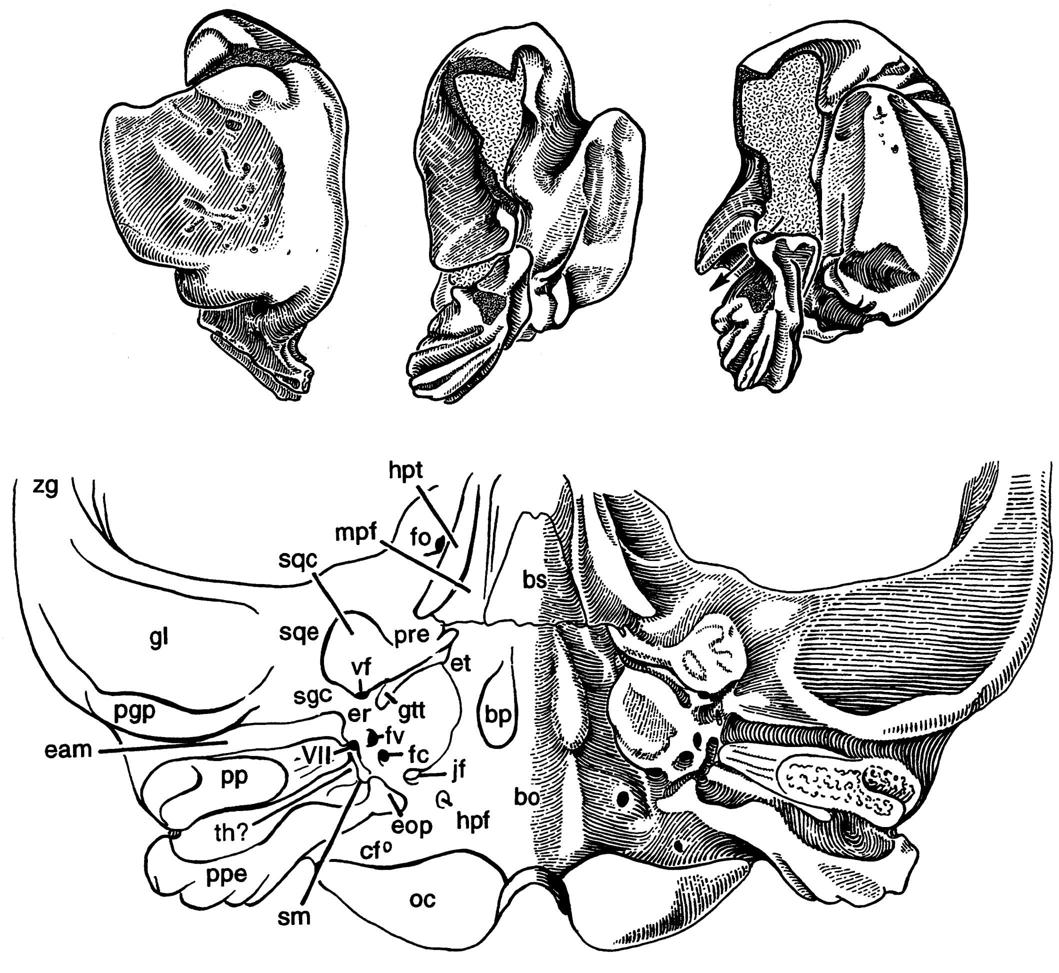
TERRESTRIAL MESONYCHIA TO AQUATIC CETACEA: TRANSFORMATION OF THE BASICRANIUM AND EVOLUTION OF HEARING IN WHALES

ZHEXI LUO and PHILIP D. GINGERICH



Pakicetus inachus

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TERRESTRIAL MESONYCHIA TO AQUATIC CETACEA: TRANSFORMATION OF THE BASICRANIUM AND EVOLUTION OF HEARING IN WHALES

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Morphological and stratigraphic evidence indicates that land-living mesonychian ungulates are broadly ancestral to early amphibious and later aquatic cetaceans. The transition from terrestrial ungulates to aquatic whales is a transition from life in air to life in water. Air and water differ in density and are very different media for sound propagation. Thus perception of air-borne sound by land mammals and perception of water-borne sound by whales require markedly different functional adaptations. Here we describe and compare the basicranial morphology of mesonychian ungulates and archaeocete cetaceans to establish stages of morphological transformation of the basicranium and evolution of hearing in whales.

We describe the basicranium of three mesonychians: Eocene *Hapalodectes hetangensis* as a representative of Hapalodectidae, and Paleocene *Dissacus praenuntius* and *Sinonyx jiashanensis* as representatives of Mesonychidae. In mesonychians the ectotympanic bulla is surrounded by squamosal and basioccipital bones of the basicranium, having little or no contact with the exoccipital or the mastoid process of the petrosal. This condition is shared by artiodactyls, and we consider it the primitive condition, or stage 0 in the evolution of hearing in cetaceans.

The basicranium of early middle Eocene *Pakicetus inachus* is representative of pakicetid archaeocetes (stage 1). *Pakicetus* retained a functional external auditory meatus with a tympanic annulus and, by inference, a tympanic membrane capable of hearing air-borne sound. The auditory bulla contacts the mastoid process of the petrosal, the squamosal, the exoccipital, and possibly the basioccipital, and there are no extracranial sinuses. Presence of a tympanic involucrum represents the beginning of pachyostosis and osteosclerosis of the bulla, enhancing its density contrast to surrounding bones, soft tissues, and water.

Basicrania of middle Eocene *Gaviacetus razai* and *Indocetus ramani* are described and compared to other protocetid archaeocetes (stage 2). These lack a functional external auditory meatus and have a conical apophysis rather than a tympanic annulus, indicating that the tympanic membrane has been transformed into a tympanic ligament. This means that the capacity to hear air-borne sound was reduced or lost. Incipient peribullar sinuses are present in protocetids, but these are not fully developed.

We describe basicrania of middle-to-late Eocene *Dorudon atrox*, *Basilosaurus isis*, and *Saghacetus osiris* and compare these to other basilosaurid archaeocetes (stage 3). These have a well-developed pterygoid sinus that extends to the exoccipital region. Bullar contact with the squamosal is partially replaced by contact with the petrosal. Bullar articulation with the basioccipital and exoccipital is completely lost in adults. The petrosal is both pachyostotic and osteosclerotic. We infer that basilosaurids had substantial capacity for directional hearing in water, but did not achieve the high resolution required for echolocation.

In modern mysticetes and odontocetes (stage 4), the sigmoid process of the bulla is detached from the squamosal. The petrosal is at least partially excluded from the braincase and isolated in a peribullar cavity. Finally, in odontocetes (stage 5), the petrotympanic complex is completely enclosed in a peribullar cavity and almost completely isolated from the rest of the cranium.

Stages of transformation of the middle ear and evolution of hearing in archaeocetes parallel similar stages of transformation of the postcranial skeleton and evolution of locomotion. Stage 1 pakicetids were probably as terrestrial as they were aquatic. Stage 2 protocetids were similar at the beginning of the middle Eocene but almost fully aquatic by the end of the middle Eocene. Stage 3 basilosaurids had hydrodynamically streamlined bodies, hind limbs too small to be useful in swimming or to support the body on land, no real sacrum, and powerful tail-powered locomotion similar to that of modern cetaceans.

Transformation of the basicranium in the transition from terrestrial ungulates to aquatic whales involved: (1) substantial augmentation of the density of bones involved in hearing, enhancing the density contrast from surrounding soft tissues and pterygoid sinuses; (2) reduction of the tympanic membrane to a conical tympanic ligament, decreasing any capacity for hearing air-borne sound in later archaeocetes; and (3) shifting of the tympanic articulation to the petrosal permitting more complete isolation of the petrotympanic complex from the rest of the cranium.

Degree of development of pachyosteosclerosis of the petrotympanic complex, isolation of the petrotympanic complex from surrounding bones, and development of vascular sinuses in the basicranium, indicate that *Pakicetus* retained full capacity for hearing air-borne sound; protocetids could hear water-borne sound but directional hearing was weakly developed; and basilosaurids probably had at least some capacity for directional hearing. High resolution directional hearing using high-frequency sound, indispensable for echolocation, was not achieved in any known archaeocete. Divergence of ultrasonic hearing in odontocetes from infrasonic hearing in mysticetes occurred after modern cetaceans diverged from basilosaurids.

Key Words: Mesonychia, Archaeoceti, Cetacea, petrotympanic complex, phylogeny, evolution of hearing

I

INTRODUCTION

The origin of cetaceans from terrestrial ungulate ancestors and their progressive adaptation to life in an aquatic environment have brought forward many fundamental changes in cetacean ears and hearing. The spectacular radiation of whales that we know today can be attributed, at least in part, to remarkable specializations of their ear structures. Submersion in an aquatic environment limits vision and olfaction, and whales depend greatly on hearing for navigation, feeding, and communication. Thus the evolution of specialized underwater hearing in cetaceans during the ungulate-cetacean transition is a crucial part of their phylogenetic history.

The two extant groups of whales, odontocetes (toothed whales) and mysticetes (baleen whales), have very different adaptations for underwater hearing. Toothed whales (odontocetes) have the capacity for echolocation (ultrasonic sonar) and use this for underwater sensory perception. This involves generating high frequency sound from a "biosonar signal generator" associated with the nasal passage (Pilleri et al., 1986; Heyning, 1989; Ketten, 1992; Cranford et al., 1996), and beaming the sound primarily through the melon in the forehead (Fleischer, 1978; Ketten, 1992; Cranford et al., 1996). The returning echo from the surrounding aquatic environment can be received in the ear via two possible routes (reviewed in Ketten, 1992; see discussion below). The ability to hear ultrasonic frequencies is indispensable for sensitive perception in an aquatic environment, and toothed whales' greater sensitivity to higher frequencies enables them to echolocate and to obtain a more accurate acoustic perception of their environment. In contrast, baleen whales have no ability to perceive high-frequency sound nor to echolocate, but they can hear very low frequency ("infrasonic") sounds. Lower frequencies have greater penetrating power underwater and travel farther, enabling baleen whales to communicate over a wider geographic range.

Hearing in cetaceans

The most probable sites for receiving echoed sound in odontocetes are through the fat-filled mandibular canal and the thin "pan bone" or "acoustic window" of the posterior part of the mandible (Norris, 1980; Ketten, 1992). It is still difficult to trace the exact anatomical route of sound conduction from the mandible to the middle ear because the petrotympanic complex is enclosed around much of its periphery by sinuses separating it from most other basicranial bones in most odontocetes. In some derived extant odontocete groups, such as delphinoids, the petrotympanic complex is completely detached on all sides from other bones and it is only suspended by ligaments and vascular tissues (see reviews by Fleischer, 1978; Ketten, 1992). Nonetheless, several functional studies strongly support the mandible as the primary (and possibly only) site for receiving sound (McCormick et al., 1970; Norris and Harvey, 1974; Brill et al., 1988; Ketten, 1992).

An alternative hypothesis with far less support is that odontocetes receive sound through the external auditory meatus (Fraser and Purves, 1960; Purves, 1966; Purves and Pilleri, 1983). This idea is put forward in spite of the fact that there is no bony canal for the external auditory meatus, and soft tissues of the meatus have degenerated to vestigial ligaments suspended in the fatty blubber of extant odontocetes. Nonetheless, there is some experimental evidence for possible conduction of sound in lower frequencies via this alternative route (Ketten, 1992).

Mysticetes retain a bony canal for the external auditory meatus, a general and undoubtedly primitive feature of land mammals. However, the internal part of the external auditory meatus is plugged by ceruminous wax and its external part is completely occluded by blubber (Lillie, 1910; Fraser and Purves, 1960; Reysenbach de Haan, 1966). The mandibular canal is greatly reduced due to development of baleen on the mandible, and it is unclear whether sound passes via the mandibular route or the external auditory meatus to enter skulls of mysticetes. No experimental evidence is available concerning pathways of sound conduction in the skulls of mysticetes (Ketten, 1992).

Directional perception

Directional perception is a crucial requirement for effective underwater hearing using both high and low frequencies. Water and the body tissues of cetaceans are more similar to each other in density than either is to air. Thus waterborne sound enters the skulls of aquatic mammals with relatively little attenuation, and this generates greater acoustic interference between the two ears of an aquatic whale (Reysenbach de Haan, 1966; Fleischer, 1978; Oelschläger, 1986a) than airborne sound can between the two ears of a terrestrial ungulate. To maintain directional perception in underwater hearing it is important to reduce interference of the waterborne sound by isolating both ears from the rest of cranium and from each other.

To maintain directional hearing of waterborne sound, all extant cetaceans have at least some degree of acoustic isolation of left and right ears. In general, acoustic isolation is better developed in odontocetes with high-frequency hearing than in mysticetes with low-frequency hearing, for the simple reason that high frequency sound is more susceptible to interference than low-frequency sound.

Anatomically, acoustic isolation can be achieved in two ways. The first is to increase the density of the ear bones, such as the petrosal, the tympanic, and the middle ear ossicles, relative to the density of soft tissues surrounding these ear bones. As a result, these ear bones become osteosclerotic (very dense and almost glassy in texture). The higher the contrast in density between the ear bones and surrounding soft tissues and cranial bones, the more effective is isolation of the two ears against acoustic interference (Fleischer, 1978; Currey, 1979).

The second way to archive acoustic isolation is to develop pneumatic vascular sinuses filled with air (Fraser and Purves, 1960; Fleischer, 1978). The sinuses are formed by mucous membranes, spongy vasculature, and fibrous connective tissues in which numerous tiny air pockets are enclosed (Fraser and Purves, 1960). The foam-like vascular sinuses surround much of each petrotympanic complex and isolate left and right ears from the rest of skull and from each other—except for narrow posterior processes of the petrosal and ectotympanic that articulate with the squamosal and the exoccipital. The vascular supply to the sinuses can engorge the sinus tissue in response to increasing ambient pressure during diving. The vascular supply also regulates the volume of air in the sinus cavity as a part of the diving adaptation (Fleischer, 1978). Air entrapped in the sinuses decreases the density of soft tissues around the ear bones, thereby maintaining acoustic isolation of the two ears.

The ectotympanic bulla and the petrosal bone surround and enclose the middle ear, and the petrosal encloses the inner ear. As these two bones become more tightly articulated or fused to each other in cetaceans, they are also separated from most other basicranial bones by surrounding sinuses. Consequently, the middle and inner ears on both sides of the skull are decoupled from the cranium and from each other. This decoupling of the two ears enhances directional hearing (Fraser and Purves, 1960; Kasuya, 1973; Oelschläger, 1990; Ketten, 1992), which is an essential component necessary for underwater hearing of modern whales.

Basicranium of archaic whales

The cetacean basicranium has numerous osteological specializations or apomorphies that are not found in terrestrial ungulate relatives. Almost all of these apomorphies are related either to the development of pachyostosis and osteosclerosis, or to development of vascular sinuses. Development of vascular sinuses alters the pattern of articulation of the basicranial bones and opens large sinus cavities. This results in some large gaps or open spaces between bones, and modified bone articulations in the petrotympanic complex and adjacent skull bones. Numerous osteological characteristics associated with development of sinuses are commonly preserved in fossil skulls, making it possible to understand the size and distribution of pneumatic vascular sinuses in the basicrania of extinct cetaceans. Consequently, if the systematic distribution of petrotympanic and sinus structures can be established for fossil whales, especially archaic cetaceans or archaeocetes, it can contribute to our understanding of the morphological evolution of the anatomical structures crucial for directional underwater hearing.

Because of the great complexity of the mammalian basicranium, it is a rich source of information for inferring phylogenetic relationships (van der Klaauw, 1931; MacPhee, 1981; Novacek, 1993). However, archaeocete basicrania have not received very much attention since the landmark review by Kellogg in 1936. Our current understanding of the relationships of archaeocetes was primarily based on the skull roof (Miller, 1923; Kellogg, 1936), the dentition (Van Valen, 1966; Barnes and Mitchell, 1978), and the pelvis and hind limbs (Gingerich et al., 1990, 1994; Thewissen et al., 1994, 1996, 1998; Hulbert et al., 1998). The rich information of the basicranium of archaeocetes needs to be explored in the wake of the recent discoveries of excellent cranial fossils spanning much of the Eocene (Sahni and Mishra, 1975; Kumar and Sahni, 1986; Gingerich et al., 1983, 1994, 1995; Geisler et al., 1996; Gingerich and Uhen, 1996; Thewissen and Hussain, 1998; Hulbert et al., 1998). A systematic survey of basicranial features can provide new information bearing on current phylogenetic hypotheses of the relationships of archaeocetes.

The petrosal, the tympanic, and other basicranial structures in archaic archaeocetes and their terrestrial ungulate relatives are examined in this study with three goals: (1) to provide a full description of new basicrania, especially the petrotympanic complex and associated basicranial structures, of archaic whales and their ungulate relatives; (2) to present a parsimony analysis of these morphological characters for inference of relationships among archaeocetes; and (3) to establish the anatomical evolution of the petrotympanic complex and bony structures related to surrounding sinuses. By establishing the evolution of anatomical characters crucial for directional hearing in water, we hope to achieve a better understanding of the evolution of hearing in archaeocetes, and the divergence of the ultrasonic hearing specialization of odontocetes from the infrasonic hearing specialization of mysticetes.

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York
AUMP — Auburn University Museum of Paleontology, Auburn, Alabama
CGM — Cairo Geological Museum, Cairo (Egypt)
ChM — Charleston Museum Vertebrate Fossil Collection, Charleston, South Carolina
CMM — Calvert Marine Museum, Solomons, Maryland
CMNH — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
GSP-UM — Geological Survey of Pakistan-University of Michigan collection, Islamabad (Pakistan)
GSM — Georgia Southern Museum, Statesboro, Georgia

H-GSP — Geological Survey of Pakistan-Howard University collection, Islamabad (Pakistan)
IVPP — Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (China)
LUVP — Lucknow University vertebrate paleontology collection (India)
VPL/K — Panjab University, Vertebrate Paleontology Laboratory, Kumar collection, Chandigarh (India)
SMF — Senckenberg Museum, Frankfurt (Germany)
SMNS — Staatliches Museum für Naturkunde, Stuttgart (Germany)
UM — University of Michigan Museum of Paleontology, Ann Arbor
USNM — United States National Museum of Natural History, Smithsonian Institution, Washington, DC

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II

MATERIALS AND METHODS

The ear region of cetaceans is complex like those of other mammals, but differs in having the petrosal and ectotympanic bones densely ossified with distinctively hard, almost glassy, osteosclerotic bone. Complex structures are always preferred in systematic studies because they provide more information than simple structures, and the hardness and density of bones associated with hearing in whales enhances their preservation potential as fossils. Taken together, these characteristics provide an unusual opportunity to study changes in the basicrania of fossil cetaceans and in auditory function through evolutionary time.

Fossils studied here are listed in Table 1. For outgroup comparison with terrestrial mammals, we examined mesonychians (outgroup 1), which are generally considered to be closely related to archaeocetes (Van Valen, 1966; Gingerich et al., 1983; Prothero et al., 1988; Prothero, 1993; Zhou et al., 1995; Geisler and Luo, 1998). We studied *Hapalodectes* (IVPP 5253, Ting and Li, 1987), *Sinonyx* (IVPP 10760, Zhou et al., 1995), *Dissacus* (UM 75501) and *Mesonyx* (AMNH 12643; Geisler and Luo, 1998). We did not include the enigmatic *Andrewsarchus* because details of the ear region of the type specimen (AMNH 20135) are missing or obscured by plaster.

We included two additional outgroups representing ungulates that survive to the present. The first of these (outgroup 2) includes the Eocene artiodactyls *Diacodexis* (Coombs and Coombs, 1982; Russell et al., 1983) and *Homacodon* (Coombs and Coombs, 1982). The second (outgroup 3) includes the Eocene perissodactyl *Heptodon* (Radinsky, 1965). Artiodactyls and perissodactyls were included because they have been suggested to be more closely related to cetaceans than to other orders of extant placental ungulate mammals (Kellogg, 1936; Boyden and Gemeroy, 1950; Czelusniak et al., 1990; Novacek et al., 1988; Novacek, 1992; Prothero, 1993; Milinkovitch et al., 1993, 1994; Arnason and Gullberg, 1994).

Some aspects of the interrelationship of odontocetes and mysticetes have not been fully resolved (Milinkovitch et al., 1993, 1994; Arnason and Best, 1991; Arnason and Ledje, 1993; Arnason and Gullberg, 1994; see also McLeod et al., 1993; Geisler and Luo, 1996; Messenger and McGuire, 1998). The main emphases of the present study are the relationships and anatomical evolution of archaeocetes, not the family level phylogeny of odontocetes or mysticetes. Nevertheless, several taxa of odontocetes and mysticetes were included to expand the taxonomic coverage of each group. This is to insure that alternative and controversial placements of extant odontocete and mysticete clades would not adversely affect interpretation of the relationships of archaeocetes and the course of their character evolution.

ANATOMICAL TERMINOLOGY

Anatomical terms used to describe cetacean basicranial osteology were standardized by Kellogg (1928, 1936) in a series of papers on fossil whales. Kellogg inherited his terminology from earlier studies of fossil cetaceans by Fraas (1904) and Pompeckj (1922). The terminology was further elaborated in two detailed monographic studies on the basicrania of extant cetaceans by Fraser and Purves (1960) and Kasuya (1973). Descriptive terminology for the cetacean petrosal and ectotympanic, as developed by Kellogg (1928, 1936) and adopted by later students, is quite different from the terminology more widely used for terrestrial mammals (e.g., van Kampen, 1905; van der Klaauw, 1931; MacIntyre, 1972; MacPhee, 1981; Williams et al., 1989; Wible, 1990).

Some differences in descriptive terms are justifiable because they reflect unique cetacean aquatic specializations that are absent in terrestrial eutherians: e.g., terms related to the complex pterygoid sinus system in cetaceans. However, other synonyms only differ semantically. Many cetacean basicranial structures bear different terms even though they are morphologically similar and homologous to their counterparts in other mammals (Figs. 1-4, and Tables 2-6). For example, the prefacial commissure and the tegmen tympani of the petrosal of terrestrial eutherian mammals are termed the superior process in cetaceans. The term 'mastoid process' can refer either to the posterior process of the petrosal (Kellogg, 1936), or to a mastoid process of the squamosal (Oelschläger, 1986).

Due to the lack of understanding of the highly transformed basicranial structures in cetaceans, there has been a far greater proliferation of anatomical terms for cetaceans than for any other mammalian order. Use of many synonyms for homologous basicranial structures has made it difficult to compare cetaceans to their terrestrial ungulate relatives. Without an adequate understanding of the homologies of the synonymous structures, it would be next to impossible to establish character evolution.

The issue of unnecessary synonyms needs to be addressed because the practice of phylogenetic systematics requires a comparison of cetaceans to ungulate outgroups and other non-

TABLE 1 — Taxonomic scope of this study. The focus is on early cetacean Archaeoceti, in comparison to outgroups Mesonychia, Artiodactyla, and Perissodactyla, and in comparison to later cetacean Odontoceti and Mysticeti. Specimens listed here include most of those relevant for our understanding of the evolution of hearing in Archaeoceti.

Taxon	Specimens and references	Illustrations in this study
Mesonychia (outgroup 1)		
Dissacus praenuntius	UM 75501 (Zhou, 1995; this study)	Figs. 2B; 3B; 6A-B; 7A-D
Sinonyx jiashanensis	IVPP 10760 (Zhou et al., 1995)	Fig. 8
Mesonyx obtusidens	AMNH 12643 (Geisler and Luo, 1998)	—
Hapalodectes hetangensis	IVPP 5253 (Ting and Li, 1987)	Fig. 5
Artiodactyla (outgroup 2)		
Diacodexis metsiacus	(Coombs and Coombs, 1982; Geisler and Luo, 1998)	—
Diacodexis pakistanensis	(Russell et al., 1983)	—
Homacodon vagans	(Coombs and Coombs, 1982)	—
Perissodactyla (outgroup 3)		
Heptodon posticus	(Radinsky , 1965; Cifelli, 1982)	—
Archaeoceti		
Pakicetus inachus	GSP-UM 84 (adult; Gingerich et al., 1983)	Figs. 9; 10B-C
" "	GSP-UM 1632 (this study)	Fig. 10A (pt.); 11A-C; 12A-C
P. attocki	H-GSP 96334 (Luo, 1998)	Fig. 10A (pt.)
Ichthyolestes pinfoldi	H-GSP 18391 (Luo, 1998)	Fig. 10A (pt.)
Ambulocetus natans	H-GSP 18507.10111 (Thewissen et al., 1996)	—
'Habib Rahi protocetid'	GSP-UM 1858 (adult; Gingerich, 1991)	—
Rodhocetus kasrani	GSP-UM 3012 (adult; Gingerich et al., 1994)	—
Gaviacetus razai	GSP-UM 3095 (adult; Gingerich et al., 1995)	Figs. 13; 14A-B
Protocetus atavus	SMNS 11084 (Fraas, 1904)	—
Indocetus ramani	LUVP 11034 (Sahni and Mishra, 1975)	Figs. 15A-B; 16A-B
Remingtonocetus harudiensis	VPL/K 15001 (Kumar and Sahni, 1986)	—
Georgiacetus vogtlensis	GSM 350 (Hulbert et al., 1998)	—
'Cross protocetid'	ChM 5401 (Geisler et al., 1996; Geisler and Luo, 1998)	—
Dorudon atrox	SMF 4451 (adult; Pompeckj, 1922)	—
" "	UM 93220 (subadult; Uhen, 1996)	Figs. 1C (pt.); 17 (pt.); 18A (pt.); 21A-E (pt.)
" "	UM 93232 (subadult; Uhen, 1996)	—
" "	UM 94812 (adult?; Uhen, 1996)	Figs. 1C (pt.); 2C; 4C-E; 17 (pt.); 18A (pt.); 20A,C; 21A-E (pt.)
" "	UM 97512 (adult; Uhen, 1996)	—
" "	UM 100139 (subadult; Uhen, 1996)	—
" "	UM 100142 (subadult; Uhen, 1996)	—
Ancalecetus simonsi	CGM 42290 (adult; Gingerich and Uhen, 1996)	Fig. 18B (pt.)
Basilosaurus cetoides	USNM 4647 (Kellogg, 1936)	—
" "	USNM 6087 (Kellogg, 1936)	—
B. isis	UM 97507 (adult; this study)	Figs. 18B (pt.); 19A-D; 20B,D
Zygorhiza kochii	USNM 4748 (Kellogg, 1936)	—
" "	USNM 11962 (Kellogg, 1936)	—
" "	USNM 12977 (Kellogg, 1936)	—
" "	USNM 13773 (Kellogg, 1936)	—
" "	AUMP 2368 (Lancaster, 1990)	—
" "	ChM 5065 (this study)	—
Saghacetus osiris	UM 97550 (adult; Gingerich, 1996)	Fig. 21A-E (pt.)
" "	UM 101227 (subadult; this study)	—

TABLE 1 (cont.) — Taxonomic scope of this study. The focus is on early cetacean Archaeoceti, in comparison to outgroups Mesonychia, Artiodactyla, and Perissodactyla, and in comparison to later cetacean Odontoceti and Mysticeti. Specimens listed here include most of those informing our understanding of the evolution of hearing in Archaeoceti.

Taxon	Specimens and references	Illustrations in this study
Odontoceti		
Xenorophus sp.	CMNH 72655, 72670 (Whitmore and Sanders, 1976; Luo and Marsh, 1996; this study)	—
Platanista gangetica	(Kasuya, 1973; de Muizon, 1987, 1994; Oelschläger, 1990; Luo and Marsh, 1996)	—
Squalodon sp.	(Kellogg, 1928; Fordyce, 1983, 1994; Luo and Eastman, 1995)	Fig. 27C
Physeter catodon	(Kasuya, 1973; Luo and Marsh, 1996)	—
Mesoplodon sp.	(Kasuya, 1973; de Muizon, 1990; Luo and Marsh, 1996)	—
Tursiops truncatus	(Kasuya, 1973; Oelschläger, 1986a,b; Luo and Marsh, 1996)	Fig. 24, Fig. 27D
Mysticeti		
Parietobalaena palmeri	(Kellogg, 1968; Geisler and Luo, 1996)	Fig. 25A-D, Fig. 27B
Pelocetus calvertensis	CMM 935, 1605 (Kellogg, 1965; Geisler and Luo, 1996)	—
Herpetocetus sp.	CMNH specimens (Geisler and Luo, 1996)	—
Balaenoptera physalis	USNM 239307, 239707 (Geisler and Luo, 1996)	—
Eubalaena glacialis	AMNH 169829 (Geisler and Luo, 1996)	—

cetacean mammals. Only true neomorphic features of cetaceans should be given new anatomical terms. Outgroup comparison is a basic part of phylogenetic systematics (Wiley, 1979; Maddison et al., 1984). Outgroups are crucial for establishing the primitive eutherian condition from which the more specialized cetacean features could have evolved. Rooting of the trees in parsimony analysis depends on outgroups (Swofford, 1990; Maddison and Maddison, 1992). Thus it is imperative to eliminate redundant synonyms before cetaceans and non-cetacean outgroups can be incorporated into a character-by-taxon matrix for parsimony analysis.

Synonymy of terms for cetacean cranial osteology can now be considered anew in the light of more recent discoveries of transitional taxa linking cetaceans to land mammals (Gingerich and Russell, 1981, 1990; Gingerich et al., 1983, 1994; Thewissen et al., 1994). These new taxa clearly have intermediate postcranial features between the primitive condition of terrestrial ungulates and the specialized cetacean condition adapted to aquatic life, such as a streamlined body with vestigial pelvis and no hind limbs. For some cranial features, such as those of the bullae (Gingerich et al., 1983; Thewissen and Hussain, 1993; Luo, 1998), the newly discovered transitional fossil taxa have shown intermediate characteristics between the conspicuously different anatomical features of extant terrestrial mammals on one hand, and cetaceans on the other, bridging some morphological gaps that seemed previously insurmountable.

The use of different names for basicranial structures in cetaceans were based, at least in part, on the conspicuous differences between extant cetaceans and other mammals. If the basicrania of the newly discovered transitional taxa turn out to have the intermediate conditions between ungulates and extant cetaceans, as is the case in the postcranial skeleton, they will help to clarify the homology of the seemingly different basicranial characters of cetaceans and terrestrial mammals.

For these reasons, wherever the homology of the structures of cetaceans and basal eutherians can be established (Tables 2-6), we prefer to use the terms for primitive eutherians employed by de Beer (1929), MacIntyre (1972), MacPhee (1981), Cifelli (1982), Novacek (1986), Wible (1990), or the terms of human anatomy (Williams et al., 1989). When a special term for cetaceans has to be used, we also identify the corresponding synonym for basal eutherians in an effort to illustrate the underlying homology. For cetacean apomorphic characters that have no counterparts in basal eutherians, we adopt the terminology of Kasuya (1973), Fordyce (1983, 1994), Whitmore (1986), Oelschläger (1986, 1990), de Muizon (1987), Pilleri et al. (1987, 1989), Luo and Marsh (1996), and Geisler and Luo (1996, 1998). Our interpretation of the homology of the basicranial characters of cetaceans and non-cetacean mammals is summarized in Tables 2-6. Some of these homologous characters are illustrated in Figures 1, 2, 3, and 4.

PHYLOGENETIC ANALYSIS

Our preferred hypothesis of relationships of ungulate and cetacean taxa is based on the distributions of 64 character states of the basicranium across 22 taxa of ungulates and cetaceans. The main focus of this study is on the basicranial morphology of cetaceans—thus archaeocetes (seven taxa), odontocetes (five taxa), and mysticetes (three taxa) are considered to be the ingroups of this study. Mesonychian ungulates (e.g., *Dissacus praenuntius*, *Sinonyx jiashanensis*, *Mesonyx obtusidens*, and *Hapalodectes hetangensis*) are considered as the closest outgroup to cetaceans (Van Valen, 1966; Barnes and Mitchell, 1978; Ting and Li, 1987; Prothero, 1993; Zhou et al., 1995; Geisler and Luo, 1998). Additional ungulate mammals are regarded as more distant outgroups, including Perissodactyla (represented by Eocene *Heptodon*) and Artiodactyla (represented by Eocene *Diacodexis metsiacus*, *D. pakistanensis*, and *Homacodon vagans*).

In the analysis of the characters listed in Chapter 4 and Table 6, morphological characters are grouped together by their anatomical association to demonstrate that characters are logically independent and to avoid the potential over-splitting of characters and/or redundancy. In the parsimony analyses of PAUP (Swofford, 1990), all multiple character states are treated as unordered to avoid a priori bias in interpreting character transformations. In cases where a character is variable in a taxon, the character is treated as polymorphic in the analysis (Maddison and Maddison, 1992).

Many of these characters have been discussed extensively in previous studies of the petrosals (periotics) of odontocetes (Kellogg, 1928, 1965; Fraser and Purves, 1960; Kasuya, 1973; Fordyce, 1983, 1994; Barnes, 1978, 1984; Oelschläger, 1986, 1990; Pilleri et al., 1987, 1989; de Muizon, 1987, 1988, 1990, 1994; Whitmore, 1987; Luo and Eastman, 1995; Luo and Marsh, 1996). To a lesser extent, some archaeocete basicranial characters were also described by Pompeckj (1922) and Kellogg (1936); and the mysticete characters were discussed in Fraser and Purves (1960) and Geisler and Luo (1996). However, there have been few basicranial studies that attempt to compare archaeocetes with extant cetaceans and with non-cetacean ungulates (Geisler and Luo, 1998). In this study, we intend to expand the taxonomic scope of parsimony analyses from odontocetes and mysticetes to archaeocetes. The definitions of some basicranial characters employed in previous studies have been revised in this study.

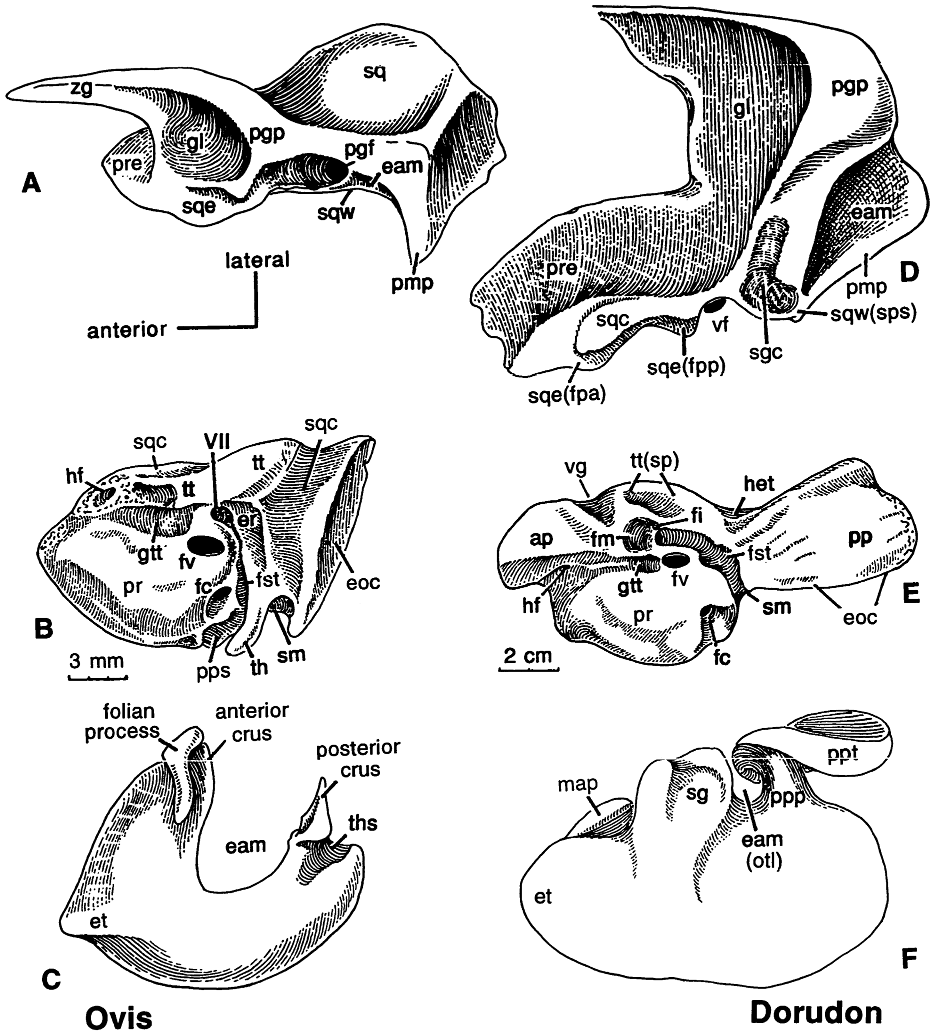

FIGURE 1. Homology of basicranial structures in the extant artiodactyl *Ovis aries* (domestic sheep) and Eocene archaeocete *Dorudon atrox*. A-C, *Ovis* modified from van Kampen (1905), based on new-born fetal specimens CMNH G995 and G997: A, squamosal (ventrolateral view); B, petrosal (ventrolateral view); C, ectotympanic bulla (lateral view). D-F, *Dorudon* composite restoration based on UM 93220 and 94812: D, squamosal (ventral view); E, petrosal (ventrolateral view); F, ectotympanic bulla (lateral view). All figures are from left side, not to the same scale. Homologous basicranial structures of cetaceans and non-cetacean ungulates are summarized in Tables 2-5. Abbreviations: *ap*, anterior process (= anterior extension of tegmen tympani of petrosal); *apt*, anterior process of tympanic (= processus tubarius); *eam(otl)*, external auditory meatus (= opening for conical tympanic ligament in the bulla [*otl*]); *eoc*, contact for the exoccipital on petrosal; *er* epitympanic recess; *et*, bony eustachian tube formed by the ectotympanic bulla; *fc*, fenestra cochleae (= round window); *fi*, fossa incudis on petrosal (= part of epitympanic recess); *fm*, fossa for malleus head (= part of epitympanic recess on petrosal); *fpa*, anterior falciform process (= part of entoglenoid process of squamosal [*sqe*]); *fpp*, posterior falciform process (= part of entoglenoid process of squamosal); *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli (= oval window); *gl*, glenoid fossa of the squamosal for temporomandibular joint; *gtt*, groove for tensor tympani; *het*, hiatus epitympanicus; *hf*, hiatus fallopii (= anterior exit for the greater superficial petrosal nerve); *otl*, opening for the tympanic ligament; *pgp*, postglenoid process; *pgf*, postglenoid foramen; *pmp*, postmeatal crest of the squamosal (= the postmastoid process of the squamosal in artiodactyls with the amastoid condition, such as *Ovis*); *pp(mas)*, posterior process of petrosal (= mastoid process of the petrosal); *ppp*, posterior pedicle of ectotympanic bulla; *pps*, postpromontorial tympanic sinus; *ppt*, posterior process of ectotympanic; *pr*, promontorium; *pre*, preglenoid process of squamosal; *sg*, sigmoid process; *sgc*, contact for sigmoid process of the tympanic (on squamosal); *sm*, stylomastoid notch; *sq*, cranial moiety of squamosal; *sqc*, contact for the squamosal (on the petrosal); *sqe*, entoglenoid process = falciform process of the squamosal; *sqw*, wing of squamosal (= spinous process of squamosal); *th*, tympanohyal; *ths*, tympanohyal sulcus (on the tympanic bulla); *tt (sp)*, tegmen tympani (= "superior process of petrosal"); *vf*, vascular foramen; *vg*, vascular groove for the ramus superior of stapedial artery or a vein (see Geisler and Luo, 1998 for discussion on homology); *VII*, facial nerve foramen; *zg*, zygoma.

