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Basicranial Morphology of Early Tertiary Erinaceomorphs and the Origin of Primates

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CONTENTS

Abstract	2
Introduction	2
Acknowledgments	4
Abbreviations	5
Materials and Methods	6
Basicranial Morphology of Early Tertiary Erinaceomorphs	7
Amphilemuridae	7
<i>Pholidocercus hassiacus</i> HLMD Me 7577	7
Ectotympanic	7
Other Features	8
<i>Pholidocercus hassiacus</i> SMF 81/619	9
Petrosal	13
Basisphenoid and Basioccipital	15
Alisphenoid and Squamosal	15
Tympanic Roof	16
Pneumatization	16
Blood Vessels	17
Dormaliidae	18
<i>Macrocranium tupaiodon</i> Feist Collection	18
<i>Macrocranium nitens</i> AMNH 48697	20
Erinaceomorpha incertae sedis	21
<i>Diacodon alticuspis</i> AMNH 48587	21

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Basicranial Characters and the Erinaceomorph Basicranial Morphotype	23
Primate Basicranial Morphotype	36
A Test of Hypotheses of Primate-Erinaceomorph Relationships	38
References	40

ABSTRACT

In this paper, we provide original descriptions of the earliest known erinaceomorph taxa represented by basicranial remains — *Pholidocercus*, *Macrocranium*, and *Diacodon*. We then assess their affinities with euprimates and certain other primitive eutherian groups via a detailed character analysis. Unlike the Neogene brachyricines emphasized in other analyses, Early Tertiary erinaceomorphs exhibit notably primitive auditory regions. They differ from both later hedgehogs and primates in a number of important ways, including absence of significant tympanic processes developed from the basisphenoid and the petrosal. A number of similarities to microsyopids exist, but these seem to be exclusively primitive resem-

blances carried over from their mutual joint ancestor. Given existing doubts about the proper taxonomic position of Microsyopidae, erinaceomorph-microsyopid resemblances—whatever their significance—are of little help in sorting out the nature of primate-hedgehog relationships. The basicranial morphology of Early Tertiary hedgehogs does not corroborate a hypothesis of close primate-erinaceomorph relatedness. No synapomorphies can be quoted in support of the contention that primates originated from an adapisoricid insectivoran, with a basicranium not very different from that of the erinaceotan morphotype. Accordingly, we shall have to look elsewhere for the sister-group of primates.

INTRODUCTION

Erinaceomorpha is an insectivore suborder which contains the familiar hedgehogs of the Old World (Erinaceidae) and a variety of Early Cenozoic groups, including Dormaalidae,⁴ Amphilemuridae, and others (for a recent treatment of erinaceomorph systematics, see Novacek et al., 1985). Erinaceomorphs are frequently regarded as either ancestral to or closely allied with several major clades of eutherian mammals. One suggestion, repeatedly raised by paleontologists (e.g., Simpson, 1945; McKenna, 1966; Szalay, 1968; Clemens, 1974) but rarely considered by neontologists, is that primates originated from erinaceomorphs, either directly or from a near ancestor. Most discussions of erinaceomorph-primate relationships are more or less exclusively devoted to the analysis of dental

traits, for the very good reason that the majority of fossil taxa having some relevance to this issue are known only from their dentitions. In this paper we shall be concerned with the information content of another morphological domain, the basicranium.

In 1975, F. S. Szalay published a seminal paper on the significance of the basicranium for understanding primate phylogeny. Although principally concerned with how best to portray the internal arrangement of the Order Primates, Szalay (1975) also attempted to identify derived features of the basicranium shared by primates and hedgehogs. Several candidate synapomorphies were specified: large petrosal contribution to the tympanic floor, rounded promontorium, bone-enclosed divisions of the internal carotid system, absence of a “medial internal carotid,” and “shielding” of the aperture of the fossula fenestrae cochleae. His conclusion (Szalay, 1975: 100) was that these similarities were extensive enough to make it “a likely possibility” that primates originated “from a eutherian I would dub, *faute de mieux*, an

⁴ *Adapisorex*, the nominotypical taxon of Adapisoricidae (Schlosser, 1887) has been removed to Erinaceidae by Novacek et al. (1985). They proposed, and in this paper we shall use, Dormaalidae as the family-group name for remaining “adapisoricids” of some older classifications.

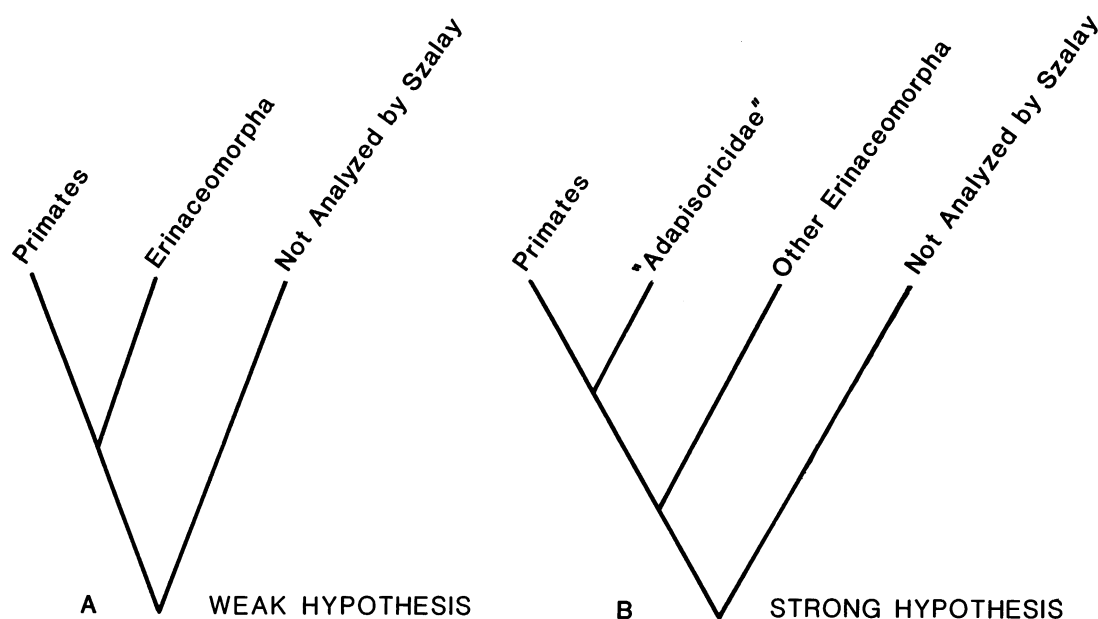


Fig. 1. Cladograms illustrating hypotheses to be tested. Szalay (1975) did not present his views regarding the extraordinal relationships of primates in a cladistic format, and the sister-group of Primates + Erinaceomorpha (hypothesis A) is not identified. He mentioned (ibid.: 100) that Primates may have evolved from "a genus phenetically not far removed from *Leptacodon*." However, this would appear to amount to a restatement of his strong hypothesis, because *Leptacodon* was referred to "Adapisoricidae" by Van Valen (1967), Szalay's cited authority for erinaceomorph classification. The sister-group of Primates + "adapisoricids" (hypothesis B) is likewise not mentioned by Szalay, but since he concludes that "adapisoricids" are also ancestral to Erinaceidae, it is reasonable to infer that the appropriate sister taxon is "Other Erinaceomorpha." As explained in the text, "Adapisoricidae" is not definable except as a wastebasket for certain Early Cenozoic erinaceomorphs. The dormaaliid *Macrocranion* is the only ex-"adapisoricid" whose basicranium is known. However, in order to air all of the possibilities, we also consider *Diacodon* and the amphiemurid *Pholidocercus* in our analyses.

adapisoricid insectivoran, with a basicranium not very different from that of the erinaceotan morphotype." (See also Szalay and Delson, 1979: 27.)

It should be noted that Szalay (1975) also viewed "adapisoricids" as ancestral to erinaceids. Most current workers (e.g., Russell et al., 1975; Novacek et al., 1985) do not regard "adapisoricids" as the basal group that Szalay (1975) believed they were, and the concept of this family is now quite different from what it was only a decade ago. In order to preserve the formal intent of Szalay's argument in light of new views on erinaceomorph evolution, we feel that it is appropriate to recast his language so that it embraces two phylogenetic hypotheses (hereafter, the "weak" and "strong" hypotheses) of primate-erinaceomorph relationship.

Simply stated, the weak hypothesis predicts that Primates and Erinaceomorpha are sister-groups (fig. 1A). Demonstration of this hypothesis has no necessary implication for erinaceomorph monophyly: Primates and Erinaceomorpha could be treated as sister taxa without disturbing the internal arrangements of either group as usually construed. The strong hypothesis (fig. 1B) is derived from Szalay's original formulation, namely that primates arose from some Early Cenozoic taxon of erinaceomorphs, possibly but not necessarily Dormaaliidae *sensu stricto*. This argument necessarily implies that the existing concept of Erinaceomorpha is not monophyletic. To recover monophyly, either Primates would have to be inserted into a more inclusive Erinaceomorpha, or vice versa, depending on detailed resolution of the actual cla-

dogeny and one's preference for the appropriate name for the resulting higher taxon.

At the time Szalay (1975) undertook his review, no nonerinaceid erinaceomorph basicranial fossils had been described (but see Gawne, 1968; T. Rich and P. Rich, 1971; and T. Rich, 1981 for excellent descriptions of the basicranial morphology of early Neogene erinaceids). A short time later, however, Maier (1979) published a detailed paper on the morphology and adaptations of the dormaalid *Macrocranium tupaiodon* from Grube Messel. Maier (ibid.) maintained that this species possessed a short, tubular external acoustic meatus formed by the ectotympanic, and a swollen auditory bulla of indefinite composition. Although Maier did not pursue the systematic implications of his findings, he noted that these particular features were rare or absent in other Early Cenozoic eutherians—save for plesiadapoids and euprimates.

More recently, Novacek et al. (1983) briefly described and analyzed the basicranial anatomy of *Diacodon alticuspis*, an early Eocene (Wasatchian) erinaceomorph from New Mexico of uncertain placement as to family. They pointed out that, because *Diacodon* possessed neither a complete petrosal bulla nor any other identifiable apomorphy of plesiadapoids and euprimates, Primates could not have originated from within Erinaceomorpha. Such a pattern would be allowed only if the latter taxon was not monophyletic, which they regarded as improbable. They did not, however, attempt to evaluate the significance of Maier's preliminary observations on *Macrocranium*, thus leaving Szalay's strong hypothesis unimpeached.

We report here on a third Early Tertiary erinaceomorph represented by basicranial remains, the amphilemurid *Pholidocercus hassiacus* (Koenigswald and Storch, 1983), also from Grube Messel. Like dormaalids, amphilemurids have figured prominently in discussions of primate origins: *Amphilemur* (Heller, 1935), *Gesneropithecus* (Hürzeler, 1946), and *Alsaticopithecus* (Hürzler, 1947), as their nomina insinuate, were all taken to be in or near Primates by their discoverers (see also Simons, 1962; Russell et al., 1967). Current consensus, however, holds that none

of these claims can be substantiated on dental grounds (Szalay, 1971), and Amphilemuridae is nowadays usually relegated to Erinaceomorpha.

The basicranial remains of *Pholidocercus* described here are much more complete than any yet known for *Macrocranium* and *Diacodon*, and are therefore of special significance for testing the strong and weak versions of Szalay's argument. Because of certain inaccuracies in Maier's (1979) description of the auditory region of *Macrocranium tupaiodon*, we also provide corrective notes on this species. Finally, we briefly describe the petrosal anatomy of *Macrocranium nitens*, a North American congener of *M. tupaiodon*. As far as we know, these four taxa (table 1) are the only early Paleogene erinaceomorphs for which reliably referred basicranial material exists.

Since we will repeatedly refer to "Szalay's hypotheses" in this paper, it is only fair to note that this author now favors a different concept of the extraordinary relationships of primates (a version of the so-called "archontan hypothesis;" see Szalay, 1977; Novacek, 1986). Although erinaceomorphs are not mentioned in any of Szalay's recent statements on archontan relationships, he is the only author who has made any effort to proffer basicranial evidence for an idea that has been supported by several other distinguished paleontologists. This evidence deserves a hearing, independent of its association with the name of any individual researcher.

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TABLE 1
List of Specimens Described

Taxa	Described specimens	Age and locality
<i>Diacodon alticuspis</i>	AMNH 48587 ^a	Lower Eocene, San Jose Formation, Quarry 58, Regina, New Mexico
<i>Macrocranium nitens</i>	AMNH 48697	Lower Eocene, San Jose Formation, Quarry 88, Arroyo Blanco, New Mexico
<i>Macrocranium tupaiodon</i>	Feist 1, Feist 2	Middle Eocene "oil shales" of Grube Messel, Hessen, Fed. Rep. Germany
<i>Pholidocercus hassiacus</i>	HLMD Me 7577, SMF 81/619a, b	Middle Eocene "oil shales" of Grube Messel, Hessen, Fed. Rep. Germany

^a Not AMNH 48597 as reported by Novacek et al. (1983).

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ABBREVIATIONS

Institutional

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History
HLMD	Hessisches Landesmuseum, Darmstadt, FRG
PU	Princeton University
SMF	Senckenberg Museum, Frankfurt/Main, FRG

Anatomical

ac	auricular cartilage
acf	anterior carotid foramen
ap	tympanic process of alisphenoid (often confluent with bp)
bs	basisphenoid
bo	basioccipital
bp	tympanic process of basisphenoid
bsp	basisphenoid "pit"
cat	channel for auditory tube
cc	cochlear canaliculus
cfs	<i>Chordafortsatz</i> (bony support for chorda tympani)
ch	ceratohyal
cp	caudal tympanic process of petrosal
cri	canal for ramus inferior
df	fossa for origin of posterior belly of digastricus m.
e	ectotympanic
eam	external acoustic meatus

er	epitympanic recess
esps	epitympanic sphenopetrosal suture
fcf	fossula of cochlear fenestra
ff	foramen faciale
fo	foramen ovale
fri	foramen for ramus inferior of stapedial a.
frs	foramen for ramus superior of stapedial a.
fs	sulcus for facial n.
fv	vestibular fenestra
g	gonial
gf	glaserian fissure
hf	hypoglossal foramen
i	incus
ics	sulcus for internal carotid a.
iri	incisure for ramus inferior of stapedial a.
ld	lambdoidal dehiscence
lp	lateral process
lpl	lateral pterygoid lamina
m	malleus
mn	mandible
mnf	mandibular fossa
mpl	medial pterygoid lamina
ms	malleolar sulcus
pce	posterior crus of ectotympanic
pcf	posterior carotid foramen
pf	piriform fenestra
pgf	postglenoid foramen
pgp	postglenoid process
plf	posterior lacerate foramen
pmc	paratympanic marrow cavities
pr	promontory of cochlea
prc	canal for promontory a.
prs	sulcus for promontory a.
rp	rostral tympanic process of petrosal
rrs	sulcus for ramus posterior of stapedial a.
sf	fossa for stapedius m.
sh	stylohyal

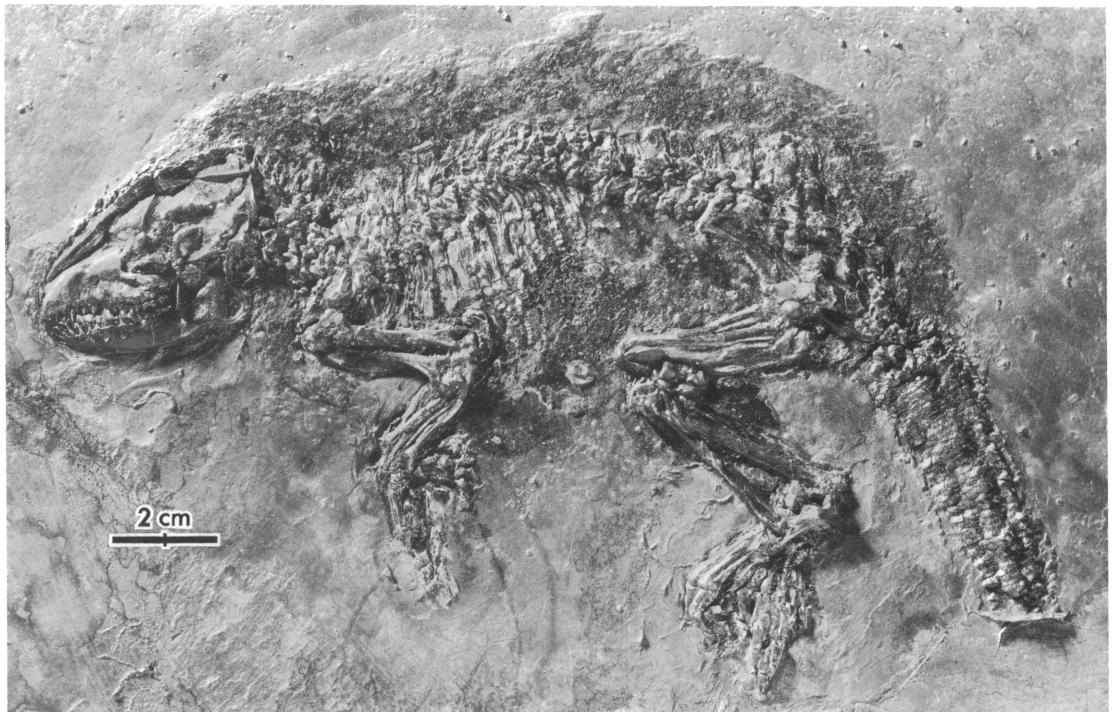


Fig. 2. *Pholidocercus hassiacus* HLMD Me 7577 (holotype; Middle Eocene, Messel, FRG). This specimen is substantially complete except for the distal part of the tail and portions of the feet. Soft tissue impressions are responsible for the dark "halo" around the specimen's trunk. Photography by E. Haupt (SMF).

smf	stylomastoid foramen
sq	squamosal
sqe	entoglenoid process of squamosal
sqw	epitympanic wing of squamosal
sri	sulcus for ramus inferior of stapedial a.
ss	sulcus for proximal part of stapedial a.
sw	epitympanic wing of sphenoid
th	tympanohyal
tsps	tympanic sphenopetrosal suture
tvf	transverse venous foramen
v	vertebral fragment

MATERIALS AND METHODS

The condition of each of the fossils described here is discussed under appropriate headings in the text. Because of the central importance of the Messel finds, however, a few general notes on fossil preservation at Grube Messel are warranted (for complete introductions to the published literature on Grube Messel and its flora and fauna, see Koenigswald, 1980, and Koenigswald and Michaelis, 1984).

Although many Messel fossils are remarkably complete, they almost always show the effects of compression and plastic deformation due to the weight of overlying sediments (Koenigswald and Schierning, 1987). Skulls of laterally deposited specimens (i.e., ones laid down on their right or left sides, parallel to the then-existing surface) are usually crushed flat. Specimens in this condition are of limited use for basicranial studies, since only the lateralmost parts of the auditory region can be prepared. Individuals that were deposited on their backs or bellies are recovered more rarely, perhaps because dead or dying vertebrates falling through a water column are unlikely to end up on the bottom in fully prone or supine positions. However, when available, such specimens (e.g., *Pholidocercus* SMF 81/619) are especially useful because their basicrania tend to be less distorted and more readily preparable than those of laterally deposited individuals.

