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Earliest Eutherian Ear Region: A Petrosal Referred to *Prokennalestes* from the Early Cretaceous of Mongolia

JOHN R. WIBLE,¹ GUILLERMO W. ROUGIER,² MICHAEL J. NOVACEK,³
AND MALCOLM C. McKENNA³

ABSTRACT

A right petrosal from the ?Aptian or Albian Khoobur locality is referred on the basis of size and morphology to *Prokennalestes trofimovi*, the earliest eutherian previously known only from dentigerous elements. The petrosal shows a mosaic of primitive and derived features, bearing on the purported therian and eutherian morphotypes. Among the primitive features shared with the Early Cretaceous prototribosphenidan *Vincelestes* and other more basal taxa that are modified in later eutherians and metatherians are the pattern of basicranial arterial and venous circulation, including a prootic canal and an intrapetrosal inferior petrosal sinus; a vertical paroccipital process; and a fenestra semilunaris, an incomplete wall between the cavum epiptericum and cavum supracochleare. Among the derived features shared with therians is a cochlea coiled through a minimum of 360°, with *Prokennalestes* extending the range of the oldest occurrence of such a coiled cochlea by at least 10 million years. Shared with Late Cretaceous eutherians is a shallow internal acoustic meatus with a thin prefacial commissure. The petrosal referred to *Prokennalestes* is intermediate in having a reduced anterior lamina and lateral flange, both of which are well developed in *Vincelestes* and essentially lacking in later eutherians and metatherians. Features previously held to be part of the therian and eutherian morphotypes, such as the absence of the anterior lamina and lateral flange, may have been lost independently in metatherians and in post-*Prokennalestes* eutherians.

¹ Research Associate, Division of Vertebrate Zoology, American Museum of Natural History; Associate Curator, Section of Mammals, Carnegie Museum of Natural History, 5800 Baum Boulevard, Pittsburgh PA 15206.

² Research Associate, Division of Paleontology, American Museum of Natural History; Assistant Professor, Department of Anatomical Sciences and Neurobiology, School of Medicine, University of Louisville, Louisville KY 40292.

³ Curator, Division of Paleontology, American Museum of Natural History.

INTRODUCTION

Remains of eutherian mammals from the Early Cretaceous are exceedingly rare. The only undoubted eutherians from this interval are *Prokennalestes* from the ?Aptian or Albian of Mongolia (Kielan-Jaworowska and Dashzeveg, 1989; Sigogneau-Russell et al., 1992) and *Bobolestes* from the late Albian of Uzbekistan (Nessov, 1985; Nessov and Kielan-Jaworowska, 1991; Nessov et al., 1994). The former is known from nearly complete lower dentitions and fragmentary uppers (Kielan-Jaworowska and Dashzeveg, 1989; Sigogneau-Russell et al., 1992), whereas the latter is known from a maxillary fragment with two molars (Nessov, 1985). Other purported Early Cretaceous eutherians known from incomplete lower jaws include *Ausktribosphenos* from the Aptian of Australia (Rich et al., 1997, 1998, 1999) and *Endotherium* from not later than the Aptian of northeast China (Shikama, 1947; Wang et al., 1995). The eutherian designation of *Ausktribosphenos* has been contested by Kielan-Jaworowska et al. (1998) and Rougier and Novacek (1998), and the original specimen of *Endotherium* has been lost. Other possible Early Cretaceous eutherians include *Montanalestes* from the Aptian-Albian of Montana (Cifelli, 1999) and, according to Kielan-Jaworowska (1992), *Tribotherium* known from four isolated, incomplete upper molars from the ?Berriasian of Morocco (Sigogneau-Russell, 1991, 1995).

Khoobur (also variously spelled Khobur, Khoboor, and Khovboor), Guchin Us Somon, Mongolia is the ?Aptian or Albian locality yielding *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989). Discovered by the Joint Soviet-Mongolian Paleontological Expeditions (Beliajeva et al., 1974), additional collecting at Khoobur has been conducted by the Geological Institute of the Mongolian Academy of Sciences, and in the summer of 1991, 1997, and 1999, by the Mongolian Academy of Sciences–American Museum of Natural History Expeditions (MAE). In addition to *Prokennalestes*, a diverse mammalian fauna has been reported from fragmentary mandibular remains, including multituberculates (Trofimov, 1980; Kielan-Jaworowska et al., 1987), gobiconodontids

(Trofimov, 1978), symmetrodonts (Trofimov, 1980, 1997), cladotherians (Dashzeveg, 1979, 1994), and tribosphenidans (Dashzeveg, 1975; Dashzeveg and Kielan-Jaworowska, 1984).

In 1995, Wible et al. described a well-preserved petrosal bone (PSS-MAE 104) from Khoobur yielded through screen washing by the MAE. They concluded (Wible et al., 1995: 10), based on its size and the results of their cladistic analysis, that this specimen belonged “to either an as yet unknown triconodont or to a primitive holotherian, which in the context of the known Khoobur fauna would be the symmetrodont *Gobiodon infinitus* Holotheria includes the common ancestor of *Kuehneotherium* and therians plus all its descendants.” In a subsequent contribution, Rougier et al. (1996a) reported a second petrosal (PSS-MAE 129), which was identified as the sister group of PSS-MAE 104 in their cladistic analysis. However, the triconodont versus holotherian relationships of both specimens were left unresolved. More recently, another well-preserved, smaller petrosal has been found in the MAE screen wash collection from Khoobur. A preliminary announcement of this specimen (PSS-MAE 136) was made in Wible et al. (1997). These authors identified this as the petrosal of ?*Prokennalestes*. A full description of this specimen, the earliest known eutherian ear region, is provided here.

METHODS

For the descriptions of PSS-MAE 136, we employ the anatomical terminology that we have used in reports on basicrania of other Mesozoic mammals (e.g., Wible, 1990; Rougier et al., 1992, 1996a; Wible et al., 1995). In addition to describing the outer surfaces of the petrosal, we report some of the internal features of the PSS-MAE 136 as revealed through radiographic analysis. The specimen was digitally imaged at the University of Louisville School of Dentistry using a small dental intraoral charged-coupled device (RadioVisioGraphy Model PCi sensor; Trophy Radiography, Vincennes, France) and a dental X-ray generator operating at 70 kVp, 7mA at an exposure time of approximately 0.1 seconds. Multiple projec-

tions of the specimen were taken and resultant images enhanced in Adobe Photoshop.

We also reconstruct the major vessels and nerves associated with the petrosal bone. Our research on the anatomy of recent mammals (e.g., Novacek, 1986, 1993; Wible, 1986, 1987, 1990; Rougier et al., 1992; Wible and Hopson, 1995) serves as background for this vascular and nervous reconstruction. Recently, several authors (e.g., Bryant and Russell, 1992; Witmer, 1995) have offered explicit methods for reconstructing soft tissues in fossils and for evaluating levels of confidence in those inferences. In formulating hypotheses about soft-tissue reconstruction here, we accept that PSS-MAE 136 is attributable to *Prokennalestes* and, following the recent phylogenetic analysis by Rougier et al. (1998), identify *Prokennalestes* as a basal eutherian (fig. 5). Consequently, under the terminology proposed by Witmer (1995), the extant phylogenetic bracket (minimally, the first two extant outgroups) for *Prokennalestes* consists of placentals and marsupials. Inferences that are based on soft-tissue structures and osteological correlates occurring in both extant outgroups are considered more decisive than those occurring in only one.

INSTITUTIONAL ABBREVIATIONS

AMNH Department of Vertebrate Paleontology, American Museum of Natural History, New York

MACN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires

MAE Collections of joint Mongolian Academy of Sciences–American Museum of Natural History Paleontological Expeditions

PSS Paleontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Science, Ulaan Baatar

UCMP University of California, Museum of Paleontology, Berkeley

DESCRIPTIONS

In Recent mammals, the petrosal houses the organs of hearing and equilibration. For descriptive purposes, the therian petrosal historically (e.g., Voit, 1909; Fawcett, 1918) has been divided into two parts: the more anter-

oventral pars cochlearis, enclosing the cochlea, and the more posterodorsal pars canalicularis, enclosing the vestibule and the semicircular canals. We describe the petrosal of *Prokennalestes* here in three views—ventral, dorsal, and lateral—with the orientation based on the presumed position in the skull. However, given that the specimen is isolated and incomplete, its precise orientation in the skull is subject to interpretation. We have provided an estimate in figure 1, but must admit that the angulation to the midline may be considerably different depending on the proportions of the surrounding cranial elements. Following our descriptions, the morphology of the osseous inner ear as revealed through radiographic analysis and a reconstruction of the courses of the major vessels and nerves suggested by grooves, canals, and foramina on PSS-MAE 136 are presented.

PSS-MAE 136 is a right petrosal (fig. 1). The pars cochlearis is largely intact, with the only substantive damage being to the anteromedial surface, which has exposed spongy bone within the petrosal. In contrast, the pars canalicularis has suffered considerable damage such that roughly the lateral, posterodorsal half of it is missing. Of the three semicircular canals, the lateral one is almost wholly enclosed in bone, as is the bulk of the posterior one. However, little remains of the anterior semicircular canal or the bone between it and the other two canals.

VENTRAL VIEW

(fig. 1A, D)

In ventral view, the pars cochlearis is represented chiefly by the oval promontorium of the petrosal. The shape and topography of the promontorium closely reflect the enclosed cochlear duct (fig. 2), which does not coil in a single plane but in a ventrally directed spiral. Consequently, the ventralmost bulge of the promontorium, which is situated posteromedially, underlies the end of the coil. Extending from the anterior and medial border of the promontorium is a narrow, flattened shelf. The full extent of the anterior part of this shelf is uncertain because of damage, but the medial part is intact. We identify this shelf as an epitympanic wing following MacPhee (1981), who used that term for out-

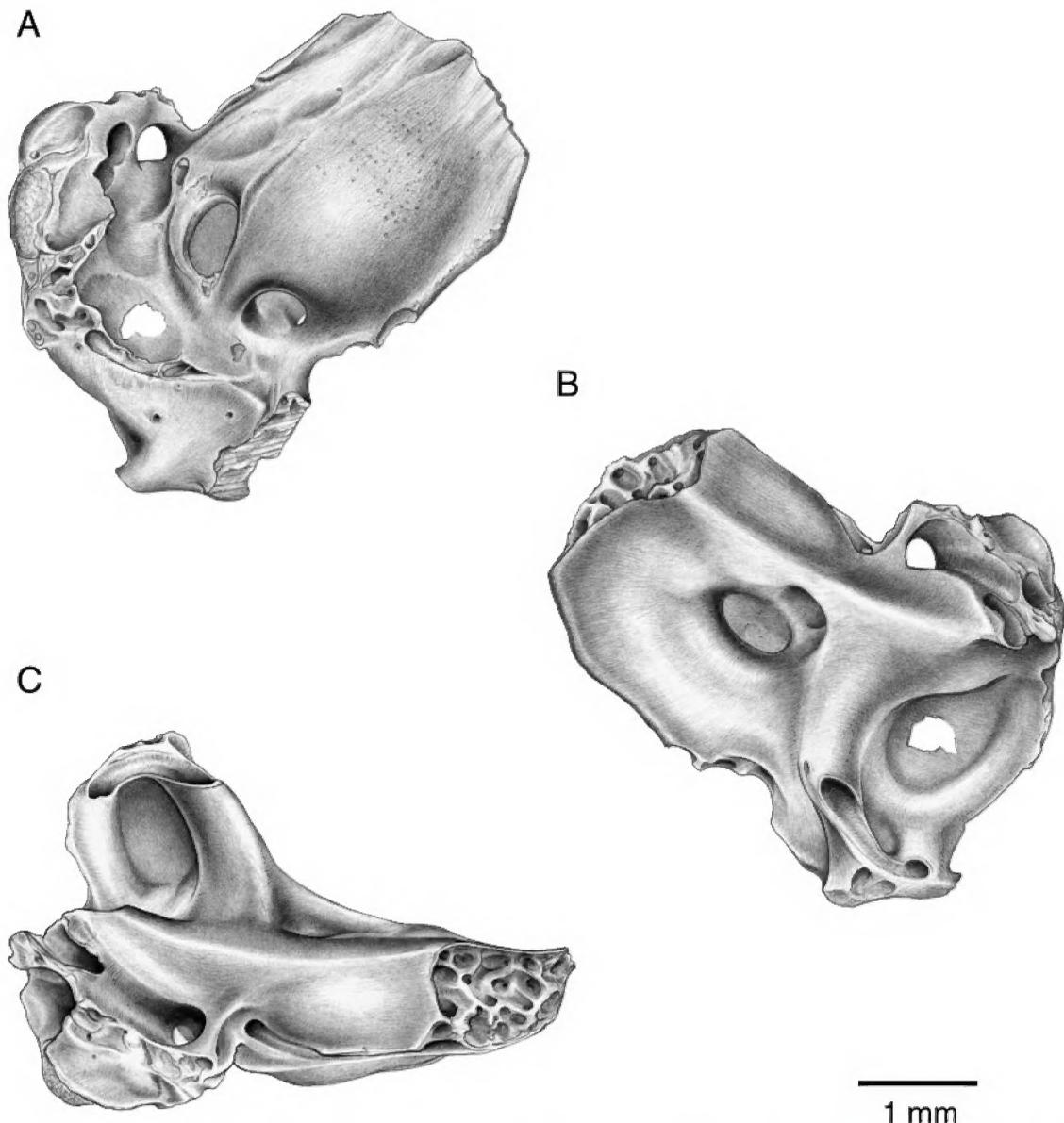


Fig. 1. Three views of right petrosal referred to *Prokennalestes trofimovi*, PSS-MAE 136. **A, D**, Ventral view. **B, E**, Dorsal view. **C, F**, Lateral view. Given that the petrosal is both isolated and incomplete, providing the precise orientation for the bone in the complete skull is difficult. One estimate is shown here. Scale = 1 mm.

growths from any basicranial bones contributing to the tympanic roof.

Two large apertures open into the posterior aspect of the promontorium. The anterolateral and larger of the two is the fenestra vestibuli or oval window, which in life accommodated the footplate of the stapes. The fe-

fenestra vestibuli is recessed slightly from the surface of the promontorium; this is most pronounced along the lateral border. As a result of breakage, the posteromedial section of the rim of the fenestra vestibuli is missing. Despite the damage, the shape and orientation of the fenestra can be reasonably recon-

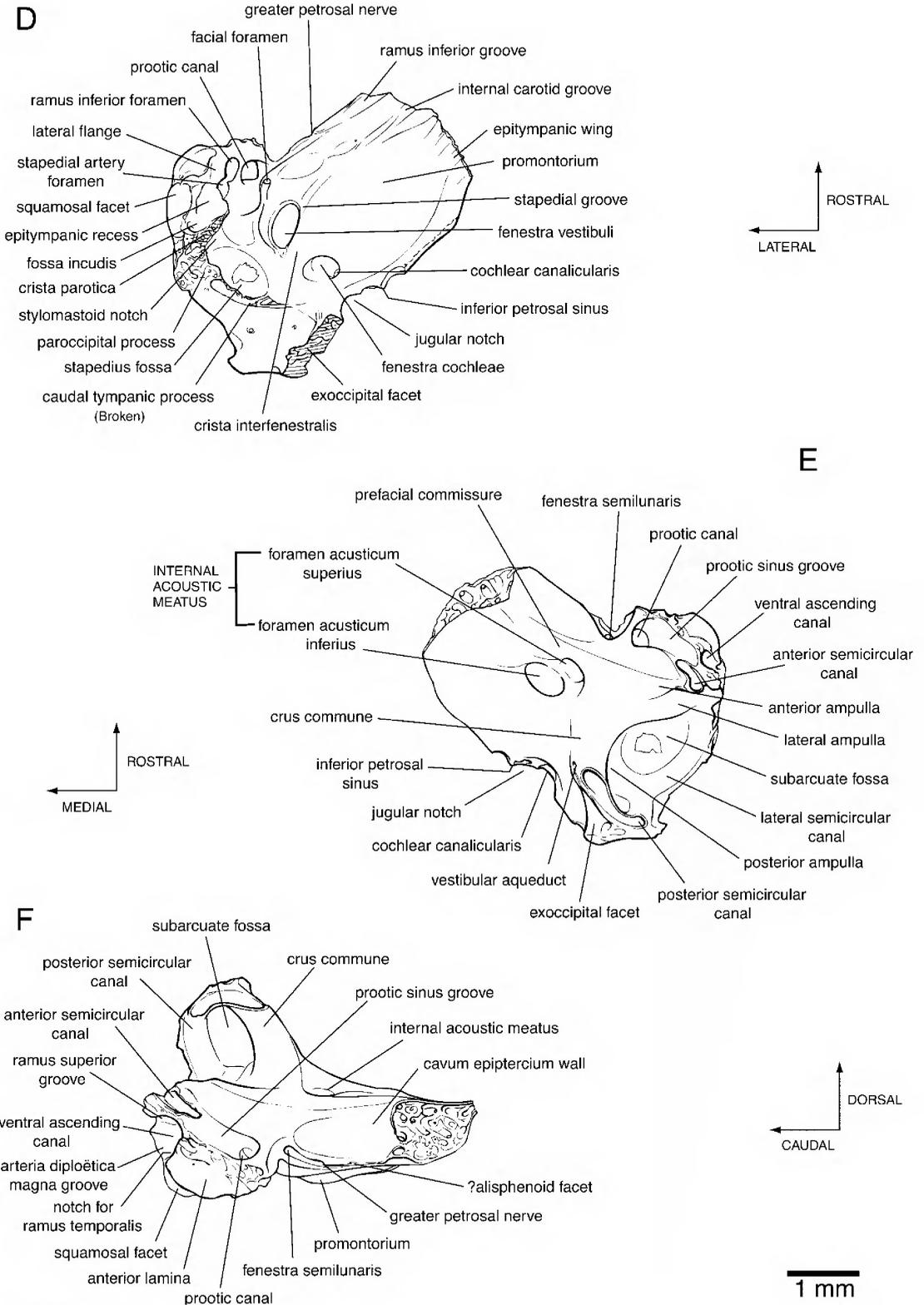


Fig. 1. Continued.

structed. As a measure of shape, and assuming that the outline of the fenestra vestibuli reflects the stapedia footplate morphology, Segall's (1970) stapedia ratio (length/width of the oval window or footplate) is approximately 1.7, that is, somewhat elliptical. Regarding orientation, the opening is directed ventrolaterally and slightly posteriorly. The other large aperture is into the posterior aspect of the promontorium. This is the fenestra cochleae or round window, which was closed by the secondary tympanic membrane in life. We identify this aperture as a round window and not a perilymphatic foramen as in monotremes (Kuhn, 1971; Zeller, 1985, 1989, 1991), because PSS-MAE 136 has a separate canal for the perilymphatic duct as in Recent therians ("cochlear canaliculus" in fig. 1E). The bone flooring this canal in extant therians is derived from the processus recessus of the chondrocranium (De Beer, 1937; Zeller, 1985). In PSS-MAE 136, the processus recessus is the narrow bridge of bone between the medial border of the fenestra cochleae and the jugular notch. The fenestra cochleae is directed posteriorly and somewhat ventrally, and is subcircular, slightly wider in the horizontal plane than vertically. Separating the round and oval windows is a narrow, near vertical bar of bone, the crista interfenestralis.