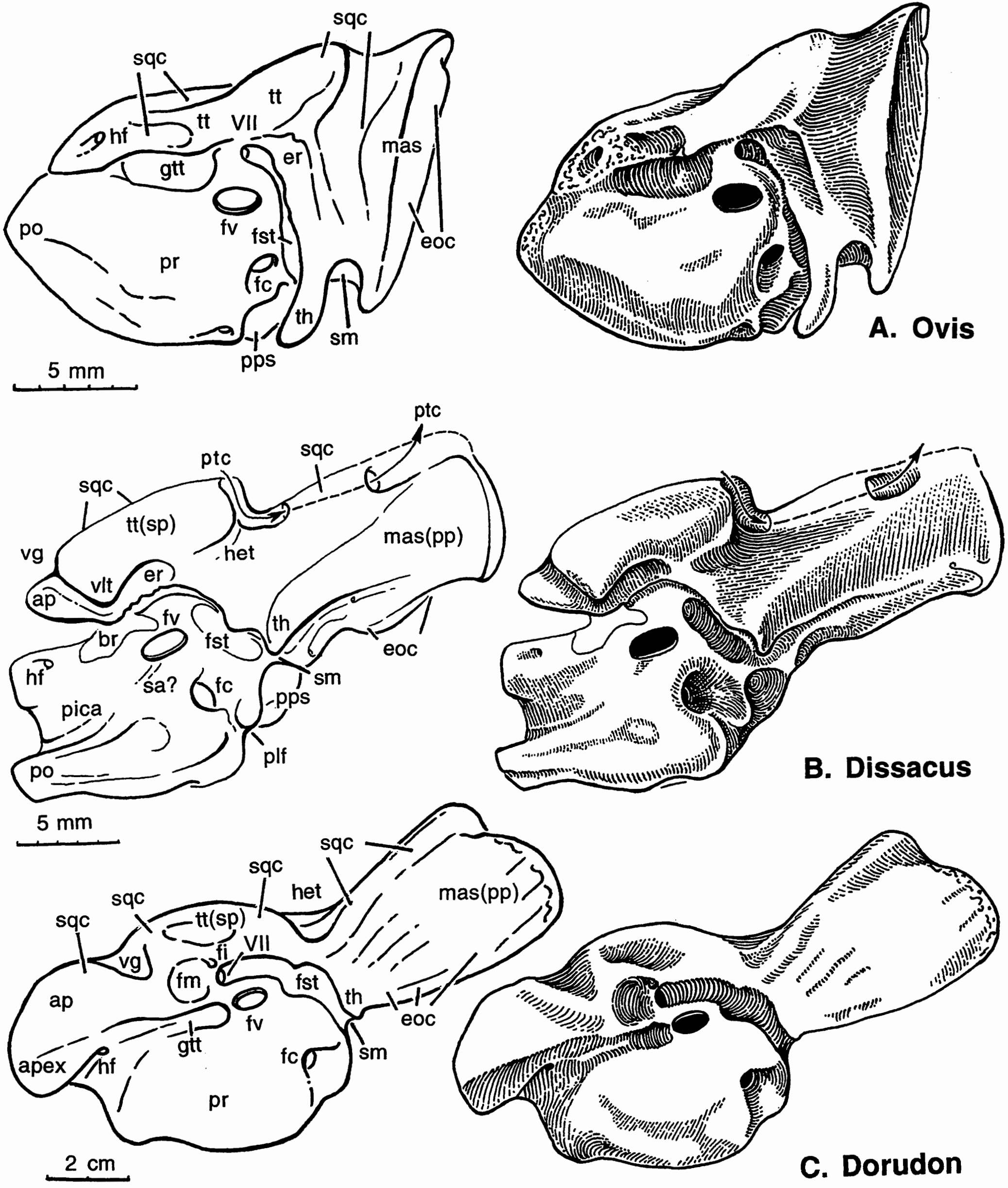

FIGURE 2. Homology of petrosal structures in ungulates and cetaceans. All are left petrosals (periotics) shown in tympanic or ventral views (not to same scale). A, extant artiodactyl *Ovis aries* (domestic sheep). B, Paleocene mesonychian *Dissacus praenuntius* (reversed from UM 75501 for comparison). C, Eocene archaeocete *Dorudon atrox* (UM 94812; posterior process partially restored). Tables 2-5 provide a complete list of synonyms of homologous basicranial structures of cetaceans and ungulates. Abbreviations: *ap*, anterior process (= anterior extension of tegmen tympani or superior process); *apex*, apex of the anterior process; *br*, breakage and/or matrix; *eoc*, contact for the exoccipital (on petrosal); *er*, epitympanic recess; *fc*, fenestra cochleae (= round window); *fi*, fossa incudis (= part of epitympanic recess); *fm*, fossa for malleus head (= part of epitympanic recess); *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli (= oval window); *gtt*, groove for tensor tympani; *het*, hiatus epitympanicus; *hf*, hiatus fallopii (= anterior exit for the greater superficial petrosal nerve); *mas*, mastoid process of the petrosal (= posterior process); *pica*, promontorial course of the internal carotid artery; *plf*, perilymphatic foramen; *po*, pole of promontorium; *pp*, posterior process of petrosal; *pps*, postpromontorial tympanic sinus on the petrosal; *pr*, promontorium; *ptc*, post-temporal canal through the mastoid process of petrosal for blood vessels (for discussion on the reconstruction of vessels see Geisler and Luo, 1998); *sa*?, sulcus for the proximal stapedial artery; *sm*, stylomastoid notch; *sqc*, contact between the squamosal and the petrosal; *th*, the base for tympanohyal; *tt (sp)*, tegmen tympani (= "superior process of petrosal"); *vg*, vascular groove (see Geisler and Luo, 1998, for discussion of homology); *vlt*, ventrolateral tuberosity; *VII*, facial nerve foramen.

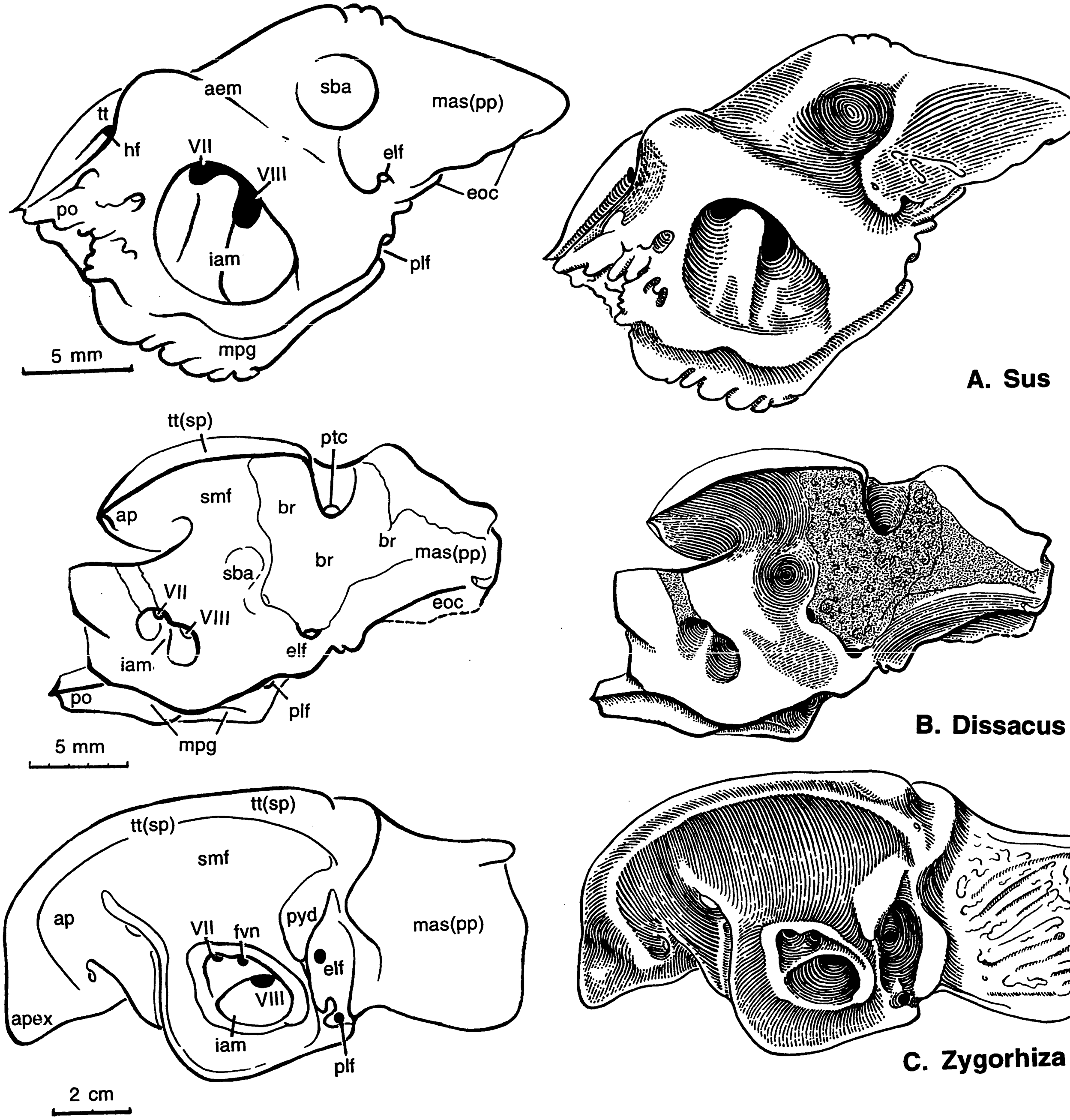

FIGURE 3. Homology of petrosal structures in ungulates and cetaceans. All are right petrosals (periotics) shown in endocranial or internal view (not to same scale). A, extant artiodactyl *Sus scrofa* (domestic pig). B, Paleocene mesonychian *Dissacus praenuntius* (UM 75501). C, Eocene archaeocete *Zygorhiza kochii* (USNM 4748, 12977, and 13773; posterior process modified from Kellogg, 1936). Tables 2-5 provide a complete list of synonyms of homologous basicranial structures of cetaceans and ungulates. Abbreviations: *aem*, arcuate eminence; *ap*, anterior process; *apex*, apex of anterior process of petrosal; *br*, breakage and/or matrix; *elf*, endolymphatic foramen; *eoc*, contact for the exoccipital; *fvn*, foramen for vestibular nerve; *hf*, hiatus fallopii; *iam*, internal auditory meatus; *mas(pp)*, mastoid process of petrosal (= posterior process of petrosal); *mpg*, medial promontory groove on pars cochlearis for inferior petrosal sinus; *plf*, perilymphatic foramen; *po*, pole of the promontorium; *pyd*, pyramidal process; *ptc*, post-temporal canal through the mastoid process of petrosal for blood vessels (for discussion on the reconstruction of vessels see Geisler and Luo, 1998); *sba*, subarcuate fossa; smf, suprameatal fossa; *tt (sp)*, tegmen tympani (= superior process); *VII*, facial nerve canal, endocranial opening; *VIII*, foramina for cochlear nerve.

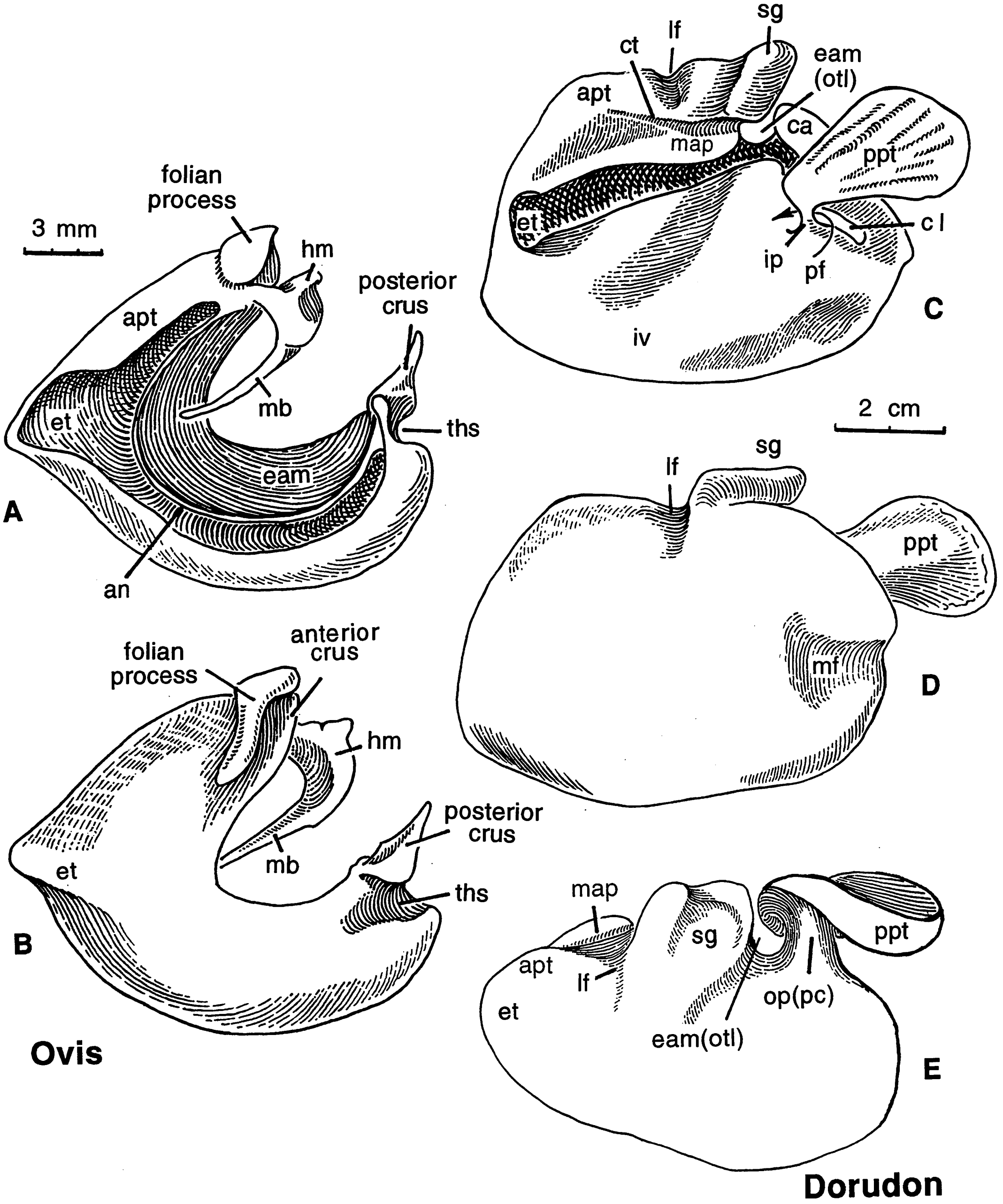

FIGURE 4. Ectotympanic bullae of artiodactyls and cetaceans. A-B, extant artiodactyl *Ovis aries* (domestic sheep), modified from van Kampen (1905) on the basis of new-born fetal specimens CMNH G995 and G997: A, dorsomedial view; and B, ventrolateral view. C-E, Eocene archaeocete *Dorudon atrox* (UM 94812): C, dorsal view; D, ventral view; and E, lateral view. Tables 2-5 provide a complete list of synonyms of homologous basicranial structures of cetaceans and ungulates. Abbreviations: *an*, annulus of the ectotympanic for suspension of the tympanic membrane; *apt*, anterior process or processus tubarius of the ectotympanic; *ca*, conical (middle) apophysis of the ectotympanic; *cl*, posterior cleft; *ct*, chorda tympani groove; *eam*, external auditory meatus; *et*, bony eustachian tube; *hm*, head of malleus; *ip*, internal posterior pedicle of tympanic; *iv*, involucrum; *lf*, lateral furrow; *mb*, manubrium of malleus; *mf*, median furrow; *op(pc)*, outer posterior pedicle of tympanic (= posterior crus); *pf*, posterior pedicle foramen; *ppt*, posterior process of tympanic; *sg*, sigmoid process; *ths*, tympanohyal sulcus.

TABLE 2 — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the petrosal and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
1. **Superior process of petrosal**	Present	Superior process of petrosal in cetaceans is formed by the embryonic prefacial commissure and tegmen tympani. It is hypertrophied and more massive than its homologues in non-cetaceans.
2. **Accessory structures in the epitympanic recess**	Present and modified	Tegmen tympani (superior process) forms the roof of the epitympanic recess — a dorsal extension of the tympanic cavity that houses the incudomalleolar articulation. Several structures are present in the area of the epitympanic recess and on the ventral aspect of the tegmen tympani.
2a. Ventrolateral tuberosity or process	Present only in some taxa	Ventrolateral tuberosity or process is a protuberance on the ventral side of the tegmen tympani (= superior process) in cetaceans. It is present but poorly developed in most non-cetacean mammals other than mesonychians.
2b. Fossa for the head of the malleus	Present only in some taxa	Fossa is a depression medial to the ventrolateral tuberosity in cetaceans; homologous to that part of the epitympanic recess that overhangs the incudo-malleolar joint in other mammals.
2c. Fossa incudis	Present in most taxa	Fossa incudis is a small pit on the tegmen tympani for the incus articulation. It is a part of the epitympanic recess. It is present in many non-cetacean mammals, but much better developed in cetaceans.
2d. Sulcus peripetrous anterior	Present in only some taxa	Sulcus peripetrous anterior is a vascular groove anterior to the ventrolateral tuberosity in archaeocetes and mesonychians (but absent in mysticetes and odontocetes). The groove may be for either the superior ramus of the stapedial artery (Geisler and Luo, 1998) or, less likely, the petrosquamous vein.
2e. Hiatus epitympanicus	Present only in some taxa	Hiatus epitympanicus is a concave area between the tegmen tympani and the mastoid process of the petrosal. Its lateral part forms a transverse trough, which may receive the spinous process of the squamosal. Its medial part is contiguous with the epitympanic recess.
3. **Accessory endocranial structures on the superior process**	Present and modified	The endocranial aspect of the superior process is formed in large part by ossification of the embryonic prefacial commissure in cetaceans, with some contribution from the tegmen tympani.
3a. Suprameatal fossa 3b. Suprameatal groove	Present in mesonychians	If the cranial surface of the superior process (prefacial commissure + tegmen tympani) is broadly concave, the concavity is termed the suprameatal fossa; if the concave structure is deep and narrow, then it is termed the suprameatal groove.
4. **Anterior process of petrosal**	Present in mesonychians	Anterior process of the petrosal of cetaceans and mesonychians is an anterior extension of the tegmen tympani. It is equivalent to a hypertrophied part of the tegmen tympani in other mammals.
5. **Accessory structures of anterior process**	Absent in most taxa	Not developed in most non-cetacean mammals.
5a. Dorsomedial angle	—	—
5b. Ventrolateral angle	—	—
5c. Lateral process	—	—
5d. Contact of anterior process to pterygoid	Absent in most taxa	Absent in non-cetacean mammals; present only in some cetaceans (basilosaurids, some archaic odontocetes, and some mysticetes)

TABLE 2 (cont.) — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the petrosal and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
6. **Articulating structures on anterior process for the ectotympanic**	Absent	Articulation of tegmen tympani (= anterior process) with the ectotympanic is not present in most non-cetacean mammals and pakicetids. Most articulating structures between the anterior process and the ectotympanic are neomorphic for basilosaurids and crown group cetaceans.
6a. Fossa (fovea) epitubaria	Absent	Fossa or fovea epitubaria is a depression anterior to the ventrolateral tuberosity to receive the accessory ossicle of the ectotympanic in most odontocetes. In some odontocetes it obliterates the lateral part of the sulcus peripetrous partially or replaces the sulcus entirely.
6b. Bullar facet for anterior process of ectotympanic	Absent	This structure is only present in some odontocetes with very elongated anterior processes, in which the anterior bullar facet and fovea epitubaria are separate. It may be continuous with and indistinguishable from the fovea epitubaria on a petrosal with a short anterior process.
6c. Pedicle for anterior process of ectotympanic	Absent	Pedicle for anterior process of the tympanic connects the ectotympanic to the anterior process of the petrosal. It is developed by fusion of the embryonic accessory ossicle with an anterior extension of the embryonic tegmen tympani (anterior process). This feature is unique to mysticetes.
7. **Features of the pars cochlearis**	—	—
7a. Pyramidal process	Present and modified	Pyramidal process (sensu Kasuya, 1973; Luo and Eastman, 1995) is considered to be homologous with the arcuate eminence in non-cetacean mammals. Both have identical topographical relations to the underlying anterior semicircular canal. The pyramidal process may be variable, especially in mysticetes.
7b. Medial promontorial groove	Present in some taxa	Medial promontorial groove is present in some non-cetacean mammals, for the inferior (medial) petrous sinus. This groove probably housed the inferior petrosal sinus in protocetids; but in most cetaceans it is incorporated into the medial pterygoid sinus.
8. **Hiatus fallopii**	Present in several conditions	Hiatus fallopii is the foramen or opening by which the greater superficial petrosal nerve exits the petrosal anteriorly. Its location may be endocranial, extracranial, or intramural (on the anterior aspect of the pars cochlearis) in different cetacean taxa and non-cetacean mammals.
8a. Hiatus fallopii on tympanic side of petrosal	—	This condition is present in archaeocetes, mesonychians, and some non-cetacean mammals.
8b. Hiatus fallopii on endocranial side of petrosal	—	This condition is present in most odontocetes, and most non-cetacean mammals.
8c. Hiatus fallopii intramural	—	This condition is present in most mysticetes and some non-cetacean mammals.
9. **Loss of subarcuate fossa**	Subarcuate fossa	Subarcuate fossa is a cavity between three semicircular canals in the pars canaliculus of the petrosal. It opens endocranially and its margin is formed by the anterior semicircular canal. The subarcuate fossa is present in most non-cetacean mammals, but absent in cetaceans in which the semicircular canals associated with the fossa are extremely reduced (Luo and Marsh, 1996), and it is absent in some ungulates (Novacek, 1986; Geisler and Luo, 1998).

TABLE 2 (cont.) — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the petrosal and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
10. **No separation of vestibular nerve foramina**	Separate nerve foramina to utricle and semicircular canals	In non-cetacean mammals, vestibular nerve branches to the saccule, utricle, and semicircular canals have separate foramina in the internal acoustic meatus. In all basilosaurids and more derived cetaceans, there is only one foramen for the vestibular nerve, in correlation with the very reduced utricle and semicircular canals.
11. **Posterior process of petrosal**	Mastoid process	The posterior process in cetaceans represents an elongated mastoid process (pars mastoides). It is relatively short in most non-cetacean mammals, but more elongate in mesonychids and cetaceans. Its distal part is expanded in most archaeocetes.
11a. Very reduced in derived odontocetes	Present in very modified condition	Very reduced posterior (mastoid) process is present in some odontocetes (kogiids, phocoenids, iniids, pontoporiids, and some delphinids). Its enclosure by the squamosal and exoccipital in most odontocetes is convergent to the amastoid condition of some derived artiodactyls.
11b. Extremely long in mysticetes	Present in very modified condition	Not developed in non-cetacean mammals.
12. **Articulation of posterior processes between petrosal and ectotympanic**	Present and modified	This cetacean feature is homologous with the articulation between the crista parotica of the petrosal and the posterior crus of the ectotympanic ring in many non-cetacean mammals. The key modification in cetaceans is that the area of articulation or contact is extended beyond the crista parotica onto most of the mastoid process. This differs from non-cetaceans, in which the articulation is restricted to the crista parotica of the petrosal.
12a. Posterior process of tympanic covers half of posterior (mastoid) process	Present and modified	This condition is present only in pakicetids among all cetaceans. Limited coverage of the bulla on the mastoid process of petrosal may occur in some non-cetacean mammals, but this usually far less than half of the length of the mastoid process.
12b. Posterior process of tympanic covers the full length of posterior process	Absent	Not developed in non-cetacean mammals and pakicetids; derived condition of post-pakicetid cetaceans.
12c. Smooth contact between posterior processes of petrosal and ectotympanic	Absent	Not developed in non-cetacean mammals. Among cetaceans, this condition is only present in some derived odontocetes, such as kogiids, phocoenids, and some delphinids.
12d. Fusion of posterior processes of petrosal and ectotympanic	Absent	Not developed in non-cetacean mammals; only present in mysticetes among all cetaceans.
13. **Articulation of posterior process of petrosal with squamosal**	Present	Primitive condition of non-cetacean mammals.

TABLE 2 (cont.) — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the petrosal and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
13a. Articulating flange and fossa on the posterior process of petrosal for squamosal	Absent	Not developed in non-cetacean mammals; only present in mysticetes among cetaceans.
13b. Ridge-like articulation on posterior process of the petrosal for squamosal	Absent	No homologous structure on the mastoid process of petrosal in non-cetacean mammals. It is present in squalodontids among odontocetes.
13c. Hook-like process on posterior process to articulate with squamosal	Absent	No homologous structure on the mastoid process of petrosal in non-cetacean mammals; only present in *Platanista*, *Zarhachis* and primitive "river-dolphins" among all cetaceans.
13d. Little or no articulation of posterior process with squamosal	—	Not developed in non-cetacean mammals. A derived condition in some odontocetes.
14. **Articulation of posterior process of petrosal with exoccipital**	Present	Primitive condition of non-cetacean mammals.
14a. Absence of articulation of posterior process with exoccipital	Present	Not developed in non-cetacean mammals. A derived condition in some odontocetes.

TABLE 3 — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the ectotympanic and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
15. **Anterior process (processus tubarius) of ectotympanic**	Present	Anterior process of ectotympanic (the processus tubarius of van der Klaauw, 1931) is the same in *Pakicetus* as in such terrestrial ungulates as *Ovis* in its morphology and proportion. We consider the anterior process of primitive cetaceans to be homologous with the anterior process of the bulla as in ungulates.
15a. Anterior process of ectotympanic formed by a hollowed bullar shell	Present	Same as the processus tubarius (sensu van der Klaauw, 1931) in ungulate outgroups; present only in pakicetids among cetaceans.
15b. Anterior process of ectotympanic forms an external ridge	Absent	This condition is not developed in non-cetacean mammals and pakicetids. Derived condition of basilosaurids and *Xenorophus*. Condition in protocetids is unknown.
15c. Accessory ossicle	Present and modified	Accessory ossicle of the ectotympanic is present in embryogenesis of mysticetes and odontocetes. It grows to be an independent structure separated from (although related to) the processus tubarius in adult odontocetes. It is fused with the anterior process of the petrosal to form the pedicle for the anterior process of the bulla in adult mysticetes. In non-cetaceans, the homologous accessory ossicle (ossiculum accessorium of van Kampen, 1905) is a distinctive structure in development, but co-ossifies with the anterior process of the bulla and the long process of the malleus in adults. Therefore, homologues of the accessory ossicle of odontocetes are present in mysticetes and non-cetacean mammals in some modified form.
15d. Pedicle for the anterior process	Absent	Fusion of the embryonic accessory ossicle to the anterior process of the tegmen tympani of the petrosal is a derived condition for mysticetes.
16. **Articulation of the anterior process (and its homologues) of the bulla to the basicranium**	Present in modified condition	—
16a. Contacting the squamosal	Present in some taxa	Anterior process of bulla contacts the entoglenoid process of the squamosal in *Ovis* (van Kampen, 1904; this study) and mesonychians (Zhou et al., 1995; Geisler and Luo, 1998). Articulation of anterior bullar process with the squamosal is present in archaeocetes, but absent in mysticetes and odontocetes.
16b. Contacting the anterior process of petrosal	Absent	This condition is not developed in non-cetacean mammals. A small bullar articulation with the anterior process of the petrosal is present in some protocetids and all basilosaurids. Full articulation occurs in mysticetes and odontocetes.
17. **Sigmoid process**	Modified	Sigmoid process of cetaceans is a structure homologous to the anterior wall of the auditory meatal tube (of some non-cetacean mammals) and developed from the anterior crus of the ectotympanic ring (present in all mammals). A putative sigmoid process is present in *Diacodexis pakistanensis* (Russell et al., 1983).
17a. Plate-like sigmoid process	Modified	Similar to the anterior wall of the ectotympanic part of the external auditory meatus. This condition is present only in *Pakicetus* and *Ichthyolestes* among all cetaceans (Luo, 1998).
17b. Margin of sigmoid process is flaring and recoiled	Absent	This condition is not developed in non-cetacean mammals and pakicetids. It is an apomorphy for cetaceans more derived than pakicetids.

TABLE 3 (cont.) — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the ectotympanic and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
18. **Lateral furrow**	Absent	Not developed in non-cetacean mammals.
19. **Articulation of sigmoid process**	Absent	Not developed in non-cetacean mammals.
19a. Articulation of sigmoid process with squamosal	Present in modified condition	Anterior crus of the ectotympanic ring articulates with the squamosal in many non-cetacean mammals. As the anterior crus of the ectotympanic is homologous to a part of the sigmoid process of cetaceans, contact of the sigmoid process with the squamosal in archaeocetes is a primitive condition for cetaceans. Absence of a sigmoid-squamosal articulation is a derived character of mysticetes and most odontocetes.
19b. Contact of sigmoid process with ventrolateral tuberosity	Absent	Derived condition of some odontocetes (See Luo and Marsh, 1996, for discussion).
20. **Malleolar process (or the malleolar accessory ossicle) of ectotympanic**	Present	Articulation (or even fusion) of the long process of the malleus to the anterior crus of the ectotympanic ring is primitive for non-cetacean mammals. In cetaceans, a modified part of the anterior crus of the ectotympanic is fused to the gonial, and, indirectly, the medial conical process. This compound structure provides attachment for the long process of the malleus (Ridewood, 1922).
21. **The conical apophysis (middle process) of the bulla**	Absent	The conical apophysis (middle process) of the ectotympanic develops from an early folding of the embryonic ectotympanic ring (Hanke, 1914). The apophysis is absent in non-cetacean mammals and pakicetids, but present in protocetids and more derived cetaceans.
21a. Appressed to sigmoid process	Absent	Not developed in non-cetacean mammals and archaeocetes; present in mysticetes and odontocetes.
22. **Posterior process of ectotympanic**	Present	The posterior process of the tympanic in cetaceans is homologous with the posterior crus of the ectotympanic ring of non-cetacean mammals. The main distinction is that the posterior process is distally expanded in cetaceans, whereas the posterior crus tapers posteriorly in most non-cetacean mammals.
23. **Base of posterior process**	Present	Posterior crus of the ectotympanic ring.
23a. Broad	Present	Present in pakicetids, mesonychids, and other ungulates, but absent in other cetaceans.
23b. Constricted neck (pedicle) of posterior process	Absent in most	Not developed in most non-cetacean mammals; present in post-pakicetid cetaceans.
23c. Double posterior pedicles with a pedicle foramen	Absent	Not developed in non-cetacean mammals; present in several protocetids and all basilosaurids.
24. **Distal plate of posterior process**	Present in modified condition	The distal plate of the posterior process of the ectotympanic is homologous with the posterior wall of the external auditory meatus, or an expanded posterior crus of the ectotympanic in some ungulate mammals.

TABLE 3 (cont.) — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the ectotympanic and its articulation with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
24a. Thin and vertical plate	Present in modified condition	Present in pakicetids, among cetaceans.
24b. Thick horizontal plate of posterior process of ectotympanic	Absent	This condition is not developed in non-cetacean mammals and pakicetids; present in all post-pakicetid cetaceans.
24c. Distal end of the posterior process contacting squamosal	Absent	Not developed in non-cetacean mammals; present in physeterids and ziphiids among all cetaceans.
25. **Involucrum**	Absent	The involucrum is a pachyosteosclerotic condition of the medial rim of the bulla.
26. **Morphology of eustachian tube**	Present	—
26a. With recoiled rim	Present in some taxa	The recoiled rim of the eustachian tube is the adult condition in artiodactyls. Among cetaceans, it is also present in non-odontocete cetaceans, including pakicetids.
26b. With sharp (uncoiled) edge	Present in some taxa	Juvenile condition in artiodactyls and mesonychians; present in only odontocetes among cetaceans.
27. **Position of bony eustachian opening**	—	—
27a. At the anteromedial corner of the bulla	Present	Position of the eustachian tube in the anteromedial corner of the bulla is typical of non-cetacean mammals, and therefore a primitive condition.
27b. On the medial side of the bulla	Absent	A derived condition seen only in protocetids, but not in other cetaceans including *Pakicetus*.
28. **Interprominential notch**	Present	The interprominential notch and the tympanohyal sulcus have identical positions on the tympanic bullae in the artiodactyls and pakicetids. The two structures are considered to be homologous.
29. **Median furrow or ridge**	Absent	Non-cetacean mammals lack such features; also absent in *Pakicetus*.
29a. Median furrow	Absent	Derived character of protocetids, basilosaurids, and odontocetes.
29b. Median ridge	Absent	Derived character of mysticetes among all cetaceans.
30. **Medial petrotympanic fissure**	Absent	A gap between the ectotympanic involucrum and the petrosal promontorium—a derived character of cetaceans. In most non-cetacean mammals with a full bulla, the medial bullar rim of bulla contacts the basioccipital, which represents a primitive condition. This is different from the Glasserian fissure on the anterolateral side of the bulla (van der Klauuw, 1931; MacPhee, 1981).
31. **Basicapsular fissure**	Present	Gap of unossified area between the pars cochlearis (promontorium) and the basioccipital, present in some (but not all) non-cetacean mammals. It is secondarily enlarged by the pterygoid sinus in cetaceans.

TABLE 4 — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the squamosal, and its articulations with other basicranial bones

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
32. **Falcate process of squamosal**	Present and modified	The falcate process of the squamosal in cetaceans is homologous with the entoglenoid process of the squamosal in non-cetacean mammals; but in some cetaceans the falcate process is highly modified (see below).
32a. Divided (anterior and posterior) falcate processes	Absent	Derived characters of some cetaceans; incipient in basilosaurids; fully developed in odontocetes.
32b. Interlock of the squamosal with the hiatus epitympanicus	Absent	Presence of a spinous process — the part of squamosal that inserts between the pars cochlearis and the pars canaliculus of the petrosal — is primitive for non-cetacean mammals. Also present in mysticetes. Present in mesonychians, mysticetes, platanistids, and *Zahrachis* among odontocetes.
33. **Preglenoid region of squamosal**	Present and modified	An anterior expansion of the entoglenoid process of squamosal occurs in archaeocetes and mysticetes.

TABLE 5 — Homology of basicranial structures in cetaceans and non-cetacean eutherians: characters of the occipitals and related features

Cetacean apomorphy	Condition in non-cetacean mammals	Description of character, comments on homology, and systematic distribution
34. **Jugular foramen**	Present	Presence of jugular foramen (= posterior lacerate foramen) is a primitive character of non-cetacean mammals.
34a. Confluence of jugular foramen	Absent	Basicapsular fissure between the basioccipital and the petrotympanic complex may be enlarged by the medial pterygoid sinus so it becomes confluent with the jugular foramen. This condition is present in cetaceans.
34b. Jugular foramen is enlarged into the petrosoparoccipital fissure	Absent	This condition is not developed in most non-cetacean mammals and protocetids. Enlargement of the jugular foramen occurs as the posterior part of the pterygoid sinus expands into the exoccipital region; present in basilosaurids, mysticetes, and odontocetes.
35. **Basal (falcate) process of basioccipital**	Absent	Not developed in non-cetacean mammals; present in cetaceans including pakicetids.
35a. Lateral protuberance	Absent	Not developed in non-cetacean mammals; a derived condition only in pakicetids.
35b. Basal or falcate process	Absent	A process on the lateral margin of the basioccipital. Derived condition of post-pakicetid cetaceans.
35c. Crest or plate-like falcate process	Absent	Basioccipital process is plate-like, and extending ventrally to accommodate an expanded medial pterygoid sinus.

III

MORPHOLOGICAL DESCRIPTIONS

The transition from terrestrial ungulates to aquatic whales is now known from fossils representing a basal Paleocene and Eocene group of Mesonychia, comprising two families Hapalodectidae and Mesonychidae (combined in our outgroup 1), and three Eocene archaeocete families, Pakicetidae, Protocetidae, and Basilosauridae, that are transitional from earlier Mesonychia to later Odontoceti and Mysticeti. Some members of these groups have been described by others. Here we provide new descriptions of *Hapalodectes hetangensis* (Hapalodectidae), and of *Dissacus praenuntius* and *Sinonyx jiashanensis* (Mesonychidae). *Hapalodectes* is described first as it appears to be a little more primitive than *Dissacus* and *Sinonyx.* These are followed by new descriptions of *Pakicetus inachus* (Pakicetidae) and of *Gaviacetus razai* and *Indocetus ramani* (Protocetidae). Finally, we provide new descriptions of Basilosauridae based on *Dorudon atrox*, *Basilosaurus isis*, and related middle and late Eocene forms. All of our descriptions are based on original specimens, except for that of *Indocetus*, which is based on a good cast. Characteristics described here are considered in the context of a broader range of comparative taxa in the following chapters.

HAPALODECTES HETANGENSIS (HAPALODECTIDAE)

Hapalodectes hetangensis is represented here by the type skull (IVPP 5253) described by Ting and Li (1987). It is clearly subadult, as evidenced by unerupted P_4 and M_3 (Ting and Li, 1987). This means that cranial sutures are generally not fully ossified and remain visible. The bulla is not present, and its absence may be due to (1) lack of preservation, or (2) lack of full ossification of this structure due to its immaturity. As a result, the petrosal is fully exposed in tympanic view (Fig. 5).

Petrosal.—The promontorium of the petrosal (Fig. 5: *pr*) is separated anteriorly from the alisphenoid by a large piriform fenestra (Fig. 5: *pif*; also see Ting and Li, 1987). The medial rim is separated from the basioccipital by the basicapsular fissure (Fig. 5: *bf*) that is continuous with the jugular foramen (= posterior lacerate foramen; Fig. 5: *jf*). The basicapsular fissure (= "medial course for internal carotid artery, or *mica*" of Ting and Li, 1987, p.181) was most likely a venous (instead of arterial) channel filled by the inferior petrosal sinus (Wible, 1983, 1986). Lack of a direct contact or a suture between the promontorium of the petrosal and the surrounding bones could be due to the lack of full ossification in this subadult skull.

The promontorium has a clearly marked groove for the transpromontorial course of the internal carotid artery (Fig. 5: *pica*; see Ting and Li, 1987). The groove extends first from the jugular foramen to the fenestra cochleae (round window), then anteriorly from the fenestra cochleae across the promontorium to reach the anterior pole of the promontorium (Fig. 5: *po*; MacPhee, 1981; Wible 1990). The course for the proximal stapedial artery is not preserved on the left side of the specimen. There is a faint groove between the fenestra cochleae and the fenestra vestibuli on the right side, which is tentatively interpreted to be for the proximal stapedial artery (Fig. 5: *sa?*). Ting and Li (1987) placed the stapedial artery on the promontorial surface anterior the fenestra cochleae. Geisler and Luo (1998) revised their interpretation by placing the course of the proximal stapedial artery between the fenestra vestibuli and fenestra cochleae. This latter placement of the proximal stapedial artery (Fig. 5) is more consistent with the well established pattern known from many (but not all) eutherians, in which the branching point of the stapedial artery from the internal carotid artery is located lateral to the fenestra cochleae (MacPhee, 1981; Wible, 1986).

