

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

Guillermo W. Rougier^{a,b,1}, John R. Wible^b, Robin M. D. Beck^c, and Sebastian Apesteguía^{d,e}

^aDepartment of Anatomical Sciences and Neurobiology, University of Louisville, Louisville, KY 40202; ^bSection of Mammals, Carnegie Museum of Natural History, Pittsburgh, PA 15206; ^cSchool of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia; ^dCEBBAD–Fundación de Historia Natural ‘Félix de Azara’, Universidad Maimónides, 1405 Buenos Aires, Argentina; and ^eConsejo Nacional de Investigaciones Científicas y Técnicas de Argentina, C1033AAJ Buenos Aires, Argentina

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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.

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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), palaeonodonts (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 re-interpret 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,

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¹To whom correspondence should be addressed. E-mail: grougier@louisville.edu

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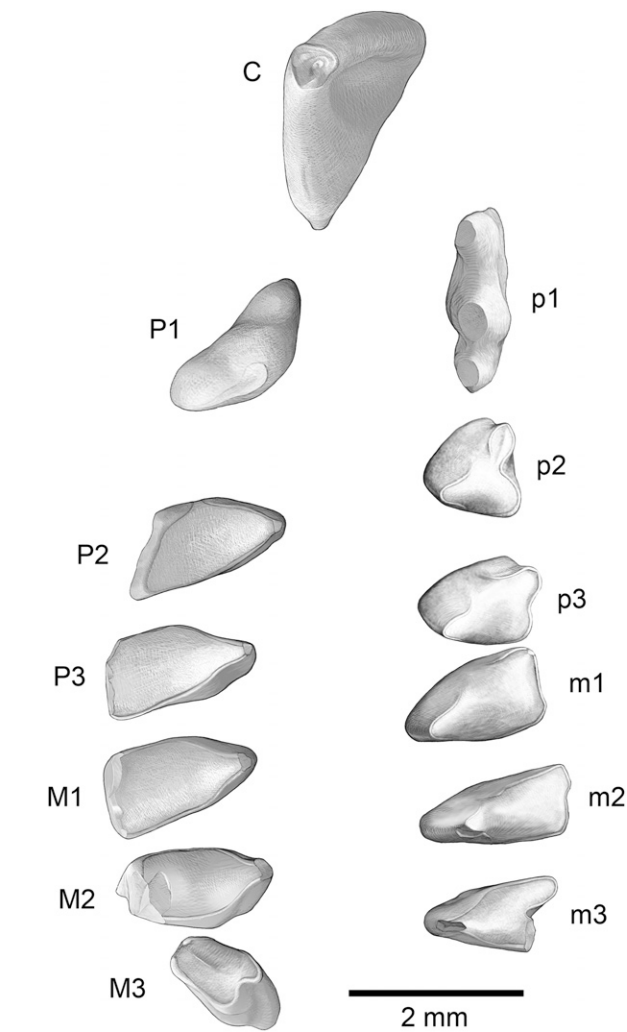


Fig. 1. Composite illustration of the partial upper and lower dentitions (occlusal view, lingual toward the midline) of *N. patagonensis* from the early Miocene of Argentina, ~16 MYA (2), based on YPM PU 15384 and 15699. C, upper canine; P/p, premolar; M/m, molar; YPM PU, Yale Peabody Museum Princeton 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 4C).

