Basicranial Anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the Late Jurassic of Colorado, and a Reappraisal of Mammaliaform Interrelationships

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ABSTRACT

Left and right petrosals and exoccipitals of the triconodontid *Priacodon fruitaensis* from the Late Jurassic Morrison Formation of western Colorado are described. To elucidate the phylogenetic relationships of *Priacodon*, a cladistic analysis of 51 basicranial characters across 18 ingroup and two outgroup taxa is performed. A monophyletic Triconodontidae, including *Priacodon, Trioracodon,* and *Triconodon* is identified in the six equally most parsimonious trees obtained; a fourth triconodont from the Early Cretaceous Cloverly Formation is a sister taxon to this grouping. In three of the six most parsimonious trees, the four triconodonts are more closely related to therians than are multituberculates; the reverse is true in the remaining three trees. The next more inclusive node is Mammalia, formed by the common ancestor of monotremes and therians and all its descendants. A petrosal from the Early Cretaceous of Mongolia, considered previously to be related either to triconodonts or Prototribosphenida, is shown here to be allied with the latter. The phylogenetic relationships of a number of Jurassic taxa traditionally held to be members of Triconodonta are weakly resolved, resulting in a paraphyletic series: (*Adelobasileus* (*Sinoconodon* ((*Morganucodon* + *Dinnetherium*) (*Megazostrodon* (*Haldanodon* + Mammalia))))). Basicranial characters employed in previous cladistic analyses are discussed, and the implications of our phylogenetic proposal for taxa known primarily from dentitions, such as *Kuehneotherium,* are examined.

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INTRODUCTION

Traditionally the order Triconodonta included a diverse assemblage of Mesozoic mammals usually with three anteroposteriorly aligned, main cusps in the postcanine teeth (Hopson and Crompton, 1969; Jenkins and Crompton, 1979). Among the taxa included in this grouping were the Early Jurassic "morganucodonts," *Sinoconodon, Dinnetherium,* and four Late Jurassic/Cretaceous families—Triconodontidae, Gobiconodontidae, Austrotriconodontidae, and Amphilestidae (Simpson, 1925, 1928, 1929; Hopson, 1970; Jenkins and Crompton, 1979; Bonaparte, 1986, 1992; Kielan-Jaworowska, 1992). However, Amphilestidae has alternatively been suggested to have therian affinities because of similar occlusal patterns (Simpson, 1961; Patterson and Olson, 1961; Mills, 1971). Cladistic analyses of mammaliamorph relationships have shown that these taxa do not form a monophyletic assemblage, with the Early Jurassic forms occupying a basal position among mammaliamorphs (Rowe, 1988, 1993; Wible and Hopson, 1993; Wible et al., 1995). The relationships of the four Late Jurassic/Cretaceous families have not been addressed within a cladistic framework, although Rowe (1993) reported that Triconodontidae and Gobiconodontidae were identified as sister taxa in some of the trees yielded by his analysis.

The bulk of the material attributed to the four Late Jurassic/Cretaceous families, which we informally call triconodonts here, comprises upper and lower jaws. However, additional cranial and postcranial remains of triconodontids and gobiconodontids have been reported. Regarding triconodontids, Simpson (1928) noted fragmentary cranial bones, axis, and possible radius associated with dentitions of *Triconodon mordax* from the Late Jurassic Purbeck Formation of England. Included among the cranial elements were both petrosals, a basisphenoid, and part of an alisphenoid. These were redescribed by Kermack (1963) along with two petrosals attributed to the triconodontid *Trioracodon ferox,* also from the Purbeck. Jenkins and Crompton (1979) reported 20 dental specimens of unnamed triconodontids, ranging from fragmentary jaws to complete skulls,

some with associated postcranial remains, from the Early Cretaceous Cloverly Formation of Montana. Basicrania of these specimens have been figured and partially described by Crompton and co-workers (Crompton and Jenkins, 1979; Crompton and Sun, 1985; Crompton and Luo, 1993). Regarding gobiconodontids, Jenkins and Schaff (1988) described two partial skeletons found in association with upper and lower jaws of *Gobiconodon ostromi* also from the Cloverly Formation of Montana. A fragmentary squamosal and frontal were found with one of the skeletons. This material included postcranial remains originally reported by Jenkins and Crompton (1979) to be from an unnamed amphilestid.

A new triconodontid species, *Priacodon fruitaensis,* was named by Rasmussen and Callison (1981) based on a left lower jaw with teeth from the Late Jurassic Morrison Formation of western Colorado. Subsequent work on the original block revealed several additional bones in association with the left lower jaw. The partial right mandible, both maxillae, and some postcranial elements are described elsewhere (Engelmann and Callison, in prep.). We report here on the right and left petrosals and exoccipitals of the holotype of *P. fruitaensis.* In addition to describing these elements, a cladistic analysis of petrosal and exoccipital anatomy addresses the relationships of triconodonts within Mammaliamorpha.

MATERIALS AND METHODS

Rasmussen and Callison (1981) designated the holotype of *Priacodon fruitaensis* as LACM 120451, Natural History Museum of Los Angeles County, Los Angeles, CA. It was recovered near Fruita, Colorado, in the uppermost part of the Salt Wash Member, Morrison Formation, Upper Jurassic. In the original description, only the left lower jaw was studied. Subsequently, however, Engelmann and Callison (in prep.) described additional material of the holotype, the right lower jaw, right and left maxillae, and several postcranial elements. The right and left petrosals and exoccipitals are described here.

The definition of taxonomic units employed

here follows Gauthier (1986) and Rowe (1987). We use the following terms in the senses of the cited authors: Mammaliamorpha, Mammaliaformes, Mammalia, Theriiformes, and Theria (Rowe, 1988), Holotheria (Hopson, 1994), Trechnotheria and Tribosphenida (McKenna, 1975), Triconodontidae (Jenkins and Crompton, 1979), Symmetrodonta (Prothero, 1981), and Prototribosphenida (Rougier, 1993). However, we note that Rowe's (1988) definition of Mammalia—the clade including the most recent common ancestor of living mammals plus all its descendants—is not universally accepted. We accept Jenkins and Crompton's (1979) composition of the family Triconodontidae and define this taxon as the last common ancestor of *Alticonodon, Astroconodon, Priacodon, Triconodon,* and *Trioracodon* plus all its descendants. The basicrania from the Cloverly Formation (MCZ 19969, 19973) figured and partially described by Crompton and co-workers (Crompton and Jenkins, 1979; Crompton and Sun, 1985; Crompton and Luo, 1993) have been attributed variously to triconodontids, triconodontines, and triconodonts. Because the associated dentitions have not been described, we refer to these basicrania here as indeterminate Cloverly triconodonts. Our use of the term triconodonts for the Triconodontidae, Gobiconodontidae, Austrotriconodontidae, Amphilestidae, and the indeterminate Cloverly triconodonts (which may ultimately be members of one of the previous groups) is an informal one and does not imply monophyly of this assemblage, which has yet to be tested.

To evaluate the affinities of *Priacodon fruitaensis* and other triconodonts known from basicranial remains, a cladistic analysis of petrosal and exoccipital anatomy was performed using the method of simultaneous outgroup analysis (Nixon and Carpenter, 1993). Following recent cladistic analyses by Luo (1994) and Wible et al. (1995), the ingroup was selected to include the common ancestor of *Adelobasileus, Sinoconodon,* and Mammaliaformes plus all its descendants, and Tritheledontidae and Tritylodontidae were chosen for the outgroups. Fifty-one transformation series were identified largely from the literature, including characters to resolve the outgroups, and scored across 20 taxa (18 ingroup plus two outgroup) (see, ap-

pendices 1 and 2). An unrooted cladistic analysis was performed using the branch and bound algorithm of PAUP (Swofford, 1993). All multistate characters were treated as unordered, and the multiple states occurring in some taxa were interpreted as uncertainties, because in most instances the multiple states resulted from incomplete specimens and not from true polymorphism. The unrooted analysis confirmed the monophyly of the ingroup and the resulting cladograms were rooted between the outgroup and ingroup.

The basicranial anatomy of most taxa included here has been described elsewhere, and scores for these taxa were taken from the original literature, supplemented by our own direct observations. The literature sources consulted were: Simpson (1928), Kühne (1956), Crompton (1958, 1964), Kermack (1963), Hopson (1964), Kuhn (1971), MacIntyre (1972), Kermack et al. (1981), Sun (1984), Crompton and Sun (1985), Gow (1986a, 1986b), Kielan-Jaworowska et al. (1986), Novacek (1986), Sues (1986), Hahn (1988), Rowe (1988), Zeller (1989), Wible (1990, 1991), Lillegraven and Krusat (1991), Rougier et al. (1992), Lillegraven and Hahn (1993), Crompton and Luo (1993), Wible and Hopson (1993, 1995), Lucas and Luo (1993), Hopson and Rougier (1993), Rougier (1993), Luo (1994), Luo and Crompton (1994), Luo et al. (1995), and Wible et al. (1995).

The basicrania of three taxa included here have been only partially described or figured, and scores for these were taken from the available published reports: the tritheledontid *Pachygenelus* (Wible, 1991; Allin and Hopson, 1992; Hopson and Rougier, 1993; Wible and Hopson, 1993; Lucas and Luo, 1993; Luo, 1994; Luo et al., 1995); *Dinnetherium* (Crompton and Luo, 1993; Luo, 1994); and the unnamed Cloverly triconodonts (Crompton and Jenkins, 1979; Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, 1994). In addition, observations on the endocranial surface of the petrosal in *Sinoconodon* and the shape of the promontorium in *Megazostrodon* were taken from Luo and Crompton (personal common). Finally, observations from three specimens collected in the Gobi Desert by the Joint Paleontological Expedi-

tions of the Mongolian Academy of Sciences and the American Museum of Natural History and cataloged in the Geological Institute, Ulaan Baatar are included here. Two of these specimens are isolated petrosals from the Early Cretaceous locality of Khoobur: PSS-MAE-104 (referred to as Khoobur petrosal 1), which was described by Wible et al. (1995), and PSS-MAE-119 (referred to as Khoobur petrosal 2), which is to be reported on elsewhere. The third specimen, PSS-MAE-113, is a well-preserved skull of a taeniolabidoid multituberculate, *Kryptobaatar dashzevegi,* from the Late Cretaceous locality of Tugrugeen Shireh.

The terminology for anatomical terms used here follows Wible (1987, 1990), Rougier et al. (1992), and Wible et al. (1995).

Abbreviations

AMNH-DM	American Museum of Natural History, Department of Mammalogy
AMNH-DVP	American Museum of Natural History, Department of Vertebrate Paleontology
FMNH	Field Museum of Natural History, Department of Geology
LACM	Natural History Museum of Los Angeles County
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"
MAE	Collections of the joint Mongolian Academy of Sciences-American Museum of Natural History Paleontological Expeditions
PSS	Paleontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences
ZPAL	Institute of Paleobiology, Polish Academy of Sciences

DESCRIPTIONS

In addition to the cranial and postcranial elements of *Priacodon fruitaensis* described by Rasmussen and Callison (1981) and Engelmann and Callison (in prep.), right and left petrosals and exoccipitals and an indeterminate laminar component are also pre-

served. Isolated petrosals are frequently recovered in the fossil record, because they are composed of dense, compact bone. This is a fortunate accident because, other than the dentition, the petrosal is the only cranial element that allows for assignment of isolated specimens to particular higher-level taxa (MacIntyre, 1972; Wible, 1990; Wible et al., 1995). Additionally, there is a growing database on petrosal morphology for systematic studies of early mammals (Crompton and Luo, 1993; Wible and Hopson, 1993; Luo, 1994). In contrast, the exoccipital in early mammals is poorly known and, consequently, has played virtually no role in phylogenetic analyses to date.

PETROSAL

In Recent mammals, the petrosal is the ossified otic capsule housing the organs of hearing and balance. For descriptive purposes, the petrosal can be divided into two components: the more anterior pars cochlearis, enclosing the cochlear duct and saccule, and the more posterior pars canalicularis, enclosing the utricle and semicircular canals. We base our description of the petrosal of *Priacodon* on the more complete left one, supplementing it with details from the right. The petrosal is described in three views: ventral, dorsal, and lateral, with the orientation based on the inferred position of the petrosal in the skull in relation to the exoccipital.

In the left petrosal, most of both the pars cochlearis and pars canalicularis are present. Missing are the anterior tip of the promontorium, the paroccipital process, and part of the anterior lamina and lateral flange. The right petrosal is represented only by the promontorium and anterior half of the pars canalicularis.

VENTRAL VIEW (fig. 1A, D)

The most distinctive feature in this view is the promontorium or cochlear housing. It is fingerlike, suggesting that it contained a straight cochlear duct. On the posterior aspect of the promontorium are two openings separated by a narrow bridge of bone, the crista interfenestralis. The more medial opening is the perilymphatic foramen, which faces posteroventrally. Preserved on the ven-

tral and dorsal margins of the perilymphatic foramen are thin, sharp crests (fig. 2). The gap between these crests at the posterior margin of the foramen is a preservation artefact, interrupting what would have been a continuous rim. Anteriorly, both the preserved ventral and dorsal portions of the continuous crest abruptly turn medially toward the jugular foramen, marking the posterior limit of a deep sulcus, the perilymphatic groove. As interpreted here, the continuous crest so described marks the boundary between the cavum tympani and the perilymphatic system, and attached on the edge of the crest in life was the secondary tympanic membrane. This membrane extended over the perilymphatic foramen, along the posterior aspect of the perilymphatic groove, and finally entered the cranial cavity via the jugular foramen. On the right petrosal, the perilymphatic groove was nearly closed to form a canal by the crest for the attachment of the secondary tympanic membrane; unfortunately, additional preparation damaged the crest and the enclosure now is not as complete as before. Medial to the crista interfenestralis and posterior to the perilymphatic foramen is a deep recess delimited anterolaterally by the crest for the attachment of the secondary tympanic membrane. This recess is reminiscent of a depression in the platypus called the recessus scalae tympani by Zeller (1989, 1991), but differs in its relationship to the secondary tympanic membrane. In extant mammals, the recessus scalae tympani is on the labyrinthine side of the membrane (Goodrich, 1930; Kuhn, 1971; Zeller, 1989), whereas the depression in *Priacodon* is on the tympanic side.

The opening lateral to the crista interfenestralis is the fenestra vestibuli. It is larger than the perilymphatic foramen, faces ventrolaterally, and is elongate anteroposteriorly, with an average stapedial ratio (Segall, 1970) of 1.45. Anterior to the fenestra vestibuli is a tiny opening with a narrow sulcus running forward (foramen in promontorium in fig. 1C, F); the opening corresponds to the foramen for small nerves and blood vessels identified in *Trioracodon ferox* by Kermack (1963: fig. 3). The crista interfenestralis extends posteriorly from the promontorium to the base of the broken paroccipital process.

It is a high, horizontal ridge continuous with the ventral surface of the promontorium that separates the space behind the perilymphatic foramen from the main tympanic cavity lateral to the promontorium. Consequently, a post-promontorial tympanic sinus (Wible, 1990) is lacking.

Along the medial margin of the promontorium anterodorsal to the perilymphatic foramen is an opening that leads into the petrosal (inferior petrosal sinus in fig. 1D). There is a second opening at the anterior tip of the promontorium (inferior petrosal sinus in fig. 1E). In the less complete right petrosal, the medial promontorial surface is broken, exposing a canal that in the left petrosal would be continuous between the two openings. In connecting these two openings, the canal would have to turn laterally at the anterior end of the promontorium. We interpret this canal as housing the inferior petrosal sinus (see Discussion).