There are two smaller openings into the outer contour of the ventral surface of the pars cochlearis. Anterior to the fenestra vestibuli is a posteriorly directed, oval aperture, the facial foramen, which transmitted the main or hyomandibular branch of the facial nerve into the middle-ear space. Running posteriorly from the facial foramen is a very short, shallow facial groove that ends just in front of the oval window. The other opening, barely visible in ventral view, lies at the posteromedial corner of the pars cochlearis, just in front of the jugular notch, the petrosal's contribution to the border of the jugular foramen. As preserved, there are actually two openings in this area: a smaller, circular posterior one and a larger, oval anterior one. We believe that the latter is a product of damage and only the smaller, circular foramen was present during life. Visible through both openings is spongy bone laterally and a narrow canal in the epitympanic wing anteriorly.

Although the endpoint of this canal cannot be confirmed, we believe that its terminus is in the spongy bone exposed via damage at the anteriormost surface of the pars cochlearis (visible in dorsal and lateral view, fig. 1B, C). As discussed in the vascular reconstruction, and following similar examples in other Mesozoic mammals, we interpret this canal as for the inferior petrosal sinus.

Two moderately developed vascular sulci run nearly the length of the ventral surface of the pars cochlearis. The more medial one starts posteriorly at the medial rim of the fenestra vestibuli and extends anteromedially to the end of the epitympanic wing. This is the transpromontorial sulcus for the internal carotid artery (Wible, 1986). The sulcus notches the medial rim of the fenestra vestibuli, with the occupant of this notch interpreted to be the stapedia artery (Wible, 1987; Rougier et al., 1992). The second sulcus runs along the lateral edge of the promontorium, beginning just in front of the facial foramen and extending onto the epitympanic wing. The major occupant of this groove is interpreted to be the ramus inferior of the stapedia artery (Wible, 1987; Rougier et al., 1992). About halfway along the length of the sulcus for the ramus inferior, a second, much smaller groove flows into it from the endocranial surface. This would have transmitted the greater petrosal nerve (palatine ramus) of the facial nerve. Continuous posteriorly with the well-developed sulcus for the ramus inferior and anterior to the facial foramen, there is what might be a very faint sulcus (see Vascular and Nervous Reconstruction).

The pars canicularis in ventral view is roughly L-shaped, with the short arm posterior to the promontorium and the long arm lateral to the posterior half of the promontorium. The outer contour of both arms of the L is raised as crests and eminences, whereas the inner contour is depressed as troughs and fossae. For descriptive purposes, we treat the short and long arms separately.

The crest on the posterior edge of the short arm, the caudal tympanic process (MacPhee, 1981), forms the back wall of the middle-ear space. It does not extend medially all the way to the jugular notch, but fades out posterior to the middle of the fenestra cochleae. The

small section immediately behind the fenestra cochleae is the only undamaged part of the caudal tympanic process. It is lower than the broken lateralmost part of the caudal tympanic process, but slightly higher than the intervening middle part. The broken base of the caudal tympanic process, which contained a pneumatic space, extends laterally from behind the round window and connects with the raised outer edge of the long arm of the L. Between the caudal tympanic process and the fenestra cochleae is a flattened shelf, which forms the posterolateral border of the jugular notch. Lateral to this shelf is a depression containing a broad, flat, oval fossa, which is roughly twice the area of the fenestra vestibuli. This fossa housed the origin of the stapedius muscle. The bone roofing the stapedius fossa is thinner than that surrounding it and post mortem damage has opened a hole in the fossa that connects to the endocranial surface of the petrosal. It is apparent from study of the endocranial surface that the rim around the stapedius fossa is formed by the bone containing the lateral semicircular canal. Consequently, the caudal tympanic process, which forms the posterior wall of the stapedius fossa, lies directly ventral to the lateral semicircular canal.

The morphology of the lateral edge of the long arm of the L is more complex than that of the short arm. Posteriorly is the broken base of a broad eminence, which contained a pneumatic space continuous with that in the adjacent caudal tympanic process. This eminence is equivalent to what is called the lateral section of the caudal tympanic process of the petrosal in various placentals (MacPhee, 1981) or the paroccipital process in more basal taxa, such as the prototribosphenidan *Vincelestes* from the Early Cretaceous of Argentina (Rougier et al., 1992). We employ the latter term here. Although the ventral extent of the paroccipital process in PSS-MAE 136 is uncertain, it apparently was well developed and vertical in orientation. Anterior to the paroccipital process is a triangular depression, whose apex points posteriorly. The deepest part of this depression is at the apex and in life housed the crus breve of the incus. Anterior to the fossa incudis is the shallower and broader epitympanic recess, which housed the articulation between the

malleus and incus. Forming the medial wall of the fossa incudis is the crista parotica, continuous with the paroccipital process behind. Only the broken base of this crest is preserved, and it also contained a pneumatic space, likely continuous with that in the paroccipital process. In extant mammals, the crista parotica provides the point of attachment to the embryonic auditory capsule of Reichert's cartilage (the second or hyoid arch cartilage), the proximate segment of which often ossifies to form a tympanohyal element in the adult (De Beer, 1937). Although not preserved in PSS-MAE 136, the point on the crista parotica where the tympanohyal (whether cartilaginous or osseous) would have attached is indicated by slight notching in the medial wall of the crest. This stylo-mastoid notch transmitted the facial nerve from the middle-ear space. The tympanohyal would have attached to the crista parotica immediately in front of the notch. Forming the lateral wall of the fossa incudis and epitympanic recess is a thickened, rounded ridge, continuous with the paroccipital process behind. Judged by the surface texture, this ridge also likely contained a pneumatic space. Moreover, it is apparent that the bulk of this ridge was covered in life by another bone, presumably the squamosal, which therefore was the major element in the wall lateral to the mallear-incudal articulation. In front of the epitympanic recess, this ridge narrows and continues to the anterior limit of the pars canalicularis. As described below, the narrower anterior section of this ridge floors several prominent vascular foramina. Because of its continuity with the paroccipital process and crista parotica, we identify this ridge as the lateral flange of the petrosal, as occurs in more basal taxa (Rougier et al., 1992; Wible and Hopson, 1993).

In the interval between the promontorium on the one side and the paroccipital process, crista parotica, and lateral flange on the other, the pars canalicularis is marked by a broad, smooth-walled, longitudinal trough. This trough ends at a subcircular aperture at the anterior limit of the pars canalicularis. This aperture is directed anterosuperiorly and slightly laterally, and leads into a short, near vertical prootic canal opening on the endocranial surface of the petrosal. Lateral to the

prootic canal, above the lateral flange, is a figure-eight-shaped aperture, which we interpret as having accommodated two arteries. The smaller posterior opening of the figure eight was for the stapedial artery; the larger anterior aperture was for the ramus inferior. The figure-eight-shaped aperture, which is directed laterally, leads into a canal that bends superiorly to open on the lateral surface of the petrosal. This canal is equivalent in position and general orientation to the ventral ascending canal in more basal taxa, such as *Vincelestes* (Rougier et al., 1992).

DORSAL VIEW
(fig. 1B, E)

As in the case of the ventral view, the shape of the pars cochlearis in dorsal view closely reflects that of the enclosed cochlear duct (fig. 2). The most prominent feature is the internal acoustic meatus for the facial and vestibulocochlear nerves, which is an ovoid opening offset laterally from the center of the pars cochlearis. Within the meatus are two unequal-sized, oval apertures separated by a low transverse septum. The smaller, lateral aperture, the foramen acusticum superius, is directed ventrolaterally and ends in two subequal-sized, circular structures. The larger anterior one is a canal transmitting the facial nerve. The smaller posterior one is a blind pit with tiny perforations in it. This is the cribriform dorsal vestibular area for the passage of bundles of the vestibular nerve. The larger, medial aperture in the internal acoustic meatus, the foramen acusticum inferius, is directed ventrally into a pit, whose anterior, medial, and posterior walls have three irregular apertures into the inner ear, which we believe are the result of damage. The spicules of bone between these three openings have a rough, pitted surface resembling that in the cribriform dorsal vestibular area. The remaining surfaces in the foramen acusticum inferius are smooth. We interpret this rough surface as evidence of another cribriform area, in this case the spiral cribriform tract (tractus spiralis foraminosus), tiny perforations in a spiral belt that transmit the fascicles of the cochlear nerve in other therians (Meng and Fox, 1995a, 1995b).

The surface of the pars cochlearis anterior

and medial to the internal acoustic meatus is broad and flat. The surface posterior to the meatus slopes posterodorsally into the pars canicularis (see below). The lateral wall of the meatus is formed by a thin bar of bone, the prefacial commissure. The aspect of the pars cochlearis lateral to the prefacial commissure slopes steeply ventrally and is more fully visible in lateral view (fig. 1C). This smooth-walled surface formed the posteromedial wall of the cavum epipericum, the extradural space housing the trigeminal ganglion and other nervous and vascular structures (Gaupp, 1902, 1905; Kuhn and Zeller, 1987). The only other feature on the endocranial surface of the pars cochlearis is just lateral to the jugular notch, where there is a depression with two dorsomedially directed foramina. The larger ventral one transmitted the perilymphatic duct. This foramen is often called the cochlear aqueduct, but following the *Nomina Anatomica Veterinaria* (1994, 4th ed.) we refer to it as the cochlear canaliculus. The smaller dorsal foramen likely transmitted a vein accompanying the perilymphatic duct.

Less than half of the endocranial surface of the pars canicularis is preserved; it rises steeply posterodorsally from the pars cochlearis. The area just behind the internal acoustic meatus housed the vestibule of the inner ear, and projecting from that were the three semicircular canals (fig. 2). The most prominent feature on the pars canicularis is a deep depression in the preserved posterior edge. When closed by the complete pars canicularis, this depression would have been the anterior part of a very wide, deep subarcuate fossa, which housed the paraflocculus of the cerebellum. The loss of the posterior edge of the subarcuate fossa has made visible parts of the bony housing for all three semicircular canals.

The only complete canal preserved is the lateral (horizontal) semicircular canal, which lies in the floor of the subarcuate fossa. The bone between the lateral semicircular canal and vestibule is very thin and is perforated by a jagged, irregular opening, the artifact within the stapedius fossa described above. A bulge between the lateral terminus of the lateral semicircular canal and the vestibule reflects the underlying lateral ampulla. The

posterior (inferior) semicircular canal lies in the medial wall of the subarcuate fossa, and that for the anterior (superior) would have formed most of the rim of the now incomplete opening into the subarcuate fossa. Ventrally the posterior canal connects with the lateral one just distal to a bulge representing the posterior ampulla. Dorsally the posterior canal is broken open, exposing a groove and two openings. It is in this broken area, in the medial rim of the subarcuate fossa, that the posterior and anterior canals join to form the crus commune. From there the crus commune continues forward in the anteromedial rim of the subarcuate fossa to connect with the vestibule. Along the ventral surface of the bone enclosing the crus commune is a small posterodorsally directed foramen, the vestibular aqueduct for passage of the endolymphatic duct. The anterior semicircular canal is broken open just distal to the bulge over the anterior ampulla in the anterolateral rim of the subarcuate fossa.

The surface of the pars canalicularis anteromedial to the subarcuate fossa is smooth. Often in eutherians, this area has a sulcus transmitting the sigmoid sinus to the jugular foramen. Posterior to this smooth-walled surface is a roughened, medially facing, crescentic facet for contact with another bone, presumably the exoccipital. The surface of the pars canalicularis lateral to the vestibule contains a posterodorsally directed, round foramen; this is the endocranial aperture into the prootic canal. Leading into this foramen from above and behind is a broad sulcus for the prootic sinus, which likely continued onto the missing posterior part of the pars canalicularis. Ventrolateral to this sulcus, the endocranial aperture into the ventral ascending canal is visible. As with the tympanic aperture, the endocranial one is somewhat figure-eight shaped, with the posteroventral opening larger than the anterodorsal one. The shape of this aperture is fully visible only in an oblique dorsal view (not shown). Anterolateral to this aperture is a smooth, crescentic surface exposed on the lateral braincase wall (see below).

LATERAL VIEW (fig. 1C, F)

The pars cochlearis presents two main surfaces in lateral view. Anteriorly is the broken

anterior pole with spongy bone exposed by post mortem damage. Posterior to that is the smooth, laterally facing surface that contributed to the posteromedial part of the cavum epiptericum described above. The ventral edge of this smooth surface bears a narrow, ventrolaterally directed ridge, except where is it notched by a narrow groove (see below). The edge of this ridge is flattened, serving as a facet for contact with another bone, presumably the alisphenoid. Just above the posterior end of this ridge is a subcircular depression, within which is an oval foramen. The foramen opens into a small space within the petrosal that has two other points of egress: the facial foramen in the middle ear and the canal for the facial nerve in the internal acoustic meatus. The space in the petrosal is the cavum supracochleare (Voit, 1909), which housed the geniculate ganglion of the facial nerve. We name the opening into the cavum supracochleare visible in lateral view the "fenestra semilunaris", following Rougier et al. (1992). Running anteroventrally from the fenestra semilunaris is a narrow groove interpreted to be for the greater petrosal nerve, a branch of the facial nerve, which notches the ridge bearing the alisphenoid facet and, therefore, would have been closed as a foramen between the petrosal and alisphenoid in life. The groove continues onto the ventral surface of the pars cochlearis and merges with the groove for the ramus inferior of the stapedia artery.

Two distinct regions of the pars canalicularis are visible in lateral view, a ventrolateral one (see below), and a more dorsomedial one exposed through post mortem damage. The latter is the deep, medial portion of the subarcuate fossa, rimmed by the semicircular canals. Forming the anteroventral rim of the subarcuate fossa is the crus commune, the conjoined anterior and posterior canals. The remainder of the rim is formed by the posterior semicircular canal, including its broken portion at the dorsal apex.

The ventrolateral region of the pars canalicularis in lateral view shows postmortem damage, and it is uncertain how much of the original bone has been lost through breakage. The ventralmost part of what is preserved has a small, bowed, crescentic surface that we believe was exposed on the sidewall of

the braincase. Consequently, we identify this as an anterior lamina such as occurs in extinct non-therian mammaliaforms (Kermack and Kielan-Jaworowska, 1971; Wible and Hopson, 1993). The ventral edge of the anterior lamina is the lateral flange (see above under Ventral View, fig. 1A, D). The anterior lamina in *Prokennalestes* was larger than the preserved crescentic surface, because there is evidence of breakage along most of its anterior and dorsal border. However, the unbroken edges that are preserved, especially posterodorsally, reveal that, overall, the anterior lamina in *Prokennalestes* was smaller than that in extinct non-therian mammaliaforms.

Immediately behind the anterior lamina in PSS-MAE 136 is a deep notch (visible in ventral view lateral to the lateral flange, fig. 1A, D). Most of the bony surface of this notch is roughened for contact with another bone, presumably the squamosal. The only exception is the surface adjacent to the anterior lamina, which is smooth and may not have been covered.

Running adjacent to the anterior lamina are two major vascular channels. Immediately medial to the anterior lamina is the ventral ascending canal, and anterior to it the sulcus for the prootic sinus. Both of these channels run at about a 45° angle to the horizontal, sloping posterodorsally. The sulcus for the prootic sinus ends ventrally at the endocranial aperture of the prootic canal, which is situated between the anterior lamina and fenestra semilunaris. Two major vessels were transmitted by the ventral ascending canal in light of grooves emanating from this canal's figure-eight-shaped endocranial aperture. The larger posterior groove, interpreted to be the posttemporal groove for the arteria diploëtica magna, bends posteromedially, and the smaller anterior one, identified as the dorsal ascending groove for the continuation of the ramus superior, runs dorsally. A third smaller vessel apparently arose from the arteria diploëtica magna. The posterodorsal border of the anterior lamina (and the figure-eight-shaped aperture into the ventral ascending canal) has a shallow, smooth, concave edge that we interpret as contributing to the ventral border of a foramen on the sidewall of the braincase. Completing the borders of this small foramen was likely the squamosal.