For definitions and characterizations of

morphological terms relating to the auditory region, see MacPhee (1981) and Novacek (1986).

BASICRANIAL MORPHOLOGY OF EARLY TERTIARY ERINACEOMORPHS

AMPHILEMURIDAE

Pholidocercus hassiacus HLMD Me 7577

This specimen, the holotype of *P. hassiacus* (fig. 2), consists of a nearly complete, laterally deposited individual (Koenigswald and Storch, 1983). The posterior part of the neurocranium of HLMD Me 7577 has been crushed flat, with the result that some right-side structures (e.g., right parietal) are exposed on the same plane as the prepared left side of the specimen (fig. 3). The exposed left auditory region is also somewhat damaged: for example, although the ectotympanic is seemingly well-preserved, the promontorium has been pushed into the external acoustic meatus and has displaced the ectotympanic's posterior crus (fig. 3).

Ectotympanic

The ectotympanic appears to be essentially intact save for detachment of the end of the posterior crus and minor breakage along the anteromedial rim (fig. 3). The only feature on the ectotympanic's medial surface that can be made out with some confidence is the crista tympani, the attachment site of the tympanic membrane. This feature can be identified by sharply tilting the specimen under the microscope in order to gain an oblique view into the middle ear through the external acoustic meatus. The crista can be traced from the upper part of the anterior crus around to the termination of the posterior crus. A small part of the crista can be seen in figure 3, on the detached and somewhat externally rotated tip of the posterior crus.

Compared with the ontogenetically primary state of the ectotympanic in all therians (MacPhee, 1981), the medial aspect of this bone is expanded in *Pholidocercus*. Since the medial expansion lies directly on the plastic preparation slab, we cannot be certain that it really ends where it appears to, or was yet wider. The smooth curvature of its border

makes the latter possibility unlikely. For a similar reason, we cannot be sure that any additional floor components intervened between the ectotympanic and the petrosal. However, there is certainly no positive evidence of other structures in the form of bone fragments or plates, and we prefer to conclude that *Pholidocercus* possessed only the components detectable in this and the following specimen (SMF 81/619).

Moderate expansion of the ectotympanic is found in all extant erinaceids and a great variety of other mammals. In living hedgehogs (fig. 4A–D), expansion varies in degree from *Hylomys* (slight broadening) to *Erinaceus* (notable broadening). If, as argued, the ectotympanic of HLMD Me 7577 is essentially complete, it agrees most with that of *Hylomys*. The nearly vertical orientation of the ectotympanic in the fossil is surely artificial and due to its displacement by sediment pressure.

The spikelike posterior crus terminates in a small, broadened tip (fig. 3). A short distance below the tip is a projection, apparently complete, which may have supported the lower margin of the pars flaccida of the tympanic membrane. A similar feature is found in living erinaceids.

The anterior crus has a more complicated shape. Externally, it exhibits a deep and broad gutter, the malleolar fossa. No structure was preserved within this fossa at the time of study, but during life it almost certainly accommodated a massive goniale, as does the equivalent groove of many other primitive mammals (Fleischer, 1973; see also fig. 4B). In the depths of the fossa there is an indistinct groove which we interpret as a slot for the chorda tympani (and not for the stapedial ramus inferior, which left the middle ear more medially). There are a few bone chips in the uppermost part of the fossa (not illustrated in fig. 3), but whether they belong to the goniale, malleus, or some other structure cannot be determined. According to Wassif (1948) and Henson (1961) the goniale does not fuse with the ectotympanic in living hedgehogs, although fusions are frequently encountered in other mammals (e.g., in tree shrews; Fleischer, 1973).

The tympanic notch is wide and situated at a considerable distance from the external

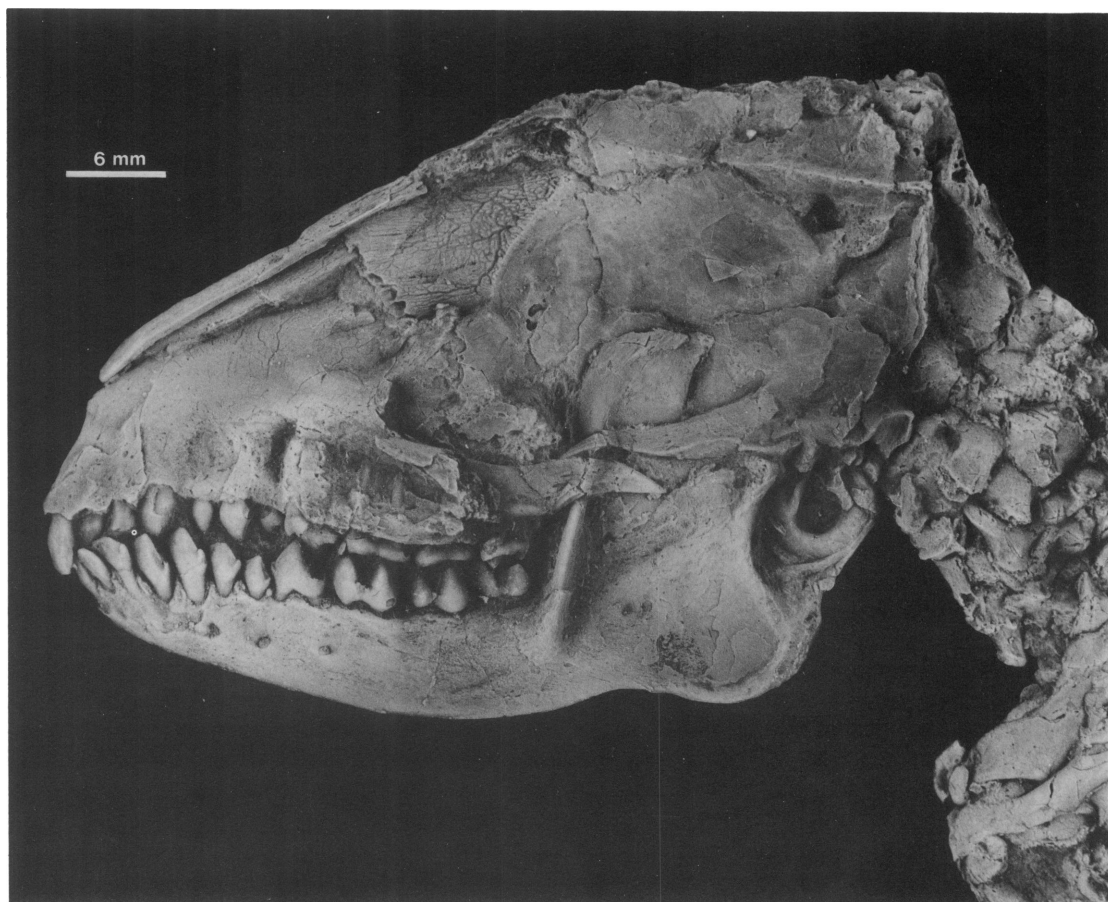


Fig. 3. *Pholidocercus hassiacus* HLMD Me 7577 (holotype): skull, left lateral aspect. Photograph by Dr. W. von Koenigswald (HLMD).

margin of the tympanic roof. In life this large space would probably have been ventrally covered by the pars flaccida, as in living erinaceids (cf. fig. 4C).

Because of the possibility that artificial displacement has disturbed the relations of the ectotympanic, it is not clear whether the broadened tip of the anterior crus was closely appressed to the skull just behind the large postglenoid process. In living erinaceids, the ectotympanic is "free" in the sense that it is not fused to any contiguous bone, but its play is limited by bony overlaps (goniale, basisphenoid tympanic wing, hyoid apparatus) and strong soft tissues in the tympanic floor (fibrous membrane of tympanic cavity).

Other Features

A few other features can be reliably made out in the general vicinity of the auditory region of this specimen (fig. 3). Ventrally, the body of the ectotympanic is overlapped by portions of the hyoid apparatus. The best-preserved portion is the long bar, probably the ceratohyal, which extends toward the laryngeal region. Dorsal to the posterior termination of the ceratohyal is a small slab of bone which is apparently the stylohyal, and dorsal to that is a small pronglike projection which we take to be the tympanohyal. Artificial displacements may have increased the size of the gaps between these elements, al-

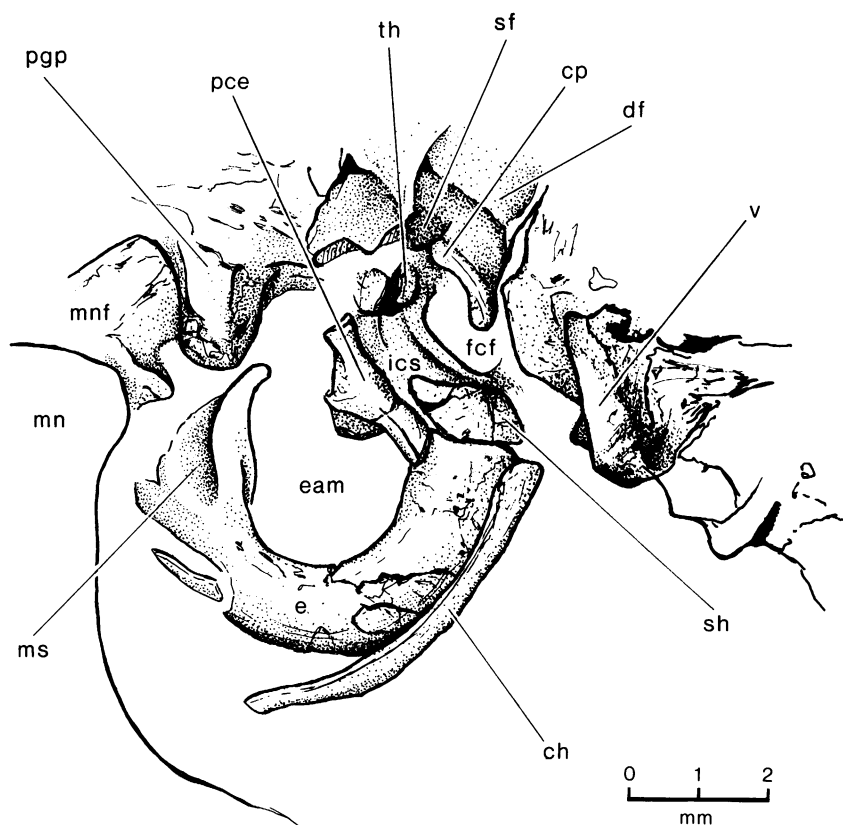


Fig. 3. *Continued.* Detail of left auditory region. Perspective of detail is slightly different from that of opposite figure, and shows results of additional cleaning.

though it is not improbable that these gaps were largely filled with persistently unossified remnants of Reichert's cartilage during life.

During cleaning, the lumen of the external acoustic meatus was found to be partly filled with fragments of bone. A few of these pieces could be recognized as parts of the promontory of the petrosal (fig. 3), but most were unidentifiable.

Although pits and small foramina exist in the suprameatal portion of the squamosal, none could be cleaned or followed far enough to be certain that they represent apertures for either rami temporales of the stapedia ramus superior or small veins emptying into the petrosquamus sinus (Cartmill and MacPhee, 1980). Foramina in this location are common in living erinaceids, as they are in many other mammals (Wible, 1984). The region behind the mastoid area is filled by a jumble of small

fragments, but most seem to be pieces of cervical vertebrae rather than cranial parts.

Pholidocercus hassiacus SMF 81/619

SMF 81/619 was discovered in the usual manner of "excavating" fossils at Grube Messel, namely by splitting up thick blocks along bedding planes. In this instance the split went directly through the specimen (a sub-adult skull), cleaving it into ventral and dorsal halves (fig. 5). This was a propitious accident, because it permitted the preparation of both the upper and lower parts of the skull on separate slabs.

The midventral section of the basicranium is noticeably warped in the zone between the pterygoids and the auditory region, but the posterior section has suffered less damage. On the right side the tympanic roof has been

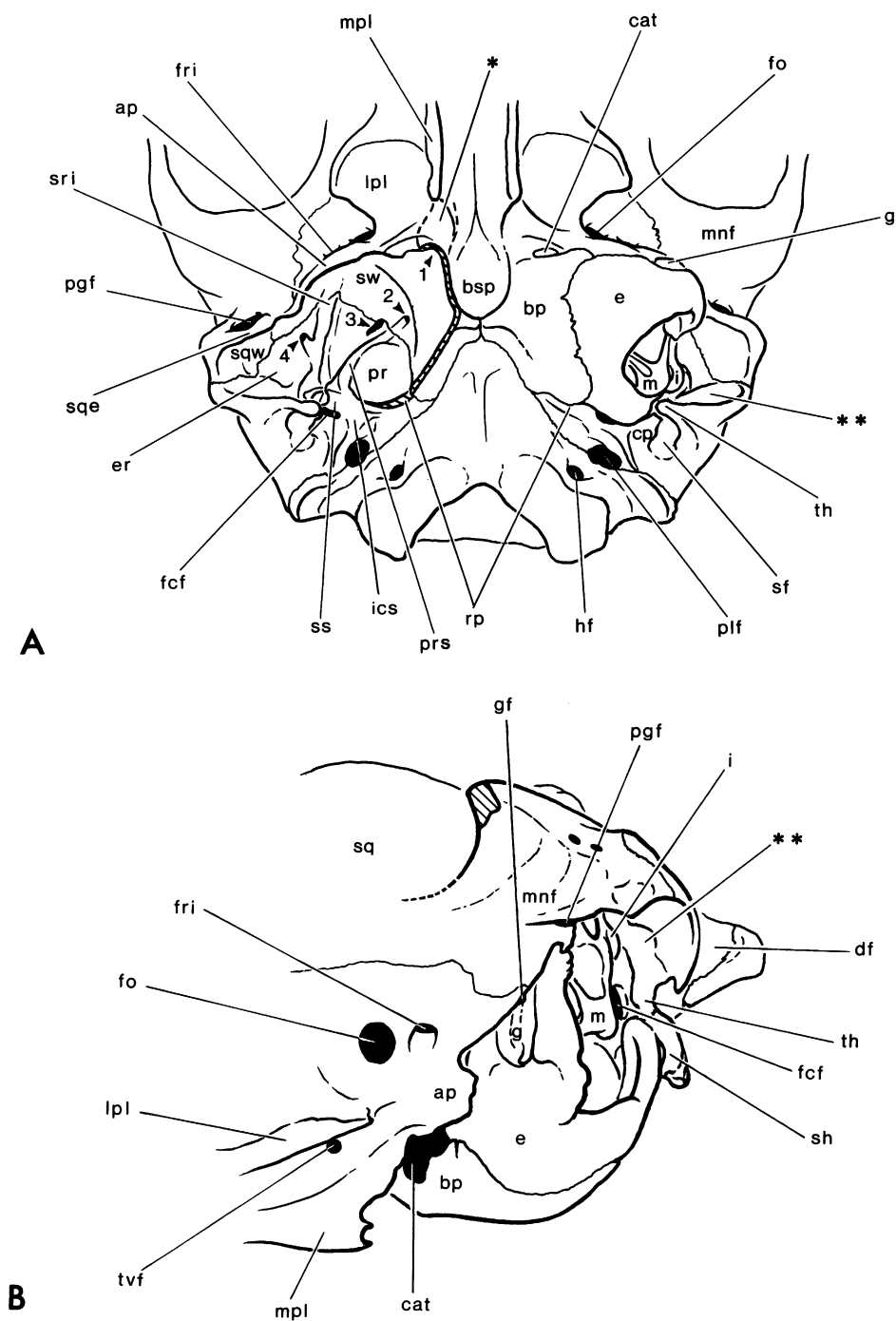


Fig. 4. Basicrania of representative extant erinaceomorphs and other lipotyphlans (semidiagrammatic; variable scales). Ventral aspect depicted in each case except B, which is an oblique ventrolateral view. Right tympanic floors have been partly dissected away in order to show hidden structures. A, B, *Hemiechinus*; C, *Hylomys*; D, *Echinosorex*; E, *Desmana*; F, *Chlorotalpa*. Numbered features: 1, entrance to pterygoid canal; 2, anterior carotid foramen; 3, remnant of piriform fenestra (and foramen

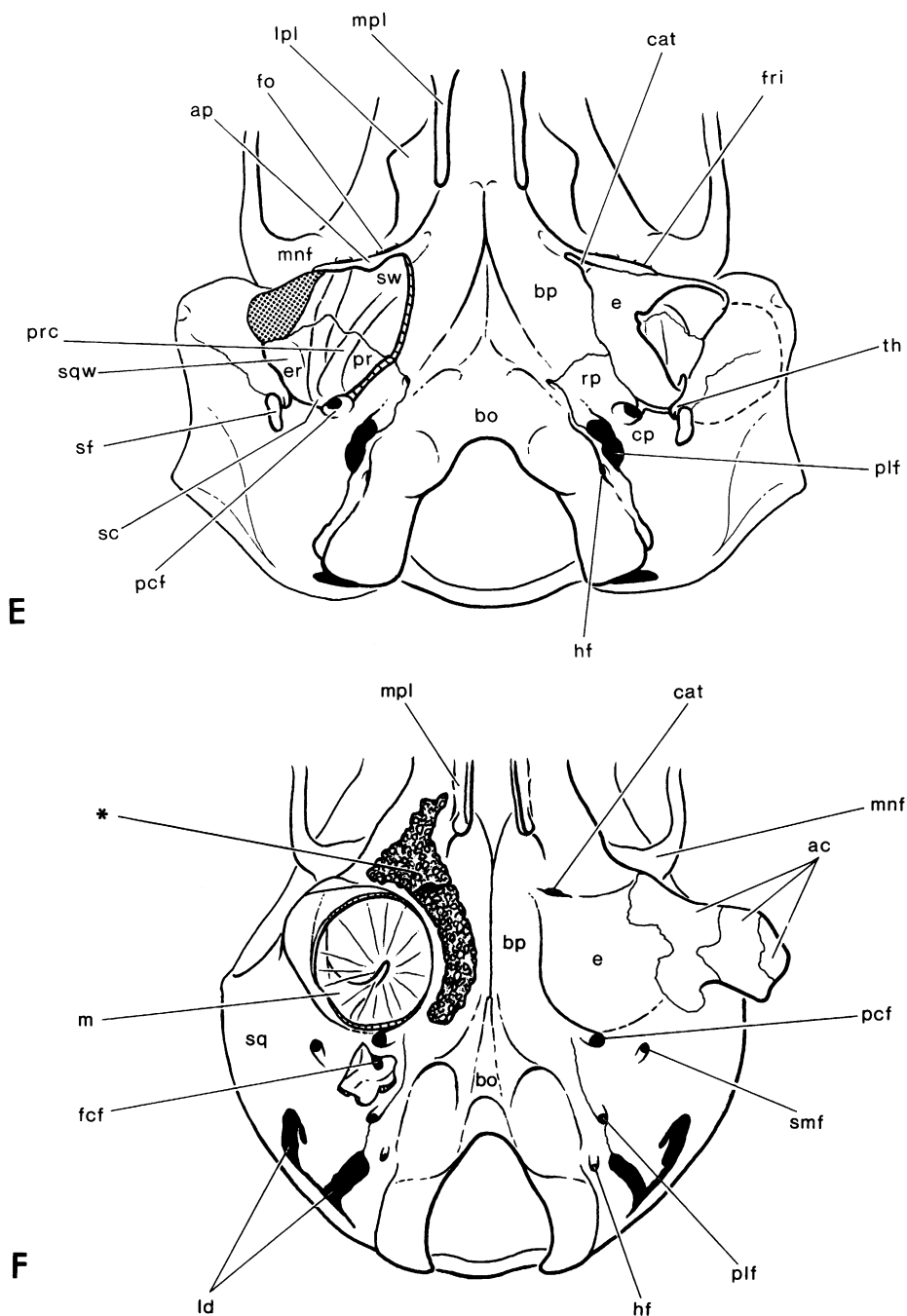


Fig. 4. *Continued.*

spaces as defined by the attachments of the pars flaccida of the tympanic membrane (left in situ in C). In *Desmana* (E), there is a relatively enormous pocket (dashed line) in the same position which bores deeply into the squamosal and mastoid. Stippled area in E represents sphenosquamosal articular surface for anterior crus of ectotympanic (shown as removed on right side of skull). Drawings based on specimens in collections of Department of Mammalogy, AMNH.