Medial to the perilymphatic foramen is the jugular notch, which, when completed by the exoccipital, enclosed a nearly square jugular foramen subequal in size to the perilymphatic foramen. The perilymphatic and jugular foramina are housed in a common depression, the jugular fossa. Posterior to the jugular notch is a medially directed, barrel-shaped process on the petrosal that ends medially in an articular surface for the exoccipital. Posterolateral to the perilymphatic foramen is a distinct, cuplike depression (pocket in fig. 1D). It is bordered anterolaterally by the crista interfenestralis, posterolaterally by the base of the paroccipital process, posteromedially by a faint crest, and anteromedially by a low, sharp process. We are uncertain of the function of this depression, though E. F. Allin, a reviewer on an earlier version of this manuscript, suggested it might house the levator hyoidei. This muscle is found in extant monotremes (Edgeworth, 1914), but does not have a distinct depression of origin on the petrosal.

The paroccipital process is broken in both petrosals, but is more complete in the right one. It was a massive, subrectangular structure that projected ventrally. Although the full extent of the ventral projection cannot be established, the paroccipital process descended at least to the level of the ventral pro-
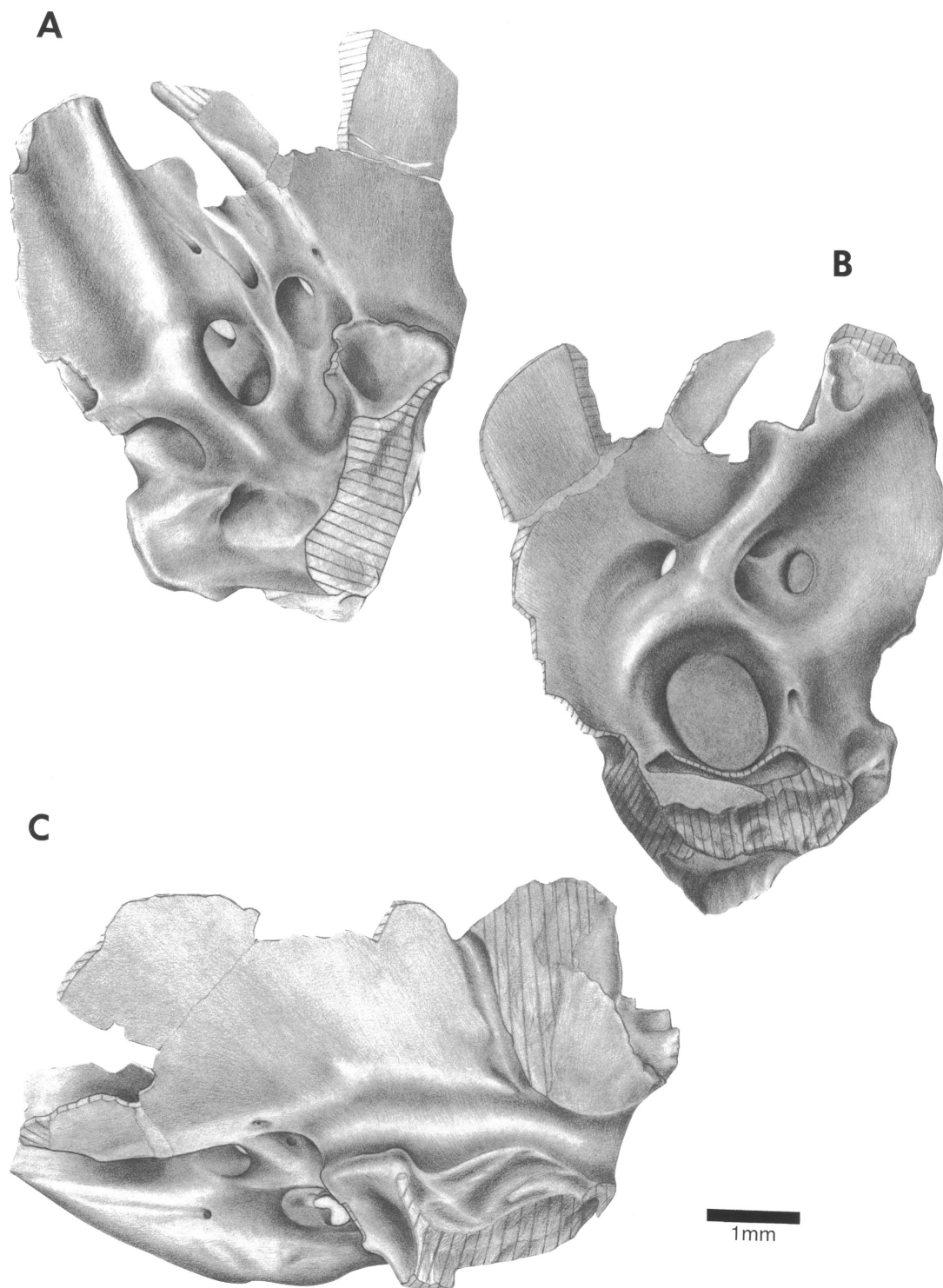
Fig. 1.   Three views of left petrosal of *Priacodon fruitaensis,* LACM 120451. **A, D,** Ventral view. **B, E,** Dorsal view. **C, F,** Lateral view. Parallel lines represent damaged surfaces.
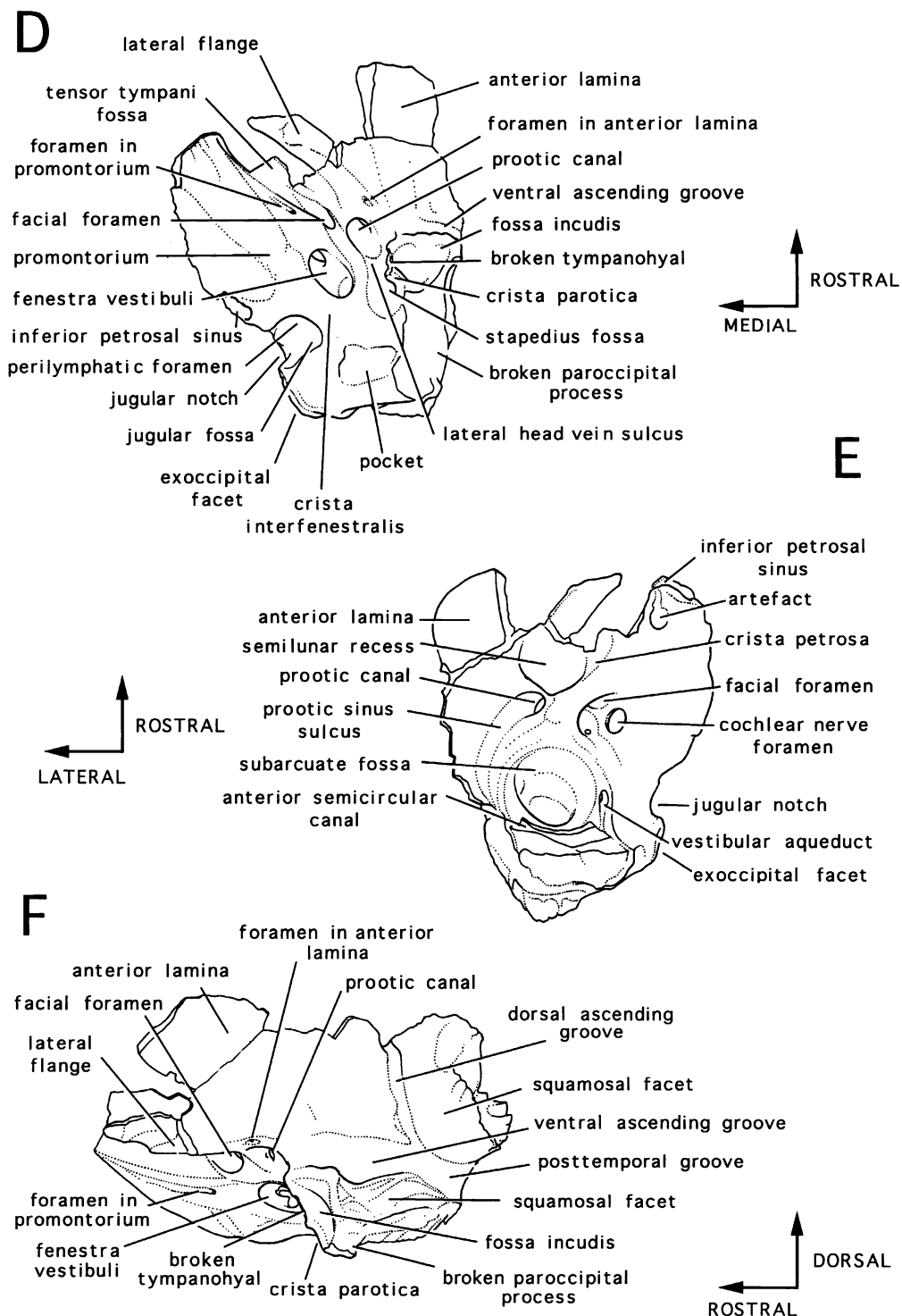
D

lateral flange

tensor tympani
fossa

foramen in
promontorium

facial foramen

promontorium

fenestra vestibuli

inferior petrosal sinus

perilymphatic foramen

jugular notch

jugular fossa

exoccipital
facet   crista
interfenestralis

pocket

anterior lamina

foramen in anterior lamina

prootic canal

ventral ascending groove

fossa incudis

broken tympanohyal

crista parotica

stapedius fossa

broken paroccipital
process

lateral head vein sulcus

ROSTRAL

MEDIAL

E

anterior lamina

semilunar recess

prootic canal

prootic sinus
sulcus

subarcuate fossa

anterior semicircular
canal

inferior petrosal
sinus

artefact

crista petrosa

facial foramen

cochlear nerve
foramen

jugular notch

vestibular aqueduct

exoccipital facet

ROSTRAL

LATERAL

F

foramen in anterior
lamina

anterior lamina

facial foramen

lateral
flange

prootic canal

dorsal ascending
groove

squamosal facet

ventral ascending groove

posttemporal groove

squamosal facet

fossa incudis

broken paroccipital
process

foramen in
promontorium

fenestra
vestibuli   broken
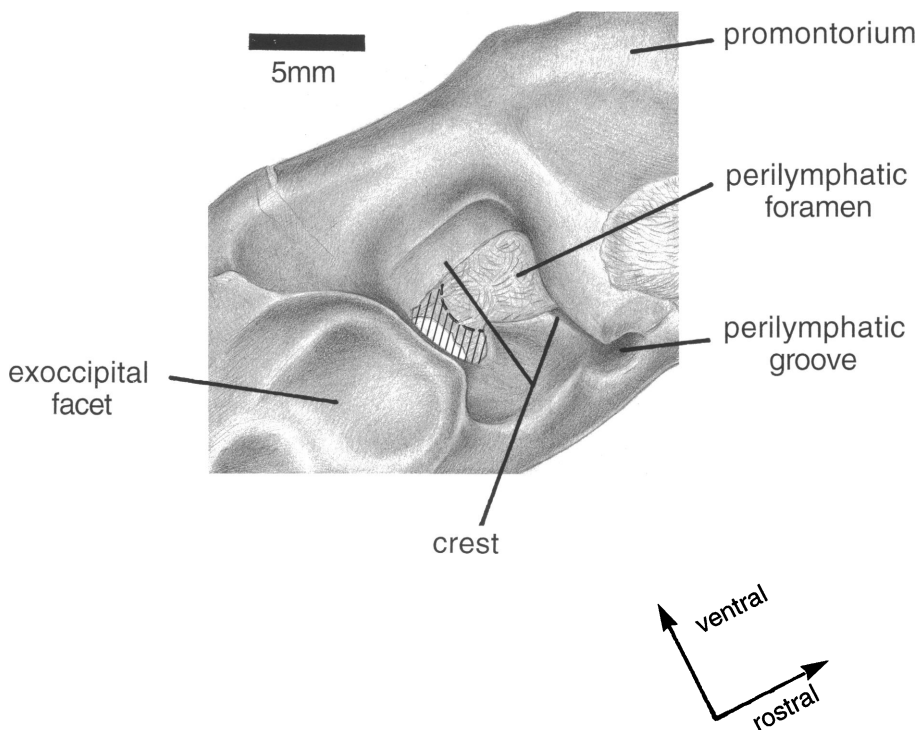tympanohyal   crista parotica

DORSAL

ROSTRAL

Fig. 1.   Continued.

Fig. 2. Detail of area about the perilymphatic foramen of the right petrosal of *Priacodon fruitaensis*, LACM 120451. The irregular pattern indicates matrix, the dashed line the probable posterior margin of the perilymphatic foramen, and the parallel-line pattern the missing posterior portion of the crest for the attachment of the secondary tympanic membrane.

montorial surface (fig. 1C, F). A sharp crest, the crista parotica, whose anteroventral surface is damaged, runs anterodorsally from the base of the paroccipital process. Preserved on the ventromedial edge of the left petrosal, near the midpoint of the crista parotica is a small bump with a notch posterior to it; we interpret these features as the broken base of the tympanohyal (fig. 1D, F) and the stylomastoid notch, respectively. A second crest extends dorsally from the base of the paroccipital process in an anterolateral direction. Between this crest and the crista parotica is a deeply concave, subtriangular surface, the fossa incudis, for the reception of the crus breve of the incus. Whereas the fossa incudis is delimited by well-developed crests medially (the crista parotica) and posteriorly (the paroccipital process), its anterolateral and lateral margins lack crests altogether and its anteromedial margin has only a weakly developed ridge. The contact facet

for the squamosal extends rostrally on the lateral surface of the petrosal, almost to the level of the anterior border of the fossa incudis (fig. 1C, F); in life, the squamosal may have contributed to the lateral margin of the fossa.

Z. Luo, another reviewer of an earlier version of this manuscript, expressed concerns that our reconstructed tympanohyal is positioned too far anteriorly and, given the location of the fossa incudis, would have interfered with the incudostapedial articulation. However, a similar positional relationship between the base of the tympanohyal and the fenestra vestibuli occurs in *Trioracodon ferox* (fig. 5E; Wible and Hopson, 1993) and also in some extant forms (e.g., *Echinosorex*, MacPhee et al., 1988: fig. 4D), yet the tympanohyal does not interfere with the incus and stapes because it is directed posteromedially. Additionally, we know of no explanation for a notch in the crista parotica other

than for the facial nerve, and the tympano-hyal is invariably placed anterior to that notch in extant mammals (Goodrich, 1930).

Anterior to the fossa incudis and fenestra vestibuli are two openings, the larger, more lateral one being the ventral opening of the prootic canal and the other the primary facial foramen. Running posteriorly from the proot-ic canal, between the crista parotica and fe-nestra vestibuli, is the wide sulcus for the lateral head vein (Wible and Hopson, 1995). It ends posteriorly in a shallow depression, the stapedius fossa, between the cristae in-terfenestralis and parotica. In life, the lateral head vein presumably ran medially from the posterior end of its sulcus, ventral to the sta-pedius fossa, to join the internal jugular vein ventral to the jugular foramen, as occurs in didelphid marsupials (Rougier et al., 1992; Wible and Hopson, 1995). The primary fa-cial foramen opens into the deep recess that in life housed the geniculate ganglion. The bone surrounding the recess is unbroken, in-dicating that there was no bony floor ventral to it; consequently, a bone-enclosed cavum supracochleare for the geniculate ganglion is lacking. This arrangement is an unique one in mammals (Wible, 1990; Wible and Hop-son, 1993). Two sulci notch the anterior and posterior edges of the primary facial fora-men, marking the course of the branches of the facial nerve. The anterior sulcus for the palatine ramus is the deeper of the two, but it can only be traced a short distance forward from the foramen. After a short course, the posterior sulcus for the hyomandibular ramus merges with the sulcus for the lateral head vein lateral to the fenestra vestibuli. In life, after sharing a short common course with the lateral head vein, the hyomandibular ramus presumably diverged laterally, running ven-tral to the vein, and left the middle-ear cavity through the stylomastoid notch behind the tympanohyal.

