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Source: American Museum Novitates, 2007(3546) : 1-40

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2007)3546[1:NARNAP]2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3546, 40 pp., 21 figures, 1 table January 15, 2007

Neither a Rodent nor a Platypus: a Reexamination of *Necrolestes patagonensis* Ameghino

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ABSTRACT

We present new descriptions, figures, and interpretations of well-preserved cranioskeletal elements of the early Miocene, fossorial mammal *Necrolestes patagonensis* from Argentina. As previously noted, this animal is highly apomorphic and its phylogenetic affinities are difficult to interpret. Its derived features include hypsodont upper cheek teeth, a partially fused cervical spine, an unfused atlas consisting of separate right and left *massae*, and a distally ossified flexor tendon of the forearm. Characters that support its status as a therian mammal include a coiled cochlear housing of the inner ear. Consistent with its status as a metatherian is the presence of five upper incisors, transverse canal foramina, and a broad proximal fibula. However, we cannot confirm other characters claimed by previous researchers as evidence for affinity with marsupial or nonplacental mammals, such as the presence of an inflected mandibular angle and epipubic bones. Furthermore, *Necrolestes* shows similarities to eutherian mammals, such as small incisive foramina and possibly three molars. On biogeographic and some anatomical grounds, identification of *Necrolestes* as a metatherian remains a compelling option. However, pending a combined-data phylogenetic analysis encompassing Theria and accounting for the anatomical diversity of *Necrolestes*, possible membership in Eutheria should not be ruled out.

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ISSN 0003-0082

INTRODUCTION

Necrolestes patagonensis was first described by Florentino Ameghino in 1891 from the early Miocene Santa Cruz beds of Patagonia. Ameghino, followed by Scott (1905), compared this animal favorably with African golden moles (Chrysochloridae). It has subsequently been associated with marsupial moles (Leche, 1907), didelphoids (Winge, 1941; Patterson, 1958), palaeanodonts (Saban, 1954), xenarthrans (McDowell, 1958), ameridelphian marsupials (Szalay, 1994: 346), and even as a middle Cenozoic holdover of the Gondwanatheria (Van Valen, 1988). Some authors have doubted the marsupial affinities of *Necrolestes*, but have not offered an alternative placement (Turnbull, 1971; Archer, 1984). The initial publication (Ameghino, 1891) did not include figures or refer to a type specimen, but based on Ameghino's descriptive notes (p. 303), the material first described consisted of a relatively complete lower jaw with an intact mandibular condyle. Shortly after Ameghino's initial work, more complete material of *Necrolestes* was collected by J. B. Hatcher and O.A. Peterson between 1896 and 1899 consisting of partial skeletons of three individuals (Scott, 1905). Since then, expeditions from the MACN–La Plata and Duke University have recovered more material (e.g., Goin et al., in press), but the skeletons first described by Scott (1905) remain the most complete yet discussed in the literature.

"Insectivoran" (i.e., lipotyphlan and tenrecoid sensu Asher, 2005) and palaeanodont placental mammals are largely absent throughout the South American Cenozoic. Among these taxa, only the single genus *Cryptotis* (Soricidae) has had a post-Pliocene distribution in northern South America. Due in part to the biogeographic enigma that would be caused by the presence of either group in the South American Miocene, most recent authors have followed Patterson (1958) in identifying *Necrolestes* as a marsupial. In this paper we reassess the status of *Necrolestes*, and focus on the hypothesis that this extinct South American mammal is in fact a metatherian. Both Scott (1905) and Patterson (1958) provided fairly detailed descriptions of certain parts of the Hatcher-Peterson specimens. We do not repeat all of their descriptions, but point out issues of disagreement between the two authors, our view of who is correct, and describe several anatomical regions not discussed by either author. In addition, we present the first detailed photographs of these fossils ever published.

Like *Plesiorycteropus* (MacPhee, 1994), *Necrolestes* has posed an enigma for multiple generations of paleontologists. Despite the high quality of its osteological remains, making sense of its relationships within the framework of modern mammal diversity has proven difficult. In terms of the attention paid to it by scientists over the past 100 years, *Necrolestes* shows an interesting resemblance to the Malagasy subfossil *Plesiorycteropus*: both were first named in the closing years of the 19th century; both remained in obscurity for much of the 20th century; and both were the subjects of seemingly conclusive revisions by Bryan Patterson (1958 for *Necrolestes*, 1975 for *Plesiorycteropus*). Like MacPhee (1994) did for *Plesiorycteropus*, we too take issue with some of the conclusions made by Patterson, in our case regarding *Necrolestes*.

Institutional Abbreviations

BMNH	The Natural History Museum London, United Kingdom
TM	Transvaal Museum Pretoria, South Africa
YPM-PU	Yale Peabody Museum Princeton University collection, USA
ZIUT	Zoologisches Institut Universität Tübingen, Germany
ZMB	Zoologisches Museum Berlin, Germany

ANATOMICAL DESCRIPTIONS

Cranium

Dentition: Scott gave the formula 4.1.3.3/4.1.3.3; Patterson suggested 5.1.2.4/4.1.2.4. Regarding the incisor count, Patterson was correct. Posterior to the intact upper I1s there are clearly four alveoli, including a partial right I5 in YPM-PU 15065 (fig. 1). In addition, the left side of YPM-PU 15699 preserves the anterior four single-rooted incisors, with a root fragment of left I5 just anterior to the canine; on the right side I5 is entirely intact (fig. 2; Patterson, 1958: 6). Identification of incisors vs. more posterior teeth is possible using morphology and origin, with incisors rooted at least partially in the premaxilla, and canines, premolars, and molars in the maxilla. YPM-PU 15065 shows breaks just anterior to the upper canines, within the fossa that receives each lower canine, which we believe correspond to the premaxilla-maxilla boundary (fig. 1). All of the aforementioned upper incisors occur within the region we identify as the premaxilla. Lower incisors are more difficult to homologize. Of the anterior four lower teeth (i.e., the putative incisors), the first is the largest, showing a root extending approximately to the base of the jaw below the lower canine. The succeeding three teeth are small and nonhypsodont, and in YPM 15699 appear to show enamel restricted to the crown, in contrast to *Necrolestes*' hypsodont cheek teeth. We follow both Scott and Patterson in identifying the pair of hypertrophied, trenchant lower antemolars as canines based on their form.

The best criterion to distinguish molars from premolars is tooth replacement, a feature for which we unfortunately do not have any direct evidence in the YPM-PU specimens. However, new material described by Goin et al. (in press) shows an erupting premolar anterior to three more posterior cheek teeth, suggesting that Scott (1905) was correct in identifying three molars. We would therefore argue that the correct dental formula for *Necrolestes* is 5.1.3.3/4.1.3.3.

A break in the maxilla posterolateral to the lacrimal foramen on the right side of YPM-PU 15065 exposes the dorsal extremes of two posterior cheek teeth (M1 and M2 following Goin et al., in press). These teeth are hypsodont, without roots, and retain enamel on their lingual aspect dorsally into the maxilla (fig. 1D). When viewed from an anterior perspective, the cheek teeth of *Necrolestes* are curved from dorsal apex to occlusal surface, showing a lateral concavity. From a lateral perspective the cheek teeth are also curved, showing a posterior concavity (fig. 1C).

JAW: Patterson (1958: 8) suggested that although the angular process was small, it "bears an internal ledge and this is inflected and concave dorsally." Ameghino (1891: 303) also described the angular process with a small and internally directed inflection. However, we do not regard this kind of inflection to be comparable to that of, for example, didelphids or borhyaenids. Rather, it shows some resemblance to that of *Gypsonictops* (Clemens, 1973: figs. 2, 3). In fact, and somewhat ironically, the dentary of the placental afrotherian *Chrysochloris* shows a much more prominent, medially directed angular process than that of *Necrolestes* (fig. 3), considerably broader than that of the marsupial mole *Notoryctes* (fig. 3D). The morphology of the chrysochlorid angular process is no doubt influenced by its articulation with the hyoid apparatus (Bronner, 1991).

Scott (1905: 369) suggested that the dentary of *Necrolestes* is "exceedingly" like that of *Chrysochloris*. Because the coronoid process of the YPM-PU 15384 *Necrolestes* dentary (fig. 3B) is broken off close to its base, it shows a somewhat chrysochlorid-like form. However, not only is the coronoid process prominent in an intact specimen (YPM-PU 15699), but it also shows an additional, posteriorly directed process close to its apex (fig. 3A). Furthermore, compared with the jaw of *Chrysochloris* (fig. 3C), *Necrolestes* has a more gracile mandibular angle, a prominent masseteric fossa, a more inferiorly situated mandibular foramen, and a shorter, dorsoventrally deeper mandibular symphysis. Hence, we disagree with Scott's assessment of similarity in jaw structure between the two taxa.

CUSP HOMOLOGIES: Patterson (1958:4) referred to the main cusp of the upper molars of *Necrolestes* as "presumably paracones," an interpretation that at first glance might be shared by many contemporary paleomammalogists. However, we note that the main cusp in molars of zalambdodont marsupials such as *Notoryctes* has been interpreted to be the metacone, not the paracone (Archer et al., 2000; Long et al., 2002: 67; Asher and Sánchez-Villagra, 2005). Similarly, Goin and Candela (2004) recently described the putative metatherian genus *Kiruwamaq* based on a zalambdodont-like upper cheek tooth, showing a large metacone and diminutive paracone. Occlusal relations can elucidate some of these

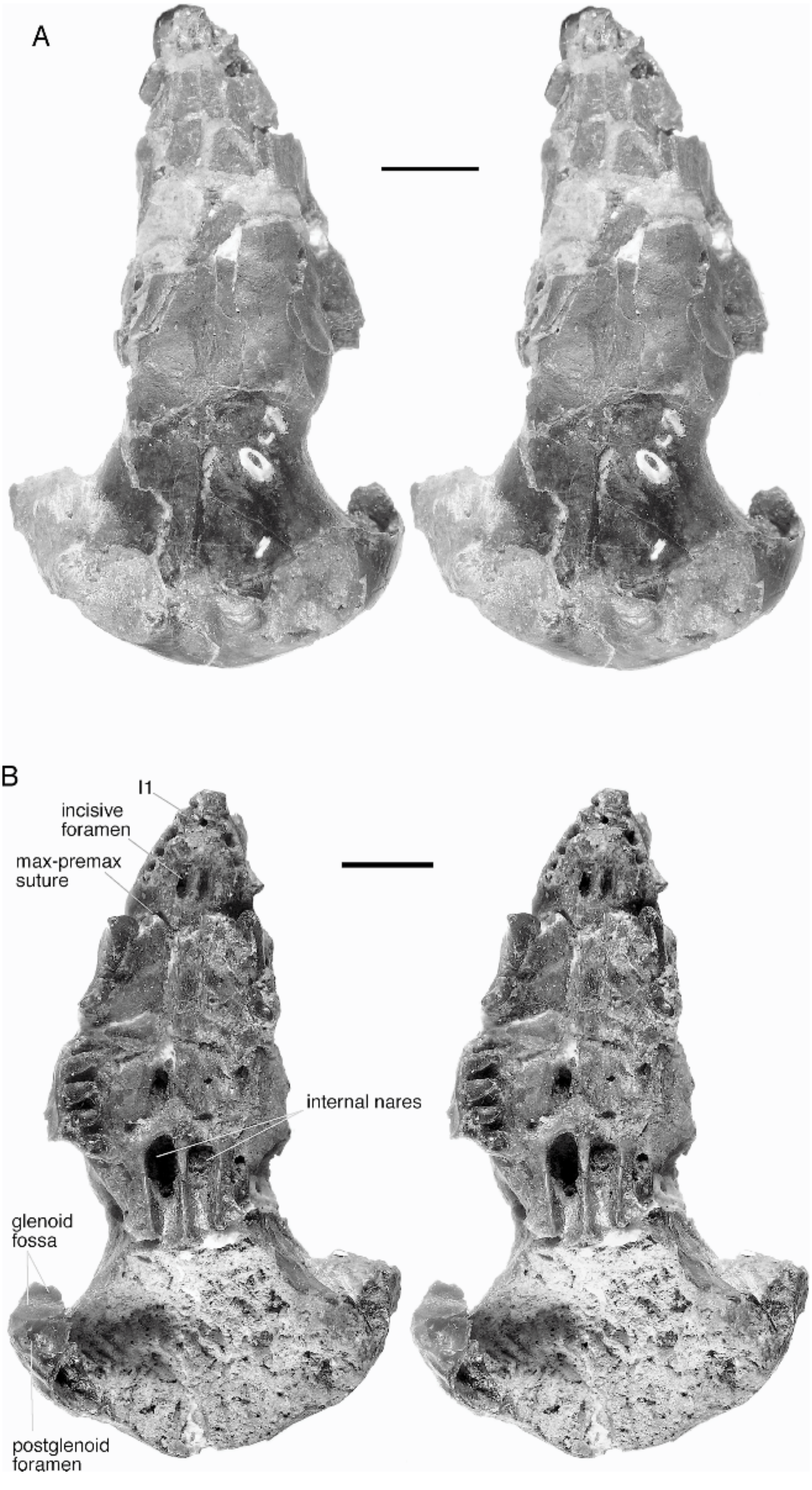
A
B
I1
incisive foramen
max-premax suture
internal nares
glenoid fossa
postglenoid foramen

Fig. 1. Continued.

Fig. 1. Skull of *Necrolestes* YPM-PU 15065 in stereo (**A**) dorsal, (**B**) ventral, (**C**) lateral views with (**D**) closeup of dorsal maxillary region showing hypsodont, rootless cheek teeth. Arrows in **C** and **D** indicate location of internal temporal space and course of infraorbital canal, respectively. Scale bars = 5 mm.

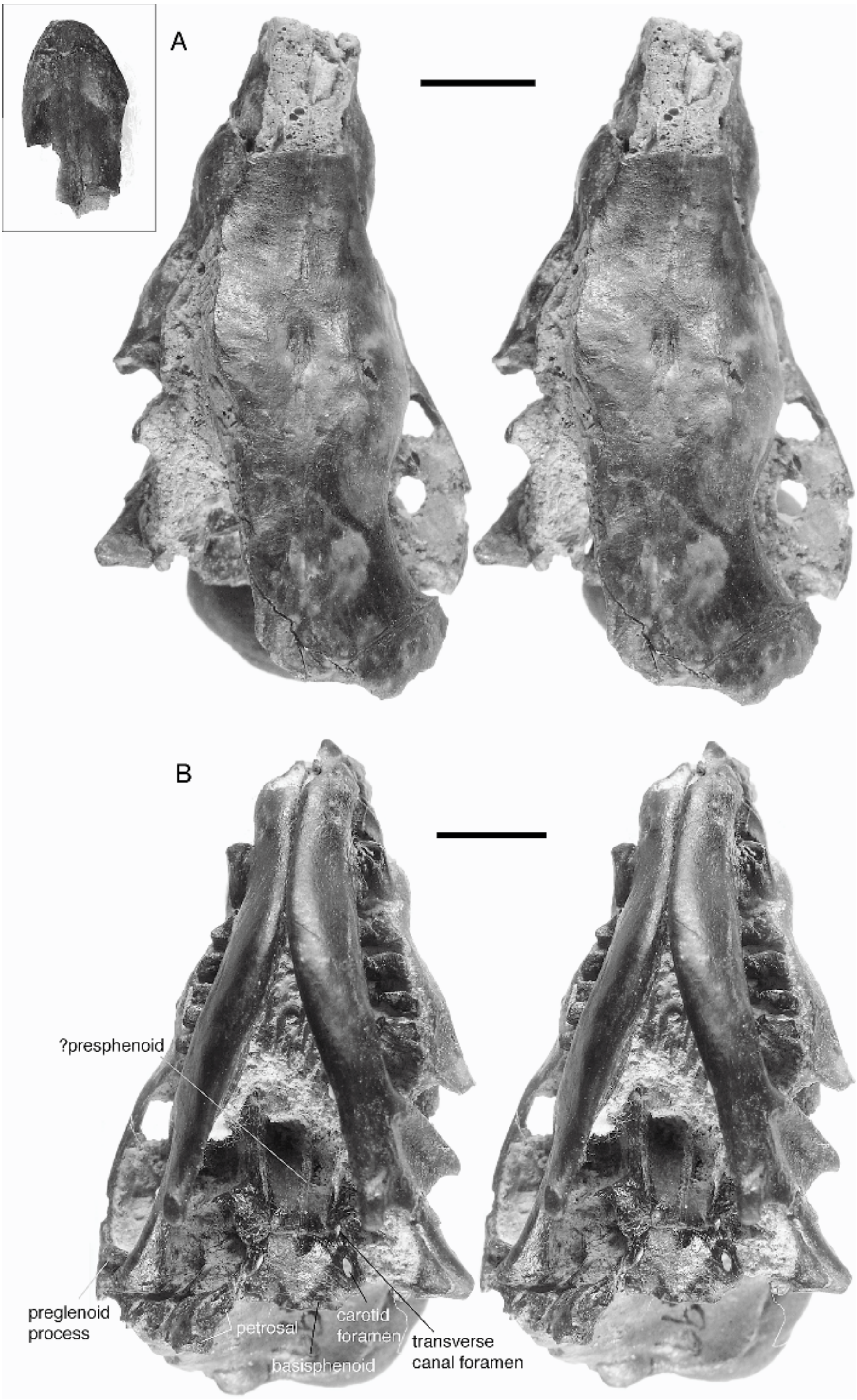

Fig. 2. *Necrolestes* YPM-PU 15699 in stereo (**A**) dorsal, (**B**) ventral, and (**C**) lateral views, with inset showing anterior fragment of nasal bone in dorsal view. Scale bars = 5 mm.

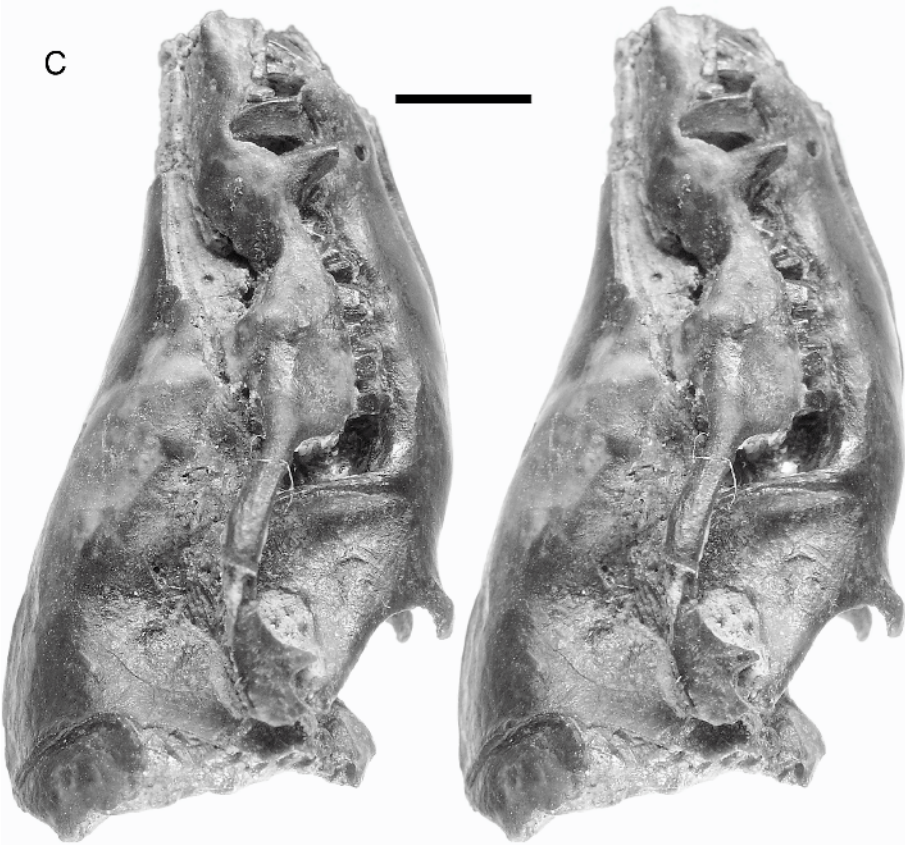

Fig. 2. Continued.

cusp homologies: for example, the paracone occludes in or adjacent to the lower ectoflexid, lateral to the talonid basin; the protocone occludes within the talonid basin; and compared to the paracone, the metacone occludes closer to the paracristid of the more posterior lower molar (e.g., M1 metacone-m2 paracristid). With the caveat that occlusal relations across tooth loci are obviously contingent upon jaw mobility, and that noninterlocking upper and lower teeth are not as canalized as those that interlock (Polly et al., 2005), we tentatively note that the main upper cusp of *Necrolestes* could be the metacone. As discussed by Asher and Sánchez-Villagra (2005: fig. 2), the main upper cusp of each molar in YPM-PU 15699, which preserves uppers and lowers in occlusion, shows closer proximity to the preparacristid of the next most-posterior lower molar than to any structure on the lower molar of the same tooth locus. We regard this occlusal pattern as suggestive that the main upper molar cusp in *Necrolestes* is the metacone, not the paracone.