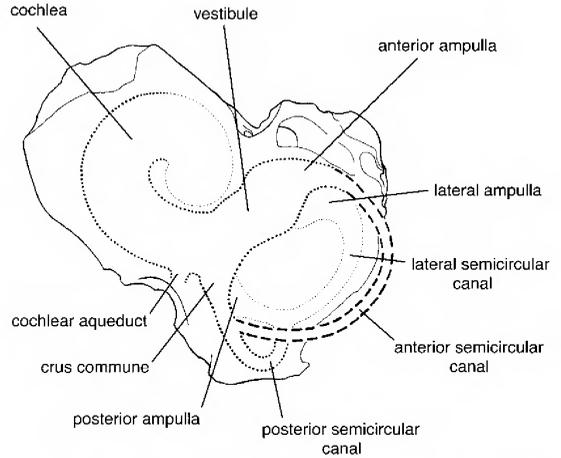


Fig. 2. Reconstruction of the osseous labyrinth of the right petrosal referred to *Prokennalestes trofimovi*, PSS-MAE 136, in dorsal view, based on radiographs. Bone housing lateral semicircular canal and enclosing subarcuate fossa is missing.

Transmitted via this foramen was a ramus temporalis to the temporal musculature.

OSSEOUS INNER EAR

Figure 2 shows our restoration of the osseous labyrinth, cavities hollowed out within the petrosal that in life contained perilymph in which the membranous labyrinth was suspended. Our restoration is based on radiographic analysis of PSS-MAE 136 along with the surface topography as well as the internal morphology exposed through post-mortem damage. The osseous labyrinth consists of three parts: the cochlea, which contained the cochlear duct; the vestibule, which contained the utricle and saccule; and the semicircular canals, which contained the semicircular ducts.

The most prominent feature of the osseous labyrinth is the cochlea. It is a coiled, hollow tube of uniform diameter that occupies the majority of the available space in the par cochlearis with little room to spare. The connection between the cochlea and vestibule is at the posteromedial aspect of the pars cochlearis. Anteromedial to its origin, the cochlea is joined by the short, narrow cochlear canaliculus, which transmitted the cochlear aqueduct of the perilymphatic duct. Beyond the cochlear canaliculus, the cochlea coils in a

clockwise direction, spiraling ventrally and ending anterior to the fenestra vestibuli. In counting the degrees of curvature of the cochlea, we follow West (1985: 1092), who measured the number of turns in the spiral "starting at the inflection point at the round window, where the cochlear duct leaves the basal hook region to begin its spiral course, continuing up the apex of the cochlea where the cochlear duct terminates." With no indication of the round window on the radiographic images of PSS-MAE 136, we used the cochlear canaliculus instead, drawing a straight line from the back edge of this canal to the axis of the coil. The apex of the coil intersected the straight line, meaning that the coil was 360°. The basal segments of the osseous primary and secondary spiral laminae are visible through the oval window. These are delicate laminae that project outward and inward from the inner and outer walls of the cochlea, respectively. The gap between the primary and secondary laminae is filled in life by the basilar membrane, which supports the organ of Corti. In extant mammals, the basilar membrane divides the cochlear duct into two passages, the scala tympani and scala vestibuli, which communicate with each other by a small opening, the helicotrema, at the apex of the cochlear duct.

The vestibule communicates with the cochlea anteriorly and the semicircular canals posteriorly. It consists of an irregular, oval, central space and three distal swellings or ampullae on the semicircular canals at their junction with the vestibule. The anterior and lateral ampullae lie dorsolateral and ventrolateral to the vestibule, respectively. The posterior ampulla is ventromedial, and the crus commune, formed by the union of the non-ampullated ends of the anterior and posterior semicircular canals, is dorsomedial. The position of the ampullae and the semicircular canals was not well resolved in the radiographs, but were determinable from the specimen, as reported above. The lateral semicircular canal lies in a nearly horizontal plane in the floor of the subarcuate fossa. The posterior semicircular canal is in a nearly vertical plane in the medial wall of the subarcuate fossa; it joins the anterior canal in the crus commune dorsally and the posterior canal ventrally. The anterior ampulla is the only

direct evidence for the anterior semicircular canal, which in life formed the rim for the orifice into the subarcuate fossa. We saw no evidence of the vestibular aqueduct for the endolymphatic duct on the radiographs, but its endocranial aperture is on the crus commune in the specimen as expected.

VASCULAR AND NERVOUS RECONSTRUCTION

The foramina, grooves, and canals associated with the major basicranial vessels and nerves have already been noted in the above descriptions. We provide a comprehensive restoration of the basicranial vessels and nerves here to account for the pathways between the major conduits into and out of the skull (fig. 3). For comparative purposes, Figure 4 shows the major basicranial vessels and nerves in representatives of the three groups of extant mammals—the monotreme *Ornithorhynchus* (based on Wible and Hopson, 1995, with amendments from Rougier et al., 1996a), the marsupial *Didelphis* (based on Wible and Hopson, 1995), and the placental *Solenodon* (based on McDowell, 1958, with amendments from personal obs.)—plus the prototribosphenidan *Vincelestes* (based on Rougier et al., 1992; Rougier, 1993). The platypus and *Vincelestes* are distinguished from therians in having well-developed vessels in the posttemporal canal between the petrosal and squamosal and on the basicranial surface. In contrast, in therians, the posttemporal vessels are either reduced (e.g., *Didelphis*) or lacking (e.g., *Solenodon*), armadillos being a notable exception (Tandler, 1899, 1901; Bugge, 1979). Moreover, in marsupials, the major basicranial arteries are lost and the veins reduced, and in placentals, the major basicranial veins are lost.

VEINS (fig. 3)

PSS-MAE 136 preserves two channels that we interpret to be part of the venous system: the prootic canal and the intrapetrosal inferior petrosal sinus. The prootic canal transported the prootic sinus from its endocranial sulcus to the lateral head vein within the middle-ear space. The lateral head vein ran posteriorly in the trough between the promontorium and lateral flange, and turned medially to join the inferior petrosal sinus below

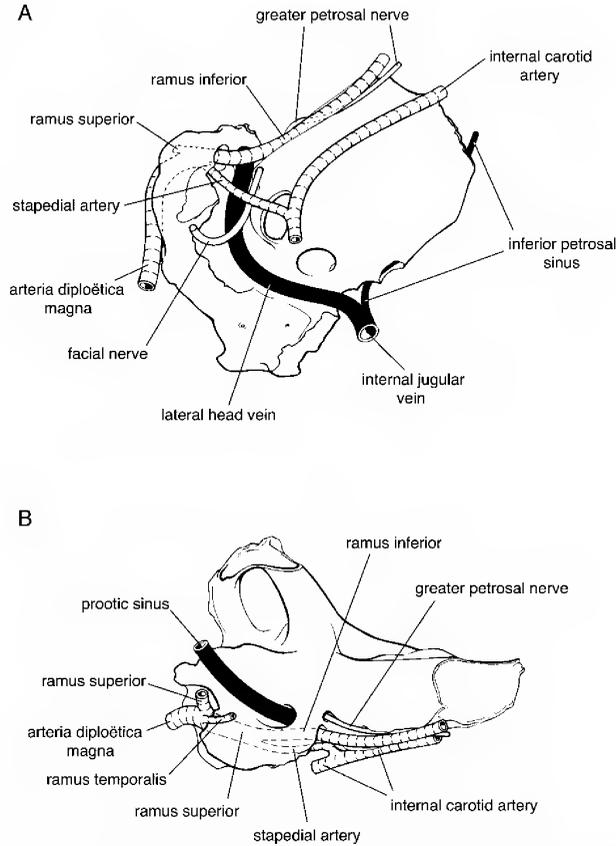


Fig. 3. Reconstruction of major arteries, veins, and nerves on the right petrosal referred to *Prokennalestes trofimovi*, PSS-MAE 136. **A**, Ventral view. **B**, Lateral view.

the jugular foramen to form the internal jugular vein. Among extant mammals, a prootic canal occurs only in monotremes and some marsupials (Wible, 1990; Wible and Hopson, 1995). Of these, the prootic canal and associated sulci in *Prokennalestes* most closely resembles that in monotremes in size and orientation (fig. 4A); the marsupial prootic canal is narrow and laterally directed (fig. 4C).

Our reconstruction of the intrapetrosal inferior petrosal sinus in *Prokennalestes* is more problematic. It is clear that there is a channel of some sort enclosed within the medial edge of the pars cochlearis in PSS-MAE 136. Similar channels have been described for the vast majority of extinct non-therian mammaliaforms (fig. 4B; Rougier et al., 1996a; Wible and Rougier, 2000). As noted by Rougier et al. (1996a), comparable structures are not known in extant mammals. There are small venous sinuses within the pe-

trosal in some (e.g., monotremes), but these are highly anastomotic and do not form a single continuously walled canal. Given that the only substantial venous structure in this vicinity in extant mammals is the inferior petrosal sinus, Rougier et al. (1996a) suggested that this vessel occupied the intrapetrosal canal in extinct non-therian mammaliaforms. An analogous arrangement is found, for example, in some living carnivorans in which the inferior petrosal sinus is within a deep sulcus in the medial edge of the petrosal that is closed by the basioccipital and auditory bulla to form a petrobasilar canal (Hunt, 1977; Evans and Christensen, 1979).

Prokennalestes likely had a sigmoid sinus, a distributary of the transverse sinus running within the tentorium cerebelli, given that this vein is invariably present in extant mammals. The absence of a sulcus for the sigmoid sinus on the petrosal directed toward the jugular

foramen suggests that the major exit of this vein was via the foramen magnum in *Prokennalestes*, as in monotremes (fig. 4A) and marsupials (Hochstetter, 1896; Archer, 1976; Wible, 1990).

Veins likely accompanied some of the branches of the basicranial arterial system. Certainly, this was the case for the internal carotid artery and the arteria diploëtica magna, as veins accompany these vessels in extant monotremes, marsupials, and placentals (Wible, 1984; Wible and Hopson, 1995; personal obs.). It is less certain that veins accompanied the ramus superior and ramus inferior in *Prokennalestes*. Among extant mammals, such companion veins are known for the platypus (fig. 4A; Wible and Hopson, 1995; Wible and Rougier, 2000), but are thought to be generally lacking in therians preserving the ramus superior and ramus inferior. The faint indication of a sulcus anterior to the facial foramen in PSS-MAE 136 that merges with the well-developed groove for the ramus inferior might have transmitted a companion vein of the ramus inferior, a post-trigeminal vein, into the lateral head vein. However, to date, a post-trigeminal vein has not been described in extant therians.

ARTERIES (fig. 3)

PSS-MAE 136 has a groove that runs the length of the promontorium, from just medial to the oval window to the anterior pole. Among extant mammals, when such a transpromontorial groove is present, with few exceptions (Conroy and Wible, 1979) it transmits the internal carotid artery with accompanying vein and sympathetic nerve (fig. 4D; Wible, 1986).

The transpromontorial groove nicks the medial rim of the fenestra vestibuli in PSS-MAE 136, an arrangement which in extant mammals invariably indicates the presence of the stapedial artery, the major extracranial branch of the internal carotid (Wible, 1987). Judging from the size of the notch at the oval window, the stapedial artery was considerably smaller than the internal carotid. A small stapedial artery is also suggested by the relatively small caliber of the posterior portion of the figure-eight-shaped foramen

on the lateral flange. The stapedial artery forms during development in all extant mammals, with the exception of the echidna (Hochstetter, 1896), but is lost by the adult stage in all marsupials as well as in various placentals (Wible, 1984, 1987).

The general pattern in those mammals retaining the stapedial artery in the adult is for that vessel to have two major branches: a ramus superior and a ramus inferior (fig. 4A, D; Tandler, 1899, 1901; Bugge, 1974; Wible, 1984, 1987). The ramus superior runs forward through the braincase, sends branches to the temporalis musculature and meninges, and enters the orbit as the ramus supraorbitalis to send branches with the ophthalmic nerve. Dorsal to the ear region, the ramus superior joins a vessel running forward from the occiput in the posttemporal canal between the squamosal and petrosal, the arteria diploëtica magna. The ramus inferior leaves the middle ear anteriorly and sends branches with the maxillary and mandibular nerves. We believe that *Prokennalestes* exhibits the essentials of this pattern. The ramus inferior is indicated by the longitudinal groove on the lateral edge of the promontorium of the petrosal; this vessel follows a similar pathway in the platypus (Wible and Hopson, 1995) and erinaceomorphs (MacPhee et al., 1988). The ramus superior is indicated by the ventral ascending canal, which is remarkably like that transmitting the ramus superior in the platypus (fig. 4A; Wible and Hopson, 1995). Continuous with the endocranial aperture of the ventral ascending canal are a well-developed posttemporal groove directed posteromedially for the arteria diploëtica magna and a dorsal ascending groove directed dorsally for the continuation of the ramus superior. A notch in the anterior lamina represents the petrosal's contribution to the borders of a foramen for a ramus temporalis, resembling that in the platypus and *Vincelestes*. The figure-eight-shaped tympanic aperture of the ventral ascending canal is unusual among mammals, but must have contained components of the stapedial system. We believe that the smaller, posterior opening, which is directed toward the oval window, transmitted the stapedial artery. Because the larger, anterior foramen is directed toward the groove on the promontorium for the ra-

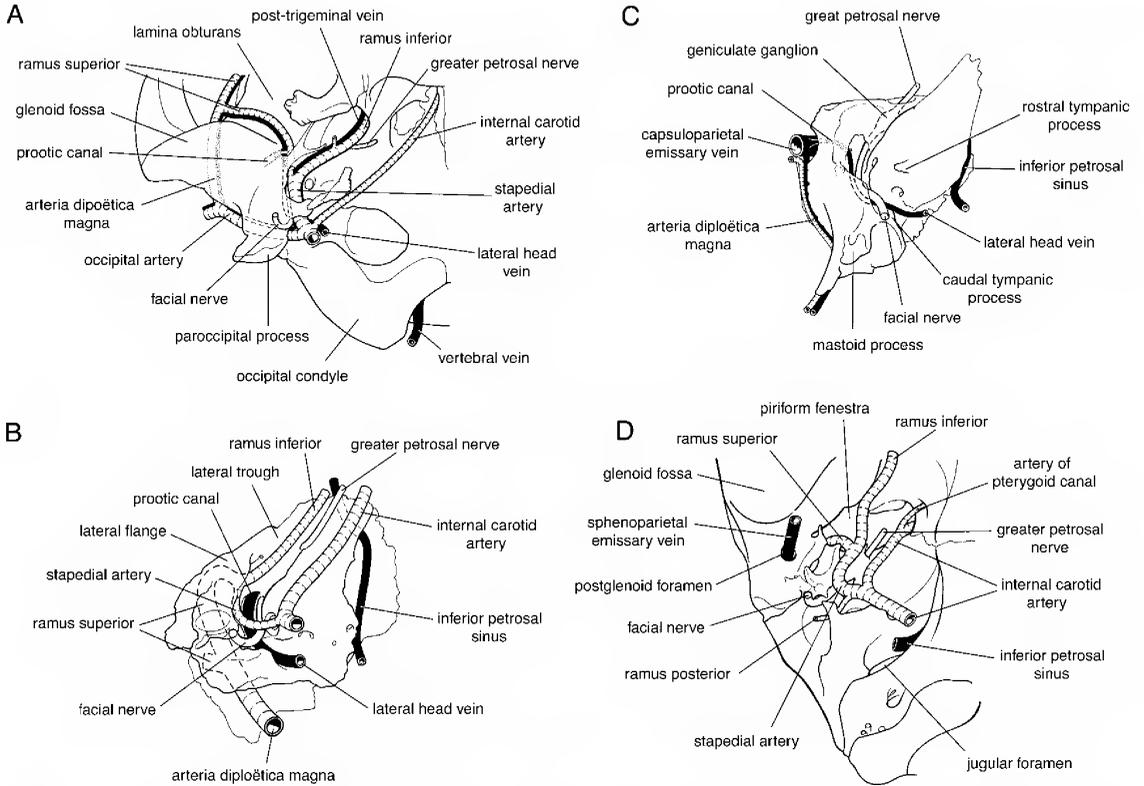


Fig. 4. Right ear regions in ventral view, with major arteries, veins, and nerves. **A**, The basicranium of the monotreme *Ornithorhynchus anatinus*, modified and redrawn from Wible and Hopson (1995: fig. 4B). **B**, The petrosal of the prototribosphenidan *Vincelestes neuquenianus*, modified and redrawn from Rougier et al. (1992: fig. 3C). **C**, The petrosal of the marsupial *Didelphis virginiana*, modified and redrawn from Wible and Hopson (1995: fig. 5A). **D**, The basicranium of the placental *Solenodon paradoxus*, modified and redrawn from McDowell (1958: fig. 7B). The opossum has an internal carotid artery (not shown), but it does not contact the petrosal, which also occurs in the platypus.

mus inferior, we interpret it as transmitting that vessel. Consequently, the ramus inferior arose from the stapedial artery within the ventral ascending canal.