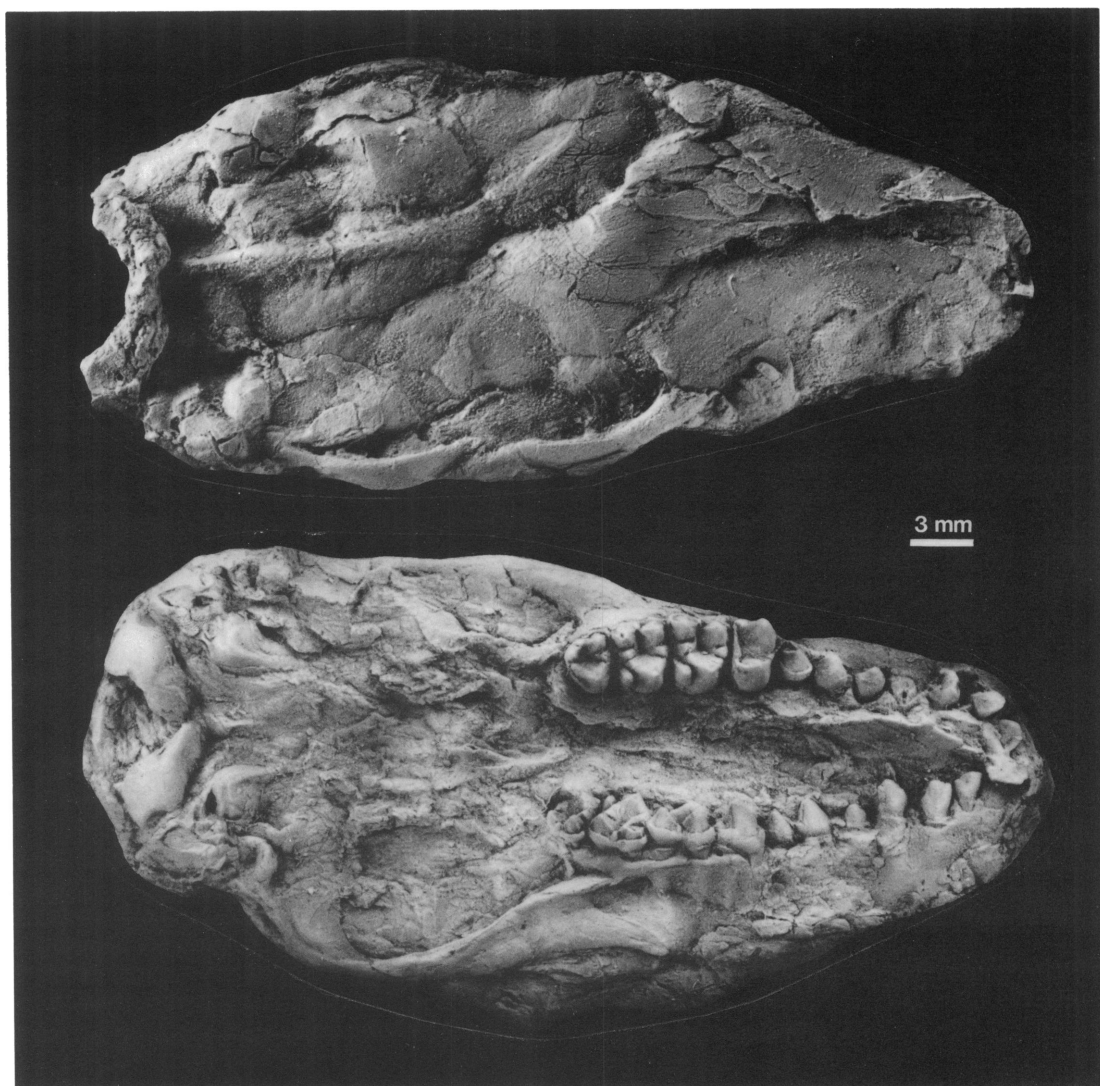


Fig. 5. *Pholidocercus hassiacus* SMF 81/619 (paratype); middle Eocene, Messel (FRG). **Top**, dorsal aspect; **bottom**, ventral aspect, prior to additional cleaning in 1986. Photograph by A. Gorzitze (SMF).

considerably narrowed as a result of medialward displacement of the squamosal. On this side the basisphenoid is buckled, apparently because the auditory capsule was forced against it by sediment pressure. The pterygoid processes were shorn off near their origins, and the ectotympanics and hyoid ossifications are missing on both sides. The latter elements were not present at the original time of cleaning, and they may have simply fallen away after death and maceration—additional evidence that the ectotympanic was

comparatively “free.” As an aid to description, the left auditory region was drawn in a way which eliminates obvious sources of distortion (fig. 6). This figure should be compared to figure 5 as one reads the following descriptions.

Petrosal

A low but broad eminence begins posteriorly at the margin of the internal carotid sulcus and runs anteriorly beyond the ante-

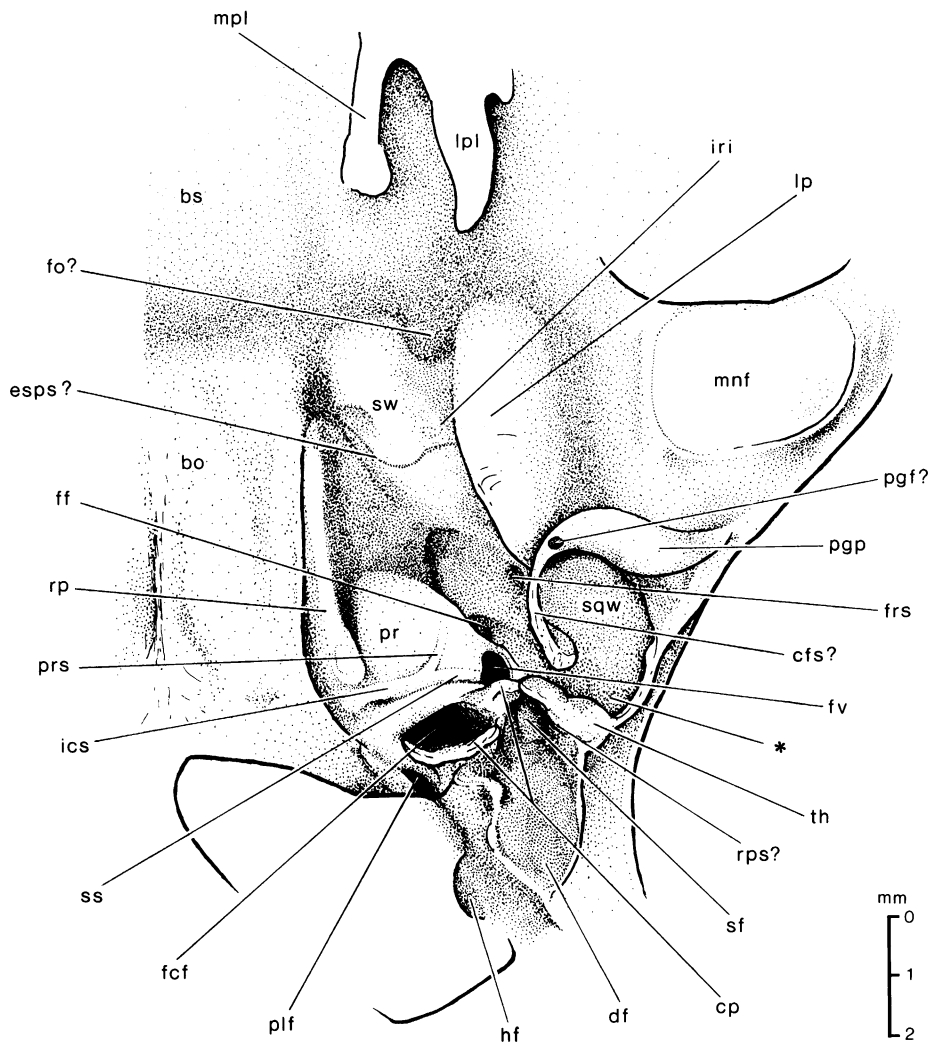


Fig. 6. Reconstruction of the auditory region of *Pholidocercus hassiacus* based on SMF 81/619 (ventral aspect). Reconstruction is based largely on the newly cleaned left side, with some details added from right side. Asterisk identifies small diverticulum related to crista parotica and base of tympanohyal.

rior pole of the promontory onto the elongated petrosal apex (anteromedial corner of the petrosal). There is no sign of suture remnants between this crest and the cochlear capsule per se, and we doubt that it is anything other than what it appears to be—a rostral tympanic process of the petrosal (MacPhee, 1981). The ventral surface, or leading edge, of the rostral process is smooth, suggesting that sutural tissues were not elaborated between this process and the ectotympanic. The smooth leading edge may be evidence that

these elements were separated by a significant interval, which in life would have been closed by membrane (fibrous membrane of the tympanic cavity). In living erinaceids the ventral edge of the rostral process is usually roughened.

Posterior and slightly lateral to the internal carotid sulcus is another petrosal process, corresponding to the caudal tympanic process of the petrosal (MacPhee, 1981). The medial section of this process closely confines the small diverticulum leading into the elon-

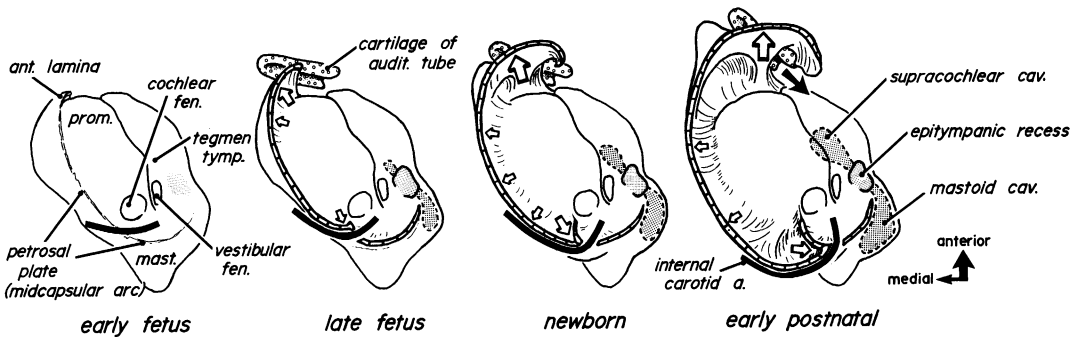


Fig. 7. Development of tympanic floor in a representative euprimate (in this instance, a lemuriform). The petrosal contribution to the tympanic floor arises from two sources, the rostral and caudal tympanic processes, which coalesce early in bullar ontogeny to form the petrosal plate. The plate expands both by apposition along its leading edge and by pneumatization (remodeling). Outline arrows illustrate relative strength of bullar pneumatization in various parts of the middle ear. Stippled areas represent specific pneumatic spaces in dorsal aspect of auditory region. Black arrow represents path of the tubal canal and auditory tube. Modified from MacPhee and Cartmill (1986).

gated aperture of the fossula fenestrae cochleae. The lateral section is produced into a tapering spike which articulates with the tympanohyal, thereby creating a narrow floor for the foramen stylomastoideum.

All investigated euprimates (fig. 7) elaborate a large dependent plate, formed by the coalescence of the rostral and caudal tympanic auditory bullae (MacPhee, 1981; MacPhee and Cartmill, 1986). In this they differ from living erinaceomorphs (fig. 4A–D) in which petrosal outgrowths are normally little larger than in *Pholidocercus* (except in some extinct Neogene forms, in which the petrosal shares equally with the sphenoid in delimiting the bulla [T. Rich, 1981]).

The caudal process is closely comparable to the one in living erinaceids. In extant forms the medial section is large enough to cover, at least partly, the apertura of the fossula; the lateral section is variably prominent, but frequently touches the tympanohyal (Butler, 1956; MacPhee, 1981). Neither section encloses the stapedius fossa, a difference from strepsirhine, but not all haplorhine, primates (MacPhee, 1981).

Basisphenoid and Basioccipital

Since it is not possible to determine the location of the synchondrosis between the basioccipital and basisphenoid in this specimen, these two elements may be considered

together as the bones of the “posterior central stem.”

Although *Pholidocercus* obviously lacked the well-developed basisphenoid tympanic process characteristic of all known post-Paleogene erinaceomorphs, it should be noted that on the right side the posterior central stem has a puffy appearance adjacent to the petrosal. The equivalent area on the left, however, is flattened. It is possible that the flattening is artificial, considering the battered condition of the bone in this area, but it is more likely that the left aspect of the posterior central stem has been warped or buckled by compression. In any event, even if natural, the enlargement does not extend beyond the level of the low rostral process of the petrosal, and therefore obviously did not function as a true tympanic process.

Alisphenoid and Squamosal

These two bones must be considered together as well: both probably contribute to the delimitation of the anterior wall of the tympanic cavity, but their separate contributions cannot be discriminated in the absence of detectable sutures.

The anterior margin of the tympanic cavity is bounded by a low, sinuous crest which conforms to the “preotic crest” described by McDowell (1958) for lipotyphlan insectivores. The preotic crest is formed by the ali-

sphenoid in all investigated lipotyphlans (MacPhee, 1981). This was presumably also true of *Pholidocercus*, whose preotic crest is essentially identical to that of living erinaceids in its form and relations. The only real difference may lie in the composition of the anterolateral extremity of the anterior wall. In *Pholidocercus* there is a large sheet of bone (lp, fig. 6) medial to the mandibular fossa, which ends freely beneath a deep sulcus. In living erinaceids (fig. 4A–D) there is a much smaller sheet of bone in this position, and it delimits a sulcus or short tube for the stapedia ramus inferior. In the latter group this structure is typically formed by the alisphenoid, but in the absence of detectable sutures in *Pholidocercus* it cannot be settled whether the same bone or the squamosal is responsible for this outgrowth. We would not hesitate to ascribe homology to these processes were it not for the fact that *Pholidocercus* is quite different morphologically in the conformation of the lateral portion of its squamosal. Not only does it have a large postglenoid process (absent or vestigial in recent lipotyphlans [McDowell, 1958]), but it also seems probable that it has a larger entoglenoid component than do living erinaceids. Thus the “lateral process” may actually be formed by the entoglenoid process and not the alisphenoid. The foramen ovale (fo?, fig. 6) was apparently situated anterior to the preotic crest, as in living erinaceids. There is no definitive sulcus for the tubal cartilage at the medial edge of the preotic crest. In some living erinaceids (e.g., *Echinosorex*) the basisphenoid tympanic wing spreads over this area, forming an incomplete canal for the auditory tube.

Tympanic Roof

Sutures are also difficult to detect in the tympanic roof, and we cannot be certain of the precise arrangement of roof elements. The best candidate for a suture is an indistinct groove that passes laterally from the anterior limit of the rostral process of the petrosal toward the “lateral process,” where it loses definition. This is similar, but not identical, to the track of the epitympanic sphenopetrosal suture of living erinaceids (MacPhee, 1981). If this feature is interpreted correctly,

Pholidocercus had a rather small sphenoid epitympanic wing, comparable to that of some soricomorphs rather than living erinaceids (MacPhee, 1981). By contrast, the epitympanic wing of the petrosal and probably the tegmen tympani would have been comparatively very large (for the distinction between petrosal epitympanic wing and tegmen tympani, see MacPhee, 1981). There is a second candidate for an epitympanic sphenopetrosal suture, a groove which sweeps posterolaterally rather than directly laterally from the anterior tip of the petrosal apex. However, this feature can only be traced for a few millimeters before it becomes too indistinct to trace further; it may not be a suture at all, but instead the distal track of the promontory artery (see Blood Vessels). The piriform fenestra, if present, cannot be detected.

The squamosal's contribution may have been rather large, if all of the region between the postglenoid process and the tympanohyal is mostly squamosal in origin. The morphology of this area, which includes the epitympanic recess, is considered later (see Pneumatization), but here it may be noted that the marked ridge (cfs?) which continues the arc of the postglenoid process is probably a part of the squamosal, as is everything lateral to it. Living erinaceids possess a small squamosal epitympanic wing, but that of *Pholidocercus* appears to be relatively larger and more anatomically complex than any of its homologs in extant hedgehogs.

Pneumatization

Extensive bone remodeling in the auditory region, correlated with the expansion of the cavum tympani during ontogeny, can follow widely different courses in mammals (MacPhee, 1981). The auditory regions of living erinaceids, however, are little pneumatized, and this also appears to have been true of *Pholidocercus*. There is no evidence of a mastoid cavity in SMF 81/619, nor is it likely that the low tympanic processes which bound the middle ear have undergone much ontogenetic displacement. The fossae deeply indenting the tympanic roof adjacent to the promontorium are not pneumatic spaces, but impressions for the muscle of the malleus (fossa for tensor tympani m.) and the facial

nerve (facial sulcus). The stapedius muscle would have been situated somewhere in the broad gap between the caudal tympanic process of the petrosal and the crista parotica, but its location is not marked by any special feature.

The area between the lateral limit of the middle ear (the roof of the external acoustic meatus) and the prominent ridge connected to the posteromedial aspect of the postglenoid process may have accommodated the incudomalleolar joint, in which case it should be identified as the epitympanic recess. However, the recess is unusually wide and deep for an erinaceomorph, and it could therefore be an accessory diverticulum. The ridge which medially delimits this fossa ends sharply and seems to have a broken end, implying that it may have continued up to the tympanohyal. Cracks in the ridge reveal a canal of unknown function. Butler (1956) and MacPhee (1981) have interpreted a similar (but much lower and shorter) ridge in *Erinaceus* as a *Chordaforstz*, i.e., an ossified channel for the chorda tympani. The limits of the fossa appear to extend well into the substance of the crista parotica/tympanohyal. Modern erinaceids also exhibit this excavation; it is not homologous with the fossa incudis because it does not contain the short process of the incus, nor does it appear to be comparable to the mastoid antrum of primates and some other mammals.

Blood Vessels

Information about the vascular network of extinct animals has to be based on impressions left by vessels and associated foramina. In the auditory region, the only vessels that ordinarily leave evidence of their passage are the internal carotid and its dependencies (promontory artery and divisions of the stapedial); more rarely, diagnoseable impressions are left by the ascending pharyngeal artery and veins draining to the major venous channels of the posterior parts of the head (mostly intradural sinuses). Excellent reviews of the ontogeny and evolutionary history of the cranial vasculature may be found in papers by Wible (1984, 1986, 1987).