Enamel Microstructure: An isolated right molar from YPM-PU 15384 was embedded in resin and sectioned longitudinally and transversely to obtain information about its enamel microstructure. Enamel terminology follows Koenigswald and Sander (1997a) and Martin (1999a, b); for preparation techniques, see Martin (2004). The schmelzmuster of *Necrolestes* (fig. 4) was compared to that of various Mesozoic taxa, as well as to data on small placentals and marsupials drawn from a large body of literature (see Koenigswald and Sander [1997b] and literature cited therein). In addition, we compared the pattern of *Necrolestes* with that of sectioned right upper molars of *Chrysochloris* (ZMB 76872), *Notoryctes* (ZIUT SZ10068), and *Potamogale* (ZMB 71592).

The enamel distribution on the *Necrolestes* upper molar is very asymmetrical. Enamel is thickest (140 µm) on the lingual side and very thin or even missing on the labial side. In the longitudinal section (fig. 4A) two zones are evident. The inner zone consists of radial enamel with the prisms inclined about 40° apically. After three fifths of the enamel thickness, prisms turn simultaneously in horizontal direction (inclination 0°), forming an outer layer of tangential enamel. Prisms and interprismatic matrix (IPM) run parallel in the outer zone and therefore are difficult to distinguish. Prisms and IPM seem to be at least partially confluent, forming a prismless external layer (PLEX). In the cross section (fig. 4B), prisms are cut transversely in the inner zone and longitudinally in the outer zone. In this section the distinction between prisms and IPM in the outer zone is somewhat more clear. From the cross section it is evident that the PLEX apparently is restricted to the outer 10–20 µm of the enamel layer. The radial enamel of *Necrolestes* with a single turn of prisms is very similar to that of the other small placentals and marsupials that have been studied.

In longitudinal section (fig. 4C), the marsupial mole *Notoryctes* exhibits a schmelzmuster with radial enamel and steeply apically inclined prisms in the inner zone and a simultaneous antapical turn of prisms in the outer zone. In the cross section (fig. 4D), the prisms are cut obliquely transversely in the inner zone and almost longitudinally in the outer zone; the thick IPM is well exposed. The golden mole *Chrysochloris* has a very similar schmelzmuster with radial enamel in the inner zone and tangential enamel in the outer zone; prisms and IPM tend to be confluent. In the longitudinal section of the protocone, the radial prisms of the inner zone are cut longitudinally (fig. 4E), and in the cross section they are cut transversely (fig. 4F).

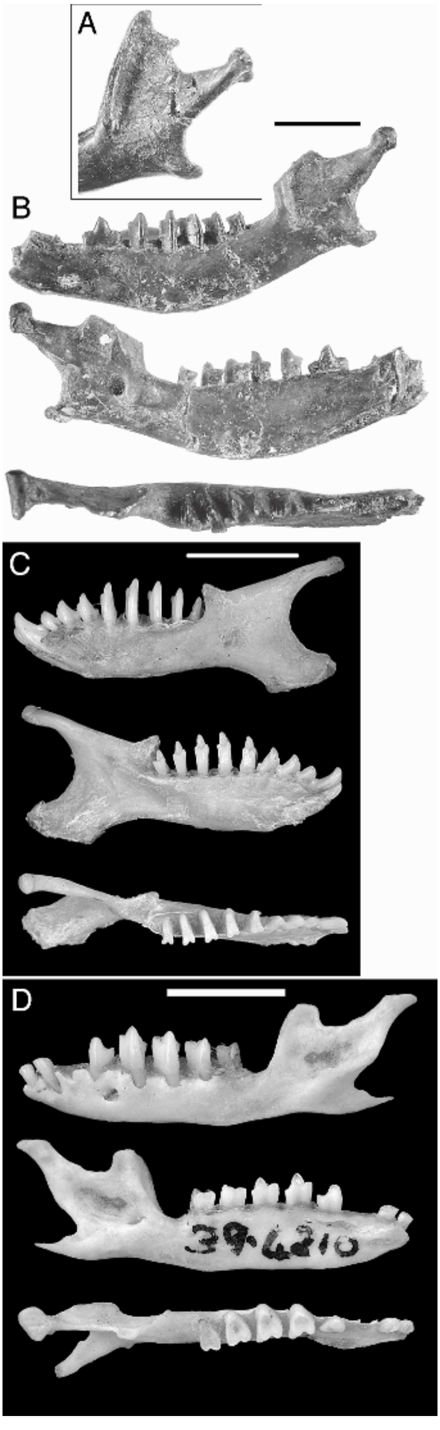

Fig. 3. Mandibles of (**A**, **B**) *Necrolestes patagonensis* (A shows coronoid process of YPM-PU 15699; B shows jaw of YPM-PU 15384), (**C**) *Chlorotalpa leucorhina* ZMB 31505, and (**D**)

←

Notoryctes typhlops BMNH 39.4210 in external (top), internal (middle) and occlusal (bottom) views. Scale bars = 5 mm.

The rounded-prism cross sections are surrounded by thick IPM. In the outer zone, prisms and IPM are confluent and hardly distinguishable. The otter shrew *Potamogale* has a generally similar schmelzmuster with apically inclined prisms in the inner zone and a simultaneous antapical turn in the outer zone (figs. 4G, 4H). Prisms and IPM are more clearly distinct in the outer zone than in the other taxa studied.

The schmelzmuster of *Necrolestes* and the other taxa studied here represent the plesiomorphic therian schmelzmuster type that is typical for small marsupials (Peradectia and Didelphimorphia) and placental insectivorans (Koenigswald, 1988, 1997a, b; Koenigswald et al., 1987; Koenigswald and Goin, 2000). A very similar schmelzmuster has also been detected in the molars of various Mesozoic non-therian taxa (Wood and Stern, 1997; Wood et al., 1999) as well as in the incisors of zalambdalestids, pseudictopids, and early gliriforms such as *Eurymylus* and *Eomylus* (Martin, 1999a, b, 2004). Evidently derived characters of gondwanatheres (Koenigswald et al., 1999), such as an IPM that runs at a distinct angle to the prisms in the radial enamel of the molars and prisms increasing in thickness towards the exterior of the tooth, are not evident in our observations of *Necrolestes*. The schmelzmuster of *Necrolestes* represents the plesiomorphic therian condition that characterizes many small placentals and marsupials.

BASICRANIUM: Scott (1905: 368) referred to an ‘‘ossified and moderately inflated’’ auditory bulla. However, we agree with Patterson (1958) that Scott was actually referring to the ventrum of the pars cochlearis itself. None of the *Necrolestes* material shows any sign of ossifications enclosing the middle ear (figs. 1, 2). In fairness, the YPM-PU specimens do not have completely intact, articulated basicrania. The most complete is on 15699, which has a petrosal still articulated with the skull, bounded laterally by the jaw joint and anteromedially by the basisphenoid; however, regions posterior and medial to the petrosal are missing (fig. 2). YPM-PU 15384 preserves a fragment consisting of petrosal, squamosal, and a part of the still-articulated mandibular condyle (fig. 5). Neither specimen preserves an ectotympanic. They nevertheless clearly lack alisphenoid, basisphenoid, and petrosal contributions to an ossified bulla. Terrestrial mammals with prominent, ossified ecto- or entotympanic bullae tend to have strong coossifications and/or articulation scars, such that the contribution of tympanic elements to a bulla can often be inferred. Since the basicranial remains of *Necrolestes* show no sign of an ecto- or entotympanic bulla, we agree with Patterson (1958) that it lacked an ossified bulla.

CT scans of the inner ear of YPM-PU 15699 and 15384 indicate that the cochlea was coiled, making nearly a full turn. While this degree of coiling is not as tight as in some placental mammals, it is considerably more than that seen in monotremes. Interestingly, hedgehogs, sea cows, vombats, and the marsupial mole *Notoryctes* are among the only extant therians that also show reduced cochlear coiling (Gray, 1907; Sánchez-Villagra and Schmelzle, in press).

Adult monotremes, didelphids, dasyurids, and other metatherians such as *Pucadelphys* and *Deltatheridium*, but not *Dromiciops*, *Mayulestes*, or borhyaenids, possess a prootic canal (Wible and Hopson, 1995; Wible et al., 2001). In didelphids, this structure transmits venous blood from the prootic sinus (Sánchez-Villagra and Wible, 2002), passes through an osseous canal connecting the ventrum of the pars canalicularis of the petrosal and a small foramen immediately lateral to the secondary facial foramen, and leaves the tympanic region posteroventrally adjacent to the facial nerve. Except for petrosals assigned to the eutherian taxon *Prokennalestes* (Wible et al., 2001) and specimens assigned to the taxonomically ambiguous ‘‘zhelestids’’ (Ekdale et al., 2004), the prootic canal has not been explicitly documented in any eutherian mammal. The anteroventral pars canalicularis of *Necrolestes* is smaller than that of didelphids and shows no sign of a prootic canal (fig. 5).

Wible et al. (2001: character 153) noted that the state of the internal acoustic meatus (‘‘shallow, with thin prefacial commissure’’) comprises a synapomorphy for Eutheria in an analysis of selected crown and stem Theria, focusing on extinct taxa (Rougier et al., 1998). However, they noted in addition that the

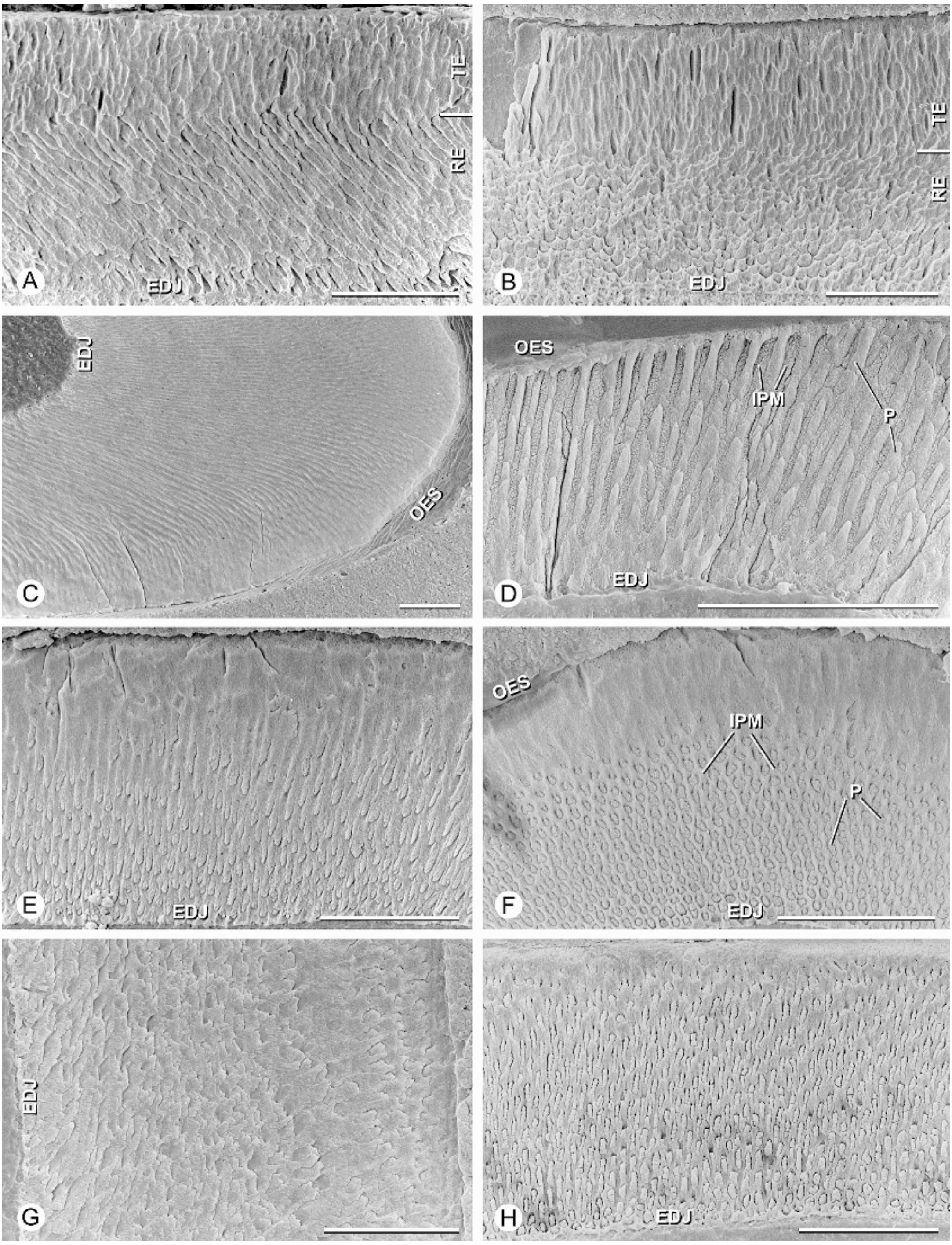

Fig. 4. Scanning electron microscope (SEM) photos of sectioned and etched right M1s showing enamel microstructure of (**A**, **B**) *Necrolestes* (YPM-PU 15384; occlusal surface to the left in A), (**C**, **D**) *Notoryctes* (ZIUT SZ10068; tip of protocone to the right in **C**), (**E**, **F**) *Chrysochloris* (ZMB 76872), and (**G**, **H**) *Potamogale* (ZMB 71592; occlusal surface to the top in **G**). Longitudinal sections are listed in the left

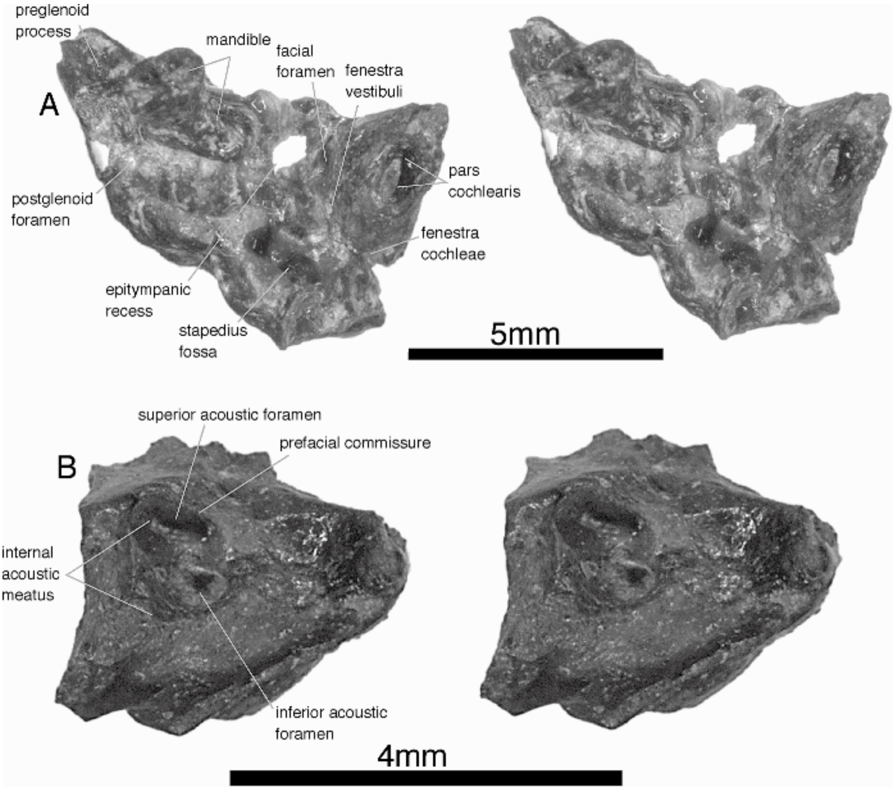

Fig. 5. Stereo views of *Necrolestes* (YPM-PU 15384): (**A**) right petrosal and glenoid region in ventral view; (**B**) left petrosal fragment in dorsal view showing internal acoustic meatus (bottom). Anterior is at top, lateral towards left. Note that the articulated mandibular condyle in **A** has been slightly displaced medially.

"shallow-thin" state also occurs in certain metatherians (e.g., *Turgiodon*, deltatheridians, *Pucadelphys*, *Marmosa*, *Didelphis*, *Dromiciops*, and dasyurids). *Necrolestes* also exhibits a relatively thin prefacial commissure (fig. 5), similar to that of *Monodelphis*.

Neither Patterson nor Scott mentioned the unusual character of the *Necrolestes* skull near the mandibular glenoid articulation. Although YPM-PU 15065 is missing most of the basicranium (fig. 1B), it still retains the right glenoid articulation for the jaw, and shows considerable similarity to the jaw articulation in golden moles and *Notoryctes*. As opposed to the morphology seen in *Monodelphis* (fig. 6), and resembling that of golden moles and *Notoryctes*, the mandibular glenoid fossa in *Necrolestes* is situated posteriorly, lateral to the pars cochlearis of the petrosal (fig. 2B) and probably also dorsal to the external auditory meatus, although the latter structure is not intact in any of the YPM-PU specimens. In addition, the postglenoid process in *Necrolestes* is diminutive, much smaller than that of *Monodelphis*.

Dorsal to the mandibular glenoid fossa, the external sidewall of the braincase in YPM-PU 15065 shows a deep excavation, creating a space internal to the squamosal root of the zygomatic arch (fig. 1C). As in chrysochlorids such as *Eremitalpa*, this space probably served

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column, cross sections in the right. EDJ, enamel-dentine junction; IPM, interprismatic matrix; OES, outer enamel surface; P, prism(s); RE, radial enamel; TE, tangential enamel. Scale bars = 50 μm.