NERVES (fig. 3)

As in all extant mammals, the internal acoustic meatus in *Prokennalestes* gave passage to the facial and vestibulocochlear nerves. The latter divided into two bundles that occupied different compartments within the internal acoustic meatus: the larger, medial cochlear nerve and the smaller, lateral vestibular nerve. The latter terminated by ramifying into numerous fascicles that entered the inner ear through tiny pores in the internal acoustic meatus; the former does not appear to show the same pattern. The facial

nerve entered the facial canal in the lateral part of the internal acoustic meatus. The facial canal ran ventrolaterally into a wider space, the cavum supracochleare, where the geniculate ganglion of the facial nerve was situated. The main stem or hyomandibular branch of the facial nerve left the posterior aspect of the geniculate ganglion and entered the middle-ear space via the facial foramen, anterior to the oval window. The nerve ran posteriorly dorsal to the lateral head vein and left the middle ear via the stylomastoid notch in the crista parotica. This is the pattern exhibited by these structures in the platypus and opossum (fig. 4A, C). The greater petrosal nerve or palatine ramus of the facial nerve left the anterior aspect of the geniculate ganglion and entered the rear of the ca-

vum epiptericum via the fenestra semilunaris. It then ran anteroventrally out of the cavum in a groove that merged with that for the ramus inferior on the tympanic surface of the petrosal. In the intact skull, this groove would have been closed to form a foramen, a hiatus Fallopii, by the alisphenoid bone. This contrasts with the pattern of the hiatus Fallopii in other mammals, which is entirely within the petrosal, either in the tympanic roof (fig. 1A, B, D) or along the anterior edge (fig. 1C).

DISCUSSION

TAXONOMIC ALLOCATION OF PSS-MAE 136

Wible et al. (1997) noted that PSS-MAE 136 exhibits a mosaic of primitive features also found in the prototribosphenidan *Vincelestes* from the Hauterivian of Argentina and derived features shared with therians. Among the former is the inferred vascular pattern, whereas among the latter is the coiling of the cochlea. These authors also noted that PSS-MAE 136 was intermediate in some features between *Vincelestes* and therians. For example, in contrast to therians, PSS-MAE 136 has an anterior lamina, but one that is reduced compared with the structure occurring in *Vincelestes*. The anterior lamina in *Vincelestes* extends forward to the level of the anterior pole of the promontorium, whereas in PSS-MAE 136 it barely extends forward to the level of the back of the promontorium. Based on the morphology and size of PSS-MAE 136, Wible et al. (1997) concluded it most likely belonged to *Prokennalestes*.

To elaborate on the rationale followed by Wible et al. (1997) regarding size, we offer the following remarks. To associate PSS-MAE 136 with a Khoobur taxon known from dentitions, we used the nearly complete skulls of *Vincelestes* (Rougier, 1993) and the basal eutherian *Asioryctes* (Kielan-Jaworowska, 1981) to predict the length of the skull associated with an isolated petrosal. Using *Vincelestes*, which has a relatively longer petrosal than does *Asioryctes*, we estimate the skull length for PSS-MAE 136 to be 26.5 mm; using *Asioryctes*, the estimate is 25.3 mm. These estimates fall in the range of the skull length of 24–27 mm predicted for *Pro-*

kennalestes trofimovi by Kielan-Jaworowska and Dashzeveg (1989) from lower jaws and teeth. The smaller species *P. minor* was estimated by these authors as having a skull 21 mm in length. The other described Khoobur taxa are either smaller than *P. minor* (i.e., the tribosphenidan *Kielantherium gobiensis*, Dashzeveg, 1975; Dashzeveg and Kielan-Jaworowska, 1984; the cladotherians *Arguimus* and *Arguitherium*, Dashzeveg, 1979, 1994; the gobiconodontid *Gobiconodon hoburensis*, Trofimov, 1978; Kielan-Jaworowska and Dashzeveg, 1998; and the multituberculates *Arginbaatar dimitrievae*, Trofimov, 1980; Kielan-Jaworowska et al., 1987; and *Eobaatar minor*, Kielan-Jaworowska et al., 1987) or considerably larger than *P. trofimovi* (i.e., the gobiconodontid *Gobiconodon borissiakii*, Trofimov, 1978; the multituberculate *Eobaatar magnus*, Kielan-Jaworowska et al., 1987; and the symmetrodont *Gobiodon infinitus*, Trofimov, 1980; see Wible et al., 1995). Consequently, of the currently described Khoobur taxa, PSS-MAE 136 accords best in size with *P. trofimovi*.

Kielan-Jaworowska and Dashzeveg (1989) contend that the dentition of *Prokennalestes* is the most primitive known for Eutheria. This view has been supported subsequently by Butler (1990). The morphology of PSS-MAE 136 is congruent with taxonomic assignment to *Prokennalestes*, as its petrosal structure is intermediate between *Vincelestes* on the one hand and Late Cretaceous eutherians (e.g., asioryctitheres, zalambdalestids) on the other. Already mentioned is the intermediate condition of the anterior lamina of PSS-MAE 136. Another example concerns the lateral flange, which runs the length of the petrosal in *Vincelestes* and more primitive mammals (Rougier et al., 1992, 1996a; Wible and Hopson, 1993, 1995), but is restricted to the posterolateral corner of PSS-MAE 136 and is greatly reduced or absent in Late Cretaceous and younger eutherians (Wible, 1990; Rougier et al., 1998). This feature, however, may be at least partially correlated with the presence and development of an anterior lamina.

An alternative is that PSS-MAE 136 belongs to an as yet undescribed or unknown Khoobur taxon that occupies a phylogenetic position between *Vincelestes* and Late Cre-

taceous eutherians. There is, in fact, another form from Khoobur that has been named but not formally described—*Prodeltheridium kalandadzei* (Trofimov in Reshetov and Trofimov, 1984)—and, therefore, is considered a nomen nudum (Kielan-Jaworowska and Dashzeveg, 1989; Kielan-Jaworowska and Nessov, 1990). In light of the name, this form was presumably thought to have affinities with the basal metatherian *Deltatheridium* (Gregory and Simpson, 1926; Rougier et al., 1998) and, therefore, to occupy a position between *Vincelestes* and Late Cretaceous eutherians. The alternative that PSS-MAE 136 belongs to this or some other unknown form cannot be eliminated, of course, with total certainty. However, because of the reasonable match regarding both size and morphology, we follow Wible et al. (1997) in attributing PSS-MAE 136 to *Prokennalestes trofimovi*.

PHYLOGENETIC ANALYSIS OF *PROKENNALESTES*

The only phylogenetic analysis with a taxon-character matrix to include *Prokennalestes* as a terminal taxon is that by Rougier et al. (1998), a study designed to evaluate the relationships of Late Cretaceous deltatheroidans. Their matrix included 156 characters (66 dental, 11 mandibular, and 79 cranial) and 48 terminal taxa, 7 of which are eutherians. In addition to *Prokennalestes*, these included the Late Cretaceous Asian taxa *Otlestes*, Asioryctidae (*Asioryctes* + *Ukhaatherium*), *Kennalestes*, *Zalambdalestes*, and *Zhelestes-Aspanlestes*, and the Early Tertiary leptictids. *Prokennalestes* was identified as the basal-most eutherian in the most parsimonious trees recovered (fig. 5). In their analysis, Rougier et al. (1998) followed Wible et al. (1997) by including PSS-MAE 136 with *Prokennalestes*. Altogether, *Prokennalestes* was scored for 67% of the characters (105 of 156), including 35 basicranial characters. Because of space restrictions, Rougier et al. (1998) were unable to provide detailed descriptions and discussions of the characters they considered. We take this opportunity to elaborate on these 35 basicranial characters, providing justification for their coding of *Prokennalestes*. Based on new interpretations or additional preparation, we also amend the

scoring of 10 character states; the vast majority of these concern *Zalambdalestes*, for which there are new specimens (Novacek et al., 1997; Wible et al., 1998) currently being described (Wible et al., in prep.). The character numbers, descriptions, and initial references below are those used by Rougier et al. (1998), available as supplementary information at www.nature.com and repeated here in the appendices. The other taxa considered by Rougier et al. (1998) were either investigated by direct observation or taken from the literature, which is listed at the Internet site. For scoring of some characters in the metatherian *Andinodelphys*, Rougier et al. (1998) acknowledged Dr. Christian de Muizon. Among the eutherian taxa, basicrania are not yet described for *Otlestes* and *Zhelestes-Aspanlestes*.

Since the publication of Rougier et al. (1998), new descriptions of some extinct therians relevant to that analysis have appeared. The most pertinent of these for the present discussion is *Daulestes nessovi* from the Coniacian of Uzbekistan assigned tentatively to the Asioryctitheria (McKenna et al., 2000), the clade including Asioryctidae and *Kennalestes* (Novacek et al., 1997). *Daulestes* is represented by a single incomplete skull that includes partial petrosals. Based on the descriptions and illustrations in McKenna et al. (2000), we were able to identify character states in *Daulestes* for only 11 of the 35 basicranial characters scored for *Prokennalestes* in the Rougier et al. (1998) matrix. We include these observations below.

103. Orbitotemporal canal—*present (0) or absent (1)* (Rougier et al., 1992): In extant mammals, the orbitotemporal canal transmits the ramus superior from its union with the arteria diploëtica magna forward to the orbit, where it emerges as the ramus supraorbitalis (Rougier et al., 1992; Wible and Hopson, 1995). *Prokennalestes* preserves the most proximal part of the orbitotemporal canal on its petrosal, the dorsal ascending groove. In light of the size of the dorsal ascending groove (“ramus superior groove” in fig. 1F), it seems likely that the ramus superior reached the orbit in *Prokennalestes*. An orbitotemporal canal is widely present among Mesozoic mammals, with the exception of metatherians (Rougier et al., 1998). Based on

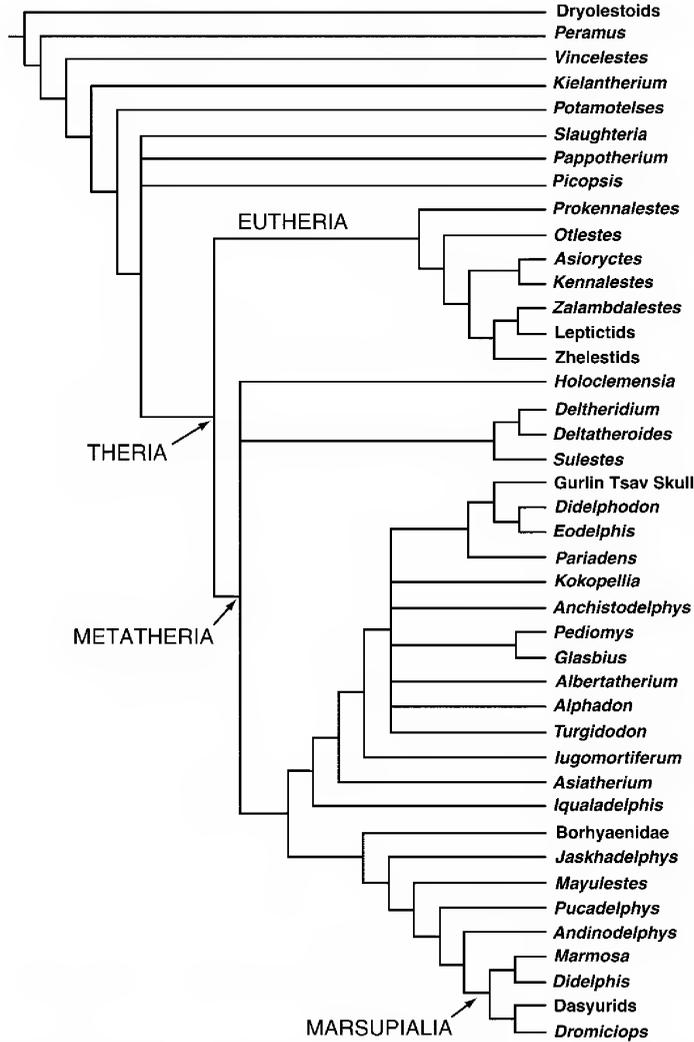


Fig. 5. Strict consensus tree of 144 equally most parsimonious trees, taken from the phylogenetic analysis by Rougier et al. (1998). Trees were obtained by using PAUP on a database of 156 craniodental characters, representing 365 morphological transformations across 48 taxa (see appendices). Six taxa were subsequently pruned from the study because of incompleteness, all being represented by only one tooth (*Aegialodon*, *Comanchea*, *Trinititherium*, *Kermackia*, *Falepetrus*, and *Zygiocuspis*). Tree length of the individual trees is 570; consistency index = 0.444; and retention index = 0.663.

the incidence of an orbital aperture of the orbitotemporal canal, Rougier et al. (1998) scored this vascular channel present among early eutherians in asioryctids, *Kennalestes*, and leptictids. This foramen is also present in *Zalambdalestes* (personal obs.) and likely in *Daulestes* ("?sinus canal foramen" in McKenna et al., 2000).

108. Anterior lamina exposure on lateral braincase wall—*present (0)*, *rudimen-*

tary (1), or *absent (2)* (Modified from Kermack, 1963; Hopson and Rougier, 1993): An extensive anterior lamina contributes to the sidewall of the braincase in Mesozoic mammaliaforms, with the exception of eutherians and metatherians (Wible and Hopson, 1993; Hopson and Rougier, 1993). Marshall and Muizon (1995) described a reduced anterior lamina for the Paleocene metatherian *Pucadelphys*, but this element has no exposure on

the sidewall of the braincase. *Prokennalestes* is unique among therians (including apparently *Daulestes*, McKenna et al., 2000: fig. 8) in that it has an anterior lamina that was exposed on the lateral braincase (fig. 1C, F). Although this element is damaged in *Prokennalestes*, it is apparent that it was reduced compared with the extensive anterior lamina of more basal taxa. In extant monotremes, the anterior lamina forms as an independent intramembranous ossification called the lamina obturans (fig. 4A; Kuhn, 1971; Presley, 1981; Zeller, 1989), and this pattern may have been repeated in extinct taxa as well.

109. Cavum epiptericum—flooded by petrosal (0), petrosal and alisphenoid (1), primarily or exclusively by alisphenoid (2), or primarily open as piriform fenestra (3) (Modified from Wible and Hopson, 1993): The composition of the floor of the cavum epiptericum, including the fossa for the trigeminal ganglion, varies among Mesozoic mammaliaforms (Wible and Hopson, 1993; Luo, 1994). Among the taxa considered by Rougier et al. (1998), the cavum epiptericum is flooded by the petrosal only in *Vincelestes*. In metatherians, the floor is formed by the alisphenoid, either alone or in concert with the petrosal. In eutherians, there is a well-developed piriform fenestra (fig. 4D) beneath the cavum epiptericum in asioryctitheres and *Zalambdalestes*, and a floor formed by the alisphenoid and petrosal in leptictids (and presumably *Daulestes*, McKenna et al., 2000: fig. 8). The posteromedial part of the trigeminal fossa is preserved on the petrosal of *Prokennalestes* (“cavum epiptericum” in fig. 1F). The remainder was either in another bone, the alisphenoid, or was open, as a piriform fenestra. It appears that bone, presumably alisphenoid, contacted the lateral surface of the promontorium and flooded at a minimum the posterolateral part of the trigeminal fossa (character state 1).

111. Foramen ovale composition—in petrosal (anterior lamina) (0), between petrosal and alisphenoid (1), or in alisphenoid or between alisphenoid and squamosal (2) (Modified from Gaudin et al., 1996): It has been noted by various authors that the composition of the foramen ovale, which transmits the mandibular division of the trigeminal nerve, varies among mammals. The most

recent detailed accounting of the distributions of morphologies across Mammalia is by Gaudin et al. (1996). Rougier et al. (1998) modified the three states identified by Gaudin et al. (1996) to those above. As presented on the Internet, state 1 of Rougier et al. (1998) inadvertently was “between petrosal and squamosal” instead of “between petrosal and alisphenoid” as above. In the taxa scored by Rougier et al. (1998), the foramen ovale is in the petrosal in *Vincelestes*; between the petrosal and alisphenoid in most metatherians and *Zalambdalestes*; and in the alisphenoid (or between that bone and the squamosal) in *Dromiciops*, asioryctitheres, and leptictids. In addition, the foramen ovale is not in the petrosal in the metatherians *Asiatherium* and the Gurlin Tsav skull (see Szalay and Trofimov, 1996), but it is unclear whether these forms exhibit state 1 or 2. The character state in *Prokennalestes* is uncertain.

113. Squama of squamosal—absent (0) or present (1): In his phylogenetic analysis of Mammaliaforma, Rowe (1988) employed as a character whether the cranial moiety of the squamosal was confined to the zygomatic root or contributed broadly to the cranial wall. Rougier et al. (1998) modified this description to refer to the presence/absence of the squama of the squamosal. In their analysis, the squama is lacking in *Vincelestes* and present in therians, including *Prokennalestes*, asioryctitheres, *Zalambdalestes*, and leptictids. A clear facet for the squama is not preserved in PSS-MAE 136. However, in light of the reduced size of the anterior lamina compared with the condition in non-therian mammaliaforms, the squamosal must have contributed broadly to the braincase wall in *Prokennalestes*. A well-developed squama is tentatively identified for *Daulestes* by McKenna et al. (2000).