Anterior to the facial foramen, contribut-ing to the floor of the cavum epieptericum and the roof of the anterior part of the middle-ear cavity, is a broken laminar projection from the promontorium, which forms the lat-eral trough. In light of broken edges on the preserved lateral trough, the promontorium anterior to it, and the lateral flange (see be-low), the petrosal probably constituted the bulk of the floor of the cavum epieptericum. A large depression in the anteromedial part of the preserved lateral trough, delimited me-dially by the steep lateral wall of the pro-montorium, is the fossa muscularis major for the tensor tympani muscle. It is not delimited by a well-marked posterior crest as occurs, for example, in *Trioracodon ferox* (fig. 5E; Wible and Hopson, 1993). The lateral margin of the lateral trough is formed by a ventrally projecting ridge, the lateral flange, which is broken anteriorly. The shallowest part of the preserved lateral flange is at its posterior lim-it where it forms part of a broad notch; the deepest part is at the preserved anterior limit. The ventral surface of the lateral flange (to the extent preserved) shows no facet for ar-ticulation with the quadrate ramus of the al-isphenoid. However, the presence of a well-developed quadrate ramus underlying the missing anterior part of the lateral flange can-not be excluded. In the roof of the lateral trough, between the primary facial foramen and the lateral flange, is a shallow longitu-dinal sulcus, which we interpret as contain-ing the ramus inferior of the stapedial artery, inasmuch as this vessel lies in the same po-sition in the platypus (Rougier et al., 1992; Wible and Hopson, 1995).

A horizontal sulcus on the lateral surface of the petrosal (ventral ascending groove in fig. 1D, F) has an anterior limit that is con-tinuous with the broad notch in the rear of the lateral flange. Within the sulcus and pass-ing through the posterior part of the notch, we restore the ramus superior of the stapedial artery (see below). Given this reconstruction, the notch is homologous with the medial wall of the pterygoparoccipital foramen (the fo-ramen for the ramus superior), which is al-most universally present in Cynodontia (Wi-ble and Hopson, 1993).

DORSAL VIEW (fig. 1B, E)

Four major features are visible in this view: medially, the internal acoustic meatus and subarcuate fossa; and laterally, the semi-lunar recess and the endocranial aperture and sulcus of the prootic canal.

The internal acoustic meatus for the facial and vestibulocochlear nerves is delimited lat-erally and posteriorly by a raised surface.

However, anteriorly and medially, it is continuous with the dorsal surface of the pars cochlearis and, therefore, is not a distinct depression. Of the three foramina within the meatus, the largest and most medial is for the cochlear nerve. Posterolateral to it is the opening for the vestibular nerve and anterolateral to it is the opening for the facial nerve. The last is the smallest and lies in a common depression with the vestibular nerve opening. The right petrosal is broken, which exposes the course and orientation of the facial canal. It is a long, narrow passageway that extends to the primary facial foramen on the ventral surface. There is no enlarged space along the canal that might have housed the geniculate ganglion, and, as stated above, that ganglion occupied a depression ventral to the primary facial foramen. Given that the facial canal is long, the prefacial commissure—the segment of the crista petrosa dorsal to the facial canal, in this specimen placed anterolateral to the internal acoustic meatus—is very deep.

Separated from the internal acoustic meatus by a stout, low crest is the deeply excavated subarcuate fossa, housing the paraflocculus of the cerebellum. A small groove and foramen for the endolymphatic duct (vestibular aqueduct) are located on the medial margin of the subarcuate fossa. The bone dorsal to the subarcuate fossa is damaged, exposing the anterior semicircular canal. It is in this broken area that the sulcus for the sigmoid sinus would be expected. The sigmoid sinus is ubiquitous in extant mammals (Gelderen, 1924) and exits the braincase either from the foramen magnum or jugular foramen (Wible, 1990). This vessel was probably present in *Priacodon* as well. We believe that it exited via the foramen magnum because (1) the jugular foramen is too small to have transmitted a sigmoid sinus in addition to the glossopharyngeal, vagus, and accessory nerves and (2) no sulcus is found between the preserved medial margin of the subarcuate fossa and the jugular foramen. There is a faint, very narrow sulcus extending dorsally from the posterior margin of the jugular foramen, but it does not reach the medial margin of the subarcuate fossa.

A deep sulcus for the prootic sinus runs parallel to the dorsal and lateral margins of

the subarcuate fossa. It leads into the endocranial aperture of the prootic canal. Because the endocranial aperture is essentially dorsal to the ventral aperture, the prootic canal is nearly vertical in orientation. It is also very short and anteriorly positioned, at the level of the foramen for the vestibular nerve.

Anterior to the endocranial aperture of the prootic canal is the recessed area that housed the semilunar ganglion. The walls of the semilunar recess are formed medially by the crista petrosa (and prefacial commissure), laterally by the anterior lamina, and posteriorly by a distinct, narrow crest immediately in front of the endocranial aperture of the prootic canal. The floor of the semilunar recess is incompletely preserved and so the full extent of the closure of the cavum epiptericum cannot be ascertained. The existence of a pila antotica is also uncertain because breakage in the anterior pole of the pars cochlearis.

LATERAL VIEW (fig. 1C, F)

The lateral view is dominated by the anterior lamina in front and the articular surface for the squamosal behind. The latter includes two well-developed sulci, one running horizontally, the other vertically. Also visible in lateral view are the promontorium, the lateral flange, the crista parotica, the fossa incudis, and the damaged base of the paroccipital process.

The horizontal sulcus mentioned above extends from the narrow mastoid exposure of the petrosal to the broad notch anterior to the fossa incudis. Running anterodorsally from the dorsal margin of the horizontal sulcus is a vertical sulcus, the dorsal ascending groove, which divides the horizontal sulcus into anterior and posterior parts. Given the location of the squamosal facet on the posterior third of the lateral petrosal surface, the preserved portion of the dorsal ascending groove and the posterior part of the horizontal sulcus (posttemporal groove in fig. 1F) were enclosed in canals walled laterally by the squamosal. The posterior part of the horizontal sulcus was thus enclosed in life to form the posttemporal canal, opening on the occiput at the posttemporal foramen; the dorsal ascending groove was enclosed as the

dorsal ascending canal. The anterior part of the horizontal sulcus was open, forming the ventral ascending groove. Following Rougier et al. (1992) and Wible and Hopson (1995), we reconstruct arteries as the major occupants of these channels: the arteria diploëtica magna in the posttemporal canal, the ramus superior of the stapedial artery in the ventral ascending groove, and the ramus supraorbitalis of the stapedial artery in the dorsal ascending canal. The area around the posttemporal foramen on the mastoid exposure shows no trace of a sulcus for the occipital artery, the source for the arteria diploëtica magna in, for example, monotremes and armadillos (Wible, 1987).

Dorsal to the preserved part of the lateral flange and the ventral ascending groove is a broken bony lamina forming the anterior lamina of the lateral braincase wall. Two foramina are preserved in the anterior lamina, both opening into the temporal fossa. A smaller posterodorsal one lies at the level of the posterior extent of the semilunar recess (foramen in anterior lamina in fig. 1F), corresponding in position to foramen 3 described in *Trioracodon ferox* by Kermack (1963: fig. 3). Given that this foramen lacks an endocranial opening, it is likely a nutrient foramen. A large anteroventral foramen is represented only by a notch; it is the foramen pseudovale of the same author and is presumed to be the exit for the mandibular division of the trigeminal nerve.

EXOCCIPITAL (fig. 3)

Both exoccipitals are preserved, but are incomplete. Illustrated here is the more complete left one. Its most conspicuous feature is the occipital condyle (fig. 3A, B), which is long, subcylindrical, and dorsoventrally compressed. The condyle is not sharply demarcated from the surrounding bone and both dorsal and ventral condylar fossae are absent. The condyle is restricted to the ventral part of the foramen magnum, contributing to less than half of the height of the foramen (fig. 3B). Extending dorsally from the condyle and contributing to the margin of the foramen magnum is an incomplete occipital plate. It is laminar and tilted anteriorly.

In ventral view (fig. 3A), the exoccipital is roughly triangular, with the posterior face formed by the condyle, the medial face by the basioccipital surface, and the lateral face by the petrosal surface. The medial face is complete, exposing an extensive articular facet for the basioccipital. In life, the exoccipital-basioccipital sutures diverged anteriorly. Between the medial border of the condyle and the articular facet for the basioccipital is a notch lacking an articular surface; this indicates that the left and right condyles were not continuous ventrally and were separated by an odontoid notch. Most of the articular surface with the petrosal is lost. Preserved is a stout anterolateral process in front of the condyle that in life faced the barrel-shaped process of the petrosal described above (exoccipital facet in fig. 1D, E). Anteromedial to this process a single large hypoglossal foramen is preserved.

Endocranially, in the part of the exoccipital that floors the cranial cavity, are two foramina of which the more posterior one is slightly the larger (fig. 3C). Both foramina lead to canals that converge on the single aperture present on the ventral surface and presumably transmitted branches of the hypoglossal nerve.

PAUP ANALYSIS

As stated above, a cladistic analysis of 51 petrosal and exoccipital characters across 20 taxa was performed to evaluate the affinities of *Priacodon fruitaensis* and other triconodonts to one another and to other groups of mammaliamorphs. Scores for several characters included here differ from those in our prior published analyses (Wible and Hopson, 1993; Rougier, 1993; Wible et al., 1995). Character reevaluation on the basis of additional specimens has uncovered some incongruences and mistakes that are amended here. Character numbers follow the numeration in Appendices 1, 2, and 3, as well as in figures 4 and 5.

CHARACTER DISCUSSION

PETROSAL PROMONTORIUM (1)

We consider a promontorium to be a petrosal eminence on the tympanic side of the cochlear housing. Under such a definition, a
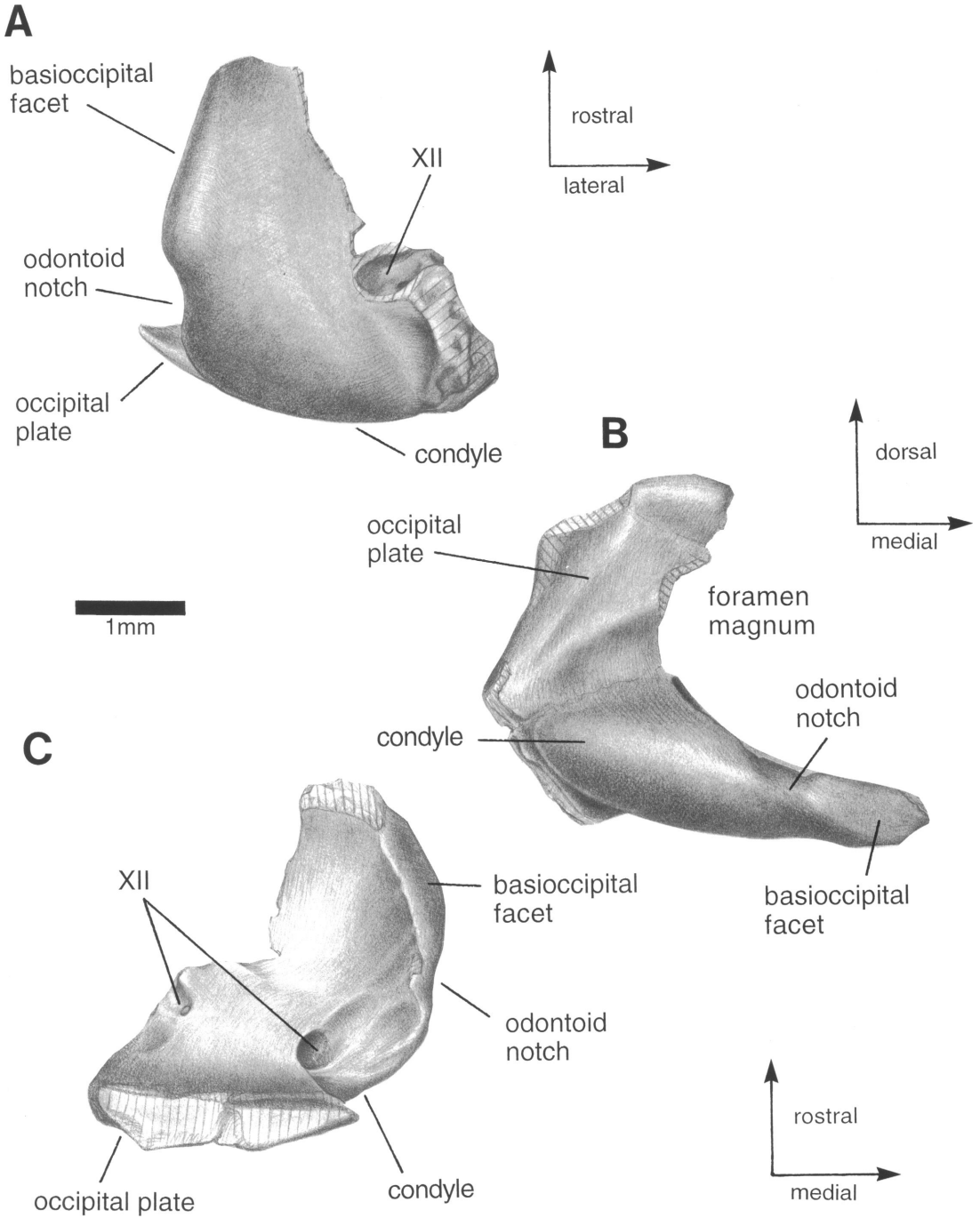
Fig. 3. Three views of left exoccipital of *Priacodon fruitaensis,* LACM 120451. **A,** Ventral view. **B,** Posterior view. **C,** Dorsal view. Parallel lines represent damaged surfaces.

promontorium is present in all the ingroup taxa included here with the exception of tachyglossids. In these forms (fig. 5B), a prominent bulge on the cochlear housing is lacking, although a raised area is present on the posteroventral aspect of the petrosal related to the abutment of the hyoid arch (Kuhn, 1971). Consequently, we code tachyglossids as lacking a promontorium.

PARA/BASISPHENOID WING (2)

Lucas and Luo (1993) reported that a wing of the basisphenoid covers the anterior pole of the promontorium in *Adelobasileus*. They interpreted this condition as intermediate between that in non-mammalian cynodonts in which the wing reaches the fenestra vestibuli (fig. 4B) and in mammaliaforms in which the wing is absent. As the parasphenoid is thought to be fused to the basisphenoid in non-mammalian cynodonts and early mammaliaforms (Miao, 1988), we here call this the para/basisphenoid wing.

COCHLEAR HOUSING SHAPE (3)

Fitting the cochlear housing of *Ornithorhynchus* (fig. 5A) into a shape category posed problems, and we ultimately coded it as fingerlike in outline; this is the shape of the pars cochlearis clearly evident from the endocranial aspect, but it is masked in ventral view by additional bone growth along the medial border. Additionally, we coded the cochlear housing shape as indistinctive for tachyglossids as well as the outgroup taxa.