According to our analyses, *Pholidocercus* possessed an unenclosed internal carotid sys-

tem that was closely comparable to that of most living erinaceids (fig. 4A, C), a pattern which is essentially primitive for Eutheria (MacPhee, 1981; Wible, 1986). The internal carotid entered the middle ear between the rostral and caudal tympanic processes of the petrosal. After a course of a few millimeters across the posterior part of the promontory (transpromontorial route of Cartmill et al., 1981) the carotid sulcus furcated into a large stapedial channel and a smaller one for the promontory artery.

A number of authors have discussed whether inferences about arterial caliber can be reliably made from osteological features like sulci and canals (Conroy and Wible, 1978; Cartmill and MacPhee, 1980; MacPhee and Cartmill, 1986). While there is doubtless a strong positive correlation between channel width and vessel caliber, the relationship is not linear (MacPhee, 1981). Vessels of substantial size may leave an insignificant impression, and some basicranial sulci, canals, and foramina may contain several structures (arteries, veins, nerves). Thus, we can only conclude that it is probable, but not entirely certain, that the stapedial artery was substantially larger than the promontory artery in *Pholidocercus*. The promontory artery, when preserved through ontogeny in a eutherian, is always accompanied by the sympathetic internal carotid nerve and, occasionally, by small veins. The stapedial, however, normally travels independently. Therefore, however stringently we wish to interpret the present fossil evidence for circulation in *Pholidocercus*, the evidence favors reconstruction of a large proximal stapedial. The stapedial is larger than the promontory vessel in living erinaceids studied by dissection, injection, and histological methods (Tandler, 1899; Bugge, 1974; MacPhee, 1981).

The channel for the promontory artery fades anteriorly, and we cannot confidently state where its foramen of exit into the braincase was situated. The likeliest possibility is that the artery swung medially and anteriorly after leaving the promontory, as it does in many eutherians. As noted earlier, the indistinct groove that leads toward a depression in front of the petrosal apex may actually be the sulcus for the promontory artery. The

basicranium is noticeably warped in this area and the depression may or may not be a natural feature. If it is (see description of *Diacodon alticus*) its position and relations are those of an anterior carotid foramen as defined by MacPhee (1981). Our reconstruction suggests that the borders of this possible foramen may have been comparatively wide, but beyond stating this little else can be said. There is no evidence of a vidian artery or a "medial internal carotid" and we have no independent reason for suspecting that the anterior pharyngeal anastomosed with the circulus arteriosus through this aperture. In living erinaceids, the anterior carotid foramen is inside the middle ear cavity rather than on its anteromedial margin, due to the hyperdevelopment of the lateral part of the basisphenoid.

The sulcus for the proximal stapedia cannot be traced beyond the fenestra vestibuli, although there are some features which suggest that the artery divided into superior and inferior rami, as it does in living erinaceids. Directly dorsal to the large ridge which defines the media extent of the epitympanic recess is the probable aperture of exit for the ramus superior. As already noted, the groove crosscutting the preotic crest allowed the ramus inferior to escape the middle ear. Both features, in precisely the same place, are seen in living erinaceids.

The perfect preservation of the crista parotica and tympanohyal allowed delicate cleaning of a groove which begins in the roof of the stapedia fossa. This groove may have held a third primitive division of the proximal stapedia, the ramus posterior. This vessel is known to exist in fetal stages of *Erinaceus* and several soricomorphs (MacPhee, 1981; MacPhee and Cartmill, 1986) and has recently been recognized in *Homo* (Diamond, 1987).

The dorsal section of the skull of SMF 81/619 is too mangled to provide any additional information on the homologies of the small squamosal foramina detected in HLMD Me 7577. With respect to the venous circulation, the only point worth making is that we do not have a good candidate for the postglenoid foramen. The reconstruction shows a hole (pgf?, fig. 6), of decidedly insignificant size,

in the medial part of the postglenoid process. Similar but not identical apertures are found in roughly the same place on both sides of the specimen, but each postglenoid process is slightly damaged and we are not convinced that these apertures are natural. In addition to being in an unusual place, their diminutive size implies that *Pholidocercus* would have had a more limited drainage from the petrosquamous sinus than is the case in living erinaceids. It is not out of contention that the true postglenoid foramen was situated more medially, within the deep (and uncleanable) cleft between the postglenoid and the "lateral process" or even within the area identified as the epitympanic recess (cf. description of *Diacodon*). Suprameatal foramina cannot be identified.

DORMAALIIDAE

Macrocranium tupaiodon (Feist Collection)

Although numerous specimens of *M. tupaiodon* have been recovered from Grube Messel by public institutions and private individuals, in all cases known to us the basicranium is either missing, inaccessible, or too crushed for reliable interpretation. Maier's (1979) preliminary analysis of the ear region of this species is based on two specimens (denominated by him as F.1 and F.2) in the Feist collection, an important private collection of Messel vertebrates (figs. 8, 9). F.1 is a nearly complete, laterally deposited specimen with a well-preserved cranium. The cranium of F.2 was ventrally deposited, but it is unfortunately very badly crushed and distorted.

Maier's (1979: 45) notes on the auditory region of *Macrocranium* are as follows:

In specimen F.1, the left postglenoid process and the external otic meatus are separated by structures which look like parts of a mastoid and bullar region displaced by sediment pressure. . . . F.1 shows a short but distinct bony tube forming the external otic meatus. Dorsally, this tube seems to be fused to the squamosal, although in F.2 faint sutures are distinguishable. In F.1, this meatus suddenly expands to form a broad bony plate of semicircular shape; most probably this plate is to be interpreted as the lateral wall of a middle ear bulla of considerable size. Unfortunately no specimen permits the study of the medial parts of the supposed bullae



Fig. 8. *Macrocranium tupaiodon* from Feist Collection (F.2 of Maier, 1979; middle Eocene, Messel, FRG). Lateral aspect of nearly complete subadult.

and their connections with the basicranium. It is difficult to decide whether the visible structures of the meatus and the bulla belong to the ectotympanicum or some kind of entotympanicum. Specimen F.2, although damaged to some degree, shows some morphological differences which might elucidate this problem. A broad, ring-shaped ectotympanic is exposed, which seems to have formed at least parts of the meatus, whereas the covering parts of a supposed entotympanic are removed. The composition of the bullar capsule of *Macrocranium*, however, is not yet known exactly but its existence alone, and its basic similarity to the middle ear regions in primitive primates are interesting.

Regrettably, the evidence for these morphological interpretations and the attendant implications mentioned by Maier (1979) have to be rejected. Reexamination of F.1 and F.2 (fig. 9) reveals that the structure which Maier regarded as the ectotympanic is actually made up of portions of the posterior and superior semicircular canals, fortuitously exposed on the specimens' exteriors as a result of crushing and loss of parts of the cranial roof. He interpreted the walls of the parafloccular fossa as the external acoustic meatus, which in turn led him to conclude that the raised eminences of the semicircular canals were the crura of the ectotympanic, and so on. With

correct relations established, it can be seen that the "suture" on the posterior aspect of the "ectotympanic" is in reality the lip of the sigmoid sulcus (or possibly the lingula covering the entrance to the endolymphatic canal), and the piece of bone posterior to this complex could be either a section of pars canalicularis or the occipital—but not an "os bullae." Hence, we conclude that there is no evidence of an ossified auditory bulla in *M. tupaiodon*.

Unfortunately, nothing of the real middle ear can be made out in either specimen. The squamosal margin of the external auditory meatus can be identified behind the large postglenoid process in F.1, but no additional details can be resolved because the area cannot be further cleaned.

In recent years, more than ten additional skeletons of *Macrocranium* have been recovered from the Messel site. Our study of these specimens discloses little new information, as most skulls are badly crushed and bony elements are often distorted or lacking. A subadult *Macrocranium* (SMF Me 1209) with a bilaterally compressed skull shows a small, crescent-shaped, dorsally open element directly posterior to the back of the jaw on the exposed right side of the cranium. This is probably an ectotympanic, suggesting that

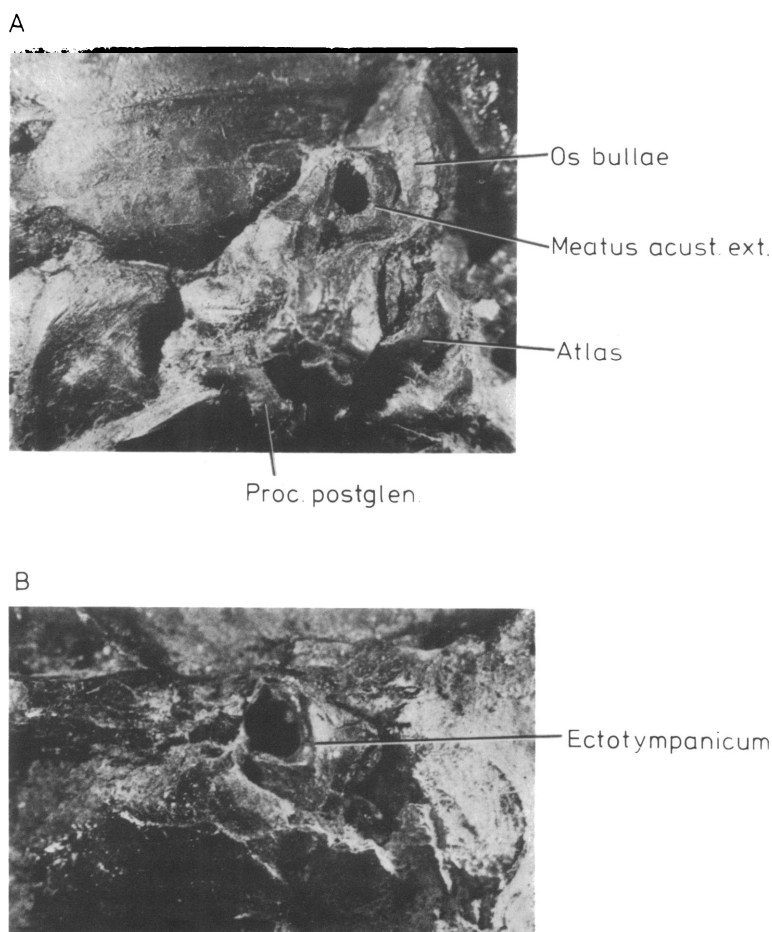


Fig. 9. Maier's (1979) interpretation of otic features in *Macrocranium tupaiodon* as exposed on left side of skulls of Feist 1 (A) and 2 (B). Because of crushing and loss of bone from the cranial roof, the features exposed are actually endocranial, not ectocranial. Thus, "Meatus acust. ext." is really the entrance to the parafloccular fossa; "Os bullae" represents either part of the petrosal pars canalicularis or the adjacent occipital; and the "Ectotympanicum" consists of the eminences of the posterior and superior semicircular canals framing the entrance of the parafloccular fossa.

this element was a simple structure not expanded into a bulla. The presence of a little-expanded ectotympanic in SMF Me 1209 would tend to corroborate our reassessment of Maier's (1979) original description of the Feist skulls.

Macrocranium nitens AMNH 48697

The associated specimens bearing this accession number include a crushed cranial roof, left maxilla (with M^{1-3} in situ), and left petrosal. The petrosal's medial aspect is well

preserved, but its lateral and posterior portions are much battered (fig. 10). The tegmen tympani and the contiguous part of the mastoid area were broken off during preparation and reattached with glue.

The petrosal morphology of *M. nitens* is strikingly similar to that of *Pholidocercus*, and both resemble in turn the petrosal of *Hylo-mys* (cf. figs. 6, 10A, B). The medial aspect of the petrosal bears rostral and caudal processes which are essentially identical to those of the Messel amphilemurid. The undamaged ventral edge of the rostral process is smooth

rather than rough. The caudal process is not complete, but it has the same position and relationship to the aperture of the fenestra cochleae described for *Pholidocercus*. Because the tympanohyal of AMNH 48697 has been slightly displaced by breakage, it is not certain that it articulated with the lateral aspect of the caudal process, although this is probable.

The only transpromontorial arterial tracks which can be made out with some confidence are poorly defined sulci for the internal carotid and proximal stapedia in the same places as in *Pholidocercus* and *Hylomys*. There is no identifiable groove for a promontory artery, although a small indentation in the anterior border of the petrosal apex may have accommodated this vessel as it passed into the endocranium (cf. similar indefinite indications of the promontory artery track in living *Solenodon* [Novacek et al., 1983]). The foramen for the ramus superior is not represented in the preserved part of the tegmen tympani; the hole lateral to the promontorium is definitely for the facial nerve and not the artery (fig. 10).

Since material has been lost from the lateral side of the auditory capsule, it is not known how extensively the petrosal participated in the tympanic roof. A small fragment of the mastoid area, collected with the rest of the skull but not recognized as part of the petrosal until after this study was completed, has a noticeable scar for the digastric m. There is no sign of inflation, so *Macrocranium*, like *Pholidocercus*, lacked a mastoid cavity.

ERINACEOMORPHA INCERTAE SEDIS

Diacodon alticuspis AMNH 48587

This specimen was briefly described by Novacek et al. (1983). Although parts of both auditory regions are preserved, the specimen is crushed and is missing large sections of its basicranium. Most of the observations reported below are based on the specimen's better preserved right side (fig. 11).

Judging from the relative sizes of their promontoria, *Diacodon* was a slightly larger animal than *Macrocranium nitens*, but in other regards their comparable basicranial features are essentially identical. As in the other fos-

sils considered here, the petrosal makes only insignificant contributions to the medial wall of the tympanic cavity. The rostral processes are slightly abraded on both sides, and it cannot be directly established whether they were smooth-surfaced as in *Pholidocercus* and *Macrocranium*. However, there is no positive sign that the rostral process was comparatively larger than in the other two genera, and we doubt that there was a well-developed suture between the ectotympanic and the petrosal in *Diacodon*. The caudal process is also abraded, but it corresponds in all particulars to its homolog in the other early erinaceomorphs described here.

Enough of the basisphenoid is preserved to be certain that it did not form a tympanic process. Unlike *Pholidocercus* SMF 81/619, crushing has not affected the basisphenoid's planum, which is slightly raised adjacent to the auditory capsule but otherwise featureless. This raised area, which occurs at the "notch" where the alisphenoid and basisphenoid components of the sphenoid meet, was tentatively interpreted as the wall of a vascular channel by Novacek et al. (1983). As noted above, the equivalent area in *Pholidocercus* may have helped to define the anterior carotid foramen. In *Diacodon* the petrosals seem to have been slightly displaced, artificially enlarging the aperture. In any event, the presence of an anterior carotid foramen in this position cannot be taken as evidence for a pharyngeocarotid anastomosis, since it may have transmitted only the promontory artery. Alternatively, the raised rim and its adjacent shelf of bone may have acted as an articular surface for the petrosal apex, which in life would have been firmly wedged into the basisphenoid-alisphenoid "notch."

As in *Macrocranium nitens*, there is a definite sulcus for the proximal stapedia, but the track of the promontorial artery cannot be discriminated with certainty. This is not surprising, given the poor preservation of these specimens and the indistinctness of the promontory sulcus even in the excellent material of *Pholidocercus*. Novacek et al. (1983) noted the lack of a definite promontory sulcus and speculated that there might have been an arterial pathway medial to the petrosal in *Diacodon*. After study and discussion, we now

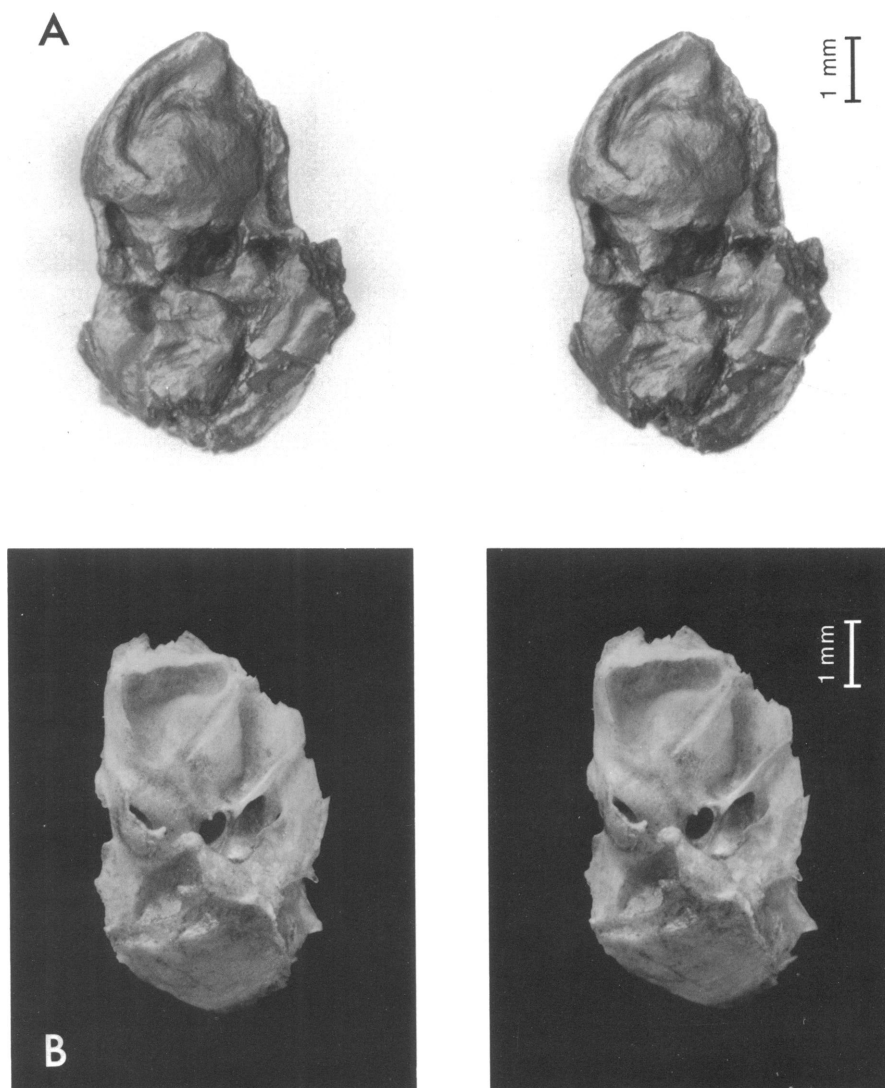


Fig. 10. Stereopairs of ventral aspect of petrosal in **A**, *Macrocranium nitens*, AMNH 48697 (lower Eocene, San Jose Formation, New Mexico); and **B**, *Neotetracus sinensis*, AMNH 11552 (Dept. of Mammalogy), an extant erinaceid.

agree that it is far more likely than not that the promontory artery, transpromontorial in position, was constantly present in this and other Early Tertiary erinaceomorphs reviewed here.

The stapedia system appears to have been organized as in living erinaceids, with large superior and inferior branches. There is also a small groove on the posterior aspect of the crista parotica which may imply the presence

of a ramus posterior (see description of *Pholidocercus*). The ramus superior evidently passed into the endocranium soon after arising from the proximal stapedia (fig. 11), but the ramus inferior continued forward in a deep groove, to surmount the preotic crest and exit from the middle ear.