122. Epitympanic wing medial to promontorium—absent (0), flat (1), undulated (2), or confluent with bulla (3): An epitympanic wing extends medially from the promontorium in many therians, but is wholly lacking in extinct non-therian mammals (Rougier et al., 1996a, 1998). In *Prokennalestes* (fig. 1A, D), the epitympanic wing is flat, as it is in asioryctitheres, *Zalambdalestes*, and leptictids, and certain metatherians as well, including *Deltatheridium*. The epi-

tympenic wing presents an undulated morphology in the metatherians *Didelphodon* and *Pediomys* (following the attribution of isolated petrosals by Wible, 1990), and is confluent with the bulla in *Asiatherium* and *Dromiciops*. The flat bony shelf on the anteromedial aspect of the promontorium in *Daulestes* identified as a rostral tympanic process by McKenna et al. (2000) is actually a flat epitympenic wing.

123. Tympanic aperture of hiatus Fallopii—in roof through petrosal (0), at anterior edge of petrosal (1), or absent (2) (Modified from Wible, 1990): In describing isolated petrosals of Late Cretaceous metatherians, Wible (1990) employed a character concerning the length of the hiatus Fallopii, which transmits the greater petrosal nerve forward from the geniculate ganglion of the facial nerve. Following Rougier et al. (1998), we believe that the position of the distal aperture of the hiatus Fallopii more objectively accounts for the differences noted by Wible (1990). In *Vincelestes* and asioryctids, the distal aperture of the hiatus Fallopii is in the tympanic roof (e.g., fig. 4B, D). In contrast, in leptictids and in the metatherians scored by Rougier et al. (1998) with one exception, the hiatus Fallopii opens distally at the anterior edge of the petrosal (e.g., fig. 4C). The one exception is *Deltatheridium*, which has no separate canal for the greater petrosal nerve. The condition in *Prokennalestes* was scored as in the roof by Rougier et al. (1998), but it differs in one regard from the condition in *Vincelestes* and asioryctids: the aperture is not wholly in the petrosal, but between the petrosal and another bone, presumably the alisphenoid (fig. 1C, 3A). The hiatus Fallopii in *Zalambdalestes* is at the anterior edge of the petrosal (personal obs.).

124. Prootic canal—long and vertical (0), short and vertical (1), short and horizontal (2), or absent (3) (Modified from Wible, 1990): Among extant mammals, monotremes have a long, vertical prootic canal that transmits the prootic sinus from the cranial cavity to the middle ear where it joins the lateral head vein (fig. 4A), and some marsupials have a short, horizontal prootic canal that encloses the lateral head vein (fig. 4C; Wible and Hopson, 1995). *Prokennalestes* is unique among eutherians in having a prootic canal

(fig. 1), and Rougier et al. (1998) recognized an intermediate condition for it: short and vertical.

125. Position of sulcus for anterior tributary of transverse sinus relative to subarcuate fossa—anterolateral (0) or posterolateral (1): In extant mammals, the anterior tributary of the transverse sinus is the prootic sinus in monotremes, the sphenoparietal emissary vein in marsupials, and the capsuloparietal emissary vein in placentals (Gelderen, 1924; Wible, 1990; Wible and Hopson, 1995). Despite the apparent non-homology of these veins based on embryological grounds, each occupies a sulcus on the endocranial surface of the petrosal in the vicinity of the subarcuate fossa. Rougier et al. (1998) identified this character to account for the difference in the position of this sulcus between metatherians and other mammals, with the sulcus not extending as far forward in the former forms. Although the sulcus is not fully preserved in *Prokennalestes*, it does extend anterolateral to the subarcuate fossa to the endocranial aperture of the prootic canal (“prootic sinus groove” in fig. 1E, F) as it does in *Kennalestes*, *Zalambdalestes*, and leptictids.

126. Lateral flange—parallels length of promontorium (0), restricted to posterolateral corner (1), or greatly reduced or absent (2) (Modified from Rougier et al., 1996a): Running the length of the promontorium in non-therian mammals is an extensive lateral trough, the lateral edge of which is downturned to form the lateral flange (fig. 4B; Wible et al., 1995). In therians, the lateral flange is either greatly reduced or absent (Wible et al., 1995). *Prokennalestes* preserves a well-developed lateral flange, but it is restricted to the posterolateral corner of the petrosal (fig. 1A, D).

127. Stapedial ratio—rounded, less than 1.8 (0) or elliptical, more than 1.8 (1) (Segall, 1970): Segall (1970) quantified the shape of the stapedial footplate and oval window as a ratio of length to width for various extant mammals. He discovered that monotremes and most marsupials that he considered have a slightly oval footplate, with a stapedial ratio less than 1.8, whereas it tends to be more elliptical in placentals, with a stapedial ratio higher than 1.8. Among the the-

rians coded by Rougier et al. (1998), *Prokennalestes* with a value of 1.71 was unique among the eutherians in having a stapedial ratio less than 1.8 and *Dromiciops* was unique among the metatherians with a stapedial ratio greater than 1.8.

128. Complete wall separating cavum supracochleare from cavum epiptericum—*absent (0) or present (1)* (Modified from Wible and Hopson, 1993): In the platypus, the geniculate ganglion of the facial nerve lies immediately posterior to the trigeminal ganglion in the cavum epiptericum (Kuhn and Zeller, 1987; Zeller, 1989). In contrast, in the echidna, the geniculate ganglion is enclosed in the petrosal bone, creating a cavum supracochleare separate from the cavum epiptericum (Kuhn, 1971; Kuhn and Zeller, 1987). Most extant therians exhibit the echidna condition, but the wall between the two cava is incomplete in some marsupials (Wible, 1990). The aperture connecting the two cava in such instances has been named the fenestra semilunaris by Rougier et al. (1992). Among the taxa considered by Rougier et al. (1998), a fenestra semilunaris (and so an incomplete wall) occurs in *Vincelestes* and *Prokennalestes* (fig. 1C, F). The fenestra semilunaris in *Prokennalestes* is unusual in that it transmits the greater petrosal nerve (fig. 3B). Rougier et al. (1998) scored this character as unknown for *Zalambdalestes*, but we now know that the wall is complete (personal obs.).

129. Coiling of cochlea—*less than 360° (0) or more than 360° (1)*: Because the cochlea of *Prokennalestes* is coiled through just 360°, we propose amending the derived state of this character to “360° or greater”. As far as we currently know, all therians (including *Daulestes*, McKenna et al., 2000) have a cochlea coiled through at least one turn (see below). In contrast, the cochlea of *Vincelestes* is coiled through about three-fourths of one turn (Rougier, 1993).

130. Rostral tympanic process of petrosal, on posteromedial aspect of promontorium—*absent or low ridge (0) or tall ridge, occasionally contacting ectotympanic (1)* (Modified from Wible, 1990): Many therians have a low ridge on the promontorium near the fenestra cochleae (fig. 4C; Wible, 1990), which in some forms (e.g., primates,

MacPhee, 1981; dasyurids, Archer, 1976) expands to a tall ridge making a significant contribution to the tympanic bulla. Wible (1990) employed the term rostral tympanic process of the petrosal for both conditions, following MacPhee (1981). None of the eutherians considered by Rougier et al. (1998), including *Prokennalestes*, has a rostral tympanic process. This is also the condition in *Daulestes* contra McKenna et al. (2000; see character 122 above). In the Rougier et al. (1998) matrix, the only forms with the derived state are the metatherians *Didelphodon* and *Asiatherium*.

131. Paroccipital process (sensu Wible and Hopson, 1993) orientation and shape—*vertical (0), slanted, projecting anteroventrally as flange toward back of promontorium (1), or indistinct or absent (2)*: Non-therian mammaliaforms have a well-developed process on the tympanic surface of the pars canalicularis of the petrosal that serves for muscle attachment (fig. 4A; Rowe, 1988; Wible, 1991; Wible and Hopson, 1993). This process is equivalent to what MacPhee (1981) called the lateral section of the caudal tympanic process of the petrosal in various placentals. In most of the taxa considered by Rougier et al. (1998), the paroccipital process is either vertical (e.g., *Vincelestes*, *Asiatherium*) or indistinct to absent (e.g., didelphids, asioryctitheres, leptictids). However, in some metatherians (i.e., *Deltatheridium*, *Mayulestes*, and borhyaenids), the paroccipital process is slanted anteriorly toward the back of the promontorium. Although the paroccipital process is damaged in *Prokennalestes* (fig. 1A, D), it is apparent that this process was well developed and vertical. This condition also was scored for *Zalambdalestes* by Rougier et al. (1998), but we now know the bulk of this process is on the squamosal bone (as the posttympanic process) and that the paroccipital process is indistinct.

132. Caudal tympanic process of petrosal development—*tall wall behind postpromontorial recess (0), tall wall decreasing in height markedly medially (1), or notched between stylomastoid notch and jugular foramen (2)* (Modified from Wible, 1990): We use the term caudal tympanic process of the petrosal sensu Wible (1990) for the wall on

the tympanic surface of the pars canalicularis of the petrosal, medial to the paroccipital process and posterior to the postpromontorial recess. In Rougier et al.'s (1998) matrix, the caudal tympanic process is a well-developed wall in *Vincelestes* and some metatherians, but it decreases in height markedly as it nears the jugular foramen in other metatherians (e.g., *Didelphodon*, *Pediomys*; fig. 4C). In contrast, in the eutherians considered by Rougier et al. (1998), including *Prokennalestes*, the caudal tympanic process has a notch in it between the stylomastoid notch laterally and the jugular foramen medially. In reviewing the scoring of *Prokennalestes* here, we believe that this character should be scored a 1 or 2. The preserved medial end of the caudal tympanic process in PSS-MAE 136 indicates that a tall wall was not present (character state 0). However, damage to the remainder of this element does not allow us to discriminate between the remaining two states (fig. 1A, D).

133. Crista interfenestralis and caudal tympanic process of petrosal connected by curved ridge—*absent (0) or present (1)* (Modified from Rougier et al., 1996a): The crista interfenestralis is the strut of bone separating the oval and round windows (Wible et al., 1995). In asioryctitheres and *Zalambdalestes*, the crista interfenestralis is connected to the medial part of the notched caudal tympanic process of the petrosal by a curved ridge. This condition is lacking in the remaining taxa considered by Rougier et al. (1998), including *Prokennalestes* (fig. 1A, D).

134. "Tympanic process"—*absent (0) or present (1)* (Kielan-Jaworowska, 1981): Kielan-Jaworowska (1981) described in the asioryctitheres *Asioryctes* and *Kennalestes* a prominent, fingerlike vertical process on the petrosal posterior to the fenestra cochleae, which she dubbed the "tympanic process". This process also occurs in *Zalambdalestes*, but is lacking in *Prokennalestes* (fig. 1A, D) and the remaining taxa considered by Rougier et al. (1998).

136. Rear margin of auditory region—*marked by a steep wall (0) or extended onto a flat surface (1)*: In most of the taxa in Rougier et al.'s (1998) matrix, the pars canalicularis posteriorly ends abruptly at the lev-

el of the caudal tympanic process of the petrosal, which forms a steep wall for the rear margin of the auditory region. In contrast, in asioryctitheres, *Zalambdalestes*, and leptictids, there is a flat shelf posterior to the caudal tympanic process, which extends the rear margin of the tympanic region. Despite the damage to the caudal tympanic process in *Prokennalestes*, it is apparent that this element formed a steep wall behind the middle-ear space (fig. 1A, D).

137. Fossa incudis—*continuous with (0) or separate from (1) epitympanic recess*: An epitympanic recess is restricted to multituberculates, *Vincelestes*, and therians, whereas a fossa incudis is more widely distributed among mammaliaforms (Rougier et al., 1996a). In forms having both an epitympanic recess and fossa incudis, Rougier et al. (1998) noted that these two spaces are either continuous or separated by a distinct ridge. The epitympanic recess and fossa incudis are continuous in most of the taxa considered by Rougier et al. (1998), including *Prokennalestes* (fig. 1A, D), asioryctids, *Zalambdalestes*, and leptictids. The derived state is restricted to some metatherians, i.e., *Didelphodon*, *Pediomys*, borhyaenids, and dasyurids.

138. Epitympanic recess—*with small contribution to posterolateral wall by squamosal (0) or with extensive contribution to lateral wall by squamosal (1)*: In *Vincelestes* and most metatherians scored by Rougier et al. (1998), the lateral wall of the epitympanic recess is formed largely by the petrosal, and the squamosal is confined posterolaterally. However, in the eutherians *Prokennalestes* (fig. 1A, D), asioryctids, *Zalambdalestes*, and leptictids, and in the metatherians *Didelphodon*, *Andinodelphys*, *Turgidodon* (following the attribution of isolated petrosals by Wible, 1990), and the unnamed Gurlin Tsav skull (see Szalay and Trofimov, 1996), the squamosal contributes extensively to the lateral wall of the epitympanic recess.

139. Stapedius fossa—*twice the size of fenestra vestibuli (0) or small and shallow (1)*: Rougier et al. (1998) observed that the fossa of the stapedius muscle varied significantly in size among the taxa they investigated. In the majority including *Prokennalestes* (fig. 1A, D), asioryctitheres, and leptictids, the stapedius fossa is roughly twice the size of

the oval window. In contrast, the stapedius fossa is small and shallow in most metatherians, the exceptions being *Deltatheridium*, *Pediomys*, *Turgidodon*, and borhyaenids. The derived state was identified as an unambiguous synapomorphy of the grouping of post-borhyaenid South American and Australian metatherians. Rougier et al. (1998) scored *Zalambdalestes* as unknown, but it exhibits the primitive state (personal obs.).

140. Hypotympanic sinus—*absent (0), formed by squamosal, petrosal, and alisphenoid (1), or formed by alisphenoid and petrosal (2)* (Modified from Muizon, 1994): A variety of names have been employed in describing the various spaces in the middle ear enclosed by the auditory bulla. Klaauw (1931) used the term hypotympanic sinus to include the parts of the middle ear that do not contain the principal elements, such as the auditory ossicles. Muizon (1994) noted that the alisphenoid hypotympanic sinus, which is situated anterior to the epitympanic recess, in his Borhyaenoidea (borhyaenids plus *Mayulestes*) is formed by the squamosal and petrosal in addition to the alisphenoid. Rougier et al. (1998) identified three states for the alisphenoid hypotympanic sinus in the taxa they considered. It is absent in *Vincelestes*, *Deltatheridium*, *Pucadelphys*, *Andinodelphys*, asioryctitheres, and *Zalambdalestes*; formed by the squamosal, petrosal, and alisphenoid in *Didelphodon*, *Mayulestes*, borhyaenids, and leptictids; and formed by the petrosal and alisphenoid in *Marmosa*, *Didelphis*, *Dromiciops*, and dasyurids. The last state was an unambiguous synapomorphy of Marsupialia. In addition to the above, there are several metatherians that have an alisphenoid hypotympanic sinus, but the contributing elements are uncertain. Included are *Eodelphis*, *Pediomys*, *Turgidodon*, *Asiatherium*, and the Gurlin Tsav skull (see Szalay and Trofimov, 1996). Finally, the petrosal of *Prokennalestes* shows no involvement in an alisphenoid hypotympanic sinus (states 1 and 2), and so this taxon was scored 0. The same state occurs in *Daulestes* (McKenna et al., 2000: fig. 8).

143. Foramina for temporal rami—*on petrosal (0), on parietal and/or squama of squamosal (1), or absent (2)*: The platypus

has a foramen in the lamina obturans on the lateral braincase wall that transmits an artery off the ramus superior and vein associated with the temporalis muscle (fig. 4A; Rougier et al., 1992; Wible and Hopson, 1995). *Vincelestes* has three similarly situated foramina in the anterior lamina that likely had the same function (Rougier et al., 1992). In contrast, in therians, foramina for the temporal rami are either on the squamosal and/or parietal or are absent (Wible, 1987). The one exception noted by Rougier et al. (1998) is *Prokennalestes*, which has a temporal foramen between the petrosal and presumably the squamosal (“notch for ramus temporalis” in fig. 1F). Rougier et al. (1998) scored the absent state for *Zalambdalestes*, but temporal foramina have been subsequently identified in the squamosal (personal obs.).

144. Posttemporal canal—*large (0), small (1), or absent (2)* (Modified from Wible, 1990): Among extant mammals, the posttemporal canal is found between the petrosal and squamosal in monotremes and some therians, where it transmits the arteria diploëtica magna and accompanying vein (fig. 4A, C; Wible, 1987; Wible and Hopson, 1995). Wible (1990) used the presence or absence of the aperture on the occiput into the posttemporal canal as a character in his analysis of isolated Late Cretaceous metatherian petrosals. Rougier et al. (1998) modified this character to the above, noting the size disparity in addition to the presence/absence. In the taxa investigated by Rougier et al. (1998), the posttemporal canal is large only in *Vincelestes*; small in most metatherians and *Zalambdalestes*, and absent in borhyaenids, dasyurids, *Dromiciops*, asioryctitheres, and leptictids. Absence of the posttemporal canal was an unambiguous synapomorphy of dasyurids and *Dromiciops*. *Prokennalestes* was scored as having a small canal, because the posttemporal groove on the petrosal is small compared with that in *Vincelestes* (cf. figs. 3B and 4B).

145. Foramen for ramus superior of stapedial artery—*on petrosal (0), on petrosal-squamosal suture (1), or absent (2)* (Modified from Rougier et al., 1992): Various authors (e.g., Wible, 1987; Rougier et al., 1992) have noted that the composition of the foramen by which the ramus superior leaves the

middle ear differs among mammals. Rougier et al. (1998) identified three states: on the petrosal as in *Vincelestes* (fig. 4B) and *Prokennalestes* (fig. 1D, 3A); on the suture between the petrosal and squamosal as in leptictids (e.g., fig. 4D); and absent as in metatherians (fig. 4C). Rougier et al.'s (1998) phylogenetic analysis identified absence of the foramen as an unambiguous synapomorphy of Metatheria. Originally scored as unknown for *Zalambdalestes*, the foramen for the ramus superior has been found to lie on the petrosal-squamosal suture (personal obs.).