VENTRAL CREST ON COCHLEAR HOUSING (4)

Among the taxa considered here, a distinct longitudinal crest on the ventral surface of the cochlear housing (fig. 4G, H) is found in *Sinoconodon* (Crompton and Luo, 1993), *Megazostrodon* (Gow, 1986b), and *Haldanodon* (Lillegraven and Krusat, 1991). This crest is reported to be absent in *Morganucodon* (Crompton and Luo, 1993), though we note that a raised area is present in some isolated petrosals of *M. watsoni* (Kermack et al., 1981: figs. 73C, 80D, F). Until we restudy *M. watsoni*, we code *Morganucodon* following Crompton and Luo (1993). E. F. Allin, a reviewer of an earlier version of this manuscript, suggested that this crest may represent the lateral limit of the longus capitis muscle insertion.

SECONDARY SPIRAL LAMINA (7)

Recent papers by Meng and Fox (1993, 1995a, 1995b) have focused attention on the phylogenetic utility of inner ear structures, including the secondary spiral lamina. A character concerning the presence/absence of the secondary spiral lamina was used in the phylogenetic analyses by Rougier (1993) and Wible et al. (1995). In the taxon-character matrix of the latter paper, the condition in *Sinoconodon* was scored as unknown. However, cross sections through the cochlear canal of *Sinoconodon* published by Luo et al. (1995) reveal that a secondary spiral lamina is absent. The presence of a secondary spiral lamina in *Vincelestes* is documented by a sulcus on the endocast of the cochlea (Rougier, 1993: fig. 34).

PERILYMPHATIC DUCT (11, 12)

In the primitive condition in amniotes, the perilymphatic duct leaves the cranial cavity via the jugular foramen and reaches the inner ear through the perilymphatic foramen in the rear of the otic capsule (Gauthier et al., 1988). This condition is repeated in *Ornithorhynchus* (Zeller, 1991, 1993), except that the perilymphatic foramen also provides partial attachment for the secondary tympanic membrane (Presley, 1980). This membrane, which is said to be absent primitively in amniotes (Gauthier et al., 1988), lies at the lateral limit of an extracranial space behind the perilymphatic foramen, the recessus scalae tympani, where the perilymphatic duct contacts the cavum tympani (Zeller, 1991, 1993). In therians, in contrast to the condition in *Ornithorhynchus*, a chondrocranial process, the processus recessus, encloses the perilymphatic duct within a canal, the cochlear aqueduct; this process ossifies with the petrosal in the adult and delimits another aperture in the rear of the otic capsule, a true round window or fenestra cochleae (fenestra rotunda), which is closed by the secondary tympanic membrane (Goodrich, 1930; Zeller, 1985).
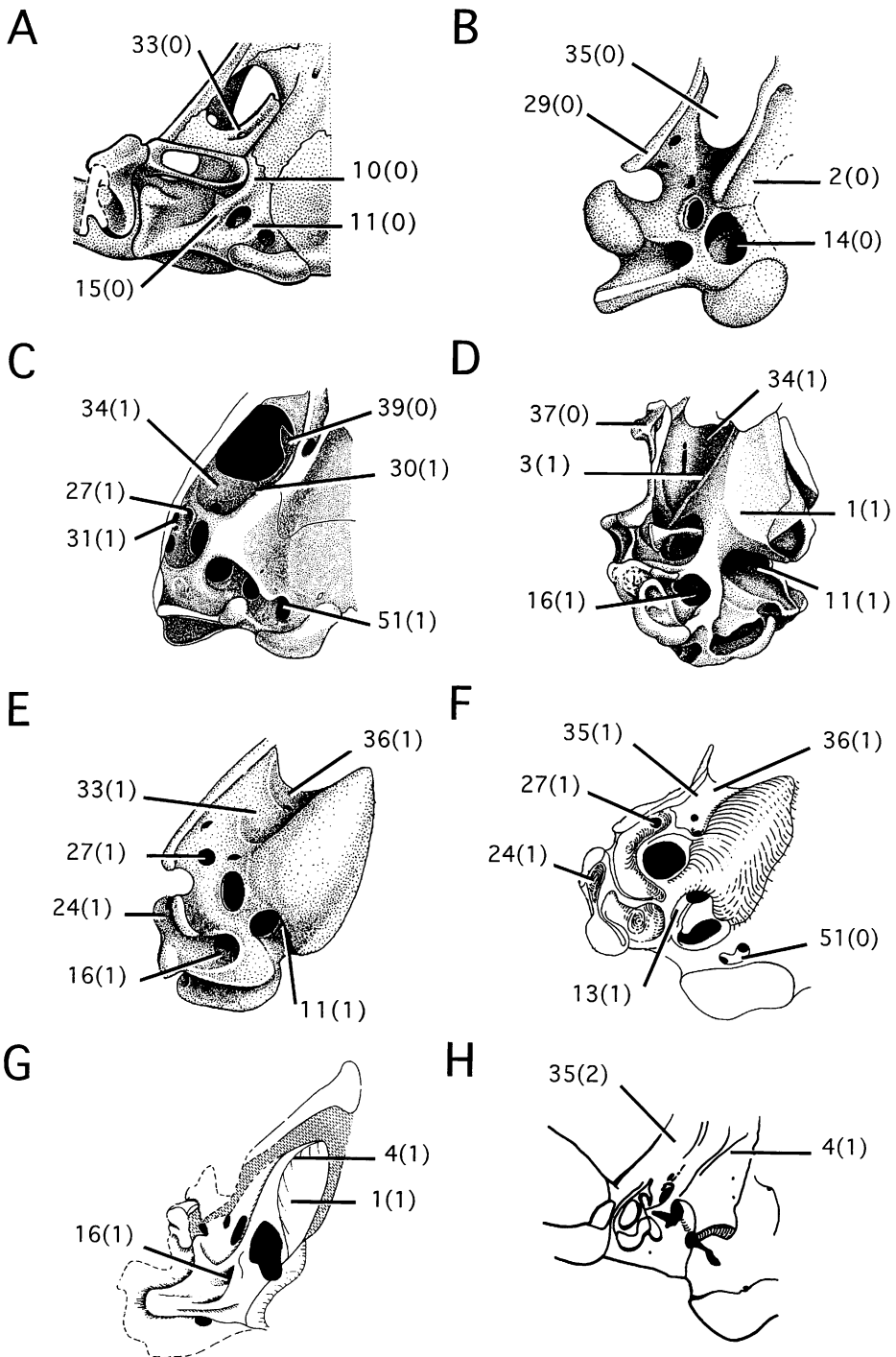
Tachyglossus presents a problem in deter-

Fig. 4. Right petrosals or ear regions in ventral view; not to scale and some have been reversed from the original. Numbers correspond to characters (and states) in appendices 1–3. **A,** The tritheledontid *Pachygenelus*; **B,** generalized tritylodontid; **C,** *Adelobasileus*; **D,** *Sinoconodon*; **E,** *Morganucodon oehleri*; **F,** *Dinnetherium*; **G,** *Megazostrodon*; **H,** *Haldanodon*. The figures are reprinted and modified with permission or redrawn from the following sources: **A,** Wible and Hopson (1993); **B, E,** Luo (1994); **C,** Luo et al. (1995); **D, F,** Crompton and Luo (1993); **G,** Gow (1986b); **H,** Lillegraven and Krusat (1991).

mining the homologies of the canal for the perilymphatic duct. As in *Ornithorhynchus,* the perilymphatic duct in *Tachyglossus* enters the inner ear via the perilymphatic foramen. However, whereas the duct runs to the foramen in an open groove in *Ornithorhynchus*; it is enclosed in a canal in *Tachyglossus* (Kuhn, 1971). Our study of macerated skulls of *Tachyglossus* and *Zaglossus* reveals that the degree of enclosure of the perilymphatic duct varies both ontogenetically and individually. For example, in juvenile *Tachyglossus* the duct lies in a sulcus and is open ventrally (Kuhn, 1971: fig. 40; Wible and Hopson, 1995: fig. 3). On the other hand, adult specimens may show extensive closure on one side of the skull but not on the other (e.g., AMNH-DM 42176). In at least some *Zaglossus* (AMNH-DM 190863), the ossification enclosing the perilymphatic duct, the "processus recessus" of Kuhn (1971), is even more developed than in *Tachyglossus* and circumscribes a larger portion of the duct within a canal. The homology of the "processus recessus" in *Tachyglossus* (and by extension also in *Zaglossus*) with the processus recessus in therians has been questioned by Kuhn (1971), because that of echidnas encloses the glossopharyngeal nerve in addition to the perilymphatic duct. We agree that the relationships of the tachyglossid "processus recessus" are unique among living mammals, which may suggest the nonhomology of the tachyglossid and therian cochlear aqueducts, despite their striking osteological similarities. In addition to the canal for the perilymphatic duct present in tachyglossids and therians, enclosure of the duct is also thought to have occurred independently on at least three other occasions in amniotes: in squamates, in crocodilians, and in birds (Gauthier et al., 1988).

Only the presence or absence of the canal for the perilymphatic duct can be ascertained for extinct taxa in our cladistic analysis. With no soft tissues preserved, we cannot know whether the perilymphatic duct was the only occupant of the cochlear aqueduct as in therians or if it was accompanied by the glossopharyngeal nerve as in tachyglossids. Consequently, despite the risk of treating nonhomologous canals as homologous in a transformation series, we subsume all taxa exhibiting osseous enclosure of the perilymphatic duct under the same character state.

In considering the complex transformations related to the enclosure of the perilymphatic duct and associated structures, we recognize two multistate characters. These are: (11) degree of enclosure of the perilymphatic duct; and (12) position of the lateral aperture of the cochlear aqueduct.

Among the basal taxa considered here, the position of the perilymphatic duct is not marked on the bridge of bone separating the perilymphatic and jugular foramina (fig. 4A). This condition, present in tritheledontids, tritylodontids, *Adelobasileus,* and *Sinoconodon,* can be considered primitive for mammaliamorphs. In most of the remaining taxa, the position of the duct is marked by an osseous channel that shows differing degrees of enclosure; the exceptions are *Megazostrodon, Dinnetherium, Triconodon,* and the unnamed Cloverly triconodonts in which the appropriate part of the petrosal is not preserved, described, or figured. An open sulcus for the perilymphatic duct (fig. 4D, E) is found in the Jurassic mammaliaforms *Morganucodon* and *Haldanodon,* and in ptilodontoid multituberculates (e.g., compare *Mesodma thompsoni* FMNH PM 53904; *Ptilodus montanus* AMNH-DVP 35490). The sulcus is deeper and a ventral lappet of bone extends posteriorly and dorsally from the promontorium, nearly flooring a canal, in isolated petrosals of taeniolabidoid multituberculates (e.g., cf. "*Catopsalis*" *joyneri* AMNH-DVP 118533, 119445) from the Late Cretaceous of North America. The Late Jurassic paulchoffatiid multituberculates also have a deep sulcus (Hahn, 1988; Lillegraven and Hahn, 1993), but the presence of a ventral bony lappet from the promontorium cannot be ascertained in the fragmentary material available. The bony lappets on the edges of the sulcus are expanded further in *Priacodon* and produce a nearly complete canal (fig. 2). A sulcus is also present in *Trioracodon* (Kermack, 1963: fig. 3), but the presence of bony lappets is uncertain from the published figures.

The Khoobur petrosals and prototribosphenidans exhibit a cochlear aqueduct (fig. 5I), but a morphocline exists regarding the degree of enclosure. The Early Cretaceous
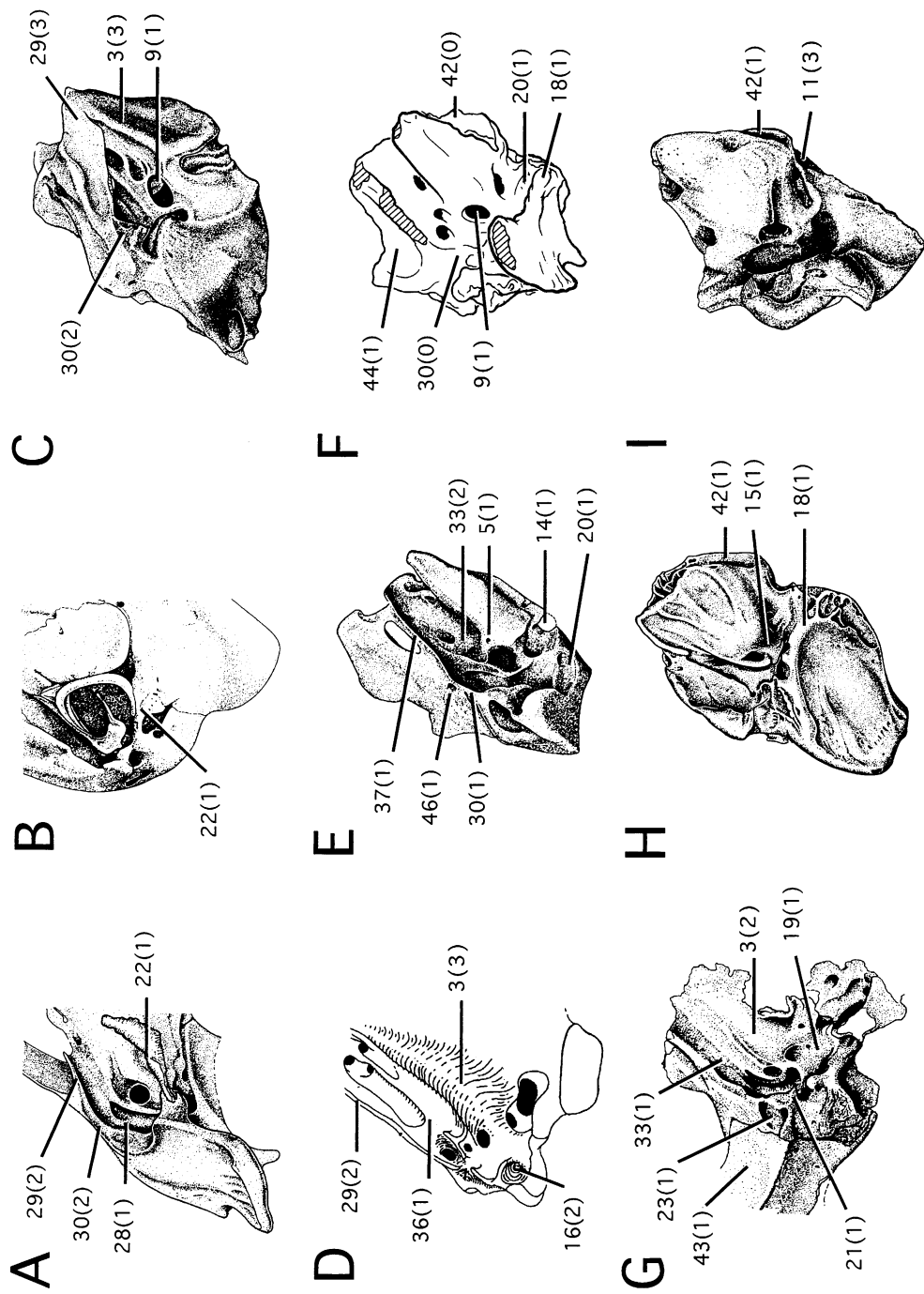
Fig. 5. Right petrosals or ear regions in ventral view; not to scale and some have been reversed from the original. Numbers corresponds to characters (and states) in appendices 1–3. A, *Ornithorhynchus*; B, *Tachyglossus*; C, the multituberculate ?*Catopsalis joyneri*; D, Cloverly triconodont; E, the triconodontid *Trioracodon*; F, Khoobur petrosal 1; G, *Vincelestes*; H, Bug Creek marsupial; I, Bug Creek placental. Figures are reprinted and modified with permission or redrawn from the following sources: A, C, E, H, I, Wible and Hopson (1993); B, Kuhn (1971); D, Crompton and Luo (1993); F, Wible et al. (1995); G, Rougier (1993).