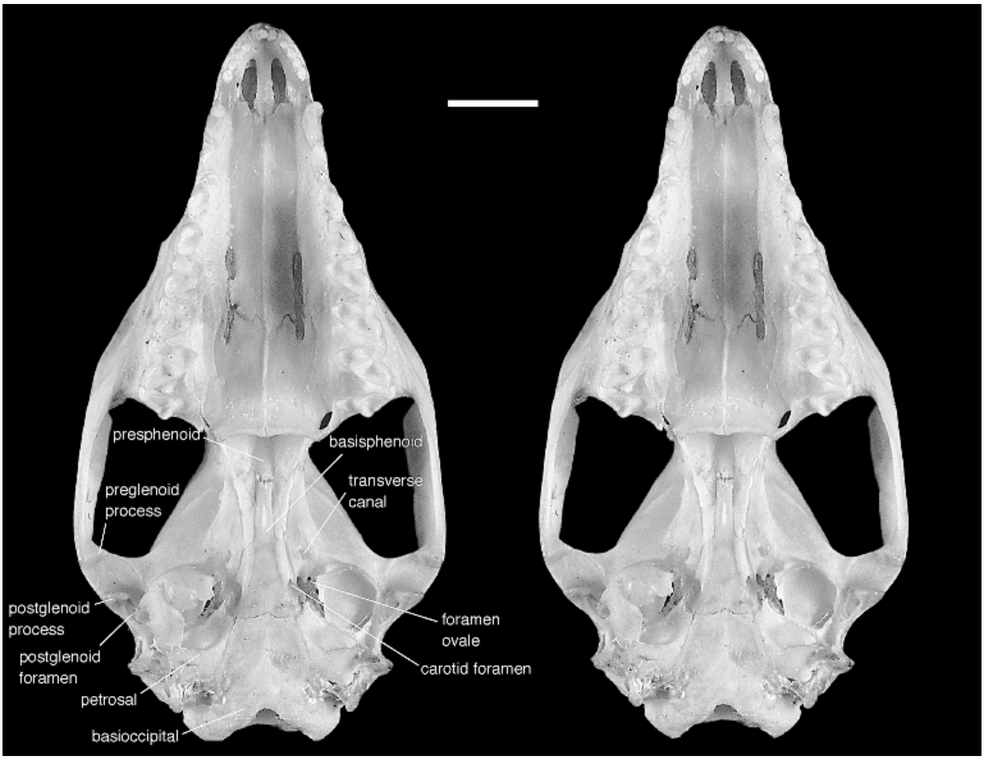

Fig. 6. *Monodelphis domestica* (ZMB 35522) skull in stereo ventral view. Scale bar = 5 mm.

to increase surface area for the attachment of temporalis musculature.

Immediately lateral to the exit foramen for the facial nerve in the tympanic roof, a space is evident that we believe housed the epitympanic recess (fig. 5A). This region is best preserved (with a damaged roof) in the semiarticulated petrosal-squamosal fragment of YPM-PU 15384, and is consistent with the enlargement of an element within the ossicular chain, as in most golden moles. However, because the internal temporal region (fig. 1C) dorsal to the mandibular glenoid remains relatively flat, a hyperinflated malleus of the kind observed in *Chrysochloris asiatica* (Mason, 2003) was not present in *Necrolestes*.

Scott (1905: 370) stated that "the condylar and carotid foramina are not displayed in any of the specimens," whereas Patterson suggested the presence of the carotid foramen in YPM-PU 15065. We agree with Patterson regarding the presence of a carotid foramen, but on the basis of a different specimen. Unfortunately, except for an isolated right petrosal, the "good deal of the structure of the basicranium and auditory region" mentioned by Patterson for YPM-PU 15065 now appears to be lost. Nevertheless, YPM-PU 15699 retains an articulated right petrosal and part of the basisphenoid, within which are right and left foramina anteromedial to the petrosal, and which correspond closely in position and morphology to carotid foramina in *Monodelphis*. In contrast to *Monodelphis*, the carotid foramina in *Necrolestes* open directly onto the dorsum of the basisphenoid, whereas in *Monodelphis* each carotid foramen defines a short, anteroposteriorly directed canal within the basisphenoid. In addition, *Monodelphis* possesses a transverse canal that is situated anterior to the carotid foramen and is intramural, not exposed within the braincase (see character 2 of Sánchez-Villagra and Wible, 2002). In *Necrolestes*, slitlike openings on the dorsum of the basisphenoid are evident medial to the dorsal exposure of each carotid foramen (fig. 7); these are continuous with foramina exposed on either side of the midline anterior to the carotid

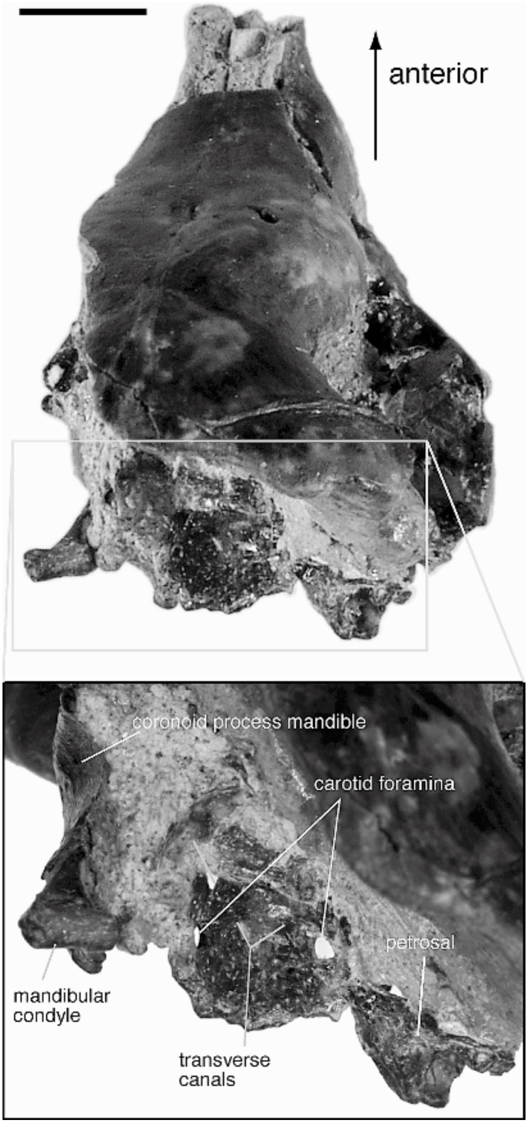

Fig. 7. Dorsal view of mid-braincase floor in *Necrolestes* (YPM-PU 15699), showing intracranial apertures of carotid foramina and transverse canals. Scale bar = 5 mm.

foramina and comprise the intracranial apertures of each transverse canal (fig. 2B).

YPM-PU 15384 preserves fragments of both occipital condyles, one of which is associated with a partial atlas (see below). Neither is sufficiently well-preserved to document the presence/absence of a hypoglossal (= "condylar") foramen.

Both Scott (1905) and Patterson (1958) noted the unusual internal nares of *Necrolestes*, which show a narrow, posteriorly expansive element dividing the internal nasal aperture into two halves (figs. 1B, 2B). A clear suture with the basisphenoid is evident immediately posterior to the rodlike element dividing the internal nares. The identity of this element is unclear. In *Leptictis* (Novacek, 1993: fig. 9.5), *Monodelphis* (Wible, 2003: fig. 5), and *Euphractus* (Wible and Gaudin, 2004: fig. 2), the ventral, midline element immediately anterior to the basisphenoid has been labeled the presphenoid; whereas in another figure of *Monodelphis* (Novacek, 1993: fig. 9.4), it is depicted as the vomer. Starck (1995: 41) labeled as "praesphenoid" a small, midline-exposed element anterior to the basisphenoid in a newborn *Mirounga* (Carnivora); on the same figure he depicts as the "orbitosphenoid" the adjacent ossification that also shares a ventral suture with the basisphenoid.

According to McDowell (1958: 127), the presphenoid comprises a "median structure of the endochondral cranium anterior to the basisphenoid and formed by the fusion of mediad extensions of the two orbito-sphenoids." McDowell goes on to state that in golden moles, some species of which (e.g,. *Amblysomus gunningi*, TM 42117) resemble *Necrolestes* in the morphology anterior to the basisphenoid, the orbitosphenoids are "absent". In fact, the orbitosphenoids are present in golden moles, but are too small to exhibit a ventral midline junction (Broom, 1916). Similarly, Starck (1995: 42) states that the presphenoid results from the ossification of midline, ventral extensions of the cartilaginous "Alae orbitales" and "Radices pro- und metopticae" of the developing mammalian central stem. Starck (1995: fig. 31) repeats the conclusion of Roux (1947) that golden moles possess the cartilaginous precursor of a presphenoid.

Debate on the homologies of the elements comprising the "central stem" of the mammalian cranial base dates from Parker (1885), Broom (1927), and Roux (1947), among others. Both Broom and Roux argued for the presence of a presphenoid in golden moles based on their observation of a median, unpaired ossification center, independent of the orbitosphenoids, anterior to the cartilaginous precursor of the basisphenoid. The term "parasphenoid" has been used in reference to an element in nonmammalian amniotes, hypothesized to be the homologue of the vomer and/or presphenoid in mammals (e.g., DeBeer, 1937: 433; see Novacek, 1993: 453–454). The vomer itself comprises much of the bony nasal septum throughout mammals, but does not typically articulate with the basisphenoid. Hence, for present purposes, we use the term presphenoid for the skull-base element anterior to the basisphenoid in *Necrolestes*.

In *Monodelphis*, *Euphractus*, *Leptictis*, and most other therian mammals, the bony roof of the posterior nasal fossa, corresponding to the ventrum of the posterior lamina transversalis or posterior-most "choanal passage" of Cave (1948: fig. 73), is flat and undivided; division of the nasal fossa occurs more anteriorly, within the nasal fossa proper. *Necrolestes*, in contrast, shows a median ridge extending posterior to the internal nares, probably composed of the presphenoid and, more anteriorly, the vomer. This ridge appears to be continuous with the median nasal septum within the nasal fossa.

LACRIMAL AND ORBIT: Patterson (1958: 7) stated that the lacrimal foramen is "very similar to that of various didelphids as regards both position and size." In our view, however, the two taxa are roughly similar only in that both have foramina dorsal to a relatively long infraorbital canal, as is common in several marsupial and placental groups. Didelphids typically show multiple lacrimal foramina (Sánchez-Villagra and Asher, 2002), whereas only one is evident in *Necrolestes* (fig. 2). Furthermore, didelphids show lacrimal foramina at the anterior margin of the orbit, facing posteriorly (Wible, 2003: fig. 3); *Necrolestes*, in contrast, shows the lacrimal foramen situated in a groove dorsal to the infraorbital canal, medial to a broad emargination in the maxilla (figs. 2C, 2D).

Patterson (1958: 7) also stated that "the optic foramen appears to be confluent with the sphenorbital fissure." However, the orbital region is poorly preserved in all available specimens, and we can confirm neither the contour of the sphenorbital fissure nor the confluence of an optic foramen with it.

JUGAL BONE: Although he acknowledged that sutures in the zygomatic region were obliterated, Patterson (1958: 6) suggested that in *Necrolestes*, the jugal extends posterior to the glenoid surface of the jaw, and regarded this morphology as indicative of marsupial affinities. However, without intact sutures, neither the posterior nor anterior extent of the jugal bone in *Necrolestes* can be confidently identified. Hence, we do not believe this element can be interpreted as didelphid-like. *Necrolestes* resembles the marsupial *Monodelphis* in showing a preglenoid process anteriorly buttressing the mandibular condyle in its glenoid articulation. As noted by Patterson, the immediate postglenoid region in *Necrolestes* is relatively flat (see above), whereas *Monodelphis* shows a large postglenoid process (fig. 6). Several eutherian groups also possess processes of the jugal contributing to the glenoid jaw articulation (Asher et al., 2003).

PALATE AND ROSTRUM: We agree with Patterson's (1958: 7) statement that "the long, slit-like incisive foramina are very didelphid-like". The incisive foramina appear anterior to a roughly symmetrical, slightly distorted break that we believe corresponds to the maxilla-premaxilla suture (fig. 1). We also agree with his comment that *Necrolestes'* palate is solid and lacks palatal vacuities. YPM-PU 15065 is the only specimen to expose this region (fig. 1B). It shows a break in the posterior palate just right of the midline, but this is not repeated on the left side, indicating that in life the hard palate was not perforate.

Scott (1905: 368) claimed the "nasals are long and tapering" in *Necrolestes*. We suspect he was referring to the general contour of the rostrum. As Patterson (1958) pointed out, actual sutures for most of the dermal cranium, including the nasals, are completely fused. Hence, it is not possible to infer the extent to which the posterior nasal bones widen posteriorly, or if they articulate with the lacrimal, as is often the case in marsupial groups (e.g., *Didelphis*; see Horovitz and Sánchez-Villagra, 2003).

AXIAL SKELETON

CERVICAL SPINE: In most mammals (e.g., *Chrysochloris*, fig. 8C), the atlas is composed of a right and left lateral mass, connected dorsally by a neural arch and ventrally by an intercentrum and/or a ventral arch. Several diprotodont marsupials, some specimens of the peramelid *Echymipera* (e.g., ZMB 37012), and some Mesozoic therians (Kielan-Jaworowska, 1977; Kielan Jaworowska et al., 2004: 483) show an incomplete atlantal ventral arch (and no intercentrum) but still show a fused neural arch (Horovitz and Sánchez-Villagra, 2003). Juvenile monotremes display an unfused or only partially fused suture between left and right neural arches (Griffiths, 1978; Lessertisseur and Saban, 1967a, b), as do the presumably juvenile specimens of the basal prototribosphenidan *Vincelestes neuquenianus* (Rougier, 1993). Later in ontogeny, the neural arches of monotremes fuse to each other; adult monotremes possess a complete, ring-like atlas. In *Vincelestes* the intercentrum is missing, but may have been present in life. Separate atlantal hemiarches (and a separate intercentrum) have also been reported in several close relatives of mammals, such as nonmammalian cynodonts (Jenkins, 1971), the basal mammaliamorph *Oligokyphus* (Kühne, 1956) and the basal mammaliaform *Megazostrodon* (Jenkins and Parrington, 1976).

McKenna et al. (2000) reported that a juvenile specimen of the Cretaceous eutherian *Daulestes* may have possessed unfused ventral and neural arches of the atlas; whether this condition characterized adult specimens is unclear. Ontogenetic studies of the development of beagle dogs report fusion of the atlantal hemiarches by postnatal day 106 and fusion of the intercentrum to the massae laterales by postnatal day 115 (Watson et al., 1986, cited in Evans, 1993); ontogenetic studies of *Didelphis* also indicate differential timing in fusion: fusion of the ventral arch occurs "much later" than that of the dorsal arch (Oliveira et al., 1998: 117).

Based on five preserved hemiatlantes and/or fragments thereof, representing all three of the Hatcher-Peterson specimens, *Necrolestes* may be added to the very short list of mammals with completely separate right and left atlantal halves (fig. 8A). Neither Scott (1905) nor Patterson (1958) mentioned any details of atlantal morphology in *Necrolestes*, perhaps because its atypical appearance hindered identification. Nevertheless, we believe this attribution is correct for two main reasons:

(1) YPM-PU 15384 (fig. 9) preserves a fragmentary right lateral mass associated with a fragmentary right occipital condyle. These have been slightly disarticulated postmortem, such that the atlas has been pushed anteriorly into the foramen magnum and the atlantal cotyle no longer articulates with the occipital condyle. Nevertheless, the close association of these two elements in the original matrix supports the interpretation that in life they were articulated.

(2) The right lateral mass, neural arch, and articular facets for the cranium and axis of YPM-PU 15065 (fig. 8A) are relatively complete. The cranial (anterior) cotyles correspond closely in shape and size with the occipital condyle of YPM-PU 15384 (fig. 9); similarly, the anterior articular facets of the axis in 15065 and 15384 closely match the axial (posterior) articular facets of the atlantes in the same specimens.

Unfortunately, there remains some uncertainty as to the correct provenance of certain elements among the three YPM-PU specimens. The right atlas fragment that we now associate with YPM-PU 15699 (fig. 9A) based on preservation, color, and nonduplication of elements had been in the same box with elements from YPM-PU 15384. We do not believe these atlantal elements are associated with 15384 because the atlantal fragment shown in figure 9B, associated with YPM-PU 15384 based on preservation and association with a fragmentary petrosal on which "15384" is written, duplicates the right atlantal lateral mass shown in figure 9A. The black-colored right lateral mass in figure 9A is in our view a better candidate for association with the YPM-PU 15699 skull, and in addition is associated with a left atlas fragment preserving most of the neural arch (fig. 9).

The left neural arch of the YPM-PU 15699 atlas and the right neural arch of the YPM-PU 15065 atlas (fig. 8) preserve undistorted apices without signs of breakage. This is consistent with an unfused soft-tissue joint between right

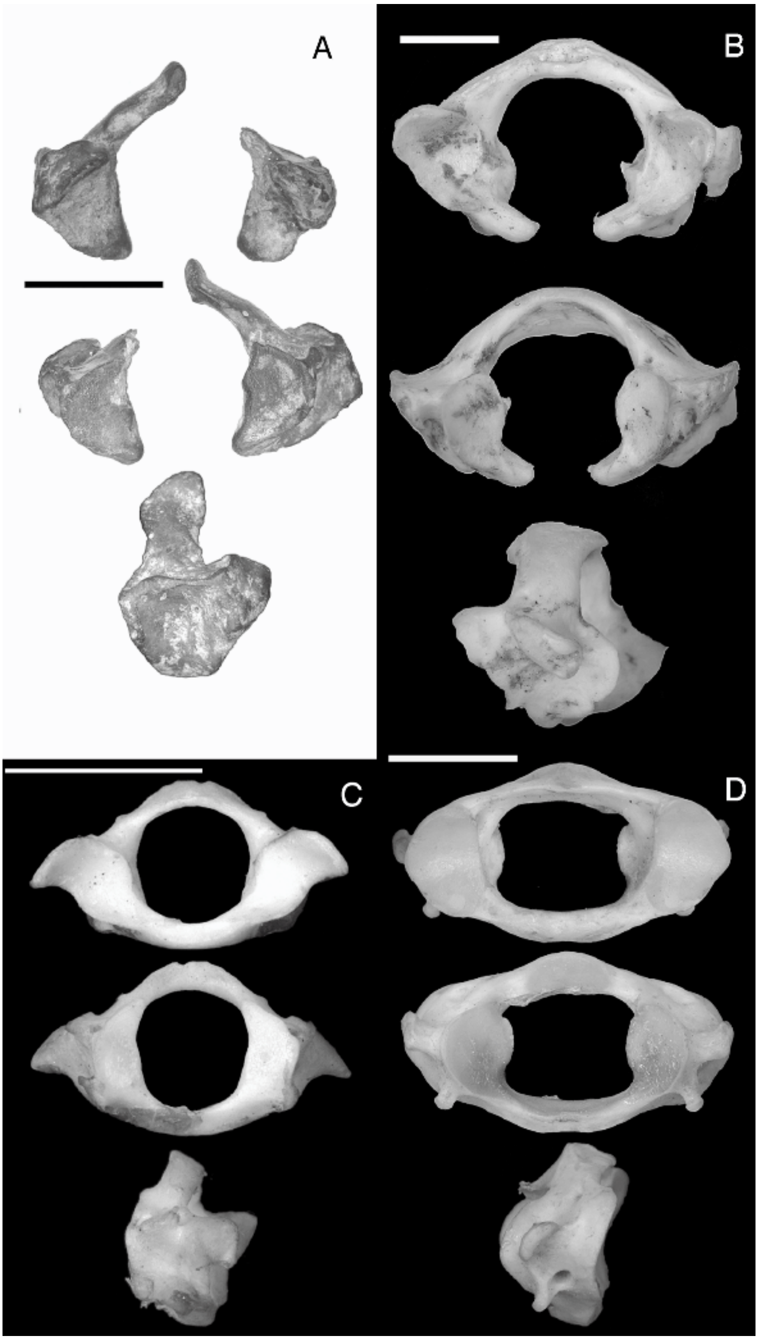

Fig. 8. Atlantes of (**A**) *Necrolestes* (YPM-PU 15065), (**B**) *Echymipera* (ZMB 37012), (**C**) *Chrysochloris* (ZMB 76896), and (**D**) *Chlamyphorus* (ZMB 6007). For each specimen, anterior view is at top, posterior middle, and lateral bottom. Scale bars = 5 mm.