146. Transpromontorial sulcus—present (0) or absent (1) (Wible, 1986): The internal carotid artery in extant mammals follows one of three extracranial courses en route to the cranial cavity, according to Wible (1986): extrabullar (medial to the auditory bulla), intrabullar (through a canal in the bulla), or transpromontorial (across the tympanic surface of the promontorium). Often the last is marked by a sulcus running forward from the vicinity of the fenestrae cochleae and vestibuli toward the anterior pole. Among the taxa considered by Rougier et al. (1998), a transpromontorial sulcus is present in *Vincelestes* (fig. 4B), *Prokennalestes* (fig. 1A, D, 3A), and leptictids; and absent in metatherians (fig. 4C), asioryctitheres, and *Zalambdalestes*. McKenna et al. (2000) report a transpromontorial sulcus in *Daulestes*.

147. Sulcus for stapedia artery—present (0) or absent (1) (Wible, 1987): Among adult extant mammals, the stapedia artery is found in the platypus (fig. 4A) and various placentals (fig. 4D; Tandler, 1899, 1901; Bugge, 1974; Wible, 1987). Among the former, the course of the stapedia artery is often marked by a sulcus in the vicinity of the fenestra vestibuli. Rougier et al. (1998) reported a sulcus for the stapedia artery in *Vincelestes* (fig. 4B), *Prokennalestes* (fig. 1A, D), asioryctitheres, *Zalambdalestes*, and leptictids. A stapedia sulcus also occurs in *Daulestes* (McKenna et al., 2000). In contrast, the sulcus was absent in all metatherians preserving the petrosal (fig. 4C) and was identified as an unambiguous synapomorphy of Metatheria.

148. Deep sulcus for internal carotid artery excavated on anterior pole of pro-

montorium—absent (0) or present (1) (Modified from Muizon et al., 1997): Muizon et al. (1997) figured a well-developed sulcus on the anterior pole of the promontorium in the South American metatherians *Pucadelphys*, *Andinodelphys*, and *Mayulestes*. Although this sulcus carried the internal carotid artery, it is not equivalent to the transpromontorial sulcus described above, which runs the length of the cochlear housing (fig. 1A, D). In addition to these three taxa, Rougier et al. (1998) scored this sulcus for borhyaenids. It is lacking in all other taxa studied, including *Prokennalestes* (and *Daulestes*, McKenna et al., 2000). In Rougier et al.'s (1998) phylogenetic analysis, the presence of this sulcus was an unambiguous synapomorphy of the clade of South American and Australian metatherians.

149. Jugular foramen size relative to fenestra cochleae—subequal to (0) or larger than (1): Rougier et al. (1996a) employed the size of the jugular foramen relative to the fenestra cochleae (or perilymphatic foramen) in their phylogenetic analysis of Mammaliaformes. Rougier et al. (1998) modified this character to account for the very large jugular foramen occurring in some metatherians. The derived state was scored for *Mayulestes*, *Pucadelphys*, *Andinodelphys*, and borhyaenids, and was an unambiguous synapomorphy of the clade of South American and Australian metatherians. Given the size of the jugular notch on the petrosal of *Prokennalestes* (fig. 1A, D), the jugular foramen was likely subequal to the round window and was scored accordingly by Rougier et al. (1998). In the remaining eutherians considered by Rougier et al., the primitive state occurs in asioryctitheres and *Zalambdalestes* and the derived state in leptictids.

150. Jugular foramen—confluent with (0) or separated from (1) opening for inferior petrosal sinus: Extant marsupials have two openings in the jugular fossa: an anterior one transmitting the inferior petrosal sinus to the internal jugular vein and a posterior one for cranial nerves IX, X, and XI (Archer, 1976). Archer (1976) and others (e.g., Muizon et al., 1997) have called the anterior foramen, the internal jugular canal, and the posterior, the posterior lacerate foramen. We believe that the term "opening for the inferior petrosal

sinus” better reflects the function of the anterior aperture, as the internal jugular vein forms ventral to the skull base in the dog (Evans and Christensen, 1979), humans (Williams et al., 1989), and presumably marsupials. Rougier et al. (1998) employed the presence of one versus two foramina in the jugular fossa as a character, with the derived state found only in metatherians and an unambiguous synapomorphy of Metatheria. *Prokennalestes* was scored as unknown, because either state is possible depending on the structure of the exoccipital. Leptictids were scored as confluent, but separate is more appropriate (see Novacek, 1986: figs. 22, 23, 26).

151. Inferior petrosal sinus—*intrapetrosal* (0), *between petrosal, basisphenoid, and basioccipital* (1), *or endocranial* (2) (Modified from Rougier et al., 1996a): Wible (1983) reported that the inferior petrosal sinus in extant placentals follows one of three possible courses between the cavernous sinus and internal jugular vein along the suture between the petrosal, basisphenoid, and basioccipital: intracranial, extracranial, or intramural. Rougier et al. (1996a) identified a variant on the intramural state that occurs in many Mesozoic mammaliaforms: rather than between the petrosal, basisphenoid, and basioccipital, the sinus is wholly within the petrosal. In the taxa considered by Rougier et al. (1998), the inferior petrosal sinus is intrapetrosal in *Vincelestes* (fig. 4B), *Didelphodon* (UCMP 53896), and *Prokennalestes* (fig. 3A); and between the petrosal, basisphenoid, and basioccipital in other metatherians (fig. 4C) and in asioryctitheres, *Zalambdalestes*, and leptictids.

152. Ascending canal—*intramural* (0), *intracranial* (1), *or absent* (2) (Rougier et al., 1992): Kielan-Jaworowska et al. (1986) coined the term “ascending canal” for the intramural canal in multituberculates within the suture between the anterior lamina and the squamosal, dorsal to the middle ear. These authors suggested this canal was more widespread among Mesozoic and extant taxa, and a more detailed evaluation of its homologies was offered by Rougier et al. (1992). Reconstructed as the major occupants were the ramus superior of the stapedia artery and accompanying veins (Wible, 1989; Rougier

et al., 1992; Wible and Hopson, 1995). In comparisons among cynodonts, Rougier et al. (1992) reported that the ascending canal can be an extracranial sulcus, an intramural canal, an intracranial sulcus, or absent. Among the taxa considered by Rougier et al. (1998), only the last three states are present: intramural in *Vincelestes* (fig. 4B) and *Prokennalestes* (fig. 1C, F, 3B); intracranial in leptictids; and absent in metatherians (fig. 4C). Absence of the ascending canal was an unambiguous synapomorphy of Metatheria. An ascending canal is present in asioryctitheres, given the presence of a foramen for the ramus superior in the tympanic roof. However, it is unclear if their ascending canal is intramural or intracranial. *Zalambdalestes* was scored as unknown by Rougier et al. (1998). Given that a foramen for the ramus superior is now known (personal obs.), then an ascending canal (either intramural or intracranial) must have been present as well.

153. Internal acoustic meatus—*deep, with thick prefacial commissure* (0) *or shallow, with thin prefacial commissure* (1): The presence or absence of an internal acoustic meatus, housing cranial nerves VII and VIII, has been used as a character in phylogenetic analyses of Mammaliaomorpha and Mammaliaformes (e.g., Rowe, 1988; Luo, 1994; Rougier et al., 1996a). A distinct depression for the meatus is present in all the taxa with petrosals considered by Rougier et al. (1998). What varies among them is the relative depth and the thickness of the bone forming the anterolateral wall of the meatus, the prefacial commissure. The meatus is deep with a thick prefacial commissure in *Vincelestes* and some metatherians (i.e., *Deltatheridium*, *Didelphodon*, *Pediomys*, and borhyaenids); and shallow with a thin prefacial commissure in the remaining metatherians (i.e., *Turgidodon*, *Pucadelphys*, *Marmosa*, *Didelphis*, *Dromiciops*, and dasyurids) and in the eutherians *Prokennalestes* (fig. 1B, E), asioryctitheres, *Zalambdalestes*, and leptictids. The derived state was identified as an unambiguous synapomorphy of Eutheria.

154. Mastoid-squamosal fusion—*absent* (0) *or present* (1): Among the taxa studied by Rougier et al. (1998), the mastoid portion of the petrosal exposed on the occiput and the squamosal are fused in the stagodontids

Didelphodon (UCMP 53896) and *Eodelphis* (AMNH 14169). Enough of the pars canalicularis of the petrosal is preserved in *Prokennalestes* to ascertain that the squamosal was not fused to the mastoid.

After making the above changes, the amended Rougier et al. (1998) matrix (appendix 1) was run on PAUP (Swofford, 1993). We followed the parameters enumerated in the supplementary information at www.nature.com by Rougier et al. (1998). The number and topology of the 144 most parsimonious trees recovered by Rougier et al. (1998) were not altered in our reanalysis. We made two additional PAUP analyses with the amended matrix. First, we ran the 35 basicranial characters described above with the 21 taxa having scores for these characters. PAUP found 2604 equally most parsimonious trees, the strict consensus of which showed little resolution. Rather than at the base of Eutheria as in the analysis using the complete matrix (fig. 5), *Prokennalestes* was the outgroup to the remaining therians, because it retains the primitive state for 5 characters modified in most other therians. These concern the hiatus Fallopii (#123), the fenestra semilunaris (#128), the temporal rami foramina (#143), the inferior petrosal sinus (#151), and the ascending canal (#152). The only resolution within Theria was a unresolved trichotomy with asioryctids, *Kennalestes*, and *Zalambdalestes*, supported by derived states for the caudal tympanic process (#133) and the "tympanic process" (#134). In the second analysis, *Daulestes* was added to the amended matrix and scored for 11 of the 35 basicranial characters (see above). After exhausting memory at 10,000 equally most parsimonious trees, the resulting strict consensus had no resolution whatsoever. Our future goal is to include information from the dentition and other cranial regions of *Daulestes* in an expanded phylogenetic analysis to evaluate early eutherian relationships, using the Rougier et al. (1998) matrix as the starting point.

IMPLICATIONS FOR THE EUTHERIAN MORPHOTYPE

Rowe (1988) presented the first comprehensive phylogenetic analysis of extant

mammals and near relatives to include a taxon-character matrix. Extant mammals were represented by three terminal taxa: monotremes, marsupials, and placentals. Rowe (1988) did not specify how characters were scored for these diverse groups, but it is likely that in the case of polymorphisms a morphotype was constructed. Since 1988, a number of additional studies addressing the higher-level relationships of extant mammals have been published (e.g., Rougier et al., 1996a, 1996b; Hu et al., 1997; Ji et al., 1999). These analyses have included more fossil forms and characters than did Rowe (1988). However, the extant forms have continued to be represented by three terminal taxa, with the exception of Rougier et al. (1996a, 1996b) who considered ornithorhynchids and tachyglossids separately in order to test monotreme monophyly. Regarding eutherians, in the studies in which we have participated (e.g., Wible et al., 1995; Rougier et al., 1996a, 1996b), states have been scored that are either universally present or from a morphotype based on in-group analyses (e.g., Novacek and Wyss, 1986; Novacek et al., 1988; Novacek, 1992; Gaudin et al., 1996). If *Prokennalestes* falls at the base of Eutheria, as proposed by Rougier et al. (1998), then its petrosal will impact the eutherian morphotype employed in higher-level phylogenetic studies. Below we highlight some of the features of the eutherian morphotype affected by the discovery of the petrosal attributed to *Prokennalestes*.

Anterior Lamina—The presence/absence of the anterior lamina exposed on the sidewall of the braincase has been employed in most phylogenetic analyses of mammalia-morph and mammaliaform relationships (e.g., Rowe, 1988; Wible, 1991; Rougier, 1993; Wible et al., 1995; Rougier et al., 1996a, 1996b). In each instance, the only taxa lacking the anterior lamina are Eutheria and Metatheria, which reflects the state of affairs before the discovery of the petrosal of *Prokennalestes*. However, *Prokennalestes* has a small exposure of petrosal on the braincase wall, which we identify as an anterior lamina (fig. 1C, F), as did Rougier et al. (1998). The incidence of this requires that the anterior lamina has either been (1) lost in the common ancestor of eutherians and me-

tatherians, and redeveloped in reduced form in *Prokennalestes*; or (2) lost independently in metatherians and eutherians other than *Prokennalestes*.

Lateral Flange—Wible et al. (1995) reported that the lateral flange is greatly reduced or absent in eutherians and metatherians, whereas it is a ventrally directed crest extending the length of the promontorium in other mammals, usually in continuity with the crista parotica (see also Rougier et al., 1996a, 1996b). *Prokennalestes* has the posterior part of the lateral flange (fig. 1A, D). As with the anterior lamina, the lateral flange has either been (1) lost at the base of Theria and regained in part in *Prokennalestes*; or (2) retained in part in *Prokennalestes*, and lost independently in metatherians and eutherians more derived than *Prokennalestes*.

Prootic Canal—Features of the prootic canal have been used in most phylogenetic analyses of mammalian morph and mammalian relationships (e.g., Rowe, 1988; Wible and Hopson, 1993; Luo, 1994). When included, Eutheria has been scored as lacking the prootic canal, with one exception: Rowe (1988) scored the prootic canal present for eutherians, but provided no justification. Wible (1991) questioned this, observing that the prootic sinus and lateral head vein, the prootic canal occupants in monotremes and marsupials (fig. 4A, C), are not known for any extant placentals nor is the canal known for any extinct eutherians (see Wible and Hopson, 1995). However, *Prokennalestes* changes this conclusion, because its petrosal has a canal that resembles the prootic canal of monotremes and extinct non-therian mammals, the only significant difference being its relatively shorter length (fig. 1). Absence of the prootic canal has been considered to be a synapomorphy of Eutheria, but is now a synapomorphy of post-*Prokennalestes* eutherians.

Posttemporal Canal—Monotremes have a well-developed posttemporal canal that transmits the arteria diploëtica magna and accompanying vein (fig. 4A), the artery being a major supplier of the stapedia system (Tandler, 1899, 1901; Wible, 1984, 1987). The corresponding osseous structure is ubiquitous among extinct non-therian mammalian forms, with the arteria diploëtica magna in-

terpreted to be larger than the stapedia artery (fig. 4B; Rougier et al., 1992). In contrast, in most metatherians, the posttemporal canal is reduced (fig. 4C; Wible, 1990; Rougier et al., 1998) and, therefore, so is the contribution of the arteria diploëtica magna to the stapedia system. The posttemporal canal is lacking in most forms considered to be basal eutherians, such as asioryctitheres (Kielan-Jaworowska, 1981; Rougier et al., 1998), leptictids (Novacek, 1986), and palaeoryctids (Thewissen and Gingerich, 1989). *Prokennalestes* (fig. 1F, 3) and *Zalambdalestes* are exceptions (Rougier et al., 1998). Although small compared with that in non-therian mammalian forms, the posttemporal canal in *Prokennalestes* is larger than the osseous markings left by the stapedia artery on the petrosal, suggesting that the arteria diploëtica magna was a more significant contributor to the stapedia system. Consequently, the eutherian morphotype likely retains a well-developed arteria diploëtica magna as the major supplier of the stapedia system.

Stapedia Ratio—It is generally (e.g., Segall, 1970; Fleischer, 1978) accepted that a round stapedia footplate represents the primitive mammalian condition and more elliptical ones are derived. In previous studies (e.g., Segall, 1970; Archibald, 1979; Wible, 1990), eutherians are reported to have a more elliptical footplate than metatherians: with stapedia ratios for the former between 1.8 and 2.9, and for the latter between 1.1 and 1.8 with two exceptions: *Dromiciops* and *Macropus* at 2.1 (Segall, 1970). *Prokennalestes*, with a ratio of 1.7, has a rounder footplate than Late Cretaceous eutherians, which are in the range of 2.0 and higher (Archibald, 1979; Wible, 1990). Consequently, the basal eutherian morphotype may not be quite so elliptical as previously held.

Fenestra Semilunaris—A fenestra semilunaris connecting the cavum epiptericum and cavum supracochleare has been reported among extant taxa for caenolestids and some marmosine didelphids (Wible, 1990), and among extinct forms for *Vincelestes* (Rougier et al., 1992) and PSS-MAE 104 and 129, the isolated petrosals from Khoobur that fell between prototribosphenidans and triconodontids in the analyses by Wible et al. (1995) and Rougier et al. (1996a, 1996b). In light of

this distribution, the fenestra semilunaris in *Prokennalestes* (fig. 1C, F) either is a retained plesiomorphy or is convergent on that in *Vincelestes* and the non-therian Khoobur petrosals. Supporting the latter is the observation that the fenestra semilunaris in *Prokennalestes* is unique in that it transmits the greater petrosal nerve (fig. 3B); the remaining forms have a canal in the petrosal leading to the hiatus Fallopii.

Paroccipital Process—Various authors (e.g., Rowe, 1988; Luo, 1994; Rougier et al., 1996a, 1996b) have employed different aspects of the mammalian paroccipital process of the petrosal in phylogenetic analyses, including its orientation and size. In the vast majority of non-therian mammaliaforms, the paroccipital process is a well-developed, vertical muscular process continuous anteriorly with the crista parotica (fig. 4A; Wible and Hopson, 1993; Rougier et al., 1996a). An exception is the echidna, in which the paroccipital process is essentially lacking (see Wible and Hopson, 1995: fig. 3). Identifying the paroccipital process in therians has been problematic, because by and large these forms do not have a well-developed, vertical muscular process posterior to the crista parotica (Wible, 1990; Rougier et al., 1998). Rather than a paroccipital process, what many therians do have that may serve a comparable function is a more posterolaterally directed shelf, which is usually termed the mastoid process (Novacek, 1986; Wible, 1990). In contrast to other therians, *Prokennalestes* has a well-developed, vertical paroccipital process (fig. 1A, D) resembling that in *Vincelestes* (not easily visualized in the ventral view in fig. 4B). The paroccipital process has either been (1) retained in *Prokennalestes* and lost independently in other eutherians and in metatherians; or (2) lost at the base of Theria and redeveloped in *Prokennalestes*.