Khoobur petrosal 2 exhibits a more enclosed state than that in tachyglossids, with a processus recessus that is thicker and that shields the perilymphatic duct all the way from the endocranial surface of the petrosal to immediately posteromedial to the perilymphatic foramen, just outside the inner ear. The processus recessus is even thicker in Khoobur petrosal 1, enclosing the perilymphatic duct more deeply within the petrosal. It shields the perilymphatic duct all the way from the endocranial surface to inside the inner ear and, thereby, contributes to the formation of a true round window (contra Wible et al., 1995; see below). The lateral aperture of the cochlear aqueduct is immediately rostral to the anteromedial rim of the fenestra cochleae, within the inner ear. Finally, *Vincelestes,* a prototribosphenidan from the Early Cretaceous of Argentina, shows an even more enclosed perilymphatic duct with a massive processus recessus and a medial aperture for the cochlear aqueduct recessed from the round window, well within the inner ear. This is also the condition present primitively in marsupials and placentals.

In their original description of Khoobur petrosal 1, Wible et al. (1995) observed the absence of a sulcus for the perilymphatic duct and considered the opening in the back of the promontorium as a perilymphatic foramen because no likely cochlear aqueduct was to be found. Restudy of the material after further preparation shows a cochlear aqueduct to be present. Its medial aperture lies in a narrow seam in the jugular notch and the lateral aperture is a small opening within the cochlear cavity just in front of the fenestra cochleae.

JUGULAR FOSSA (13)

Primitively in non-mammalian cynodonts, the jugular and perilymphatic foramina are confluent (Quiroga, 1979). In the taxa included in our analysis, these two apertures are separated (Wible, 1991). Additionally, in tritheledontids, tritylodontids, and most Jurassic mammaliaforms, including multituberculates, these two apertures open into a common recessed area referred to here, following Kielan-Jaworowska et al. (1986), as the jugular fossa (fig. 4F).

CAUDAL TYMPANIC PROCESS OF THE PETROSAL (18)

The caudal tympanic process is a crest on the petrosal situated medial to, and usually continuous with, the paroccipital process, forming the posterior wall of the tympanic cavity (fig. 5F, H; Wible, 1990). In the cladistic analyses by Wible and Hopson (1993) and Wible et al. (1995), Multituberculata is scored as lacking a caudal tympanic process, the condition present in (for example) the ptilodontoid *Ptilodus* (AMNH-DVP 35490) and the taeniolabidoid *Nemegtbaatar* (ZPAL MgM-I/76). However, the recently recovered skull of the taeniolabidoid *Kryptobaatar dashzevegi* (PSS-MAE-113) from the Late Cretaceous of Mongolia shows a distinct caudal tympanic process, as does *Kamptobaatar* (ZPAL MgM-I/33). Reexamination of other multituberculate ear regions, including the Late Jurassic paulchoffatiids (Hahn, 1988; Lillegraven and Hahn, 1993), reveals that the area medial to the paroccipital process is often subject to considerable damage. We score Multituberculata as polymorphic because both states are clearly present.

DEEP POCKET MEDIAL TO PAROCCIPITAL PROCESS (20)

The distinct cuplike depression of uncertain function medial to the paroccipital process and crista interfenestralis in *Priacodon* (fig. 1D) is also found in two other taxa considered here: *Trioracodon ferox* (fig. 5E) and the Khoobur petrosal 1 (fig. 5F). In *Trioracodon,* this depression has been identified as a possible pit for the hyoid by Kermack (1963) and as the fossa for the stapedius muscle by Wible and Hopson (1993). Neither interpretation is likely for *Trioracodon,* because the proximal segment of the hyoid arch, the tympanohyal, is already fused to the crista parotica and a stapedius fossa is clearly present lateral to the crista interfenestralis. In both regards, *Trioracodon* closely resembles the condition in *Priacodon.* In their description of Khoobur petrosal 1, Wible et al. (1995) did not recognize this pocket, which is nevertheless visible in their figure 2 (between the lines indicating the caudal tympanic process of the petrosal and the postpromontorial tympanic sinus).

The Liassic *Morganucodon* has a depression on the crista interfenestralis anterior to the paroccipital process that was identified as the pit for the levator hyoidei muscle by Kermack et al. (1981). However, we follow Crompton and Sun (1985) and others in identifying this feature as for the stapedius muscle. In addition to *Morganucodon,* a similar depression on the crista interfenestralis occurs in tritylodontids, *Sinoconodon, Dinnetherium, Megazostrodon,* and *Haldanodon.* This condition of the stapedius fossa is distinguished from the deep pocket occuring in *Priacodon, Trioracodon,* and Khoobur petrosal 1, because the latter occurs medial to the crista interfenestralis along with a more laterally-placed stapedius fossa.

CRISTA PAROTICA/SQUAMOSAL CONTACT (23)

Presence or absence of contact between the crista parotica and squamosal was recently used as a character in the cladistic analysis by Wible et al. (1995). The following scores in their matrix we amended here. *Megazostrodon* is altered from contact present to unknown, because this feature is not described or illustrated in the only descriptive treatment of the skull of this taxon (Gow, 1986b). *Haldanodon* is changed from unknown to contact absent, as illustrated in Lillegraven and Krusat (1991: fig. 8). Marsupialia and Placentalia, both of which were scored as contact absent, are treated as polymorphic here, because both conditions are evident in isolated petrosals from the North American Late Cretaceous (MacIntyre, 1972; Wible, 1990). Finally, Multituberculata, scored by Wible et al. (1995) as contact absent, is amended to contact present. Few multituberculates preserve this region, and the only form that clearly shows absence of contact between the crista parotica and squamosal is the Late Paleocene taeniolabidoid *Lambdopsalis,* a specialized fossorial form from China (Miao, 1988). Contact is clearly present in more generalized taeniolabidoids from the Mongolian Late Cretaceous, e.g., *Chulsanbaatar, Nemegtbaatar* (Kielan-Jaworowska et al., 1986), and *Kryptobaatar dashzevegi* (PSS-MAE-113). In addition, although none of the Late Jurassic paulchoffatiids can be scored for this character, in at least one ear region (Hahn, 1988: fig. 1), the squamosal is ventrally prolonged and as reconstructed by us would have contacted the crista parotica.

VASCULAR FORAMEN IN LATERAL FLANGE (31)

First used in cladistic analysis by Wible (1991), the absence or presence of a vascular foramen through the lateral flange (fig. 4C) has been included in subsequent analyses by Wible and Hopson (1993), Lucas and Luo (1993), Rougier (1993), Luo (1994), and Wible et al. (1995). We offer the following amendments to the matrix in Wible et al. (1995). *Haldanodon* is changed from foramen present to unknown, because the appropriate part of the petrosal is damaged. *Vincelestes* is altered from absence of the foramen to polymorphic, because as reported by Rougier et al. (1992) this aperture is variably present. Finally, the foramen in Multituberculata, said to be absent by Wible et al. (1995), is scored here as present. Following Rougier (1993), we interpret the supraglenoid foramen of multituberculates and the lateral flange vascular foramen of other taxa as equivalent, because they occupy essentially the same location and connect with similar vascular canals. This contrasts with the discussion in Wible and Hopson (1995), who did not consider the multituberculate supraglenoid foramen to be equivalent to the lateral flange vascular canal of other taxa.

FACIAL GANGLION FLOOR (33)

Wible et al. (1995) scored the floor of the facial ganglion as open ventrally in Tritylodontidae. An exception to this is *Oligokyphus,* which has a bony floor (Kühne, 1956). Given the putative basal position of *Oligokyphus* within Tritylodontidae (Clark and Hopson, 1985), the primitive condition for this group is equivocal. Accordingly, we code Tritylodontidae has having two states for this character: open ventrally and a broad petrosal bridge.

PILA ANTOTICA (39)

Wible et al. (1995) scored the presence of the ossified base of the pila antotica (fig. 4C)

as uncertain for *Megazostrodon.* However, this is altered to presence here, following Lucas and Luo (1993).

POSITION OF INFERIOR PETROSAL SINUS (42)

In Recent mammals, the inferior petrosal sinus drains blood from the cavernous sinus to the internal jugular vein via a course along the petrosal-basioccipital suture. Its course may be largely endocranial, intramural, or extracranial (Wible, 1983). A comparable vein does not occur in Recent non-mammalian amniotes (Shindo, 1915), and therefore the sinus is a neomorph originating within synapsids. However, the only synapsids with any osseous indication for the inferior petrosal sinus are certain mammaliaforms.

Kermack et al. (1981) illustrated a number of petrosals of *Morganucodon watsoni* in which foramina open into internal canals within the promontorium. Within these foramina and canals, they reconstructed a circumpromontorial venous plexus. The largest and most consistent of these foramina are at the anterior and posterior ends of a major internal canal along the medial edge of the promontorium (best seen in their fig. 83B). The anterior opening lies at the anterior pole of the promontorium within the cranial cavity, and the posterior opening is extracranially placed, rostral to the jugular notch. No comparable structure is known in any group of living mammals, although in some (e.g., monotremes) the petrosal houses small venous sinuses (Rougier et al., 1992). These small sinuses are highly anastomotic and do not form a single continuously walled canal that could account for the structure present in *M. watsoni.* Given that the only major venous element in this area of the skull in Recent mammals is the inferior petrosal sinus, we interpret this vein as the likely occupant of the canal in *M. watsoni.* A similar arrangement is found, for example, in some living carnivorans in which the inferior petrosal sinus occupies a deep sulcus in the medial edge of the promontorium that is transformed into the petrobasilar canal by contact with the basioccipital and auditory bulla (Hunt, 1977; Evans and Christensen, 1979). A striking difference between the canal in the petrosal in *M. watsoni* and the petrobasilar canal is that

the former bends laterally and opens at the apex of the promontorium. Canals resembling that in *M. watsoni* are found in *Haldanodon* (Lillegraven and Krusat, 1991), paulchoffatiid multituberculates (Lillegraven and Hahn, 1993), the Khoobur petrosal 1 (fig. 5F; Wible et al., 1995), *Priacodon,* *Trioracodon,* and *Vincelestes* (MACN-N05, N09). The coding of the inferior petrosal sinus by some of us in a prior analysis (Wible et al., 1995) is altered here to reflect our new interpretation. We note, however, that Kermack et al. (1981) offered a different restoration of the inferior petrosal sinus in *Morganucodon,* as an endocranial vessel vertically piercing the petrosal-basioccipital suture. An appropriate sutural gap is not illustrated in any of their specimens.

ANTERIOR LAMINA (45)

In Wible et al. (1995), the contribution of the anterior lamina to the cranial wall was coded in reference to the foramina for the maxillary and mandibular branches of the trigeminal nerve. In the case of two nerve apertures in or near the anterior lamina, two models of nerve restoration have been proposed. First, Simpson (1937) identified two foramina in the ventrolateral braincase of the multituberculate *Ptilodus montanus* and reconstructed branches of the mandibular nerve within them. This model was based on Hill's (1935) observation of two foramina for the mandibular nerve within the alisphenoid in some living rodents. Second, Patterson and Olson (1961) identified two major apertures in the anterior lamina of *Sinoconodon* as transmitting the maxillary and mandibular nerves, respectively. The same restoration was proposed for *Morganucodon* (Kermack, 1963, 1967), and the placement of the maxillary nerve in the anteriormost opening was justified by a shallow, anteriorly directed groove extending from the foramen, which represented an appropriate course for the maxillary nerve (Kermack et al., 1981). However, this restoration was challenged by Kielan-Jaworowska (1971), who considered both foramina in the anterior lamina of "triconodonts" (i.e., *Trioracodon* and *Morganucodon*) to be for mandibular nerve branches. Kermack et al. (1981: 97) acknowledged

that "this may well be a possible alternative interpretation of the condition in *Morganu-codon.*"

Although the presence of an anteriorly directed sulcus seems to be a reasonable criterion for identifying a foramen for the maxillary nerve, the fact is that such grooves may accommodate branches of the mandibular nerve as well, such as deep temporal nerves (see Evans and Christensen, 1979). Further doubts concerning the identification of foramina in the ventrolateral wall of the braincase are raised by the position of the two foramina in paulchoffatiid multituberculates. In Cretaceous and Tertiary multituberculates, such as *Ptilodus,* the foramina are directed ventrally and anterolaterally, as is the case in rodents. In contrast, in the Early Jurassic paulchoffatiids, both foramina seem to be directed laterally (see Hahn, 1988)— reminiscent of the condition in *Morganuco-don.* If nerves are restored in paulchoffatiids as in other multituberculates (Simpson, 1937; Kielan-Jaworowska, 1971), then both of the paulchoffatiid foramina are for the mandibular nerve. However, if the *Morganucodon* model (Kermack et al., 1981) is followed, then the two foramina in paulchoffatiids are for the maxillary and mandibular nerves, respectively. Recently discovered crania of *Sinoconodon* and *Adelobasileus* pose additional problems. Both forms have three large foramina occupying similar positions in the anterior lamina. Whereas Crompton and Luo (1993) allocated two foramina to the mandibular nerve and one to the maxillary nerve in *Sinoconodon,* Lucas and Luo (1993) allocated one foramen for each of these nerves in *Adelobasileus,* with the third said to be indeterminate in function.

Resolution of these problems awaits careful comparison of the relevant extinct and extant taxa as well as the identification of criteria allowing an unambiguous recognition of maxillary and mandibular nerve exits. In the meantime, reflecting the doubts raised above (and contra Wible et al., 1995), we do not characterize the anterior lamina's contribution to the lateral braincase wall with reference to the exits for the maxillary and mandibular nerves. Our reworded character description considers whether the anterior lamina does or does not contact the orbitosphenoid external-

ly. An additional character (**48**), also used by Wible et al. (1995), treats the number of openings for the trigeminal nerve posterior to the alisphenoid as either none, single, or multiple.

AFFINITIES OF *Priacodon fruitaensis*

Running the taxon-character matrix in appendix 2 on the branch and bound algorithm of PAUP produced six equally most parsimonious trees (147 steps.) They differ in the relationships among the triconodontid taxa and in the positions of triconodonts and multituberculates with respect to Prototribosphenida + the Khoobur petrosals. The strict consensus of these six trees is shown in figure 6A. Reweighting the data set, using the rescaled consistency index on PAUP's reweighting option, yielded three equally most parsimonious trees, the consensus of which is shown in figure 6B and diagnosed in appendix 3. These three trees differ only in the relationships among the triconodontids. It is noteworthy that the most incomplete taxon included here is *Triconodon mordax,* which is scored for only 17 of the 51 characters. This low degree of completeness (33.3%), which undoubtedly accounts for the unresolved relationships within Triconodontidae, is well below the 86.7% average completeness of the taxa in the matrix.