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

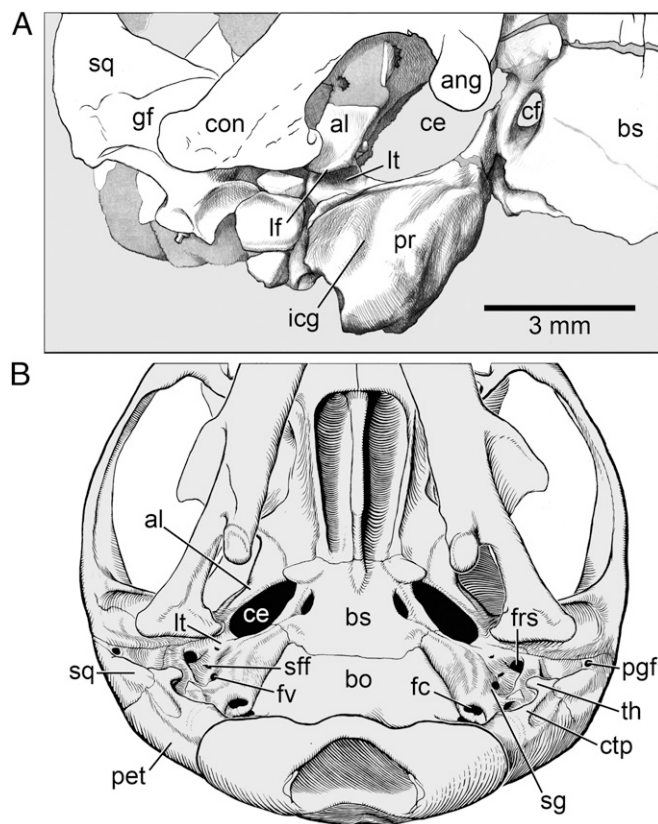


Fig. 2. Basicranium of *N. patagonensis* in ventral view. (A) Ventral view of YPM PU 15699 showing partial right petrosal and lower jaw in articulation; missing is the basioccipital and posterior parts of the petrosal and squamosal, as well as a portion of the lateral braincase sidewall. (B) Reconstruction 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.

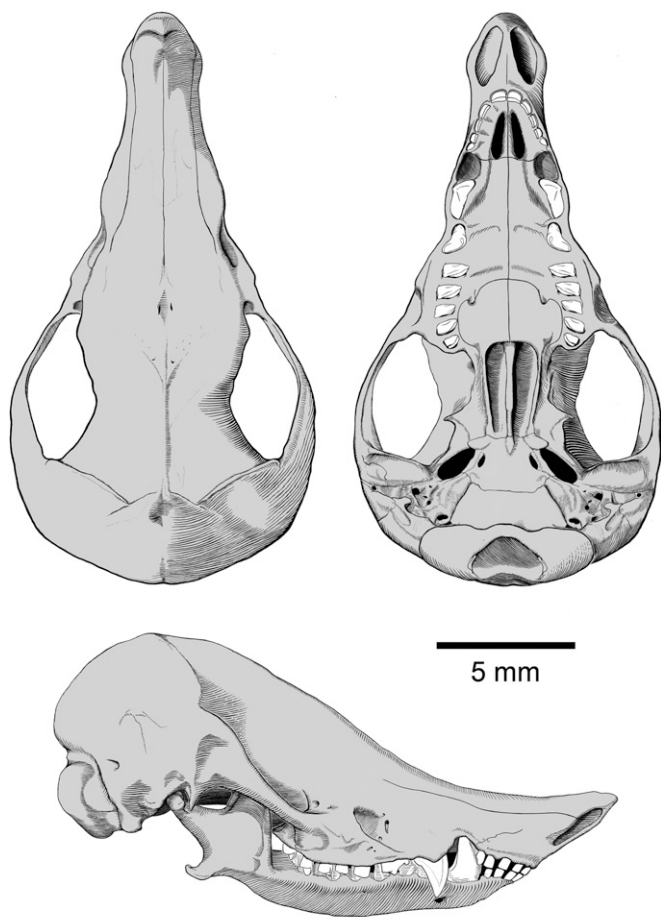


Fig. 3. Reconstruction of the skull of *N. patagonensis* in dorsal, ventral, and lateral views.

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 reparation. Our reparation 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. 2A); together, these specimens allow us to make a robust reconstruction of the basicranium (Fig. 2B; 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. 2A). 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. 2A). 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 stapedia artery (Fig. 2B), an opening for the ramus superior of the stapedia artery (Fig. 2B), and a large posttemporal canal. As reconstructed by us, the stapedia 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 stapedia 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