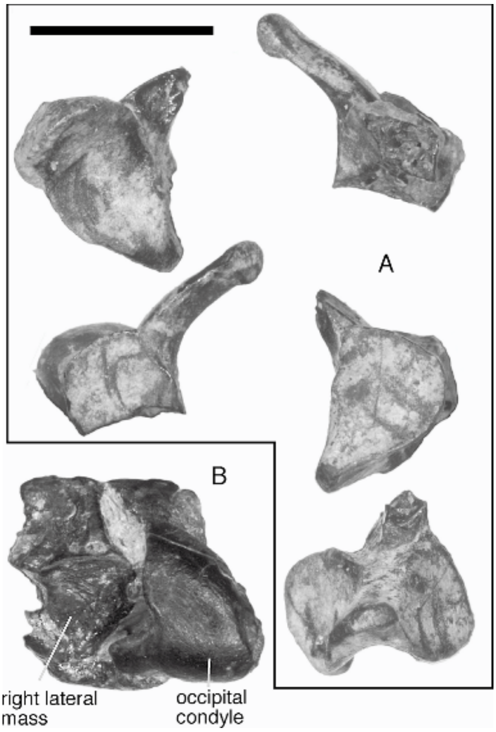

Fig. 9. (**A**) atlas of *Necrolestes* (YPM-PU 15699) in anterior (top), posterior (middle), and internal (bottom right) views. (**B**) associated right atlantal and occipital fragments from YPM-PU 15384 in posterior view. Right atlantal fragment has been displaced postmortem and does not occlude naturally with occipital condyle; however, association between atlantal and occipital fragments is genuine. Scale bar = 5 mm.

and left atlantal neural arches. The neural arch is missing on the YPM-PU 15384 atlantal fragment.

The process for the cranial articular fovea on the atlas protrudes anteriorly beyond the neural arch. There are no lateral vertebral foramina, just a groove on the medial side of the root of the process for the cranial articular fovea on the left and right sides as in *Notoryctes* and *Amblysomus*. There are no wings per se, but just ridges along the lateral sides of the *massae laterales*, a morphology similar to that found in *Amblysomus, Scapanus,* and *Condylura*. A foramen on each side perforates the lateral ridges and opens dorsally in the anterior area of the neural arch just medial to the processes for the cranial articular facets, to the area just ventral to the lateral ridges, also in the anterior area of the vertebra.

The right neural arch is preserved in YPM-PU 15065. It is narrower anteroposteriorly than the *massa lateral*, with a dorsal tubercle insinuated in the medial-most end of what is preserved of the neural arch. The caudal articular fovea is preserved in both specimens. It is almost flat, with a roughly triangular outline. It converges ventrally with the cranial articular fovea, from which it is separated by a very narrow surface pointing medioventrally. This narrow surface bridges the separation between the cranial and caudal articular facets and is smooth like an articular facet; it was therefore not part of an unfused suture with an intercentrum. It may have made contact with an (unpreserved) intercentrum or with the dens of the axis.

A partial axis is preserved for both YPM-PU 15384 and 15065 (fig. 10). The dens, cranial articular surface, part of the body, and a very small portion of the left neural arch are preserved. The ventral surface of the body is smooth with no traces of ridges or median keel. The cranial articular facets end at the dens and do not extend ventral to the dens. Not enough of the neural arches are preserved to assess the presence of an enclosed transverse foramen. However, the body of the axis is anteroposteriorly much longer than those of other vertebrae, including those in the thoracic and lumbar regions (fig. 11). We believe this is due to fusion. Contrary to Scott's statement (1905: 371) that the cervical vertebrae of *Necrolestes* do not resemble the fused cervicals of *Notoryctes*, we believe that the cervical spine of *Necrolestes* was extensively fused, possibly including C2 to C6 (fig. 11). In addition to its fragmentary but relatively elongate axis, YPM-PU 15384 shows another cervical fragment with an antero-posteriorly elongate body. This does not show a clear fit to the 15384 axis, but may still have been fused to it, separated by fragments that are now missing (fig. 11). Both elements are considerably more elongate than an isolated vertebra that we interpret to be a posterior (or posterior-most) cervical.

THORACIC AND LUMBAR SPINE: Scott (1905: 371) stated that in both chrysochlorids and *Necrolestes*, spinous processes throughout the

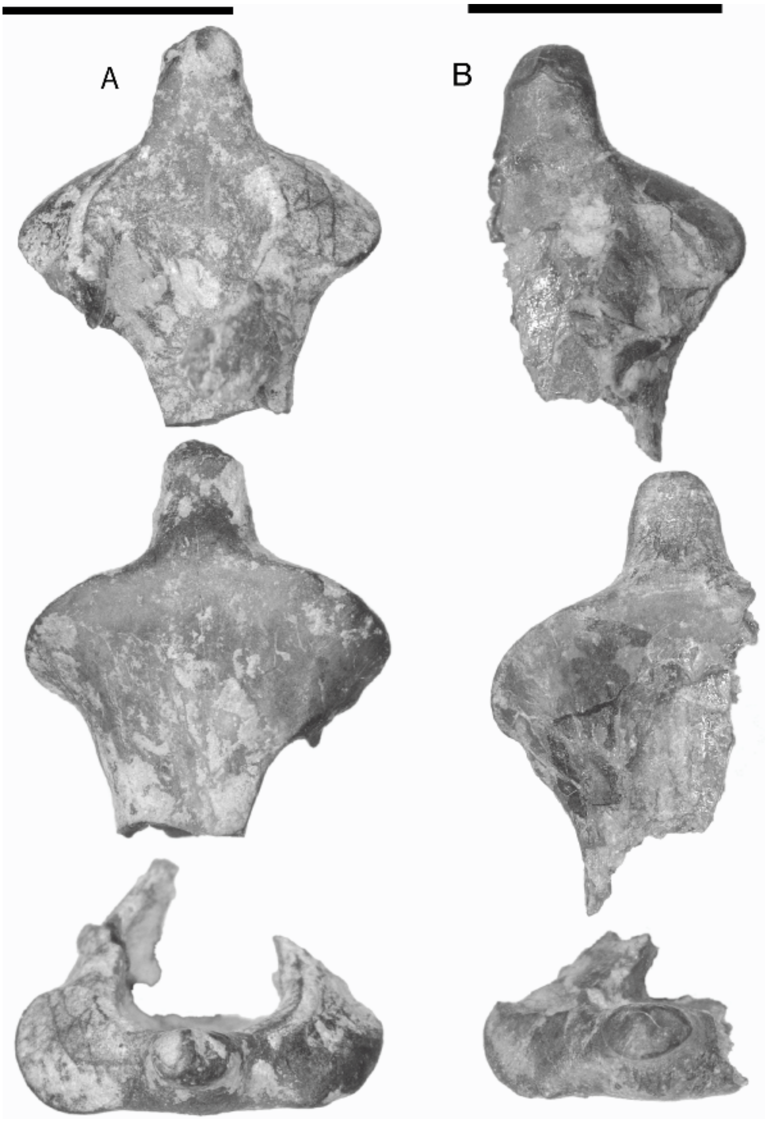

Fig. 10. Axes of *Necrolestes* (**A**) YPM-PU 15065, (**B**) YPM-PU 15384, in dorsal (top), ventral (middle), and anterior (bottom) views. Scale bars = 5 mm.

vertebral column extended posterodorsally; neither taxon possessed anticlinal (extending dorsally at a right angle to the vertebral column) or anterodorsally extending spinous processes. We agree with Scott based on the material available to us. The lack of anticlinal and anterodorsally directed vertebral spinous processes is also evident in *Dasypus*, but contrasts with *Talpa*, which shows anterodorsally directed spinous processes in the anterior

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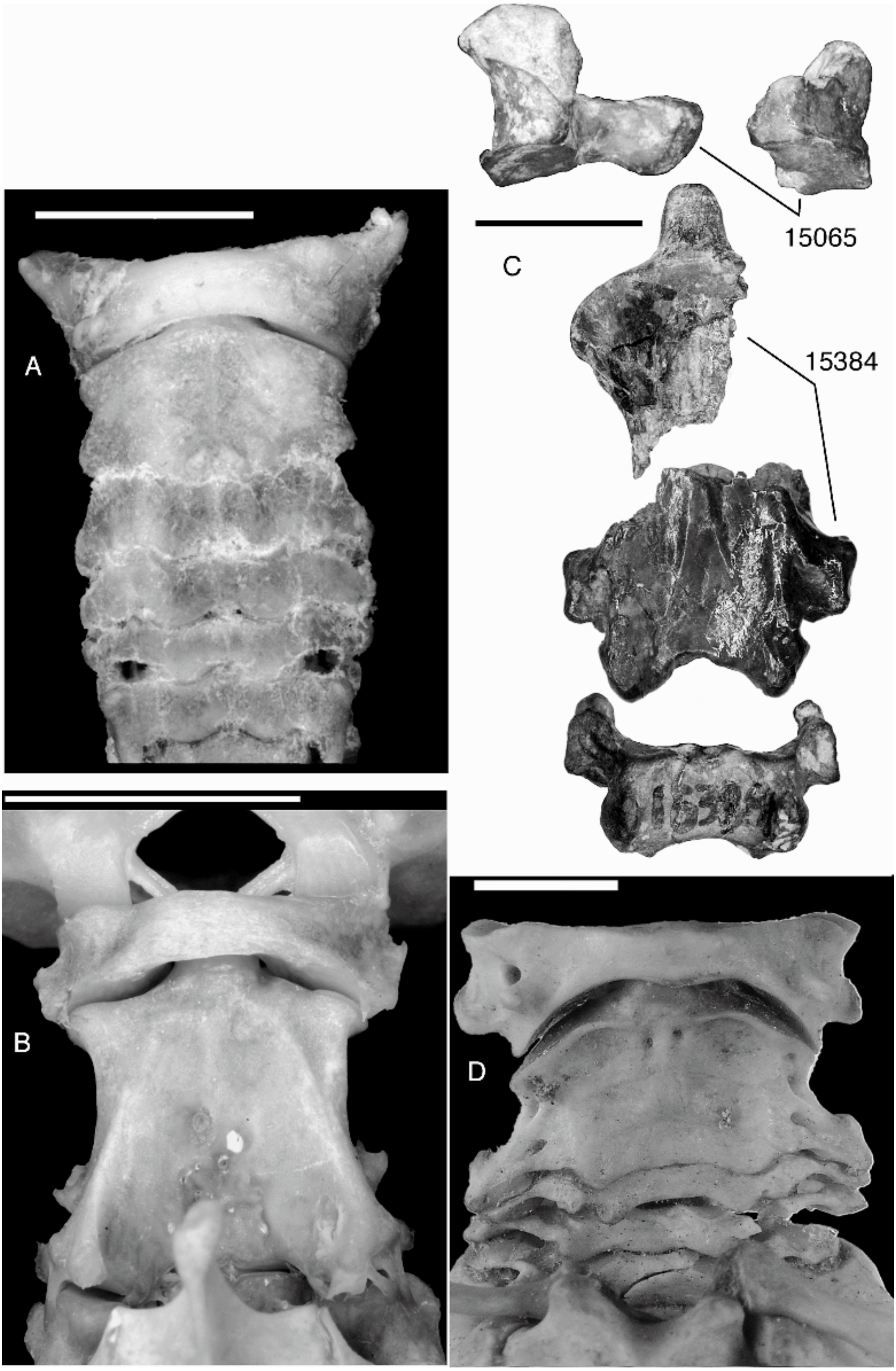
Fig. 11. Ventral views of cervical vertebral skeleton in (**A**) *Amblysomus* (Asher's collection), (**B**) *Notoryctes* (ZMB 35694), (**C**) *Necrolestes* (atlas, YPM-PU 15065; axis and cervical vertebrae, YPM-PU 15384), and (**D**) *Chlamyphorus* (ZMB 6007). Scale bars = 5 mm.


A
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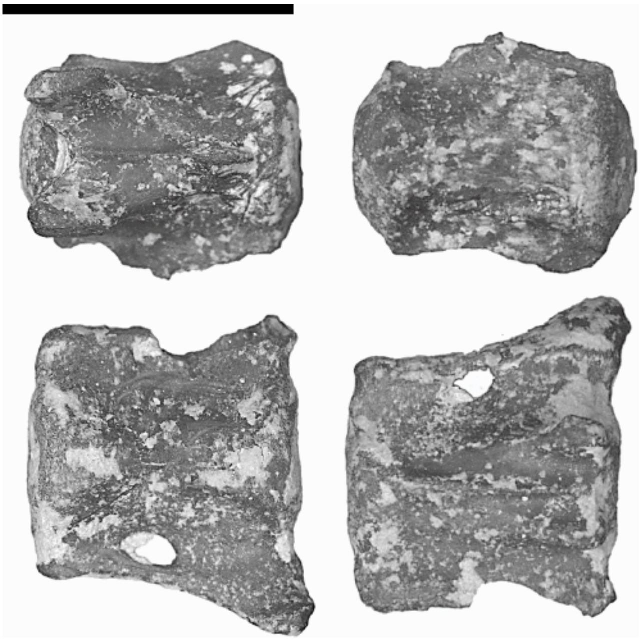


Fig. 12. Dorsal (left) and ventral (right) views of caudal vertebrae in *Necrolestes* (YPM-PU 15384). Scale bar = 5 mm.

lumbar and posterior thoracic region. Articulations between vertebrae in this region are limited to zygapophyses and vertebral centra, as in other non-xenarthrous mammals.

SACRUM: see "pelvic girdle" section under "hind limb".

TAIL: Patterson (1958: 9) noted a "well-developed tail" in *Necrolestes* as a similarity to didelphoids. Here again it seems that some of the YPM-PU *Necrolestes* material may have been lost, because we can identify just two caudal vertebrae, both from YPM-PU 15384 (fig. 12). One of these is broad at one end and may have been the proximal-most caudal vertebra, adjacent to the sacrum. Both caudal vertebrae are considerably larger than any vertebrae in the tails of *Amblysomus hottentotus* and *Talpa europaea*, both of which are similar in overall size to *Necrolestes* but have reduced tails. *Necrolestes* may have resembled *Notoryctes* in terms of tail size, but unlike the latter shows relatively small transverse processes and neural spines on the two preserved caudal vertebrae. We cannot infer too much detail about the tail in *Necrolestes*, but agree with Patterson that it was probably longer and more robust than that of *Talpa* or golden moles.

FORELIMB

SCAPULA: For our descriptions we orient the scapula in the anatomical position of most quadrupedal tetrapods, rather than humans. That is, the "dorsal" margin of the scapula refers to its vertebral margin; its ventral aspect includes the glenoid articulation with the humerus; and its lateral surface anchors the scapular spine.

Only the humeral articular regions of the right and left scapulae from YPM-PU 15384 remain intact (fig. 13A). These show a scapular spine defining infra- and supraspinous fossae; however the spine itself is incomplete, missing the metacromion and acromion. In didelphids and xenarthrans (e.g., *Dasypus*, *Zaedyus*, *Chlamyphorus*), the scapular spine transversely bifurcates the lateral scapular surface into cranial (supraspinous) and caudal (infraspinous) regions of similar size; i.e., the spine is situated in roughly the middle of the lateral surface. *Necrolestes* resembles the condition

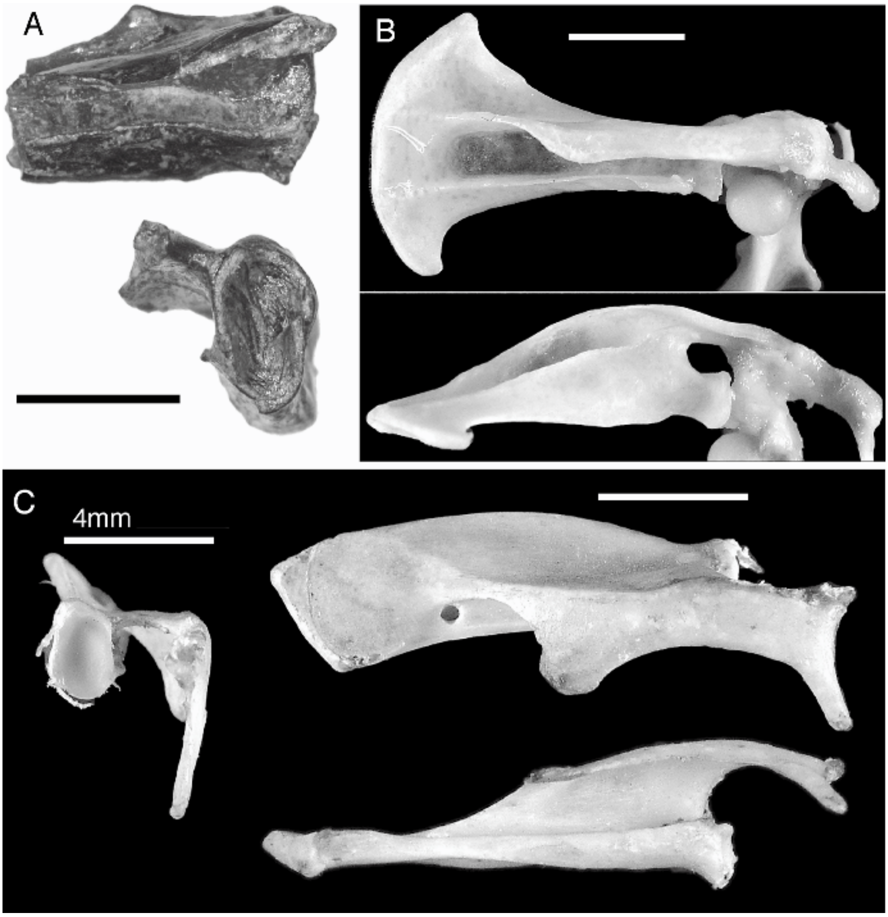


Fig. 13. Scapulae in (**A**) *Necrolestes* (YPM-PU 15384), lateral fragment in lateral (top) and inferior (bottom) views; (**B**) *Notoryctes* (ZMB 35694) in lateral (top) and posterior (bottom) views, and (**C**) *Chrysochloris* (ZMB 76897) in inferior (left), lateral (top right) and posterior (bottom right) views. Scale bars = 5 mm.

shown in *Notoryctes* (fig. 13B) and golden moles (fig. 13C) in which the scapular spine originates closer to the cranial border of the scapula. Furthermore, as in *Amblysomus* and the talpid *Galemys*, the root of the scapular spine in *Necrolestes* extends ventrally to a point close to the glenoid fossa, unlike that of xenarthrans, didelphids, *Metacheiromys*, and *Notoryctes*, which stops well dorsal to the scapular neck. Another similarity to *Amblysomus*, *Galemys*, some xenarthrans (e.g., *Tamandua*), and epoicotheres (e.g., *Metacheiromys*) is the caudal border of the scapula, which curves and approaches the scapular spine, giving the infraspinous fossa a tube-like appearance (fig. 13A). Otherwise, the scapula of *Necrolestes* does not resemble the elongate, narrow scapula of talpids. Furthermore, it shows no sign of a coracoid process. Overall, *Necrolestes* most closely resembles the golden mole *Amblysomus* in its scapular morphology.