Two other phylogenetic analyses of basicranial characters across mammaliamorphs have been completed recently by some of us (Wible and Hopson, 1993; Wible et al., 1995). The current analysis considers more ingroup taxa and characters. The additional ingroup taxa result from including a second isolated petrosal from Khoobur and from splitting Monotremata into OTU's for the platypus and echidnas and Triconodontidae into OTU's for *Priacodon, Triconodon, Trioracodon,* and the unnamed Cloverly triconodonts. The additional characters include features unique to triconodonts as well as features not considered previously, such as that of the exoccipital (see appendix 1). The phylogenetic results of the current report most closely resemble those of Wible et al. (1995), with the main difference being that all taxa, except triconodonts and multituberculates, are fully resolved in the strict consensus tree of the original analysis here (fig.
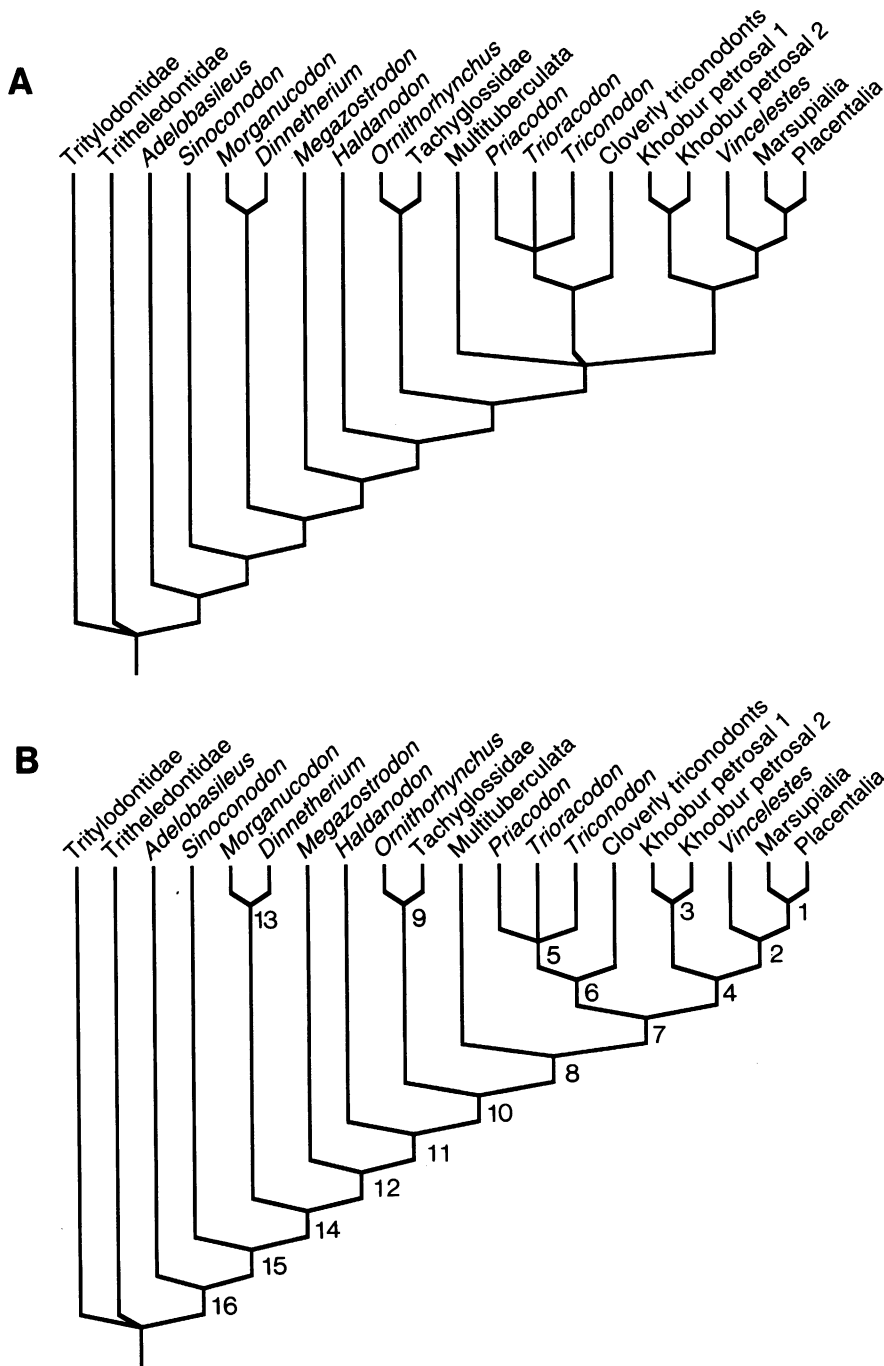
Fig. 6. **A,** Strict consensus of the six most parsimonious trees resulting from the PAUP analysis of the matrix in appendix 2. Tree length = 148 steps; consistency index = 0.568; retention index = 0.708; these values on the individual trees are 147, 0.571, and 0.712 respectively. **B,** Strict consensus of the three most parsimonious trees resulting from the reweighted (rescaled consistency index) PAUP analysis. This tree is diagnosed in appendix 3, and the numbers here correspond to the diagnosed nodes.

6A); the strict consensus tree in Wible et al. (1995) has three unresolved trichotomies between Mammaliaformes and Prototribosphenida. However, using MacClade (Maddison and Maddison, 1992) to reproduce one of the most parsimonious trees recovered in Wible et al. (1995) requires that four steps be added to the most parsimonious trees here. The most striking difference between the current report and Wible et al. (1995) on the one hand and Wible and Hopson (1993) on the other is the position of triconodonts with regard to Mammalia; here and in Wible et al. (1995) triconodonts are included within Mammalia, whereas they are excluded in Wible and Hopson (1993). Yet, the position of triconodonts is very labile in all three analyses, and in some trees that are one step longer than the most parsimonious ones presented here, triconodonts are excluded from Mammalia. Within the framework provided by the current cladistic analysis, we address below triconodont interrelationships and other issues of mammaliamorph phylogeny.

TRICONODONT INTERRELATIONSHIPS

Four taxa (the indeterminate Cloverly triconodontids, *Priacodon*, *Trioracodon*, and *Triconodon*) are considered to be triconodonts here, based on one unequivocal and four equivocal synapomorphies (appendix 3: node 6). The unequivocal feature is a wide separation between the lateral flange and the crista parotica into which the ventral ascending groove opens (fig. 5E). In non-triconodont mammals, the lateral flange is in closer proximity to the crista parotica (or is absent), and the ventral ascending groove opens into a notch between the two or is enclosed in a foramen by them.

As defined above, the family Triconodontidae is the group including the last common ancestor plus descendants of the five genera included in Triconodontidae by Jenkins and Crompton (1979): *Alticonodon*, *Astroconodon*, *Priacodon*, *Triconodon*, and *Trioracodon*. In our analysis, the Cloverly triconodonts are identified as the sister taxon of an unresolved monophyletic group including *Priacodon*, *Triconodon*, and *Trioracodon*. Whether or not the Cloverly triconodonts should be included ultimately in Triconodon-

tidae is dependent upon their relationship with *Alticonodon*, *Astroconodon*, and the remaining triconodont families (Amphilestidae, Austrotriconodontidae, and Gobiconodontidae) for which no petrosals, have yet been identified.

Triconodontidae here is supported by three unequivocal synapomorphies and one equivocal synapomorphy (appendix 3: node 5). Among the unequivocal characters are the presence of a small foramen on the cochlear housing in front of the fenestra vestibuli and a very small jugular foramen (fig. 5E).

TRICONODONT RELATIONSHIPS

Our analysis is inconclusive regarding the phylogenetic position of triconodonts among Mammaliaformes. In three of the six most parsimonious trees obtained, triconodonts are more closely allied with therians than are multituberculates; the reverse is true in the remaining three trees. Reweighting of our data set identified the same three trees that allied triconodonts with therians to the exclusion of multituberculates (fig. 6B). In this instance, the clade of triconodonts + the Khoobur petrosals + Prototribosphenida (Theriimorpha, see below) is supported weakly by a single unequivocal and four equivocal synapomorphies (appendix 3: node 7). The unequivocal synapomorphy, the craniomandibular joint anterior to the fenestra vestibuli, is unknown in *Priacodon*, *Trioracodon*, *Triconodon*, and Khoobur petrosal 2.

The term Theriimorpha was coined by Rowe (1993) as a stem-based taxon including all mammals more closely related to Theria than are monotremes. In the strict consensus trees obtained in our initial analysis (fig. 6A) as well as in the reweighted analysis (fig. 6B), Theriimorpha (Rowe, 1993) is synonymous with Theriiformes (Rowe, 1988). In order to avoid redundant and novel terms, following Wible et al. (1995), we use Theriimorpha here to include the last common ancestor of Triconodontidae and Theria plus all its descendants.

Although, as shown above, the phylogenetic relationships of triconodonts are uncertain, our results are congruent with those of recent cladistic analyses (e.g., Rowe, 1988; Wible, 1991; Wible et al., 1995) in denying

the monophyly of Triconodonta in the traditional sense. This deeply rooted concept, which groups several Jurassic taxa (e.g., *Morganucodon, Sinoconodon,* and *Dinnetherium*) with triconodonts as understood here, is still used in formal systematics and represents the archetypal Mesozoic "mammal" for many investigator (e.g., Carroll, 1988; Bonaparte, 1992; Kielan-Jaworowska, 1992; Stucky and McKenna, 1993). Given that all recent cladistic analyses that include the pertinent taxa (e.g., Rowe, 1988, 1993; Wible, 1991; Wible and Hopson, 1993; Wible et al., 1995) have denied the monophyly of Triconodonta in the traditional sense, we recommend that this use of the term be abandoned. Whether or not the four families of triconodonts recognized by us (Triconodontidae, Amphilestidae, Austrotriconodontidae, and Gobiconodontidae) form a natural group has not been established. Studies identifying dental synapomorphies have yet to be published, and because amphilestids, austrotriconodontids, and gobiconodontids are not yet known from petrosals, they cannot be incorporated into our analysis. Furthermore, because the four triconodont families may constitute a paraphyletic assemblage, we shall not formally define Triconodonta as the last common ancestor of Triconodontidae, Amphilestidae, Austrotriconodontidae, and Gobiconodontidae plus all its descendants.

The only recent researcher to postulate characters in support of Triconodonta in the traditional sense is Luo (1994). He offered one dental and five cranial features allying morganucodontids and triconodontids. However, as he pointed out, Mammalia as we understand it (i.e., the last common ancestor of monotremes and therians-plus its descendants) was excluded from his study. In fact, Luo's five purported cranial synapomorphies are found in Mammalia, in multituberculates and/or living mammals and their extinct relatives (e.g., *Vincelestes*). Additionally, as Luo noted, the single dental character (lower cusp a occluding between upper cusps A and B) is not present in amphilestids. The monophyly of Triconodonta in the traditional sense has not yet been rigorously tested and is not feasible without consideration of all relevant mammaliamorph taxa.

The phylogenetic position for triconodonts

obtained in our study is congruent with basicranial evidence presented previously by some of us (Wible et al., 1995) as well as, for example, the evidence of the shoulder girdle. As in *Vincelestes* (Rougier, 1993) and therians, the scapula of gobiconodontids (Jenkins and Schaff, 1988) and the scapula attributed to the Cloverly triconodonts (Jenkins and Crompton, 1979) has a spine separating supra- and infraspinous fossae, both of which extend to the glenoid. In contrast, in more basal taxa, a supraspinous fossa is small and dorsally placed (tritylodontids; Sues, 1983; Sun and Li, 1985), rudimentary (multituberculates; Sereno and McKenna, 1995), or lacking altogether (monotremes). However, as is evident by the strict consensus tree (fig. 6A), the position of triconodonts with respect to multituberculates is open to question. In general, the tree topology recovered here is labile with respect to a few changes in the data set, and 123 additional trees only one step longer than the most parsimonious ones (148 steps) were identified using the branch and bound algorithm on the matrix. The strict consensus of the 129 trees (147 + 148 steps) erases much of the resolution recovered in the six most parsimonious trees. It is evident from the low number of unequivocal characters defining some clades (appendix 3) that the least stable relationships are those of the pre-*Haldanodon* Jurassic taxa (see below) and those of triconodonts, multituberculates, and monotremes. In the 123 trees one step longer (148 steps), triconodonts are either grouped paraphyletically with the Khoobur petrosals or are the sister taxa to Prototribosphenida + the Khoobur petrosals (as in fig. 6B), to Theriiformes (Multituberculata plus Prototribosphenida + the Khoobur petrosals), or to Mammalia.

PROTOTRIBOSPHENIDA

Prototribosphenida (Rougier, 1993), the grouping of *Vincelestes* and therians, is one of the most robustly supported clades in our analysis, with four unequivocal and five equivocal characters (appendix 3: node 2). All cladistic analyses of cranial morphology considering *Vincelestes* (e.g., Wible, 1991; Rowe, 1993; Rougier, 1993; Wible and Hop-

son, 1993) have arrived at the same phylogenetic conclusion.

RELATIONSHIPS OF THE KHOOBUR PETROSALS

In their description of a mammalian petrosal from Khoobur (PSS-MAE-104), Khoobur petrosal 1 of the current report, Wible et al. (1995) left the affinities of this specimen to Prototribosphenida and to triconodonts unresolved. Subsequently, a second petrosal was identified from the same locality (PSS-MAE-119), referred to here as Khoobur petrosal 2. In the current analysis, these two specimens are weakly linked in a monophyletic group (appendix 3: node 3), which in turn is the sister group of Prototribosphenida. Supporting affinities with prototribosphenidans are five unequivocal synapomorphies and one that is equivocal (appendix 3: node 4), all of which relate to the enclosure of the perilymphatic duct or to the development of the posterior wall of the tympanic cavity. If the Khoobur specimens and Prototribosphenida are monophyletic, then given the dental taxa known from Khoobur, these petrosals are likely those of symmetrodonts. However, among the 123 trees one step longer than the most parsimonious trees obtained here, varying monophyletic groupings of the Khoobur petrosals and triconodonts are identified. Given this, Wible et al.'s (1995) uncertainties regarding the affinities of the Khoobur petrosals to either Prototribosphenida or triconodonts cannot be considered fully resolved.

MULTITUBERCULATE RELATIONSHIPS

Multituberculate ear regions are probably the most distinctive of those pertaining to the extinct taxa considered here. Of the numerous multituberculate autapomorphies, the most striking are a lateral flange that is bent medially to contact the promontorium and an extensive epitympanic recess on the ventrolateral surface of the lateral flange. Theriiformes, the clade encompassing the last common ancestor of multituberculates and therians plus all its descendants (Rowe, 1988), is diagnosed by four unequivocal and four equivocal synapomorphies (appendix 3: node 8). As mentioned above, three of the six most parsimonious trees of our analysis ally multituberculates more closely with ther-

ians than are triconodonts. Supporting this relationship are one unequivocal (51: state 0) and three equivocal (18, 25, 48: state 1) synapomorphies. Recent phylogenetic proposals have revived Broom's (1914), Kielan-Jaworowska's (1971), and Kermack and Kielan-Jaworowska's (1971) hypotheses of multituberculate-monotreme affinities (Wible and Hopson, 1993; Meng and Wyss, 1995). Such relationships are not sustained by our most parsimonious trees (fig. 6), although a monophyletic Monotremata/Multituberculata appears in six of the 123 trees one step longer.