The epitympanic recess area (Fig. 5: *er*) is positioned lateral to the fenestra vestibuli on the petrosal (Fig. 5: *fv*). It is a relatively flat and almost featureless area, and it does not appear to have extended onto the adjacent squamosal. Both the fossa incudis for the incus and the fossa malleus to accommodate the malleolar head are absent. The tegmen tympani that forms the dorsal roof of the epitympanic recess is small and weakly ossified. The shallow stapedial muscle fossa (Fig. 5: *fst*) is located posterior to the fenestra vestibuli and posterodorsal to the relatively large base for attachment of the tympanohyal. The facial nerve sulcus for the hyomandibular branch of the facial nerve extends from the facial foramen (Fig. 5: *VII*) to the stylomastoid notch (Fig. 5: *sm*), which is located medial to the base of the tympanohyal (Fig. 5: *th*), and lateral to the stapedial muscle fossa. The hiatus fallopii, the foramen for the greater superficial petrosal nerve (= the palatine branch of the facial nerve; Fig. 5: *hf*), is visible on the ventral side of the tegmen tympani. A faint groove for the greater superficial petrosal nerve extends from the hiatus fallopii to the anterior margin of the promontorium. The greater petrosal nerve was probably

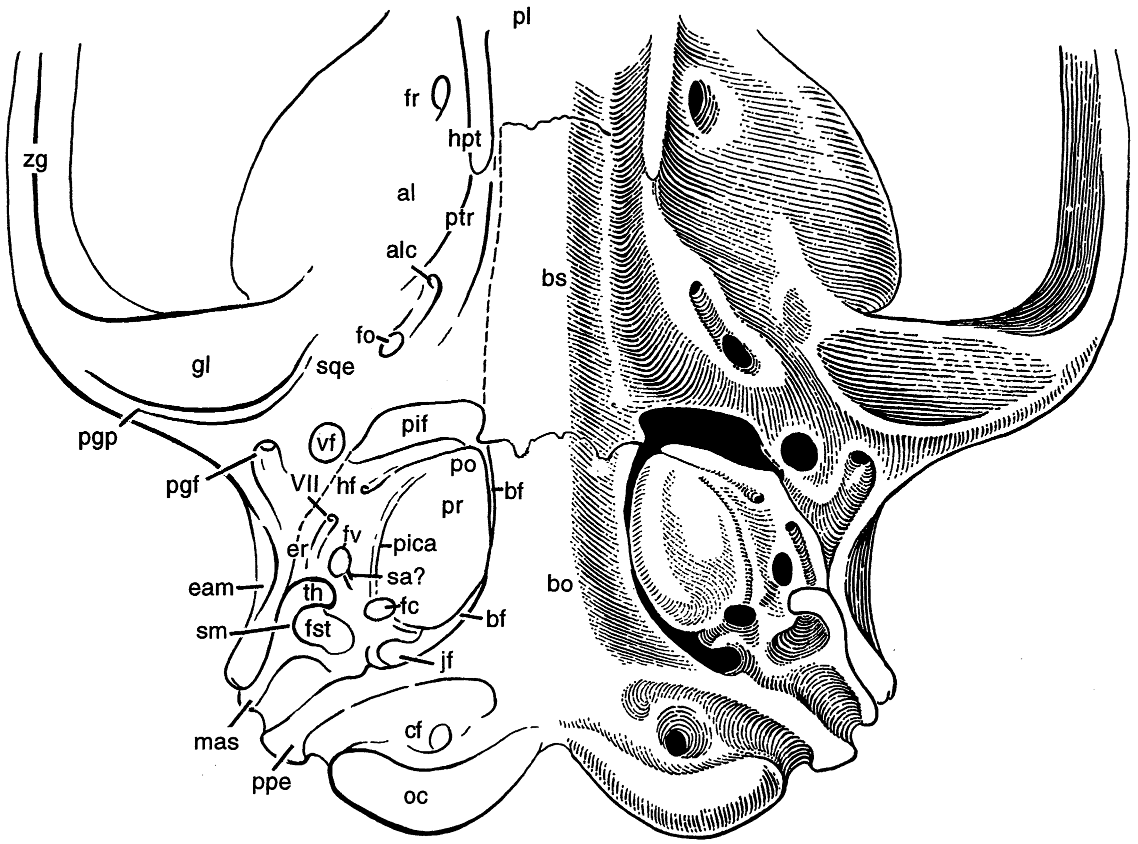

FIGURE 5. Basicranium of Eocene mesonychian *Hapalodectes hetangensis* (IVPP 5253; modified from Ting and Li, 1987). Abbreviations: *al*, alisphenoid; *alc*, alisphenoid canal; *bf*, basicapsular fissure; *bo*, basioccipital; *bs*, basisphenoid; *cf*, condylar foramen for hypoglossal nerve; *eam*, external auditory meatus; *er*, epitympanic recess; *fc*, fenestra cochleae; *fo*, foramen ovale; *fr*, foramen rotundum; *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli; *gl*, glenoid; *hf*, hiatus fallopii for the great petrosal nerve; *hpt*, hamulus of pterygoid; *jf*, jugular foramen (= posterior lacerate foramen); *mas*, mastoid process; *oc*, occipital condyle; *pgf*, postglenoid foramen; *pgp*, postglenoid process; *pif*, piriform fenestra; *pica*, promontory groove for the internal carotid artery; *pl*, palatine; *po*, pole of the promontorium; *ppe*, paroccipital process of exoccipital; *ptr*, pterygoid ridge; *sa?*, sulcus for stapedial artery?; *sm*, stylomastoid notch; *sqe*, entoglenoid process of the squamosal; *th*, tympanohyal; *VII*, facial nerve foramen; *vf*, vascular foramen for the superior ramus of the stapedial artery (for possible homology see Geisler and Luo, 1998); *zg*, zygoma.

exposed on the tympanic side of the tegmen tympani after exiting from the hiatus. The geniculate ganglion where the greater petrosal nerve bifurcates from the hyomandibular nerve (VII) was enclosed by bone and not exposed on the tympanic side of the tegmen.

The mastoid part of the petrosal (= posterior process; Fig. 5: *mas*) is short and proportionally comparable in length to the mastoid process of *Leptictis* (Novacek, 1986) and other basal eutherians (MacPhee, 1981), as well as contemporary ungulates from the Eocene (Radinsky, 1965; Coombs and Coombs, 1982). Its ventral surface is slightly concave. Its posterolateral end is exposed ventral to the lambdoidal crest of the skull. The mastoid exposure of the petrosal forms a wedge between the squamosal and the paroccipital process of the exoccipital (Fig. 5: *ppe*). The post-temporal canal is present in the skull near the junction of the mastoid process of the petrosal, the squamosal, and the supraoccipital. This canal is interpreted to be for arteria diploetica magna (possibly also for the vena diploetica magna, see discussion by Geisler and Luo, 1998), a vessel that has a broad distribution in mammals (Wible, 1987).

Squamosal.—The squamosal has an oval-shaped glenoid fossa for the temporomandibular joint. The glenoid fossa has a prominent postglenoid ridge, known as the postglenoid process (Fig. 5: *gl* and *pgp*; Ting and Li, 1987), posterior to which is a large postglenoid foramen for a branch of the capsuloparietal emissary vein, known either as the postglenoid vein or as the petrosquamous vein (Fig. 5: *pgf*; Ting and Li, 1987). Between the postglenoid foramen and the piriform fenestra is a large vascular foramen (Fig. 5: *vf*), which could be for the ramus superior of the stapedial artery (as interpreted by Geisler and Luo, 1998).

Pterygoid.—The oropharyngeal passage is flanked on either side by a slightly elevated and broad pterygoid ridge (Fig. 5: *ptr*). A similar ridge is present in many eutherians (e.g., *Leptictis*, Novacek, 1986; *Canis*, Evans, 1992). The sutures of the pterygoid, alisphenoid and basisphenoid are not clear on the type specimen of *Hapalodectes*. The alisphenoid-basisphenoid suture is both parallel to and medial to the pterygoid ridge in *Sinonyx* (Zhou et al., 1995) and other eutherians (Novacek, 1986; Evans, 1992). So we interpret the suture of the alisphenoid to be positioned just medial to the pterygoid ridge. The foramen ovale and the posterior opening of the alisphenoid canal are present in an elongated depression on the top of this ridge (Fig. 5: *fo* and *alc*). The foramen ovale was the exit for the mandibular branch of the trigeminal nerve. The alisphenoid canal was the passage for the ramus inferior of the stapedial artery or an artery derived from the maxillary branch of the external carotid artery (Wible, 1987; Wible and Hopson, 1995). The alisphenoid canal appears to open anteriorly into the orbital fissure (not figured here, but see Ting and Li, 1987). There is no visible pneumatic sinus in the area of the pterygoid, basisphenoid, alisphenoid, or petrosal.

Basioccipital.—The basioccipital has a very shallow median ridge that extends posteriorly toward (but does not reach) the foramen magnum. There are two foramina on the ventral side of the exoccipital in the right side (one for the hypoglossal nerve, the other for an emissary vein), but only one condylar foramen for the hypoglossal nerve on the left (Fig. 5: *cf*, based on the left side of the skull). This interpretation implies that the condylar foramen for the condylar emissary vein is more variable, while the hypoglossal foramen (for cranial nerve XII) is a more conservative feature of the exoccipital, at least in mesonychians.

DISSACUS PRAENUNTIUS (MESONYCHIDAE)

The basicranium of *Dissacus praenuntius* (UM 75501) consists of a partial alisphenoid, a complete squamosal, a complete but broken petrosal, and a complete exoccipital. The tympanic bulla is missing. All basicranial bones of UM 75501 are disarticulated but preserved in close association. A composite restoration of the partial basicranium is illustrated in Figure 6.

Petrosal.—The petrosal has a nearly complete but fractured mastoid process (or posterior process; Fig. 6: *mas* or *pp*). It is elongate, and much longer than that of *Hapalodectes*. Its anterior aspect is flanked by the squamosal (Figs. 6 and 7: *sqc*). Its posterior aspect (Figs. 6 and 7: *eoc*) is covered by the paroccipital process of the exoccipital (Fig. 6: *ppe*). Its ventral surface is slightly concave. The mastoid process has a smooth periosteal surface, indicating that it was not covered by the posterior process of the tympanic as is the case in cetaceans. The distal end of the mastoid process is exposed between the exoccipital and the postmeatal crest of the squamosal, as seen in ventral and lateral views of the skull (Fig. 6: *pmp*). On the dorsal aspect of the petrosal (near the notch of the hiatus epitympanicus), there is the dorsal and internal opening of the post-temporal canal (Fig. 7A, B, and D: *ptc*). The ventral and external opening of this canal is located on the distal end of the mastoid process, near the paroccipital process of the exoccipital. The canal is completely enclosed by the mastoid process of the petrosal. A similar canal is present in *Erinaceus* (Luo, 1989) and *Leptictis* (Novacek, 1986; Luo, 1989), and it is known to be present in some 26% of human skulls (Boyd, 1930; Hollinshead, 1968). The post-temporal canal may be either for the arteria diploetica magna (Wible, 1987; Geisler and Luo, 1998), or for both the arteria and vena diploetica magna (Geisler and Luo, 1998).

The tegmen tympani is a very prominent structure on petrosals of *Dissacus* (Figs. 6 and 7: *tt*) and *Mesonyx* (Geisler and Luo, 1998). It is greatly inflated, making it much larger than those of other extant and archaic ungulates (see the tegmen tympani of *Ovis*, Fig. 1; also see Cifelli, 1982). The tegmen tympani is identical in most major characteristics to the so-called superior process of archaeocetes (sensu Kellogg, 1928, 1936; Kasuya, 1973). The tegmen tympani in *Dissacus* and the "superior process" of archaeocetes have about the same size in proportion to both the pars cochlearis and to the mastoid process (Fig. 2). Based on these similarities, we interpret the so-called superior process of archaeocetes (and probably all cetaceans) to be homologous to a compound structure of the tegmen tympani and the prefacial commissure of non-cetacean eutherian mammals (Tables 2-6; Fig. 2: *tt* or *sp*).

The lateral aspect of the tegmen tympani is convex and smooth. When in situ, the lateral side of the tegmen tympani has a broad contact with the entoglenoid part of the squamosal (Fig. 1A and Fig. 5: *sqe*). The ventral surface of the tegmen tympani bears a simple concavity and a small protuberance. The concavity represents a part of the larger epitympanic recess. Most of the recess is in the petrosal but a small portion of it is also squamosal in the intact skull (Figs. 6 and 7: *er*). The protuberance is identical in position to (but smaller in size than) the ventrolateral tuberosity of the cetacean petrosals (Figs. 6B and 7A: *vlt*).

On the lateral surface of the tegmen tympani and anterior to the ventrolateral tuberosity is a large and prominent vascular groove (*vg*), forming a bony channel between the brain cavity and the tympanic cavity. In the intact skull, this vascular groove is enclosed by the entoglenoid part of the squamosal to form a vascular foramen (Fig. 6A: *vf*). This vascular channel was most probably occupied by the ramus superior of the stapedial artery (Geisler and Luo, 1998).

Another (albeit less likely) hypothesis would be that the bony channel carried a tributary vein of the capsuloparietal emissary vein or the prootic-lateral head venous system (for more information see Wible and Hopson, 1995; Geisler and Luo, 1998). However, it is unclear as to how this putative vein would exit the tympanic cavity because the ectotympanic bulla is tightly appressed to the entoglenoid part of the squamosal in mesonychians (see the descriptions of *Sinonyx* below, and *Mesonyx* in Geisler and Luo, 1998), and there is no opening for this venous vessel.

The anterior part of the tegmen tympani forms a distinctive projection (Figs. 6 and 7: *ap*), which is interpreted as an incipient anterior process because of its striking resemblance to the anterior process of the cetacean petrosals. The incipient anterior process is separated by an embayment from the lateral margin of the promontorium.

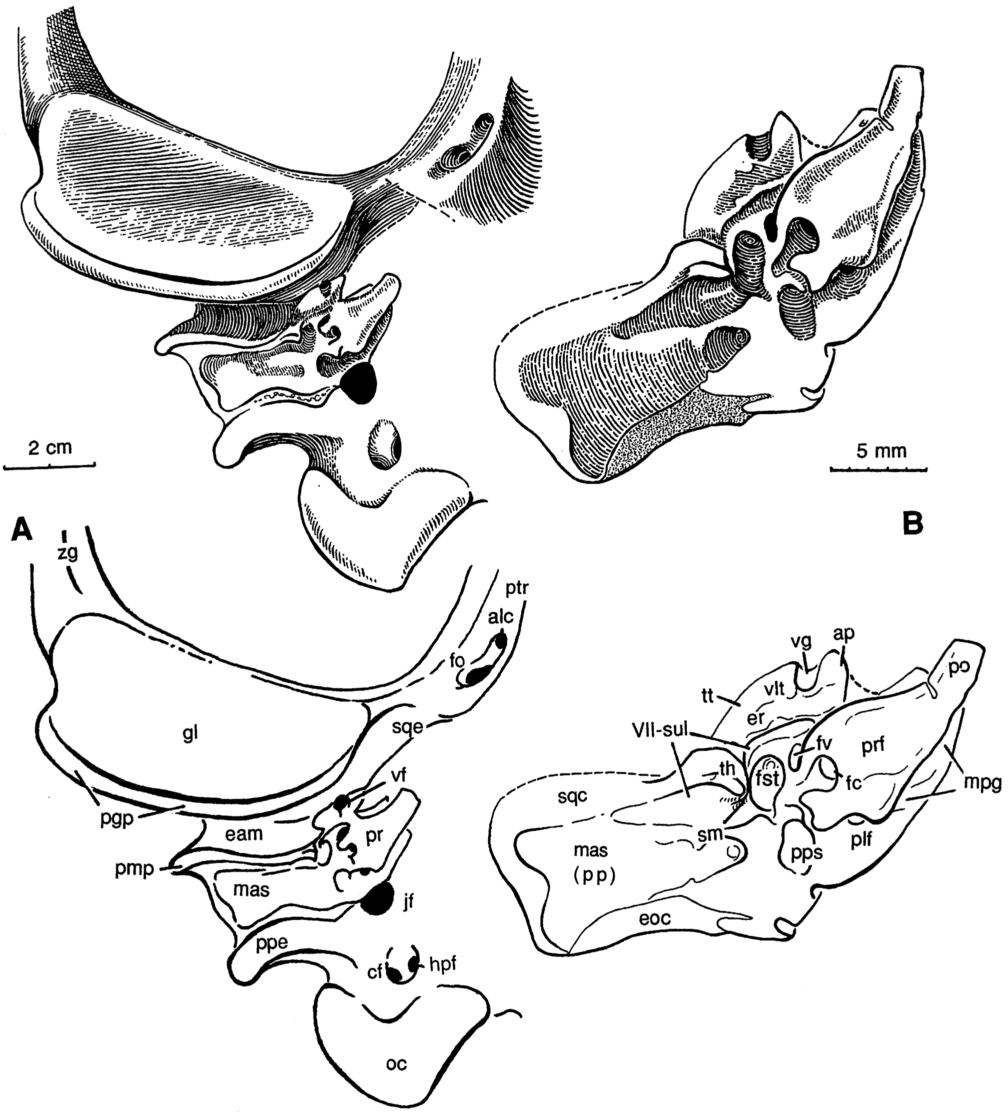

FIGURE 6. Basicranium of Paleocene mesonychian *Dissacus praenuntius* (UM 75501). A, composite illustration of right basicranium in ventral view, based on a disarticulated alisphenoid, exoccipital, petrosal and squamosal. B, isolated right petrosal in ventral view. Abbreviations: *alc*, alisphenoid canal; *ap*, anterior process; *cf*, condylar foramen (probably for a vascular vessel); *eam*, external auditory meatus; *eoc*, contact for the exoccipital; *er*, epitympanic recess; *fc*, fenestra cochleae; *fo*, foramen ovale; *fst*, stapedial muscle fossa; *fv*, fenestra vestibuli; *gl*, glenoid; *hpf*, hypoglossal foramen for cranial nerve XII; *jf*, jugular foramen; posterior lacerate foramen; *mas*, mastoid process of petrosal (= posterior process); *mpg*, medial promontory groove on the pars cochlearis, for inferior petrosal sinus; *oc*, occipital condyle; *pgp*, postglenoid process; *plf*, perilymphatic foramen; *pmp*, postmeatal process or crest of squamosal; *po*, pole of promontorium or pars cochlearis; *ppe*, paroccipital process of exoccipital; *pps*, postpromontorial sinus; *pr*, promontorium; *prf*, ventral facet of promontorium; *ptr*, pterygoid ridge; *sm*, stylomastoid notch; *sqc*, contact for squamosal on the petrosal; *sqe*, entoglenoid process of the squamosal; *th*, attachment site for tympanohyal; *tt*, tegmen tympani; *VII-sul*, facial nerve sulcus; *vf* (= *vg*), vascular foramen for the superior ramus of the stapedial artery; *vg* (= *vf*); *vlt*, ventrolateral tuberosity on the tegmen tympani; *zg*, zygoma.

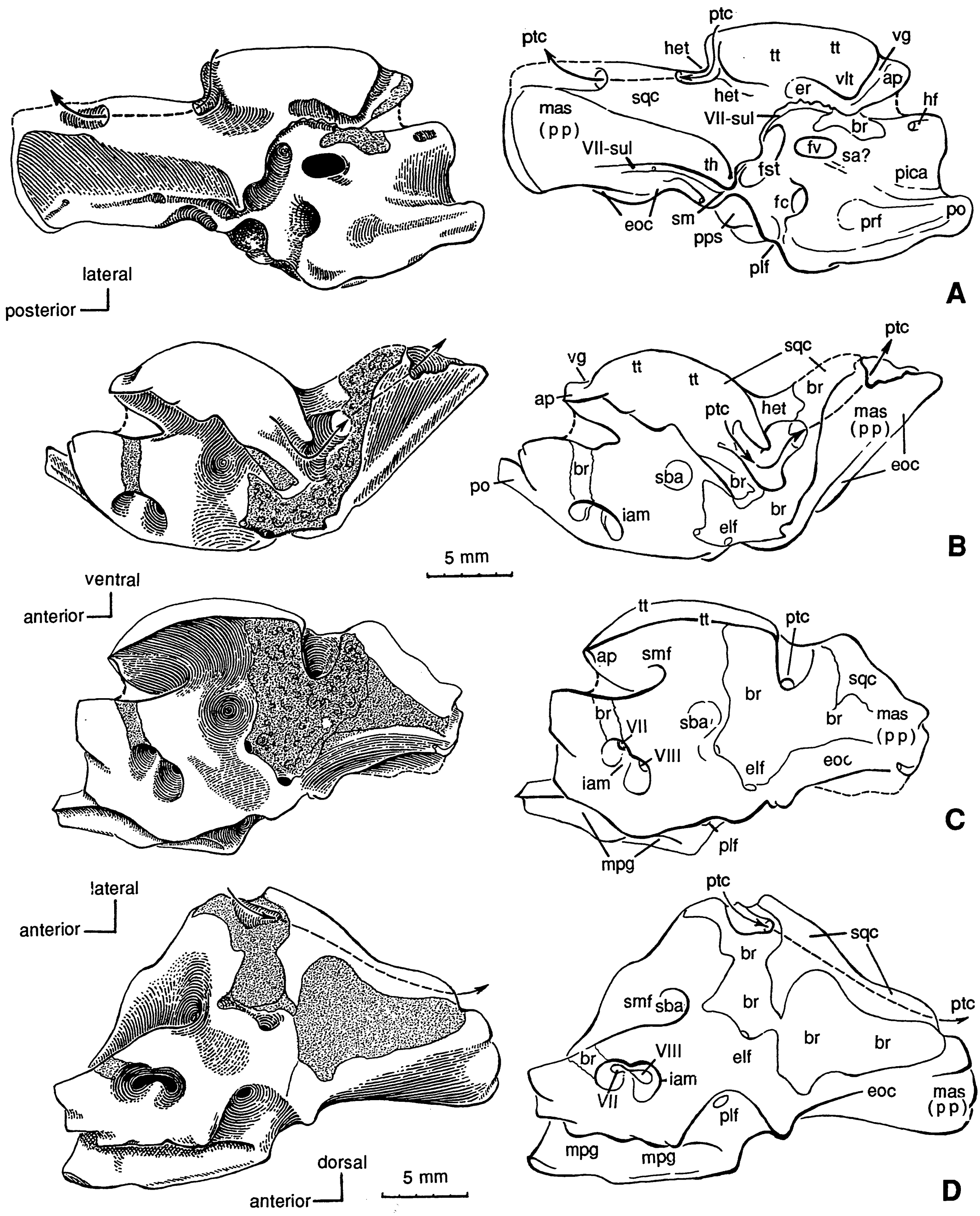

FIGURE 7. Right petrosal of Paleocene mesonychian *Dissacus praenuntius* (UM 75501). A, tympanic (tilted and ventrolateral) view. B, lateral view (tilted). C, endocranial (dorsal) view. D, medial view (tilted). Short dashed line between the anterior process and the pole of the promontorium represents a small missing part of the petrosal. Longer dashed line with arrow shows course of posttemporal canal. Abbreviations: *ap*, anterior process (= anterior extension of tegmen tympani); *br*, breakage and/or matrix; *elf*, endolymphatic foramen; *eoc*, contact for the exoccipital on the petrosal; *er*, epitympanic recess; *fc*, fenestra cochleae (= round window); *fst*, stapedial muscle fossa; *fv*, fenestra vestibuli (= oval window); *het*, hiatus epitympanicus; *hf*, hiatus fallopii for the greater superficial petrosal nerve of VII; *iam*, internal acoustic meatus; *mas(pp)*, mastoid process (or posterior process of the

Continued on page 26

The hiatus epitympanicus (Figs 6 and 7: *het*) is a broad and transverse trough located between the inflated tegmen tympani and the mastoid process. The ventral part of the hiatus epitympanicus is contiguous with the epitympanic recess (Fig. 7A, B). The lateral part of the hiatus epitympanicus receives the spinous (or spiny) process of the squamosal (not labeled), a small protruding part medial to the external auditory meatus of the squamosal. Similar articulating relationships between the hiatus epitympanicus of the petrosal and the spiny process of the squamosal are present in *Dorudon* (Fig. 1D, E), and in the platanistoid odontocetes *Notocetus* (de Muizon, 1987) and *Waipatia* (Fordyce, 1994). Therefore we consider the hiatus epitympanicus on the petrosal and its associated spinous (or "spiny") process of the squamosal to be homologous structures in both *Dissacus* and cetaceans (see Fig. 1D, E: *sqw* or *sps* and *het* of *Dorudon*).

The posterior part of the promontorium (the ventral eminence of the pars cochlearis) has a convex, smooth, and featureless surface. The anterior part of the promontorium has a flat area (Fig. 7A: *prf*). The lateral part of the promontorium has a broad and shallow groove flanked by two low and faint ridges. There are two possible interpretations of the soft tissue structures of this groove. First, it is possible to interpret the groove to be the course of the internal carotid artery, on the basis of its resemblance to the groove for the internal carotid artery in many other Paleocene and Eocene eutherian ungulates, such as *Hapalodectes* (MacIntyre, 1972; Cifelli, 1982; Coombs and Coombs, 1982; Ting and Li, 1987; Geisler and Luo, 1998). Placement of the internal carotid artery here is consistent with the position of the homologous vessel in most eutherians (Wible, 1986; Geisler and Luo, 1998). This promontorial sulcus for the internal carotid is much better developed in the closely related *Mesonyx* (Geisler and Luo, 1998). Following Geisler and Luo (1998) we interpret *Dissacus* to have had a transpromontorial groove for the internal carotid artery, as in other mesonychids (Fig 7A: *pica*). The second possible interpretation is that the groove and its associated ridges are spurious features unrelated to vessels. It is known that the grooves on the promontorium in lemurs are not necessarily correlated with the presence of a promontorial artery but may contain only nerves (Conroy and Wible, 1978). This second interpretation is far less likely but cannot be ruled out, for the groove is only present on the anterior part of the promontorium and does not extend to the posterior part, which is featureless (Fig. 7A).

A long and oval-shaped fossa for the tensor tympani muscle is present, although partially broken, on the petrosal of *Dissacus* (UM 75501). Anterior to the fossa for the tensor tympani is a small foramen, interpreted to be the hiatus fallopii for the greater superficial petrosal branch of the facial nerve (Fig. 7A: *hf*). The position of the hiatus fallopii in *Dissacus* is similar to the homologous foramen in *Hapalodectes* in its location on the tympanic side of the petrosal. The facial foramen for the hyomandibular branch of the facial nerve (partially broken in UM 75501) is located lateral to the fenestra vestibuli (Figs. 6B, 7A: *fv*). The facial nerve sulcus leads posteriorly from the facial foramen, and then passes around the large and oblong stapedial muscle fossa (Fig. 7A: *fst*) before it eventually reaches the stylomastoid notch (Figs 6B, 7A: *sm*) under the base of attachment for the tympanohyal (*th*). From the stylomastoid notch the facial sulcus extends onto the ventral surface of the mastoid (or posterior) process (Fig. 6: *VII-sul*). The portion of the facial sulcus close to the stylomastoid notch is visible, but the distal portion of the sulcus is obscured by fractures in the bone.

The fenestra cochleae is positioned on the posterior part of the promontorium (Figs 6B and 7A: *fc*). Posterior to the fenestra is a broadly concave area termed the postpromontorial tympanic sinus (Figs 6B and 7A: *pps*). A similar sinus is present at the same position in most therian mammals (Wible et al., 1995). Extending from the postpromontorial sinus along the medial edge of the promontorium is a groove, the medial promontory groove for the inferior petrosal sinus vein (Fig. 7C, D: *mpg*).

The cranial side of the petrosal is broken posterior to the subarcuate fossa. It has several features (Fig 7B, C, D): the perilymphatic foramen (*plf*), the endolymphatic foramen (*elf*), the internal acoustic meatus (*iam*) that houses the cranial openings of the facial nerve canal (*VII*) and the vestibulocochlear nerves (*VIII*). All of the above-mentioned structures are primitive characteristics of many other mammals.

The subarcuate fossa (Fig. 7: *sba*) is a shallow concavity. This is a primitive characteristic of most mammals, including many placental ungulates (MacIntyre, 1972; Cifelli, 1982). However, the subarcuate fossa is absent in *Mesonyx* (Geisler and Luo, 1998), in the domestic cow, and in a number of other artiodactyls.

The suprameatal fossa (Fig. 7C, D: *smf*) is a concave area lateral to the internal acoustic meatus on the cranial side of the tegmen tympani. The position and size of the fossa are very similar to those of cetacean petrosals. This derived feature rarely occurs in the petrosals of other eutherian mammals with a small tegmen tympani (MacIntyre, 1972; Cifelli 1982; Luo, 1989; Wible, 1990).

Exoccipital.—The exoccipital, though broken, shows several relatively well preserved features (Fig. 6). The occipital condyles are massive. The paroccipital process is very large,

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petrosal); *mpg*, medial promontory groove for inferior petrosal sinus; *pica*, promontory groove of the internal carotid artery; *plf*, perilymphatic foramen (= foramen cochleae); *po*, pole of the promontorium; *pp*, posterior process (= mastoid process); *pps*, postpromontorial sinus; *pr*, promontorium; *prf*, ventral facet of promontorium; *ptc*, post-temporal canal through the mastoid process of the petrosal; *sa?*, sulcus for stapedial artery; *smf*, suprameatal fossa; *sba*, subarcuate fossa; *sqc*, contact for squamosal (on the petrosal); *th*, attachment site for the tympanohyal; *tt*, tegmen tympani (= superior process); *vlt?*, ventrolateral tuberosity; *vg*, vascular groove; *VII*, facial foramen; *VII-sul*, sulcus for the hyomandibular branch of the facial nerve; *VIII*, foramina for vestibulocochlear nerves.

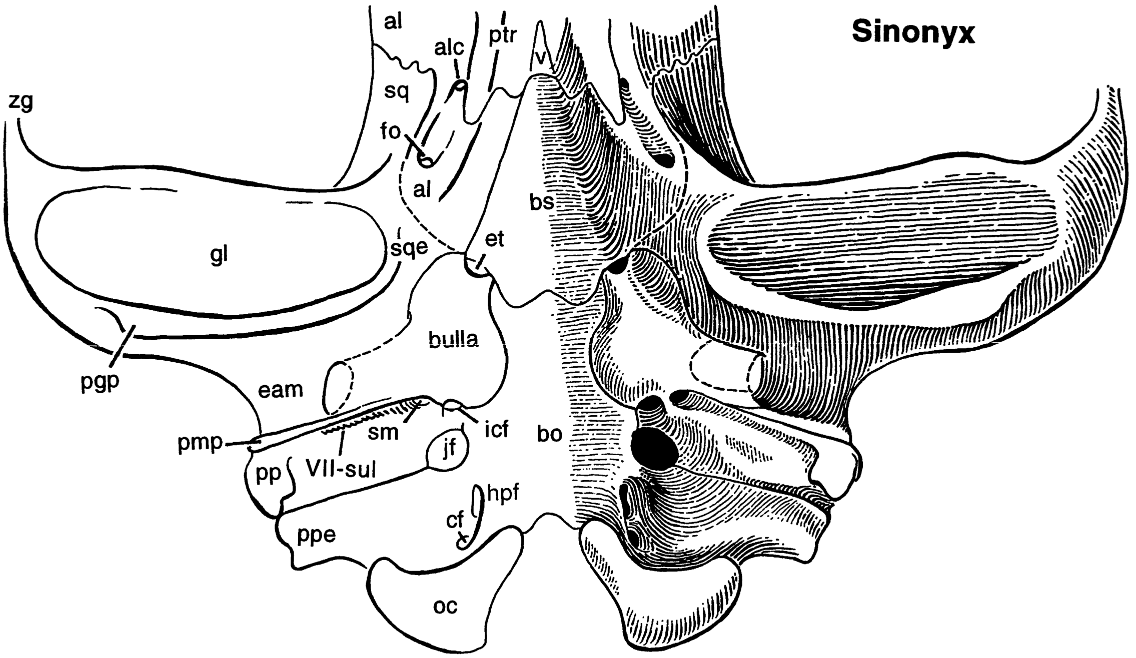


FIGURE 8. Basicranium of Paleocene mesonychian *Sinonyx jiashanensis* (IVPP 10760). The meatal floor of the bulla is restored on the basis of fragments of this specimen and a partial bulla of Eocene *Mesonyx obtusidens* (AMNH 12643). Abbreviations: *al*, alisphenoid bone; *alc*, the alisphenoid canal; *bo*, basioccipital; *bs*, basisphenoid; *cf*, condylar foramen for a vascular vessel; *eam*, external auditory meatus; *et*, bony eustachian tube opening; *fo*, foramen ovale; *gl*, glenoid fossa; *hpf*, hypoglossal foramen for cranial nerve XII; *icf*, posterior opening of the internal carotid canal; *jf*, jugular foramen (= posterior lacerate foramen); *oc*, occipital condyle; *pgp*, postglenoid process; *pmp*, postmeatal process of squamosal; *pp*, posterior (mastoid) process of petrosal; *ppe*, paroccipital process of exoccipital; *ptr*, pterygoid ridge forming the base for the pterygoid hamulus; *sm*, stylomastoid foramen; *sq*, squamosal; *sqe*, entoglenoid process of squamosal; *v*, vomer; *VII-sul*, sulcus for the facial nerve; *zg*, zygoma.

and extends laterally beyond the lateral end of the mastoid process of the petrosal, which the paroccipital process overlaps broadly. Both the hypoglossal foramen (for cranial nerve XII) and the condylar foramen (probably for a vascular vessel) are located in a depression anterolateral to the occipital condyle (Fig. 6: *cf*, *hpf*, *oc*).

SINONYX JIASHANENSIS (MESONYCHIDAE)

The ectotympanic bulla in *Sinonyx jiashanensis* (IVPP 10760) consists of two parts: a bulbous medial part that encloses the tympanic cavity, and a lateral extrabullar part that forms the ventral floor of the external auditory meatus (Fig. 8). Most of the left tympanic bulla is preserved in situ (Zhou et al., 1995). The bulbous portion of the bulla is preserved on the left side, and broken and slightly crushed on the right side. The medial rim of the bulla is sutured to the basioccipital. The anterolateral border of the bulla is sutured to the entoglenoid portion of the squamosal (Fig. 8: *sqe*). The eustachian tube has a funnel-like opening located in the anteromedial corner of the bulla (Fig. 8: *et*). The anteromedial location of the eustachian opening is typical of those early Tertiary placental mammals that have fully developed tympanic bullae.

Ectotympanic.—The lateral extrabullar part of the bulla is tubular. It is partially preserved on the right side, but entirely missing on the left. A narrow splinter of the broken bullar tube is preserved on the right side and attached to the mastoid process of the petrosal (Fig. 8: *pp*). This suggests that the meatal portion of the right bulla had formed much of the floor to the external auditory meatus. In a similar pattern, the anterior wall of the extrabullar part of the ectotympanic in *Mesonyx* (AMNH 12643) is attached to the postglenoid process of the squamosal (Geisler and Luo, 1998). We interpret that the external auditory meatus has a tubelike floor formed by the ectotympanic (Fig. 8).

The intrabullar part of the auditory meatus is not visible in *Sinonyx*. However, it is present in *Mesonyx* (AMNH 12643), where the intrabullar part of the auditory meatus protrudes into the bulla and bears an annulus for suspension of the tympanic membrane (Geisler and Luo, 1998). This is very similar to the annulus for suspension of the tympanic membrane in *Ovis* (Fig. 4: *an*), and it is the general condition of all land mammals with a well developed meatal tube of the ectotympanic.

In the posteromedial part of the bulla are two foramina, of which the larger and more medial one is tentatively interpreted as the entrance of the internal carotid artery into the posterior part of the bulla (Fig. 8: *icf*), and the smaller and more lateral foramen is the stylomastoid foramen for the facial nerve (Fig. 8: *sm*; see also Zhou et al., 1995: fig. 2).

Petrosal.—The mastoid process (posterior process) of the petrosal is elongated (Fig. 8). Its proportions are comparable to those of the mastoid process in *Dissacus* (Fig. 7) and in *Mesonyx*, but much longer than that of *Hapalodectes* (Fig. 5). The anterior border of the mastoid (or posterior) process overlaps the crest formed by the postmeatal process of the squamosal (Fig. 8: *pmp*) and the posterior wall of the meatal tube of the ectotympanic. The mastoid process of the petrosal, the squamosal, and the ectotympanic are joined to one another, forming a triple junction (Zhou et al., 1995). The posterior border of the mastoid process is sutured to the paroccipital process of the exoccipital. The ventral surface of the mastoid process is mostly flat, and exposed without any coverage by the ectotympanic. A faint groove for the facial nerve extends from the stylomastoid foramen posterolaterally along the anterior border of the mastoid process (Fig. 8: *VII-sul*). In lateral and occipital views of the skull, the distal end of the mastoid process is shaped like a wedge between the squamosal and exoccipital (Zhou et al., 1995). Although the bullae conceal most features in the tympanic cavity, two internal features of the petrosal are still visible because the right bulla is broken and slightly displaced. One visible feature is the medial promontorial groove for the inferior petrosal sinus, as in *Dissacus* and *Mesonyx* (Geisler and Luo, 1998). The second is a gap at the junction of the promontorium, the basioccipital, and basisphenoid for the internal carotid artery to enter the braincase, even though the course of this artery on the promontorium is not visible.

Occipital region.—The exoccipital has a well developed paroccipital process (Fig. 8: *ppe*). Its lateral (distal) end extends to about the same level as the distal end of the mastoid process (Fig. 8: *pp*). As in *Dissacus*, the occipital condyles are massive and separated by the odontoid notch in the midline of the skull. Both the hypoglossal foramen (for cranial nerve XII) and the condylar foramen (probably for an emissary vein in the condylar region) are present. As reported by Zhou et al. (1995), these foramina are somewhat variable and differ on the two sides of the one known skull.

PAKICETUS INACHUS (PAKICETIDAE)

The petrosal and ectotympanic of *Pakicetus inachus* (GSP-UM 84) and other pakicetids were described in several previous studies (Gingerich et al., 1983; Thewissen and Hussain, 1998; Luo, 1998). Here we provide additional information on basicranial parts that have not been described in detail. We describe a new ectotympanic bulla of *Pakicetus inachus* (GSP-UM 1632) from the type locality, and, for purposes of comparison, provide new illustrations of the type specimen (GSP-UM 84).

Pterygoid.—The pterygoid has a ridge (or crest) that decreases in height posteriorly and becomes broad near the bulla. Anteriorly, the left and right pterygoid ridges converge toward the midline on the ventral surface of the secondary palate. The specimen does not have a gracile and triangular hamulus that is commonly present in terrestrial mammals. In the comparable position where the ptergygoid hamulus was reconstructed in *Zygorhiza* by Kellogg (1936: fig. 29), the ridge is split posteriorly into medial and lateral laminae. The hamulus is interpreted by Kellogg (1936) to be attached to the medial lamina in *Zygorhiza*. It is unclear whether the pterygoid hamulus was absent in life in *Pakicetus*, or present in the skull but broken postmortem and lost during preservation. It cannot be ruled out that the broadened part of the pterygoid ridge served as the base for the hamulus of the pterygoid (Fig. 9: *hpt*).

The ptergygoid ridge is similar to its homologues in *Hapalodectes*, *Dissacus*, and *Sinonyx*. The pterygoid-alisphenoid suture is not clear. Therefore it is difficult to establish whether the posterior part of the pterygoid ridge is actually supported by the alisphenoid. The ridge does not bifurcate posteriorly into medial and lateral laminae as in basilosaurids. The medial (and internal) side of the pterygoid is a shallow trough, which is termed a medial pterygoid fossa (Fig. 10: *mpf*). The fossa is a part of the pharynx, and it is posterolaterally continuous with the shallow channel for the eustachian tube near the junction of the ectotympanic, petrosal, and basioccipital (Fig. 10). No anterior pterygoid sinus is present on the pterygoid.

Lateral to the pterygoid ridge is the foramen ovale for the mandibular nerve of the trigeminus (Fig. 9: *fo*; see also Thewissen and Hussain, 1998). The foramen ovale is positioned either in the alisphenoid, or at the suture of the squamosal and alisphenoid. Due to fusion of the suture between the two bones, the precise position of the foramen ovale is difficult to determine on this specimen. The foramen ovale appears to open directly into the braincase as is the primitive condition of mammals.

Squamosal.—The glenoid fossa of the squamosal has an oval outline, wider transversely than long (Fig. 9: *gl*). The zygoma is broken anteriorly. The preserved part of the zygoma does not have any facet or groove for articulation with the jugal. We infer that the jugal did not reach near the glenoid fossa, as is the case in *Sinonyx* (Zhou et al., 1995) and in basilosaurids. The postglenoid process is represented by a low ridge (Fig. 9: *pgp*). The external auditory meatus is a narrow and deep groove between the postglenoid ridge and the mastoid process of the petrosal (Fig. 9: *eam*). The meatus is an open trough and has no ventral floor of ectotympanic, unlike mesonychids in which a long segment of the meatus is ventrally covered by a tubular floor of the ectotympanic bulla. The meatus is much narrower than in all other cetaceans.