HUMERUS: Right and left humeri are at least semi-intact in two specimens: YPM-PU 15384 and 15065. The best preserved is the right humerus of 15384 (fig. 14A). The head of the humerus is mediolaterally compressed, reminiscent of that of moles, golden moles (Horovitz, 2004), and the epoicotheriid palaeanodonts *Xenocranium pileorivale*, *Epoicotherium unicum* (Rose and Emry, 1983: fig. 8B and D respectively), and *Dipassalus*

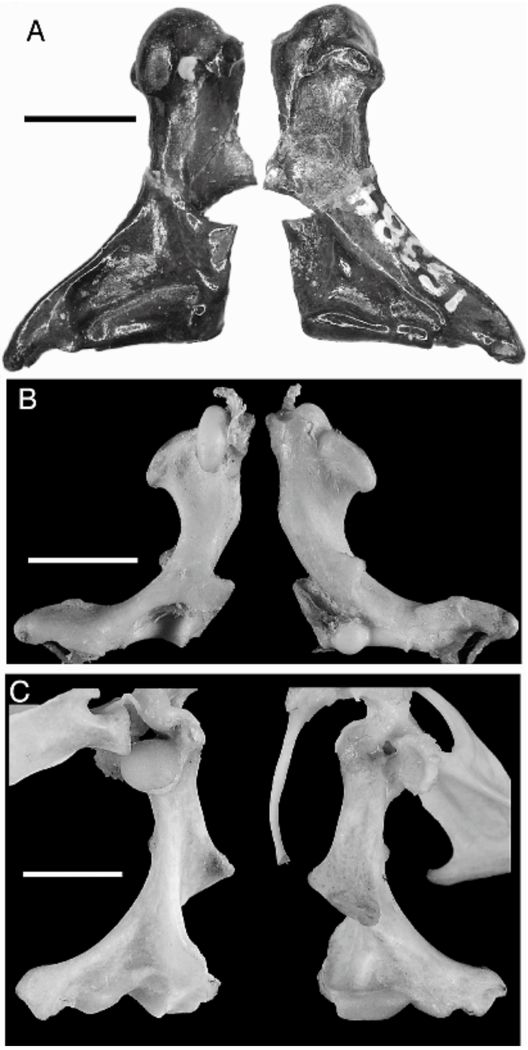


Fig. 14. Humeri of (**A**) *Necrolestes* (YPM-PU 15384), (**B**) *Chrysochloris* (ZMB 76897), and (**C**) *Notoryctes* (ZMB 35694) in posterior (left) and anterior (right) views. Scale bars = 5 mm.

oryctes (Rose et al., 1991: figs. 5A, C and D). Greater and lesser tubercles are similar in size, but the greater tubercle is located more proximally than the lesser tubercle. The head projects proximally beyond both of them. There is a conspicuous depression on the anterior side of the head, in the area of transition into the diaphysis, medial to the lesser tubercle. The diaphysis of the humerus is straight for the most part in medial/lateral view, except for the proximal end that curves forming a concavity under the head. The deltopectoral crest is raised and convex in the proximal area of the diaphysis, and its convexity is continuous with that of the head and more distally with the greater tubercle. It becomes distally thinner, in the shape of a crest with a concave edge directed laterally, and protrudes terminally in a large process on the midshaft. This process is missing its distal tip in all four YPM-PU specimens. The shape of this crest resembles that of *Plesiorycteropus* (MacPhee, 1994) and *Dasypus novemcinctus*, except that in the latter two the crest is not continuous with the head, but with the proximal end of the greater tubercle. In addition, *Necrolestes* shows an eminence running distally from the deltopectoral crest towards the medial epicondyle, forming a bridge over the entepicondylar foramen, and comprising a very prominent feature of the humeral shaft proximal to the articular surface of the trochlea and capitulum (fig. 14). *Amblysomus* possesses a similar, more gracile structure, also extending distally from the deltopectoral crest towards the medial epicondyle, defining the entepicondylar foramen (fig. 14B).

The medial epicondyle is directed mediodistally and protrudes distally beyond the trochlea and condyle, similar in this respect to that of *Epoicotherium unicum* (Rose et al., 1991: fig. 6). In *Necrolestes* there is a small process next to the trochlea (most evident in the right humerus of 15384) and a concave, distomedially directed edge between this small process and the medial epicondyle. Both of these features are absent in *Epoicotherium,* where the lateral edge of the medial epicondyle starts next to the medial edge of the trochlea. In *Notoryctes* and *Amblysomus* there are very large medial epicondyles as well, but in *Amblysomus* the epicondyle is directed almost straight medially and in *Notoryctes* it protrudes slightly distally, and is shorter. In addition, *Notoryctes* lacks an entepicondylar foramen (fig. 14C).

The supinator crest is large and laminar, reaching proximally to midshaft, close to the level of the deltopectoral process. Its proximal end extends abruptly out of the humeral shaft, at a level just inferior to the deltopectoral crest, creating a flange similar to that seen in

Amblysomus (fig. 14) and even more strongly developed in *Palaeanodon* (Rose, 1999: fig. 2), *Metacheiromys* (Simpson, 1931: fig. 16), *Epoicotherium*, and *Xenocranium* (Rose and Emry, 1983: fig. 8).

The trochlea is cylindrical, and shows a subtle transition to the capitulum defined by a waisted neck. The capitulum is also cylindrical, but broadens laterally, and is mediolaterally wider than the trochlea. The trochlea is similar in shape to that of *Epoicotherium*; however, the capitulum of *Necrolestes* differs in being cylindrical, rather than sphere-shaped as in *Chrysochloris* and *Amblysomus*. The anconeal process of the ulna articulates in a mediolaterally long depression, running dorsal to the posterior articular surface of the trochlea and capitulum.

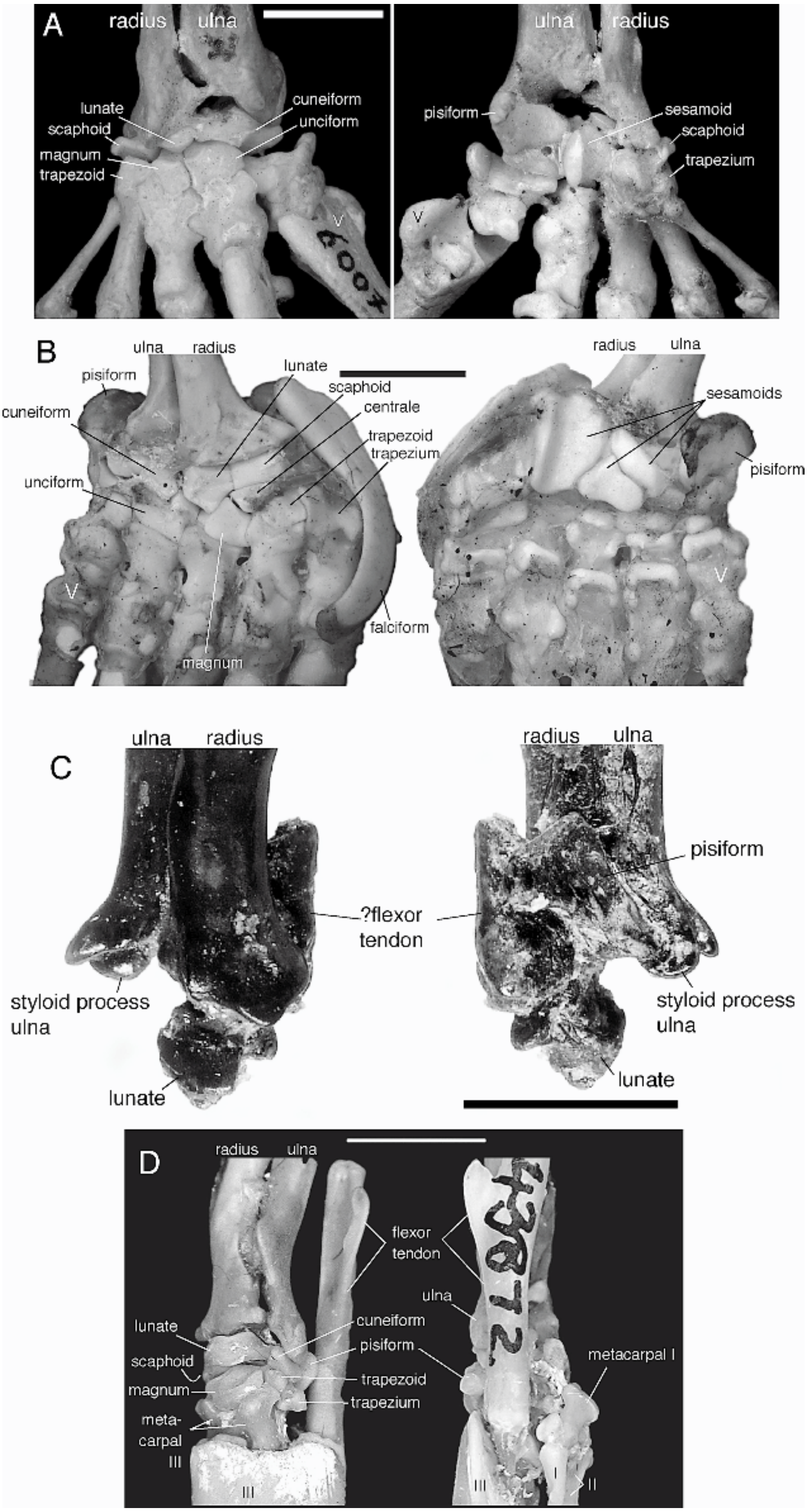
In *Amblysomus*, the articular surface on the distal humerus for the radius and ulna is fairly restricted to a lateral position. As in other fossorial taxa, the medial epicondyle provides greatly expanded surface area for attachment of extrinsic hand musculature; in golden moles, it provides the proximal support for the ossified digital flexor tendon. This "articulation" is not synovial; rather, an unossified, tendinous insertion connects the (more distally) ossified flexor tendon with the medial epicondyle.

FORELIMB: One of the most conspicuous features of the *Necrolestes* forearm is the medially curved olecranon process of the ulna (Rose and Emry, 1983: fig. 9). This feature is present to an even greater degree in the palaeanodonts *Xenocranium* and *Epoicotherium* (Rose and Emry, 1983: fig. 10). Golden moles, *Notoryctes*, and *Euphractus* show a similarly curved ulnar olecranon; in golden moles this process bends in a slightly more posterior than medial direction. The anterior face of the olecranon process in *Necrolestes* is relatively flat. A facet for the radial head is evident lateral to the ulnar coronoid process. The ulnar shaft is substantial and broadens slightly toward the carpus, coming to a point only at the styloid process on its distal extreme, which extends from the posterior surface of the distal ulnar margin. Relative to the distal radius, the ulna comprises a small component of the carpus-forearm articulation.

Golden moles possess one of the most remarkable forelimbs among Mammalia, showing three long bones of the forearm: radius, ulna, and an ossified flexor tendon that approaches the humeral epicondyle and articulates with the carpus (fig. 15D; see Dobson, 1883: 121). Based on the description of Leche (1907), who called the palmar sesamoid of *Notoryctes* "unverkennbar homolog" (unmistakably homologous) with the ossified flexor tendon of golden moles, W.K. Gregory (1910: 256) stated that the "third lower arm bone" is at least partly present in *Notoryctes*. As described in Stirling (1891, 1894), Gadow (1892), Wilson (1894), and Carlsson (1904), and as evident in an articulated skeleton available to us (ZMB 35694), the forearm of *Notoryctes* does possess a large palmar sesamoid, into which *M. flexor digitorum* inserts (Wilson, 1894). However, this element does not extend proximal to the carpus, and resembles palmar sesamoids present in, among others, *Chlamyphorus* and *Talpa* (fig. 15A, B) more than it does the ossified flexor tendon in golden moles (fig. 15D). In fact, Carlsson (1904: 116) stated explicitly that the marsupial mole lacks a third-forearm bone, contra Leche (1907) and Gregory (1910).

An articulated right ulna, radius, and some carpals are preserved for YPM-PU 15384 (fig. 15C), referred to by Patterson (1958) as "various bones of the fore foot". Other small elements with articular surfaces are present, including several phalanges, a metacarpal, and indeterminate distal carpal elements, one of which is still partly embedded in matrix. At some point these elements may have had clearer associations with one another; however, at present we restrict our discussion of carpal anatomy to those elements still articulated to the distal radius.

The right radius is articulated with a proximal carpal, probably the lunate (fig. 15C). A moderately large pisiform is also present, adjacent to the styloid process of the ulna. Between pisiform and distal radius, another ossification is evident, larger than both lunate and pisiform. This element extends from a position adjacent to the lunate towards the ulnar shaft (fig. 15C), and possibly provided


A
radius
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V
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ulna
radius
pisiform
cuneiform
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ulna
lunate
scaphoid
magnum
meta-carpal III
cuneiform
pisiform
trapezoid
trapezium
III
flexor tendon
ulna
metacarpal I
III
I
II

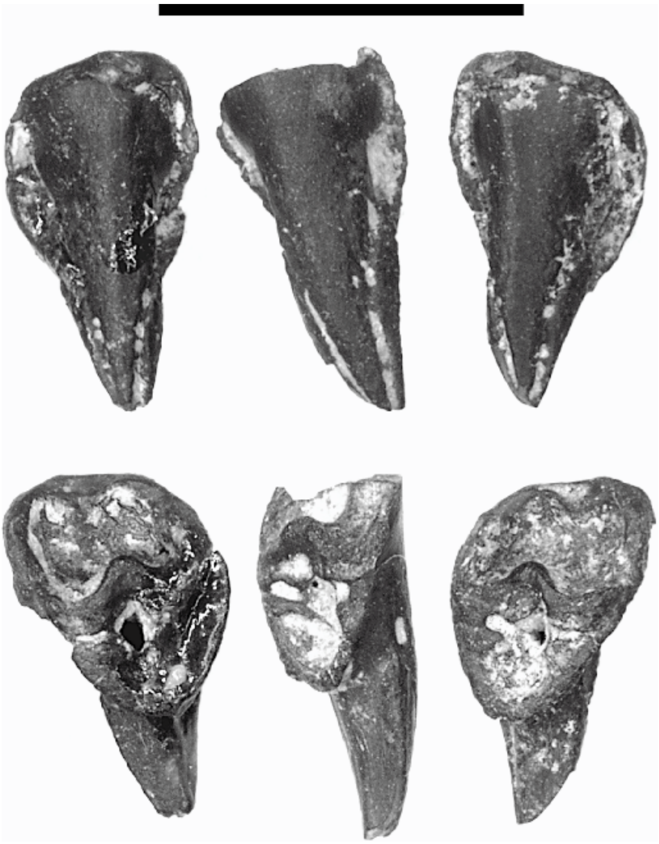

Fig. 16. Terminal phalanges of *Necrolestes* (YPM-PU 15384). Scale bar = 5 mm.

for the insertion for *M. flexor digitorum*. This proximal carpal ossification in *Necrolestes* is considerably more elongate than the palmar sesamoid of *Notoryctes* and shows a greater similarity to the ossified flexor tendon of golden moles. Scott (1905: 374) also interpreted the forearm of *Necrolestes* to have had a chrysochlorid-like flexor tendon, "though only the distal portion of it is ossified".

The phalanges show elongate fissures extending longitudinally on either side of each terminal phalanx (fig. 16), resembling those of *Xenocranium* figured by Rose and Emry (1983: fig. 15). We cannot be sure if these belong to the manus or the pes. If the former, then they would comprise an important difference from the manus of both *Notoryctes* and golden moles. In most of these species, digit III is considerably larger than the others; digit IV is reduced to a stub; and digit V is lost altogether (Hickman, 1990: fig. 4). In *Notoryctes*, digits III and IV are enlarged relative to the others (Wilson, 1894). Most golden moles (except *Eremitalpa,* which shows similarly sized claws on digits I, II, and III) and *Notoryctes* do not show three terminal digits of the hand that resemble each other in size. Such would be the condition in *Necrolestes* if the three phalanges in figure 16 belong to distinct digits of the manus. However, the lack of an

←

Fig. 15. Hands of (**A**) *Chlamyphorus* (ZMB 6007), (**B**) *Mogera* (ZMB 77008), (**C**) *Necrolestes* (YPM-PU 15384), and (**D**) *Amblysomus* (TM 43872). Roman numerals I–V indicate digital rays. For carpal terminology we follow Horovitz and Sánchez-Villagra (2003). Scale bars = 5 mm.

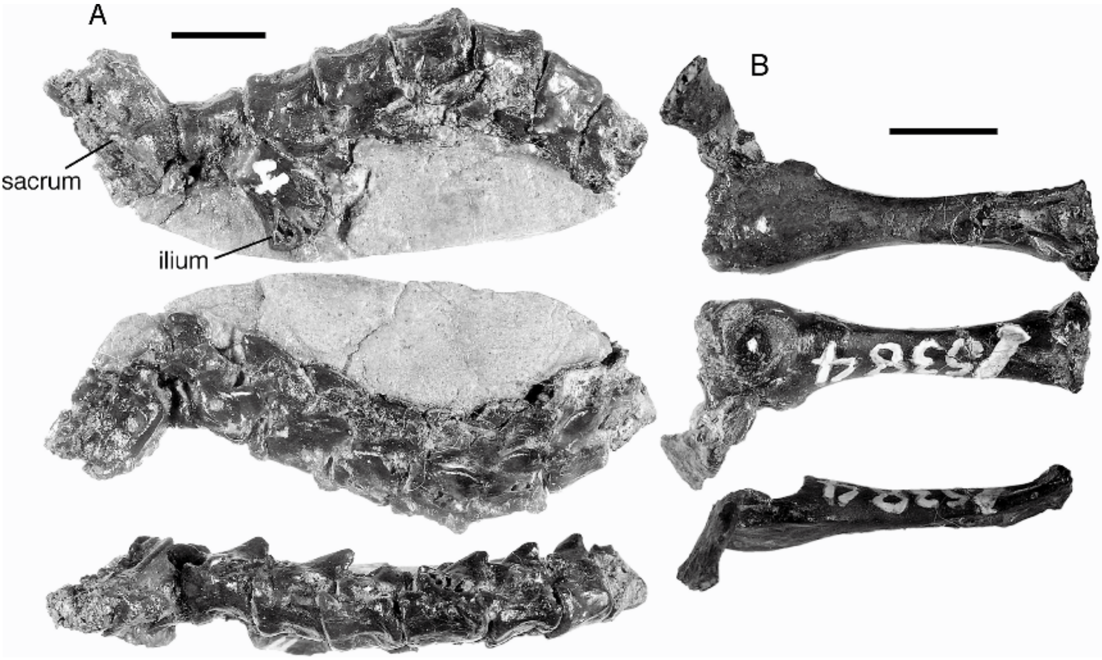

Fig. 17. (**A**) lumbar spine, sacrum, and left ilial fragment and (**B**) isolated right os coxae of *Necrolestes* (YPM-PU 15384) in internal (top), external (middle), and anterior (bottom) views. Scale bars = 5 mm.

articulated specimen prevents certainty on this point.