Diacodon possessed a relatively large post-glenoid foramen, situated in a position where the epitympanic recess is found in *Pholido-*

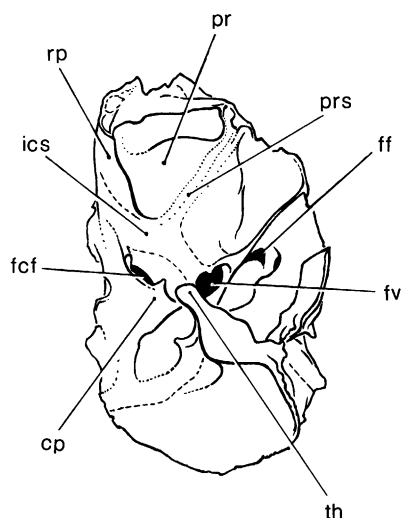
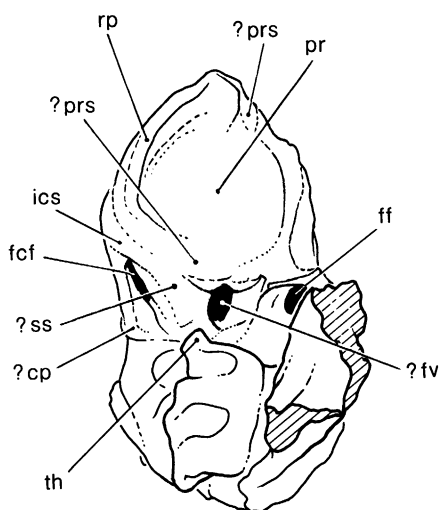


Fig. 10. *Continued.* Diagrammatic representation of petrosals in *Macrocranium nitens*, AMNH 48697 (top), and *Neotetracus sinensis*, AMNH 11552 (bottom). The aperture of the fenestra vestibuli (?fv) is broken in AMNH 48697, making it difficult to define its boundaries accurately.

cercus. The postglenoid process is also smaller and differently disposed than in the latter. Because the lateral part of the tympanic roof has been destroyed on both sides, we cannot locate the exact position of the epitympanic recess (or related accessory sinus) in *Diacodon*, but all likely interpretations indicate that

it was both smaller and more medially situated than in *Pholidocercus*. In these aspects *Diacodon* is actually more like living erinaceids than is *Pholidocercus* (cf. figs. 4A–D, 6).

Diacodon agrees with *Pholidocercus* in possessing an identifiable “lateral process,” although this feature is bilaterally broken and sutural demarcations are not identifiable in AMNH. There is a large suprameatal foramen located about 3 mm above the upper margin of the external acoustic meatus. This aperture, also found in leptictids, didelphids and some euprimates, probably communicated with the petrosquamous sinus, although we cannot determine whether it transmitted a vein or an artery (or both, as in *Tarsius* [MacPhee and Cartmill, 1986]).

BASICRANIAL CHARACTERS AND THE ERINACEOMORPH BASICRANIAL MORPHOTYPE

Szalay (1975) did not explicitly define his concept of the erinaceomorph basicranial morphotype, although his list of five “significant similarities” of hedgehogs to primates were evidently meant to be a serviceable approximation at some level. A more precise statement of the morphotype is required before a formal judgment on the phylogenetic connections of primates and erinaceomorphs can be rendered. Our character list (table 2) subsumes the traits originally defined by Szalay, and additionally includes outgroup features that should be considered in any morphotype definition. Many of these characters and their distributions within Eutheria have already been discussed by Novacek (1977, 1986) and MacPhee (1981; Cartmill and MacPhee, 1980; MacPhee and Cartmill, 1986), but we wish to record our special debt to several workers whose painstaking investigations of fossil erinaceomorphs have eased the task of morphotype reconstruction (in particular, Butler, 1948, 1956; McDowell, 1958; T. Rich and P. Rich, 1971; T. Rich, 1981). Outgroup comparisons emphasize conditions displayed by groups conventionally included within or frequently associated with Primates and Lipotyphla (table 3).

Transformation series are noted in cases where character state polarity within

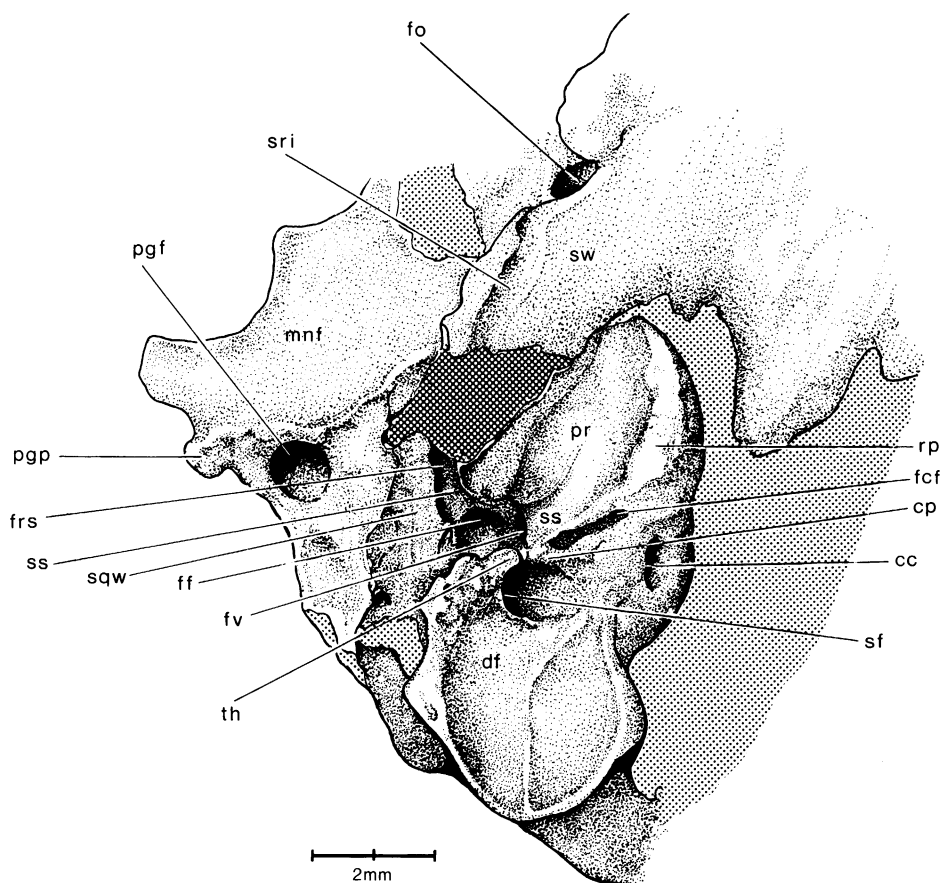


Fig. 11. *Diacodon alticuspis*, AMNH 48487 (lower Eocene, San Jose Formation, New Mexico). Ventral aspect of right auditory region. Areas covered by coarse regular stipple are either broken or filled with matrix.

subgroups of Erinaceomorpha can be determined with some confidence. In many instances, of course, the least derived state (state 0) in the comparative set is also the least derived one found in erinaceomorphs. The majority of states in this class are probably eutherian symplesiomorphies.

It should be noted that in this recension of the erinaceomorph morphotype, we have assumed that the consensus concept of Erinaceomorpha recently defined by Novacek et al. (1985) is monophyletic. Compared to some competing classifications (e.g., Sigé, 1977; Butler, 1972), this concept of Erinaceomorpha is rather narrow: in addition to the central family Erinaceidae (including subfamilies Galericinae, Erinaceinae, and Brachyericinae), it includes only Dormaaliidae, Amphi-

lemuridae, and a small handful of taxa incertae sedis (including *Diacodon*). This restricted membership is based on mutual possession, by these taxa, of a number of dental features considered by Novacek (1982) to be apomorphous. However, some of these features individually occur in a variety of other taxa not included in Erinaceomorpha as defined above. This may imply that the stated trait list includes some character states which are primitive for a wider taxon assemblage, in which case Erinaceomorpha may be paraphyletic. We control for the possibility that the consensus concept of Erinaceomorpha is not monophyletic by separately considering Early Cenozoic taxa in our comparison of morphotypes (see final section).

In order to make economical reference to

TABLE 2
Basicranial Characters and Character States of Some Eutherian Mammals^{a,b}

*1. Rostral tympanic process of petrosal
1.0 absent [some Soricoidea, some Tenrecidae]
1.1 small but distinct crest or rugosity; restricted to medial aspect of promontorium; extends to petrosal apex, but may be partially occluded by other components of tympanic floor; does not help to form meatus; roughened articular surface for other components of tympanic floor; does not form anterior tympanic wall [some Leptictidae, some Tenrecidae, ?Chrysochloridae, #Talpinae, Desmaninae, Erinaceinae, Galericinae, Microsyopidae]
1.2 small but distinct crest; restricted to medial aspect of promontorium; extends to petrosal apex; does not help to form meatus; no articular surface; does not form anterior tympanic wall [some Soricoidea, some Leptictidae, <i>Diacodon</i> , Dormaaliidae, Amphilemuridae]
1.3 large; situated on promontorium, but medially inflated; extends to petrosal apex; greatly broadened and forms posteroinferior part of meatus; roughened articular surface for basisphenoid (tympanic sphenopetrosal suture); does not form anterior tympanic wall [Brachyericinae]
1.4 extensive; situated medial to promontorium, from which it spreads as a wide sheet to ossify all of tympanic floor except for variable ectotympanic contribution; extends well beyond petrosal apex; forms anterior tympanic wall [?Plesiadapidae, ?Paromomyidae, #Adapidae, #Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthropoidea]
*2. Caudal tympanic process of petrosal
2.0 process absent or insignificant [Leptictidae, Microsyopidae]
2.1 small, incompletely encloses fossula of fenestrae cochleae only; little or not pneumatized [Soricoidea, some Tenrecidae, <i>Diacodon</i> , Dormaaliidae, Amphilemuridae, Erinaceinae, Galericinae]
2.2 extensive, closely delimits or forms apertures for surrounding structures such as facial nerve and internal carotid, little or not pneumatized [some Tenrecidae, Desmaninae]
2.3 extensive, closely delimits stylomastoid foramen and posterior carotid foramen, pneumatized from within tympanic cavity to form posterior septum [Brachyericinae, ?Plesiadapidae, ?Paromomyidae, #Adapidae, Lemuriformes]
2.4 extensive, closely delimits stylomastoid foramen and posterior carotid foramen, no posterior septum [Chrysochloridae, Talpinae, #Omomyidae, Lorisiformes, <i>Tarsius</i> , Anthropoidea]
3. Tympanic process of basisphenoid
3.0 process absent [Leptictidae, some Microsyopidae, Soricoidea, <i>Diacodon</i> , #Dormaaliidae, Amphilemuridae, Plesiadapidae, Paromomyidae, Adapidae, Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthropoidea]
3.1 small, restricted to "notch" between alisphenoid and basisphenoid components of sphenoid [some Microsyopidae]
3.2 large, but does not coalesce with alisphenoid tympanic wing under tubal foramen or reach meatus [Tenrecidae, Desmaninae, Erinaceinae, Galericinae]
3.3 large, coalesces with alisphenoid tympanic wing but does not form anteroinferior floor of meatus [Chrysochloridae, Talpinae]
3.4 large, coalesces with alisphenoid tympanic wing and forms anteroinferior floor of meatus [Brachyericinae]
4. Tympanic process of alisphenoid
4.0 process absent [Plesiadapidae, Paromomyidae, Adapidae, Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthropoidea]
4.1 small, does not completely form tubal foramen in combination with basisphenoid; little or not pneumatized [Leptictidae, Soricoidea, Tenrecidae, Desmaninae, <i>Diacodon</i> , #Dormaaliidae, Amphilemuridae, Erinaceinae, Galericinae, Microsyopidae]

TABLE 2—*Continued*

4.2	large, completely forms tubal foramen in combination with basisphenoid; strongly pneumatized [Chrysochloridae, Brachyericinae, Talpinae]
5.	Ectotympanic
5.0	crura slightly to significantly expanded relative to ontogenetically early condition; ectotympanic phaneric or slightly semiphaneric [Soricoidea, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, # <i>Diacodon</i> , # <i>Dormaaliidae</i> , Amphilemuridae, Erinaceinae, Galericinae, ?Microsyopidae, ?Plesiadapidae, ?Paromomyidae, Omomyidae, Lorisiformes, <i>Tarsius</i> , Anthroipoidea]
5.1	crura not expanded relative to ontogenetically early condition; ectotympanic aphaneric or highly semi-phaneric [Leptictidae, Brachyericinae, Lemuriformes, Adapidae]
6.	Squamosal participation in temporomandibular joint and anterior tympanic wall
6.0	entoglenoid region does not articulate with mandible (true postglenoid process present), makes little or no contribution to anteromedial wall of tympanic cavity [Leptictidae, <i>Diacodon</i> , Dormaaliidae, Amphilemuridae, Microsyopidae, Plesiadapidae, Paromomyidae, Adapidae, Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthroipoidea]
6.1	entoglenoid region articulates with mandible (true postglenoid process small or absent), makes small to large contribution to anteromedial wall of tympanic cavity [Soricoidea, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, Brachyericinae, Erinaceinae, Galericinae]
7.	Entotympanics
7.0	absent [Soricoidea, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, # <i>Diacodon</i> , # <i>Dormaaliidae</i> , Amphilemuridae, #Brachyericinae, Erinaceinae, Galericinae, ?Microsyopidae, ?Plesiadapidae, ?Paromomyidae, #Adapidae, #Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthroipoidea]
7.1	present [Leptictidae]
8.	Petrosal participation in tympanic roof
8.0	restricted to area lateral to promontory [Leptictidae, Soricoidea, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, <i>Diacodon</i> , # <i>Dormaaliidae</i> , #Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae, Microsyopidae]
8.1	petrosal greatly extended to form all of anterior part of tympanic roof [?Plesiadapidae, ?Paromomyidae, Adapidae, Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthroipoidea]
9.	Sphenoid participation in tympanic roof
9.0	large [Leptictidae, some Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, <i>Diacodon</i> , # <i>Dormaaliidae</i> , #Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae, Microsyopidae]
9.1	small because sphenoid fails to ossify piriform fenestra [Soricoidea, some Tenrecidae]
9.2	nonexistent because petrosal roof elements exclude sphenoid [?Plesiadapidae, ?Paromomyidae, Adapidae, Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthroipoidea]
10.	Squamosal participation in tympanic roof and pneumatization of lateral part of middle ear
10.0	no diverticula in crista parotica or squamosal other than epitympanic recess [Leptictidae, Tenrecidae, Soricoidea, Microsyopidae, Plesiadapidae, Paromomyidae, Adapidae, some Omomyidae, some Lemuriformes, <i>Tarsius</i>]
10.1	small intratympanic diverticulum formed in base of crista parotica [# <i>Diacodon</i> , # <i>Dormaaliidae</i> , Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae]
10.2	large intratympanic diverticulum formed in base of crista parotica which laterally invades squamosal [Desmaninae, Chrysochloridae, Talpinae]
10.3	true mastoid cavity formed [some Omomyidae, Lorisiformes, some Lemuriformes, Anthroipoidea]

TABLE 2—Continued

11. Internal carotid system
11.0 internal carotid stem large, promontorial and proximal stapedia divisions subequal (inferred from sulci or canals in case of fossils)
[Leptictidae, Soricidae, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, # <i>Diacodon</i> , Dormaaliidae, Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae, Microsyopidae, some Adapidae, some Omomyidae]
11.1 internal carotid stem large, marked caliber disparity between proximal stapedia when preserved and promontorial divisions (inferred from sulci or canals in case of fossils)
[some Adapidae, some Omomyidae, some Lemuriformes, <i>Tarsius</i> , Anthropoidea]
11.2 internal carotid insignificant or obliterates during ontogeny
[Plesiadapidae, Paromomyidae, some Lemuriformes, Lorisiformes]
12. Stapedial ramus inferior
12.0 large, exits middle ear through glaserian fissure or through trough/foramen in alisphenoid tympanic process
[Soricidae, some Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, <i>Diacodon</i> , #Dormaaliidae, Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae, Microsyopidae]
12.1 large, exits middle ear through tympanic roof, does not pass through glaserian fissure or alisphenoid process
[Leptictidae]
12.2 absent or insignificant
[some Tenrecidae, Plesiadapidae, Paromomyidae, Adapidae, Omomyidae, Lemuriformes, Lorisiformes, <i>Tarsius</i> , Anthropoidea]
13. Supply to meninges
13.0 mostly or exclusively from stapedial ramus superior
[#Leptictidae, Soricidae, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, <i>Diacodon</i> , #Dormaaliidae, Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae, Microsyopidae, Adapidae, some Omomyidae, some Lemuriformes]
13.1 ramus superior highly reduced or obliterated, blood supply to meningeal vessels mediated by other vessels (e.g., ramus anastomoticus of maxillary, posterior auricular)
[Plesiadapidae, Paromomyidae, Lorisiformes, some Lemuriformes, some Omomyidae, <i>Tarsius</i> , Anthropoidea]
*14. Supply to circulus arteriosus, additional to vertebral arteries
14.0 promontorial artery (pharyngeocarotid anastomosis insignificant or absent)
[Leptictidae, Soricidae, Tenrecidae, Chrysochloridae, Talpinae, Desmaninae, <i>Diacodon</i> , #Dormaaliidae, Amphilemuridae, Brachyericinae, Erinaceinae, Galericinae, Microsyopidae, Adapidae, Omomyidae, <i>Tarsius</i> , Anthropoidea]
14.1 pharyngeocarotid anastomosis (internal carotid system insignificant)
[some Lemuriformes, Lorisiformes]
14.2 none (internal carotid system insignificant, pharyngeocarotid anastomosis absent)
[?Plesiadapidae, ?Paromomyidae, some Lemuriformes]
*15. Arterial canals, intratympanic
15.0 none or only enclose stem of unreduced internal carotid at its entrance into tympanic cavity
[Leptictidae, Soricidae, Tenrecidae, <i>Diacodon</i> , Dormaaliidae, Amphilemuridae, Erinaceinae, Galericinae, Microsyopidae]
15.1 canals enclose stem of unreduced internal carotid and its major intratympanic divisions
[Chrysochloridae, Talpinae, Desmaninae, Brachyericinae, Adapidae, Omomyidae, some Lemuriformes, <i>Tarsius</i> , Anthropoidea]
15.2 none, internal carotid system reduced or obliterated
[Plesiadapidae, Paromomyidae, Lorisiformes, some Lemuriformes]
*16. Promontorium
unanalyzed

^a # = parsimonious inference permitted; ? = parsimonious inference not permitted. See table 3 and text.

^b * = character includes or redefines a character state defined by Szalay (1975).