The entoglenoid part of the squamosal (medial to the glenoid fossa) bears the bullar process of the squamosal (Figs. 9, 10: *sqc*) for articulation of the anterior process of the tympanic bulla (Gingerich et al., 1983). The bullar process of the squamosal is a slightly elevated stage with a round outline. It borders medially on the groove in the petrosal for the tensor tympani

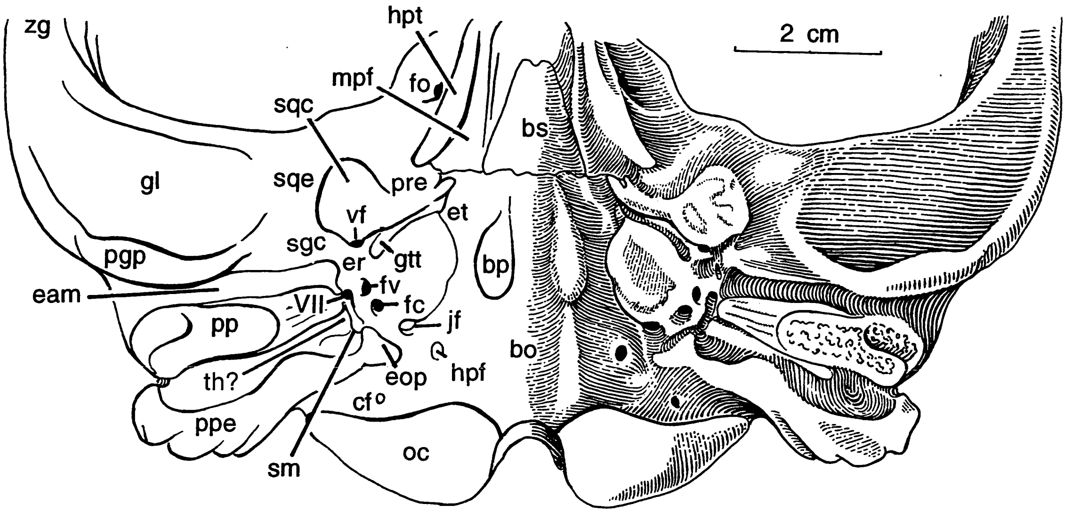


FIGURE 9. Basicranium of Eocene archaeocete *Pakicetus inachus* (GSP-UM 84; modified from Gingerich et al., 1983, to show specimen with bulla removed). Abbreviations: *bo,* basioccipital; *bp*, incipient falcate process of basioccipital; *bs*, basisphenoid; *cf*, condylar foramen; *eam*, external auditory meatus; *er*, epitympanic recess; *eop*, bullar process of the exoccipital; *et*, trough for the eustachian tube; *fc*, fenestra cochleae; *fo*, foramen ovale; *fv*, fenestra vestibuli; *gl*, glenoid fossa; *gtt*, tensor tympani groove; *hpf*, hypoglossal foramen; *hpt*, base of the pterygoid hamulus (= pterygoid ridge); *jf*, jugular foramen; *mpf*, medial pterygoid fossa; *pgp*, postglenoid process; *pp*, posterior process (= mastoid process); *ppe*, paroccipital process of exoccipital; *pre*, preglenoid portion of squamosal; *sm*, stylomastoid notch; *sqc*, contact on squamosal for the anterior process of tympanic; *th?*, possible site for attachment of tympanohyal; *vf*, vascular foramen for the superior ramus of the stapedial artery; *sqe*, entoglenoid process of squamosal; *zg*, zygoma.

muscle. Between the bullar process and the postglenoid process of the squamosal is a flat area where the sigmoid process of the ectotympanic bulla contacts the squamosal (Figs. 9, 10: *sgc*). It appears that the squamosal extends anterior to the bullar process (Figs. 9, 10: *pre*), but the suture of the preglenoid area of the squamosal with the alisphenoid is fused and difficult to determine.

Exoccipital.—The paroccipital process of the exoccipital is laterally elongated (Figs. 9, 10: *ppe*). Its enlarged distal end reaches beyond the lateral end of the mastoid process of the petrosal. This is similar to the condition in *Dissacus* and *Sinonyx,* but different from that of *Hapalodectes*. The exoccipital has a tuberosity near the jugular foramen (Fig. 9: *jf*). The tuberosity serves to support the medial prominence of the bulla, and it is therefore termed the bullar process of the exoccipital (Figs. 9, 10: *eop*; Gingerich et al., 1983). Two foramina are present on the ventral side of the exoccipital. The foramen for the hypoglossal nerve (XII) is more anteriorly positioned and closer to the jugular foramen. The close proximity of the hypoglossal foramen to the jugular foramen in *Pakicetus* is very similar to the condition of protocetids, but different from the pattern of mesonychians. The condylar foramen (probably for a vessel) is close to the occipital condyle (see also Thewissen and Hussain, 1998). The occipital condyles are enlarged both transversely and dorsally along the periphery of the foramen magnum.

Basioccipital.—The basioccipital has a basal process on either side of the bone (Figs. 9 and 10: *bp*). The process is identical in position and homologous to the falcate processes of other protocetids, such as *Protocetus* (Fraas, 1904), and other protocetids (Geisler et al., 1996, Geisler and Luo, 1998; Hulbert et al., 1998), but it is much lower and smaller than the falcate processes of other whales. The lower and smaller basioccipital process almost certainly represents a precursor state in character evolution of a fully developed basioccipital falcate process.

Petrosal.—The mastoid (posterior) process of the petrosal is elongated. Its lateral (distal) part has a rugose ventral surface, suggesting that it could have been covered by cartilage in life. This unossified distal area on the mastoid process of the petrosal is common in several pakicetid basicrania (Thewissen and Hussain, 1998; Luo, 1998). The proximoventral surface of the mastoid process has some low ridges for articulation of the posterior process of the tympanic bulla (Fig. 10: *ppt*). Based on the proportions of the posterior processes of the petrosal and ectotympanic, it is clear that only the proximoventral part of the mastoid (posterior) process was covered by the ectotympanic (Fig. 10A, B). The proximal end of the mastoid process has a small protuberance near the small stapedial muscle fossa and the stylomastoid foramen (Fig. 9: *sm*). The protuberance is interpreted as the base for the attachment of the tympanohyal (Fig. 9: *th?*) because its location is similar to the tympanohyal attachment site in ungulates and in *Tursiops* (Oelschläger, 1986b).

The anterior process of the petrosal is present, as it is in mesonychids. However, most of the anterior process of the petrosal here is covered ventrally by the entoglenoid process

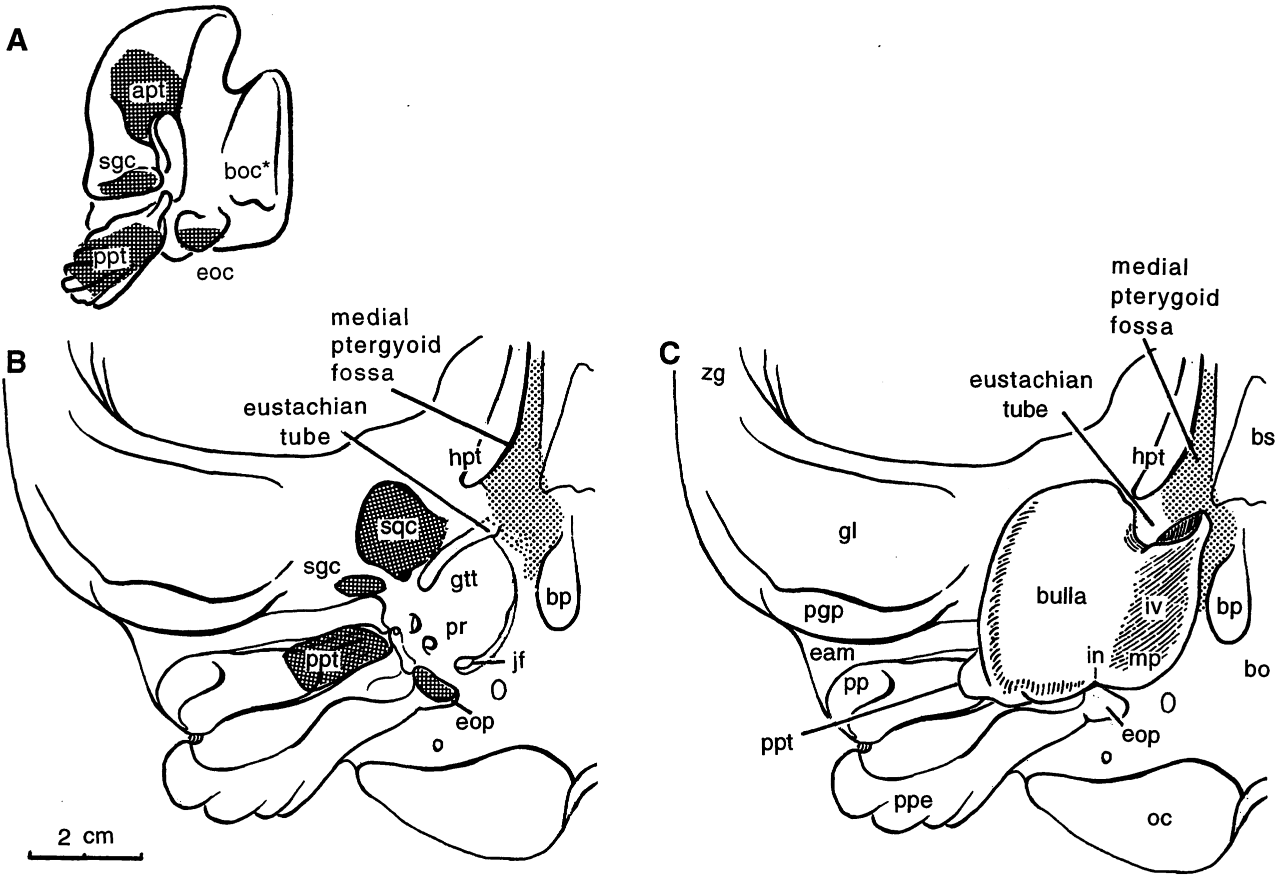


FIGURE 10. Articulation of bulla in Eocene archaeocete *Pakicetus inachus* (GSP-UM 84; modified from Gingerich et al., 1983). A, bullar articulations to other basicranial bones (composite reconstruction including information from GSP-UM 1632 *P. inachus*, H-GSP 96334 *P. attocki*, and H-GSP 18391 *Ichthyolestes pinfoldi* — the latter two specimens by courtesy of J. G. M. Thewissen). B, basicranial articulations for the bulla in GSP-UM 84 (basicranium reversed from the left side). C, basicranium of GSP-UM 84 with bulla in place. Articulations are represented by dark hatching, and the medial pterygoid fossa and its adjacent concave areas are shown in light stippled pattern. Abbreviations: *apt*, anterior process or processus tubarius of ectotympanic; *bo*, basioccipital; *boc**, contact site for basioccipital on ectotympanic bulla (*this contact may be variable); *bp*, incipient falcate process of basioccipital; *bs*, basisphenoid; *eam*, external auditory meatus; *eop*, bullar process of the exoccipital; *et*, tube for the eustachian tube; *gl*, glenoid fossa; *gtt*, tensor tympani groove; *hpt*, base of the pterygoid hamulus (= pterygoid ridge); *in*, interprominential notch or sulcus for tympanohyal; *iv*, involucrum; *jf*, jugular foramen (= posterior lacerate foramen); *mp*, medial prominence; *mpf*, medial pterygoid fossa; *oc*, occipital condyle; *pgp*, postglenoid process; *pp*, posterior process (= mastoid process); *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of tympanic; *pr*, promontorium; *sgc*, squamosal site for contact with sigmoid process of ectotympanic; *sqc*, squamosal site for contact with anterior process of tympanic; *zg*, zygoma.

of the squamosal. The groove for the tensor tympani (Figs. 9, 10: *gtt*) lies between the anterior process and the anterolateral border of the promontorium. The groove is narrower and shallower than the deep and oval-shaped fossa for the tensor tympani in ungulates (see *Ovis*, Figs. 1 and 2; and *Dissacus*, Fig. 7).

The promontorium is relatively flat. There is no trace of any vascular grooves on its ventral surface. Much of the medial periphery of the promontorium is separated from the basioccipital by the basicapsular fissure, although there appears to be a small area of contact between the promontorium and the basioccipital. It is not clear if the promontorium has a medial promontorial groove. The fenestra vestibuli is in the posterolateral part of the promontorium and the fenestra cochleae is in the posterior part of the promontorium (Fig. 9: *fv and fc*). The jugular (posterior lacerate) foramen is on the posteromedial side of the promontorium. Lateral to the promontorium is a small epitympanic recess (Fig. 9: *er*), which is mostly on the petrosal but also extends onto a small neighboring area of the squamosal. Anterior to the epitympanic recess and posterior to the bullar process of the squamosal is a vascular foramen (Fig. 9: *vf*), a feature consistently present in mesonychians and all other archaeocetes.

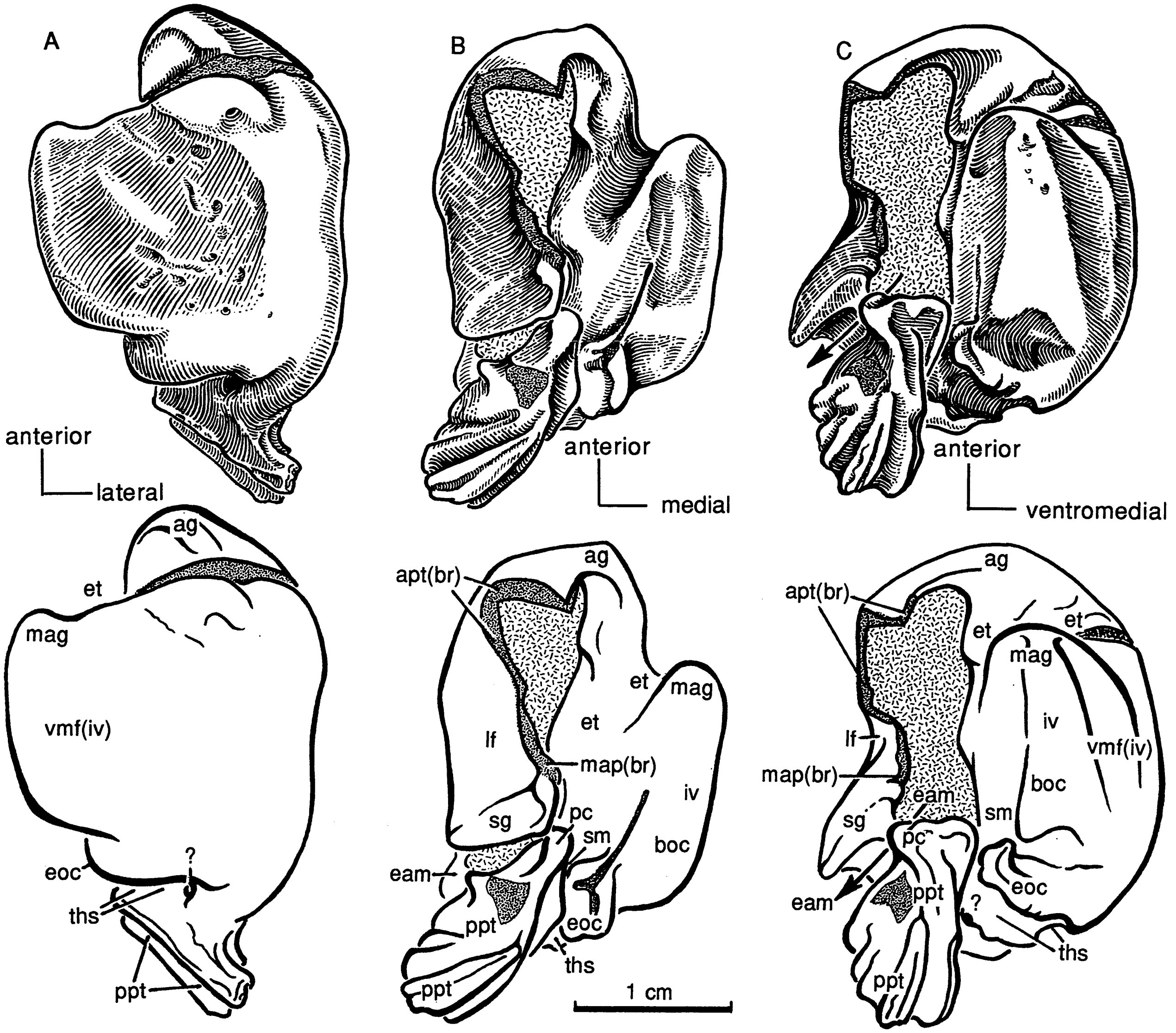


FIGURE 11. Ectotympanic bulla of Eocene archaeocete *Pakicetus inachus* (GSP-UM 1632; cf. Fig. 12). A, B, and C are ventral, dorsolateral, and dorsal views, respectively. Dense stippled pattern represents areas of breakage. Lighter granular pattern shows areas filled with matrix. Abbreviations: *ag*, anterior angle of bulla; *an*, annulus of the ectotympanic ring for suspension of tympanic membrane (present but not labeled); *apt*, processus tubarius or anterior process of the tympanic (broken here); *boc*, area of possible contact with the basioccipital; *br*, broken or incomplete structure; *eam*, external auditory meatus; *eoc*, exoccipital contact on the dorsal side of involucrum; *et*, eustachian tube; *iv*, involucrum; *lf*, lateral furrow; *mag*, anteromedial angle of involucrum; *map(br)*, attachment site for malleus on ectotympanic; *pc*, posterior crus of the tympanic annulus; *ppt*, posterior process of the tympanic bulla; *sg*, sigmoid process (= equivalent to the anterior wall of the meatus, derived from the anterior crus of the embryonic ectotympanic); *sqc*, contact site for squamosal on ectotympanic bulla; *th*, attachment site of tympanohyal; *ths*, tympanohyal sulcus (= interprominential notch of the bulla); *mf(iv)*, ventromedial facet of the involucrum; *?*, foramen of uncertain identification.

Ectotympanic.—The ectotympanic bulla has a large involucrum (Figs. 11, 12: *iv*), which is the pachyostotic and recoiled medial rim of the bulla. The ventral surface of the involucrum is almost flat, with numerous small nutritive foramina (*vmf*). The anterior extremity of the involucrum forms the anteromedial angle of the bulla (Figs. 11, 12: *mag*). The posterodorsal part of the involucrum bears a protuberance for contacting the bullar process of the exoccipital (Figs. 10, 11: *eoc*). The size of the exoccipital protuberance on the bulla is variable, large and rugose in some bullae (e.g., GSP-UM 1632), but small and relatively featureless in others (e.g., H-GSP 96334 *Pakicetus attocki*; Luo, 1998, fig. 4C). The dorsal aspect of the involucrum has a

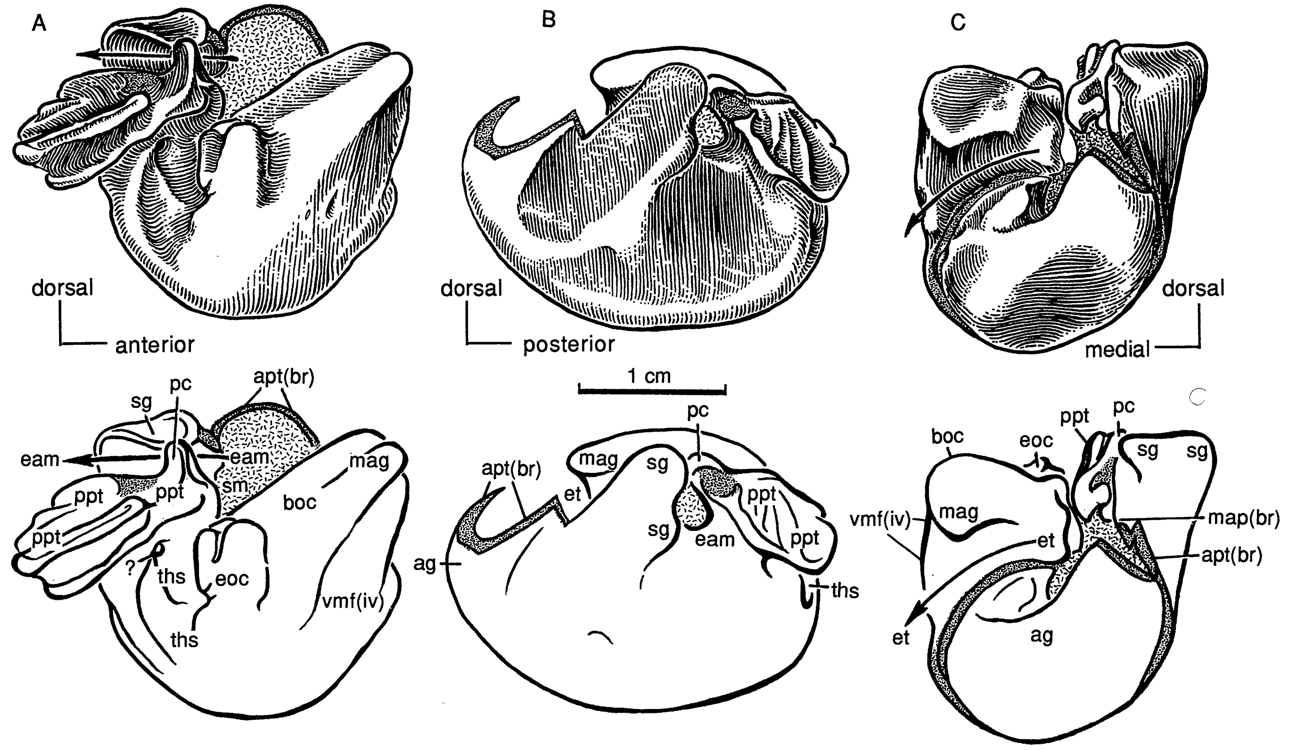


FIGURE 12. Ectotympanic bulla of Eocene archaeocete *Pakicetus inachus* (GSP-UM 1632; cf. Fig. 11). A, B, and C are posteromedial, lateral, and anterior views, respectively. Dark stippled pattern represents an area of breakage. Lighter granular pattern shows area filled with matrix. Abbreviations: *ag*, anterior angle of the bulla; *apt*, anterior process or processus tubarius of the tympanic (broken in GSP-UM 1632); *boc*, area of possible contact with the basioccipital; *br*, broken or incomplete structure; *eam*, external auditory meatus; *eoc*, contact site on involucrum for exoccipital; *et*, eustachian tube; *iv*, involucrum; *lf*, lateral furrow; *mag*, anteromedial angle of involucrum; *map*, malleolar process or ridge of the bulla; *pc*, posterior crus of the tympanic annulus; *ppt*, posterior process of the tympanic bulla; *sg*, sigmoid process homologous to the anterior wall of the meatus and derived from the anterior crus of the embryonic ectotympanic; *ths*, tympanohyal sulcus (= interprominential notch of the bulla); *mf(iv)*, ventromedial facet of the involucrum; *?*, foramen of uncertain identification.

trough-like depression that forms the ventral floor of the eustachian tube in the intact skull (Luo, 1998). The anterior opening of the eustachian tube (Figs. 9, 10: *et*) is in a large v-shaped notch located between the medial angle and the processus tubarius of the bulla.

The anterior process (processus tubarius) in the anterolateral part of the bulla is formed by a thin sheet of bone in pakicetids (Luo 1998). The anterior process is convex externally. Its hollow interior, as shown by the broken specimen (Figs. 11, 12), is similar to the anterior process in the bulla of *Ovis*. In the intact skull (GSP-UM 84), the anterior process has a large area of contact (Fig. 10A: *apt*) for the squamosal bullar process (Fig. 10B: *sqc*). Presence of this contact is evidently primitive for cetaceans as it is also found in mesonychians.

The sigmoid process of the tympanic is a thin plate, with its dorsal end contacting the squamosal. The dorsal edge of the sigmoid process is slightly recoiled in the bulla examined for this study (GSP-UM 1632), whereas the dorsal edge is almost straight in other pakicetids (Luo, 1998). The sigmoid process does not have a thick and flaring lateral margin as in the more derived cetaceans. A lateral furrow is developed in front of the base of the sigmoid process (Figs. 11, 12: *lf*), although its outline is not as well defined as in more derived cetaceans. The medial side of the sigmoid process is broken in GSP-UM 1632. In more complete specimens, this area serves as the attachment for the gracile process of the malleus (Fig. 11: *map* or *br*).

The intrabullar part of meatal tube is present in all specimens of the ectotympanic bullae of pakicetids (GSP-UM 1632; H-GSP 18391, 96334). This intrabullar part of the meatal tube protrudes into the bullar cavity. The inner (and medial) free edge has the annulus for suspension of the tympanic membrane. This structure is intact in the pakicetid *Ichthyolestes* (H-GSP 18391; Luo, 1998: fig. 4e), but incomplete in the specimen illustrated here (GSP-UM 1632). The annulus for the tympanic membrane of *Pakicetus* is similar to those of terrestrial ungulates, such as *Ovis* (Fig. 4) and *Mesonyx* (Geisler and Luo, 1998). Therefore it is reasonable to interpret the tympanic membrane in *Pakicetus* to have been similar to those of land-living ungulates capable of receiving airborne sound (Luo, 1998). No conical apophysis (middle process) is developed in the ectotympanic meatal tube in pakicetids (Luo, 1998). The ectotympanic of pakicetids lacks the extrabullar floor that covers the external auditory meatus in the squamosal as seen in mesonychids.

Luo (1998) shows that the under side of the intrabullar part of the meatus is buttressed by several septa that divide the space of the bullar cavity into several compartments. A bullar cavity with several septa is common in land mammals that have low frequency hearing. Thewissen and Hussain (1993) reported that although the incus of *Pakicetus* is partially rotated, this rotation is less developed than in other cetaceans. The incus retains some primitive characteristics of land-living ungulates. All available characters of the middle ear, including the annulus, the incus, and septa in the bullar cavity, consistently indicate that the optimal hearing range of *Pakicetus* was probably in the low frequencies of airborne sound (Luo, 1998).

The posterior process of the tympanic is a short plate-like structure. The dorsal aspect of the tympanic posterior process has several alternating grooves and ridges in parallel. This corrugated surface undoubtedly articulated very tightly with the mastoid process of the petrosal. However, in the pakicetid *Ichthyolestes*, the plate of the posterior process had an almost flat contact surface for the petrosal. Thus this feature appears to be variable among the known pakicetid genera. As mentioned above, the short posterior process of the ectotympanic does not cover the entire length of the mastoid process of the petrosal. In this feature *Pakicetus* more closely resembles the primitive condition seen in mesonychians than that of other whales.

The internal part of the posterior process bears a hook-like projection that reaches toward the sigmoid process, almost encircling the passage of the external auditory meatus (Figs. 11, 12: *pc*). This projection represents the posterior crus of the ectotympanic ring in other mammals.

The posterior side of the bulla has a broad sulcus for the tympanohyal (Figs. 11, 12: *ths*; Luo, 1998). This sulcus is broad and deep between the base of the posterior process and the exoccipital protuberance. It becomes shallow as it extends toward the involucrum. The sulcus for the tympanohyal is homologous with the interprominential notch of the bulla in previous literature on the cetacean petrotympanic complex (Figs. 9, 10: *in*). Unlike the bullae of other derived cetaceans, there is no median furrow on the ventral surface of the bulla. A notch is present near the dorsal end of the tympanohyal sulcus. This notch encircles the stylomastoid foramen for the facial nerve in the intact skull (Figs. 11, 12: *sm*).

Contact of the involucrum with the basioccipital is variable among the available specimens of pakicetids (Fig. 10A: *boc**—asterisks indicate variable characters). This contact appears to be present in the type specimen of *Pakicetus* (GSP-UM 84), but absent in other skulls of pakicetids (J. G. M. Thewissen, pers. comm.).

GAVIACETUS RAZAI (PROTOCETIDAE)

Gaviacetus razai is a protocetid archaeocete (GSP-UM 3095, Gingerich et al., 1995). Its basicranium is complete except for the right zygoma (Fig. 13). The left tympanic bulla is detached, exposing some internal characteristics of the tympanic cavity. The petrosal is not exposed on the right side, and it is poorly preserved on the left. There appears to be a large basicapsular fissure between the promontorium laterally and the basioccipital medially. This fissure may have expanded posteriorly between the promontorium and the exoccipital to the posterior, becoming confluent with the jugular foramen. This condition is also present in other protocetid cetaceans (Geisler and Luo, 1998; e.g., *Georgiacetus*, Hulbert et al., 1998)

Pterygoid.—The pterygoid has a crest-like pterygoid ridge (Fig. 13: *ptr*). The posterior part of the ridge becomes wider and flatter toward the bullar process of the squamosal. The suture between the pterygoid and alisphenoid, and the suture between the alisphenoid and the squamosal are not clear. It is probable that the posterior part of the pterygoid ridge would extend onto the alisphenoid, just as in such mesonychians as *Sinonyx*. Anteriorly the ridges of both sides of the skull converge on the midline on the ventral surface of the secondary palate. The pterygoid ridge is very similar to that of *Pakicetus* (Fig. 9) and *Protocetus* (Fraas, 1904). It does not have the bifurcated pterygoid laminae of basilosaurids (to be discussed below) or more derived cetaceans (Fraser and Purves, 1960; Fordyce, 1994). The foramen ovale for the mandibular branch of the trigeminal nerve is located in a concave area on the lateral side of the pterygoid ridge. The foramen is located either in the alisphenoid or near the alisphenoid-pterygoid suture. It appears that the foramen ovale opens into the braincase directly, as is the case in *Pakicetus* and terrestrial mammals.

No cavities of the pterygoid sinuses are present in the basicranial areas anterior to the bullae (Fig. 13). However, on the left side of the skull where the bulla has been removed, the presence of any sinus space is difficult to ascertain because the pertinent area is damaged. If a sinus cavity of any kind was present, it would have been concealed by the ectotympanic bulla in ventral view in an intact skull.

Squamosal.—The preglenoid area of the squamosal is broad, and it directly borders on the pterygoid. This part of the squamosal bears a bullar process, which is a large, circular, and elevated platform (Fig. 13: *sqc*). The process is identical to the bullar process on the squamosal in *Pakicetus*. The anterior process of the ectotympanic (= processus tubarius; Fig. 13: *apt*) rests entirely on the squamosal bullar process, as in *Pakicetus*. The entoglenoid part of the squamosal has concealed the anterior process of the petrosal, which appears to have had no contact with the anterior process of the ectotympanic. By contrast, in *Georgiacetus*, *Protocetus*, the Cross protocetid from South Carolina (Geisler and Luo, 1998), and basilosaurids, the entoglenoid part of the squamosal is slightly receded laterally to expose a part of the anterior process of the petrosal. Consequently, both the squamosal bullar process and the anterior process of the petrosal contact the anterior process of the tympanic in these more derived protocetids and basilosaurids.

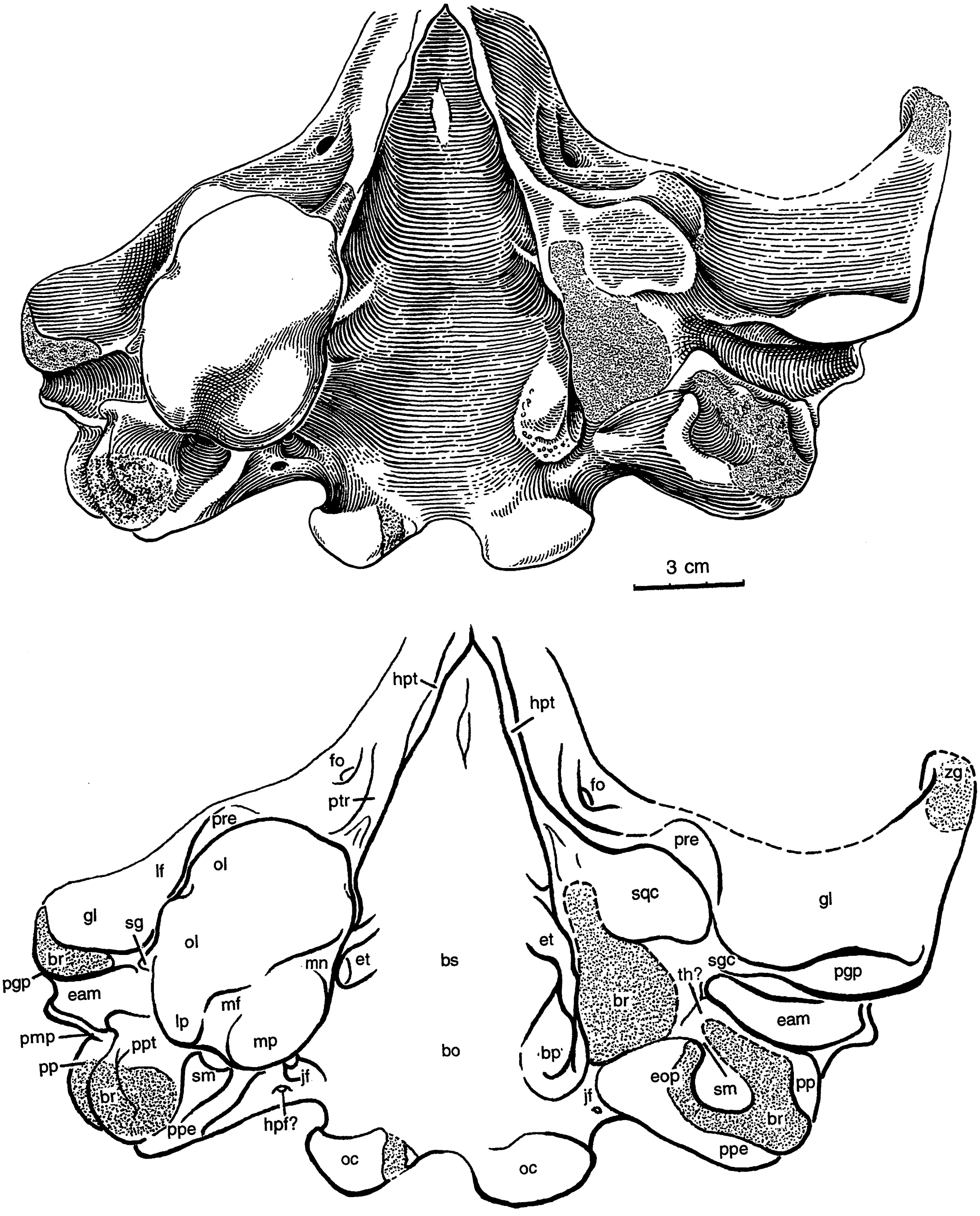


FIGURE 13. Basicranium of Eocene archaeocete *Gaviacetus razai* (GSP-UM 3095). Hatched pattern represents areas that are broken or filled by matrix. The right bulla is intact on the skull. The left bulla is preserved (Fig. 14), but the underlying promontorium is not well preserved on the basicranium. Abbreviations: *bo*, basioccipital; *bp*, falcate process of the basioccipital; *br*, broken or matrix-filled areas; *bs*, basisphenoid; *eam*, external auditory meatus; *eop*, bullar process of the exoccipital; *et*, trough for the eustachian tube; *fo*, foramen ovale; *gl*, glenoid fossa; *hpf?*, hypoglossal foramen?; *hpt*, base for the hamulus on the pterygoid; *jf*, jugular foramen; *lf*, lateral furrow of the bulla; *lp*, lateral posterior prominence of bulla; *mf*, median furrow on bulla; *mn*, medial notch of bulla; *mp*, medial posterior prominence of bulla; *oc*, occipital condyle; *ol*, outer lip of bulla; *pgp*, postglenoid process; *pmp*, postmeatal process or ridge on the squamosal; *pp*, posterior process of petrosal (= mastoid process); *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of the tympanic; *pre*, preglenoid part of the squamosal; *ptr*, pterygoid ridge; *sg*, sigmoid process of bulla; *sgc*, contact site on squamosal for the sigmoid process; *sm*, stylomastoid notch; *th?*, possible site for attachment of tympanohyal; *zg*, zygoma.

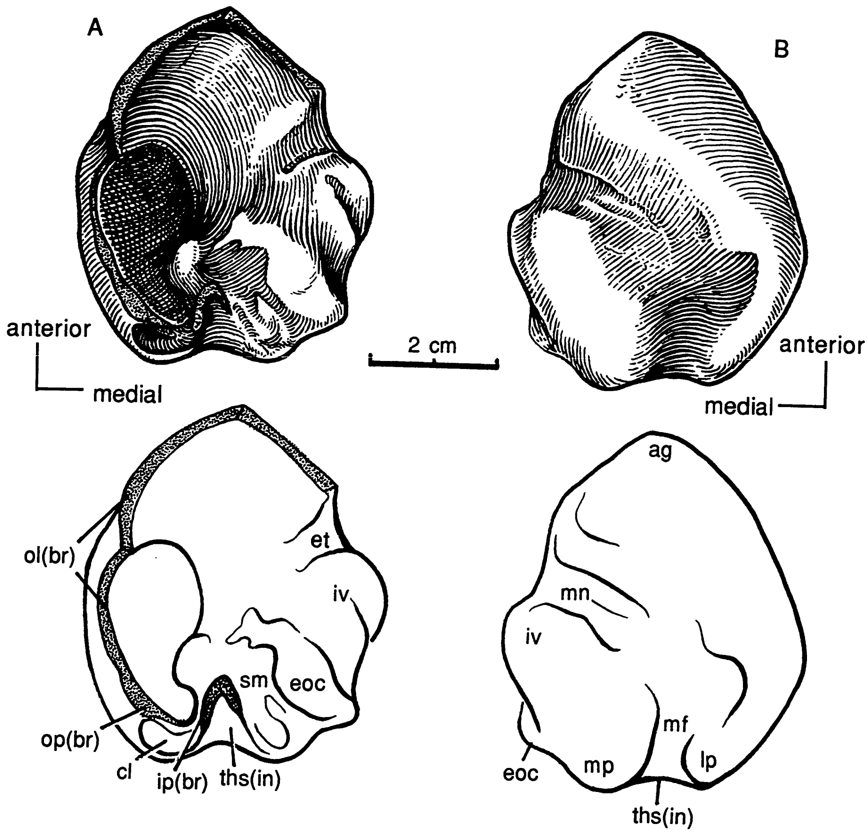


FIGURE 14. Partial left ectotympanic bulla of Eocene archaeocete *Gaviacetus razai* (GSP-UM 3095). A and B, dorsal (internal) and ventral (external) views, respectively. Dark stippled areas represent broken edges of the ectotympanic. Abbreviations: *ag*, anterior angle of the bulla; *br*, broken or incomplete structure; *cl*, posterior cleft of the bulla; *eoc*, contact site on the posterior aspect of involucrum for the exoccipital; *et*, eustachian tube; *ip*, internal pedicle of the posterior process of tympanic; *iv*, involucrum; *lp*, lateral posterior prominence; *mf*, median furrow; *mn*, medial notch; *mp*, medial posterior prominence; *ol(br)*, outer lip of the bulla (broken); *op(br)*, outer pedicle for the posterior process of tympanic (broken); *sm*, stylomastoid notch/foramen; *ths(in)*, tympanohyal sulcus (= interprominential notch of the bulla).

The glenoid fossa forming the squamosal component of the temporomandibular joint is broad and concave. The postglenoid process is a prominent and thick ridge, posterior to which is a broad external auditory meatus. The meatus has a plate-like postmeatal crest (Fig. 13: *pmp*) that overlaps the anterior face of the mastoid (posterior) process of the petrosal. A medial segment of the postglenoid ridge contacts the sigmoid process of the ectotympanic.

Ectotympanic.—The tympanic bulla of *Gaviacetus* is bulbous and oval-shaped in outline, similar to those of *Protocetus* (Fraas, 1904: fig. 2), *Georgiacetus* (Hulbert et al., 1998), and the Cross protocetid (ChM VP 5401, Geisler et al., 1996). A fully developed sigmoid process is present on the intact right bulla (Fig. 13). In lateral view it has the outline of a thin and posteriorly-oriented plate. The process is thin near its base, comparable to the condition in *Pakicetus*, but more slender than the sigmoid process of *Dorudon*. The dorsal end of the sigmoid process articulates with the entoglenoid ridge medial to (and continuous with) the postglenoid process of the squamosal. *Gaviacetus* is similar to *Dorudon* and *Basilosaurus* in the characteristics of this articulation, but differs from *Pakicetus* in that the receiving area for the sigmoid process is flat on the squamosal.