Hind limb

Pelvic Girdle: YPM-PU 15384 retains a fragmentary sacrum articulated with seven more anterior vertebrae (fig. 17). Right and left os coxae are also preserved but not articulated; the proximal tip of the left ilium remains preserved in the matrix anterodorsal to the articulated sacrum and lumbar spine. Both Scott (1905) and Patterson (1958) described a well-developed pubic symphysis for *Necrolestes*. Although none of the YPM-PU specimens available to us retains a complete pelvis, we agree that *Necrolestes* had a moderately broad pubic symphysis based on the right os coxae of YPM-PU 15384. In this specimen, the pubis broadens distally and extends in a ventromedial direction from the acetabulum (fig. 17). In contrast, the pubis of *Dasypus*, *Zaedyus*, *Talpa*, and chrysochlorids narrows distally and extends in a caudal direction from the acetabulum, rather than ventromedial. We find no evidence to support Patterson's (1958: 9) statement that *Necrolestes* had epipubic bones. The epipubic bone of *Didelphis* has a broad origin along the cranial margin of the pubis, an area which is relatively intact on the right os coxae of YPM-PU 15384 (fig. 17) and that shows no signs of articulation with another bony element. The epipubic bone of *Notoryctes* and the symphysis itself (fig. 18) are reduced but still associated with a prominent emargination along the dorsal rim of the pubic symphysis. We find in *Necrolestes* no sign of any "small fragment of bone attached to the [right pubis] by matrix [that] could be a remnant of the epipubis itself" (Patterson, 1958: 9).

Necrolestes exhibits many characters that typify fossorial mammals in several orders, particularly in its forelimb, skull, and cervical vertebrae. However, compared to those of fossorial xenarthrans, *Notoryctes*, talpids, manids, and *Orycteropus*, the sacrum and pelvis of *Necrolestes* are unremarkable. The articulated sacrum in YPM-PU 15384 is slightly distorted and incomplete caudally, but consists of three fused sacral vertebrae, with an unfused articulation between centra

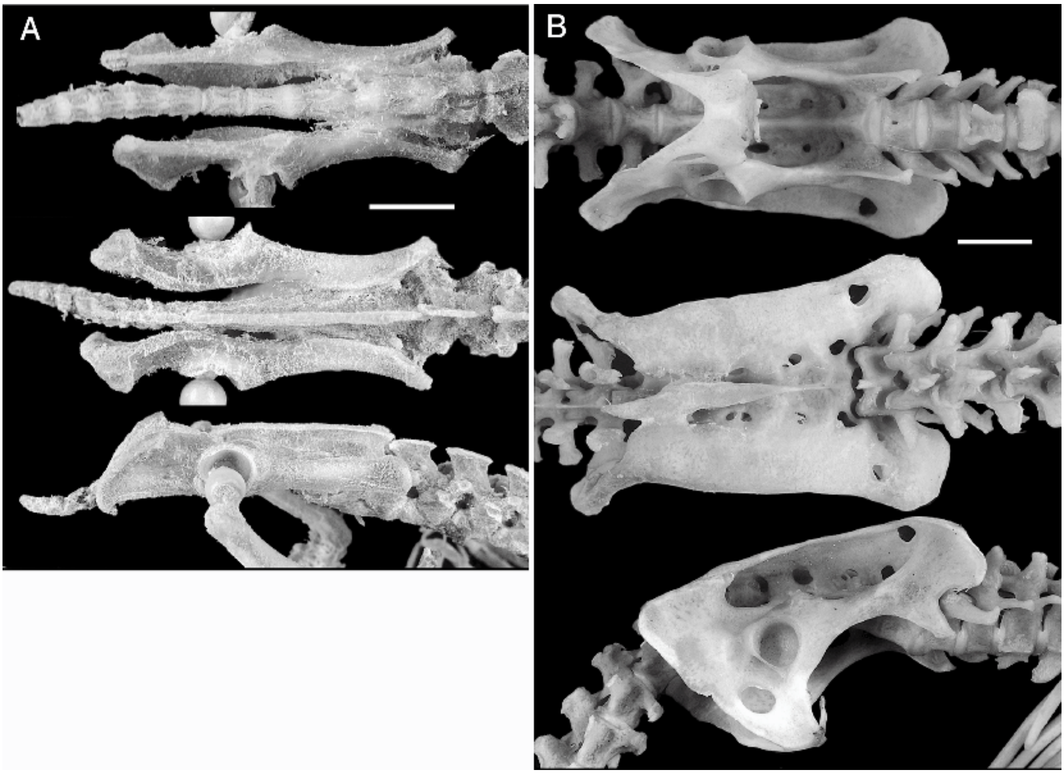

Fig. 18. Pelves of (**A**) *Amblysomus* (Asher's collection) and (**B**) *Notoryctes* (ZMB 35694) in ventral (top), dorsal (middle), and lateral (bottom) views. Lateral view in *Notoryctes* is reversed image from left side. Scale bars = 5 mm.

and zygopophyses of the proximal sacrum with the last lumbar vertebra (fig. 17). The neural spine of the last lumbar vertebra projects posterodorsally and is not fused with adjacent neural spines, unlike the fused dorsal keel evident in European talpids, for example. The only articular surface evident on the sacrum of YPM-PU 15384 fits a corresponding surface on the internal aspect of its ilium, as in golden moles and most nonfossorial mammals. Because the ischia on the two preserved innominates are both incomplete, it is impossible to rule out an ischial-sacrum articulation, as seen in many xenarthrans that possess an accessory obturator foramen (MacPhee, 1994). However, given the gracile sacrum, we believe such accessory articulations were unlikely and that *Necrolestes* possessed a relatively small pelvis without the hyperossifications seen in certain other fossorial mammals (e.g., *Notoryctes,* see fig. 18B). Pelves of *Metacheiromys* and *Alcodontulum* (Palaeanodonta) described respectively by Simpson (1931: fig. 18) and Rose et al. (1992: fig. 4) also resemble that of *Necrolestes* in showing moderate sacral fusion and a simple articulation with the vertebral column at the ilium.

The right ilium is missing the wing, although part of the auricular surface is visible on the medial side. On the lateral side the ilium ends posteriorly in a raised region on the edge of the acetabulum. This eminence is likely to be for the attachment of the *M. rectus femoris*. This position is similar to that in the palaeanodont *Alocodontulum atopum* (Rose et al., 1992: fig. 9) rather than in *Escavadodon zygus* (Rose and Lucas, 2000: fig. 11), where the eminence is located anterior to the acetabulum. This eminence contributes some articular surface to the acetabulum in *Necrolestes*. The lunate surface is therefore very wide anteriorly and becomes narrower dorsally and posteriorly. The caudal border of the lunate surface ends high up posteriorly because of breakage. The ventral edge of the cranial region of the lunate surface is damaged, and it is not possible to determine its position. The pubis has suffered some deformation; however, it is possible to discern an iliopubic eminence, as found in such mammals as *Palaeanodon ignavus* (Emry, 1970: fig. 29), *Escavadodon zygus*, and *Alocodontulum atopum*.

FEMUR: Left and partial right femora are available for YPM-PU 15384 (fig. 19A). The right femur (missing the femoral head) had been in the same box as YPM-PU 15699 in a capsule labeled "15699 or 15384", but is marked with "15384" on its diaphysis. Its potential association with 15384 may have previously been viewed as problematic based on the absent femoral head, potentially representing an unfused epiphysis of a younger individual than the left femur. However, we believe the epiphysis on the right femur had been solidly fused to the diaphysis, but broken off as a simple post-mortem artifact unrelated to age. We therefore presume that both femora belong to YPM-PU 15384.

Necrolestes lacks a femoral neck, with the femoral head projecting anteriorly as well as medially from a proximal femur compressed in an anteroposterior dimension (fig. 19). The greater and lesser trochanters are not distinct; and there is no trochanteric fossa. A very shallow trochanteric fossa has been noted in *Xenocranium* and is absent in *Manis* and *Amblysomus,* among other mammals (Horovitz, 2004).

A flattened proximal femur and absent trochanteric fossa are also found in *Notoryctes* (fig. 19B). The A-P compressed proximal femur in *Notoryctes* owes its peculiar shape to the expanded greater trochanter. As documented by Carlsson (1904), this area provides a large area for attachments of

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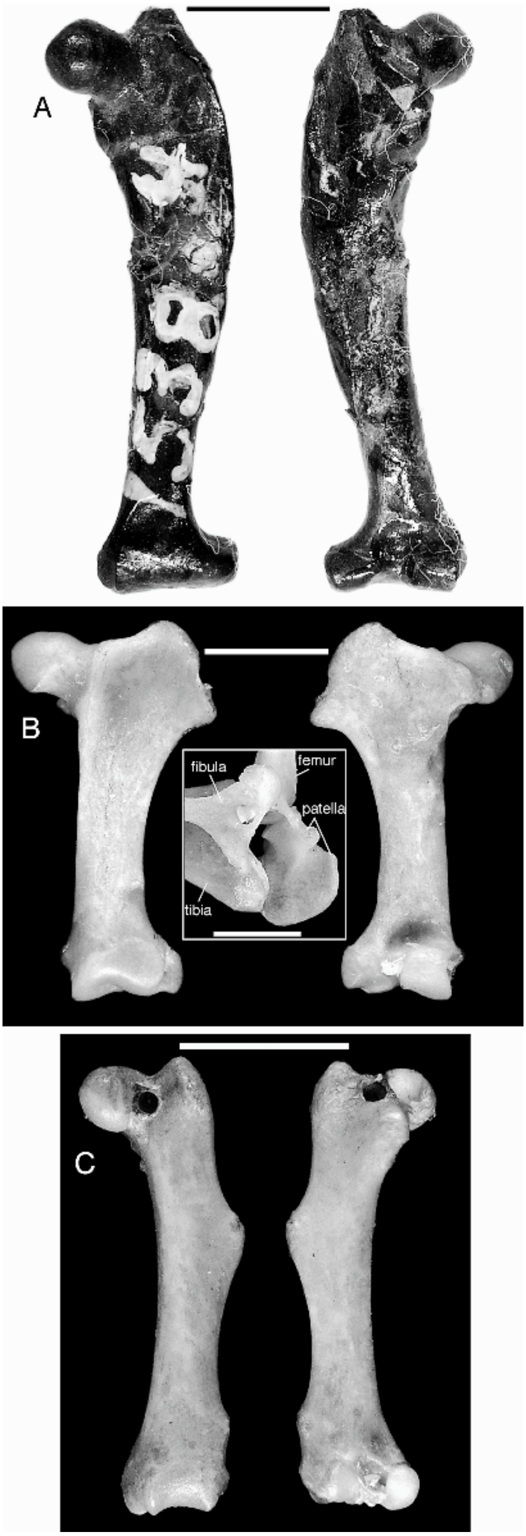

Fig. 19. Femora of (**A**) *Necrolestes patagonensis* (YPM-PU 15384), (**B**) *Notoryctes typhlops* (ZMB 35694) with inset showing lateral aspect of *Notoryctes*' left knee; and (**C**) *Chrysochloris asiatica* (ZMB 76897), in anterior (left) and posterior (right) views. Hole in *Chrysochloris* femoral neck is a post-mortem artifact. Scale bars = 5 mm.

gluteal musculature and powerful internal and external vasti, the latter two inserting onto a greatly enlarged patella (fig. 19B). These muscles contribute to hip flexion, adduction, and crus extension. Uniquely among fossorial mammals, and particularly noteworthy for a marsupial (which with the exception of peramelids generally lack patellae), the large size of the patella in *Notoryctes* may indicate some function in the animal's subterranean environment. Despite its enlarged patella, the distal femur of *Notoryctes* is smooth without a well-defined patellar trochlea.

Both *Notoryctes* and *Necrolestes* show femoral condyles that are wider mediolaterally than proximodistally. The lateral condyle in both taxa is proximodistally narrow and shows more protrusion laterally than its medial counterpart. *Necrolestes* shows a slight fossa that may correspond to a patellar trochlea, but is not as clearly defined as the trochlea in *Chrysochloris*. We have not identified a patella among the YPM-PU material attributed to *Necrolestes*.

DISTAL HIND LIMB: Patterson (1958: 3) reports the presence of the "…tibia, fibula, calcaneum, astragalus, and cuboid" for YPM-PU 15699. Unfortunately, almost all of this material appears to have been lost since Patterson's study. The only element distal to the knee remaining for any of the three Hatcher-Peterson specimens is a proximal fibula fragment (fig. 20), currently in a box with elements from YPM-PU 15384. Because it is mediolaterally flat and anteroposteriorly broad, this specimen resembles the proximal fibula of *Didelphis*, *Notoryctes*, and *Manis*. Unlike chrysochlorids and xenarthrans, the proximal fibula and tibia do not appear to have been fused.

Scott (1905: 378–379) also discusses material of the hind limb that at one point was part of the Hatcher-Peterson specimens, and goes into more detail on the structure of the foot than Patterson:

> Of the pes in *Necrolestes* only the calcaneum, astragalus and cuboid are represented. The calcaneum has a rather short and slender tuber, which is tapered toward the free end and is so curved as to be convex externally and concave internally, thus differing from both of the modern genera, in which the tuber is longer, stouter, and quite straight. The astragalus has a neck which is directed strongly toward the mesial side of the foot, ending in a very small rounded head. The cuboid is very small, but of a shape not unlike that seen in *Chrysochloris*, which, however, much exceeds it in every dimension, especially in the proximo-distal length. So much of the tarsus as is preserved displays but little resemblance to that of *Chrysochloris*.

Fig. 20. Proximal fibula of *Necrolestes* (YPM-PU 15384). Scale bar = 5 mm.

SYSTEMATIC POSITION OF *NECROLESTES*

As summarized in the introduction, the range of suggested taxonomic affinities for *Necrolestes* is broad. One might reduce this uncertainty to a simple question: Is *Necrolestes* a marsupial, placental, or part of a "prototherian" radiation on the stem leading to Theria? In order to address these mutually exclusive possibilities, we examined recently published morphological matrices with dense samples of marsupials (Horovitz and Sánchez-Villagra, 2003) and placentals (Asher et al., 2003), as well as fossil therians and their near-sister taxa, such as australosphenidans (Rougier et al., 1998; Luo et al., 2002). With these matrices and other literature-based sources specified below, we identify in table 1 characters that unambiguously optimize on mammalian trees as diagnostic for Marsupialia, Placentalia, their respective stem clades, Theria, and Australosphenida (including monotremes). A character matrix sampling gondwanatheres, suggested as a possible identification of *Necrolestes* by Van Valen (1988), is not yet available; hence, we cannot explicitly include this group in our character-based survey. Because most taxonomic treatments (e.g., McKenna and Bell, 1997) place gondwanatheres outside of Theria, we tentatively evaluate the proposed association of *Necrolestes* with gondwanatheres based on the evidence that the former is indeed a therian mammal. In other words, if *Necrolestes* is therian, it cannot be a gondwanathere. However, we acknowledge that there remains considerable uncertainty regarding the affinities of gondwanatheres (cf. Pascual et al., 1999; Koenigswald et al., 1999), and recognize that their taxonomic position may change as better fossil material is identified.

Optimizations of characters discussed in these publications are topology-dependent. For relationships among therian stem clades, we follow Luo et al. (2002: fig. 1); for Metatheria, we use the topology of Asher et al. (2004: fig. 1[left]); for Eutheria, we use Asher et al. (2005: fig. 9). Each of these topologies is reproduced here in figure 21. In addition, we use the apomorphy list in Rougier et al. (1998: supplementary data) as a source of character information for the clades discussed below.

We recognize that this comparative approach is inferior to a fully sampled, original phylogenetic analysis to determine the position of *Necrolestes*. However, the broad range of taxa previously hypothesized to be possible relatives of *Necrolestes* (e.g., golden moles, didelphoids, marsupial moles, and gondwanatheres), as well as the wide range of morphological and molecular data that would be required to understand the phylogeny of these taxa and to fit *Necrolestes* into it, would amount to a combined-data analysis of living and fossil Theria and its stem relatives. Stated differently, in order to avoid generating spurious hypotheses of sister-group relationships among, for example, fossorial golden moles and talpids, we would have to integrate more than a single data partition of osteological characters observable in *Necrolestes*, including, for example, DNA sequences for modern taxa. We are not yet in a position to undertake a phylogenetic analysis of such large scope, but attempt here to make clear the osteological characters of *Necrolestes* that could contribute to such a larger analysis.

CHARACTER OPTIMIZATIONS

AUSTRALOSPHENIDA: The clade encompassing monotremes, *Ausktribosphenos*, *Bishops*, and other southern-hemisphere tribosphenic mammals, either on the branch including the Asian taxon *Shuotherium* or immediately distal to it, shows two optimized characters in common with *Necrolestes*: a triangular alignment of the main cusps of the anterior lower molar, and pronounced shearing between molar postvallum and prevallid. Significantly, these characters are also present in northern tribosphenic mammals, and reflect the convergent acquisition of this kind of occlusion in holarctic vs. southern radiations of Mesozoic mammals (Luo et al., 2001). Otherwise, *Necrolestes* does not share any of the unambiguously optimized synapomorphies, all of which are dental, with the stem clade encompassing monotremes.

THERIA: *Necrolestes* shares with crown Theria several characters of the skull and skeleton, including a coiled cochlea of the inner ear, absence of a septomaxilla, and (following the descriptions of Scott [1905]) presence of an astragalar neck. The scapular spine, present in *Necrolestes*, has also been discussed as a therian synapomorphy (Jenkins and Weijs, 1979; Sánchez-Villagra and Maier, 2003). Furthermore, *Necrolestes* shows a therian-like glenoid articulation for the humerus (fig. 13), with no sign of the independent coracoid ossification present in monotremes. On the other hand, according to Luo et al., (2002: character 134), a supraspinous fossa defined in part from a scapular spine is present not only in therians, but also in some dryolestoids (*Henkelotherium*), triconodont (*Gobiconodon*), and amphilestids (*Jeholodens*). According to their phylogeny, the scapular spine does not optimize as a therian synapomorphy.

Necrolestes lacks many of the characters optimized for Theria. Due to its zalambdodont dentition and lack of a protocone, nearly all of its upper molar occlusal surface corresponds to the stylar region of the tribosphenic molar. Hence, many of

TABLE 1

Synapomorphies for Selected Clades

Characters from Rougier et al. (1998), Luo et al. (2002), Horovitz and Sánchez-Villagra (2003), and Asher et al. (2003) are indicated with the abbreviations R, L, H, and A, respectively. Consistency indices are calculated by optimizing characters on the relevant tree depicted in figure 21. Note that some therian synapomorphies listed in Rougier et al. (1998) are ambiguously optimized, depending on the identity of the therian sister taxon, as indicated. In addition, because we have not been able to duplicate the tree shown in Rougier et al. (1998), given the information in their supplementary data, we do not report CIs for their characters. A plus in the third column indicates correspondence of *Necrolestes* with the given synapomorphy; a minus indicates the lack thereof; a question mark indicates ambiguity.