MONOTREMATA

Significant differences in the auditory and orbitotemporal regions of the platypus and echidnas have been reported previously (Eschweiler, 1899; Kuhn, 1971; Kuhn and Zeller, 1987; Zeller, 1989, 1991; Wible and Hopson, 1995). In fact, some of the differences represent potential synapomorphies relating either the platypus or the echidnas to other taxa. Examples include the enclosure of the perilymphatic duct in a canal in the echidnas, which also occurs in Prototribosphenida + the Khoobur petrosals, and the common aperture of the prootic canal and ramus superior, which is found in the platypus (fig. 5A) and multituberculates. In previous cladistic analyses (e.g., Rowe, 1988; Wible and Hopson, 1993; Wible, et al., 1995), these morphological discrepancies were addressed by reconstructing an ancestral state for Monotremata. This approach relied on a preconceived notion about the direction of evolutionary transformation in monotremes and yielded two sources of error: attribution of potentially false ancestral states to monotremes and failure to test the monophyly of Monotremata. In order to avoid these potential pitfalls, we have coded *Ornithorhynchus* and Tachyglossidae as separate OTU's in our matrix (appendix 2). In the most parsimonious trees of our analysis, a monophyletic Monotremata is recovered and supported by three unequivocal synapomorphies and one equivocal synapomorphy (appendix 3: node 9). However, in three of the 123 trees one step longer, a paraphyletic Monotremata is identified. The four ear region synapomorphies recovered here are among the few

known for monotremes that can be directly compared with those of more primitive outgroups and supplement those of the ear ossicles reported by Zeller (1993).

Recently recovered dental remains of extinct monotremes (Archer et al., 1985, 1992, 1993; Flannery et al., 1995) have been used to advance relationships for Monotremata to a variety of taxa, all of which exhibit a reversed triangles molar pattern. Archer et al. (1985) proposed relationships with tribosphenidans; Kielan-Jaworowska et al. (1987) with advanced peramurids; Bonaparte (1990) and Archer et al. (1992, 1993) with dryolestoids; and Hopson (1994) with symmetrodonts. However, some authors (e.g., Archer et al., 1992; Flannery et al., 1995) have raised concerns about the affinities of monotremes with trechnotherians, the clade including the last common ancestor of symmetrodonts and therians plus all descendants (McKenna, 1975). Flannery et al. (1995: 419) wrote that "the basic monotreme molar structure is not therian-like [holotherian], and that any other similarities between monotremes and therians [holotherians] may be convergent."

In Wible et al. (1995), as in the current report, triconodonts along with Multituberculata are placed between Prototribosphenida and Monotremata (fig. 6). Accepting holotherian affinities for monotremes under these phylogenetic hypotheses forces one to include multituberculates and/or triconodonts within Holotheria as well. Given our current understanding of mammaliamorph dental evolution, it seems unlikely that either of these two groups had a primitive triangular arrangement of the main molar cusps. Triconodonts retain the putative primitive mammaliaform molar pattern in which the main cusps are anteroposteriorly aligned (Kemp, 1983); this contrasts with the derived condition present in tribosphenidans and their early relatives. Dentally, multituberculates are the most distinctive of the Mesozoic mammals, with the earliest representatives already showing the characteristic anteroposteriorly aligned rows of cusps on the molars. The typical multituberculate molar pattern shares no common ground for comparison with that of therians, and, therefore, hypotheses of homology are lacking (Simmons,

1988). Additionally, as stated above, the anteroposteriorly aligned cusps represent the putative basal mammaliaform pattern (Kemp, 1983). Consequently, trechnotherian affinities of triconodonts and multituberculates cannot be sustained on dental grounds. As a corollary, the purported monotreme and trechnotherian molar synapomorphies are also compromised. In fact, Archer et al. (1992: 15) in their study of the dentition of the Miocene platypus *Obdurodon dicksoni* concluded that its "molar structure is markedly autapomorphic and does not closely resemble that of any other group of mammals."

MAMMALIA

Mammalia, the clade encompassing the last common ancestor of monotremes and therians plus all its descendants (Rowe, 1988), is diagnosed by four unequivocal and seven equivocal synapomorphies (appendix 3: node 10). Of the four unequivocal characters, three are related to the lateral flange: its shape and relationship to the crista parotica and the quadrate ramus of the alisphenoid. The remaining one is a fingerlike promontorium.

RELATIONSHIPS OF LATE TRIASSIC AND JURASSIC MAMMALIAMORPHS

The relationships of the six remaining ingroup taxa are resolved as follows in all six of the most parsimonious trees obtained here (fig. 6A):

The docodont *Haldanodon exspectatus* from the Late Jurassic of Portugal is identified as the sister taxon of Mammalia, supported by four unequivocal synapomorphies and one equivocal synapomorphy (appendix 3: node 11). Among the unequivocal characters are an anteriorly positioned pterygoparoccipital foramen and a paroccipital process extending ventral to the promontorium.

Megazostrodon from the Early Jurassic of southern Africa is the sister taxon of Mammalia + *Haldanodon*. Supporting this unnamed clade are one unequivocal and an equivocal synapomorphy (appendix 3: node 12). The former, a single trigeminal foramen posterior to the alisphenoid, occurs only in *Me-*

gazostrodon and *Haldanodon* among the ingroup taxa.

The Liassic forms *Morganucodon* and *Dinnetherium* are identified as sister taxa, supported by one unequivocal and two equivocal synapomorphies (appendix 2: node 13). Following Luo (1994), we employ the term Morganucodontidae for this clade. In turn, Morganucodontidae is the sister group of Mammalia + *Haldanodon* + *Megazostrodon*. This clade, Mammaliaformes of Rowe (1988), is supported by two unequivocal (elongate, straight cochlear duct and quadrate articulation on the petrosal) and two equivocal synapomorphies (appendix 2: node 14).

The Liassic form *Sinoconodon* is the sister taxon of Mammaliaformes, based on one unequivocal (para/basisphenoid wing absent) and four equivocal synapomorphies (appendix 2: node 15).

Finally, *Adelobasileus* from the Carnian of west Texas is the sister taxon of Mammaliaformes + *Sinoconodon*. Supporting this arrangement are six unequivocal and three equivocal synapomorphies (appendix 2: node 16), with the former including a single hypoglossal foramen, a promontorium, and a cavum epinterium partially floored by the petrosal.

Only two other cladistic analyses have considered all six of the above mammaliamorph taxa: Luo (1994) and Wible et al. (1995). Of these two, the results of the current report most closely resemble those of Wible et al. (1995), which also identified *Sinoconodon* and *Adelobasileus* as the successive outgroups to Mammaliaformes and included *Dinnetherium, Megazostrodon,* and *Haldanodon* within Mammaliaformes. However, Wible et al. (1995) differed in their support of a clade of *Megazostrodon* and *Haldanodon,* which in turn was at a trichotomy with *Dinnetherium* and Mammalia. To obtain this arrangement in MacClade, four steps must be added to the most parsimonious trees in the current report. The differences between Wible et al. (1995) and the current report result from the inclusion here of more ingroup taxa (18 versus 15) and characters (51 versus 44). Scoring four separate OTU's for triconodonts in the current matrix has slightly increased the amount of missing data; the average com-

pleteness in Wible et al.'s matrix is 94.2% versus 86.7% here.

The current results differ more dramatically from those of Luo (1994), who found little resolution among the Jurassic taxa and, in fact, had Triconodontidae nested within them. Using MacClade to obtain the arrangement of Jurassic taxa congruent with that in Luo's preferred phylogenetic tree requires that 10 steps be added to our most parsimonious trees.

As shown above, our analysis does not strongly justify the interrelationships of the five pre-*Haldanodon* ingroup taxa, with only one or two unequivocal synapomorphies identified at each node. With the exception of *Morganucodon,* these taxa exhibit some missing data for the basicranial characters considered here (with the high in *Dinnetherium* and *Megazostrodon,* which are scored for only two-thirds of the characters). In contrast to the labile relationships of the basal taxa, the position of *Haldanodon* as the outgroup to Mammalia is more firmly founded in our analysis. This is congruent with the results of Wible et al. (1995) and accords with the general view that docodonts are mammaliaforms, related to morganucodontids or more derived (Crompton and Jenkins, 1979; Crompton and Sun, 1985; McKenna, 1987). A dramatically different hypothesis was offered by Lillegraven and Krusat (1991) who placed *Haldanodon* as the outgroup to *Sinoconodon* and *Morganucodon.* Their hypothesis, however, has the merit of being founded in a data set based on the anatomy of the whole skull and the drawback of too few taxa considered. Using MacClade to obtain Lillegraven and Krusat's arrangement of taxa requires that eight steps be added to the most parsimonious trees obtained here.

With regard to the outgroups employed here, there is current debate as to whether tritheledontids or tritylodontids are more closely related to mammaliaforms (see Rowe, 1993; Crompton and Luo, 1993; Hopson, 1994; Luo, 1994). This controversy was not addressed in our analysis, which in fact would require the inclusion of more non-mammaliamorph cynodonts.

IMPLICATIONS OF THE PAUP ANALYSIS FOR TAXA KNOWN ONLY FROM TEETH AND JAWS

Despite the recent dramatic increase in knowledge of the basicranium of early mammals and their relatives, the overwhelming majority of Mesozoic mammaliaform taxa are known exclusively from teeth and fragmentary jaws. This is particularly true for trechnotherians, because the only petrosals associated with dentitions for a trechnotherian prior to the Late Cretaceous are those of Early Cretaceous *Vincelestes*. Thus, our analysis has had to omit such traditionally important trechnotherians as symmetrodonts, dryolestoids, *Peramus*, and *Amphitherium*. Another influential taxon omitted is *Kuehneotherium praecursoris* from the Liassic of Wales (Kermack et al., 1968). *Kuehneotherium* has its main molar cusps forming a triangle, which has been interpreted as a derived feature supportive of affinities with trechnotherians (Kermack et al., 1968; Crompton, 1971; Prothero, 1981). In addition, the lower jaws attributed to *Kuehneotherium* retain a deep mandibular sulcus and medial dentary ridge which, when compared with contemporary taxa such as *Morganucodon*, indicate that the postdentary bones retained the primitive attachment to the dentary (Kermack et al., 1968; Cassiliano and Clemens, 1979). This implies that, like *Morganucodon*, *Kuehneotherium* lacked the definitive triossicular middle-ear system (Allin and Hopson, 1992).

Integrating *Kuehneotherium* into recently published cladograms of mammaliaform relationships (Rowe, 1988, 1993; Wible, 1991; Wible and Hopson, 1993; Wible et al., 1995), including the ones advanced here, is problematic because of the conflicting distribution of characters of the molars and the lower jaw (and, by inference, the middle ear). Accepting the topology of our most parsimonious trees, if *Kuehneotherium* is more closely related to therians than are multituberculates, triconodonts, and monotremes, as suggested by the putative molar synapomorphies, then the detachment of the postdentary bones from the lower jaw as strictly auditory structures would have occurred independently in multituberculates, triconodonts, monotremes, and therians. On the other hand, the striking resemblances in middle-ear morphology characterizing monotremes, multituberculates, and therians (Gaupp, 1913; Miao and Lillegraven, 1986; Meng and Wyss, 1995) have been considered to strongly support a single origin of the definitive triossicular middle ear (Patterson, 1981; Kemp, 1983; Novacek, 1993; Rowe, 1995). The tree topology recovered here is fully congruent with the latter alternative, a single origin of ear ossicles suspended from the skull base, which would be diagnostic of Mammalia. This suggests that the triangular arrangement of molar cusps in *Kuehneotherium* is convergent on that in therians or that it is secondarily lost in multituberculates and triconodonts, and is no longer recognizable in monotremes. The latter alternative seems unlikely for multituberculates and triconodonts and is, at present, equivocal for monotremes.

Kuehneotherium is not the only Late Triassic-Jurassic taxon known exclusively from teeth and jaws to present such problems. *Shuotherium* from the late Middle or early Late Jurassic of China has molars resembling those of *Kuehneotherium* (Hopson, 1995) and shows evidence for the retention of postdentary bones (Chow and Rich, 1982). Consequently, the previous comments regarding the conflicting characters of dental and lower jaw morphology made for *Kuehneotherium* also apply for *Shuotherium*. *Woutersia* from the Rhaetic of France is known only from isolated teeth, and, though originally included in Kuehneotheriidae (Sigogneau-Russell, 1983), has recently been assigned to a family of its own, Woutersiidae, within Holotheria (Sigogneau-Russell and Hahn, 1995). The latter authors have also observed that *Woutersia* shares some derived features of the upper molars with docodonts. Although docodont affinities for *Woutersia* were ultimately excluded by Sigogneau-Russell and Hahn (1995), the observed similarities between these taxa emphasize that alternative interpretations for the tooth morphology of kuehneotheriids are feasible.

In contrast to the abovementioned hypothesis on the single origin of the definitive triossicular middle ear, Allin and Hopson (1992) proposed a polyphyletic origin of these elements. They accepted the dental evidence that allies *Kuehneotherium* to therians

and proposed the independent separation of the articular and angular (malleus and ectotympanic) from the lower jaw in at least two and as many as four clades of mammals. Part of their argument was based on their interpretation of depressions on the inner surface of the dentary of the trechnotherians *Amphitherium,* and *Peramus* as surfaces for partial attachment of the postdentary bones to the lower jaw.

Resolution of these conflicting character sets awaits the discovery of more material and more comprehensive cladistic analyses that incorporate cranial, dental, and postcranial information from a wider array of taxa. In the meantime, however, even though only a limited number of Mesozoic taxa are known from petrosals and the relationships of some mammaliaform groups are not yet fully resolved, it is promising to note that there is some general agreement among trees produced by characters of the (1) basicranium (Wible and Hopson, 1993; Wible et al., 1995; this study), (2) cranium (Wible, 1991), and (3) cranium plus postcranium (Rowe, 1988, 1993; Rougier, 1993).

CONCLUSIONS

Our phylogenetic analysis of basicranial characters allies the triconodontids *Priacodon fruitaensis* from the Late Jurassic of Colorado with *Trioracodon ferox* and *Triconodon mordax* from the Late Jurassic of England. The nearest outgroup to these three taxa is the unnamed triconodonts from the Early Cretaceous of Montana. Whether or not the unnamed triconodonts belong in Triconodontidae is dependent on their relationships to taxa not yet known from basicrania: the two remaining triconodontid genera, *Alticonodon* and *Astroconodon,* as well as the three remaining triconodont families, Amphilestidae, Austrotriconodontidae, and Gobiconodontidae. The three triconodontids + the Cloverly triconodonts are identified as mammals, but their relationships within Mammalia are not fully resolved. In three of the six most parsimonious trees, they are more closely related to therians than are multituberculates; the reverse is true in the remaining three trees. However, the relationships of the three triconodontids + the Clov-

erly triconodonts are highly labile here. In the 123 trees one step longer than the six most parsimonious ones, these taxa are either in a paraphyletic grouping with the Khoobur petrosals or they are the sister group to Prototribosphenida + the Khoobur petrosals, to Theriiformes, or to Mammalia. Nevertheless, Triconodonta in the traditional sense (morganucodontids + triconodonts) is not supported here, or in any other recent cladistic analyses considering the pertinent taxa.

We have recently published two other phylogenetic analyses of the basicranium across mammaliamorphs that consider fewer ingroup taxa and characters (Wible and Hopson, 1993; Wible et al., 1995). The phylogenetic results of the current report most closely resemble those of Wible et al. (1995). The main difference is that here all taxa are fully resolved, except the triconodonts and multituberculates, whereas the strict consensus tree in Wible et al. (1995) had three unresolved trichotomies between Mammaliaformes and Prototribosphenida. However, the relationships of these mammaliaform taxa are not well resolved in the current report, as evidenced by the number of nodes supported by only one or two unequivocal synapomorphies. Moreover, adding one step to the most parsimonious trees identified here produces the overall topology of the most parsimonious trees of Wible et al. (1995). Adding data that are currently missing from our analysis might increase tree stability, although the present taxon-character matrix is about 87% complete. Alternatively, resolution awaits the addition of information from other anatomical systems into phylogenetic analyses. The tree topologies resulting from this study are fully congruent with the single origin of the definitive triossicular middle ear, but opposing hypotheses cannot be eliminated until some critical taxa, insufficiently known, such as *Kuehneotherium* and *Shuotherium,* are represented by more complete material.