The posterior process of the ectotympanic bulla is elongated and covers much of the ventral surface of the mastoid process of the petrosal. The posterior process of the tympanic bulla is sutured to the posterior process of the petrosal (Fig. 13: *ppt* and *pp*). Both the posterior process of the tympanic and the mastoid process of the petrosal are enlarged distally and have extensive exposure in a lateral view of the cranium. The posterior process of the ectotympanic has a constricted base. The disarticulated and broken left bulla shows the broken base of the inner pedicle for the posterior process (Fig. 14: *ip* [*br*]). Lateral to the base of the inner pedicle is the posterior cleft—a crescent-shaped groove (Fig. 14: *cl*). The outer pedicle for the posterior process of the tympanic is broken. We interpret the posterior process of the ectotympanic in *Gaviacetus* to have had double pedicles on either side of the posterior cleft. In these features *Gaviacetus* is similar to *Georgiacetus* (Hulbert et al., 1998) and to basilosaurids.

The conical apophysis (middle process) is present on the right bulla, but not preserved on the broken left bulla. Because both *Gaviacetus* and *Georgiacetus* (Hulbert et al., 1998) have the middle conical process, it is likely that this structure is present in protocetids as a group.

The conical apophysis (middle conical process) of modern cetaceans is developed from folding of the embryonic ectotympanic ring at the expense of the annulus for suspending the tympanic membrane (Hanke, 1914; Luo, 1998). The apophysis serves as one of the structures for attachment of the conical tympanic ligament and the 'glove-finger' of modern whales (Lillie, 1910; Fraser and Purves, 1960; Luo, 1998).

The presence of the conical apophysis indicates that protocetids had probably developed the conical tympanic ligament and the glove-finger—both are highly transformed cetacean homologues to the tympanic membrane of land mammals (Lillie, 1910; Fraser and Purves, 1960; Lancaster, 1990).

The median furrow is a shallow embayment on the ventral side of the bulla (Fig. 14: *mf*). It is developed only on the posterior part of the bulla, unlike the furrow in odontocetes that extends much of the length of the bulla. The furrow divides the ventral face of the bulla into a lateral posterior prominence and a medial posterior prominence (Fig. 14: *lp* and *mp*), the latter being smaller than the former, as is the case of *Protocetus* (Fraas, 1904: fig. 2).

The involucrum represented by pachyostosis along the medial rim of the bulla is developed only in the posterior half of the tympanic bulla, resulting in a wider posterior width of the bulla (Figs. 13, 14: *iv*). It appears that the anterior part of the medial rim of the bulla is thin. The outline of the anterior part of the bulla becomes narrow toward the anterior apex of the bulla. The posterodorsal part of the involucrum has an elevated contact area for the exoccipital (Fig. 14: *eoc*).

The medial part of the bulla has a broad and shallow medial notch (Figs. 13, 14: *mn*) anterior to the median posterior prominence. The notch corresponds to a basicranial trough between the pterygoid ridge and the falcate process of the basioccipital (Fig. 13: *bp*). The trough connects the tympanic cavity with the oropharynx. The groove and the corresponding notch in the bulla form the passage for the eustachian tube (Figs. 13, 14: *et*). The anterior process (or the processus tubarius) of the ectotympanic is anterior to the sigmoid process. It articulates with the squamosal bullar process. From the broken left bulla (Fig. 14), it appears that the lateral lip of the bulla is very thin. It is most likely that the anterior bullar process (which is on the lateral lip in the intact specimen) had a hollowed interior like that in pakicetids (see the discussion on *Pakicetus* above; also Luo, 1998). The hollowed interior space of the tympanic cavity does not extend as far anteriorly in *Gaviacetus* (Fig. 14) as it does in pakicetids.

Basioccipital.—The basioccipital has a prominent basal (or falcate) process with a rugose ventral surface (Fig. 13: *bp*). Unlike basilosaurids, in which the posterior part of the falcate process is formed by the exoccipital, the basal (falcate) process of *Gaviacetus* appears to be formed exclusively by the basioccipital. It is very close to the involucrum of the bulla. The process is either bound to the involucrum by ligaments, a condition that is unlikely but cannot be ruled out, or contacts the involucrum directly. A direct articulation of the basal process with the involucrum of the bulla is more likely, as this is the case in *Protocetus* (Fraas, 1904) and in remingtonocetids.

The jugular foramen is bounded anteriorly by the basioccipital process, posteriorly by the bullar process of the exoccipital, and ventrally by the ectotympanic bulla. On the left side, where the bulla is removed (Fig. 13), the jugular foramen (*jf*) appears to be a gap between the basioccipital process (*bp*) and the bullar process of the exoccipital (*eop*). Cranial nerves IX, X, and XI exited the cranial cavity from the basicapsular fissure (which had annexed the jugular foramen), and then bypassed the tympanic cavity through the jugular notch to enter the pharynx. It is possible that blood vessels entered the cranial cavity through this notch. The hypoglossal foramen for cranial nerve XII is present on the ventral surface of the exoccipital, near the jugular notch and posterior to the base of the bullar process. *Gaviacetus* is similar to *Georgiacetus* (Hulbert et al., 1998) and basilosaurids, but different from *Pakicetus* and non-cetacean ungulates, in lacking a separate condylar foramen near the occipital condyle.

The stylomastoid foramen for the facial nerve exiting the tympanic cavity (Fig. 13: *sm*) is formed laterally by the mastoid process of the petrosal, medially by the bullar process of the exoccipital, and ventrally by the stylomastoid notch of the ectotympanic. The attachment site of the tympanohyal on the petrosal is not clearly preserved. According to Oelschläger (1986b), the tympanohyal is attached to the base of the mastoid (posterior) process of the petrosal in delphinoids. If the base of the tympanohyal had been present at all, it would have been located on the proximal part of the mastoid process of the petrosal near the stylomastoid foramen (or notch; Fig. 13: *th?*).

Exoccipital.—The exoccipital has a massive bullar process (Fig. 13: *eop*). The process articulates with a rugose area on the dorsal aspect of the medial posterior prominence of the bulla. The lateral end of the paroccipital process of the exoccipital is shorter than the lateral end of the mastoid process of the petrosal, leaving the latter exposed both posteriorly and laterally. In this feature, *Gaviacetus* is similar to the protocetids *Georgiacetus* (Hulbert et al., 1998), *Protocetus* (Fraas, 1904: Plate 2, fig. 1) and basilosaurids, but different from *Pakicetus* and mesonychids. The hypoglossal foramen is on the ventral side of the exoccipital. It is located posterior to the jugular notch. The foramen's location is similar to that in *Georgiacetus* (Hulbert et al., 1998).

INDOCETUS RAMANI (PROTOCETIDAE)

The partial basicranium of *Indocetus ramani* (LUVP 11034; Sahni and Mishra, 1975) has preserved most of the ectotympanic bulla, most of the exoccipital, and broken parts of the squamo-

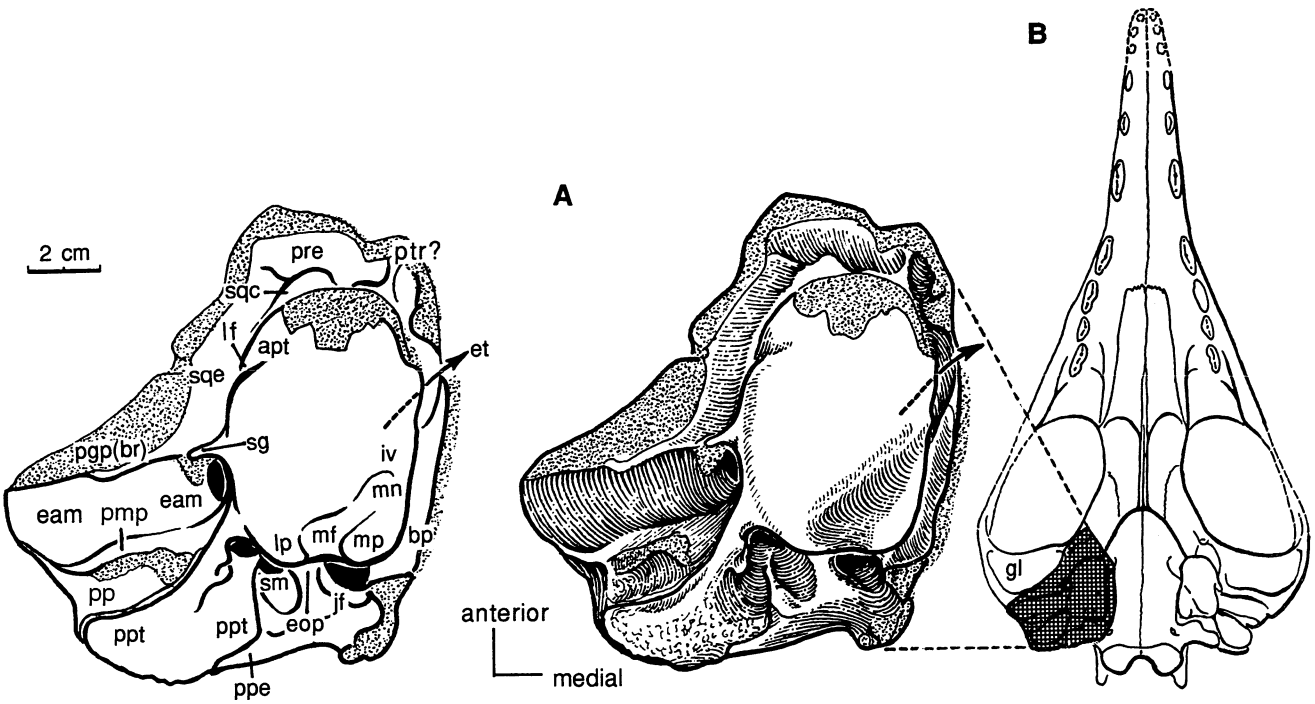


FIGURE 15. Partial basicranium of Eocene archaeocete *Indocetus ramani* (LUVP 11034, right side, drawn from cast). A, ventral view of the basicranium. B, generalized outline of protocetid skull to show the part of the skull represented by the incomplete *Indocetus* specimen (ventral view; outline modified from Gingerich et al., 1998, drawing of *Protocetus*). Abbreviations: *apt*, anterior process of tympanic; *bp*, basal or falcate process of the basioccipital; *br*, broken or matrix-filled areas; *eam*, external auditory meatus in squamosal; *eop*, bullar process of the exoccipital; *et*, eustachian tube; *gl*, glenoid fossa; *iv*, involucrum; *jf*, jugular foramen (= posterior lacerate foramen); *lf*, lateral furrow; *lp*, lateral posterior prominence of bulla; *mf*, median furrow on bulla; *mn*, medial notch of bulla; *mp*, medial posterior prominence of bulla; *gp(br)*, postglenoid process (broken); *pmp*, postmeatal process or crest of squamosal; *pp*, posterior process of petrosal (= mastoid process); *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of the tympanic; *pr*, promontorium; *pre*, preglenoid part of the squamosal (which bears an elevated stage *sqc*); *ptr*, pterygoid ridge; *sg*, sigmoid process of bulla; *sm*, stylomastoid notch; *sqc*, contact site on squamosal for the anterior process of tympanic; *sqe*, entoglenoid process of squamosal.

sal (Figs. 15 and 16). Our observations are based on a good cast provided by A. Sahni. The entoglenoid part of the squamosal bears a bullar process, which is an elevated stage medial to the glenoid fossa of the squamosal (Fig. 15: *sqc*). The preserved part of the external auditory meatus is a narrow trough on the squamosal. The petrosal is not exposed except for a small part of the mastoid process, which can be seen in a narrow ventral exposure posterior to the external auditory meatus of the squamosal.

Exoccipital.—The posterior or occipital surface of the exoccipital has a sigmoidal curvature (Fig. 16), with its lateral part being slightly convex and its medial part slightly concave. The lateral edge of the paroccipital process of the exoccipital (Figs. 15, 16: *ppe*) is shorter than the posterior processes of the petrosal and ectotympanic. The ventral aspect of the exoccipital has a prominent bullar process (Figs. 15, 16: *eop*). Medial to the exoccipital bullar process is the jugular foramen, which is represented by a notch (Figs. 13, 14: *jf*). The external opening of the stylomastoid foramen is lateral to the bullar process of the exoccipital. A short groove for the facial nerve extends posterolaterally from the stylomastoid foramen on the posterior process of the ectotympanic. A shallow embayment on the exoccipital is present near the stylomastoid foramen and in juxtaposition with the groove for the facial nerve on the ectotympanic. The basioccipital process (or falcate process) is present, and it contacts the involucrum of the tympanic bulla. The hypoglossal foramen is difficult to identify. Among other protocetids, the hypoglossal foramen is located near the jugular notch in *Georgiacetus* (Hulbert et al., 1998), and posterior to the bullar process of the exoccipital and close to the jugular notch in *Gaviacetus* (Fig. 13: *hpf*).

Ectotympanic.—The bulla in *Indocetus* is similar to that of *Gaviacetus* in most features. It has a weak and obliquely oriented median furrow. A weak lateral furrow is present anterior to the sigmoid process. The sigmoid process appears to be a thin plate in lateral view, although it cannot be ruled out that the medial part of the sigmoid process is flaring and twisted (this part is not exposed on the type specimen, Fig. 15). Near

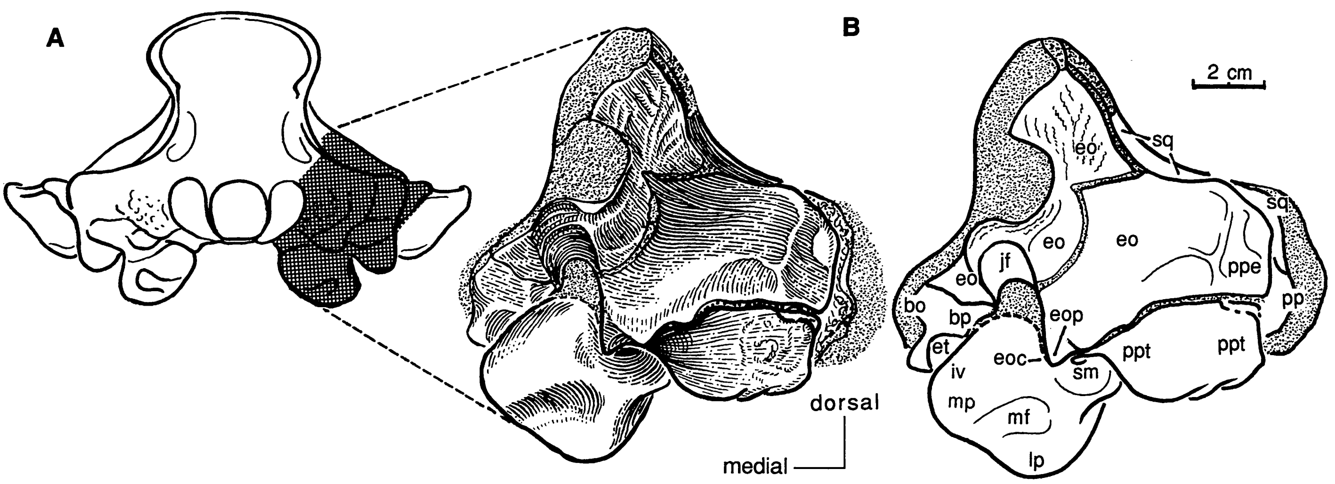


FIGURE 16. Partial basicranium of Eocene archaeocete *Indocetus ramani* (LUVP 11034, right side, drawn from cast). A, outline of protocetid skull to show part represented by *Indocetus* specimen (posterior or occipital view, modified from *Protocetus*; Fraas, 1904). B, posterior view of preserved portion of basicranium. Abbreviations: *bo*, basioccipital; *bp*, basal or falcate process of the basioccipital; *br*, broken or matrix-filled areas (granular pattern); *eo*, exoccipital; *eoc*, contact site on the bulla for the exoccipital; *eop*, bullar process of the exoccipital; *et*, trough for the eustachian tube; *iv*, involucrum; *jf*, jugular foramen; *lp*, lateral posterior prominence of bulla; *mf*, median furrow on bulla; *mp*, medial posterior prominence of bulla; *pp*, posterior process of petrosal (= mastoid process); *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of the tympanic; *sm*, stylomastoid notch; *sq*, cranial part of squamosal.

the junction of the basioccipital and the basisphenoid, there is a trough for the eustachian tube that connects with the interior of the tympanic cavity (Fig. 15). The location of the eustachian opening is medial to the bulla, as in *Gaviacetus*, but different from the more anteromedial location of the eustachian opening in *Pakicetus*.

The bulla appears to have contacted the other basicranial bones firmly on all sides. The posterior process of the ectotympanic covers almost the entire mastoid process of the petrosal and is tightly articulated with the latter. Its sigmoid process has a broad articulation with the anterior rim of the external auditory meatus of the squamosal. The processus tubarius (anterior process) has a broad contact with the squamosal bullar process. The medial posterior prominence of the bulla sits on the exoccipital bullar process. The involucrum articulates with the basioccipital crest along the posterior two-thirds of the medial side of the bulla. There is little or no sinus space around the tympanic bulla.

BASILOSAURIDAE (*DORUDON*, *BASILOSAURUS*, ETC.)

Our observations on Basilosauridae are based largely on new specimens of *Dorudon atrox*, *Ancalecetus simonsi*, *Basilosaurus isis*, and *Saghacetus osiris* collected by University of Michigan expeditions along the Qasr el-Sagha escarpment and in Wadi Hitan or Zeuglodon Valley, Fayum Province, Egypt. These complement earlier reports by Pompeckj (1922) on *D. atrox*, Kellogg (1936) on *Basilosaurus cetoides* and *Zygorhiza kochii*, and Lancaster (1990) on *Z. kochii*. New basilosaurid specimens are described together here because they represent relatively minor variations on a characteristically basilosaurid pattern.

Pterygoid.—The pterygoid bone has a prominent cavity for the anterior pterygoid sinus (Fig. 17: *aps*). The lateral and medial sides of this sinus cavity are bounded, respectively, by the lateral and the medial laminae of the pterygoid (Fig. 17: *lpl and mpl*), which merge with each other anteriorly. The lateral lamina of the pterygoid has the external opening of the foramen ovale ("foramen pseudovale" of Hulbert et al., 1998). The medial lamina of the pterygoid supports the hamulus in intact skulls of *Zygorhiza* and *Basilosaurus* (USNM 11962 and 4647, respectively; Kellogg, 1936). The hamulus of the pterygoid is not preserved on the basilosaurid skulls examined in this study. We follow Kellogg (1936) on this reconstruction. The posterior part of the medial lamina may have a contribution from the basisphenoid (e.g., in the basilosaurid *Ancalecetus simonsi*, Gingerich and Uhen, 1996).

The superior lamina of the pterygoid forms the roof of the anterior pterygoid sinus cavity in basilosaurids. The posterior edge of this sinus roof is the anterior border of the basicapsular fissure (Fig. 17: *bf*), which is a large gap in bony separation of the brain cavity and the tympanic cavity. Size of the anterior pterygoid sinus cavity and its roof (the superior lamina of the pterygoid) have some noteworthy variations in skulls of different sizes and at different ontogenetic stages (see the following discussion and Fig. 18).

Squamosal.—The preglenoid part of the squamosal extends anteriorly to join the lateral pterygoid lamina near the external opening of the foramen ovale for the mandibular nerve of the

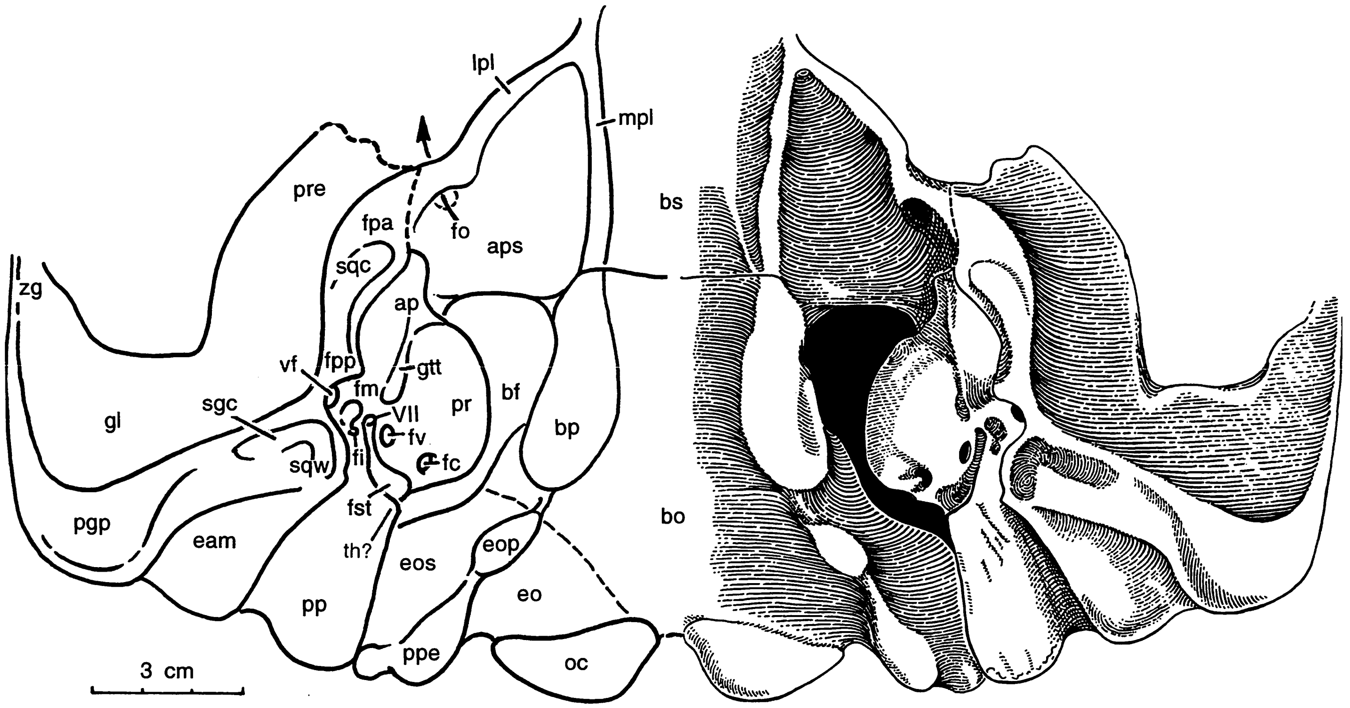


FIGURE 17. Basicranium of Eocene archaeocete *Dorudon atrox* (based on subadult specimens UM 93220 and 94812). Abbreviations: *ap*, anterior process; *aps*, anterior pterygoid sinus; *bf*, basicapsular fissure; *bo*, basioccipital; *bp*, basal or falcate process of basioccipital; *bs*, basisphenoid; *eam*, external auditory meatus; *eo*, exoccipital; *eop*, bullar process of exoccipital; *eos*, exoccipital (posterior) part of pterygoid sinus; *fc*, fenestra cochleae; *fi*, fossa incudis; *fm*, fossa for malleus; *fo*, foramen ovale; *fpa*, falciform process of the squamosal (anterior part); *fpp*, falciform process of the squamosal (posterior part); *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli; *gl*, glenoid fossa; *gtt*, groove for tensor tympani muscle; *lpl*, lateral pterygoid lamina; *mpl*, medial pterygoid lamina; *oc*, occipital condyle; *pgp*, postglenoid process; *pp*, posterior process; *ppe*, paroccipital process of exoccipital; *pr*, promontorium; *pre*, preglenoid portion of squamosal; *sgc*, contact for sigmoid process; *sqc*, contact site on squamosal for anterior process of tympanic; *sqw*, squamosal wing (= spinous process of squamosal); *th?*, possible site for attachment of tympanohyal; *vf*, vascular foramen (see Geisler and Luo, 1998, for discussion of homology); *VII*, foramen for facial nerve; *zg*, zygoma.

trigeminus (V_3; Figs. 17 and 18: *fo*). The precise location of the foramen relative to the suture of the squamosal and pterygoid is not clear on the available basilosaurid specimens. From the illustrations of Pompeckj (1922: Tafel 2: fig. 1) and Kellogg (1936: fig 5), it appears that the foramen ovale is at the suture of the squamosal and the pterygoid. The external opening of the foramen ovale has some noteworthy patterns of variation among cetacean groups other than basilosaurids (to be discussed below).

The entoglenoid area of the squamosal (Fig. 1: *sqe*) broadly overlaps the lateral but not the ventral side of the tegmen tympani and the anterior process of the petrosal. This area has several structures (Figs. 1D and 17): the squamosal wing (*sqw* or *sps*) inserting into the hiatus epitympanicus of the petrosal (*het*); the posterior falciform process (*fpp*) opposite the vascular groove (*vg*) and the fossa for the malleus (*fm*); and the anterior falciform process (*fpa*) in front of the anterior process of the petrosal (*ap*). Between the anterior falciform process and the posterior falciform process, the squamosal forms an elevated longitudinal crest that forms a part of the cranial articulation with the anterior process of the ectotympanic (Figs. 17, 18: *sqc*).

As mentioned above, articulation of the squamosal wing (or spiny process) with the hiatus epitympanicus of the petrosal is a primitive condition of artiodactyls (Fig. 1) and mesonychians. The squamosal wing of basilosaurids corresponds to the "spiny process of squamosal" of odontocetes (de Muizon, 1987; Fordyce, 1994). However, this is not nearly as well developed as it is in odontocetes.

The glenoid fossa for the dentary condyle is oblong and wider transversely than its longitudinal length. The postglenoid process is a crescentic ridge whose lateral part is thicker than its medial part. The medial segment of the postglenoid ridge bears a short transverse depression that receives the sigmoid process of the ectotympanic (Figs. 1D and 17: *sgc*). The external auditory meatus is a funnel-shaped groove posterior to the postglenoid process. The medial end of the meatus is narrow, and opposite the fossa incudis of the petrosal but does not cover the fossa. The lateral part of the meatus widens to form a broad funnel. The postmeatal crest of the squamosal is

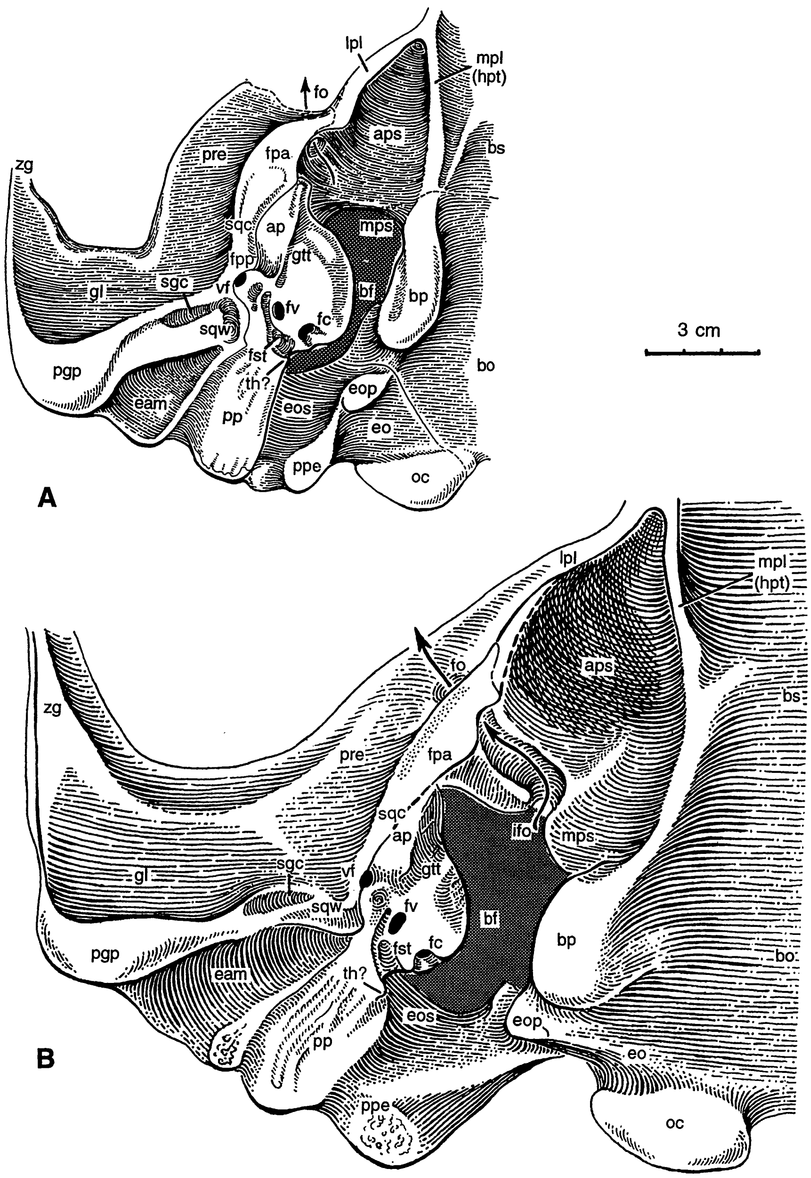


FIGURE 18. Morphological variation in the basicrania of Eocene basilosaurid archaeocetes. A, right basicranium of subadult *Dorudon atrox* (composite drawing from UM 93220 and 94812). B, right basicranium of adult *Basilosaurus isis* (UM 97507; with supplementary information from CGM 42290 *Ancalecetus simonsi*, Gingerich and Uhen, 1996). Both are drawn to the same scale. The basicapsular fissure (*bf*), anterior pterygoid sinus (*aps*), middle pterygoid sinus (*mps*), and exoccipital sinus (*eos*) are all generally disproportionately large in larger adult skulls than in smaller subadult specimens. The internal lamina of the pterygoid is expanded posteriorly to form the internal foramen ovale (*ifo*). Dark hatched pattern represents matrix-filled area. Abbreviations: *ap*, anterior process; *aps*, anterior pterygoid sinus; *bf*, basicapsular fissure (incorporating and merged with the jugular foramen); *bo*, basioccipital; *bp*, basal or falcate process of basioccipital; *bs*, basisphenoid; *eam*, external auditory meatus; *eo*, exoccipital; *eop*, bullar process of exoccipital; *eos*, exoccipital part of posterior pterygoid sinus; *fc*, fenestra cochleae; *fo*, foramen ovale (external opening); *fpa*, falciform process of squamosal (anterior part); *fpp*, falciform process of squamosal (posterior part); *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli; *gl*, glenoid fossa; *gtt*, groove for tensor tympani muscle; *ifo*, internal foramen ovale; *jf*, jugular foramen (incorporated into basicapsular fissure); *lpl*, lateral pterygoid lamina; *mpl*, medial pterygoid lamina; *mps*, middle pterygoid sinus; *oc*, occipital condyle; *pgp*, postglenoid process; *pp*, posterior process; *ppe*, paroccipital process of exoccipital; *pre*, preglenoid part of the squamosal; *sgc*, contact for sigmoid process; *sqc*, contacting site on the squamosal for the anterior process of tympanic; *sqw*, squamosal wing (= spinous process of squamosal); *th?*, possible site for attachment of tympanohyal; *vf*, vascular foramen (see Geisler and Luo, 1998 for homology); *zg*, zygoma.

broadly sutured to the mastoid process of the petrosal. It is more reduced than those of protocetids and *Pakicetus*.

Basioccipital.—The falcate process of the basioccipital (or basioccipital process; Figs. 17 and 18: *bp*) is well developed in *Dorudon* and *Basilosaurus*. This part of the falcate process forms a massive ridge with a rounded top. The posterior part of the falcate process overhangs the hollow space of the basicapsular fissure (Figs. 17 and 18: *bf*). The anterior part of the falcate process is a thin crest. The crest decreases its height anteriorly and grades into the medial lamina of the pterygoid (Figs. 17 and 18: *mpl*), which would bear the hamulus in an intact skull (according to Kellogg, 1936; Fig. 18: *hpt*). The basioccipital falcate process and the medial lamina of the pterygoid flank both sides of the pharyngeal passage, which is roofed over by the basioccipital and basisphenoid in the basicranial region.

Exoccipital.—The paroccipital process of the exoccipital is shorter than the lateral (distal) end of the mastoid process of the petrosal in all basilosaurids, which resemble protocetids more closely than pakicetids and mesonychians in this characteristic. The paroccipital process has two distinct patterns among the basilosaurid taxa examined here. The process swings anterolaterally toward the temporomandibular joint in *Zygorhiza* (Kellogg, 1936: *fig. 30*). In contrast, it swings posterolaterally to the same level of the occipital condyles in *Dorudon*, *Basilosaurus* and *Ancalecetus* (Fig. 18).

The exoccipital has a bullar process (Figs. 17 and 18: *eop*), which is separated by the jugular notch from the posterior part of the basioccipital falcate process. The jugular notch is narrow and the exoccipital bullar process is relatively close to the basioccipital falcate process in larger basilosaurids, such as *Ancalecetus* and *Basilosaurus* (Fig. 18B). In contrast, in smaller skulls of basilosaurids, such as that of a subadult *Dorudon*, the bullar process of the exoccipital is separated farther from the basioccipital falcate process (Fig. 18A). Whether the basioccipital falcate process and the bullar process of the exoccipital contact the bulla appears to depend on the overall size of the skulls (see the following discussion on variation of basicranial features in basilosaurids).

The external aperture of the hypoglossal foramen (for cranial nerve XII) is positioned on the saddle of the jugular notch of the exoccipital in basilosaurids. In the basilosaurid *Zygorhiza* (USNM 11962, 13773), the external aperture of the hypoglossal foramen in the jugular notch would be visible in the tympanic cavity if the bulla is removed, but concealed from the ventral view if the ectotympanic bulla is intact on the basicrania. We confirm the general observation by Kellogg (1936) that the external aperture of the hypoglossal foramen is in the tympanic cavity. However, we note that the precise location of the aperture may be slightly variable on the *Zygorhiza* specimens of different sizes. The aperture of the hypoglossal foramen may be on the tympanic side of the jugular notch, or right on the saddle of the jugular notch.

In the skulls of other basilosaurids examined in this study, there is no hypoglossal foramen outside the tympanic cavity on the external (ventral) surface of the exoccipital. We interpret that *Ancalecetus*, *Dorudon*, and *Basilosaurus* are similar to *Zygorhiza* in that the hypoglossal foramen is located within the tympanic cavity. However, the precise location of this foramen within the tympanic cavity is not known for these other basilosaurids because most of our specimens are damaged or poorly preserved in this area. There is no condylar foramen in the exoccipital. This is different from *Pakicetus* (Fig. 10) and protocetids (see *Gaviacetus*, Fig. 13) in which the hypoglossal foramen is on the ventral surface of the exoccipital. In *Pakicetus* and protocetids (e.g., *Georgiacetus*, Hulbert et al., 1998) this foramen is closer to the jugular notch than to the occipital condyle, whereas in non-cetacean ungulates the foramen is closer to the occipital condyle than to the jugular foramen.

The basilosaurid condition, as best represented by *Zygorhiza*, is similar to odontocetes. In *Xenorophus* (CMNH 72655), the hypoglossal foramen is located on the tympanic side of the exoccipital falcate crest and is concealed from ventral view in the intact skull. In this feature *Xenorophus* is similar to early platanistoids (Fordyce, 1994) and squalodontids. The hypoglossal cranial nerve (XII) exits the cranial cavity through the cranial hiatus in mysticetes. It does not have a separate foramen. However the pathway of the hypoglossal nerve of mysticetes resembles those of both odontocetes and basilosaurids in exiting into the tympanic (and/or peribullar) cavity before emerging on the ventral surface of the skull.

The absence of the hypoglossal foramen on the ventral surface of the exoccipital in basilosaurids, mysticetes, and odontocetes contrasts with the condition in protocetids and pakicetids, where the foramen is present on the ventral side of the exoccipital. The latter is more comparable to the primitive condition of non-cetacean mammals.

Petrosal.—Petrosals of basilosaurids have several components: the tegmen tympani and its anterior process; the mastoid (posterior) process, and the pars cochlearis.

The tegmen tympani (= "superior process" of Pompeckj, 1922; Kellogg, 1936) is a thick and broad structure (Figs. 20, 21: *tt* or *sp*). Its proportion relative to the pars cochlearis is larger (wider) in basilosaurids than in both outgroup mesonychids and odontocetes. The lateral surface of the tegmen tympani is strongly convex, and it is partially covered by the entoglenoid part of the squamosal. The dorsal edge of the tegmen tympani extends from the apex of the anterior process to near the hiatus epitympanicus (Figs. 19-20). The dorsal extent of the tegmen tympani has a considerable range of variation, which appears to be correlated to the overall size of the skull (Figs. 20, 23). In subadult to adult skulls of medium-sized basilosaurids (such as UM 93220 and 94812 of *Dorudon atrox*), the endocranial contact between the tegmen tympani and the squamosal is flush with the dorsal edge of the tegmen, so that there is no sinus groove between the dorsal edge of the tegmen and the endocranial wall of the squamosal (Fig. 23A). In contrast, in large adult skulls like UM 97507 of *Basilosaurus isis* the coverage of the tegmen by the squamosal is short of the dorsal edge (Fig. 23B). As a result, the dorsal edge of the tegmen tympani becomes free standing, and a vascular groove is formed between the free edge of the tegmen and the squamosal. The groove probably housed the enlarged superior petrosal sinus and the sigmoid sinus in larger adult skulls, as has

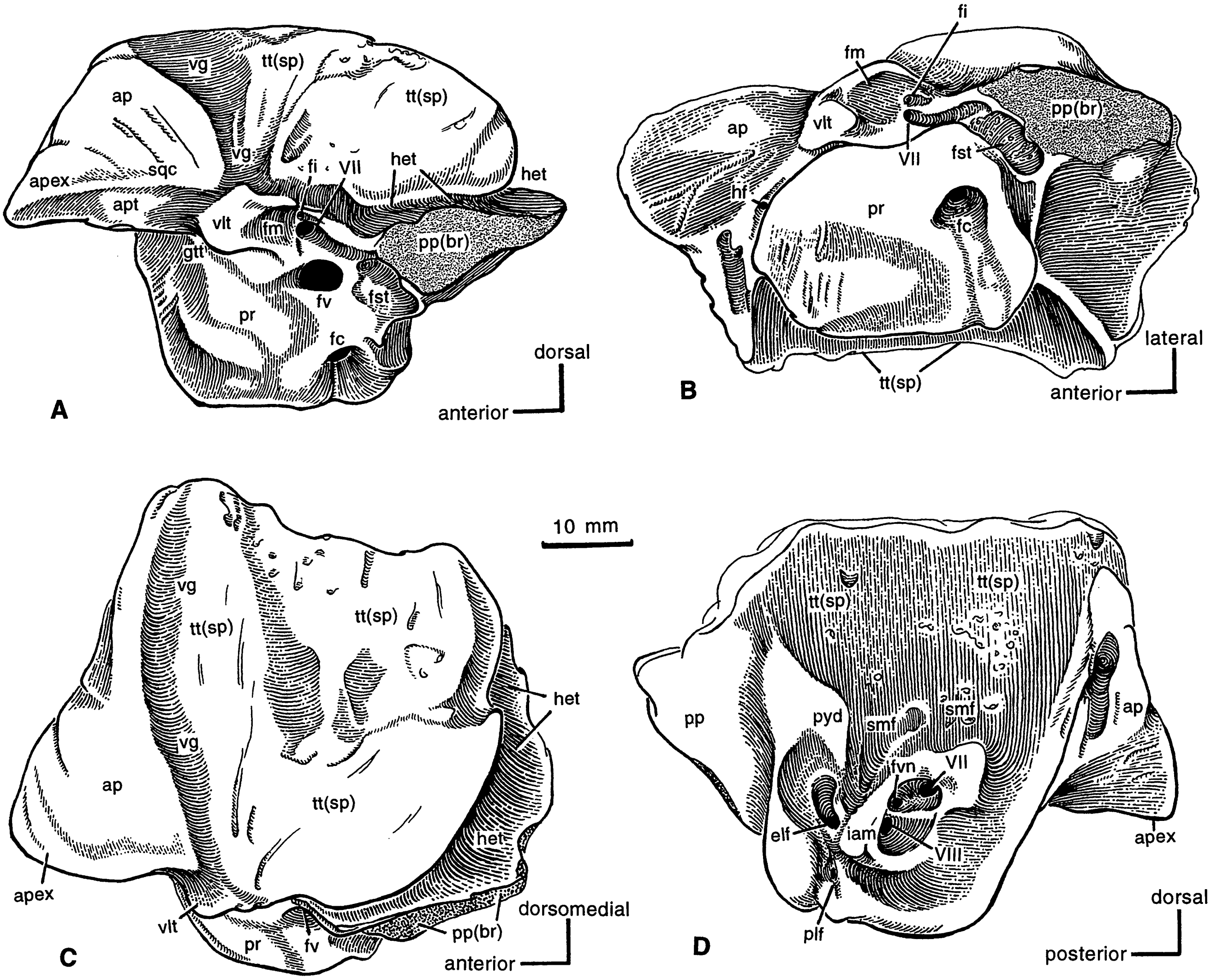


FIGURE 19. Left petrosal of the Eocene archaeocete *Basilosaurus isis* (UM 97507; incomplete, posterior process broken). A, ventral (tympanic) view. B, medial view. C, lateral view. D, dorsal (cranial or internal) view. All figures drawn to the same scale. Abbreviations: *ap*, anterior process of the petrosal; *apex*, apex of the anterior process; *br*, breakage (represented by stippled pattern); *elf*, endolymphatic foramen or aquaeductus endolymphaticus; *fc*, fenestra cochleae (= round window); *fi*, fossa incudis; *fm*, fossa for the head of the malleus (a part of the epitympanic recess); *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli (= oval window); *fvn*, foramen for vestibular nerve (VIII); *gtt*, groove for tensor tympani; *het*, hiatus epitympanicus (a part of the epitympanic recess); *hf*, hiatus fallopii (= anterior opening for the greater superficial petrosal nerve); *iam*, internal auditory meatus (= fundus of internal auditory meatus); *plf*, perilymphatic foramen (= aquaeductus cochlearis); *pp*, posterior process of the petrosal; *p(br)*, broken base of the posterior process; *pr*, promontorium (= ventromedial eminence of the pars cochlearis); *pyd*, pyramidal process; *smf*, suprameatal fossa; *t(sp)*, tegmen tympani (= superior process); *vg*, vascular groove (becoming a foramen when enclosed by the squamosal in an intact skull); *vlt*, ventrolateral tuberosity; *VII*, internal or external opening for the facial nerve canal; *VIII*, internal opening of the cochlear nerve.

been noted by several authors (Pompeckj, 1922; Kellogg, 1936; Pilleri et. al., 1989; Fordyce, 1994). However, we would point out that this feature is ontogenetically variable, and poorly developed in the smaller skulls of subadult basilosaurids (see below for further discussion of ontogenetic variability of vascular structures).