	CI	*Necrolestes* description
Australosphenida plus *Shuotherium*		
(L32-1) Labial cingulid on last premolar present along crown length	0.50	− no cingulids
(L33-1) Lingual cingulid on premolars present	0.20	− no cingulids
(L39-1) Alignment of main cusps of anterior lower molar makes acute angle	0.50	+ trigonid triangular
(L66-1) Hypoconulid present, elevated above cingulid and labially positioned	0.67	− no talonid cusp or hypoconulid
(L87-3) First lower molar oblong with labial bulge	0.42	− no bulges
(L93-2) Occlusal facets match at dental eruption	0.50	?
Australosphenida		
(L29-1) Triangular shape of cusps/crests on last lower premolar	0.75	− lower premolars zalambododont
(L30-2) Presence of distal cingulid on last lower premolar	0.33	− cingulids absent
(L31-2) Last lower premolar transversely wide	0.67	− cheek teeth uniform in width
(L34-1) Last lower premolar cusp c present but lower than cusp a	0.33	?
(L40-2) Postvallum/prevallid shearing strongly developed and transverse	0.33	+ transverse shearing strong
(L44-1) Anterior lower molar metaconid and protoconid similar in height	0.17	− protoconid taller
(L46-1) Cingulid base of paraconid and metaconid elevated	1.00	− cingulids absent
(L47-3) Cristid obliqua present and directed between protoconid and meta- protoconid notch	0.60	− cristid obliqua absent
(L48-3) Lower molar talonid heel crest, "pre-entocristid" extends anteriorly past metaconid	1.00	− talonids absent
(L52-0) Posterior lingual cingulid of lower molars weak/ absent	0.33	− cingulids absent
(L63-2) Molar (m2) talonid wider than trigonid	0.50	− talonids absent
(L64-2) Lower molar hypoflexid deep	0.67	− hypoflexid absent
(L65-4) Molar talonid present as functional basin rimmed with 3 cusps	0.67	− talonids absent
(L98-1) Wear facets 3 and 4 present	0.67	?
Theria		
(R33-1) Preprotocrista extends labially past the base of paracone (with *Pappotherium* as outgroup)		? paracone absent, main cusp possibly metacone (see text)
(R60-2) Paraconid shorter than metaconid (with *Slaughteria* as outgroup)		− lingual lower molar cusps similar in height
(R77-1) Two large mental foramina present, one under p2-p3, the other under m1-m2 (with *Slaughteria* as outgroup)		− single, large mental foramen present, ventral to posterior aspect of canine root
(L41-1) Development of the postprotocrista on the upper molar labially beyond the metacone;	1.00	− protocone and postprotocrista absent

TABLE 1
(Continued)

	CI	*Necrolestes* description
Theria (continued)		
(L79-1) A "moderately" developed lingual region of the upper molars, with distance between conules 31-50% of total tooth length;	0.67	− nearly entire molar crown homologous to "labial" region of tribosphenic tooth
(L80-2) Presence of upper molar conules showing cristae.	0.50	− conules absent
(H12-1) Articular facets of C2 dens continuous with C2 prezagopophyses;	0.33	− dens-C2 prezygopophyses separate
(H95-1) Astragalonavicular facet continuous on medial side of astragalar head;	0.33	?
(H100-1) Astragalar neck present;	1.00	+ neck present based on Scott (1905: 378)
(H151-1) Three lower incisors;	0.29	− four lower incisors
(H187-1) Presence of a postglenoid process;	1.00	− absent
(H190-1) Presence of a postglenoid foramen;	1.00	+ present, but small and located within epitympanic recess
(H201-0) Absence of a septomaxilla;	0.50	+ septomaxilla absent
(H222-1) Fully coiled cochlea.	1.00	+ fully coiled
Metatheria		
(R1-2) Three premolars		+ assuming canine and molar homology from Goin et al. (in press)
(R7-1) Seven postcanine tooth families		− 3 premolars, 3 molars, six postcanine tooth loci
(R10-1) Upper canine with one root		− upper canine two-rooted
(R11-2) Procumbent first upper premolar separated by diastema		− molariform anterior premolar, no diastema
(R19-1) Deep ectoflexus on the penultimate and preceding molar		− ectoflexus absent
(R27-1) Metacone slightly smaller than paracone		− paracone absent, metacone main upper cusp
(R62-1) Last lower molar rotates during eruption		?
(R65-1) Deciduous canine absent		?
(R66-1) Replacement of dP1/dp1 and dP2/dp2 absent		?
(R70-1) Labial mandibular foramen absent		+ labially no foramen evident
(R75-1) "Meckelian" groove absent		+ internal ventrum of jaw is smooth
(R76-1) "Coronoid" facet absent		+ area at anterior base of coronoid process smooth
(R79-1 and H203-1) Palatal process of premaxilla reaches nearly or to canine alveolus		+ premaxilla reaches canine alveolus
(R125-1) Sulcus for anterior distributary of transverse sinus posterolateral to subarcuate fossa		?
(R145-2) Foramen for ramus superior of stapedial artery absent		?
(R147-1) Sulcus for stapedial artery absent		+ sulcus absent
(R150-1) Jugular foramen separated from inferior petrosal sinus opening		?
(R152-2) Ascending canal absent		?
(L34-1) Posterior cusp C of the last lower premolar is distinctive but less than 30% the size of cusp A	0.33	?
(L47-3) Short cristid obliqua of the lower molars connecting anteriorly at a point between the metaconid-protoconid notch and the protoconid	0.60	? inapplicable, talonid/cristid obliqua absent
(L57-1) Postcingulid oblique and connected to hypoconulid	0.67	? inapplicable, hypoconulid absent

TABLE 1
(Continued)

	CI	*Necrolestes* description
Metatheria (continued)		
(L62-1) Mesiolingual surface of lower molar paraconid forms a keel	1.00	− paraconid simple
(L63-2) m2 talonid width equal to or wider than that of m2 trigonid	0.50	? inapplicable, talonid absent
(L69-1) Hypoconulid-postcingulid shelf present as crest from apex of hypoconulid to base of hypoconid	0.69	? inapplicable, hypoconulid absent
(L72-1) Paraconid, metaconid, and entoconid aligned	0.50	? inapplicable, entoconid absent
(H152-0) Four upper molars	1.00	− three molars following Goin et al. (in press)
(H172-1) Staggered lower i3	0.33	− alveoli of lower incisors evenly spaced
(H175-1) Single premolar dental replacement	1.00	?
(H178-1) Medially inflected angular process of dentary	0.33	− angular process not inflected
Crown Marsupialia		description
(H52-1) Proximal extent of humeral capitulum and trochlea similar	0.40	− capitulum extends farther proximally
(H60-0) Distal process of ulna spherical, contributing to ball-socket articulation	1.00	+ styloid of ulna spherical
(H91-2) Tibial posterior shelf present and extending posteriorly beyond medial astragalotibial facet	0.29	? distal tibia missing
(H118-1) Calcaneal sustentacular facet dorsally oriented	0.50	? calcaneus missing
(H185-1) Alisphenoid tympanic wing present	0.67	− alisphenoid bulla absent
(H196-1) Transverse canal foramen anterior to carotid foramen	0.80	+ small foramina anteromedial to carotid fmna indicate transverse canal
(H202-2) Palatal vacuities present	0.57	− palate solid
Eutheria		
(R3-1) Tall, trenchant premolar in penultimate premolar position		− all premolars molariform
(R4-2) Three molars		+ three molars following Goin et al. (In Press)
(R6-0) Size of molars does not increase posteriorly		+ molars similar in size
(R12-1) Penultimate upper premolar protocone is a small lingual bulge		− protocones absent
(R14-2) Last upper premolar molariform		+ all premolars molariform
(R34-1) Postprotocrista does extend labially past base of metacone		− protocone and associated cristae absent
(R132-2) Caudal tympanic process of petrosal notched between stylomastoid notch and jugular foramen		− CTPP absent
(A50-1) Optic foramen present	0.40	? indistinguishable from sphenorbital fissure
(A63-1) Jugal does not contribute to anterior articular surface of glenoid	0.10	? jugal–squamosal suture indistinct
(A65-1) Zygomatic process squamosal small, tapering	0.33	+ zygomatic process posteriorly gracile
(A92-0) Incisive foramen small, oval	0.14	+ incisive foramina small
(A116-0) Jaw angle not inflected	0.33	+ jaw angle not inflected
(A133-1) Scapular coracoid anteroventral to humerus	0.15	− scapular coracoid reduced
Crown Placentalia		
(A159-1) Absence of epipubic bones	1.00	+ absence likely but pelvic region not fully intact
(A39-1) Single condyloid foramen adjacent to each occipital condyle	0.38	? region obscured in available specimens

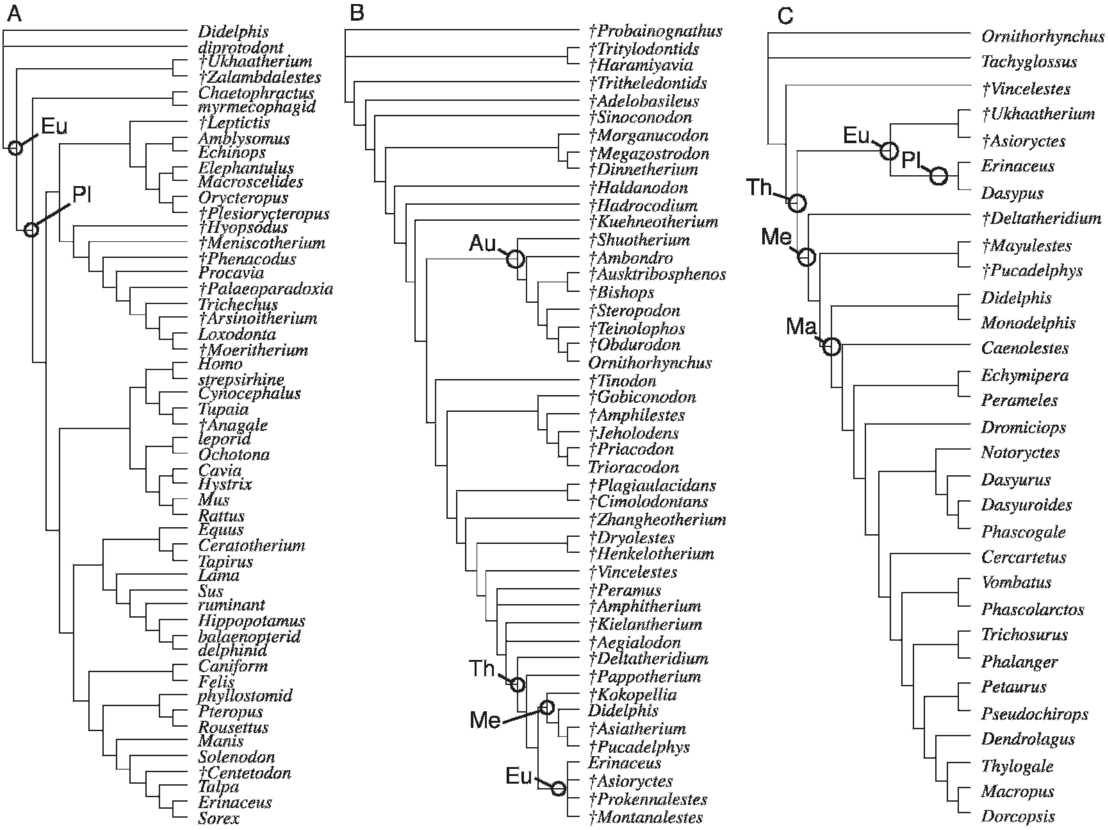

Fig. 21. Trees used to optimize morphological data sets from **(A)** Asher et al. 2003 (topology from Asher et al. 2005: fig. 9), **(B)** Luo et al. 2002 (topology from Luo et al. 2002: fig. 1) and, **(C)** Horovitz and Sánchez-Villagra 2003 (topology from Asher et al. 2004: fig. 1[left]). Abbreviations indicate the following clades: Au, Australosphenida; Eu, Eutheria; Ma, Marsupialia; Me, Metatheria; Pl, Placentalia; Th, Theria.

the dental characters listed by Rougier et al. (1998) and Luo et al. (2002) as diagnostic for Theria are absent (e.g., extent of pre- and postprotocristae, molar conule morphology). In addition, unlike the character reconstruction hypothesized for basal Theria in Rougier et al. (1998: supplementary data), *Necrolestes* shows only a single mental foramen on the exterior of its mandible, inferior to its canine.

METATHERIA: Of the characters optimized unambiguously as metatherian synapomorphies by the data sets identified above, *Necrolestes* shares several: lack of a stapedial artery sulcus, palatal process of the premaxilla reaching the canine alveolus, and presence of three premolars (see discussion of dental homologies above). Of the features of the jaw hypothesized by Rougier et al. (1998: supplementary data) to be derived for Metatheria, *Necrolestes* shares three, all of which are "absence" characters: it lacks a labial mandibular foramen (Kielan Jaworowska and Dashzeveg, 1989: 18), a Meckelian groove, and a coronoid facet.

Several other characters contrast with those optimized for the metatherian common ancestor, such as a double-rooted upper canine, and a noninflected mandibular angle (a derived feature of some marsupial species such as the koala). Without ontogenetic data, we cannot infer the condition for dental replacement (Horovitz and Sánchez-Villagra, 2003: character #175). However, based on the observation of Goin et al. (In Press) that the jaw of *Necrolestes* shows an erupting posterior premolar anterior to three molar loci, one may infer that this animal had three upper and three lower molars, unlike the four reconstructed for the common ancestor of metatherians.

MARSUPIALIA: Compared to the reconstructed common ancestor of crown marsupials, *Necrolestes* shares a ball-shaped distal (=styloid) process of the ulna. It also shows two small foramina anteromedial to the carotid foramina, also exposed on the dorsum of the basisphenoid. We interpret these to be transverse canal foramina (fig. 7). Otherwise, unlike the marsupial common ancestor, it lacks an alisphenoid tympanic process, shows a solid, nonperforated palate, and the capitulum of the distal humerus has an articular surface extending farther proximally than the trochlea.

EUTHERIA: The inferred presence of three molars, all similar in size, fits the morphology of the eutherian common ancestor as reconstructed by Rougier et al. (1998). In addition, characters from the matrix of Asher et al. (2003, 2005) show additional similarities: the zygomatic process of the squamosal is posteriorly gracile; the incisive foramina are relatively small; and the angle of the jaw is not inflected (fig. 3). Features of *Necrolestes* that do not match the reconstructed eutherian ancestor include the molariform appearance of the premolars, absence of protocones and protocristae, absence of a caudal tympanic process of the petrosal, and a reduced coracoid process of the scapula (fig. 13A).

PLACENTALIA: The only two unambiguously optimized characters of crown Placentalia from Asher et al. (2003, 2005) are absence of epipubic bones and a single hypoglossal (= "condylar") foramen. Patterson (1958) believed that the Hatcher-Peterson *Necrolestes* specimens indicated presence of epipubic bones. However, as summarized above, we see no sign of these in any of the specimens available to us. Similarly, fragmentary occipital remains of the *Necrolestes* material do not clearly show the morphology or number of hypoglossal foramina that may have been present.

SUMMARY AND CONCLUSIONS

Previously underappreciated aspects of the anatomy of *Necrolestes* include the hypsodont upper cheek teeth (fig. 1D) and bilaterally unfused atlas (figs. 8, 9). The former comprise an interesting similarity to the gondwanatheres mentioned by Van Valen (1988) as potential close relatives of *Necrolestes*. If true, this would comprise a range extension of the gondwanathere fossil record by some 20 million years, from their previously recognized last occurrence in the middle Eocene (Bond et al., 1990; Reguero et al., 2002) to Santacrucian time. Regarding atlantal fusion, some diprotodonts, peramelians, and the Cretaceous eutherian *Asioryctes* (Kielan-Jaworowska et al., 2004) show an incomplete ventral arch. However, with the possible exception of *Daulestes* (McKenna et al., 2000), unfused ventral and dorsal arches of the atlas are unknown among adult therians, having been documented only in the therian sister taxon *Vincelestes* (Rougier, 1993).

Nevertheless, when sampled in previous morphological matrices, these characters do not show unambiguous changes on the mammalian nodes summarized in table 1. Based on characters that do exhibit such change, we believe there is a basis for supporting the status of *Necrolestes* as a therian mammal. With the possible exception of atlantal nonfusion, characters it shares with southern-hemisphere radiations are also present in northern tribosphenic mammals (e.g., hypsodont cheek teeth). More importantly, *Necrolestes* possesses diagnostically therian characteristics such as the coiled cochlear housing of the inner ear and (based on the descriptions of Scott, 1905) an astragalar neck.

We cannot completely exclude the possible identity of *Necrolestes* as some kind of eutherian mammal. The idea that it is related to golden moles was favored in the first two publications describing its anatomy (Ameghino, 1891; Scott, 1905). Although we do not agree with several of the anatomical conclusions made by Scott (e.g., number of incisors, shape of the mandibular coronoid process, bullar ossification, presence of carotid foramina, and fusion of cervical vertebrae), we believe he was correct on a few important points. Perhaps most striking is the resemblance, first pointed out by him (1905: 374) but not mentioned by subsequent authors, that *Necrolestes* and golden moles share at least some ossification of the digital flexor tendon. As discussed above, the external digital flexor in *Chrysochloris* ossifies along nearly the entire forearm, from the humeral medial epicondyle to the carpus (fig. 15D). *Necrolestes* shows a similarly elongate element stretching proximally from the carpus (fig. 15C). Furthermore, we agree with Scott that *Necrolestes* lacks an inflected mandibular angle; we also agree with Goin et al. (in press) that *Necrolestes* appears to have just three cheek teeth, presumably molars, following an erupting premolar.

Hence, we do not believe Patterson's contention that the status of *Necrolestes* as a marsupial is "virtually assured". In our analysis, its mandibular angle is emphatically not marsupial-like in appearance (fig. 3), and the evidence for epipubic bones is inconclusive. It is worth pointing out here that the oldest metatherian, *Sinodelphys szalayi* (Luo et al., 2003), does not have an inflected mandibular angular, which is otherwise legitimately viewed as a shared derived character among more nested metatherians (Sánchez-Villagra and Smith, 1997). Likewise, epipubic bones are a primitive mammalian feature and have been found in basal eutherians (Novacek et al., 1997). *Necrolestes* also lacks the prootic canal present in the petrosal of most metatherian mammals (Sánchez-Villagra and Wible, 2002). On the other hand, positive evidence for a marsupial identification of *Necrolestes* is evident in the basicranium, which shows transverse canal foramina anteromedial to the carotid foramina (fig. 6). In addition, *Necrolestes* lacks the reduction of premaxillary teeth and the stapedial artery sulcus characteristic of most eutherian mammals.

On a more definitive note, features such as the lack of enamel Hunter-Schreger bands, the presence of radial enamel, a coiled inner-ear cochlea, and scapular morphology strongly indicate that *Necrolestes* is not a rodent or a monotreme—hence our somewhat tongue-in-cheek, but accurate, reference to these taxa in the title of this paper (cf. Kirsch and Mayer, 1998). Nevertheless, we admit that the list of possible taxonomic affiliations for this animal still remains long. If the affinities of *Necrolestes* were easy to infer, it would have long ago been placed securely among a well-defined group of mammals, and not incertae sedis at the base of "Insectivora" (Simpson, 1945) or Theria (McKenna and Bell, 1997). Despite availability of a fair amount of cranioskeletal material that provides insight into the morphology of a number of anatomical regions, our review does not compel us to unequivocally embrace any previous diagnosis of its affinities. A marsupial identification would present a less complicated biogeographic scenario, and may lead some to agree with Patterson and view its marsupial-like characters (e.g., incisor count, transverse canal foramina) as most indicative of its relationships.