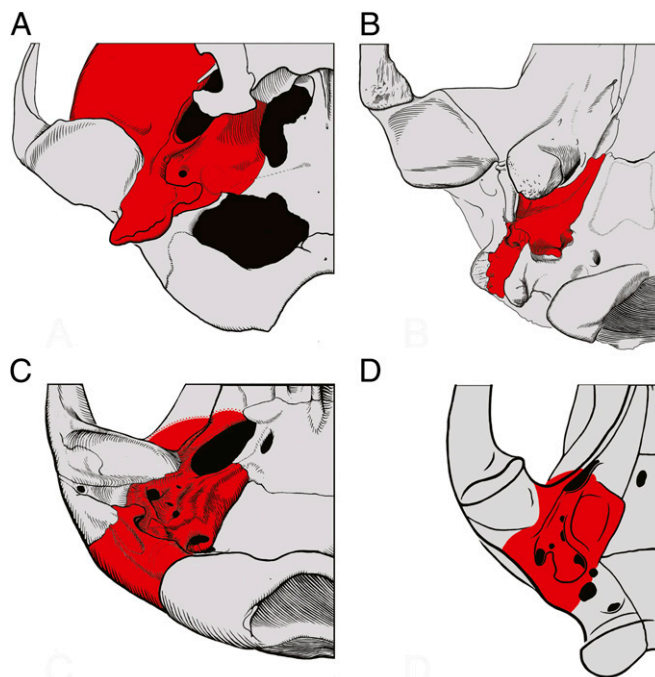


Fig. 4. Right basicrania in ventral view. (A) *Ornithorhynchus anatinus*, based on CM 50815. (B) *Didelphis virginiana*, based on CM 39794. (C) *Necrolestes patagonensis*, as reconstructed here. (D) *Cronopio dentiacutus*, based on MPCA 453. Petrosal contribution to basicranium and extension into the braincase sidewall 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.

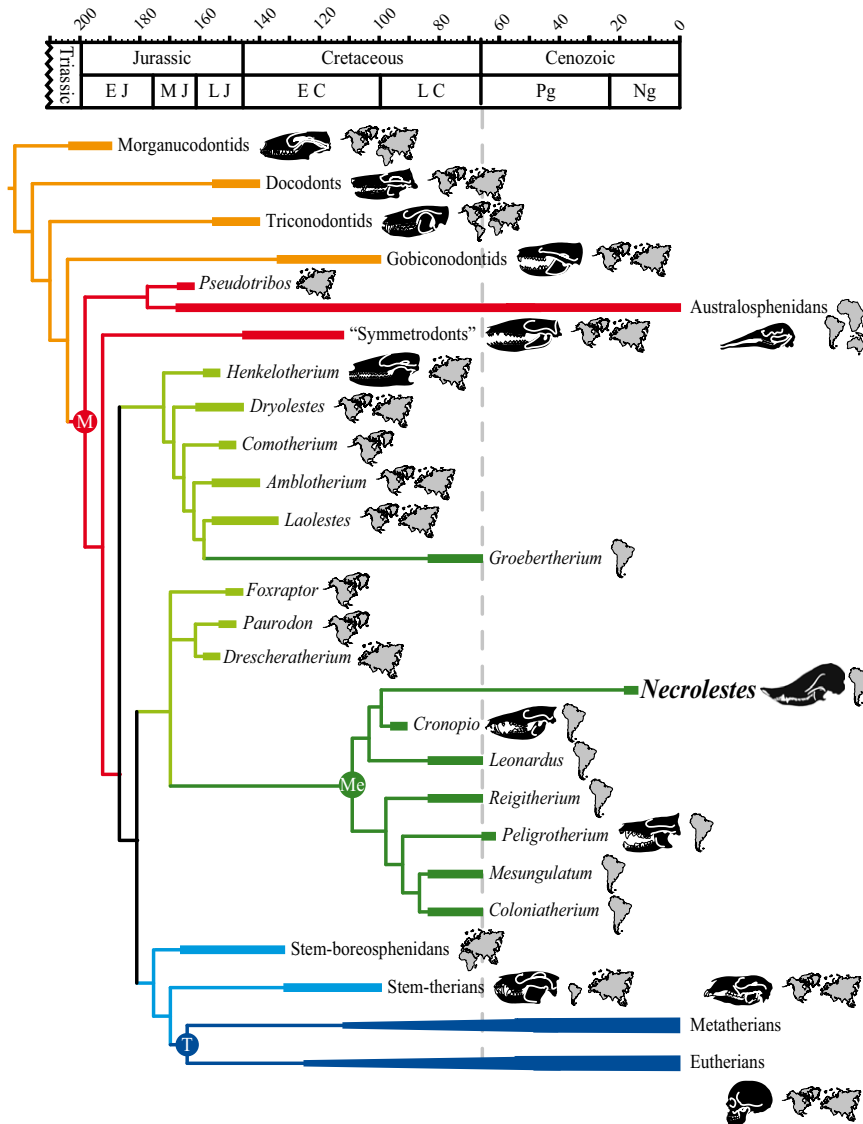


Fig. 5. Simplified phylogenetic tree showing *Necrolestes* as a member of the Meridiolestida, a group widely represented in SA. Some of the archaic Mesozoic lineages survived into the Cenozoic only in SA, Antarctica, and Australia. This tree is the strict consensus of 36 equally most parsimonious trees (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. 4A) and extinct nontherian mammals (Fig. 4D), *Necrolestes* (Fig. 4C) has a large anterior lamina, lateral flange, and lateral trough, and the ventral opening of the cavum epiptericum is large. In therians (Fig. 4B), 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 diplœtica 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 gondwanatherians, 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.

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