The anterior process is triangular in shape in lateral view, with a pointed apex. Its lateral side is convex and nestles within the anterior falciform process of the squamosal (Fig. 1: *sqe/fpa*). The ventral part of the anterior process, which is not covered by the squamosal, forms a contact with the anterior process of the ectotympanic.

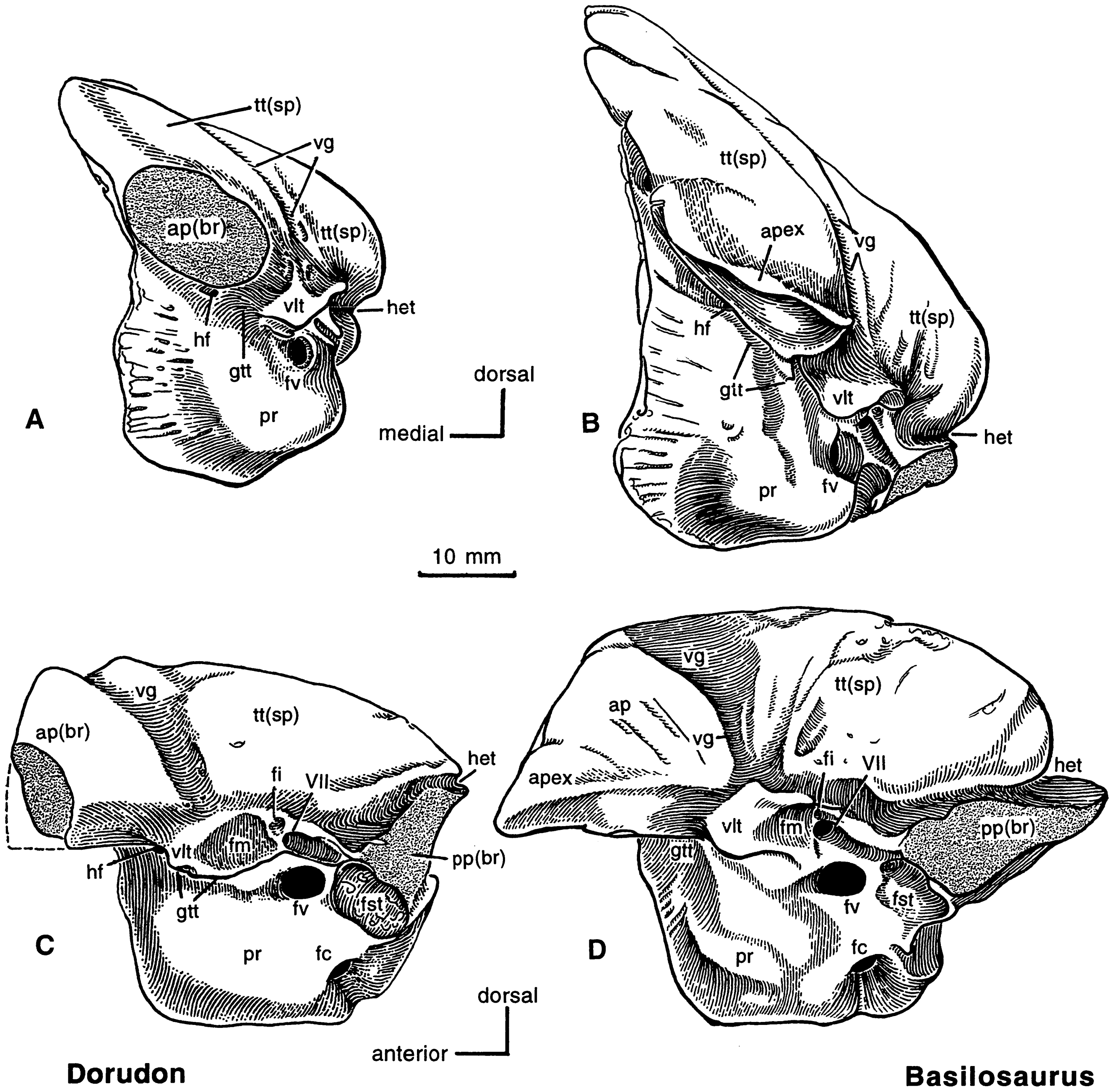


FIGURE 20. Variation in morphology and size of the petrosals of Eocene basilosaurid archaeocetes. A and C, *Dorudon atrox* (UM 94812, incomplete). B and D, *Basilosaurus isis* (UM 97507, incomplete). Both petrosals are on the same scale. A-B are anterior views; C-D are ventral (tympanic) views. This juxtaposition shows differences in the sizes of the tegmen tympani and the promontorium. Abbreviations: *ap*, anterior process of the petrosal; *ap(br)*, anterior process (broken); *apex*, apex of the anterior process; *br*, breakage in the fossil (represented by the stippled pattern); *fc*, fenestra cochleae (= round window); *fi*, fossa incudis; *fm*, fossa for the head of the malleus (a part of the epitympanic recess); *fst*, fossa for stapedial muscle; *fv*, fenestra vestibuli (= oval window); *gtt*, groove for tensor tympani; *het*, hiatus epitympanicus; *hf*, hiatus fallopii (anterior opening for the greater superficial petrosal nerve); *pp*, posterior process of petrosal; *pp(br)*, broken base of the posterior process; *pr*, promontorium (= ventromedial eminence of the pars cochlearis); *tt(sp)*, tegmen tympani (= superior process); *vg*, vascular groove (= foramen if enclosed by the squamosal); *vlt*, ventrolateral tuberosity; *VII*, external opening for the facial new canal.

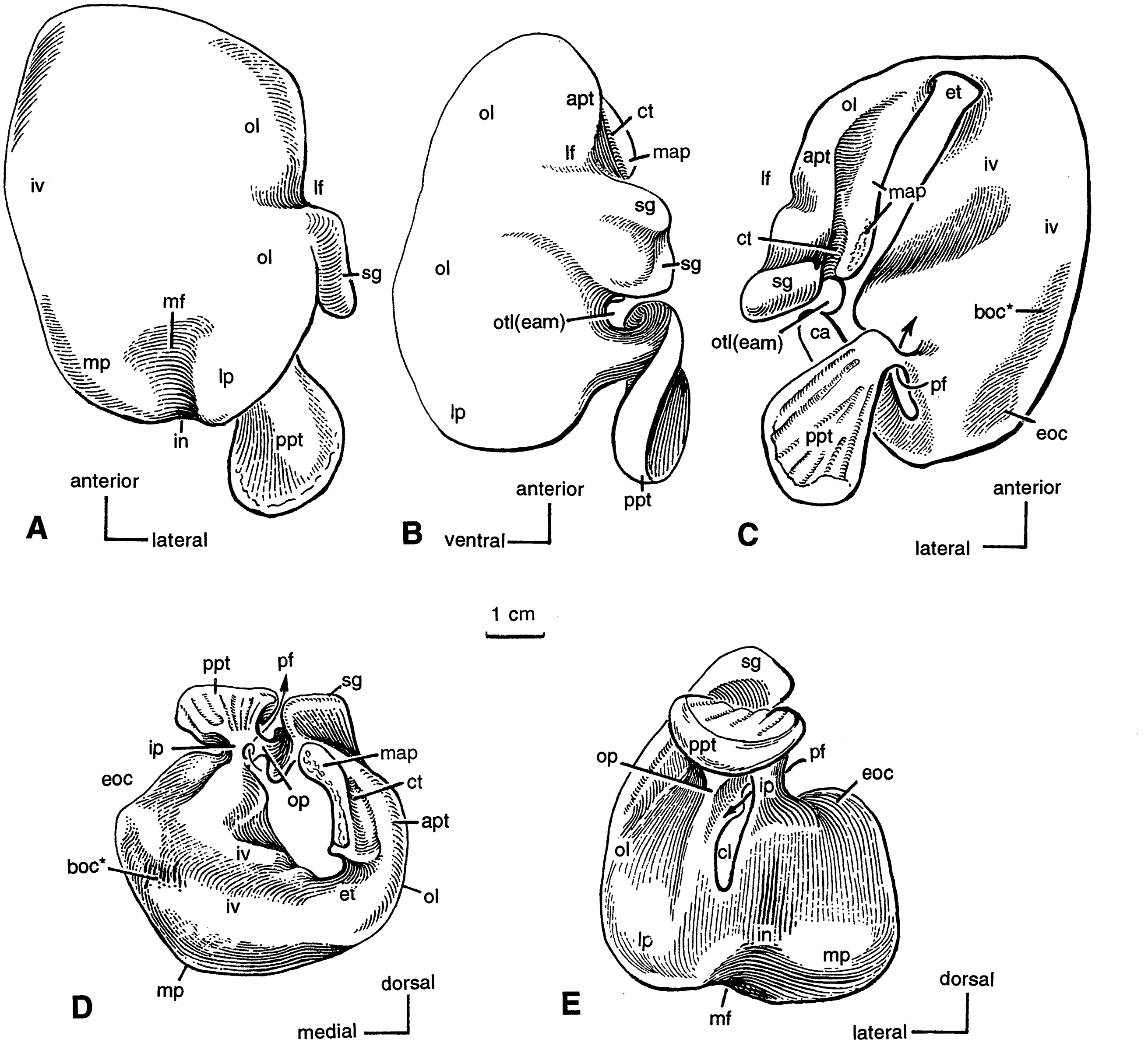


FIGURE 21. Tympanic bulla of Eocene archaeocete *Dorudon atrox* (composite drawings from *Dorudon* UM 93220 and 94812, supplemented with additional information from UM 97550 *Saghacetus isis*). A, ventral view. B, lateral view. C, dorsal view. D, oblique anterior view. E, posterior view. Abbreviations: *apt*, anterior process or processus tubarius of the ectotympanic; *boc**, contact for the basal or falcate process of basioccipital (asterisk indicates that the contact is variable and size-dependent, present in smaller skulls of smaller taxa or subadult specimens of larger taxa, but absent in larger skulls of larger basilosaurid taxa); *ca*, conical apophysis or process; *cl*, posterior cleft; *ct*, sulcus for chorda tympani; *eoc*, contact for the exoccipital, (may be absent in larger skulls); *et*, eustachian tube; *in*, interprominential notch (sensu Pilleri et al., 1987; homologous with the tympanohyal sulcus sensu Luo, 1998); *ip*, inner pedicle of posterior process of tympanic; *iv*, involucrum; *lf*, lateral furrow; *lp*, lateral or outer posterior prominence; *mf*, median furrow; *map*, malleolar process or ridge for attachment of the anterior crus of the malleus; *mp*, medial or inner posterior prominence; *ol*, outer lip of the bulla; *op*, outer pedicle of the posterior process of tympanic; *otl(eam)*, opening for tympanic ligament (= homologous to external auditory meatus); *pf*, pedicle foramen (= elliptical foramen of the posterior process); *ppt*, posterior process of the ectotympanic; *sg*, sigmoid process of the ectotympanic (homologous to the anterior wall of the meatal tube, see Luo, 1998).

On the lateral side of the tegmen tympani, there is a transverse (or dorsoventral) vascular channel (Figs. 1 and 14: *vf*). This channel is represented by a transverse groove on the lateral surface of the tegmen tympani when the petrosal is separated from the squamosal (Figs. 1E and 17: *vg*), or a foramen if the petrosal and the squamosal remain articulated (Fig. 1E, 17, 18: *vf*). As described above, an identical vascular channel is present in protocetids and pakicetids (Geisler and Luo, 1998).

The epitympanic recess area is on the ventral surface of the tegmen tympani, just lateral to the pars cochlearis (of the promontorium). Structures exposed in this area are (in an anteroposterior sequence): the ventrolateral tuberosity (lateral tuberosity of de Muizon, 1987; ventral tuberosity of Fordyce, 1994; this structure was described and illustrated in basilosaurids, but not named, by Kellogg, 1936), the fossa for the head of the malleus, and the fossa incudis.

The fossa for the malleolar head (Figs. 2C and 14: *fm*) is a large concavity, which borders on the posterior side of the ventrolateral tuberosity (Figs. 2C and 14: *vlt*). The fossa overhangs (but does not touch) the malleus (Lancaster, 1990). Posterior to the fossa for the malleus is the fossa incudis, a small deep pit for articulation of the crus brevis of the incus (Figs. 2C and 14: *fi*). Overall, these structures in the epitympanic recess area are similar to those in odontocetes in shape, size, and topographic relationship, but less so to the epitympanic structures of mysticetes. The epitympanic area of mysticetes is essentially flat and almost featureless (Geisler and Luo, 1996).

The tympanic opening for the facial nerve canal (= epitympanic aperture of the aquaeductus fallopii of Kellogg, 1936; Figs. 2D, 19D: *VII*) is positioned between the epitympanic recess and the pars cochlearis. It is medial to the fossa incudis and posterior to the fossa for the malleus. The sulcus for the hyomandibular branch of the facial nerve (Figs. 16, 17: *VII-sul*) extends from the tympanic opening of the facial nerve canal to the stylomastoid notch (Figs. 1E and 2C: *sm*).

The pars cochlearis has an almost rectangular outline in ventral view (Fig. 20). Its anterior and posterior borders are almost parallel to each other in an adult specimen (although less so in subadults). The promontorium, the ventral eminence of the pars cochlearis, has a flat to slightly concave medial face. The hiatus fallopii for the exit of the greater superficial petrosal nerve is located in the crease between the promontorium and the anterior process (Figs. 19B, 20: *hf*). The fenestra vestibuli (oval window) and the fenestra cochleae (round window) are in the posterior part of the promontorium (Fig. 2D: *fv* and *fc*). A faint groove extends from the fenestra cochleae to the medial edge of the promontorium. A similar groove is present in the mesonychid *Dissacus* (Fig. 2B) and some odontocetes (Luo and Marsh, 1996).

Unlike the petrosal of terrestrial ungulates, in which there is a large, deep and oval-shaped tensor tympani fossa, there is no distinct tensor tympani fossa in basilosaurids. Instead, the tensor tympani was attached to a groove (or crease) between the anterior process and the promontorium. The tensor tympani muscle is present on the tympanic side of the petrosal in extant whales, but its site of attachment varies from a groove in most odontocetes (Kasuya, 1973; Pilleri et al., 1987; de Muizon, 1987; Luo and Marsh, 1996) to a flat surface on the tympanic side of the petrosal in balaenopterids and eschrichtiids (Geisler and Luo, 1996).

The cranial (internal) surface of the tegmen tympani is concave, forming the suprameatal fossa (Figs. 3 and 19D: *smf*). A similar concave fossa is present in *Dissacus* (UM 75501; Fig. 3) and *Mesonyx* (Geisler and Luo, 1998). In contrast, the comparable area is flat or even convex in most odontocetes except *Xenorophus* (Luo and Marsh, 1996), and in most mysticetes (Geisler and Luo, 1996). This broad suprameatal fossa is absent in *Sus* (Fig. 3A) and other terrestrial ungulates (MacIntyre, 1972; Cifelli, 1982; Luo, 1989).

The cranial surface of the pars cochlearis is uniformly concave in basilosaurids (Figs. 3C, 19D). Near its center is the internal acoustic meatus (*iam*). The meatus usually has an oval-shaped outline, and may have an elevated rim in adult specimens (such as in adult *Basilosaurus*) but not in juvenile or subadult specimens. The transverse septum inside the internal acoustic meatus separates the medial part containing the spiral foramina for the cochlear nerve, from the lateral part containing the internal facial foramen and the vestibular nerve foramen. As in odontocetes and mysticetes (Luo and Marsh, 1996; Geisler and Luo, 1996), there is a single vestibular nerve foramen for the vestibule and the semicircular canals, based on the serial sections of two basilosaurid petrosals (UM 94812 of *Dorudon atrox* and UM 97507 of *Basilosaurus isis*). In contrast, there are separate foramina for the nerve to the saccule and the nerve for the utricle and semicircular canals in non-cetacean mammals (Williams et al., 1989; Evans, 1992).

Posterior to the internal acoustic meatus is a deep and conspicuous pit within which a large endolymphatic foramen is located (Figs. 3C, 17: *elf*). A small and circular perilymphatic foramen is present medial to the endolymphatic foramen. The surface near the endolymphatic foramen is elevated to form a pyramidal process (Fig. 3C, 19: *pyd*). The cranial face of the petrosal (in the part of the pars canaliculus) has no subarcuate fossa in basilosaurids, a common feature of terrestrial mammals (see Fig. 3B, C), except *Mesonyx* (Geisler and Luo, 1998) and some extant artiodactyls such as the domestic cow. The subarcuate fossa is a hollow cavity that occupies the space between the semicircular canals in terrestrial mammals (Fig. 3: *sba*). The rim of the fossa is formed by the anterior semicircular canal. Because the semicircular canals are greatly reduced in size in all cetaceans (Gray, 1951; Yamada and Yoshizaki, 1959; Ketten, 1992; Luo and Marsh, 1996), the subarcuate fossa is also lost as a result.

The mastoid process of the petrosal is elongated. As described by Kellogg (1936), it forms an obtuse angle with the main anteroposterior axis of the pars cochlearis. On the ventrolateral side of the petrosal, the mastoid process is separated from the tegmen tympani by a transverse groove, the hiatus epitympanicus. Medial to the mastoid process and between the process and the pars cochlearis is the stylomastoid notch (Fig. 2: *sm*). The mastoid process is wedged between the squamosal anteriorly, and the paroccipital process of the exoccipital posteriorly. The distal end of the mastoid process is exposed outside the skull. The external exposure of the process has a nearly triangular outline in posterolateral view, with an apex of the triangle pointed dorsally.

Ectotympanic.—The tympanic bulla appears to have an oval to nearly rectangular outline in ventral view. An interprominential notch is present on the posterior face of the bulla (Fig. 21: *in*), which is interpreted to be the vestige of the sulcus or groove for the tympanohyal that is less developed in basilosaurids than in *Pakicetus* and *Gaviacetus* (Luo, 1998). The median furrow is represented by a shallow embayment in the posterior part of the bulla (Fig. 21: *mf*). The extent of the median furrow is comparable to that of *Gaviacetus*, but much less than those in odontocetes. The medial rim has developed pachyostosis and formed an involucrum along the length of the bulla, as in odontocetes and mysticetes. The posterior part of the involucrum forms the medial posterior prominence, with a low and rounded ridge around the circumference of the prominence.

The anterior process of the ectotympanic (= processus tubarius of Kellogg, 1936; Fig. 21: *apt*) is formed by the swollen anterolateral rim of the outer lip of the bulla (*ol*). The process contacts both the anterior process of the petrosal and the entoglenoid part of the squamosal. The dorsal (external) aspect of this process appears to be like a longitudinal ridge, considerably narrower than the broadly convex and bulbous shape of the anterior process of the ectotympanic in pakicetids. The process is homologous to but morphologically distinct from the anterior tympanic pedicle of mysticetes (Geisler and Luo, 1996), and from the accessory ossicle of the ectotympanic of odontocetes (Luo and Marsh, 1996; see Luo, 1998: fig. 9).

The platelike sigmoid process lies posterior to the anterior process of the tympanic, and it is separated from the latter by a lateral furrow (Fig. 21: *lf*). The anterior face of the sigmoid process is convex and the posterior face is concave (Fig. 21: *sg*). The process is wider than its height, and it appears to be slightly twisted, albeit less so than in odontocetes (Pilleri et al., 1989: fig. 15). The dorsal and lateral margins of the sigmoid process are thickened and recoiled. The dorsal (or distal) end of the sigmoid process articulates with a shallow transverse groove on the entoglenoid part of the squamosal (Fig. 22: *sgc*).

The malleolar process of the bulla is a site for attachment of the processus gracilis of the malleus. It is a horizontal ridge medial to the sigmoid process and along the anterolateral rim of the bulla (Fig. 21: *map*; Pompeckj, 1922; Lancaster, 1990). Anteriorly the malleolar process grades into the anterior process of the ectotympanic. The posterior end of the malleolar process extends to the level of the sigmoid process. Between the malleolar ridge and the base of the sigmoid process is a shallow longitudinal groove, which was designated by Kellogg (1936) as the groove for the chorda tympani nerve (Fig. 21C, D: *ct*). The groove extends anteriorly but fades into the anterior process of the ectotympanic.

The posterior process of the ectotympanic is attached to the bulla through two pedicles: an outer posterior pedicle and an inner posterior pedicle (Fig. 21: *op* and *ip*). The two pedicles are separated by a pedicle foramen that is confluent posteriorly with the posterior cleft of the bulla (Fig. 21: *pf* and *cl*). The double pedicles are also present in *Gaviacetus* and *Georgiacetus*. Medial to the inner posterior pedicle is a notch on the tympanic that corresponds to the stylomastoid notch on the petrosal. The outer posterior pedicle forms the posterior periphery of the external auditory meatal opening for the conical tympanic ligament.

Between the sigmoid process and the two posterior pedicles is an opening for the conical tympanic ligament (Lancaster, 1990) that corresponds in position to and is homologous with the external auditory meatus of terrestrial mammals (Figs. 1F and 21B: *eam* /*otl*). The size of this so-called external auditory meatal opening is greatly reduced in archaeocetes as compared with terrestrial mammals. The conical apophysis (middle process) is present (Lancaster, 1990) although hidden by the flaring margins of the sigmoid process from lateral and dorsal views of the bulla. We follow Lancaster (1990) and Luo (1998) in postulating that the conical apophysis is one of the structures for attachment of the conical ligament and the glove-finger, as has been documented in extant cetaceans (Lillie, 1910; Fraser and Purves, 1960).

The opening for the bony eustachian tube (*et*) is located in the anterior end of the bulla between the outer lip (*ol*) and the involucrum (Fig. 21C, D: *in*). The rim of the bulla around the anterior opening of the tube is thickened and recoiled, similar to the eustachian opening in the bulla of mysticetes, but very different from the eustachian opening of most odontocetes, which is formed by a thin and sharp edge. The thin-edged eustachian tube opening of odontocetes is correlated with the more pointed anterior end of their bullae. The recoiled edge of the eustachian opening in the bullae of basilosaurids and mysticetes contributes to the more oblong outline of the bullae (see also Pilleri et al., 1989: fig. 14). The eustachian tube opens anteriorly into the space of the anterior pterygoid sinus (Fig. 22: *aps*). In contrast, in the more primitive *Pakicetus*, *Gaviacetus*, and *Indocetus*, the eustachian tube is located in a more medial part of the bulla, and it opens directly into the nasopharynx (Figs. 10, 13, 15) instead of the cavity of the pterygoid sinus.

PATTERNS OF VARIATION IN BASICRANIAL CHARACTERISTICS

Four basicranial features show conspicuous variability in correlation with the difference in size in basilosaurids: (1) size of the basicapsular fissure and the cavities for the pterygoid sinus (Figs. 18, 22, 23); (2) the pathway of the mandibular branch of the trigeminal nerve (Fig. 18); (3) the size of the sinus grooves between the dorsal edge of the tegmen tympani (superior process) and the adjacent wall of the squamosal (Figs. 20, 23); and (4) the articulation of the tympanic bulla with the basioccipital and exoccipital (Figs. 22, 23). Details are provided here.

Basicapsular fissure.—The space between the petrotympanic complex and the occipitals in basilosaurids is known as the "basicapsular fissure" (Figs. 18, 22, 23). This is also known as a "petrosal-paroccipital fissure," or a "cranial hiatus" in previous literature (Pompeckj, 1922; Kellogg, 1936; Kasuya, 1973; de Muizon, 1987; Fordyce, 1994; Gingerich and Uhen, 1996). The fissure corresponds in position to the embryonic

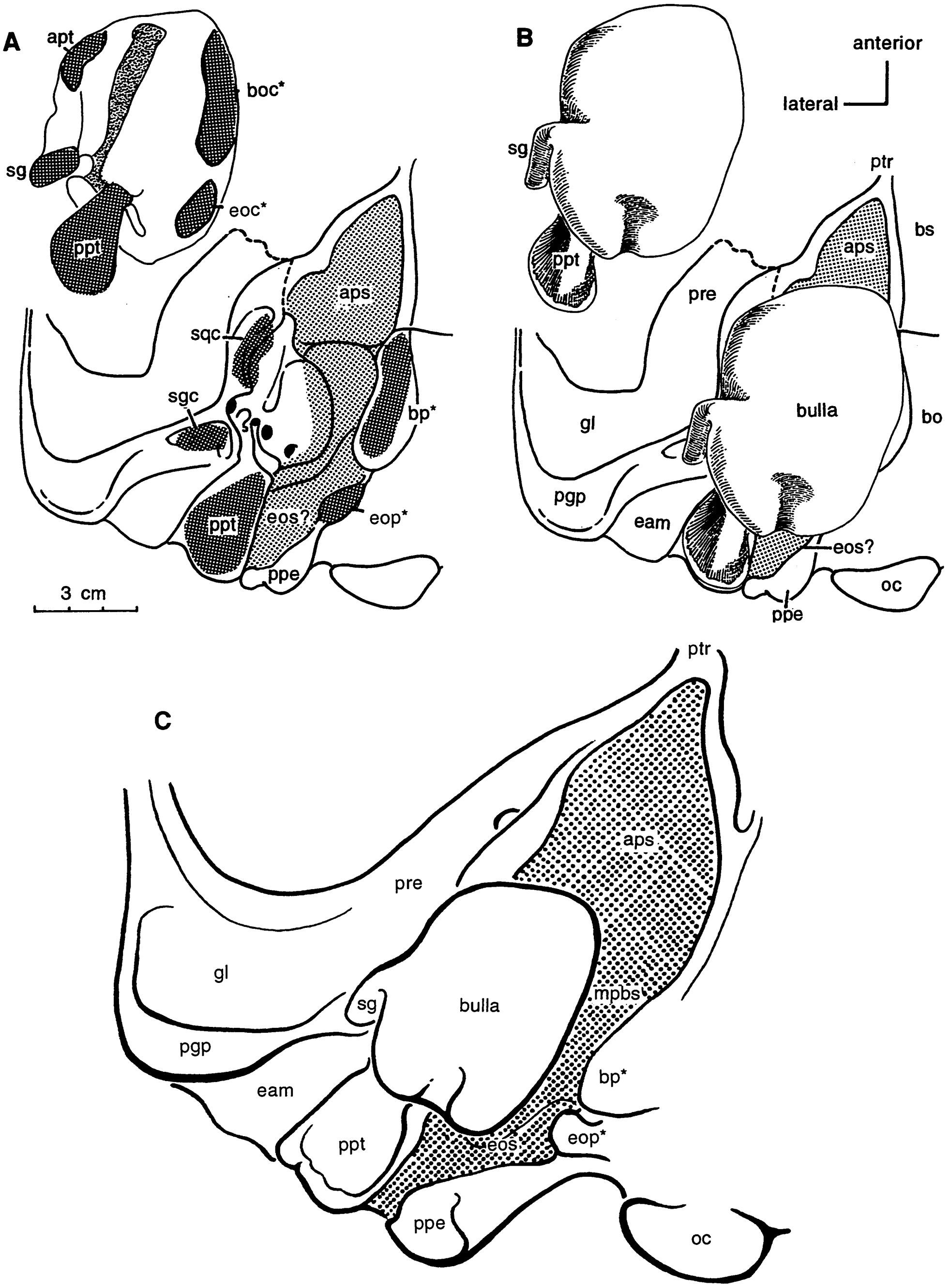
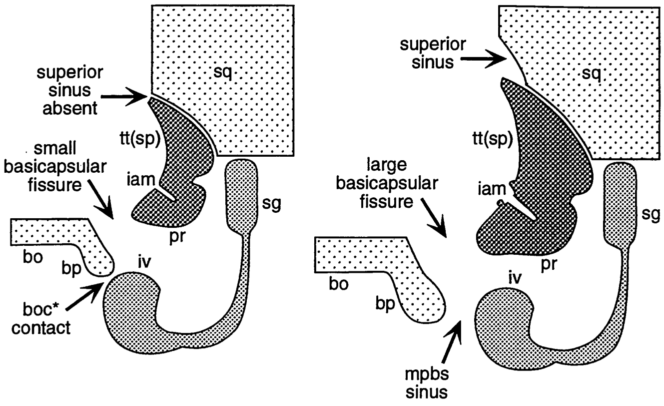


FIGURE 22. Articulation of bulla and distribution of pterygoid sinuses in Eocene basilosaurid archaeocetes. A-B, *Dorudon atrox* (subadult skull; composite of UM 93220 and 94812). C, *Basilosaurus isis* (large adult skull; UM 97507). All are drawn to the same scale. Darker hatched pattern represents sites of bullar articulation. Lighter stippling shows size and position of pterygoid sinuses. The contact between the bullar involucrum and the falcate process of basioccipital is present in small and/or subadult skulls, but this is lost in full-sized adult skulls of basilosaurids. Abbreviations: *aps*, anterior pterygoid sinus; *apt*, anterior process of tympanic; *bo*, basioccipital; *boc**, contact of the bulla to the basioccipital; *bp**, bullar contact on the falcate process of basioccipital; *bs*, basisphenoid; *eam*, external auditory meatus; *eoc*, contact of the bulla for the exoccipital; *eop*, bullar process of exoccipital; *eos*, posterior pterygoid sinus (posterior part); *gl*, glenoid fossa; *oc*, occipital condyle; *pgp*, postglenoid process; *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of tympanic; *pre*, preglenoid process of squamosal; *ptr*, pterygoid ridge; *sg*, sigmoid process; *sgc*, contact on the squamosal for the sigmoid process of the ectotympanic; *sqc(apt)*, contact on the squamosal for the anterior process of tympanic. Asterisks indicate that contacts with the bulla may be variable, present in subadult or small skulls but absent in adult and larger skulls.



A. Small (Subadult) Skull B. Large (Adult) Skull

FIGURE 23. Variation of basicranial structures in Eocene basilosaurid archaeocetes. Drawings are schematic transverse sections of right basicrania viewed posteriorly (or left basicrania viewed anteriorly). A, smaller skulls (subadult, or mature skulls of smaller taxa). B, larger skulls (mature skulls of larger taxa). Both are drawn to the same scale. Smaller skulls generally have no superior petrosal sinus groove, have a smaller basicapsular fissure, and may retain direct contact of the basioccipital process with the involucrum. Larger skulls have a larger tegmen tympani, have a groove for the superior petrosal sinus, have a larger basicapsular fissure, have a medial peribullar sinus, have a more elevated rim of internal acoustic meatus, and lack contact between the basioccipital process and the involucrum. Abbreviations: *bo*, basioccipital; *bp*, basal or falcate process of basioccipital; *iam*, internal acoustic meatus; *iv*, involucrum; *pr*, promontorium or pars cochlearis; *sg*, sigmoid process; *sq*, squamosal; *tt(sp)*, tegmen tympani or superior process of petrosal.

basicapsular (or basicochlear) fissure between the otic capsule that ossifies to form the petrosal, and the basal plate of the chondrocranium that develops into the basioccipital in most mammals (de Beer, 1937; MacPhee, 1981). The transient gap formed by the fissure between the cartilaginous basal plate and otic capsule during the development of the chondrocranium is present (albeit small) in the ontogeny of cetaceans (de Beer, 1937; or basicochlear fissure of Eales, 1951). It is clear that the large space identified as the basicapsular fissure in the adult basilosaurid skull has incorporated other structures, such as the jugular (posterior lacerate) foramen and possibly the piriform fenestra, in addition to the embryonic basicapsular fissure. The large cavity is developed secondarily in juvenile or subadult stages in correlation with the growth of the vascular (and pneumatic) sinuses. Thus the basicapsular fissure in adult skulls is not a simple retention of an embryonic precursor structure, as the term may imply.

The open space (or gap) of the basicapsular fissure is narrow in a skull fragment of *Basilosaurus* (USNM 6087), possibly subadult, illustrated by Kellogg (1936: *fig. 5*). In contrast, in other adult basilosaurid skulls like that of *Ancalecetus* (CGM 42290), this open space is much larger, as wide as the entire promontorium. The promontorium is separated much farther from the exoccipital and from the basioccipital in *Ancalecetus* (CGM 42290) than in the specimen described by Kellogg.

A similar pattern of variation, possibly ontogenetic, also occurs in *Dorudon atrox*. In this taxon, the basioccipital sinus and basicapsular fissure are smaller in subadult skulls than in larger adult skulls. In subadult skulls (e.g., UM 100139; Uhen, 1996), the promontorium is very close to the falcate (basal) process of the basioccipital, whereas in larger adult skulls the gap is much larger, being almost as wide as the promontorium.

Variation of the endocranial sinus grooves.—The endocranial sinus groove along the dorsal edge of the tegmen tympani (Fig. 23) also has ontogenetic variation in basilosaurids. In subadult skulls of *Dorudon atrox* (UM 93232, 100142), the edge of the tegmen tympani is flush with and tightly wedged to the squamosal on the endocranial surface of the braincase. There are no visible grooves for either the superior petrosal sinus or the sigmoid sinus. In contrast, in the adult skull of *Dorudon atrox* ("*Zeuglodon osiris*" of Pompeckj, 1922, Plate 2, figs. 1-7), a prominent superior petrosal sinus groove is developed between the tegmen tympani and the squamosal. This endocranial groove continues posteriorly on the endocranial surface of the pars canaliculus of the petrosal. This latter part of the groove may have housed the sigmoid sinus. A similar developmental difference is also present in *Basilosaurus*. In *Basilosaurus cetoides* (Kellogg, 1936: *fig. 5*), the tegmen tympani (= superior process of petrosal of Kellogg, 1936) abuts the squamosal. The sinus grooves are not well developed. In contrast, in an adult skull of *Ancalecetus* (CGM 42290), grooves for the superior petrosal sinus and the sigmoid sinus are very well developed; and as a result the edge of the tegmen tympani is free standing. The degree to which these vascular grooves are developed may be correlated with development of endocranial retes in the adjacent endocranial space of the cranial cavity (Breathnach, 1955; Geisler and Luo, 1998; Geisler, pers. comm.).

Variation in pathway of cranial nerve V_3.—Three characters studied here are related to the pathway of the mandibular nerve of the trigeminus (V_3): (1) the external opening in the external pterygoid lamina; (2) the groove on the roof of the anterior pterygoid sinus cavity; and (3) a highly variable feature of the internal foramen (or notch) that may be present between the pterygoid sinus cavity and the cranial cavity.

As described earlier, the external opening of the foramen ovale ("foramen pseudovale" of Hulbert et al., 1998 and some other authors) for the mandibular branch of the trigeminal nerve is located in the lateral lamina of the pterygoid that forms the lateral wall of the anterior pterygoid sinus cavity (Fig. 18). The mandibular nerve exits from the anterior pterygoid sinus cavity to the outside of the skull via this foramen. The foramen shows little variability among basilosaurids (Kellogg, 1936; Gingerich and Uhen, 1996; this study).

The internal opening for the mandibular nerve between the cranial cavity and the anterior pterygoid sinus cavity varies with size of the skull (and/or ontogenetic stages) in basilosaurids.

In some subadult skulls of basilosaurids (e.g., *Dorudon atrox*, UM 93232), the mandibular nerve entered the pterygoid-basioccipital sinus cavity from the cranial cavity through the basicapsular fissure, the gap between the basioccipital and the promontorium. On the superior pterygoid lamina that forms the roof of the anterior pterygoid sinus cavity, there is no groove for the mandibular branch of the trigeminal nerve (V_3); nor is there a foramen or notch on the posterior edge of the superior pterygoid lamina (Fig. 18A).

In skulls of adult basilosaurids like that of *Ancalecetus* (CGM 42290), the pathway of the mandibular nerve is partially enclosed by the superior lamina of the pterygoid that forms the roof of the anterior pterygoid sinus cavity. The roof of the sinus cavity shows a distinctive groove for the mandibular branch of the trigeminal nerve (V_3). The posterior edge of the superior pterygoid lamina forms a secondary and internal foramen (or notch) for the mandibular nerve. The internal secondary foramen (partially encircled by the superior lamina of the pterygoid) is comparable to the cranial foramen for the trigeminal nerve (V) in odontocetes (Fraser and Purves, 1960; Fordyce, 1994) because the foramen serves as the conduit for the mandibular nerve between the braincase and the more external pterygoid sinus cavity.

It appears that the absence of this internal foramen and the related groove for the mandibular nerve (V_3) in the small subadult skulls, and their presence in larger skulls are the results of ontogenetic expansion of the anterior pterygoid sinus cavity in larger skulls (Fig. 18). Variation of these structures associated with the mandibular trigeminal nerve is clearly related to the difference in the size of the superior lamina of the pterygoid, which grows posteriorly with the skull.

The variability of features of the mandibular nerve (V_3) with size is not only present in basilosaurids, but also in other cetacean groups. Here we briefly explore the implications of the related characters.

The foramen ovale (external opening) in the lateral lamina of the pterygoid, as described here for basilosaurids, is a primitive characteristic of pakicetids (Fig. 9), protocetids (Fig. 13; also see Geisler and Luo, 1998; "foramen pseudovale" of Hulbert et al., 1998), and mysticetes (Miocene baleen-bearing cetotheres, Kellogg, 1965; and living *Balaenoptera*, Fraser and Purves, 1960, plate 7). However it is variable in some primitive fossil odontocetes, and absent in derived odontocetes. This external opening is present in the fossil physeterid *Orycterocetus* ("ectal orifice" of the foramen ovale; Kellogg, 1965: 56), but only as an incomplete notch in the primitive odontocete *Xenorophus* (CMNH 72655, this study). In platanistoids, the external opening of the foramen ovale in the lateral lamina of the pterygoid is absent because the lateral lamina of the pterygoid associated with the foramen is completely modified by the much enlarged anterior pterygoid sinus (see de Muizon, 1987; Fordyce, 1994). The external opening is also absent in many extant families of odontocetes (Fraser and Purves, 1960; Barnes, 1984, 1985).