One of the most frustrating aspects of this study is the fact that tarsal elements of *Necrolestes* had apparently been recovered by Hatcher and Peterson in the 1890s, but have since been lost. These elements can be particularly useful in distinguishing marsupial from placental mammals (Szalay, 1994; Horovitz, 2000). We hope that new discoveries will yield more *Necrolestes* skeletal material, perhaps illuminating the anatomy of the foot, and thereby better enabling future researchers to make more precise statements on its higher-level affinities.

ACKNOWLEDGMENTS

We thank Pancho Goin, Rosendo Pascual, Daniel Brinkmann, Jaques Gauthier, Marylin Fox, and Maryann Turner for help in arranging the analysis of the YPM-PU *Necrolestes* material. We are also grateful to Bill Clemens, Ross MacPhee, and an anonymous reviewer for helpful comments on the manuscript, to Matt Skinner, Tanja Smith, Jan Ihlau, and Julia Schultz for help with CT-images, and to Robin Beck for discussion. Wolfgang Müller assisted at the SEM and Katrin Krohmann provided the artwork of figure 4. RJA acknowledges financial support from the Deutsche Forschungsgemeinschaft (DFG grant AS 245/2-1) and the European Commission's Research Infrastructure Action via the SYNTHESYS Project (GB-TAF 218); the work of TM was supported by a DFG Heisenberg grant (MA 1643/5-2).

REFERENCES

Ameghino, F. 1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas adiciones y correcciones. Revista Argentina de Historia Natural 1: 289–328.

Archer, M. 1984. Origins and early radiations of marsupials. *In* M. Archer and G. Clayton (editors), Vertebrate zoogeography and evolution in Australasia: 585–626. Carlisle: Hesperian Press.

Archer, M., S. Hand, and H. Godthelp. 2000. Australia's lost world. Carlisle: Riversleigh Books.

Asher, R.J. 2005. Insectivoran-grade placental mammals: character evolution and fossil history. *In* K.D. Rose and J.D. Archibald (editors), The rise of placental mammals: origin and relationships of the major clades: 50–70. Baltimore: Johns Hopkins University Press.

Asher, R.J., R.J. Emry, and M.C. McKenna. 2005. New material of *Centetodon* (Mammlia, Lipotyphla) and the importance of (missing) DNA sequences in systematic paleontology. Journal of Vertebrate Paleontology 25: 911–923.

Asher, R.J., I. Horovitz, and M.R. Sánchez-Villagra. 2004. First combined cladistic analysis of marsupial mammal interrelationships. Molecular Phylogenetics and Evolution 33: 240–250.

Asher, R.J., M.J. Novacek, and J. Geisler. 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. Journal of Mammalian Evolution 10: 131–194.

Asher, R.J., and M.R. Sánchez-Villagra. 2005. Locking yourself out: diversity among dentally zalambdodont therian mammals. Journal of Mammalian Evolution 12: 265–282.

Bond, M., R. Pascual, M.A. Reguero, S.N. Santillana, and S.A. Marenssi. 1990. Los primeros ungulados extinguidos sudamericanos de la Antártida. Ameghiniana 16: 240.

Bronner, G.N. 1991. Comparative hyoid morphology of nine chrysochlorid species (Mammalia: Chrysochloridae). Annals of the Transvaal Museum 35: 295–311.

Broom, R. 1916. On the structure of the skull in *Chrysochloris*. Proceedings of the Zoological Society of London 1916: 449–459.

Broom, R. 1927. Some further points on the structure of the mammalian basicranial axis. Proceedings of the Zoological Society of London 1927: 233–244.

Carlsson, A. 1904. Zur Anatomie des *Notoryctes typhlops*. Zoologisches Jahrbuch Abteilung Anatomie und Ontogenie 20: 81–122.

Cave, A.J.E. 1948. The nasal fossa in the primates. British Medical Association Proceedings of the Annual Meeting 1948.

Clemens, W.A. 1973. Fossil mammals of the Type Lance Formation, Wyoming. Part III. Eutheria and summary. University of California Publications in Geological Sciences 62: 1–122.

DeBeer, G.R. 1937 (reprinted 1985). The development of the vertebrate skull. Chicago: University of Chicago Press.

Dobson, G.E. 1883. A monograph of the Insectivora, systematic and anatomical, Part II. Including the families Potamogalidae, Chrysochloridae, and Talpidae. London: John Van Voorst.

Ekdale, E.G., J.D. Archibald, and A.O. Averianov. 2004. Petrosal bones of placental mammals from the Late Cretaceous of Uzbekistan. Acta Palaeontologica Polonica 49: 161–176.

Emry, R.J. 1970. A North American Oligocene pangolin and other additions to the Pholidota. Bulletin of the American Museum of Natural History 142: 455–510.

Evans, H.E. 1993. Miller's anatomy of the dog, 3rd ed. Philadelphia: W.B. Saunders.

Gadow, H. 1892. On the systematic position of *Notoryctes typhlops*. Proceedings of the Zoological Society of London 1892: 361–370.

Goin, F.J., and A.M. Candela. 2004. New Paleogene marsupials from the Amazonian basin, Southeastern Peru. Natural History Museum of Los Angeles County, Science Series 40: 15–60.

Goin, F.J., A. Abello, E. Bellosi, R. Kay, R. Madden, and A.A. Carlini. In press. Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno Temprano, Edad-mamífero Colhuehuapense). Parte I: Introducción, Didelphimorphia y Sparassodonta. Ameghiniana.

Gray, A.A. 1907. The labyrinth of animals. vol. 2. London: J. & A. Churchill.

Gregory, W.K. 1910. The orders of mammals. Bulletin of the American Museum of Natural History 27: 1–524.

Griffiths, M. 1978. The biology of monotremes. New York: Academic Press.

Hickman, G.C. 1990. The Chrysochloridae: studies toward a broader perspective of adaptation in subterranean mammals. *In* O. Reig and E. Nevo (editors), Evolution of subterranean mammals at the organismal and molecular levels: 23–48. New York: Alan R. Liss.

Horovitz, I. 2000. The tarsus of *Ukhaatherium nessovi* (Eutheria, Mammalia) from the Late Cretaceous of Mongolia; an apprasial of the evolution of the ankle in basal therians. Journal of Vertebrate Paleonotology 20: 547–560.

Horovitz, I. 2004. Eutherian mammal systematics and the origins of South American ungulates as based on postcranial osteology. Bulletin of Carnegie Museum of Natural History 36: 63–79.

Horovitz, I., and M.R. Sánchez-Villagra. 2003. A morphological analysis of marsupial mammal higher-level phylogenetic relationships. Cladistics 19: 181–212.

Jenkins, F.A. 1971. The postcranial skeleton of African cynodonts: problems in the early evolution of the mammalian postcranial skeleton. Bulletin of the Peabody Museum of Natural History 36: 1–216.

Jenkins, F.A., and F.R. Parrington. 1976. The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. Philosophical Transactions of the Royal Society of London B 273: 387–431.

Jenkins, F.A., and W.A. Weijs. 1979. The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). Journal of Zoology London 188: 379–410.

Kielan-Jaworowska, Z. 1977. Evolution of the therian mammals in the Late Cretaceous of Asia. Part II. Postcranial skeleton in *Kennalestes* and *Asioryctes*. Palaeontologia Polonica 37: 65–83.

Kielan-Jaworowska, Z., R.L. Cifelli, and Z.X. Luo. 2004. Mammals from the Age of Dinosaurs: origins, structure, and evolution. New York: Columbia University Press.

Kielan-Jaworowska, Z., and D. Dashzeveg. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. Zoologica Scripta 18: 347–355.

Kirsch, J.A.W., and G.C. Mayer. 1998. The platypus is not a rodent: DNA hybridization, amniote phylogeny, and the palimpsest theory. Philosophical Transactions of the Royal Society of London B 353: 1221–1237.

Koenigswald, W.v. 1988. Enamel modification in enlarged front teeth among mammals and the various possible modification of the enamel. Mémoires du Musée National d'Histoire Naturelle (C) 53: 148–165.

Koenigswald, W.v. 1997a. Brief survey of enamel diversity at the schmelzmuster level in Cenozoic placental mammals. *In* W.v. Koenigswald and M.P. Sander (editors), Tooth enamel microstructure: 137–161. Rotterdam: Balkema.

Koenigswald, W.v. 1997b. Evolutionary trends in the differentiation of mammalian enamel ultrastructure. *In* W.v. Koenigswald and M.P. Sander (editors), Tooth enamel microstructure: 203–235. Rotterdam: Balkema.

Koenigswald, W.v., and M.P. Sander. 1997a. Glossary of terms used for enamel microstructures. *In* W.v. Koenigswald and M.P. Sander (editors), Tooth enamel microstructure: 267–280. Rotterdam: Balkema.

Koenigswald, W.v., and M.P. Sander. 1997b. Tooth enamel microstructure. Rotterdam: Balkema.

Koenigswald, W.v., and F. Goin. 2000. Enamel differentiation in South American marsupials and a comparison of placental and marsupial enamel. Paleontographica A 255: 129–168.

Koenigswald, W.v., F. Goin, and R. Pascual. 1999. Hypsodonty and enamel microstructure in the Paleocene gondwanatherian mammal Sudamerica ameghinoi. Acta Palaeontologica Polonica 44: 263–300.

Koenigswald, W.v., J.M. Rensberger, and H.U. Pfretschner. 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. Nature 328: 150–152.

Kühne, W.G. 1956. The Liassic thrapsid Oligokyphus. London: British Museum of Natural History.

Leche, W. 1907. Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere, zugleich ein Beitrag zur Stammengeschichte dieser Tiergruppe. Teil 2. Zoologica (Stuttgart) 49: 1–157.

Lessertisseur, J., and R. Saban. 1967a. Squelette axial. *In* P.P. Grassé (editor), Traité de zoologie: anatomie, systématique, biologie 16: 585–708. Paris: Masson.

Lessertisseur, J., and R. Saban. 1967b. Généralités sur le squelette. *In* P.P. Grassé (editor), Traité de zoologie: anatomie, systématique, biologie 16: 334–404. Paris: Masson.

Long, J., M. Archer, T.J. Flannery, and S. Hand. 2002. Prehistoric mammals of Australia and New Guinea. Baltimore: John Hopkins University Press.

Luo, Z-X., R.L. Cifelli, and Z. Kielan-Jaworowska. 2001. Dual origin of tribosphenic mammals. Nature 409: 53–57.

Luo, Z-X., Q. Ji, J.R. Wible, and C.X. Yuan. 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. Science 302: 1934–1940.

Luo, Z-X., Z. Kielan-Jaworowska, and R.L. Cifelli. 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47: 1–78.

MacPhee, R.D.E. 1994. Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. Bulletin of the American Museum of Natural History 220: 1–214.

Martin, T. 1999a. Evolution of incisor enamel microstructure in Theridomyidae (Rodentia). Journal of Vertebrate Paleontology 19: 550–565.

Martin, T. 1999b. Phylogenetic implications of Glires (Eurymylidae, Mimotonidae, Rodentia, Lagomorpha) incisor enamel microstructure. Mitteilungen des Museums für Naturkunde Berlin, Zoologische Reihe 75: 257–273.

Martin, T. 2004. Evolution of incisor enamel microsturcture in Lagomorpha. Journal of Vertebrate Paleontology 24: 414–429.

Mason, M. 2003. Morphology of the middle ear of golden moles (Chrysochloridae). Journal of Zoology (London) 260: 391–403.

McDowell, S.B. 1958. The Greater Antillean insectivores. Bulletin of the American Museum of Natural History 115: 115–213.

McKenna, M.C., and S.K. Bell. 1997. Classification of mammals above the species level. New York: Columbia University Press.

McKenna, M.C., Z. Kielan-Jaworowska, and J. Meng. 2000. Earliest eutherian mammal skull from the Late Cretaceous (Coniacian) of Uzbekistan. Acta Paleontologica Polonica 45: 1–54.

Novacek, M.J. 1993. Patterns of diversity in the mammalian skull. *In* J. Hanken and B. Hall (editors), The skull, volume 2: 438–545. Chicago: University of Chicago Press.

Novacek, M.J., G.W. Rougier, J.R. Wible, M.C. McKenna, D. Dashzeveg, and I. Horovitz. 1997. Epipubic bones in eutherian mammals from the late Cretaceous of Mongolia. Nature 389: 440–441.

Oliveira, C.A., J.C. Nogueira, and G.A. Mahecha. 1998. Sequential order of appearance of ossification centers in the opossum *Didelphis albiventris* (Didelphidae) skeleton during development in the marsupium. Annals of Anatomy 180: 113–121.

Parker, W.K. 1885. On the structure and development of the skull in the Mammalia, part 3, Insectivora. Philosophical Transactions of the Royal Society of London 176: 121–276.

Pascual, R., F.J. Goin, D.W. Krause, E. Ortiz-Jaureguizar, and A.A. Carlini. 1999. The first gnathic remains of Sudamerica: implications for Gondwanathere relationships. Journal of Vertebrate Paleontology 19: 373–382.

Patterson, B. 1958. Affinities of the Patagonian fossil mammal, *Necrolestes*. Breviora Museum of Comparative Zoology 94: 1–14.

Patterson, B. 1975. The fossil aardvarks (Mammalia: Tubulidentata). Bulletin of the Museum of Comparative Zoology 147: 185–237.

Polly, P.D., S.C. Le Comber, and T.M. Burland. 2005. On the occlusal fit of tribosphenic molars: Are we underestimating species diversity in the Mesozoic? Journal of Mammalian Evolution 12: 283–299.

Reguero, M.A., S.A. Marenssi, and S.N. Santillana. 2002. Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. Palaeogeography, Palaeoclimatology, Palaeoecology 179(3–4): 189–210.

Rose, K.D. 1999. *Eurotamandua* and Palaeanodonta: convergent or related? Paläontologische Zeitschrift 73: 395–401.

Rose, K.D., and R.J. Emry. 1983. Extraordinary fossorial adaptations in the Oligocene palaeanodonts *Epoicotherium* and *Xenocranium*. Journal of Morphology 75: 33–56.

Rose, K.D., R.J. Emry, and P.D. Gingerich. 1992. Skeleton of *Alocodontulum atopum*, an early Eocene epoicotheriid (Mammalia, Palaeanodonta) from the Bighorn Basin, Wyoming. Contributions from the Museum of Paleontology University of Michigan 28: 221–245.

Rose, K.D., L. Krishtalka, and R.K. Stucky. 1991. Revision of the Wind River faunas, Early Eocene of central Wyoming. Part 4. Palaeanodonta (Mammalia). Annals of Carnegie Museum 60: 63–82.

Rose, K.D., and S.G. Lucas. 2000. An early Paleocene palaeanodont (Mammalia, ?Pholidota) from New Mexico, and the origin of Palaeanodonta. Journal of Vertebrate Paleontology 20: 139–156.

Rougier, G. 1993. *Vincelestes neuquenianus* Bonaparte (Mammalia, Theria) un primitivo mamifero del Cretacico Inferior de la Cuenca Neuquina. Ph.D. thesis, Argentina: Universidad Nacional de Buenos Aires.

Rougier, G.W., J.R. Wible, and M.J. Novacek. 1998. New specimens of *Deltatheridium*, implications for the early history of marsupials. Nature 396: 459–463.

Roux, G.H. 1947. The cranial development of certain Ethiopian "insectivores" and its bearing on the mutual affinities of the group. Acta Zoologica 28: 165–233.

Saban, R. 1954. Phylogénie des Insectivores. Bulletin de le Muséum Nationale d'Histoire Naturelle, Ser. 2 26: 419–432.

Sánchez-Villagra, M.R., and R.J. Asher. 2002. Cranio-sensory adaptations in small, faunivorous mammals, with special reference to olfaction and the trigeminal system. Mammalia 66: 93–109.

Sánchez-Villagra, M.R., and W. Maier. 2003. Ontogenesis of the scapula in marsupial mammals, with special emphasis on perinatal stages of didelphids and remarks on the origin of the therian scapula. Journal of Morphology 258: 115–129.

Sánchez-Villagra, M.R., and T. Schmelzle. In press. Anatomy and development of the bony inner ear in the woolly opossum, *Caluromys philander* (Didelphimorphia, Marsupialia). Mastozoologia Neotropical.

Sánchez-Villagra, M.R., and K.K. Smith. 1997. Diversity and Evolution of the Marsupial Mandibular Angular Process. Journal of Mammalian Evolution 4: 119–144.

Sánchez-Villagra, M.R., and J.R. Wible. 2002. Patterns of evolutionary transformation in the petrosal bone and some basicranial features in marsupial mammals, with special reference to didelphids. Journal of Zoological Systematics and Evolutionary Research 40: 26–45.

Scott, W.B. 1905. Insectivora and Glires. Reports of the Princeton University Expedition to Patagonia 1896–1899 5: 365–499.

Simpson, G.G. 1931. A new classification of mammals. Bulletin of the American Museum of Natural History 59: 259–293.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85: 1–350.

Starck, D. 1995. Lehrbuch der Speziellen Zoologie, Band II, Wirbeltiere, Teile 1–2, Saeugetiere. Jena: Gustav Fischer Verlag.

Stirling, E.C. 1891. Description of a new genus and species of Marsupialia, *Notoryctes typhlops*. Transactions of the Royal Society of South Australia 14: 154–187.

Stirling, E.C. 1894. Supplemental note on the osteology of *Notoryctes typhlops*. Transactions of the Royal Society of South Australia 18: 1–2.

Szalay, F.S. 1994. Evolutionary history of the marsupials and an analysis of osteological characters. New York: Cambridge University Press.

Turnbull, W.D. 1971. The Trinity therians: their bearing on evolution in marsupials and other therians. *In* A.A. Dahlberg (editor), Dental morphology and evolution: 151–179. Chicago: University of Chicago Press.

Van Valen, L.M. 1988. Faunas of a southern world. Nature 333: 113.

Watson, A.G., H.E. Evans, and A. DeLahunta. 1986. Ossification of the atlas-axis complex in the dog. Zentralblatt für Veterinärmedizin. Reihe C: Anatomie, Histologie, Embryologie 15: 122–138.

Wible, J.R. 2003. On the cranial osteology of the short-tailed opossum Monodelphis brevicaudata (Didelphidae, Marsupialia). Annals of the Carnegie Museum 72: 137–202.

Wible, J.R., and T.J. Gaudin. 2004. On the cranial osteology of the yellow armadillo *Euphractus sexcinctus* (Dasypodidae, Xenarthra, Placentalia). Annals of the Carnegie Museum 73: 117–196.

Wible, J.R., and J.A. Hopson. 1995. Homologies of the prootic canal in mammals and non-mammalian cynodonts. Journal of Vertebrate Paleontology 15: 331–356.

Wible, J.R., G.W. Rougier, M.C. McKenna, and M.J. Novacek. 2001. Earliest eutherian ear region: a petrosal referred to *Prokennalestes* from the Early Cretaceous of Mongolia. American Museum Novitates 3322: 1–44.

Wilson, J.T. 1894. On the myology of *Notoryctes typhlops*, with comparative notes. Transactions of the Royal Society of South Australia 18: 3–74.

Winge, H. 1941. The interrelationships of the mammalian genera. Copenhagen: C.A. Reitzels Forlag.

Wood, C.B., and D.N. Stern. 1997. The earliest prisms in mammalian and reptilian enamel. *In* W.v. Koenigswald and M.P. Sander (editors), Tooth enamel microstructure: 63–83. Rotterdam: Balkema.

Wood, C.B., E.R. Dumont, and A.W. Crompton. 1999. New studies of enamel microstructure in Mesozoic mammals: a review of enamel prisms as a mammalian synapomorphy. Journal of Mammalian Evolution 6: 177–213.

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