ACKNOWLEDGMENTS

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APPENDIX 1

BASICRANIAL CHARACTERS

1. Petrosal promontorium—absent (0) or present (1).
2. Para/basisphenoid wing—present (0) or absent (1).
3. Cochlear housing shape—indistinct (0), triangular in outline, wider posteriorly with steep lateral wall (1), triangular in outline, wider posteriorly without steep lateral wall (2), or finger-like in outline (3).
4. Ventral crest on cochlear housing—absent (0) or present (1).
5. Small foramen on cochlear housing anteromedial to fenestra vestibuli—absent (0) or present (1).
6. Cochlear duct—short (0), elongate and straight (1), bent (2), or coiled, 360° or more (3).
7. Secondary spiral lamina—absent (0) or present (1).
8. Semicircular canals enclosed by petrosal only—absent (0) or present (1).
9. Fenestra vestibuli shape—rounded, stapedial ratio less than 1.2 (0) or ellipsoidal, stapedial ratio greater than 1.4 (1).
10. Fenestra vestibuli margin—with thickened osseous ring (0) or without osseous ring (1).
11. Channel for perilymphatic duct—no indication (0), open sulcus (1), partially enclosed by bony lappets (2), or fully enclosed to form a canal, a cochlear aqueduct (3).
12. Lateral opening of cochlear aqueduct—absent (0), medial (external) to perilymphatic foramen (1), or within inner ear (2).
13. Jugular fossa including jugular foramen and perilymphatic foramen/fenestra cochleae—present (0) or absent (1).
14. Jugular foramen size relative to perilymphatic foramen/fenestra cochleae—equal to or larger (0) or smaller (1).
15. Crista interfenestralis—tall and horizontal, extending to base of paroccipital process (0), vertical, delimiting back of promontorium (1), or not distinguishable from surrounding elements (2).
16. Fossa for stapedius muscle—absent (0), on crista interfenestralis (1), or lateral to crista interfenestralis (2).
17. Paroccipital process—not extending ventral to level of cochlear housing (0) or extending ventral to level of cochlear housing (1).
18. Caudal tympanic process of petrosal—absent (0) or present (1).
19. Post-promontorial tympanic recess—absent (0) or present (1).
20. Deep pocket medial to paroccipital process—absent (0) or present (1).
21. Tympanohyal—separate (0), attached to petrosal, posteromedially directed (1), or attached to petrosal, medially directed (2).
22. Tympanohyal/promontorial contact—absent (0) or present (1).
23. Crista parotica/squamosal contact—present (0) or absent (1).
24. Fossa incudis or quadrate articulation on petrosal—absent (0) or present (1).
25. Epitympanic recess on petrosal—absent (0) or present (1).
26. Cranial aperture of prootic canal—absent (0), in rear of cavum epitericum (1), between the cavum and anterodorsal margin of subarcuate fossa (2), or at anterodorsal margin of subarcuate fossa (3).
27. Tympanic aperture of prootic canal—absent (0), separate from (1), or confluent with pterygoparoccipital foramen (2).
28. Pterygoparoccipital foramen—at same level or posterior to fenestra vestibuli (0), anterior to it (1), or absent (2).
29. Lateral flange—laterally directed shelf (0), with vertical and horizontal components in lateral view (1), ventrally directed crest (2), contacting cochlear housing (3), or absent (4).
30. Lateral flange/crista parotica relationship—narrowly separated (0), widely separated (1), continuous (2), or lateral flange greatly reduced (3).
31. Vascular foramen in lateral flange—absent (0) or present (1).
32. Post-trigeminal canal—absent (0) or present (1).
33. Facial ganglion floor—open ventrally (0), broad petrosal bridge, flooring part of hyomandibular and palatine rami (1), or narrow petrosal bridge, flooring only primary facial foramen (2).
34. Lateral trough of petrosal—absent (0) or present (1).
35. Cavum epitericum floor—open ventrally (0), partially floored by petrosal (1), floored, primarily by petrosal (2), or floored, primarily by alisphenoid (3).
36. Tensor tympani fossa—indistinct (0), deep recess on lateral trough anterior to hiatus Fallopii (1), or deep recess on lateral trough posterior to secondary facial foramen (2).
37. Petrosal contact with quadrate ramus of alisphenoid (epipterygoid)—elongate (0) or small or absent (1).

38. Internal acoustic meatus—without distinct medial rim (0) or with medial rim (1).

39. Pila antotica—ossified base present (0) or absent (1).

40. Wall separating cavum supracochleare from cavum epiptericum—absent (0), present with small fenestra (fenestra semilunaris) (1), or complete (2).

41. Sulcus for sigmoid sinus extending to jugular foramen—absent (0) or present (1).

42. Sulcus for inferior petrosal sinus—enclosed in petrosal, laterally directed at rostral end (0), between petrosal and basioccipital, anteroposteriorly directed (1), or endocranial (2).

43. Craniomandibular joint position relative to fenestra vestibuli—level with (0) or anterior to (1).

44. Thick, laterally directed surface of petrosal related to glenoid fossa—absent (0) or present (1).

45. Anterior lamina—separated externally from orbitosphenoid by alisphenoid (0), contacts orbitosphenoid (1), or absent (2).

46. Small vascular foramen in anterior lamina—absent (0) or present (1).

47. Number of trigeminal nerve exits posterior to alisphenoid—single (0), multiple (1), or none (2).

48. Ventral ascending groove or canal—open laterally (0), intramural, within petrosal (1), in-tramural, between petrosal and squamosal (2), endocranial (3), or absent (4).

49. Orientation of ventral ascending groove or canal—vertical (0), horizontal (1), or without groove or canal (2).

50. Dorsal ascending groove or canal—open laterally dorsal to posttemporal canal (0), intramural, covered laterally by parietal and/or squamosal (1), or endocranial (2).

51. Hypoglossal foramina—double or multiple (0), single (1), or confluent with jugular foramen (2).

Most of the above characters are taken directly or are modified from the following references, to which the reader is referred for additional information. Characters used for the first time are 5, 12, 13, 14, 15, 20, 25, 30, 32, 41, and 46.

Characters:

1, 2, 4, 10, 51—Lucas and Luo (1993)
3, 7, 23, 24, 28, 42, 44—Wible et al. (1995)
6, 21, 22, 39, 43—Rowe (1988)
8, 34, 47—Lillegraven and Krusat (1991)
9, 18, 19—Wible (1990)
11—Kermack et al. (1981)
16, 17, 27, 35, 36, 38, 40, 45, 48, 49, 50—Wible and Hopson (1993)
29—Luo (1994)
31, 37—Wible (1991)
26, 33—Crompton and Sun (1985)

APPENDIX 2

Taxon-Character Matrix

Taxon	Character*										%compl.
	5	10	15	20	25	30	35	40	45	50	
Tritheledontidae	000N0	0?000	00000	00000	00000	00000	00000	00000	0?000	00000	0	96.1
Tritylodontidae	000N0	0?000	00000	10000	10110	00010	10A00	00102	0?000	01001	0	96.1
Adelobasileus	10100	A??01	00000	00000	00?00	?1010	10011	0??0?	??000	01001	1	80.4
Sinoconodon	11110	00101	A0000	10000	00000	11010	10?11	00100	??000	01000	1	92.2
Morganucodon	1110A	10101	10000	10000	00110	31010	10111	10000	10000	11001	1	100
Dinnetherium	11100	1?111	??000	1?000	00110	D1010	10C11	10???	???0A	?A00?	0	68.6
Megazostrodon	11110	1?101	A00?0	10000	?0???	D1010	1?C11	?0?0?	??000	0000?	1	68.6
Haldanodon	11110	1?101	10110	11000	10110	21110	?0C12	00010	10000	1000C	1	92.2
Multituberculata	11300	10111	C0A00	21A00	10011	32132	11212	21100	10001	01111	0	100
Clov. triconodonts	11300	1?111	??100	21000	10010	E1121	?0212	1???2	??10A	?AB1?	1	70.6
Priacodon	1130A	1?111	20110	21001	C011?	21121	0?012	1?0?2	00?0A	1A211	1	84.3
Trioracodon	11301	1?111	C0110	21001	10011	11121	00212	110?2	00?0A	1A211	?	86.3
Triconodon	11301	1?1?1	??110	?1???	?0???	21???	???1?	?????	???0?	?????	?	33.3
Khoobur petrosal 1	11300	10111	32101	21111	20000	21120	00212	111?1	0011?	??211	?	90.2
Khoobur petrosal 2	11300	10111	31101	21?1?	?00??	21120	0?212	1?1?1	00?0A	0A211	?	76.5
Vincelestes	11200	21111	32101	21110	20111	31122	A0112	01111	?0110	01111	0	98.0
Tachyglossidae	010N0	20101	31102	00000	11110	31143	01112	01102	02101	00201	2	100
Ornithorhynchus	11300	20101	10100	01000	21110	32122	00112	01100	02001	00000	2	100
Marsupialia	11200	31111	32101	21110	20A11	31243	00C03	01112	01102	02422	0	100
Placentalia	11200	31111	32101	21110	20A11	00143	00103	01112	0C102	02302	A	100

*? = missing data; N = not applicable; 0–4 = character states (see appendix 1); A = 0 & 1; B = 0 & 2; C = 1 & 2; D = 2 & 3; E = 1 & 2 & 3; %compl. = % of scoreable characters.

APPENDIX 3

Diagnoses of Nodes

The tree diagnosed here is the strict consensus tree of the three equally most parsimonious trees obtained using the PAUP reweighting procedure (rescaled consistency index) on the matrix in appendix 2 (fig. 6B). Nodes are diagnosed by listing the derived condition for characters in appendix 1. Multistate characters or reversals are depicted within parentheses following the character number. Asterisks (*) denote equivocal characters. Characters are optimized under an accelerated transformation (ACCTRAN) assumption.

Node 1. Theria

29(4), 30(3)—lateral flange absent
34(0)—lateral trough absent
35(3)—cavum epiptericum floored primarily by alisphenoid
42(1)—sulcus for inferior petrosal sinus between petrosal and basioccipital, anteroposteriorly directed
47(2)—no foramina for trigeminal nerve posterior to alisphenoid
50(2)—dorsal ascending groove endocranial

6(3)*—cochlear duct coiled
40(2)*—complete wall separating cavum supracochleare from cavum epiptericum
45(2)*—anterior lamina absent
48(3)*—ventral ascending groove endocranial
49(0)*—ventral ascending groove vertical

Node 2. Prototribosphenida

3(2)—cochlear housing triangular, wider posteriorly without steep lateral wall
7—secondary spiral lamina
25—epitympanic recess on petrosal
33(1)—broad petrosal bridge flooring facial nerve branches
6(2)*—cochlear duct bent
23*—crista parotica/squamosal contact absent
26(3)*—cranial aperture of prootic canal at anterodorsal margin of subarcuate fossa
36(0)*—tensor tympani fossa indistinct
48(1)*—ventral ascending canal intramural within petrosal

Node 3.

30(0)—lateral flange narrowly separated from crista parotica

20*—deep pocket medial to paroccipital process
24(0)*—fossa incudis on petrosal absent

Node 4.

12(2)—lateral opening of cochlear aqueduct within inner ear
15(1)—crista interfenestralis vertical, delimiting back of promontorium
18—caudal tympanic process of petrosal
19—post-promontorial tympanic recess
21(2)—medially directed tympanohyal attached to petrosal
11(3)*—cochlear aqueduct

Node 5. Triconodontidae

5—small foramen on cochlear housing anteromedial to fenestra vestibuli
14—jugular foramen smaller than perilymphatic foramen/fenestra cochleae
20—deep pocket medial to paroccipital process
23*—crista parotica/squamosal contact absent

Node 6. triconodonts

30(1)—lateral flange widely separated from crista parotica
38(0)*—internal acoustic meatus without distinct medial rim
40(2)*—complete wall separating cavum supracochleare from cavum epiptericum
46*—small vascular foramen in anterior lamina
51(1)*—single hypoglossal foramen

Node 7. Theriimorpha

43—craniomandibular joint anterior to fenestra vestibuli
26(2)*—cranial aperture of prootic canal between cavum epiptericum and anterodorsal margin of subarcuate fossa
39*—pila antotica absent
40(1)*—fenestra semilunaris
45(0)*—anterior lamina separated from orbitosphenoid by alisphenoid

Node 8. Theriiformes

9—fenestra vestibuli ellipsoidal
33(2)—narrow petrosal bridge flooring primary facial foramen
47(1)—multiple foramina for trigeminal nerve posterior to alisphenoid
49(1)—ventral ascending canal horizontal
11(2)*—channel for perilymphatic duct partially enclosed
16(2)*—stapedius fossa lateral to crista interfenestralis
23(0)*—crista parotica/squamosal contact absent

36(1)*—deeply recessed tensor tympani fossa on lateral trough anterior to hiatus Fallopii

Node 9. Monotremata

6(2)—cochlear duct bent
22—tympanohyal contacts promontorium
42(2)—sulcus for inferior petrosal sinus endocranial
51(2)*—hypoglossal and jugular foramina confluent

Node 10. Mammalia

3(3)—cochlear housing shape fingerlike in outline
29(2)—lateral flange ventrally directed
30(2)—lateral flange continuous with crista parotica
37—quadrate ramus of alisphenoid small or absent
4(0)*—ventral crest on cochlear housing absent
16(0)*—stapedius fossa absent
38*—internal acoustic meatus with distinct medial rim
41(0)*—sulcus for sigmoid sinus extending to jugular foramen absent
45(1)*—anterior lamina contacting orbitosphenoid
48(2)*—ventral ascending groove endocranial
51(0)*—double or multiple hypoglossal foramina

Node 11.

13—jugular fossa absent
17—paroccipital process extending ventral to cochlear housing
28(1)—pterygoparoccipital foramen anterior to fenestra vestibuli
35(2)—cavum epiptericum floored primarily by petrosal
31(0)*—vascular foramen in lateral flange absent

Node 12.

47(0)—single trigeminal foramen posterior to alisphenoid
21(1*)—posteromedially directed tympanohyal attached to petrosal

Node 13. Morganucodontidae

36(1)—deeply recessed tensor tympani fossa on lateral trough anterior to hiatus Fallopii
4(0)*—ventral crest on cochlear housing absent
46*—small vascular foramen in anterior lamina connecting to cavum epiptericum

Node 14. Mammaliaformes

6(1)—cochlear duct elongated and straight
24—quadrate articulation on petrosal

23*—crista parotica/squamosal contact absent

26(3)*—cranial aperture of prootic canal at anterodorsal margin of subarcuate fossa

Node 15.

2—para/basisphenoid wing absent

4*—ventral crest on cochlear housing absent

11(1)*—open sulcus for perilymphatic duct

16(1)*—stapedius fossa on crista interfenestralis

33(1)*—broad petrosal bridge flooring facial nerve branches

Node 16.

1—promontorium

3(1)—cochlear housing triangular in outline, wider posteriorly with steep lateral wall

10—fenestra vestibuli margin without thickened osseous ring

27(1)—tympanic aperture of prootic canal separate from pterygoparoccipital foramen

34—lateral trough on petrosal

35(1)—cavum epptericum partially floored by petrosal

51(1)—single hypoglossal foramen

8*—semicircular canals enclosed by petrosal only

26(1)*—cranial aperture of prootic canal in rear of cavum epptericum

41*—sulcus for sigmoid sinus extending to jugular foramen