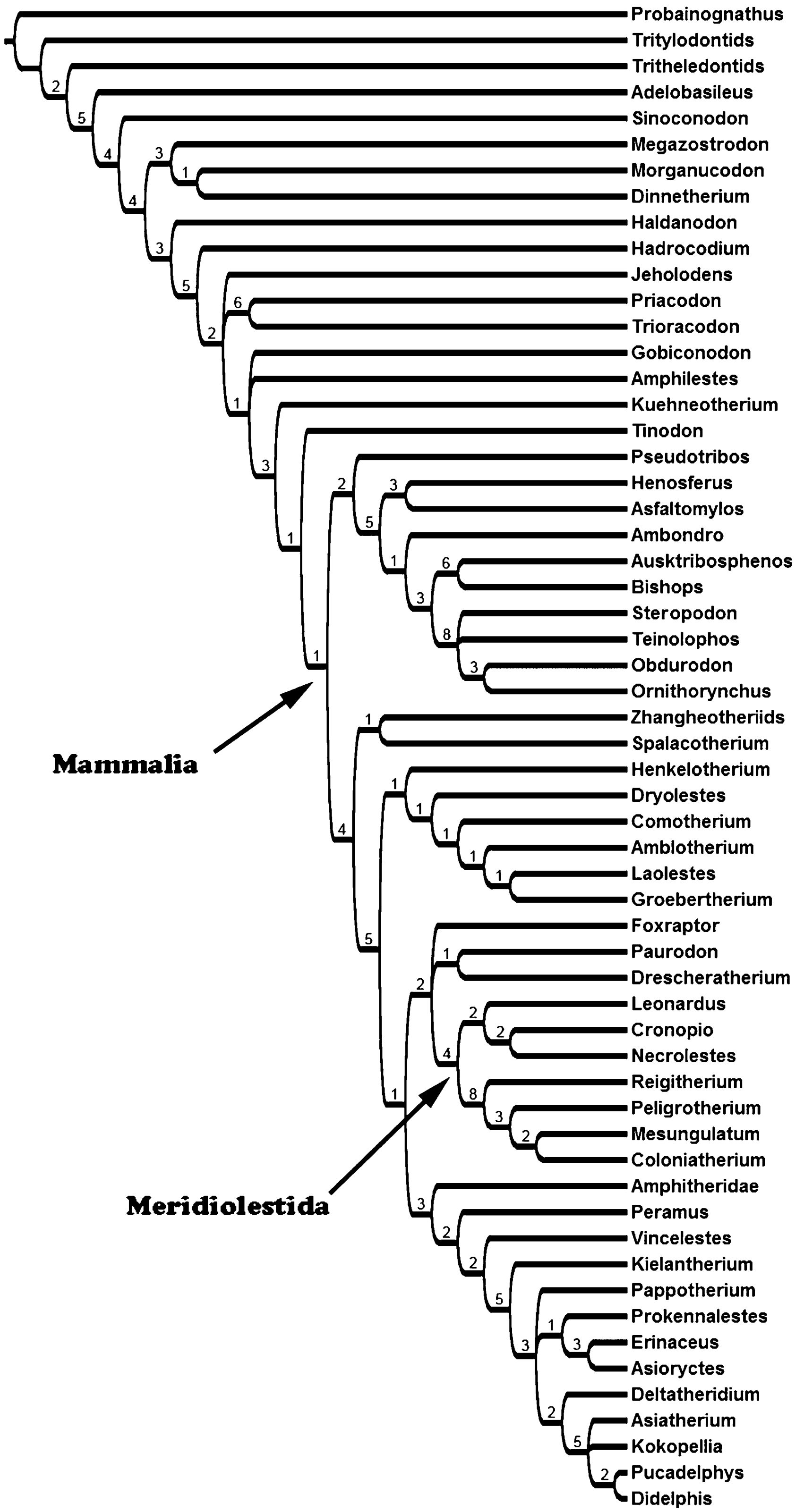


**Fig. S5.** Consensus tree of 36 trees (1,154 steps). The phylogenetic trees were obtained by using tree-search maximum parsimony ratchet analyses (1) using the program NONA (2), spawned through the program Winclada (3) (Asado, version 1.7 beta, by K. Nixon, Cornell University). Numbers at the nodes represent Bremer support values.

1. Nixon KC (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15(4):407–414.
2. Goloboff PA (1999) Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics* 15(4):415–428.
3. Nixon KC (2002) *Winclada/Asado Version 1.7* (Nixon KC, Ithaca, NY).

## Other Supporting Information Files

Dataset S1 (DOC)