Ascending Canal—In extant placentals, the course of the ramus superior of the stapedial artery is largely endocranial (Wible, 1987), whereas in the platypus the proximal part of the artery's course is intramural and the distal part is extracranial (fig. 4A; Wible and Hopson, 1995). *Vincelestes* presents an intermediate condition: the distal part of the ramus superior has an endocranial course,

but the proximal part is enclosed in an extended ascending canal within the petrosal (fig. 4B; Rougier et al., 1992). Extant marsupials lack the proximal portion of the ramus superior (fig. 4C); the distal part is endocranial (Wible, 1987). In previous phylogenetic analyses (Wible et al., 1995; Rougier et al., 1996a, 1996b), we have scored the course of the ramus superior as endocranial for Eutheria, because in addition to extant placentals, it is the condition suggested by isolated eutherian petrosals from the Late Cretaceous Bug Creek Anthills of Montana (Wible, 1990). *Prokennalestes*, however, has an ascending canal within the petrosal (figs. 1, 3), as in *Vincelestes* and some multituberculates (Kielan-Jaworowska et al., 1986; Rougier et al., 1992). Unfortunately, the details of the course of the proximal part of the ramus superior, whether intramural or endocranial, are not known for many extinct eutherians, including asioryctitheres and zambdalestids. Therefore, it is uncertain whether *Prokennalestes* has retained the primitive state of an ascending canal or developed one independently.

Foramen for Ramus Temporalis—In the platypus, the foramen for the ramus temporalis is within the lamina obturans on the sidewall of the braincase (see "ramus superior" in fig. 4A; Rougier et al., 1992; Wible and Hopson, 1995); extinct non-therians have similar foramina in the anterior lamina (Rougier et al., 1992; Wible et al., 1995). In contrast, in therians the foramina transmitting temporal rami are in the squamosal or between the squamosal and parietal (Wible, 1987). As interpreted here, *Prokennalestes* differs from other therians in that its foramen lies between the petrosal and squamosal (figs. 1C, F; 3B). If this is part of the eutherian morphotype, then the position of the foramina for the temporal rami in the squamosal and/or parietal has been convergently acquired in metatherians and in other eutherians.

Inferior Petrosal Sinus—MacIntyre (1972) found a sulcus along the medial aspect in isolated petrosals of North American Late Cretaceous eutherians and metatherians. He interpreted this sulcus for the inferior petrosal sinus and speculated that it was primitive for eutherians and metatherians, and present in

their common ancestor. Although not specified by MacIntyre, the likely course for the inferior petrosal sinus in these forms was largely intramural between the petrosal laterally and the basisphenoid and basioccipital medially. Wible (1990) noted that a similar course for the inferior petrosal sinus was proposed for the Liassic mammaliaform *Morganucodon* by Kermack et al. (1981) and suggested that such an inferior petrosal sinus may have predated Theria. More recently, however, Rougier et al. (1996a) have reevaluated the course of the inferior petrosal sinus in extinct non-therian mammaliaforms. These authors observed that many taxa (e.g., *Morganucodon*, Kermack et al., 1981: fig. 83B; *Vincelestes*: MACN-N05, N09) have a canal wholly within the petrosal near the basisphenoid-basioccipital contact, with an anterior opening at the anterior pole and a posterior opening at or near the jugular foramen (fig. 4B). Because no other course is indicated for the inferior petrosal sinus in these forms (contra Kermack et al., 1981), Rougier et al. (1996a) proposed that vein occupied the intrapetrosal canal. They used this condition in a multistate character concerning the course of the inferior petrosal sinus: the other states being endocranial, and intramural between the petrosal, basisphenoid, and basioccipital. Metatherians were scored intramural, and eutherians polymorphic: either intramural or endocranial. However, Rougier et al. (1998) noted that *Prokennalestes* and the metatherian *Didelphodon* have the intrapetrosal canal for the inferior petrosal sinus. This may either have been retained primitively or convergently acquired in Eutheria and Metatheria.

Cochlear Coiling—It has long been known (e.g., Pritchard, 1881; Gray, 1908a, 1908b; Fernández and Schmidt, 1963) that marsupials and placentals are distinguished from monotremes in having a fully coiled cochlea. Moreover, the degrees of coiling has been used as a character in Rowe's (1988) phylogenetic analysis of Mammaliaforma and in all subsequent studies of similar taxonomic scope (e.g., Rougier, 1993; Hu et al., 1997; Ji et al., 1999). The unique condition in each study ascribed to eutherians and metatherians is having a cochlear duct coiled through a minimum of 360°; *Vincelestes* at 270° is the

closest to that (Rougier, 1993). However, what the actual primitive condition is for Theria is uncertain. No living therian has fewer than one and a half turns (Gray, 1908b; Lewis et al., 1985), which is also the condition reported for eutherians and metatherians from the Late Cretaceous Bug Creek Anthills (Meng and Fox, 1993, 1995b). Slightly older isolated therian petrosals from the Late Cretaceous Oldman and Milk River Formations, Alberta, have even fewer turns at 1.25 (Meng and Fox, 1993, 1995a); two of the Oldman Formation petrosals are from metatherians and the Milk River specimen is from either an eutherian or a tribosphenidan. The fewest number of turns was reported from an endocast of the eutherian *Zalambdalestes* by Kielan-Jaworowska (1984: 162) as "consisting of only one whorl". However, using West's (1985) method of measuring cochlear curvature on the illustrations in Kielan-Jaworowska (1984: fig. 2C; pl. 31, figs. 1b, c), one and one quarter turns appears to be a better estimate for *Zalambdalestes*. In a recent description of the skull of the Late Cretaceous? asioryctitherid *Daulestes* from the Coniacian (about 87 million years ago) of Uzbekistan, McKenna et al. (2000) have reported that the cochlea has one full coil, although they (p. 23) admit that the degree of curvature "cannot be determined with precision". With a spiral of just 360° (fig. 2), the cochlea of *Prokennalestes* represents both the oldest example of coiling in the fossil record by a minimum of 10 million years and, likely along with *Daulestes*, the only evidence supporting 360° as the primitive eutherian condition.

Perhaps one of the more surprising features of the cochlea in *Prokennalestes* is that it is of uniform diameter to its tip (fig. 2). This has also been reported in a therian from the Late Cretaceous Milk River Formation (Meng and Fox, 1995a) and may be the condition in *Daulestes* (see below; McKenna et al., 2000). In most other mammaliaforms (e.g., *Morganucodon*, Graybeal et al., 1989; *Sinocondon*, Luo et al., 1995; *Canis familiaris*, Evans and Christensen, 1979), there is some tapering at the cochlear tip. An exception is monotremes, which have an expansion in the apical part of the cochlear duct, a lagena as in sauropsids (Pritchard, 1881; Al-

exander, 1904; Griffiths, 1978). From X-radiographs, Fox and Meng (1997) reported for an unidentified multituberculate from the Hell Creek Formation an expansion at the tip of the cochlea, comparable to that of monotremes, and suggested that it held a lagena. Interestingly, other multituberculates have a cochlea of uniform diameter (Fox and Meng, 1997) or one that tapers at the tip (Luo and Ketten, 1991). Also from X-radiographs, McKenna et al. (2000) found an unusual cochlea in *Daulestes*. Although the cochlear tip was as broad as the base, it was separated by a constriction. McKenna et al. (2000) posed two possible explanations for the constriction: it was either an artifact or an isthmus lagena, connecting the cochlear duct with a lagena as in monotremes. We believe the latter explanation is unlikely, because the "lagena" so identified for *Daulestes* by McKenna et al. (2000) shows no expansion over the remainder of the cochlea, in contrast to the condition in monotremes. If the constriction seen by McKenna et al. (2000) is an artifact, then the cochlea in *Daulestes* and *Prokennalestes* is very similar. Until more comparative data are collected, the meaning of the uniform nature of the cochlea in these Cretaceous forms is unknown.

Cochlear Nerve—In basal mammaliaforms, such as *Morganucodon* (Kermack et al., 1981), the cochlear nerve enters the inner ear via a single aperture in the internal acoustic meatus. In monotremes, however, the internal acoustic meatus has a cribriform plate through which branches of the cochlear nerve pass (Simpson, 1938; Fox and Meng, 1997). A cribriform plate also occurs in extinct and extant therians investigated to date, but differs from that in monotremes in being displayed in a spiral or radial belt (Meng and Fox, 1995b), possibly as a mechanism so that the nerves destined for the organ of Corti within the coiled cochlea have equivalent lengths and, therefore, equivalent nerve impulse conduction times (West, 1985). Meng and Fox (1995b) proposed that a cochlear nerve with such a radial pattern is a therian synapomorphy, although they noted that the condition in *Vincelestes* is unknown. Our interpretations of a cribriform plate in the foramen acousticum inferius in *Prokennalestes* support the proposal of Meng and Fox.

Secondary Osseous Spiral Lamina—Fox and Meng (1997) claimed that the development of primary and secondary osseous spiral laminae in the cochlea between which the basilar membrane is stretched is a therian synapomorphy, because these structures are not present in monotremes or extinct nontherian mammaliaforms. Earlier, these authors (Meng and Fox, 1995b: 60) stated that "the osseous laminae are unknown in the Early Cretaceous non-tribosphenic therian *Vincelestes* (Rougier et al., 1992)." However, Rougier (1993) reported the presence of the secondary osseous spiral lamina in this taxon, and we have repeated that observation elsewhere (Wible et al., 1995; Rougier et al., 1996a, 1996b). Consequently, contra Fox and Meng (1997), the secondary lamina is not a therian synapomorphy. We are uncertain about the level of origin of the primary lamina, because we can neither confirm nor deny the presence of the primary lamina in *Vincelestes*.

CONCLUSIONS

Prokennalestes has been posited to occupy a phylogenetic position at or near the base of Eutheria (Kielan-Jaworowska and Dashzeveg, 1989; Sigogneau-Russell et al., 1992). The results of the recent phylogenetic analysis by Rougier et al. (1998) are consistent with this view, identifying *Prokennalestes* as the basalmost of seven eutherian taxa in a study evaluating the position of deltatheroidans. Features uniting *Prokennalestes* with other eutherians include: tall, trenchant premolar in the penultimate premolar position; three molars; the size of the molars not increasing posteriorly; the penultimate upper premolar protocone a small lingual bulge; the postprotocrista does extend labially past the base of the metacone; and the internal acoustic meatus shallow with a thin prefacial commissure. The other eutherians in the Rougier et al. (1998) analysis (*Otlestes*, asioryctids, *Kennalestes*, *Zalambdalestes*, *Zhelestes-Aspanlestes*, and leptictids) are distinguished from *Prokennalestes* by a styler cusp B (styl-ocone) that is vestigial to absent and molar conules that are strong, labially placed, with winglike cristae.

Recent comparative studies (e.g., Nova-

cek, 1986; Wible, 1990; Rougier et al., 1996a) have generated detailed hypotheses about the structure of the ear region in basal eutherians and therians. The petrosal of *Prokennalestes* must be considered in such analyses, because of its phylogenetic position at or near the base of Eutheria. Our comparisons have identified primitive and derived features of the ear region that *Prokennalestes* shares with various taxa, which impact previous notions of the eutherian and therian morphotypes.

The ear region of *Prokennalestes* is distinguished from other therians by the number of primitive features it shares with more basal forms and by the intermediate conditions that it has between more basal forms on the one hand and other therians on the other. We believe it likely that *Prokennalestes* is not unique in this regard among Theria and that ear regions of other forms falling near the base of Eutheria and Metatheria yet to be discovered will show similar characteristics. If our prediction is correct, then some of the features of the ear region shared by extant marsupials and placentals long held to be therian synapomorphies will have been convergently acquired from basal forms resembling *Prokennalestes* (see below).

Primitive features that *Prokennalestes* shares with the prototribosphenidan *Vincelestes* and more basal forms (PSS-MAE 104 and 129) include (1) an intrapetrosal inferior petrosal sinus (also in *Didelphodon*); (2) an ascending canal within the petrosal; (3) a well-developed arteria diploëtica magna within the posttemporal canal (also in most metatherians and *Zalambdalestes*); (4) a foramen for temporal rami on the petrosal; (5) a vertical paroccipital process; (6) a fenestra semilunaris (also in extant caenolestids and some marmosine didelphids); and (7) the rear margin of the auditory region marked by a steep wall (also in metatherians). All seven of these features are modified in other therians, with the exceptions noted above. Regarding #1–3, different modifications have occurred in other eutherians on the one hand and in metatherians on the other. Consequently, the most parsimonious explanation is that *Prokennalestes* has retained the primitive state, with different modifications occurring in the eutherian and metatherian lin-

eages. Regarding #4–6, the same modifications are found in other eutherians and metatherians. Consequently, the primitive state in *Prokennalestes* is either a retention with convergent modification in other eutherians and metatherians, or modification at the base of Theria with redevelopment of the primitive state in *Prokennalestes*. We deem the former the more likely in light of the above. Regarding #7, only post-*Prokennalestes* eutherians have modified the rear of the auditory region through the addition of a flat surface; *Prokennalestes* and metatherians have retained the primitive condition with a steep wall here. Another feature that *Prokennalestes* shares with *Vincelestes* is the absence of a groove for the sigmoid sinus extending to the jugular foramen. This also occurs in metatherians, asioryctitheres, and zalambdalestids, but has been modified in most extant placentals.

For four characters, *Prokennalestes* exhibits an intermediate condition between that in *Vincelestes* on the one hand and in other therians on the other. (1) The anterior lamina has an expansive exposure on the sidewall of the braincase in *Vincelestes* and more basal forms, a small exposure in *Prokennalestes*, and is wholly lacking in other eutherians and metatherians. (2) The lateral flange extends forward from the crista parotica the length of the promontorium in *Vincelestes* and more basal taxa, a short distance in *Prokennalestes*, and is essentially lacking in other therians. (3) The cochlea is coiled through 270° in *Vincelestes*, 360° in *Prokennalestes* (and also likely *Daulestes*), and 450° to 540° in Late Cretaceous eutherians and metatherians. (4) The prootic canal is vertical and long in *Vincelestes* and more basal taxa, vertical and short in *Prokennalestes*, horizontal and short in basal metatherians, and wholly lacking in other eutherians. Again, in light of the above, we deem it likely that the intermediate condition exhibited by *Prokennalestes* is primitive for Eutheria and perhaps even Metatheria. Consequently, metatherians and eutherians other than *Prokennalestes* have convergently lost the anterior lamina and lateral flange, and coiled the cochlea beyond 360°. The eutherian and metatherian lineages have modified the prootic canal differently.

As follows from the above discussion, the

petrosal of *Prokennalestes* is very generalized, with most features representing either a primitive therian condition or an intermediate condition not found in the crown-group Placentalia. The only petrosal synapomorphy linking *Prokennalestes* and Placentalia in the stem group Eutheria is the presence of a shallow internal acoustic meatus with a thin pre-facial commissure. The eutherian affinities of *Prokennalestes* are, therefore, only weakly supported by the basicranium (a single synapomorphy), but more strongly by the dentition (eight synapomorphies in Rougier et al., 1998). Although partitioning the morphological data sets is probably not defensible from a philosophical point of view, the fossil record itself partitions the evidence available, with ensuing phylogenies generally emphasizing either dental or basicranial characters. In Rougier et al. (1998) and in the revised analysis presented here, the position of *Prokennalestes* responds to the signal provided by the dentition. An analysis with the basicranial characters from the Rougier et al. (1998) matrix identified the "intermediate" morphology of *Prokennalestes* as the therian plesiomorphic condition and placed *Prokennalestes* as the sister taxon to Theria. Therefore, the petrosal attributed to *Prokennalestes* seems to contradict the position suggested by the dentition. This may be because: (1) the attribution of the petrosal in question is erroneous and, therefore, we are merging two phylogenetic signals into one; (2) the dentition is precocial with regard to the basicranium and the basal eutherians early on accumulated dental synapomorphies; or (3) the supposed discrepancies between the basicranium and the dentition are a sampling artifact. The relatively more complete dental record of extinct mammals, in particular on the nodes relevant to the position of *Prokennalestes*, may distort the diagnostic utility of the characters. The petrosals of the immediate outgroups of Theria are not known, the prototribosphenidan *Vincelestes* being the first outgroup reference. The morphology of the petrosal of forms such as *Pappotherium* and *Potamotelses* are crucial for attaining a more complete picture of the basicranial evolution of early therians and close relatives. Until a more even sampling of dental and basicranial characters is obtained for basal

therians, the few petrosal characters known well enough to be diagnostic at some level are likely to be like ornaments that can be alternatively hung from one branch or another on a tree constructed mostly on dental characters. Based on the arguments presented here, we believe that proposition #1 is unlikely, but we cannot be certain. With the evidence at hand, we are unable to evaluate the impact of #2 and #3, and either a decoupling of the dental and basicranial features, a sampling problem, or both are possible.