TABLE 3
Distribution of Basicranial Character States in Primates, Erinaceomorphs, and
Some Other Eutherians^{a,b}

Taxa	Characters														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Tarsius</i>	4	4	0	0	0	0	0	1	2	0	1	2	1	0	1
Lorisiformes	4	4	0	0	0	0	0	1	2	3	2	2	1	1	2
Lemuriformes	4	3	0	0	2	0	0	1	2	0, 3	1, 2	2	0, 1	1, 2	1, 2
Adapidae	(4)	(3)	0	0	2	0	(0)	1	2	0	0, 1	2	0	0	1
Plesiadapidae	?	3	0	0	?	0	?	?	?	0	2	2	1	2	2
Paromomyidae	?	(3)	0	0	?	0	?	?	?	0	2	2	1	2 ^c	2
Microsyopidae	1	0	0, 1	1	?	0	?	0	0	0	0	0	0	0	0
Leptictidae	1, 2	0	0	1	2	0	1	0	0	0	0	1	(0)	0	0
Soricoidea	0, 2	1	0	1	0	1	0	0	1	0	0	0	0	0	0
Tenrecidae	0, 1	1, 2	2	1	0	1	0	0	0, 1	0	0	0, 2	0	0	0
Chrysochloridae	?	4	3	2	0	1	0	0	0	2	0	0	0	0	1
Talpinae	(1)	4	3	2	0	1	0	0	0	2	0	0	0	0	1
Desmaninae	1	2	2	1	0	1	0	0	0	2	0	0	0	0	1
<i>Diacodon</i>	2	1	0	1	(0)	0	(0)	0	0	(1)	(0)	0	0	0	0
Amphilemuridae	2	1	0	1	0	0	0	(0)	(0)	1	0	0	0	0	0
Dormaliidae	2	1	(0)	(1)	(0)	0	(0)	(0)	(0)	(1)	(0)	(0)	(0)	(0)	0
Galericinae	1	1	2	1	0	1	0	0	0	1	0	0	0	0	0
Brachyericinae	3	3	4	2	2	1	(0)	0	0	1	0	0	0	0	1
Erinaceinae	1	1	2	1	0	1	0	0	0	1	0	0	0	0	0
Anthropoidea	4	4	0	0	0	0	0	1	2	3	1	2	1	0	1
Omomyidae	4	4	0	0	0	0	0	1	2	0, 2	0, 1	2	0, 1	0	1

^a Soricoidea = Soricidae, Solenodontidae, and Nesophontidae; Tenrecidae = Tenrecinae, Oryzictinae, and Potamogalinae. Lemuriformes = all Malagasy primates (including Cheirogaleidae). Lemuriformes usually includes Eocene Adapidae, but Szalay and Delson (1979) placed this family in its own infraorder (Adapiformes). While not necessarily endorsing this move, we separately denote conditions in adapids in this table and in the text.

^b Characters whose states cannot be directly evaluated in fossils or living taxa are treated in one of two ways:

Parsimonious inference permitted [()]: In the case of highly substantiated sister dyads (i.e., living lemuriformes + adapids, living haplorhines + omomyids, plesiadapids + paromomyids, talpines + desmanines, and erinaceines + brachyerictines), states known to exist in one member of a dyad are inferred to be present in its sister taxon, if there is no evidence to the contrary. Character states inferred from parsimony considerations in this matter are flagged by enclosing the state in question in parentheses. This procedure was also followed for Dormaliidae, Amphilemuridae and *Diacodon*, although sister group relationships among these taxa are not clear.

Parsimonious inference not permitted [?]: Where the first rule cannot be applied, there is no parsimonious solution and the character state is indicated by a question mark. According to this criterion, it is not determinable whether nonmicrosyopid plesiadapoids, whose sister-group relationship to euprimates is unsubstantiated, had tympanic floors mainly formed by the petrosal (Character 1), the ectotympanic (Character 5), or the entotympanic (Character 7).

^c A new, well-preserved skull of *Ignacius*, to be described by the senior author's colleague, R. F. Kay, unquestionably lacks an exposed middle lacerate foramen. Thus MacPhee et al. (1983) were in error in inferring the existence of a pharyngeocarotid anastomosis in this paromomyid.

various combinations of taxa, in this and the following section we employ a convention of the general form [taxon A] + [taxon B] + ... + [taxon N]. This convention makes explicit which taxa are being associated without having to use higher-level names whose definition and ambit vary widely from author to author.

1. Rostral tympanic process of the petrosal [Szalay: Large petrosal contribution to the tympanic floor]

At first glance the erinaceid character states (CS 1.1, 1.3) appear to be quite distinct from the one found in Early Cenozoic hedgehogs (CS 1.2). In Recent erinaceines and galericines, the visible portion of the rostral pro-

cess of the petrosal is limited to the small flange (named the "median tympanic process of the petrosal" by Butler, 1956) intervening between the posterior aspect of the basisphenoid tympanic process and the sulcus for the internal carotid. However, removal of the basisphenoid process in extant hedgehogs reveals that the flange continues onto the tip of the promontory as a low, rugose crest. The more complex petrosal outgrowth of living hedgehogs is thus equivalent in length and position to the featureless rostral process identified in *Diacodon*, *Pholidocercus*, and *Macrocranium*. The brachyericine condition can be interpreted as a more elaborate version of the one characteristic of erinaceines and galericines, produced by additional growth and consequent merger of the rostral and caudal petrosal processes. In this subfamily, the petrosal ossifies all of the posterior tympanic floor and helps to form the aperture of the meatus. Among known erinaceomorphs, only brachyericines can be considered to have a substantial petrosal floor component (fig. 12).

Polarity in Erinaceomorpha: CS 1.1 (morphotypic); CS 1.2, CS 1.3 (derived).

CS 1.0, complete absence of the rostral process (promontorium smooth), may be regarded as the primitive eutherian condition (MacPhee, 1981). The incidence of this character state in Lipotyphla has not been fully documented, but it is known to occur (e.g., in the tenrecid *Hemicentetes*). The definitions of CS 1.1 and 1.2 differ in only one significant respect, which concerns the morphology of the process' leading edge. If the basisphenoid tympanic process is morphotypic for Erinaceomorpha (see character 3), then it may have articulated with the rostral process—in which case CS 1.1 can reasonably be regarded as the antecedent condition. Following this analysis to its logical conclusion, the early Tertiary forms derivedly lost surface complication on the rostral process after the disappearance of the basisphenoid's tympanic outgrowth.

Although CS 1.2 might be regarded as a possible synapomorphy of a clade which includes Amphilemuridae, Dormaliidae, and *Diacodon*, phenetically similar crests occur in some soricomorphs and palaeoryctids (cf. McDowell, 1958; McKenna et al., 1984). One

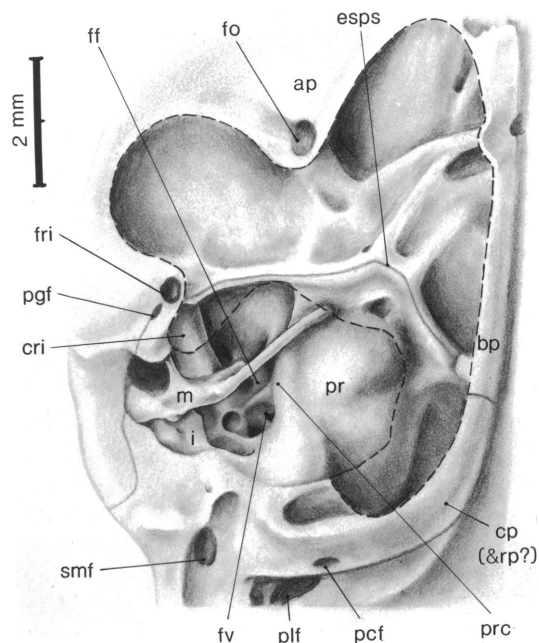


Fig. 12. Ventral view of right auditory region of North American Miocene erinaceid, *Brachyerix macrotis*, largely based on AMNH 21335 and originally figured by Rich and Rich (1971). Bulla partially dissected to reveal tympanic cavity.

also occurs in the putative new leptictid genus. The only known skull of this genus, PU 14526 currently being studied by Novacek, lacks any sign of an entotympanic; one might have been present, but, if so, it clearly did not form a large sutural complex with the promontorial crest. We therefore acknowledge the possibility that a small, elongated, but nonrugose crest on the medial aspect of the promontorium could be primitive at a higher level. However, the alternative possibility, that several unrelated "insectivore" lineages may have developed CS 1.2 in parallel, cannot be excluded. This forces us to regard CS 1.2 as a character state of rather low valency. In any case, we emphasize that small processes on the promontorium have evidently been convergently developed in several therian groups (see MacPhee, 1981, for additional examples), and the mere presence of such a process cannot be decisively counted as a similarity to primates.

While there is no a priori reason to believe that large processes cannot undergo reduc-

tion during evolution, the restricted occurrence of the brachyericine condition (CS 1.3) suggests that it is a derived state dependent on the remarkable degree of middle-ear pneumatization in this subfamily.

2. Caudal tympanic process of the petrosal [Szalay: "Shielding" of the aperture of the fossula fenestrae cochleae]

Two character states (CS 2.1, 2.3) of the caudal tympanic process of the petrosal can be discriminated in our erinaceomorph sample. Early Cenozoic taxa group with Neogene Erinaceinae and Galericinae in possessing a rather small, unpneumatized caudal process that actually "shields" very little. Brachyericines once again differ in that the caudal process is not only expanded and seamlessly fused with the rostral process, but is somewhat pneumatized as well. Moreover, "shielding" is complete, for there is a sheet of bone (posterior septum) which completely hides the fossula when the posterior pole of the promontory is viewed from the ventromedial aspect. No equivalent sheet occurs in other erinaceomorphs, but there is a startlingly similar arrangement in adapids and living lemuriforms. Whether the posterior septum developed in both groups in the same way can only be conjectured, but there can be little doubt that its appearance is dependent on the scale of pneumatization in the rear part of the middle ear.

Polarity in Erinaceomorpha: CS 2.1 (morphotypic), 2.3 (derived).

In view of the absence of pronounced middle-ear inflation in any members of Erinaceomorpha other than Brachyericinae, posterior septum development and complete "shielding" of the fossula are best construed as derived features. Complete or near-complete absence of the caudal process is uncommon in eutherians (MacPhee, 1981), although Novacek (1986: 87, character 55) defined absence, in different wording, as the primitive condition for Eutheria. However, we agree that a small process (= partial concealment of the fossula) is primitive for Erinaceomorpha, whether or not this trait is derived relative to the eutherian morphotype. CS 2.2, although a logical intermediate state between CS 2.1 and 2.3, does not occur in known erinaceomorphs (but does in the tenrecid *Potamogale*, for example).

3. Tympanic process of the basisphenoid

Three character states of the basisphenoid's contribution to the tympanic floor can be discriminated among erinaceomorphs. However, one of these states (CS 3.0) is complete absence, and morphotype construction is further complicated by the fact that the true tympanic process of the basisphenoid is virtually restricted among mammals to several families classically included in Lipotyphla (in addition to Erinaceidae, only Talpidae, Chrysochloridae, and Tenrecidae). These occurrences must be interpreted either as examples of multiple retention of a synapomorphy inherited from the stem lipotyphlan, or as examples of multiple convergence on the same derived state within Lipotyphla.

It has long been known (e.g., Van Kampen, 1905; Van Der Klaauw, 1931) that talpines and chrysochlorids differ from erinaceids and desmanines in that the area of the middle ear protected by the basisphenoid in the first-named pair is filled with cellules (as is the area protected by the alisphenoid). However, the anatomy of basisphenoid tympanic processes is more complicated than this simple contrast suggests. Dissection reveals that living erinaceids possess small diverticula *within* their basisphenoid processes (fig. 4A–E). These diverticula do not communicate, as far as we have been able to discover, with the tympanic or nasal cavities via pneumatic foramina. Therefore they cannot be regarded as air spaces in the conventional sense, because they evidently do not develop as outgrowths of part of the primitive nasopharynx. We confirmed this by dissecting an adult specimen of *Hylomys suillus* (AMNH 229738, Dept. of Mammalogy) preserved in alcohol. In this erinaceid, the large diverticula situated in the base of the basisphenoid tympanic process are completely filled with yellow marrow, flecked with small concentrations of cells that we interpret as red blood cells. We suspect, but cannot prove without appropriate ontogenetic evidence, that these chambers are important centers of hematopoietic activity during the subadult portion of the life cycle (and possibly later). These marrow spaces are apparently served by vascular channels that originate intracranially, for in all skulls in which the point could be checked, small apertures led into these diverticula from the region of the hypophyseal

fossa. It is probable that the transverse venous foramina (fig. 4B) found in many lipotyphlans and marsupials (McDowell, 1958) are also related to this system.

Other galericines also exhibit large diverticula, but it is not known whether they are fat-filled. In *Echinosorex* (fig. 4D) large and often asymmetrically placed foramina open into the diverticula from the basicranial exterior; similar apertures, usually quite small, are seen in some other hedgehogs. They are presumably venous ports and similar in function to the endocranial apertures found in *Hylomys*.

The incidence of marrow tissue in spaces that might otherwise be regarded as paratympanic sinuses has not been investigated in other insectivores. Whether talpines (and chrysochlorids) exhibit such tissue in the cellules composing the medial aspects of their auditory regions has, as far as we know, never been investigated. The capability to produce marrow in these locations is obviously absent in soricids, which lack both basisphenoid tympanic processes and cellules, and presumably absent in desmanines (which have well-inflated processes but no diverticula or cellules). Desmanines are intermediate in the sense that they have well-inflated processes outwardly resembling those of talpines, but lack exposed cellules as do erinaceids (fig. 4E). Soricoids lack both the tympanic process and cellules.

The only other taxon in the comparative sample which displays a basicranial outgrowth that might be classified as a basisphenoid tympanic process is *Microsyps annectens* (Novacek and Eaton, in prep.). This species exhibits a small, tablike outgrowth of the basisphenoid that partly shelters the anterior carotid foramen. As far as may be determined from existing material, the outgrowth is not inflated. *Cynodontomys* (fig. 13) apparently lacked this excrescence, which suggests that its appearance is derived in *Microsyps* (fig. 13). The only other mammals in which tympanic processes of the basisphenoid have been identified are macroscelideans and *Plagiomene* (MacPhee et al., in prep.); their processes differ in many details from each other and from the basisphenoid processes of lipotyphlans, which we take as evidence of their nonhomology.

Polarity in Erinaceomorpha: 3.2 (morphotypic); 3.0, 3.4 (derived).

MacPhee (1981) noted, but did not endorse, the argument that the tympanic process of the basisphenoid appeared in the ancestral line of lipotyphlans, but was later lost in certain groups. He pointed out that this sequence could not be evaluated in a satisfactory manner because so few basicrania of early Cenozoic lipotyphlans were then known. We now know that *Pholidocercus* and *Diacodon* lacked any sort of basisphenoid outgrowth in their tympanic floors, which raises a major interpretive problem. If absence of the process is a lipotyphlan symplesiomorphy, erinaceids possess a derived state (presence) found in talpids, tenrecids, and chrysochlorids but not in early Cenozoic eutherians here regarded as definite erinaceomorphs. Conversely, if presence of the process is the symplesiomorphous condition for lipotyphlans, *Pholidocercus* and *Diacodon* (and probably *Macrocranium* as well) possess a derived state (absence) found in Soricidae, Solenodontidae, and Nesophontidae, but not in any Neogene erinaceomorph.

Having to make a choice between the alternatives just listed is not comfortable, but CS 3.2 appears to us to be preferable not only as the morphotypic state for Erinaceomorpha but for Lipotyphla as a whole. Although our character analysis specifies that tympanic outgrowths of the basisphenoid have evolved on more than one occasion during eutherian phylogeny, the total number of such convergent developments is very low. If every such development is autapomorphic, then we are faced with having to explain why the potentially derived state (presence of the basisphenoid tympanic process) repeatedly arose in lipotyphlan lineages but virtually never in nonlipotyphlans. It seems more plausible to us that McDowell (1958) was correct in portraying the tympanic process of the basisphenoid as having arisen only once in Lipotyphla, at or near their origin. This permitted him to argue that it was therefore lost only once, at the base of the soricoid radiation. Our interpretation of the new evidence presented here requires that we accept a second instance of loss, this time within Erinaceomorpha.

Within Erinaceomorpha, then, there are two transformation series for Character 3. The

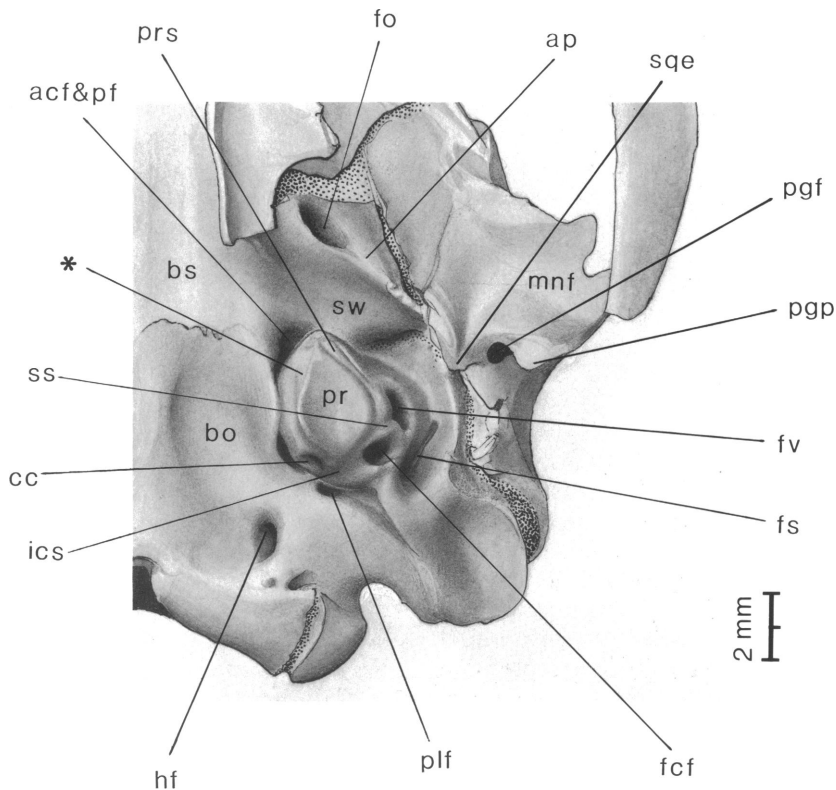


Fig. 13. Ventral view of left auditory region of *Cynodontomys latidens*, AMNH 55286 (middle Eocene, Huerfano Formation, Colorado); based on a figure published by McKenna (1966), modified here to include some features better seen on specimen's right side. Asterisk identifies a small ?articular surface on the medial side of the promontorium (for the ectotympanic or possibly an entotympanic). The crest on the promontorium, sometimes interpreted as the equivalent of the euprimate petrosal plate, is simply the raised lateral margin of this surface (cf. equivalent crest associated with entotympanic bulla in tree shrews; MacPhee, 1981). *Cynodontomys* lacks a basisphenoid process, but a small one is present in its confamilial *Microsyops*.

erinaceomorph initiator possessed a small tympanic process of the basisphenoid, inherited from the ancestral lipotyphlan. This process was lost in the line(s) leading to Amphilemuridae, Dormaaliidae, and *Diacodon*. The line leading to Erinaceidae retained the process in something close to its primitive form, but in Brachyericinae it underwent an important transformation (to CS 3.4). Adoption of these sequences allows us to consider the tympanic process of talpids and erinaceomorphs as homologs, a robust conclusion incidentally supported by other evidence for the phyletic association of these taxa (McDowell, 1958). Soricomorphs underwent a similar sequence: soricoids lost the process, but tenrecids and chrysochlorids preserved it.