The groove for the mandibular nerve (V_3) as it runs its course on the roof of the anterior pterygoid sinus cavity is variable. The bone that forms the groove may be the superior lamina of the pterygoid in basilosaurids (this study) and extant mysticetes (Fraser and Purves, 1960), or the internal laminae of the alisphenoid and basisphenoid in odontocetes (Fraser and Purves, 1960; Barnes, 1985; Fordyce, 1994). This groove can be well developed in some (e.g., the Miocene baleen-bearing cetotheres) but poorly in others (e.g., some living genera of mysticetes; Fraser and Purves, 1960; Kellogg, 1965, 1968). In odontocetes, it is known to be present in some platanistoids (Fordyce, 1994: fig. 8A), *Xenorophus* (this study), and physeterids (Kellogg, 1965: p. 56). However it is absent in most extant odontocetes and many fossil odontocetes.

The mandibular nerve (V_3) passes from the braincase into the anterior pterygoid sinus through the basicapsular fissure in some basilosaurids (Gingerich and Uhen, 1996; this study), and in the mysticetes for which this feature has been studied (e.g., Fraser and Purves, 1960; Kellogg, 1965, 1968). No separate internal opening or notch for V_3 is present in these groups, although the internal (and cranial) opening is partially developed and represented by a notch in some larger skulls of basilosaurids (Fig. 18B). In contrast, in all odontocetes for which this character has been studied, there is an internal foramen in the well-formed internal wall that excludes the peribullar sinus cavity from the braincase. It is this foramen in the internal wall of the peribullar sinus cavity that has been termed a foramen ovale in almost all anatomical literature on odontocetes (e.g., Fraser and Purves, 1960; Barnes, 1985; de Muizon, 1987; Fordyce, 1994).

We point out that the foramen ovale, as commonly identified in mysticetes (Fraser and Purves, 1960, plate 7; and Kellogg, 1965, 1968) is anatomically equivalent to the external opening for V_3 in basilosaurids. This is different from the foramen ovale as commonly identified in odontocetes (Fraser and Purves, 1960, plates 8 and 13) which is equivalent to the internal notch of the mandibular nerve path in large skulls of basilosaurids.

In some previous literature, the term "foramen ovale" was used for different openings of V_3 in mysticetes and odontocetes (e.g., compare Fraser and Purves, 1960: plate 7 versus plates 8 -10). In light of this anatomical distinction of the external vs. internal openings of the "foramen ovale," and their different systematic distributions in basilosaurids, mysticetes, and odontocetes, it is important to provide more explicit clarification in description of these features. The external opening of the mandibular nerve V_3 is the same as the foramen ovale in non-cetacean mammals, and thus a primitive mammalian character. However, the groove for V_3 is a more derived feature associated with formation of the roof of the anterior pterygoid sinus cavity in basilosaurids and crown-group cetaceans. The internal opening, which is best developed in odontocetes, is a neomorphic structure that is associated with the internal wall of the peribullar cavity. The so-called "foramen ovale" of odontocetes as identified in previous literature, has no equivalent in non-cetacean mammals.

Variation in articulation of the bulla.—Articulation of the ectotympanic bulla with the basioccipital and exoccipital shows dramatic variations that are seemingly caused largely by growth of the basioccipital sinus and the basicapsular fissure (Figs. 22, 23). In subadult skulls of *Dorudon* (UM 100139) and *Saghacetus* (UM 101227), the flat surface of the involucrum of the bulla has either a direct contact or a very close ligamentous connection to the falcate process of the basioccipital, and possibly also a close connection to the bullar process of the exoccipital (Figs. 18, 22: *bp* and *eop*). In a larger skull of *Dorudon* (UM 93220; not fully adult) and in adult *Basilosaurus* (UM 97507), the involucrum of the bulla is removed from both the falcate process of the basioccipital and the bullar process of the exoccipital. The larger sinus cavity separates the involucrum widely from these processes of the basioccipital and the exoccipital, which become free standing crests or projections.

Ossification of the petrotympanic complex occurs early in the ontogenetic development of mysticetes and odontocetes. In the growth stages of juvenile and subadults, the bulla has become fixed in size and does not grow with the rest of the skull structures, such as the peribullar sinuses. As a result, the bulla becomes separated farther from the surrounding structures in successively later growth stages (e.g., refer to the observation on mysticetes by Fraser and Purves, 1960). We believe that variability of the bullar articulation with the basioccipital and the exoccipital (although not the bulla itself) in basilosaurid skulls of different sizes is a manifestation of the same growth phenomenon.

IV

CHARACTER ANALYSIS

The basicranium of mammals is a complex anatomical region of the skull traversed by cranial vessels and nerves and encompassing specialized structures of the middle and inner ear that make hearing possible. Thus the basicranium is important for understanding how mammals hear and the functional limits of their hearing, and the very complexity of the basicranium makes it interesting and important for understanding mammalian phylogeny and evolution. Our objective in this chapter is to make sense of the basicranial complexity of archaeocetes, both in comparison to earlier mesonychians and in comparison to later odontocetes and mysticetes.

Basicranial characteristics discussed here are organized together by anatomical association, meaning that they are in close positional proximity or share common traits of soft anatomy (e.g., nerves, blood vessels, or membranes). Grouping characters by anatomical association can help to reveal shared gestalt functional patterns that are not always evident by serial treatment of characters individually. This helps to expose and avoid over-splitting of anatomical characteristics to be used in phylogenetic and functional analyses. To examine characters by anatomical association may also illuminate possible coevolution of related structures. Characters and character state distributions are summarized in Table 6 at the end of this chapter.

TEGMEN TYMPANI (SUPERIOR PROCESS) OF PETROSAL

The tegmen tympani forms a part of the roof of the epitympanic recess that overhangs the malleus and the incus in adult eutherians. In embryogenesis, the tegmen tympani is a highly conservative structure of the eutherian auditory region (de Beer, 1937; MacPhee, 1981). According to MacPhee (1981: p.64), the tegmen is a *wing, initially formed in cartilage, that springs from the anterolateral part of the auditory capsule to form the rear section of the tympanic roof in mammals. The root of the tegmen is crossed by the facial sulcus*. The tegmen is developed as an anterior extension of the crista parotica of the auditory capsule in early embryogenesis in eutherians. Later it merges medially with the prefacial commissure.

The tegmen tympani develops in a similar pattern in extant cetaceans from the lateral part of the auditory capsule (de Beer, 1937). The tegmen is continuous posteriorly with the crista parotica, and medially with the lateral prefacial commissure in the early embryonic development of odontocetes (Eales, 1951). The tegmen tympani and the lateral prefacial commissure are connected to the cartilaginous parietal plate of the chondrocranium before ossification of the auditory capsule (de Beer, 1937; Eales, 1951). During or immediately after ossification of the auditory capsule into a petrosal, the cartilaginous parietal plate is reabsorbed, so that the combined structure of the tegmen tympani and the lateral prefacial commissure are incorporated into the petrosal. The crista parotica, a low crest (or wing-like structure) on the lateral aspect of the embryonic auditory capsule, is partially incorporated into the hypertrophied tegmen tympani in adult cetacean petrosals. The anterior process is not present in this embryonic stage (Ridewood, 1922; Eales, 1951), and it must have developed as an extension of the compound structure of the tegmen tympani and the prefacial commissure in later subadult stages.

The tegmen tympani is only weakly developed in the most primitive eutherian ungulates (such as arctocyonids of the early Paleocene; MacIntyre, 1972; Luo, 1989; Wible 1990), but it is slightly enlarged in other archaic ungulates, such as *Hyopsodus*, *Meniscotherium*, *Phenacodus*, and Eocene taxa of extant ungulate orders, such as the perissodactyl *Heptodon* and artiodactyl *Diacodexis* (Gazin, 1965; Cifelli, 1982; Coombs and Coombs, 1982). A weakly developed tegmen tympani is an omnipresent and primitive condition of most eutherians; while a slightly enlarged tegmen tympani is a general condition of eutherian ungulates such as *Sus* (Fig. 2A, 3A: *tt*).

In contrast to the more primitive condition of a moderately enlarged tegmen tympani in most other ungulates, the tegmen tympani is hypertrophied in mesonychians and cetaceans (Figs. 2B, 3B). This structure was first termed a "Processus superior" by Pompeckj (1922), and this term was used in subsequent studies of cetacean petrosals by Kellogg (1928, 1936) and Kasuya (1973). The inflated tegmen tympani of mesonychians and the "superior process" of cetaceans are identical (Figs. 2 and 3). It is clear that the "superior process" of cetaceans is a synonym of the homologous tegmen tympani of non-cetacean mammals.

Expansion and inflation of the tegmen tympani are correlated with several characters, which include: (1) its overall size; (2) exposure of the tegmen tympani in the tympanic cavity; (3) the dorsolateral edge of tegmen tympani; (4) the suprameatal region on the medial side of the tegmen tympani; (5) the ventrolateral tuberosity; (6) the epitympanic recess or fossa for the malleolar head; (7) the epitympanic hiatus; and (8) the position of the hiatus fallopii.

1. Size (width) of the tegmen tympani (Fig. 2: tt*)*

The width of the tegmen tympani relative to the transverse width of the promontorium is measured in ventral view at the level of the tympanic foramen for the facial canal. This character is indicative of the size of the tegmen tympani, especially its dorsal expansion as a consequence of its hypertrophy. Character states: 0 = less than 50% (*Heptodon* and *Hapalodectes*); 1 = 60%-80% (mesonychids such as *Dissacus*); 2 = ca. 100% (protocetids based on the Cross protocetid of Geisler et al., 1996; basilosaurids; and odontocetes); 3 = >120% (mysticetes); ? = unknown (*Pakicetus*, *Ambulocetus*, and *Indocetus*).

The tegmen tympani is slightly developed or entirely absent in arctocyonids, the most primitive of all archaic and extant ungulates (Van Valen, 1978; Archibald, 1996); we interpret this as the primitive character state (0). In other archaic ungulates (Cifelli, 1982), the tegmen tympani is slightly enlarged, with a width approximately 40% to 50% of the promontorium width; this is designated as character state 1. In mesonychids, such as in *Dissacus* (UM 75501) and *Mesonyx* (Geisler and Luo, 1998), the tegmen tympani is greatly inflated (60% to 80% of the promontorium width) in comparison to the above-mentioned ungulates, and more similar to archaeocetes (Figs. 2 and 3). This inflated tegmen tympani is designated as character state 2. The largest tegmen tympani occurs in mysticetes, usually over 120% of the promontorium width (see Geisler and Luo, 1996).

2. Exposure of the tegmen tympani in the tympanic cavity (Fig. 1: tt*)*

Character states: 0 = tegmen tympani mostly covered by the entoglenoid process of the squamosal, with a small exposure in the tympanic cavity (ungulates, *Pakicetus*, *Ambulocetus*); 1 = the lateral edge of the tegmen tympani is covered by the squamosal, but the medial part is exposed (where the ventrolateral tuberosity and fossa for the malleus are located; all basilosaurids); 2 = no contact between the tegmen tympani and the squamosal, and the tegmen is fully exposed ventrally (mysticetes and odontocetes).

The tympanic exposure of the tegmen is independent of the size of tegmen tympani. The ventral coverage of the tegmen by the squamosal varies among the taxa considered in this analysis. A tegmen tympani of a moderate size may have very broad exposure in the tympanic cavity, such as in early artiodactyls (Coombs and Coombs, 1982). A large tegmen tympani may have a relatively small tympanic exposure, such as in mesonychians and archaeocetes (Figs. 15, 16; also see Pompeckj, 1922), or a very large exposure as in mysticetes and odontocetes.

3. Dorsolateral edge of the tegmen tympani

Character states: 0 = presence of a weakly developed edge; 1 = tegmen tympani developed into a prominent edge; 2 = rounded and no edge; 3 = edge is obliterated by the rugose surface of the hypertrophy of the tegmen tympani.

The dorsal (lateral) crest of the tegmen is almost nonexistent in therian petrosals of the Cretaceous and early Paleocene, and weakly developed in other archaic ungulates (Cifelli, 1982; Luo 1989). In contrast, as a result of the hypertrophied tegmen tympani, a prominent ridge (or crest) is present in mesonychids (e.g., *Dissacus*, UM 75501) and cetaceans (Fig. 3B, C). The dorsal edge of the tegmen tympani is further modified in most odontocetes, in which much of the tegmen tympani is inflated and rounded, and no crest is present (Kasuya, 1973; de Muizon, 1987, 1988, 1990; Fordyce, 1994; Luo and Marsh, 1996). The most conspicuous variation in the dorsal part of the tegmen tympani occurs in mysticetes (Geisler and Luo, 1996). The tegmen tympani may develop separate ventrolateral and dorsolateral crests (*Herpetocetus*, Geisler and Luo, 1996) or hyperinflation (e.g., balaenids, Geisler and Luo, 1996). Variation of this character within mysticetes was considered in detail elsewhere (Geisler and Luo, 1996). For the purpose of the current study on archaeocetes, we consider the lateral crest on a hypertrophied tegmen tympani a general condition of mysticetes as a whole (= character state 3).

4. Suprameatal region of the petrosal (Fig. 3: smf*)*

The suprameatal fossa is a broadly concave area on the medial side of the tegmen tympani. It has three character states among the taxa surveyed in this study: Character states: 0 = absent because the tegmen tympani is absent or weakly developed (all basal eutherians including archaic ungulates); 1 = a broad concavity or fossa (*Dissacus*, UM 75501; *Mesonyx*, Geisler and Luo, 1998; Cross protocetid, Geisler and Luo, 1998; basilosaurids and *Xenorophus*); 2 = flat, or nearly flat, with no concavity (*Parietobalaena*, Geisler and Luo, 1996; most odontocetes, Luo and Marsh, 1996); 3 = bulging and rugose (balaenids and balaenopteriids; Geisler and Luo, 1996). In several mysticetes and odontocetes, the area of the suprameatal fossa is nearly flat (e.g., *Herpetocetus*, Geisler and Luo, 1996); but in the majority of mysticetes and odontocetes this area is uniformly convex. The absence of the suprameatal fossa in mysticetes is caused by pachyostosis (excessive bone growth) of the tegmen tympani and the prefacial commissure. This is regarded as a separate character state because it differs from the absence of the suprameatal fossa as a result of the lack of ossification of the tegmen tympani in primitive ungulates.

5. Ventrolateral tuberosity (Figs. 2 and 19: vlt*)*

Character states: 0 = absent; 1 = incipient (*Dissacus*; *Mesonyx* of Geisler and Luo, 1998; and *Pakicetus*); 2 = fully developed (all post-pakicetid cetaceans including *Ambulocetus*); 3 = hypertrophied and elongated to become a process (*Xenorophus*, CMNH 72655, and *Squalodon*, ChM VP 4992).

The ventrolateral tuberosity is a protuberance on the ventral surface of the tegmen tympani in all archaeocetes and odontocetes (lateral tuberosity of Barnes, 1978; Fordyce, 1983, 1994; ventral tuberosity of de Muizon, 1987; ventrolateral tuberosity of Luo and Marsh, 1995). It is absent in the taxa with a small or moderately developed tegmen tympani, such as in most archaic ungulates. The mesonychids *Dissacus* and *Pachyaena* have a small protuberance at the same location; this incipient ventrolateral tuberosity is more developed in archaeocetes. The ventrolateral tuberosity is usually well developed in odontocetes (de Muizon, 1987; Whitmore, 1987; Fordyce, 1994; Luo and Marsh, 1996), but it is developed into a large process in *Xenorophus*. The tuberosity is not developed in mysticetes (Geisler and Luo, 1996).

6. Epitympanic recess

Character states: 0 = uniformly concave without a distinctive fossa for the head of the malleus; 1 = presence of a distinct fossa for the head of the malleus (*Ambulocetus* and the more derived cetaceans); 2 = flat or near flat (mysticetes); ? = unknown (*Gaviacetus*, *Rodhocetus*, *Indocetus*, and Habib Rahi protocetid).

The epitympanic recess is the concavity overhanging the malleus and the incus. It is a primitive structure present in many primitive eutherians (van der Klaauw, 1931; de Beer, 1929; MacPhee, 1981; Novacek, 1986). Although a fossa incudis for attachment of the incus is differentiated from within the epitympanic recess in some Cretaceous therians (Wible, 1990; Wible et al., 1995), the recess is a relatively simple structure in most other eutherian mammals (including mesonychians) of the early Tertiary without the fossae for the malleus and the incus. In archaeocetes and odontocetes, the equivalent area of the epitympanic recess is differentiated into a distinctive fossa for the malleus and a fossa for the incus (Pompeckj, 1922; Kellogg, 1936; Kasuya, 1973; de Muizon, 1988; Fordyce, 1983; Luo and Marsh, 1996). Both are major apomorphies of the cetacean tympanic cavity. These fossae, however, are secondarily lost in the epitympanic area in mysticetes (Geisler and Luo, 1996).

7. Hiatus epitympanicus (Fig. 2: het*)*

Character states: 0 = poorly developed or absent; 1 = well developed as a deep transverse groove between the tegmen tympani and the mastoid (posterior) process (partially visible in *Ambulocetus*); 2 = developed into a constricted neck between pars cochlearis and the mastoid process.

The hiatus epitympanicus is a transverse groove between the inflated tegmen tympani and the mastoid process. This groove receives the squamosal wing (or the spiny process of de Muizon, 1987) that is proximal (medial) to the external auditory meatus. The groove is only weakly developed in some eutherians (such as *Ovis*, Fig. 2A). It is best developed in mesonychians, archaeocetes and odontocetes (Fig. 2B, C).

8. Hiatus fallopii (Fig. 2: hf*)*

Character states: 0 = aperture is positioned on the tympanic surface of the tegmen tympani (all non-cetacean ungulates); 1 = on the anterior part of the pars cochlearis (between the promontorium and the anterior process; Cross protocetid, based on Geisler and Luo, 1998; and all basilosaurids and mysticetes); 2 = on the medial (cranial) side of the pars cochlearis (odontocetes); ? = unknown (*Pakicetus*, *Ambulocetus*, *Gaviacetus*, *Indocetus*).

The hiatus fallopii is the anterior exit of the greater superficial petrosal nerve, a branch of the facial nerve. Its position has three different character states. In most eutherian ungulates, the hiatus fallopii is on the tympanic surface near the anterior edge of the tegmen tympani (Fig. 2A; also see MacIntyre, 1972; Cifelli, 1982; Luo, 1989). This condition is similar to the outgroup condition of marsupials (Kuhn and Zeller, 1987; Wible, 1990; Norris, 1994; Meng and Fox, 1995) and some eutherian edentates (Luo, 1989), and thus should be considered to be primitive for ungulates and cetaceans.

In archaeocetes, the pachyostosis of both the tegmen tympani and the pars cochlearis have caused a relocation of the anterior exit of the greater petrosal nerve from the tympanic side of the tegmen tympani to the anterior edge of the pars cochlearis. In primitive odontocetes the greater superficial petrosal nerve leaves the petrosal through either a fissure, or a notch on the anterior rim of the internal acoustic meatus in which the cranial opening of the facial foramen is located (*Waipatia*, Fordyce, 1994; squalodontoids, Luo and Eastman, 1995; eurhinodelphids and *Physeter*, Luo and Marsh, 1996). Among mysticetes, the anterior course of the greater petrosal nerve is in a similar fissure in the taxa of "cetotheriid" grade (Geisler and Luo, 1996). In extant mysticete families, the excessive growth of spongy bone on the cranial surface has enclosed the course of the greater petrosal nerve (Geisler and Luo, 1996). The hiatus fallopii is either in the ventral edge of the anterior process in balaenopterids and eschrichtiids, or in the crease between the promontorium and the anterior process as is the case in balaenids. Topographically, the hiatus fallopii of balaenids is almost identical to, and therefore coded the same as the character state of basilosaurids. However, assuming that mysticetes are a monophyletic group, the condition of balaenids is most likely a secondary reversal to the primitive condition of archaeocetes.

ANTERIOR PROCESS OF PETROSAL

The anterior process of cetaceans and mesonychids could have contributions from two separate embryonic precursor structures: (1) most of this process is an anterior extension of the compound structure of the tegmen tympani and the prefacial commissure, and (2) it may also have a small contribution from the epitympanic wing of the petrosal, which is the anterodorsal outgrowth of the pars cochlearis that contributes to the roof of the tympanic cavity in some eutherian mammals (MacPhee, 1981). Early in embryogenesis of the petrosal, the tegmen tympani and the epitympanic wing are separate, but the two structures may not be distinguishable after they have fused to a continuous sheet of bone in the adult petrosal (MacPhee, 1981).

In *Dissacus*, an incipient process is formed from an anterior extension of the tegmen tympani, clearly separated from the anterodorsal margin of the pars cochlearis (UM 75501; Fig. 7). There is a strong resemblance between mesonychids and cetaceans in this structure, except that the size of the process is much smaller in the former group. This suggests that most of the anterior process is formed from the tegmen tympani in cetaceans, as it is in mesonychids.

The anterior process has several characters: (9) absence versus presence; (10) if present, its proportion; (11) morphology of the apex; (12) morphology of its lateral surface; (13) the contact of anterior process with the squamosal. We follow Geisler and Luo (1996) in the definition of most of these characters.

9. Anterior process (anterior extension of the tegmen tympani)

Character states: 0 = absent (*Heptodon*, *Diacodexis*, *Hapalodectes*); 1 = present (as an anterior projection from the tegmen tympani; *Dissacus*, *Mesonyx*, *Pakicetus*, *Ambulocetus*, and some other protocetids, Geisler and Luo, 1998; and all basilosaurids, odontocetes, and mysticetes).

The anterior process is recognized as the additional portion of the tegmen tympani anterior to both the vascular groove and the gap between the tegmen and the pars cochlearis. The absence of an anterior process is the primitive condition of the eutherian ungulates (Fig. 2A: *Sus*). In most ungulates, the tegmen tympani is either small (arctocyonids and *Hyopsodus*) or moderately developed (*Meniscotherium* and *Phenacodus*, Cifelli, 1982), but not sufficiently enlarged to give rise to the anterior process. This is coded "0." The presence of the process (Fig. 2B, C: *ap*) in mesonychids and cetaceans is designated "1."

10. Size of the anterior process

Character, when present, is measured as the length of the process relative to the length of the promontorium. Character states: 0 = less than 30% (mesonychids, *Pakicetus*, and derived odontocetes such as some delphinoids); 1 = 60-80% (archaeocetes, and most primitive odontocetes); 2 = more than 90% (mysticetes, Geisler and Luo, 1996); ? = non-applicable (archaic ungulates without an anterior process, including *Hapalodectes*) or unknown (*Ambulocetus*, *Gaviacetus*, and *Indocetus*).

If the anterior process is absent in a taxon, the character is designated as nonapplicable to the taxon. The anterior process in *Dissacus* is incipient and short, less than 10% of the length of the promontorium. The distribution of this character among cetaceans was provided by Geisler and Luo (1996). In basilosaurids and primitive odontocetes (*Xenorophus*, squalodontoids and *Mesoplodon*), the anterior process is about 60-80% of the length of the promontorium. In some delphinoids and *Physeter*, the anterior process is reduced to 30-50% of the promontorium. The anterior process is large and elongate in mysticetes, usually more than 90% of the promontorial length, and grows even longer in adults than in juveniles or subadults (Geisler and Luo, 1996).

11. Apex of anterior process

Character states: 0 = pointed and continuous with the dorsolateral ridge (mesonychids, some protocetids as far as can be observed, Geisler and Luo, 1998; and all basilosaurids); 1 = pointed without a dorsolateral ridge (*Xenorophus*, *Squalodon*, Eurhinodelphids, and all mysticetes except balaenids); 2 = rounded anterior process without an apex (delphinoids, kogiids, and other derived odontocetes); 3 = anterior process truncated with no apex (balaenids, Geisler and Luo, 1996); ? = non-applicable (archaic ungulates without an anterior process, including *Hapalodectes*) or unknown (*Ambulocetus*, *Gaviacetus*, and *Indocetus*).

The apex of the anterior process is recognized as the anteroventral angle of the anterior process (Fordyce, 1994; Luo and Marsh, 1996; Geisler and Luo, 1996), instead of the anterodorsal angle that may coexist with the apex in some (but not all) odontocetes (*Waipatia*, Fordyce, 1994; *Xenorophus*, Luo and Marsh, 1996). In all basilosaurids, the dorsolateral ridge of the tegmen tympani extends anteriorly onto the anterior process and reaches the apex (state 0).

In *Herpetocetus*, there are two lateral ridges on the anterior process (Geisler and Luo, 1996: fig. 3). The dorsolateral ridge in *Herpetocetus* is equivalent to the dorsal ridge in basilosaurids (*Dorudon*, UM 94812; *Basilosaurus*, UM 97507; *Zygorhiza*, Kellogg, 1936; state 0), and the dorsal crest in *Waipatia* (Fordyce, 1994: fig. 11, but this taxon is not included in our analysis). The ventrolateral ridge in *Herpetocetus* is probably an apomorphy of only a few Miocene mysticetes (Geisler and Luo, 1996). Because the anterior process is entirely modified by pachyostotic bone growth in balaenids and balaenopterids, these ridges are not recognizable. In squalodontoids, *Xenorophus*, and *Physeter*, the apex is present, but without a clear dorsolateral ridge on the anterior process (state 1). In other odontocetes, such as kogiids (Luo and Marsh, 1996) and delphinoids (Kasuya, 1973; Whitmore, 1987), the anterior process is rounded and lacks a pointed apex. We consider these to be sufficiently different from those of *Xenorophus*, *Squalodon* and *Physeter*, and designate character state 2 for the more derived odontocetes.

12. Lateral surface of anterior process

Character states: 0 = convex; 1 = flat or concave (modified from Geisler and Luo, 1996); ? = non-applicable (non-mesonychid ungulates in which the anterior process is absent) or unknown (*Pakicetus*, *Ambulocetus*, *Gaviacetus*, and *Indocetus*).

The character is not applicable to the non-mesonychian ungulates in which the anterior process is absent. The lateral surface of the anterior process is uniformly convex in *Dissacus*, basilosaurids, some odontocetes and extant mysticetes (state 0; Geisler and Luo, 1996). The lateral surface of some cetotheriids, such as *Pelocetus*, *Parietobalaena* and *Herpetocetus*, is flat to concave (Geisler and Luo, 1996), as it is in *Xenorophus* and *Physeter* among odontocetes. This is designated as state 1.

13. Contact of anterior process with entoglenoid part of the squamosal

Character states: 0 = extensive contact along the length and over most of the lateral surface of the anterior process (mesonychids, *Pakicetus*, *Ambulocetus*, and all protocetids); 1 = partial contact on lateral side but not on the ventral side, meaning as a result that the ventrolateral tuberosity is exposed (all basilosaurids; mysticetes); 2 = reduced contact by the falciform process of the squamosal near the fovea epitubaria; 3 =

contact is lost; ? = non-applicable (*Heptodon*, *Diacodexis*, *Hapalodectes*, and other ungulates that lack the anterior process).

In *Dissacus* (Fig. 6), the incipient anterior process and the tegmen tympani have full contact with the squamosal, such that most of the tegmen tympani and the anterior process are covered by the entoglenoid process of the squamosal. This condition is present in *Pakicetus* and other protocetid whales, such as *Gaviacetus* (Figs. 9, 13), *Protocetus* (Fraas, 1904) and an unnamed protocetid (Geisler et al., 1996; Geisler and Luo, 1998). This is designated character state 0.

In basilosaurids, the lateral side of the anterior process is covered by the squamosal, but much of the ventral side of the anterior process is exposed and has no contact with the squamosal. This ventral exposure of the anterior process has a smooth contact surface (but no suture) with the anterior process of the tympanic bulla (Figs. 16, 17, *apt*). The condition of basilosaurids is designated as character state 1. In all mysticetes the lateral side of the anterior process maintains a substantial surface contact with the squamosal, despite the difference in the shape of the anterior process (Geisler and Luo, 1996). The contact surface for the anterior process of the bulla is rugose but the contact area is reduced in contrast to archaeocetes (Geisler and Luo, 1996). In archaic odontocetes, such as *Xenorophus*, squalodontoids, and platanistoids, the area of contact between the anterior process and squamosal is even more reduced, usually restricted to a very small area on the process, or by the falciform process overlapping the embayment between the anterior process and the ventrolateral tuberosity. In many extant odontocetes, this contact of the squamosal is entirely lost (Fraser and Purves, 1960; Kasuya, 1973). Limited by the scope of this analysis, we did not include all odontocetes that show variation in this character. The limited contact or the absence of contact were tactically considered a single character state 3. Contact of the anterior process of the petrosal with the tympanic bulla is considered elsewhere in the paper.

MASTOID (POSTERIOR) PROCESS OF PETROSAL

The mastoid or posterior region of the petrosal (or periotic) is formed embryonically from the canalicular part of the cartilaginous auditory capsule (de Beer, 1937). In basal therian mammals, in which the mastoid part is usually short and small, the "mastoid" region is recognized as the portion of the petrosal that contains the semicircular canals and subarcuate fossa (MacIntyre, 1972; Norris, 1994). Thus the "mastoid" is essentially synonymous with the pars canaliculus (the bony part containing the semicircular canals). This term is widely used in studies of the petrosal of therian mammals (MacIntyre, 1972; Cifelli, 1982; Luo 1989; Wible, 1990; Norris, 1994; Meng and Fox, 1995). The only exception to this widely used definition of the character was a study by Oelschläger (1986a) in which the "mastoid" was designated as a part of the squamosal instead of the petrosal.

Some mammals, such as phalangerid marsupials (Norris, 1994), may have a more derived condition, in which an elongate mastoid process (or "wing") extends distally far beyond the semicircular canals and the subarcuate fossa. This elongation of the mastoid region may have occurred convergently in marsupials and eutherians.

The posterior process of the petrosal (the mastoid "wing" of Norris, 1994) is developed both in mesonychians and in cetaceans. This homologous structure is commonly known as the "mastoid process" in terrestrial ungulates, and "posterior process" in cetaceans (Fig. 2: *mas* and *pp*). We prefer mastoid process, but use the synonyms mastoid process and posterior process more or less interchangeably. We recognize the mastoid (or posterior) process of ungulates and cetaceans as the elongate portion of the dense bone posterolateral (distal) to the pars canaliculus ("wing" of Norris, 1994). In cetaceans, the dense bone of the mastoid (posterior) process makes up most of the posterior part of the petrosal, whereas the pars canaliculus is negligibly small because the semicircular canals are extremely reduced in comparison to those of terrestrial mammals (Gray, 1951; Yamada and Yoshizaki, 1959; Ketten, 1992; Luo and Marsh, 1996).

The mastoid or posterior process of the periotic has several anatomical characters: (14) its presence vs. absence; (15) morphology of the ventral surface of the petrosal mastoid process; (16) size of the petrosal mastoid process; (17) mastoid exposure (the posterolateral end of the petrosal mastoid process exposed on the external surface of the skull); (18) stylomastoid foramen (for facial nerve); (19) external course of the hyomandibular branch of the facial nerve.

14. Mastoid or posterior portion of the petrosal

Character states: 0 = no distinctive process beyond (distal to) the pars canaliculus (the portion of petrosal formed by the semicircular canals; archaic ungulates); 1 = distinctive mastoid process extending beyond (and distal to) the pars canaliculus (mesonychids and all whales, including *Pakicetus* and *Ambulocetus*).

15. Ventral surface of the mastoid process

Character states: 0 = exposed and without cover by the tympanic except near the attachment site of the tympanohyal (*Sinonyx*, *Dissacus*, and other mesonychids; *Pakicetus*); 1 = completely covered by and sutured to the tympanic (*Ambulocetus*, *Gaviacetus*, *Indocetus*, and other protocetids; all basilosaurids; and odontocetes); 2 = mastoid process completely fused to the tympanic posterior process (mysticetes)

The ventral surface is entirely exposed behind the external auditory meatus in *Hapalodectes* (Fig. 5), *Dissacus* (Fig. 6) and *Mesonyx* (AMNH 12643, Geisler and Luo, 1998), a condition seen in the petrosals of arctocyonids (MacIntyre, 1972; Luo, 1989). In the skull specimen of *Pakicetus* (Gingerich et al., 1983), the mastoid processes of the left and right petrosals are much longer and larger than the posterior process of the tympanic. As a result, a part of the mastoid (posterior) process is exposed ventrally in *Pakicetus* (Fig. 10). Thus we interpret the mastoid process of the petrosal as partially covered by the tympanic in *Pakicetus* (state 0). The posterior process of the tympanic has completely covered the mastoid process of the petrosal in protocetids (e.g., *Gaviacetus*; Fig. 13; Fraas, 1904; *Indocetus*, Fig. 15) and basilosaurids (Fig. 22). This condition is designated as character state 1. The mastoid process of the petrosal is completely fused with the posterior process of the tympanic in baleen-bearing mysticetes (Fraser and Purves, 1960; Geisler and Luo, 1996); this is coded state 2.

16. Length of the mastoid process relative to the length of promontorium

Character is modified from Geisler and Luo (1996). Character states: 0 = short (<50%; *Protungulatum*, *Diacodexis*, *Hapalodectes*); 1 = elongated (50-70%; *Sinonyx* and all archaeocetes, most odontocetes); 2 = extremely elongated (>100%; mysticetes).

The size of the mastoid process is best represented by the ratio of its length to the length of the promontorium. The length of the mastoid process is measured from the stylomastoid notch (foramen) to the distal end of the mastoid process (Geisler and Luo, 1996). The mastoid process is short and small in most ungulates including *Hapalodectes* (state 0). However, mesonychians have a long mastoid (posterior) process (*Dissacus*, Figs. 6, 7 and *Sinonyx*, Fig. 8), as is seen in protocetids, basilosaurids and most odontocetes (Fig. 2). This is regarded as character state 1. In mysticetes, the mastoid process is very long, and further developed to the extreme in the adult skulls of larger extant mysticetes (Geisler and Luo, 1996).

17. External mastoid exposure

Character states: 0 = present (all archaic ungulates except some derived artiodactyls; all archaeocetes including *Pakicetus*, *Ambulocetus* and *Indocetus*); 1 = reduced (mysticetes); 2 = absent (odontocetes).

In most mammals, the posterolateral aspect of the mastoid region is exposed on the outside of the skull, whether the mastoid process is elongated or not. This primitive condition is present in all Paleocene ungulates (although some later artiodactyls secondarily developed the amastoid condition in which the mastoid process is not exposed on the outside of the skull), as well as in all archaeocetes (state 0). In mysticetes, because the exoccipital and squamosal have compressed the mastoid process of the petrosal, the distal exposure of the petrosal mastoid process is very small. In odontocetes, the expanded exoccipital and squamosal have completely enclosed the mastoid process of the petrosal inside the skull. As a consequence the outside exposure of the mastoid process is lost. This condition is a convergence with the secondarily derived amastoid condition of some (but not all) artiodactyls (Whitmore, 1953; Novacek, 1993).

18. Morphology of the stylomastoid foramen

Character is related to bullar articulation with the basioccipital and exoccipital. Character states: 0 = open notch (*Heptodon*, *Hapalodectes*, and other ungulates without complete bullae; convergent in basilosaurids, odontocetes, and mysticetes, in which development of the petrotympanic fissure secondarily opens the stylomastoid notch); 1 = small circular foramen (*Diacodexis*, mesonychids, *Pakicetus*, and *Ambulocetus*); 2 = enlarged slot (*Gaviacetus*, *Rodhocetus*, *Indocetus*, and all other protocetids; Geisler and Luo, 1998; Hulbert et al., 1998).

The stylomastoid foramen is the exit for the hyomandibular branch of the facial nerve from the tympanic cavity. In isolated petrosals, it is often represented by a notch posterior to the stapedial muscle fossa and between the pars cochlearis and the mastoid process. The base for attachment of the tympanohyal overhangs the stylomastoid notch (Oelschläger, 1986b; Luo and Eastman, 1995), although the latter has not been documented in many cetaceans. Its morphology may be influenced by the tympanic bulla and its relationship to the petrosal. In primitive eutherian ungulates, the tympanic is a simple ring-shaped structure. The posterior crus of the tympanic ring is attached to the tympanohyal, but does not contribute to enclosure of the stylomastoid notch (state 0). In *Diacodexis*, *Sinonyx*, *Pakicetus* and *Ambulocetus* the expanded tympanic forms a complete bulla. The posterior part of the tympanic bulla encircles the exit of the facial nerve from the cranium, forming a small stylomastoid foramen (state 1). In some protocetids, such as *Gaviacetus* and *Indocetus*, the stylomastoid foramen is much enlarged by an incipient exoccipital sinus (state 2). In basilosaurids, odontocetes, and mysticetes, a posterior pedicle (or double pedicles in the case of basilosaurids and some protocetids) is present between the posterior process of the tympanic and the bulla itself. The development of the more gracile pedicle (or pedicles) helps to enlarge the stylomastoid foramen from a circular foramen into an oblong notch. This larger stylomastoid notch is present in all basilosaurids, odontocetes, and mysticetes surveyed here, but it is especially well developed in taxa with larger bullae (such as *Basilosaurus* and extant mysticetes). The condition in basilosaurids, odontocetes and mysticetes represents a reversal to state 0.

19. External course of the hyomandibular branch of the facial nerve

Character states: 0 = absent; 1 = present as a sulcus imprinted on the ventral surface of the petrosal mastoid (posterior) process; 2 = course of the facial nerve is separated from the petrosal by the posterior process of the tympanic, no sulcus is present on the posterior process of the petrosal; 3 = sulcus on the compound posterior process is formed by both the tympanic and the mastoid process of the petrosal (Geisler and Luo, 1996).

In basal eutherians, the facial nerve has no sulcus outside the stylomastoid foramen (or notch; state 0). In contrast, in mesonychids the facial nerve follows a sulcus on the ventral surface of the mastoid process after exiting the stylomastoid foramen (Figs. 6, 7, and 8). This is designated as character state 1. In post-pakicetid cetaceans, the ventral surface of the mastoid (posterior) process is completely covered by the tympanic. The posterior process of the tympanic excludes the course of the facial nerve from the mastoid process (state 2). In mysticetes, the posterior process of the tympanic is completely fused to the mastoid (posterior) process of the petrosal in adults

(Fraser and Purves, 1960; Geisler and Luo, 1996), forming a compound posterior process. The facial sulcus is imprinted on this compound posterior process in all mysticetes (Geisler and Luo, 1996). This condition is regarded as character state 3. Odontocetes are reversed secondarily to the primitive condition (state 0).

OTHER PETROSAL CHARACTERS

20. Articulation of the promontorium with the basioccipital

Character is correlated with the presence or absence of a basicapsular fissure. Character states: 0 = present (ungulates; *Pakicetus*); 1 = absent (most post-*Pakicetus* cetaceans, such as the Cross protocetid, Geisler and Luo, 1998; *Georgiacetus*, Hulbert et al., 1998); ? = unknown (*Ambulocetus*, *Indocetus* and *Gaviacetus*).

The promontorium maintains at least some contact with the basioccipital in most mesonychids (*Sinonyx*, Zhou et al., 1995; *Hapalodectes*, Ting and Li, 1987) and other ungulates (Radinsky, 1965; Coombs and Coombs, 1982; Russell et al., 1983). This is a primitive condition that can be traced to the earliest mammals with a promontorium (Luo et al., 1995), thus designated as character state 0. In *Pakicetus*, the promontorium partially overlaps the basioccipital (Fig. 9) and is similar to the primitive condition.

In other protocetids, basilosaurids, odontocetes, and mysticetes, the promontorium is separated by a wide basicapsular fissure (petropterygoid fissure) that has been incorporated into the middle portion of the pterygoid sinus. This is designated as character state 1.

21. Surface topography of the promontorium

Character states: 0 = flat (all outgroup ungulates; *Pakicetus*); 1 = bulbous promontorium with a flat or concave medial facet (some mesonychids; Cross protocetid, *Georgiacetus*; basilosaurids); 2 = fully convex and bulbous (all mysticetes and odontocetes); ? = unknown (*Ambulocetus*, *Gaviacetus* and *Indocetus*).

The surface of the promontorium is relatively flat in *Hapalodectes* (Fig. 5) but more bulbous in mesonychians (Fig. 7). Among cetaceans, *Pakicetus* also shows a flat promontorium. This is designated character state 0. In protocetids and basilosaurids, the promontorium is more inflated, especially near the fenestrae vestibuli and cochleae. However, the medial part of the promontorium is flat or slightly concave (Figs. 19-20); this is coded as state 1. In mysticetes (Geisler and Luo, 1996) and odontocetes, the entire pars cochlearis becomes so inflated that it is nearly spherical, or even hyperinflated. As a result, the flat medial facet is absent (character state 2).