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APPENDIX 1
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APPENDIX 1
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Alphadon

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?????????? ????111010 00A1222111 0011231101 0??????112 12?2111?12

Turgidodon

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??12120110 0?00?0010B ??B121100? 121???

Glasbius

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?????????? ????111010 00A2222B01 0011241111 1??1110112 2202111012

Asiatherium

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Mayulestes

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0113?20?10 1000000011 1?1??11111 12?001

Borhyaenids

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0113120110 10001001011 02B211111 120010

Pucadelphys

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0112120110 0000000010 1?2?211111 1210?1

Andinodelphys

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0112?20?10 0A00?001?0 1???211111 ?2?0??

Jaskhadelphys

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Marmosa

2001011001 2000112002 0211122211 1010031101 0011010112 2202011002
0101111111 1111101111 0111111001 0011101111 0011010221 1111101111
1112120111 2000100012 0021211001 121011

Didelphis

2001011001 2000112002 0211122211 1010031101 0011010112 2202011002
0101111111 1111101111 0111111011 0011101111 0011010221 1111101111
1112120111 2000100012 0021211001 121010

Dasyurids

2001011111 0000112012 0210222211 1010030101 1111000112 2202111102
0101111111 1111101011 A101111011 0011110011 0011010221 1111101121
1112120111 2000101012 0222211001 121011

Dromiciops

2021011011 0000112012 0100222201 0010041101 1001000112 1202011102
1?01111111 1011111101 0111111001 0011100111 0010010221 2111101121
1313?21?10 20000000?2 0222211000 12101?

APPENDIX 1
Continued.

Prokennalestes

0012000??? ?102111000 1001120100 0011130001 00?0100111 0111001002
0?0???0000 ?021001??? 011??????? 0?0??????? ?0?0???11? ?1?1??????
?101010010 B200?00100 ??A100000? 0010??

Oilestes

0012000??? ????114000 0100220100 001123??01 ???1001111 1111001002
0?0???0000 ??21000??? ?????????? ?????????? ?????????? ??????????
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Asioryctids

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0?0???0001 0021111101 0110101010 1100101001 1100??0231 2011010112
0103?21110 2211010100 0112?10000 1A1001

Kennalestes

1012001?10 0212114001 1100220100 0011230111 0100000211 1111001002
000??00001 ?021111?01 011010?010 0100101001 110??0231 2?110?0112
01?3021110 221101??00 0112?10000 1A100?

Zalambdalestes

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0113021110 2211010100 ?011110000 1B1001

Zhelestids

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0?0???0000? ?02??1?0? ?1????????? 0????????? ?????????? ??????????
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Leptictids

1012001121 0212114022 0100211101 0011240111 0101012212 1111001012
0000001001 1121110101 0111110110 1100101011 1100111221 2011120111
0113021110 2200010101 0012100011 111011

APPENDIX 2

Character list for the data matrix in appendix 1 taken from Rougier et al. (1998) and available at www.nature.com. Changes to characters #58, 111, and 129 from the original list are indicated here in italics. Multistate characters are unordered unless otherwise noted.

DENTITION—GENERAL

1. Number of premolars—five (0), four (1), three (2), or less than three (3). Ordered.
2. Premolar cusp form—sharp, uninflated (0) or inflated, with apical wear strongly developed (1).
3. Tall, trenchant premolar—in last premolar position (0), in penultimate premolar position (1), or absent (2) (Upper dentition considered when possible).
4. Number of molars—more than four (0), four (1), or three (2). Ordered.
5. Molar cusp form—sharp, gracile (0) or inflated, robust (1).
6. Size of molars increasing posteriorly—absent (0), moderate posterior increase (1), or marked posterior increase (2) (all molars considered in lower jaw, and all but the last considered in upper jaw).
7. Number of postcanine tooth families—eight or more (0), seven (1), or less than seven (2). Ordered.

DENTITION—UPPER

8. Number of upper incisors—five (0) or less than five (1).
9. First upper incisor—enlarged, anteriorly projecting, separated from I2 by small diastema (0), subequal or smaller than remaining incisors, without diastema (1), or lost (2).
10. Number of roots on upper canine—two (0) or one (1).
11. First upper premolar—erect, without diastema (0), erect, with a short diastema (1), or procumbent, separated by diastema (2).
12. Penultimate upper premolar protocone—absent (0), small lingual bulge (1), or with an enlarged basin (2). Ordered.
13. Number of roots on penultimate upper premolar—two (0) or three (1).
14. Last upper premolar—simple (0), complex, with small protocone (1), or molariform (2). Ordered.
15. Upper molar shape—as long as wide, or longer (0) or wider than long (1).
16. Upper molar outline in occlusal view—does (0) or does not (1) approach isosceles triangle.
17. Styler shelf—uniform in width, 50% or more of total transverse width (0), uniform in width, but less than 50% of total transverse width

(1), slightly reduced labial to paracone (2), strongly reduced labial to paracone (3), or strongly reduced or absent (4) (penultimate molar considered when present).

18. Metastylar area on penultimate upper molar—large (0) or reduced (1).

19. Deep ectoflexus—present only on penultimate molar (0), on penultimate and preceding molar (1), or strongly reduced or absent (2).

20. Styler cusp A—distinct, but smaller than B (0), subequal to larger than B (1), or very small to indistinct (2) (penultimate molar considered when available).

21. Preparastyle—absent (0) or present (1).

22. Styler cusp B size relative to paracone—smaller but distinct (0), vestigial to absent (1), or subequal (2).

23. Styler cusp C—absent (0) or present (1).

24. Styler cusp D—absent (0), smaller or subequal to B (1), or larger than B (2).

25. Styler cusp E—directly lingual to D or D position (0), distal to D (1), or small to indistinct (2).

26. Preparacingulum—absent (0), interrupted between styler margin and paraconule (1), or continuous (2) (penultimate molar considered when available).

27. Metacone size relative to paracone—noticeably smaller (0), slightly smaller (1), or subequal to larger (2).

28. Metacone position relative to paracone—labial (0), approximately at same level (1), or lingual (2).

29. Metacone and paracone shape—conical (0) or subtriangular, with labial face flat (1).

30. Metacone and paracone bases—adjoined (0) or separated (1).

31. Centrocrista—straight (0) or V-shaped (1).

32. Salient postmetacrista—weakly developed (0) or strongly developed, with paraconid enlarged and metaconid reduced on lower molars (1).

33. Preprotocrista—does not (0) or does (1) extend labially past base of paracone (double rank prevallum/postvallid shearing).

34. Postprotocrista—does not (0) or does (1) extend labially past base of metacone (double rank prevallum/postvallid shearing).

35. Conules—absent (0), small, without cristae (1), or strong, labially placed, with wing-like cristae (2). Ordered.

36. Protocone on upper molars—lacking (0), small, without trigon basin (1), small, with distinct trigon basin (2), somewhat expanded anteroposteriorly (3), or with posterior portion expanded (4). Ordered.

37. Procumbent protocone—absent (0) or present (1).

38. Protocone height—low (0) or tall, approaching para- and/or metacone height (1).

39. Protocingula—absent (0) or pre- and/or postcingulum present (1).

40. Lingual root position—supporting paracone (0) or supporting trigon (1).

41. Last upper molar width relative to penultimate upper molar—subequal (0) or smaller (1).

DENTITION—LOWER

42. Number of lower incisors—four (0) or less than four (1).

43. Staggered lower incisor—absent (0) or present (1).

44. Roots on lower canine—biradicated (0) or uniradicated (1).

45. First lower premolar—oriented in line with jaw axis (0) or oblique (1).

46. Second lower premolar—smaller than third premolar (0) or larger (1).

47. Last lower premolar—simple (0), complex, with a partial trigonid and/or talonid (1), or molariform (2). Ordered.

48. Trigonid configuration—open, with paraconid anteromedial (0), more acute, with paraconid more posteriorly placed (1), or anteroposteriorly compressed (2).

49. Lower molar talonid—small heel (0) or multicuspitated basin (1).

50. Talonid width relative to trigonid—very narrow, subequal to base of metaconid, developed lingually (0), narrower (1), or subequal to wider (2). Ordered.

51. Lower molar cristid obliqua—incomplete, with distal metacristid present (0), complete, attaching below notch in metacristid (1), or complete, labially placed, at base of protoconid (2). Ordered.

52. Hypoconulid—absent (0), in posteromedial position (1), or lingually placed and “twinned” with entoconid (2). Ordered.

53. Hypoconulid of last molar—short and erect (0) or tall and sharply recurved (1).

54. Entoconid—absent (0), smaller than (1), or subequal to larger than (2) hypoconid and/or hypoconulid.

55. Labial postcingulid—absent (0) or present (1).

56. Paraconid and metaconid—metaconid at extreme lingual margin (0) or aligned (1).

57. Metacristid orientation to lower jaw axis—oblique (0) or transverse (1).

58. First lower molar *paraconid*, low and confluent with precingulid—absent (0) or present (1).

59. Protoconid height—tallest cusp on trigonid (0) or subequal to para- and/or metaconid (1).

60. Paraconid height relative to metaconid—taller (0), subequal (1), or shorter (2) (molars other than the first considered when available).

61. Last lower molar size relative to penultimate lower molar—subequal (0) or smaller or lost (1).

62. Rotation of last lower molar during eruption—absent (0) or present (1).

63. Space between last lower molar and coronoid process—present (0) or absent (1).

TOOTH REPLACEMENT

64. Deciduous incisors—present (0) or absent (1).

65. Deciduous canine—present (0) or absent (1).

66. Replacement of dP1/dp1 and dP2/dp2—present (0) or absent (1).

LOWER JAW

67. Masseteric fossa—restricted dorsally by crest reaching condyle (0) or extended ventrally to lower margin of dentary (1).

68. Posterior shelf of masseteric fossa—absent (0) or present (1).

69. Convex ventral margin behind tooth row continuous to condyle—absent (0) or present (1).

70. Labial mandibular foramen—present (0) or absent (1).

71. Condyle shape—ovoid (0) or cylindrical (1).

72. Condyle position relative to tooth row—above (0) or very high (1).

73. Lower jaw angle—posteriorly directed (0), medially inflected (1), or posteroventrally directed (2).

74. Mandibular foramen—below (0) or posterior to (1) anterior edge of coronoid process.

75. “Meckelian” groove—present (0) or absent (1).

76. “Coronoid” facet—present (0) or absent (1).

77. Two large mental foramen, one under second and third premolar and the other under first and second molar—absent (0) or present (1).

SKULL

78. Septomaxilla—present (0) or absent (1).

79. Premaxilla, palatal process—does not (0) or does reach nearly to (1) canine alveolus.

80. Premaxilla, facial process—does not (0) or does (1) reach the nasal.

81. Lateral margin of paracanine fossa—formed by maxilla (0) or maxilla and premaxilla (1).

82. Exit(s) of infraorbital canal—multiple (0) or single (1).

83. Flaring of cheeks behind infraorbital foramen, as seen in ventral view—present (0) or absent (1).

84. Naso-frontal suture with medial process of frontals wedged between nasals—present (0) or absent (1).

85. Nasal foramina—present (0) or absent (1).

86. Frontal-maxillary contact—absent (0) or present (1).

87. Lacrimal tubercle—present (0) or absent (1).

88. Lacrimal foramen exposed on face—present (0) or absent (1).

89. Lacrimal foramen number—double (0) or single (1).

90. Preorbital length relative to postorbital length—two-thirds or more (0) or less than two-thirds (1).

91. Maxillary-jugal contact bifurcated—absent (0) or present (1).

92. Zygomatic arch—stout (0) or delicate (1).

93. Palatal vacuities—absent (0) or present (1).

94. Palatal expansion behind last molar—absent (0) or present (1).

95. Postpalatine torus—absent (0) or present (1).

96. Palate and basicranium at same level, connected by broad choanal ridges—absent (0) or present (1).

97. Minor palatine (postpalatine) foramen—small (0) or large, with thin, posterior bony bridge (1).

98. Palatine reaches infraorbital canal—present (0) or absent (1).

99. Pterygoids contact on midline—present (0) or absent (1).

100. Pterygopalatine crests—present (0) or absent (1).

101. Ectopterygoid process of alisphenoid—absent (0) or present (1).

102. Optic foramen—absent (0) or present (1).

103. Orbitotemporal canal—present (0) or absent (1).

104. Transverse canal—absent (0) or present (1).

105. Carotid foramen—within basisphenoid (0) or between basisphenoid and petrosal (1).

106. Dorsum sellae—tall (0) or low (1).

107. Alisphenoid canal—absent (0) or present (1).

108. Anterior lamina exposure on lateral braincase wall—present (0), rudimentary (1), or absent (2).

109. Cavum epiptericum—floored by petrosal (0), petrosal and alisphenoid (1), primarily or ex-

clusively by alisphenoid (2), or primarily open as piriform fenestra (3).

110. Exit for maxillary nerve relative to alisphenoid—behind (0) or within or in front (1).

111. Foramen ovale composition—in petrosal (anterior lamina) (0), between petrosal and *alisphenoid* (1), in alisphenoid or between alisphenoid and squamosal (2).

112. Foramen ovale—on lateral wall of braincase (0) or on ventral surface of skull (1).

113. Squama of squamosal—absent (0) or present (1).

114. Position of jaw articulation relative to fenestra vestibuli—at same level (0) or in front (1).

115. Glenoid fossa shape—concave, open anteriorly (0) or troughlike (1).

116. Glenoid process of jugal—present, with articular facet (0), present, without facet (1), or absent (2). Ordered.

117. Glenoid process of alisphenoid—absent (0) or present (1).

118. Postglenoid process—absent (0) or present (1).

119. Postglenoid-suprameatal vascular system—absent (0), present, below squamosal crest (1), or present, above squamosal crest (2).

120. Postglenoid foramen—absent (0), present, behind postglenoid process (1), or present, medial to postglenoid process (2).

121. Alisphenoid tympanic process—absent (0) or present (1).

122. Epitympanic wing medial to promontorium—absent (0), flat (1), undulated (2), or confluent with bulla (3).

123. Tympanic aperture of hiatus Fallopii—in roof through petrosal (0), at anterior edge of petrosal (1), or absent (2).

124. Prootic canal—long and vertical (0), short and vertical (1), short and horizontal (2), or absent (3).

125. Position of sulcus for anterior distributary of transverse sinus relative to subarcuate fossa—anterolateral (0) or posterolateral (1).

126. Lateral flange—parallels length of promontorium (0), restricted to posterolateral corner (1), or greatly reduced or absent (2).

127. Stapedial ratio—rounded, less than 1.8 (0) or elliptical, more than 1.8 (1).

128. Complete wall separating cavum supracochleare from cavum epiptericum—absent (0) or present (1).

129. Coiling of cochlea—less than 360° (0) or 360° or greater (1).

130. Rostral tympanic process of petrosal, on posteromedial aspect of promontorium—absent or low ridge (0), tall ridge, occasionally contacting ectotympanic (1).

131. Paroccipital process (sensu Wible and

Hopson, 1993) orientation and shape—vertical (0), slanted, projecting anteroventrally as flange toward back of promontorium (1), or indistinct to absent (2).

132. Caudal tympanic process of petrosal development—tall wall behind postpromontorial recess (0), tall wall decreasing in height markedly medially (1), or notched between stylomastoid notch and jugular foramen (2).

133. Crista interfenestralis and caudal tympanic process of the petrosal connected by curved ridge—absent (0) or present (1).

134. “Tympanic process”—absent (0) or present (1).

135. Tall paracondylar (“paroccipital”) process of exoccipital (sensu Evans and Christensen, 1979)—absent (0) or present (1).

136. Rear margin of auditory region—marked by a steep wall (0) or extended onto a flat surface (1).

137. Fossa incudis—continuous with (0) or separated from (1) epitympanic recess.

138. Epitympanic recess—with small contribution to posterolateral wall by squamosal (0) or with extensive contribution to lateral wall by squamosal (1).

139. Stapedius fossa—twice the size of fenestra vestibuli (0) or small and shallow (1).

140. Hypotympanic sinus—absent (0), formed by squamosal, petrosal, and alisphenoid (1), or formed by alisphenoid and petrosal (2).

141. Medial process of squamosal in tympanic cavity—absent (0) or present (1).

142. Ectotympanic—ringlike (0), fusiform (1), or expanded (2).

143. Foramina for temporal rami—on petrosal (0), on parietal and/or squama of squamosal (1), or absent (2).

144. Posttemporal canal—large (0), small (1), or absent (2).

145. Foramen for ramus superior of stapedial artery—on petrosal (0), on petrosal-squamosal suture (1), or absent (2).

146. Transpromontorial sulcus—present (0) or absent (1).

147. Sulcus for stapedial artery—present (0) or absent (1).

148. Deep groove for internal carotid artery excavated on anterior pole of promontorium—absent (0) or present (1).

149. Jugular foramen size relative to fenestra cochleae—subequal (0) or larger (1).

150. Jugular foramen—confluent with (0) or separated from (1) opening for inferior petrosal sinus.

151. Inferior petrosal sinus—intrapetrosal (0), between petrosal, basisphenoid, and basioccipital (1), or endocranial (2).

152. Ascending canal—intramural (0), intracranial (1), or absent (2).

153. Internal acoustic meatus—deep, with thick prefacial commissure (0) or shallow, with thin prefacial commissure (1).

154. Mastoid-squamosal fusion—absent (0) or present (1).

155. Interparietal—absent (0) or present (1).

156. Dorsal margin of foramen magnum—formed by exoccipitals (0) or by exoccipitals and supraoccipital (1).

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