4. Tympanic process of alisphenoid

Differences in the size of the alisphenoid floor component seem to be strongly correlated with the scale of middle-ear pneumatization in erinaceomorphs. Thus in *Hemichinus* and *Paraechinus*, which have more inflated middle ears than *Erinaceus*, the alisphenoid process forms a continuous rampart which is laterally penetrated by the departing stapedial ramus inferior. A similar arrangement is seen in *Brachyerix* (fig. 12), save that the exit-point of the ramus inferior is shifted into the domain of the squamosal. If pneumatization were insubstantial in the last common ancestor of erinaceomorphs, as most lines of evidence suggest, the low "preotic crest" is morphotypic. Its wide occurrence outside Erinaceomorpha (MacPhee,

1981) implies that minor alisphenoid participation in the tympanic floor is ancient.

Polarity in Erinaceomorpha: CS 4.1 (morphotypic), 4.2 (derived).

5. Ectotympanic

Brachyericines differ radically from erinaceines, galericines, and early Cenozoic eutherians generally in the degree to which the ectotympanic is occluded by the tympanic floor. In their original report on *Brachyerix*, Rich and Rich (1971) were unable to separate the ectotympanic from other elements of the tympanic floor. They therefore concluded that it was either indivisibly fused with other floor components, or had fallen away shortly after death in the available material. Later, T. Rich (1981) demonstrated that the slightly expanded ectotympanic of *Brachyerix* (not shown in fig. 12) is actually enclosed by the bulla, and is therefore aphaneric as in Scandentia and Lemuriformes. Although semiphany (ectotympanic partly but not completely occluded by other floor components) is the rule in living hedgehogs, it would have been a simple matter to transform the erinaceine/galericine condition into the brachyericine one (cf. MacPhee, 1981).

Semiphany and aphanery occur because a full complement of sutural tissues is not elaborated between the ectotympanic and the enclosing floor component(s) (MacPhee, 1977). At least three higher taxa in the comparative set utilized here display intragroup differences in the degree of exposure of the ectotympanic (Desmaninae vs. Talpinae, Brachyericinae vs. Erinaceinae, and Lemuriformes vs. Lorisiformes).

The mediolaterally narrow ectotympanic appears to be a primitive therian feature which has been retained in many eutherian groups. However, MacPhee (1981) distinguishes between completely unexpanded and slightly expanded forms of the anulus, arguing that the former is a rare trait which involves the retention, into the adult stage, of the fetal form of the ectotympanic. Novacek (1986) points out that it is difficult in practice to distinguish between unexpanded and slightly expanded character states, and regards all "horseshoe shaped" ectotympanics as primitive in the absence of evidence to the contrary. However, there is consensus that complete aphanery, as exhibited by Brachy-

ericinae, Lemuriformes, and Adapidae, is a derived feature. *Leptictis* may be described as intermediate in the sense that it combines an essentially unexpanded annulus with a marked degree of ectotympanic enclosure by the bulla.

Polarity in Erinaceomorpha: CS 5.0 (morphotypic), 5.1 (derived).

6. Squamosal participation in temporomandibular joint and anterior tympanic wall

The postglenoid process is weak or absent in living lipotyphlans (McDowell, 1958; Novacek, 1986). In most living hedgehogs the postglenoid process is a tiny, obliquely disposed flange which separates the mandibular fossa from the postglenoid foramen. In *Erinaceus* and *Hemiechinus*, however, only the posterolateral portion of this flange is formed, and the postglenoid foramen is not separated by a bony sheet from the mandibular fossa (fig. 4B). *Brachyerix* and *Metechinus* possess a flange which recalls that of the majority of living erinaceids. The Early Cenozoic forms notably differ from all of their later relatives in having a conspicuously large and more transversely oriented postglenoid process reminiscent of, but not as well developed as, that of *Leptictis* (Novacek, 1986).

In some living erinaceomorphs (e.g., *Echinosorex*), the entoglenoid part of the squamosal sends out a prominent, freely ending flange beneath the track of the stapedial ramus inferior. In others (*Hemiechinus*, *Paraechinus*), this part of the squamosal is integrated into the preotic crest. *Brachyerix* is similar to this latter group. In *Erinaceus*, the squamosal flange is rarely evident, and never significantly contributes to the bounding of the anterior wall. These contrasts are trivial and they involve only minor differences in the degree of elaboration of floor components common to the whole group.

Polarity in Erinaceomorpha: CS 6.0 (morphotypic), 6.1 (derived).

This transformation series requires a minimum of two independent losses of a large postglenoid process in Lipotyphla, once in soricomorphs sensu McDowell (1958) and once in the lineage leading to Neogene erinaceids. Depending on one's view of Soricomorpha as a natural group, additional losses may or may not have to be invoked. Like the basisphenoid process, the articular en-

toglenoid is a rare trait outside of Lipotyphla, but its pattern of distribution within this order is not a simple one.

7. Entotympanics

Entotympanics have never been conclusively demonstrated in any lipotyphlan, living or extinct, although one unquestionably occurs in Leptictidae (McKenna, 1966; Novacek, 1986). Their presence may or may not be morphotypic for Eutheria, depending on how one construes the homologies of these elements among the placental groups that actually possess them (MacPhee, 1981). McDowell's (1958) inference that entotympanics were functionally replaced by the tympanic process of the basisphenoid in the stem lipotyphlan has not been substantiated (Novacek, 1986).

Polarity in Erinaceomorpha: CS 7.0 (morphotypic).

8. Petrosal participation in tympanic roof

Although the petrosal is extensively involved in ossifying the lateral part of the tympanic roof in living erinaceomorphs, the anteromedial and anterolateral parts of the roof are largely formed by sphenoid material (Butler, 1948, 1956; MacPhee, 1981). In *Pholidocercus* the petrosal may contribute more extensively, but this is difficult to gauge in the absence of a good candidate for the epitympanic sphenopetrosal suture. Specimens of *Macrocranium* and *Diacodon* are seriously damaged in the relevant areas, although it is clear that their petrosal apices were anteromedially lengthened to some degree. Lengthening also occurs in some soricids (McDowell, 1958), but in this group there is usually a large piriform fenestra in the tympanic roof which is not closed by any bone (MacPhee, 1981).

Polarity in Erinaceomorpha: CS 8.0 (morphotypic).

Although there seems to be some variation among erinaceomorphs in the proportion of the tympanic roof formed by the petrosal, in the present context it is surely relevant that no erinaceomorph—even the highly derived *Brachyerix* (fig. 12)—exhibits a euprimate-like tympanic roof formed almost entirely by the petrosal (CS 8.1).

9. Sphenoid participation in tympanic roof

The sphenoid forms a large part of the tympanic roof in most lipotyphlans, and the existence of the epitympanic sphenopetrosal suture within the tympanic cavity is clearly morphotypic for the group. Although a small piriform fenestra may also be morphotypic, the presence and size of this dehiscence in the adult stage varies among and within lipotyphlan families (MacPhee, 1981). The relatively enormous fenestrae found in many soricids can reasonably be regarded as derived. If *Pholidocercus* is typical, the piriform fenestra had to have been small or absent in Early Cenozoic erinaceomorphs, as it is in living hedgehogs. Novacek et al. (1983) provisionally identified a piriform fenestra in *Diacodon*, but the relevant area is damaged in AMNH 48587 and the aperture in the tympanic roof may therefore be artificial.

Polarity in Erinaceomorpha: In our character analysis, only a single state is found in erinaceomorphs (CS 9.0), and this is taken to be morphotypic. Finer resolution of this character within the group will have to await the discovery of Early Cenozoic taxa with interpretable tympanic roofs.

10. Squamosal participation in tympanic roof and pneumatization of lateral part of middle ear

The squamosal almost always participates in the tympanic roofs of eutherians, but its contribution is usually minor (MacPhee, 1981). However, in a wide variety of groups, including some Lipotyphla, its exposure within the middle ear can be substantially increased by pneumatization.

At present we can define only three character states in Lipotyphla (CS 10.0, 10.1, 10.2). CS 10.0 is equivalent to the absence of inflation, as seen in soricoids. The difference between the CS 10.1 and 10.2 principally concerns the degree to which paratympanic sinuses inflate the lateral boundaries of the middle ear (crista parotica of the mastoid region and the meatal portion of the squamosal). Living and known extinct erinaceomorphs do not develop true mastoid cavities (i.e., sinuses comparable to that of *Homo* which develop in the rear of the epitympanic recess, in the region of the ampullar end of

the lateral semicircular canal). However, they do develop small diverticula at a more lateral position, in relation to the crista parotica and base of the tympanohyal. Despite their position on the morphological sidewall of the skull, in living species these diverticula lie medial to the attachment point of the pars flaccida of the tympanic membrane and are therefore incorporated within the middle ear (e.g., fig. 4C). We assume that this was also true of *Pholidocercus*, the only Cenozoic genus in which diverticular presence can be demonstrated with some certainty (fig. 6). Talpids are somewhat similar to *Pholidocercus*, but in them the squamosal is substantially more inflated. In Chrysochloridae (fig. 4F), the entire lateral aspect of the skull is greatly expanded in order to contain the enlarged auditory ossicles (Simonetta, 1957).

Polarity in Erinaceomorpha: CS 10.1 (morphotypic).

Considering the morphological variety found in the lateral part of the tympanic roof in erinaceomorphs, about all that can be said at present is that this group displays a pronounced tendency to form small parameatal sinuses. This may be evidence that CS 10.1 is morphotypic for Erinaceomorpha.

11. Internal carotid system

Polarity in Erinaceomorpha: Although some of the relevant fossil evidence is difficult to interpret (e.g., *Macrocranium nitens* AMNH 48697) because of damage, the basic patterning of the internal carotid system (internal carotid stem plus all of the primitive branches of its daughter vessels within the tympanic cavity) seems to be essentially invariant among known erinaceomorphs. The constant erinaceomorph character state (CS 11.0) is identical with the state here inferred for the last common ancestor of all of the taxa referenced under Character 11 in table 2. We state the primitive condition in this way because the transpromontorial pattern is not regarded by all observers as the morphotypic one for Eutheria (Presley, 1979; Wible, 1983; Novacek, 1986; but see Wible, 1986).

12. Stapedial ramus inferior

Polarity in Erinaceomorpha: Brachyericines do not differ from erinaceines or Early Cenozoic erinaceomorphs in the location of

the furcation point of the proximal stapedial, in the anteromedial corner of the middle ear. In this sense, erinaceomorphs are invariant among themselves, and compare closely to most other eutherians in the comparative set. We regard CS 12.0 as close to or identical with the eutherian morphotypic state.

13. Supply to meninges

Polarity in Erinaceomorpha: Erinaceomorphs in which the point can be checked are also clearly primitive in utilizing the ramus superior as the conduit for most or all of the blood supply to the meninges (CS 13.0). They notably lack the more derived states seen in some members of the comparative set, and may be regarded as having a stapedial circulation resembling that of the ancestral eutherian (cf. MacPhee, 1981).

14. Supply to circulus arteriosus, additional to vertebral arteries [Szalay: Absence of a "medial internal carotid"]

Prior to the publication of Presley's (1979) paper, it was generally accepted among mammalian paleontologists that the ancestral eutherian possessed two internal carotids on each side of the head. Presley (ibid.) and others (e.g., MacPhee, 1981; Wible, 1984) have demonstrated that this dual-carotid hypothesis is fallacious, and that all mammals produce only a single internal carotid during ontogeny.

Although Szalay's (1975) character state is based on a false dichotomy, it is true that the circulus arteriosus can be supplied in more than one way in mammals. Sometimes the internal carotid is reduced or absent in the adult, and most or all of the brain's blood supply is routed through the vertebral arteries (CS 14.2). Another rare condition involves diverting the cerebral supply through the ascending pharyngeal (CS 14.1).

Polarity in Erinaceomorpha: Neither of the highly derived states noted above can be legitimately inferred for any erinaceomorphs, which invariably display the primitive eutherian condition (CS 14.0).

15. Intratympanic arterial canals [Szalay: Bone-enclosed divisions of the internal carotid]

Although the presence of arterial canals in the middle ear seems derived for eutherians (Archibald, 1977; MacPhee, 1981; Novacek, 1986), the distribution of intratympanic vascular conduits is not isomorphic with any acceptable hypothesis of eutherian cladogeny. This fact is best interpreted as evidence that canals have been independently developed many times. MacPhee (1981) noted that there is an apparent correlation between the degree of middle ear pneumatization and the spread of bone around intratympanic arteries and nerves. This might account for the slight development of canals in *Paraechinus*, which has a relatively more expanded middle ear than do other living erinaceomorphs (Rich and Rich, 1971). However, the correlation is by no means perfect, since (for example) complete tubes are formed in *Desmana* but not in *Hylomys*, despite roughly equivalent degrees of pneumatization in these forms. Fleischer (1973) correlated canal production with the need to dampen noise created by arterial pulsation in order to enhance low-frequency auditory sensitivity, but here too the correlation is lower than expected (MacPhee, 1981). Either way, the little-pneumatized ears of early Cenozoic erinaceomorphs were unlikely to have been specialized for low-frequency audition, and for this reason we suspect that intratympanic canals are not morphotypic for the group. Absence or involution of intratympanic arteries (CS 15.2) is obviously antithetical to canal development, but this trait is unquestionably derived and does not occur within Erinaceomorpha.

Polarity in Erinaceomorpha: CS 15.0 (morphotypic), 15.1 (derived).

The derived state is limited to brachyericines (fig. 12) among accepted hedgehogs, since in *Paraechinus* only the internal carotid stem is covered by bone.

16. Promontorium [Szalay: Rounded promontorium]

This character is not analyzed because we are unable to distinguish any useful states for it in the groups of interest. Promontoria are flat in monotremes, rounded in leptictids and paramyids, and "towered" in some caviomorphs, which undoubtedly indicates that promontorial shape is grossly correlated with the number of cochlear turns. However, the

number of turns—conceivably of some systematic significance—cannot be inferred from relative convexity alone, and we see no essential differences within the comparative set in the degree of promontorial "roundedness."

PRIMATE BASICRANIAL MORPHOTYPE

Like the suborder Erinaceomorpha, the order Primates has proven resistant to easy diagnosis (for recent and divergent views, see Szalay and Delson, 1979; MacPhee et al., 1983; Martin, 1986; Wible and Covert, 1987; Szalay et al., 1987). Most paleoprimatologists accept the monophyly of Euprimates, but there is considerable disagreement about the status of the individual families comprising Plesiadapoidea. Although we question whether Primates can remain monophyletic if forced to include such groups as Picrodontidae and Uintasoricidae, no basicranial remains assigned to these taxa have been described. They therefore have no direct bearing on reconstructing the primate basicranial morphotype and can be safely ignored. This approach cannot be taken with Microsyopidae, since good basicranial material of *Microsyops* exists (fig. 13).

In the first two rows of table 4, we map the euprimate morphotype against that of Plesiadapidae + Paromomyidae. The morphotype of Microsyopidae is presented separately in the last row of the table.

To establish morphotypic states of euprimates, we assumed that invariant characters are euprimate symplesiomorphies (Characters 1, 3, 4, 6, 7, 8, 9, 12). The remaining characters are represented by more than one state in euprimate taxa, and their morphotypic condition is the subject of much debate in paleoprimatology. Our preference is to adopt decisions about the morphotype made by MacPhee (1981) and MacPhee and Cartmill (1986). A similar strategy was followed in defining the morphotype of Plesiadapidae + Paromomyidae. Although the external auditory meatus seems to have been formed by the ectotympanic in the paromomyid *Phenacolemur* (Szalay, 1975), we do not attribute an ectotympanic character state to Paromomyidae (table 4, Character 5) because we

TABLE 4
Comparison of Morphotypic Character States of Basicranium in Euprimates (EU),
Plesiadapidae (PL) + Paromomyidae (PA), and Microsyopidae (MI)

	Characters ^a														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
EU	4	4	0	0	0	0	0	1	2	0	0	2	0	0	1
PL + PA	?	3	0	0	?	0	?	?	?	0	2	2	1	2	2
MI	1	0	0/1	1	?	0	?	0	0	0	0	0	0	0	0

^a Characters and character states defined in table 2.

cannot tell whether these plesiadapoids were lorislake or rodentlike in their bullar composition. Although we specify a morphotypic state of Character 14 for Plesiadapidae + Paromomyidae, both families display a highly derived condition of the vascular supply to the circulus arteriosus that may not be primitive for plesiadapoids in general. Fortunately, there is some new evidence bearing on these issues which should help to clarify primitive character states of the plesiadapoid auditory region (R. F. Kay, personal commun.; see footnote *c*, table 3).

Compared to our concept of the primitive eutherian basicranial morphotype, Euprimates + Plesiadapidae + Paromomyidae mutually possess derived states of Characters 2, 12, and 15. For the remaining 12 characters, states are either primitive in both or cannot be compared because of missing data. If the mutually held derived states are taken to be homologous, then one has at least three reasons for accepting the joint monophyly of the taxa in question. Those who would do so, however, are forced to concede either that euprimates have gained intratympanic arterial canals not present in the last common ancestor of Euprimates + Plesiadapidae + Paromomyidae, or, alternatively, that Plesiadapidae + Paromomyidae lost canals primitively present (Character 15). Loss of the stapedial ramus inferior (Character 12) is the only derived basicranial character which expresses the same state in both major groups of primates. However, Plesiadapidae + Paromomyidae evidently lost the ramus inferior by involuting the entire internal carotid system; most Euprimates followed a more conservative course and reduced only the vessel primitively supplying the lower jaw. These cases of stapedial simplification are perhaps better regarded as homoplasious re-

semblances. By contrast, it is somewhat easier to believe that the derived states of the caudal tympanic process (CS 2.3 and 2.4) are on the same morphocline, although MacPhee and Cartmill (1986) have argued that CS 2.3 is actually an autapomorphy of Lemuriformes + Adapidae, and that the similar condition in Plesiadapidae + Paromomyidae is due to convergence.

However we choose to judge the derivedness and polarity of traits possibly shared by Euprimates + Plesiadapidae + Paromomyidae, it is evident from table 4 that Microsyopidae share virtually none of the character states that might be used to define a monophyletic primate clade. Nearly all of the traits that can be directly observed in the microsyopid basicranium are simply primitive for Eutheria; those that may be derived (CS 3.1, 4.1) are not found in any euprimate or non-microsyopid plesiadapoid. Indeed, the only potentially derived traits of the basicranium currently definable for *Microsyops* (presence of small alisphenoid and basisphenoid tympanic processes) otherwise occur together only in some lipotyphlans.

If the dental traits apparently shared by *Microsyops* and (other) primates are truly synapomorphies (Rose and Fleagle, 1981), then the primate basicranial morphotype is either not distinguishable from that of the basal eutherian, or not distinguishable from that of Lipotyphla + Leptictidae (assuming for the sake of argument that this latter collocation is monophyletic). For the purpose of this investigation, there is little point in making a choice between these alternatives, since each implies that any derived traits found in erinaceomorphs and specific primate groups are best interpreted as convergences or as higher-level apomorphies shared by a multiplicity of eutherians. To put it another way,

TABLE 5
Comparison of Morphotypic Character States of Basicranium in Nonmicrosyopid
Primates (NMP) and Erinaceomorphs (ER)

	Characters ^a														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
NMP	?/4	4	0	0	?/0	0	?/0	?/1	?/2	0	0	2	0	0	1
ER	1	1	2	1	0	0	0	0	0	1	0	0	0	0	0

^a Characters and character states defined in table 2.

if microsyopids are to be regarded as the sister-group of primates, the sister-group of this dyad may be Lipotyphla as a whole, Lipotyphla + Leptictidae, or some still larger assemblage—but not Erinaceomorpha alone, unless one is prepared to accept a clade that can only be defined by the common possession of primitive traits.

The alternative is to omit Microsyopidae from further consideration and relegate them to Eutheria incertae sedis. This procedure would be appropriate in any event, since Szalay had concluded by 1975 that microsyopids could not be retained in Primates if this order were to remain monophyletic (see also Szalay et al., 1987). We have therefore generated a second morphotypic list for primates, based on states inferred for the last common ancestor of Euprimates plus nonmicrosyopid plesiadapoids (table 5). To reflect the omission of Microsyopidae, the resulting taxon assemblage will be identified as "NM primates." NM primates are what Szalay had in mind when he developed his list of primate-erinaceomorph similarities, and a comparison of the morphotype of NM primates to those of different groupings of erinaceomorphs now permits us to undertake a proper test of his weak and strong hypotheses.

A TEST OF HYPOTHESES OF PRIMATE-ERINACEOMORPH RELATIONSHIPS

The states of Characters 1, 5, 7, 8, and 9 in table 5 cannot be directly observed in plesiadapids and paromomyids, and their morphotypic form in NM primates must therefore be based on distributions in living taxa and Eocene euprimates. This uncertainty is flagged in the table by combining acknowledged euprimate morphotypic states with

question marks. As previously noted, we do not regard character states associated with the cranial vasculature of plesiadapids and paromomyids as morphotypic for the order, largely because it would then be necessary to infer that the stem euprimate reinvented the carotid system of the basal eutherian. Our concept of the euprimate morphotype is the same as that of the NM morphotype, except that we strip the question marks associated with uncertain character states in the latter.

According to table 4, NM primates and erinaceomorphs morphotypically possess six character states (for Characters 5, 6, 7, 11, 13, 14) which are primitive for eutherians. NM primates are also primitive for Characters 3, 4, and 10, while erinaceomorphs are additionally primitive for Characters 8, 9, 12, and 15. They are both derived for Characters 1 and 2, but the specialized states in question are not the same. However, these states could be on the same morphocline if the last common ancestor of NM primates and erinaceomorphs possessed both rostral and caudal tympanic processes of the petrosal. There are three major problems with making this assumption. First, bullar constitution is ambiguous in plesiadapoids and paromomyids (MacPhee et al., 1983). This is a different problem from the one connected with the analysis of microsyopid bullar constitution, since we know *for certain* that microsyopids lacked petrosal contributions in their tympanic floors. Secondly, both petrosal processes are simultaneously present in taxa outside the euprimate-erinaceomorph dyad (e.g., talpids, soricids, macroselideans, some tenrecids). If any of these processes are homologous with those of primates and hedgehogs, presence of both petrosal tympanic outgrowths does not uniquely define a NM primate-erinaceomorph clade. Thirdly, were

such a clade to be erected, the few derived basicranial traits which could be counted as synapomorphies of Lipotyphla must instead be dismissed as convergences, because they do not occur in any NM primates. Therefore, the minimum price for accepting the weak version of Szalay's hypothesis involves removing Microsyopidae from Primates, demoting petrosal participation in the tympanic floor to the rank of a probable eutherian symplesiomorphy, and ignoring (as a convergence) the derived presence of a large basisphenoid process in both erinaceomorphs and a variety of other lipotyphlans. This price need not be paid if one is willing to invoke multiple convergences (and reconvergences) wherever necessary to make results conform to expectations. However, implicit in this procedure is a denial of comparative morphology as the basis for recognizing homology, and therefore of the value of undertaking character analysis in the first place. We reject all of these manipulations, and conclude that there is no material support for the weak version of Szalay's hypothesis.

Since Szalay's weak proposal is more inclusive than his strong one, if undoubted monophyletic groups were being analyzed it would ordinarily follow that rejection of the former hypothesis must necessarily result in rejection of the latter. However, if the groups in question are not likely to be monophyletic, the only thing which a cladistic analysis will demonstrate is the futility of trying to make sense of the relationships of paraphyletic or polyphyletic taxa. Rather than atomizing the constituent taxa of Primates and Erinaceomorpha and performing every possible cross-comparison in the hope that some analyses will actually involve monophyletic groups, we will consider only a single test of Szalay's strong hypothesis. This test considers the possibility that NM primates are most closely related to one or more of *Diacodon*, *Amphilemuridae*, and *Dormaalidae*, the only taxa known to fit Szalay's (1975) stipulation that primates derive from an Early Cenozoic hedgehoglike eutherian "with a basicranium not very different from the erinaceotan morphotype."

If *Diacodon*, *Pholidocercus*, and *Macrocranium* are not the closest known relatives of Erinaceidae in a cladistic sense, then we

cannot assume that the general erinaceomorph morphotype defined in the preceding section is applicable to them. The usual problems which attend morphotype reconstruction are exacerbated in this case by missing data and the obvious fact that we can offer little convincing basicranial evidence that these three taxa ought to be considered as a monophyletic unit. However, even if their combination produces a paraphyletic or polyphyletic assemblage, our character analysis would not be affected because the comparable parts of their basicrania are nearly identical. For this reason we feel justified in treating them as a single unit ("ADD group" in table 6; the first term is an acronym composed of the initial letters of *Amphilemuridae*, *Dormaalidae*, and *Diacodon*).

Inspection of table 6 demonstrates that the ADD group is, in general, no more like the NM primates than the assemblage which includes all erinaceomorphs. Once again, the only features which both taxon sets possess in a derived state are traits of Characters 1 and 2, and all that was previously said about these traits being on the same morphocline applies here as well, *mutatis mutandis*. The only additional phenetic similarity of NM primates and the ADD group that could be regarded as possibly significant is the absence of the basisphenoid tympanic process. However, absence of this process could be counted as cladistically important only if there is reason to believe that it is derived in both NM primates and the ADD group. If the ADD group is not a member of either Erinaceomorpha or a more inclusive assemblage of lipotyphlans, then there is little reason to suspect that the basisphenoid produced a tympanic outgrowth in ancestors of the ADD group. If, as we believe, the ADD taxa are cladistically erinaceomorphs, loss of the basisphenoid process becomes a stronger contender as a derived feature. However, the only hard evidence for assuming a similar sequence in Primates is the presence of a flange-like basisphenoidal outgrowth in *Microsyops*—which is, of course, irrelevant if microsyopids are neither primates nor the sister-group of primates. As already discussed, if microsyopids are indeed primates or closely related to them, most character states in the primate morphotype will have to be reset to "0", with

TABLE 6
Comparison of Morphotypic Character States of Basicranium in Nonmicrosyopid
Primates (NMP) and "ADD Group"^a

	Characters ^b														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
NMP	?/4	4	0	0	?/0	0	?/0	?/1	?/2	0	0	2	0	0	1
ADD	2	1	0	1	0	0	0	0	0	1	0	0	0	0	0

^a ADD = Acronym for Amphilemuridae, Dormaalidae, and *Diacodon*.

^b Characters and character states defined in table 2.

all that implies for future use of the basicranium as a useful source of characters in primate systematics.

In sum, we find no cladistic merit in either the weak or the strong versions of Szalay's hypothesis of primate-erinaceomorph relatedness. With the possible exception of the highly derived brachyricines, which are unarguably erinaceids (T. Rich, 1981), no known erinaceomorph displays a strong phenetic resemblance to any primate in details of basicranial architecture. The intertaxon similarities that do exist are strongest not between undoubted primates and erinaceomorphs, but between groups of less certain placement, like microsyopids and members of the ADD group. Even in the latter case the list of resemblances is not very exclusive, for similar combinations of traits appear again and again in diverse mammalian taxa. This is a good reason for considering such trait complexes as primitive, but it is a poor one for using them to make phylogenetic inferences.

REFERENCES

- Archibald, J. D.
1977. Oldest known eutherian stapes and a marsupial petrosal bone from the Late Cretaceous of North America. *Nature* 281: 669-670.
- Bugge, J.
1974. The cephalic arterial system in insectivores, primates, rodents and lagomorphs, with special reference to the systematic classification. *Acta Anat.* 87(suppl. 62): 1-160.
- Butler, P. M.
1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. *Proc. Zool. Soc. London* 1948: 446-500.
1956. The skull of *Ictops* and the classification of the Insectivora. *Ibid.* 1956: 453-481.
1972. The problem of insectivore classification. In K. A. Joysey and T. S. Kemp (eds.), *Studies in vertebrate evolution*, pp. 253-265. New York: Winchester Press.
- Cartmill, M., and R. D. E. MacPhee
1980. Tupaiid affinities: the evidence of the carotid arteries and cranial skeleton. In W. P. Luckett (ed.), *Comparative biology and evolutionary relationships of the tree shrews*, pp. 95-132. New York and London: Plenum Press.
- Cartmill, M., R. D. E. MacPhee, and E. L. Simons
1981. Anatomy of the temporal bone in early anthropoids, with remarks on the problem of anthropoid origins. *Am. J. Phys. Anthropol.* 56: 3-21.
- Clemens, W.
1974. *Purgatorius*, an early paromomyid primate (Mammalia). *Science*, 184: 903-905.
- Conroy, G. C., and J. R. Wible
1978. Middle ear morphology of *Lemur variegatus*: some implications for primate paleontology. *Folia Primatol.*, 29: 81-85.
- Diamond, M. K.
1987. Unusual example of a persistent stapedia artery in a human. *Ant. Rec.* 218: 345-354.
- Fleischer, G.
1973. Studien am Skelett des Gehörorgans der Säugetiere, einschliesslich des Menschen. *Säugetierkundl. Mitt.* 21: 131-239.
- Gawne, C. E.
1968. The genus *Proterix* (Insectivora, Erinaceidae) of the Upper Oligocene of North America. *Am. Mus. Novitates* 2315, 26 pp.
- Heller, F.
1935. *Amphilemur eocaenicus* n. g. et n. sp., ein primitiver Primate aus dem Mittel-

- eoän des Geiseltales bei Halle a. S. Nova Acta Leopoldina 2: 293–300.
- Henson, O. W.
1961. Some morphological and functional aspects of certain structures of the middle ear in bats and insectivores. Sci. Bull. Univ. Kansas 42: 151–255.
- Hürzeler, J.
1946. *Gesneropithecus peyeri* nov. gen. nov. spec., ein neuer Primate aus dem Ludien von Gösen (Solothurn). Eclogae Geol. Helv. 39: 354–361.
1947. *Alsaticopithecus leemanni* nov. gen. nov. spec., ein neuer Primate aus dem unteren Lutetian von Buchweiler in Unterelsass. Ibid. 40: 343–356.
- Koenigswald, W. von
1980. Fossilagerstätte Messel—Literaturübersicht der Forschungsergebnisse aus den Jahren 1969–1979. Geol. Jahrb. Hessen 108: 23–38.
- Koenigswald, W. von, and W. Michaelis
1984. Fossilagerstätte Messel—Literaturübersicht der Forschungsergebnisse aus den Jahren 1980–1983. Geol. Jahrb. Hessen 112: 5–26.
- Koenigswald, W. von, and H.-P. Schierner
1987. The ecological niche of an extinct group of mammals, the early Tertiary apatemyids. Nature 326: 595–597.
- Koenigswald, W. von, and G. Storch
1983. *Pholidocercus hassiacus*, ein Amphilemuride aus dem Eozän der “Grube Messel” bei Darmstadt (Mammalia, Lipotyphla). Senckenbergiana Lethaea 64: 447–495.
- MacPhee, R. D. E.
1977. Ontogeny of the ectotympanic-petrosal plate relationship in strepsirhine primates. Folia Primatol. 27: 245–283.
1981. Auditory regions of primates and eutherian insectivores: morphology, ontogeny, and character analysis. Contrib. Primatol. 18: 1–282.
- MacPhee, R. D. E., and M. Cartmill
1986. Basicranial structures and primate systematics. In D. Swindler and J. Erwin (eds.), Comparative primate biology, vol. 1, Systematics, evolution and anatomy, pp. 219–275. New York: Alan R. Liss.
- MacPhee, R. D. E., M. Cartmill, and P. D. Gingerich
1983. New Palaeogene primate basicrania and definition of the order Primates. Nature 301: 509–511.
- MacPhee, R. D. E., M. Cartmill, and K. D. Rose
In prep. Relationships of *Plagiomene*: the basicranial evidence.
- Maier, W.
1979. *Macrocranium tupaiodon*, an adapisorcid (?) insectivore from the Eocene of “Grube Messel” (Western Germany). Palaeont. Z. 53: 38–62.
- Martin, R. D.
1986. Primates: a definition. In B. Wood, L. Martin, and P. Andrews (eds.), Major topics in primate and human evolution, pp. 1–31. Cambridge Univ. Press.
- McDowell, S. B.
1958. The Greater Antillean insectivores. Bull. Am. Mus. Nat. Hist. 115: 113–214.
- McKenna, M. C.
1966. Paleontology and the origin of primates. Folia Primatol. 4: 1–25.
- McKenna, M. C., Xue Xiangxu, and Zhou Ming-zhen
1984. *Prosarcodon lonanensis*, a new Paleocene micropternodontid palaeoryctoid insectivore from Asia. Am. Mus. Novitates 2780: 17 pp.
- Novacek, M. J.
1977. Aspects of the problem of variation, origin and evolution of the eutherian auditory bulla. Mamm. Rev. 7: 131–149.
1982. *Diacodon alticuspis*, an erinaceomorph insectivore from the early Eocene of northern New Mexico. Contrib. Geol. Univ. Wyoming 20: 135–149.
1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bull. Am. Mus. Nat. Hist. 183: 1–112.
- Novacek, M. J., and J. Eaton
In prep. Cranial features of *Microsyops*: new evidence.
- Novacek, M. J., T. M. Bown, and D. Schankler
1985. On the classification of the early Tertiary Erinaceomorpha (Insectivora, Mammalia). Am. Mus. Novitates 2813: 22 pp.
- Novacek, M. J., M. C. McKenna, N. A. Neff, and R. L. Cifelli
1983. Evidence from the earliest known erinaceomorph basicranium that insectivorans and primates are not closely related. Nature 306: 683–684.
- Presley, R.
1979. The primitive course of the internal carotid artery in mammals. Acta Anat. 103: 238–244.
- Rich, T. H.
1981. Origin and history of the Erinaceinae and Brachyericinae (Mammalia, Insectivora) in North America. Bull. Am. Mus. Nat. Hist. 171: 1–116.
- Rich, T. H., and P. V. Rich
1971. *Brachyerix*, a Miocene hedgehog from

- western North America, with a description of the tympanic regions of *Paraechinus* and *Podogymnura*. *Am. Mus. Novitates* 2477: 58 pp.
- Rose, K. D., and J. G. Fleagle
1981. The fossil history of nonhuman primates in the Americas. In A. F. Coimbra-Filho and R. A. Mittermeier (eds.), *Ecology and behavior of neotropical primates*, pp. 111–117. Rio de Janeiro: Academia Brasileira de Ciencias.
- Russell, D. E., P. Louis, and D. E. Savage
1967. Primates of the French early Eocene. *Univ. Calif. Publ. Geol. Sci.* 73: 1–46.
1975. Les Adapisoricidae de l'Eocène inférieur de France: réévaluation des formes considérées affines. *Bull. Mus. Natl. Hist. Nat.* 237: 129–193.
- Schlosser, M.
1887. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten, und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. *Beiträge Palaeontol. Oesterreich-Ungarns und Orients* 6: 1–227.
- Sigé, B.
1977. Insectivores primitifs de l'Eocène supérieur et Oligocène inférieur d'Europe occidentale. *Nyctitheriidés. Mém. Mus. Natl. Hist. Nat. ser. C*, 4: 1–140.
- Simonetta, A.
1957. Anatomia e significato morfologico e sistematico dell'orecchio medio e delle strutture ad esso connesse in alcuni insettivori (*Suncus*, *Talpa*, *Chrysochloris*). *Arch. Ital. Anat. Embriol.* 62: 55–94.
- Simons, E. L.
1962. A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bull. Brit. Mus. (Nat. Hist.)* 7: 1–36.
- Simpson, G. G.
1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85: 1–350.
- Szalay, F. S.
1968. The beginnings of primates. *Evolution* 22: 19–36.
1969. Mixodectidae, Microsyopidae, and the insectivore-primate transition. *Bull. Am. Mus. Nat. Hist.* 140: 193–330.
1971. Relationships of the alleged primate *Gesneropithex peyeri* Hürzeler, 1946. *J. Mammal.* 52: 824–826.
1975. Phylogeny of primate higher taxa: the basicranial evidence. In P. W. Luckett and F. S. Szalay (eds.), *Phylogeny of the primates, a multidisciplinary approach*, pp. 91–125. New York and London: Plenum Press.
1977. Phylogenetic classification and a classification of the eutherian Mammalia. In M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), *Major patterns in vertebrate evolution*, pp. 315–374. New York and London: Plenum Press.
- Szalay, F. S., and E. Delson
1979. *Evolutionary history of the primates*. New York: Academic Press.
- Szalay, F. S., A. Rosenberger, and M. Dagosto
1987. Diagnosis and definition of the order Primates. *Yearb. Phys. Anthropol.* 30: 75–106.
- Tandler, J.
1899. Zur vergleichenden Anatomie der Kopfarterien bei den Mammalia. *Denkschr. Kaiserl. Akad. Wissensch. Wien, Math.-Naturwissensch. Kl.* 67: 677–784.
- Van Der Klaauw, C. J.
1931. The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. *Bull. Am. Mus. Nat. Hist.* 62: 1–352.
- Van Kampen, P. N.
1905. Die Tympanalgegend des Säugetierschädels. *Gegenb. Morph. Jahrb.* 34: 321–722.
- Van Valen, L.
1967. New Paleocene Insectivora and insectivore classification. *Bull. Am. Mus. Nat. Hist.* 135: 217–284.
- Wassif, K.
1948. Studies on the structure of the auditory ossicles and tympanic bone in Egyptian Insectivora, Chiroptera, and Rodentia. *Bull. Fac. Sci. Fouad I Univ.* 27: 177–213.
- Wible, J. R.
1983. The internal carotid artery in early eutherians. *Acta Palaeontol. Pol.* 28: 174–180.
1984. The ontogeny and phylogeny of the mammalian cranial arterial pattern. Ph.D. diss., Duke Univ., Durham, North Carolina, 705 pp.
1986. Transformations in the extracranial course of the internal carotid artery in mammalian phylogeny. *J. Vert. Paleontol.* 6: 313–325.
1987. The eutherian stapedial artery: character analysis and implications for superordinal relationships. *Zool. J. Linn. Soc.* 91: 107–155.
- Wible, J. R., and H. H. Covert
1987. Primates: cladistic diagnosis and relationships. *J. Human Evol.* 16: 1–22.

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