22. Tensor tympani muscle attachment

Character states: 0 = with round or oval fossa (ungulates); 1 = groove (or grooves; archaeocetes and odontocetes); 2 = broad and featureless (mysticetes); ? = unknown (*Ambulocetus*, *Gaviacetus* and *Indocetus*).

23. Petrosal participating in the wall of the brain cavity

Character is described by Pompeckj (1922), Kellogg (1936), Fordyce (1994), and Geisler and Luo (1996). Character states: 0 = present (all ungulates; archaeocetes); 1 = partial (mysticetes, especially balaenids; Geisler and Luo, 1996); 2 = absent (all odontocetes); ? = unknown (*Ambulocetus*, *Gaviacetus* and *Indocetus*).

In *Dissacus* and *Pachyaena*, the petrosal participates in the braincase, and the entire cranial surface of the petrosal is exposed internally on the braincase. The internal exposure of the petrosal on the braincase occurs in all mammals except odontocetes. This condition (character state 0) is widespread in protocetids (*Indocetus*, *Remingtonocetus*, an unnamed protocetid, Geisler and Luo, 1998) and basilosaurids (Pompeckj, 1922; Kellogg, 1936; Uhen, 1996).

The petrosal is partially excluded from the braincase in mysticetes (Fraser and Purves, 1960; character state 1). In contrast, the petrosal is excluded from the braincase in odontocetes by the internal secondary bony laminae (septa) of the basioccipital, the exoccipital, the squamosal, and the pterygoid. These internal laminae form the wall of the peribullar cavity, segregating the petrotympanic complex from the braincase (Fraser and Purves, 1960; Purves, 1966; de Muizon, 1987; Ketten, 1992; Fordyce, 1994). The odontocete condition is coded as 2.

24. Subarcuate fossa (Fig. 3)

Character is described by Luo and Marsh (1996) and Geisler and Luo (1996; 1998). Character states: 0 = present (most ungulate genera examined in this study); 1 = absent (all protocetids and later whales). Note that the subarcuate fossa may be variable in some ungulate groups. It may be present in some taxa, but absent in others of the same mammalian order. Variation of the character in different orders of extant ungulates is not considered in this study.

The subarcuate fossa is a hollow cavity in the canalicular part of the petrosal. The rim of the fossa is encircled by the anterior semicircular canal (Williams et al., 1989; Evans, 1992). The subarcuate fossa is present in most Paleogene fossil ungulates except *Mesonyx* (Geisler and Luo, 1998). There are some variations of this fossa from moderately developed to the complete absence in some extant orders of ungulates (e.g., see Novacek, 1986). The absence of the subarcuate fossa in some extant terrestrial ungulates occurs due to infilling with bone of the otherwise hollowed space in between the semicircular canals, rather than the reduction of the semicircular canals. This is different from the condition in cetaceans where the semicircular canals are reduced.

In extant cetaceans, the semicircular canals are very reduced (Yamada and Yoshizaki, 1959; Ketten, 1992; Luo and Marsh, 1996), and reduction of the semicircular canals has eliminated the subarcuate fossa altogether (Luo and Marsh, 1996; Geisler and Luo, 1996). The subarcuate fossa is also absent in all basilosaurids examined in this study and in specimens illustrated in previous publications, and it is absent in at least two protocetids: *Remingtonocetus* (Kumar and Sahni, 1986) and an unnamed protocetid from South Carolina (Geisler et al., 1996; state 1).

25. Pole of promontorium

Character states: 0 = present (all non-cetacean therian mammals); 1 = absent (all protocetids and later whales; unknown in *Pakicetus*).

ARTICULATION OF TYMPANIC WITH BASICRANIUM

In basal eutherian ungulates, the ectotympanic bulla is attached to several basicranial bones (van Kampen, 1905; van der Klaauw, 1931; Novacek, 1977). In contrast, the ectotympanic bulla (known as the "tympanic" or simply the "bulla" in most cetacean basicranial literature) has shifted its articulation from the other basicranial bones to the petrosal in extant cetaceans (Pompeckj, 1922; Kellogg, 1928; 1936; Fraser and Purves, 1960; Kasuya, 1973). These changes are correlated with development of the vascular (and pneumatic) pterygoid sinuses that isolate the petrotympanic complex from the rest of the skull (Fraser and Purves, 1960). The tightly integrated petrotympanic complex, acoustically isolated from the rest of the cranium, is generally accepted as a part of the functional adaptation for underwater hearing (Fleischer, 1978; Barnes, 1984; Pilleri et al., 1989; Oelschläger, 1990; Ketten, 1992). The characters in the articulation of the bulla provide abundant morphological information for inferring cetacean relationships (Kasuya, 1973; de Muizon, 1987; 1988; Fordyce, 1994; Luo and Marsh, 1996; Geisler and Luo, 1996).

26. Articulation of the anterior process ("processus tubarius") of the tympanic with the anterior process of the petrosal

Character states: 0 = absent or extremely small (all ungulate outgroups; *Sinonyx*, *Dissacus*, *Pakicetus*, *Ambulocetus*, and *Gaviacetus*); 1 = present along most of the length of the anterior process (all basilosaurids); 2 = by way of the accessory ossicle (all odontocetes); 3 = by way of a slender pedicle (all mysticetes).

Direct articulation of the anterior crus of the ectotympanic ring with the tegmen tympani of the petrosal is rare in eutherians. In *Sinonyx* and *Mesonyx*, the anterolateral rim of the bulla contacts the squamosal but not the petrosal (character state 0). Articulation of the anterior process of the bulla (a part of the ectotympanic) with the anterior process of the petrosal, an extension of the tegmen tympani, as in basilosaurids, odontocetes and mysticetes, is a highly derived condition for eutherians. This articulation has three different character states.

In basilosaurids, the anterolateral rim (= anterior process of tympanic) overlaps both the anterior process of the petrosal and the entoglenoid process (or anterior falciform process) of the squamosal. Partial contact of the anterior processes of the tympanic and the petrosal is designated character state 1.

The anterolateral rim of the bulla of odontocetes has an accessory ossicle, which is a separate bony element attaching to the bulla (Kasuya, 1973; Pilleri et al., 1987). The bulla indirectly articulates with the anterior process through the accessory ossicle (state 2; also see de Muizon, 1987; Fordyce, 1994; Luo and Marsh, 1996, for additional discussion of this character). The most specialized condition of the anterolateral rim of the tympanic bulla occurs in mysticetes. The anterior processes of the tympanic and the petrosal are completely fused with each other in adults, forming a compound anterior process (Geisler and Luo, 1996; Luo, 1998). The rim of the bulla is separated by a gracile anterior pedicle from this compound anterior process (state 2; Kellogg, 1965; Kasuya, 1973; Geisler and Luo, 1996).

27. Accessory ossicle of the tympanic

Character is a separate ossification of odontocetes that is homologous to the anterior tympanic process on the anterolateral rim of the bulla in basilosaurids and the anterior bullar pedicle of mysticetes. Character states: 0 = absent (all ungulates; all archaeocetes including *Pakicetus* and *Ambulocetus*); 1 = present (odontocetes); 2 = transformed to a slender pedicle (mysticetes).

The accessory ossicle is a separate ossification center distinct from the rest of the bulla in the early development of the artiodactyl *Ovis* (van Kampen, 1905). Later it becomes incorporated with the rest of the bulla, and forms a part of the processus tubarius in the adult bulla (van Kampen, 1905; Luo, 1998).

The ectotympanic bulla of mysticetes has an accessory ossicle at early embryonic stages (Ridewood, 1922). Later in development the dorsal part of the embryonic accessory ossicle is fused to the anterior process of the petrosal (Luo, 1998) and the ventral part of the accessory ossicle develops into a very gracile anterior bullar pedicle (Geisler and Luo, 1996). Therefore, the accessory ossicle is a transient ontogenetic structure. It is entirely transformed to a pedicle in adult mysticetes (Luo, 1998).

The accessory ossicle is a separate ossification attached to the anterolateral rim of the bulla in early development in odontocetes. But different from *Ovis* and mysticetes, the ossicle remains an independent structure in adults, and its "spherical" shape in early development is little changed in the adult. The adult accessory ossicle serves as the connecting structure between the bulla and the anterior process of the petrosal. It may even be fused secondarily to the anterior process in all physeterids and kogiids (Luo and Marsh, 1996) and ziphiids (Kasuya, 1973), and in some delphinoids (Kasuya, 1973). Because the number of odontocete taxa considered in this study is limited here, we have not subdivided these character states as in other studies (e.g., Luo and Marsh, 1996).

The accessory ossicle of odontocetes arises just lateral to the groove for the chorda tympani, a branch of the facial nerve. This groove is partially concealed by the ossicle if the ossicle is intact (see Pilleri et al., 1987). In basilosaurids, the anterolateral rim of the bulla has a similar groove for the chorda tympani (Fig. 21C, D; also see Pompeckj, 1922; Kellogg, 1936). Based on its topographic relationships to the chorda tympani groove, the accessory ossicle of odontocetes is interpreted to be homologous with a part of the anterior process of the tympanic (= the processus tubarius) of basilosaurids. This is consistent with observation that the embryonic accessory ossicle is incorporated into the comparable area of the bulla and forms the processus tubarius in extant artiodactyls.

Based on this interpretation of the developmental history of the accessory ossicle in living artiodactyls, mysticetes and odontocetes (Luo, 1998), we propose the following character states. The absence of the accessory ossicle in adult stages in ungulates, basilosaurids and other archaeocetes is designated as character state 0. The presence of an accessory ossicle as an independent spherical structure in adults in odontocetes is designated as character state 1 for odontocetes as a group. The highly modified anterior bullar pedicle in adult mysticetes that was transformed from an embryonic accessory ossicle is designated as character state 2.

It should be noted that alternative coding for this character is possible, given the same character distribution and development history (Luo, 1998). It would be equally reasonable to combine the conditions of mysticetes and odontocetes into a single character state. It is also possible to code the accessory ossicle as "absent" in adult mysticetes.

28. Articulation of the anterior process of the bulla with the squamosal

Character is related to character 26. Character states: 0 = present with broad contact (*Sinonyx*, *Dissacus*, and *Mesonyx*); 1 = present, with an elevated stage or tuberosity on the squamosal (*Pakicetus*, Habib Rahi protocetid, *Gaviacetus*, *Ambulocetus*, *Indocetus*, *Georgiacetus*, and the Cross protocetid); 2 = contact reduced to a crest on the anterior falciform process of the squamosal (all basilosaurids); 3 = no articulation to the squamosal (mysticetes and odontocetes).

In basal eutherians, the anterior part of the ectotympanic (homologue to the cetacean bulla) articulates with the squamosal. The anterior crus of the ectotympanic ring attaches to a pit on the postglenoid process of the squamosal (van der Klaauw, 1931; MacPhee, 1981). As the ectotympanic expands to form the floor of the auditory bulla, the ectotympanic comes into more extensive contact with the entoglenoid process of the squamosal, as well as other basicranial bones. In *Sinonyx* and *Mesonyx*, the bulla has two parts: the meatal part of the bulla contacts the postglenoid, while the bulbous tympanic portion contacts the entoglenoid process of the squamosal. In *Hapalodectes*, the ectotympanic is not preserved. But a pit medial to the postglenoid process is most likely the attachment site for the anterior crus of an ectotympanic, suggesting the ectotympanic at least had contact with the postglenoid process. In mesonychids (such as *Sinonyx*), the ectotympanic bulla is fully formed. As a result, contact of the bulla is expanded to a broader area of both the postglenoid and entoglenoid processes of the squamosal. The presence of the ectotympanic-squamosal contact is a basal eutherian condition, and thus primitive (state 0).

In cetaceans, the anterolateral rim of the bulla forms an anterior process (Fig. 21: *apt*). In *Pakicetus* and *Gaviacetus* this structure contacts a rounded and elevated stage on the entoglenoid process of the squamosal (Figs. 10, 13: *apt*). This is considered to be the general condition of protocetids as a group (state 1), although in some protocetids this character may be variable.

In basilosaurids, the anterolateral rim of the bulla contacts the ventral edge on the entoglenoid process (state 2). The rounded and elevated stage of protocetids is replaced by a thin edge in basilosaurids (Fig. 21: *apt*). As a result, the contact area between the squamosal and the tympanic bulla is more reduced in basilosaurids than in protocetids. The anterolateral rim of the tympanic bulla has lost its contact with the squamosal in odontocetes (Kasuya, 1973; Fordyce, 1994; Luo and Marsh, 1996) and mysticetes (Geisler and Luo, 1996). This condition is designated character state 3.

29. Neck of posterior process of tympanic

Character states: 0 = absent (*Heptodon*, *Sinonyx*, and other mesonychids); 1 = present (*Diacodexis*, *Pakicetus*, *Ambulocetus*, *Rodhocetus*, Habib Rahi protocetid, odontocetes); 2 = basal constriction modified into double inner and outer pedicles (*Gaviacetus*, all basilosaurids); 3 = long and gracile pedicle (mysticetes); ? = non-applicable to most archaic ungulates.

The posterior process of the tympanic and the body of the bulla have several conditions among the taxa surveyed in this study. In ungulates, such as *Ovis* (Fig. 4) and *Diacodexis* (fig. 4 of Russell et al., 1983), the posterior process has a broad base attached to the bullar body and it tapers toward the distal end. There is no constricted pedicle (or neck) in ungulates (state 0). Even though the posterior process of the tympanic is not fully preserved in *Pakicetus*, the base of process appears to be slender. In *Gaviacetus* the distal part of the posterior process of the tympanic is greatly enlarged whereas its connection to the bullar body becomes narrow, forming a neck. *Pakicetus* (Figs. 11, 12) is designated as character state 1. The neck has two pedicles in *Gaviacetus*, *Georgiacetus*, and basilosaurids (Fig. 21: *ip* and *op*; character state 2). Whether *Indocetus* (Fig. 15) has two pedicles is unknown. In mysticetes the neck of the posterior process becomes very gracile and thin (character state 3), except the extant right whale.

30. Posterior process of tympanic

Character states: 0 = absent (*Sinonyx*); 1 = present, of intermediate size and tapers posteriorly (*Diacodexis*; *Pakicetus*); 2 = distally enlarged (post-*Pakicetus* archaeocetes, including *Rodhocetus*, *Gaviacetus*, *Indocetus*; all odontocetes except *Inia* and *Pontoporia*); 3 = long, gracile, and fused to the mastoid process of the petrosal (mysticetes; Fraser and Purves, 1960; Geisler and Luo, 1996).

The posterior process of the tympanic is homologous to the posterior crus of the ectotympanic ring (Fig. 4). In most eutherian ungulates, this is represented by a small and incipient projection (*Ovis*, Fig. 4). In *Diacodexis*, the posterior crus is a gracile and elongate process (Russell et al., 1983). The posterior process of the tympanic is present and of intermediate size in *Pakicetus*. The tympanic posterior process is slightly tapering posteriorly in *Pakicetus*. The condition of *Diacodexis* and *Pakicetus* is designated as character state 1. In *Gaviacetus*, basilosaurids, and odontocetes, the posterior process is much enlarged, especially toward its distal end (character state 2). In mysticetes, the posterior process of the tympanic was sutured to the mastoid process of the petrosal in subadults and completely fused to the latter in adults (Kasuya, 1973; Geisler and Luo, 1996), which is designated as character state 3.

31. Articulation of the medial rim of the tympanic bulla with the basioccipital

Character states: 0 = present and running along the entire medial rim (*Diacodexis, Sinonyx, Dissacus*, and probably most other mesonychids); 1 = contact reduced to a small area on the basal or falcate process of the basioccipital (*Gaviacetus*); 2 = wide gap between the medial rim and the basioccipital (basilosaurids, odontocetes, and mysticetes; convergent to the primitive ungulate condition). *Pakicetus* is variable in this feature.

The bulla in mesonychids has a full contact with the basioccipital, as is the case in the early artiodactyl *Diacodexis* (Russell et al., 1983). The bullae of other early ungulates (including the fossil taxa of extant orders) are not sufficiently known to assess the distribution of this character. In most extant ungulate mammals (except tapirs), the medial rim of the ectotympanic bulla contacts the basioccipital (state 0). The medial rim in cetaceans, however, is detached from the basioccipital. In some specimens of *Pakicetus*, the medial rim of the bulla attaches to the basioccipital due to postmortem distortion (Thewissen, pers. comm.). It is also likely that the contact between the medial rim of the bulla and the basioccipital in *Rodhocetus* (Gingerich et al., 1994) was due to a slight distortion (dorsoventral compression) of the skull. In other protocetids with an intact bulla such as *Gaviacetus* (Gingerich et al., 1995) and *Georgiacetus* (Hulbert, 1993; Hulbert et al., 1998), the medial rim of the bulla is slightly detached from the basioccipital. We tentatively interpret that in all protocetids, the medial rim of the bulla is detached in local areas from the basioccipital (character state 1), although some contact is present on the posterior part of the basioccipital process.

The relationship of the medial rim of the bulla to the basicranium changes during growth in basilosaurids (Figs. 22, 23). In subadult basilosaurid specimens (UM 100139 *Dorudon atrox* and UM 101227 *Saghacetus osiris*), the falcate process of the basioccipital has a small contact with a flat surface on the medial part of the bulla. In other basilosaurids (e.g., UM 93220 *Dorudon atrox*, UM 97550 *Dorudon osiris*, and CGM 42290 *Ancalecetus simonsi*), the bulla is detached from the falcate process of the basioccipital by a wide gap. The adult condition of basilosaurids is designated as character state 2. The medial wall of the bulla is separated widely from the basioccipital in all mysticetes and odontocetes, extinct or extant (character state 2).

32. Articulation of the bulla with the exoccipital

Character states: 0 = absent (ungulate outgroups, including *Heptodon* and *Diacodexis*; *Hapalodectes* and *Sinonyx*; basilosaurids, mysticetes, and odontocetes); 1 = present (*Pakicetus;* all protocetids).

In primitive eutherian mammals, the posterior crus of ectotympanic ring articulates with the basicranium via the tympanohyal and the crista parotica. The posterior part of the ectotympanic ring does not directly contact the exoccipital. The ectotympanic has expanded to form a complete bulla in mesonychids, but it still does not expanded posteriorly enough to reach the exoccipital (character state 0).

In contrast to non-cetacean ungulates, the bullae in protocetids are all inflated to have a contact with the bullar process on the exoccipital (Figs. 10, 11, 12: *eop*). This contact between the bulla and the exoccipital is present in *Pakicetus* (Gingerich et al., 1983), *Gaviacetus*, *Georgiacetus* (Hulbert et al., 1998), and a new and unnamed protocetid whale (Geisler and Luo, 1998: fig. 8). The contact of the bulla with the exoccipital is designated as character state 1.

This feature is ontogenetically variable in basilosaurids. The exoccipital has a plate-like projection that forms the posterior extension of the falcate process of the basioccipital. In the skulls of subadults (UM 100139, UM 101227; Uhen, 1996), the bulla directly rests on this falcate process (= bullar process) of the exoccipital. However, in the adult skulls, the larger ptergyoid sinus separates the bullar (falcate) process of the exoccipital from the posterior part of the bulla, as the posterior part of the pterygoid sinus expands in the growth of the skull. In all odontocetes and mysticetes, the posterior part of the bulla is well separated from the exoccipital. The condition of adult basilosaurids, odontocetes and mysticetes is coded "0." It should be noted that the lack of articulation between the bulla and the exoccipital occurs in these taxa for a different reason (sinus expansion) from the primitive condition in non-cetacean ungulates (small or no bullae). Even though the character state is coded the same (state 0), it is clear that the condition of basilosaurids, odontocetes and mysticetes is a secondary reversal to that of non-cetacean ungulates.

SIGMOID PROCESS OF TYMPANIC AND EXTERNAL AUDITORY MEATUS

The sigmoid process of cetaceans may be homologous to one of three bullar structures in non-cetacean fossil ungulate mammals. The first of these is the anterior crus of the ectotympanic ring (Fig. 4). A slight enlargement of the anterior crus would be sufficient to transform the anterior crus into a protruding sigmoid process (Doran, 1898; Ridewood, 1922). A second structure of the eutherian bulla that could have contributed to development of the sigmoid process may be the folian process, a membranous ossification near the junction of the malleus and the anterior crus of the ectotympanic (Fig. 4). The folian process could add to the anterior crus, making the sigmoid process a compound structure (van der Klaauw, 1931). A third putative homologue to the sigmoid process in cetaceans is the tubular portion of the bulla in mesonychids and other ungulates.

Ridewood (1922) showed that there is very compelling topographic resemblance of the sigmoid process of subadult whales to the anterior crus of the tympanic ring of cetacean embryos. Based on this embryological evidence, we interpret that the sigmoid process is homologous to the anterior crus of the tympanic ring for this analysis. It cannot be ruled out that the folian process of non-cetaceans was incorporated into the sigmoid process of cetaceans, pending a further study of the embryonic development of this character. Lacking embryonic evidence, we consider this putative homology of the sigmoid process and the tubular part of the bulla as the weakest of all three alternatives (see later discussion). This assumption on the sigmoid process underlies several characters recognized in the general area of the sigmoid process of the tympanic and the external auditory meatus.

33. Sigmoid process

Character states (on the assumption that the sigmoid process is homologous with the anterior crus of the tympanic ring): 0 = undifferentiated from the rest of the ectotympanic ring or bulla (*Heptodon*, *Sinonyx*, *Dissacus*); 1 = differentiated as a thin splinter-like plate (*Diacodexis*, *Pakicetus*, *Ambulocetus*, *Rodhocetus*, *Indocetus*, and maybe also the Habib Rahi protocetid); 2 = broad and flaring (all basilosaurids, mysticetes, and odontocetes).

34. Articulation of sigmoid process with the squamosal

Character states: 0 = contacting (or in juxtaposition with) the postglenoid process of the squamosal (*Heptodon*, assuming the homology of the anterior crus of the tympanic ring and the sigmoid process; *Diacodexis*; *Pakicetus*, *Ambulocetus*, *Gaviacetus*, and *Indocetus*); 1 = contacting a broad transverse groove on the squamosal (basilosaurids); 2 = no contact with the squamosal (odontocetes and mysticetes); ? = non-applicable or unknown (*Sinonyx*, *Hapalodectes*).

The sigmoid process contacts the squamosal directly in *Pakicetus*. In other archaeocetes, a transverse groove is present medial to the postglenoid process and receives the sigmoid process of the tympanic. The contact of the tympanic ring or bulla with the squamosal is a primitive condition of eutherians. By outgroup comparison, articulation of the sigmoid process (a part of the ectotympanic) and the squamosal is interpreted to be primitive for cetaceans. The contact of the sigmoid process with the squamosal is lost in odontocetes (Kasuya, 1973) and mysticetes (Geisler and Luo, 1996).

35. Orientation of the sigmoid process

Character states: 0 = pointing posteriorly (*Diacodexis*, *Pakicetus*, *Rodhocetus*, and *Indocetus*); 1 = pointing laterally and dorsally (all basilosaurids, mysticetes, and odontocetes); ? = non-applicable (all ungulates except *Diacodexis*) or unknown (*Ambulocetus*).

36. Ventral floor of the external auditory meatus

Character states: 0 = absent (*Heptodon*, *Diacodexis*; all whales including *Pakicetus*); 1 = present (*Sinonyx*, *Mesonyx*, *Dissacus*); ? = unknown (*Hapalodectes* and *Ambulocetus*).

The ectotympanic is a simple ring, and does not extend laterally to form the ventral part of the external auditory meatus in whales. This condition is also a characteristic of the earliest perissodactyls (e.g., *Heptodon*, Radinsky, 1965) and the earliest artiodactyls (e.g., *Diacodexis*, Russell et al., 1983). In contrast, a lateral extrabullar part of the ectotympanic forms much of the ventral floor in *Sinonyx* and *Mesonyx*, and probably also *Dissacus*. The condition in mesonychids is designated as character state 1.

37. External auditory meatus on the squamosal

Character states: 0 = short or absent (outgroup ungulates *Heptodon*, *Diacodexis*, and *Hapalodectes*; odontocetes except *Xenorophus*); 1 = deep and narrow groove (*Sinonyx*, *Mesonyx*; *Pakicetus*, *Gaviacetus*, *Rodhocetus*, *Indocetus*; *Xenorophus*; mysticetes); 2 = long, shallow, and broad groove (all basilosaurids).

In most early eutherians of small size, the external auditory meatus is a shallow embayment on the squamosal just posterior to the postglenoid process (see *Hapalodectes*, Fig. 5). This is designated as character state "0" because it is a widespread condition of ungulates, such as perissodactyls (*Heptodon*), the early artiodactyl *Diacodexis*, and other archaic ungulates (*Meniscotherium* and *Phenacodus*). In contrast, an elongate and deep groove is present in both mesonychids (*Sinonyx*, *Mesonyx*, and *Dissacus*) and cetaceans (*Pakicetus*, *Gaviacetus*, *Rodhocetus*, and basilosaurids; Van Valen, 1966). Among extant cetaceans, mysticetes have retained this primitive condition, while odontocetes have lost the groove-like external auditory meatus.

TOPOGRAPHIC FEATURES OF THE BULLA

38. Tympanic annulus

The tympanic annulus is for suspension of the tympanic membrane. Character states: 0 = present (*Heptodon*; mesonychians, Geisler and Luo, 1998; *Pakicetus* and *Ichthyolestes*, Luo, 1998); 1 = absent (protocetids as represented by *Georgiacetus*, Hulbert et al, 1998; all basilosaurids, odontocetes and mysticetes); ? = unknown (*Ambulocetus*, *Gaviacetus*, and *Indocetus*).

39. Middle conical process

See Luo (1998) for discussion of homology. Character states: 0 = absent (*Heptodon*; mesonychids as represented by AMNH 12643 *Mesonyx obtusidens,* see Geisler and Luo, 1998; *Pakicetus*, Luo, 1998); 1 = present (*Indocetus*, *Georgiacetus*, and all basilosaurids; odontocetes; mysticetes); ? = unknown (*Hapalodectes*, *Gaviacetus*).

40. Lateral furrow of the tympanic bulla (Figs. 4 and 15: lf*)*

See Kasuya (1973) and de Muizon (1987) for discussion. Character states: 0 = absent (*Mesonyx*, *Sinonyx*, *Pakicetus*); 1 = present (all post-*Pakicetus* archaeocetes, including *Ambulocetus* and *Indocetus; odontocetes; mysticetes*); ? = non-applicable (ungulates other than mesonychids).

The lateral furrow is a groove that delimits the anterior border of the sigmoid process from the bullar body in some (but not all) cetaceans. It is absent in *Pakicetus,* but present in *Gaviacetus, Indocetus*, and all basilosaurids (Fig. 21: lf; Kellogg, 1936), present and well developed in all odontocetes (Kasuya, 1973; Pilleri et al., 1987; de Muizon, 1987), and many but not all mysticetes (*Parietobalaena*, CMM 935; *Pelocetus*, Kellogg, 1965; *Eubalaena*, AMNH 42752).

41. Median furrow of tympanic bulla (Figs. 11, 15: mf*)*

This character is conceived following Kasuya (1973). It is the ventral groove of de Muizon (1987). Character states: 0 = absent (mesonychids, *Pakicetus*, all mysticetes); 1 = present and oblique (*Gaviacetus*, *Indocetus*, and *Rodhocetus*); 2 = present as a broad embayment on the posterior part of the bulla (basilosaurids); 3 = present for more than half the length of the bulla (odontocetes); ? = non-applicable (ungulates without complete bulla).

The median (ventral) furrow of the tympanic bulla is present in all basilosaurids (Pompeckj, 1922; Kellogg, 1936; Fig. 21). It is visible but less developed, and more obliquely oriented in most protocetids, such as *Gaviacetus*; (Figs. 13, 14) and *Indocetus* (Figs. 15, 16; character state 1). It is absent in *Pakicetus* (Figs. 11, 12). In most basilosaurids examined here, the furrow is restricted to the posterior part of the ventral bullar surface and shaped like a broad embayment that opens up posteriorly (character state 2). The groove is best developed in odontocetes, in which it is very prominent and extending more than the half length of the bulla (character state 3; Kasuya, 1973; de Muizon, 1987; Fordyce, 1994). The median furrow is absent in mesonychids and other archaic ungulates (*Sinonyx*; Fig. 8), as well as in mysticetes (*Parietobalaena*, CMM 935; *Pelocetus*, Kellogg, 1965; *Eubalaena*, AMNH 42752, Geisler and Luo, 1996).

42. Interprominential notch

The interprominential notch forms a trough for the tympanohyal (see Luo, 1998, for discussion of homology). Character states: 0 = absent (non-cetacean ungulates except extant *Ovis;* mysticetes); 1 = present (all cetaceans). *Ovis* resembles cetaceans in this feature (Luo, 1998).

43. Medial posterior prominence

Character is conceived in the sense of Kasuya (1973; see also Pilleri et al., 1987; this is the medial lobe of de Muizon, 1987). Character states: 0 = absent (mesonychids and other ungulates; mysticetes); 1 = present and inflated (all other whales).

The medial posterior prominence on the ventral surface is formed by the extension of dense bone that forms the bulging involucrum. It is accentuated by the median furrow and the interprominential notch (Kasuya, 1973; Pilleri et al., 1987). The prominence is absent in non-cetacean ungulates in which the bullae are uniformly spherical (e.g., *Sinonyx*, Fig. 8) if the bullae are fully formed at all. The interprominential notch and the median prominence are present in *Pakicetus* (Figs. 10, 11: *mp*), which is coded character state 1. The prominence is more inflated in all other archaeocetes (including *Gaviacetus* and basilosaurids; Figs. 11 and 15) and odontocetes (Kasuya, 1973; de Muizon, 1994). This feature is designated as character state 2. In contrast, both the interprominential notch and the medial prominence are absent in all archaic mysticetes of the "cetotheriid grade" and extant mysticetes (*Parietobalaena*, CMM 935; *Pelocetus*, Kellogg, 1965; *Eubalaena*, AMNH 42752; Geisler and Luo, 1996). The mysticete condition is coded as character state 0.

44. Ventral tympanic keel

Character states: 0 = absent (all ungulates; non-mysticete cetaceans); 1 = present (mysticetes).

The ventral tympanic keel is a round and low ridge on the bulla. This keel is positioned in the midline of the bulla and extends almost the entire length of the bulla. So far, it is only found in mysticetes (character state 1) but absent in all non-mysticete cetaceans (character state 0).

45. Tympanic involucrum

Character states are related to the pachyosteosclerosis of the medial bullar rim: 0 = absent (all non-cetacean ungulates); 1 = present and extending more than half length of the bulla (odontocetes); 2 = present and extending the full length of the bulla (*Pakicetus* and all basilosaurids; all mysticetes).

The involucrum is the pachyostotic part of the medial rim of the bulla. As a result of this pachyostosis, the medial rim of the bulla becomes involuted and the ventral surface of the bulla is inflated. In ungulates, such as *Sinonyx* (Zhou et al., 1995), the broken medial rim of the bulla is thin. This condition is common in other ungulates (*Ovis*, Fig. 4), and other eutherians (van der Klaauw, 1931). The lack of thickening in ungulates is designated as the primitive condition (character state 0). In odontocetes, the thickening (pachyostosis) of the involucrum is present only in the posterior part of the rim. This condition is designated as character state 1. Unlike the condition of odontocetes, thickening of the bullar rim (pachyostosis) has spread to the anterior apex of the bulla in archaeocetes (including *Pakicetus*) and mysticetes (character state 2).

46. External opening of the eustachian tube

Character states: 0 = thin and straight edge of the bulla (mesonychids, and odontocetes); 1 = thickened and involuted (recoiled) edge of the bulla (*Pakicetus*, all protocetids, basilosaurids; mysticetes).

The eustachian tube opens at the anterior end of the bulla. The bullar rim for the eustachian tube displays two character states. In odontocetes, the more anterior part of the bulla is thinner and forms a rather sharp edge toward the eustachian opening of the bulla. In contrast, the bullar rim for the eustachian opening is involuted, rounded and thick in *Gaviacetus* (Fig. 14), basilosaurids (Fig. 21), and mysticetes (Fig. 25: *et*). Because the eustachian opening in mesonychids has a thin edge, we designated the condition in odontocetes as "0" based on its similarity to outgroup ungulates. The rounded and thick edge of the eustachian opening in archaeocetes and mysticetes is regarded as character state 1.

Phylogenetic distribution of the characters of the bullar rim of the eustachian tube among cetaceans offers a very interesting contrast to the pattern of character transformation through development in the extant ungulate *Ovis*. The anterior bullar rim of the eustachian tube opening is sharp and straight in the new-born fetus of *Ovis* (CMNH G997: Fig. 4A), but involuted and recoiled in the bullae of adult *Ovis*. In comparison, involuted and recoiled rims for the eustachian tube opening are primitive characteristics of pakicetids, protocetids, basilosaurids, mysticetes, whereas the sharp and straight rim for the eustachian opening is a derived condition of odontocetes. Adult odontocetes (with sharp rim) have the embryonic condition of their close phylogenetic relative artiodactyls (sharp rim in the fetus, involuted in the adult). Therefore, the odontocete condition (sharp rim in adult) can be regarded as a neotenic feature. The thin edge of the eustachian tube opening contributes to the more pointed anterior end in the odontocete bulla than those of non-odontocete cetaceans. (Pitteri et al., 1986: fig. 14).

47. Position of the external opening of the eustachian tube

Character states: 0 = in anterior part of the tympanic bulla (*Sinonyx*, *Mesonyx*; *Pakicetus*, and all basilosaurids; mysticetes; odontocetes); 1 = on medial side of the bulla (*Gaviacetus*, *Rodhocetus*, *Indocetus*, *Georgiacetus*, Hulbert et al., 1998); ? = non-applicable (*Heptodon*, *Hapalodectes*).

48. Position of pharyngeal opening of eustachian tube

Character states: 0 = into the nasopharynx (ungulates; *Pakicetus*, *Ambulocetus*, *Gaviacetus*, *Indocetus*); 1 = into the anterior pterygoid sinus cavity (all basilosaurids; mysticetes; odontocetes).

49. Size of tympanic bulla

Size is defined as width of the tympanic bulla relative to width of the skull at the level of the glenoid condyle. Character states: 0 = ca. 10-15% (*Diacodexis*; *Sinonyx*; *Pakicetus*); 1 = larger than 20% (or ca. 22%; *Ambulocetus*, *Gaviacetus*, *Rodhocetus*, *Indocetus*, Habib Rahi protocetid; all basilosaurids); 2 = ca. 5% (extant odontocetes; mysticetes); ? = non-applicable (*Heptodon*; *Hapalodectes*).

VASCULAR FEATURES

50. Promontorial course for the internal carotid artery

Character states: 0 = present (outgroup ungulates, *Diacodexis*; *Hapalodectes*, *Dissacus*, *Mesonyx*, see description by Geisler and Luo, 1998); 1 = absent (*Heptodon*, all whales).

The internal carotid artery is a major vessel supplying the cerebral circulation in mammals. In many orders of eutherian mammals, this artery has a transpromontorial course through the tympanic cavity and has a sulcus on the promontorium (Wible, 1986). This is generally accepted as the primitive condition of eutherians (Wible, 1983, 1986; Novacek, 1986, 1993). The absence of a promontory groove for the internal carotid artery is therefore considered to be an apomorphy for eutherians as a whole. Among ungulate groups, the transpromontorial sulcus for the internal carotid is well developed in *Protungulatum* (MacIntyre, 1972; Cifelli, 1982; Luo, 1989), *Diacodexis* (Russell et al., 1983), other early artiodactyls (Coombs and Coombs, 1982), and *Hapalodectes* (Fig. 5, also see Ting and Li, 1987). A promontorial sulcus is partially preserved on the promontorium of *Dissacus* (UM 75501; Fig. 6: *pica*) and in *Mesonyx* (Geisler and Luo, 1998), and is thus interpreted here to be characteristic of mesonychians as a group. The presence of the promontorial sulcus is regarded as character state "0."

In extant cetaceans, the internal carotid artery and its derivative stapedial artery are involuted early in embryogenesis (Walmsley, 1938; Vogl and Fisher, 1981, 1982; Wible, 1984). The branches of the stapedial artery are completely lost in the adult. The internal carotid is also degenerated to such a degree that it no long supplies blood to the cranial cavity in the adult. The areas supplied by these vessels have been either taken over by external carotid derivatives or by the spinal rete mirabile (Geisler and Luo, 1998).

The archaic whales such as *Pakicetus* and the basilosaurids have no arterial sulci on the promontorium. Either the internal carotid artery and its derivative stapedial artery were already lost in these earliest whales just as in extant whales; or the degenerated vessels were suspended by soft tissue without contacting the surface of the promontorium. The absence of the promontorial sulcus for the internal carotid artery is considered to be character state 1.

51. Medial promontory groove on the pars cochlearis

Character states: 0 = present (all ungulates); 1 = absent (basilosaurids; derived odontocetes such as delphinoids; all extant mysticete families); 2 = present and confluent with the middle pterygoid or basioccipital sinus (Cross protocetid; *Xenorophus*, squalodontoid odontocetes; cetotheriid mysticetes).

The sulcus on the medial side of the pars cochlearis is for the inferior petrosal sinus (or vein; Wible, 1987). The medial promontory groove is present in *Protungulatum* (MacIntyre, 1972; Luo, 1989), *Hyopsodus* (Cifelli, 1982), *Meniscotherium* (Gazin, 1965), *Merycoidodon* (Whitmore, 1953), *Dissacus* (UM 75501: Figs. 6 and 7), and *Mesonyx* (Geisler and Luo, 1998). Its wide distribution among eutherian ungulates suggests that the vessel is primitive for these ungulates, probably also for eutherians as a whole (Wible, 1983). The ungulate condition is character state 0.

The condition in protocetids is not sufficiently known, but one protocetid (Geisler and Luo, 1998) has a broad inferior petrosal sinus groove as is the case in noncetacean ungulates. In contrast, in basilosaurids, the medial aspect of the pars cochlearis forms a rather sharp edge (Figs. 3C and 14). There is no vascular groove along the medial edge of the pars cochlearis. This character state is designated state 1.

In mysticetes and odontocetes, the pterygoid sinus is enlarged and posteriorly expanded around the medial side of the entire petrotympanic complex. This large sinus probably incorporated the inferior petrosal sinus. The confluent inferior petrosal sinus and the pterygoid sinus together produced a shallow groove on the medial side of the pars cochlearis in almost all primitive mysticetes (Geisler and Luo, 1996), and many primitive odontocetes, such as squalodontoids (Luo and Eastman, 1995), *Xenorophus*, *Platanista*, and *Physeter* (USNM 550876; Luo and Marsh, 1996). This is designated as character state 2.

The medial face the pars cochlearis in many extant odontocetes is rounded and smooth, without any vascular groove despite the fact that the middle pterygoid sinus is best developed in odontocetes. This condition without a bony vascular groove in the more derived odontocetes is considered to be character state 0, which could be either a retention of the primitive condition, or a secondary reversal from basal odontocetes with the groove.

52. Jugular or posterior lacerate foramen

Character states: 0 = circular foramen ventrally exposed (non-cetacean ungulates); 1 = circular foramen concealed or partially concealed by the tympanic bulla (*Pakicetus*, *Ambulocetus*, *Gaviacetus*, *Indocetus*, and *Georgiacetus*); 2 = jugular foramen or notch confluent with the basicapsular fissure (basilosaurids; mysticetes; odontocetes).

The jugular foramen is the exit of the internal jugular vein and three cranial nerves (IX, X and XI). A foramen encircled by the exoccipital, the petrosal, and the basioccipital is typical of all mammals. A ventrally exposed jugular foramen is primitive for all ungulates (state 0). In *Pakicetus*, *Rodhocetus, Gaviacetus*, and other protocetids, the jugular foramen is present, but partially concealed by the enlarged bulla. This character state is designated as "1."

In adult specimens of basilosaurids (but not in subadults), the pterygoid sinus expands posteriorly into the exoccipital region. As a result, the previously separate jugular foramen and basicapsular fissure become confluent with each other, as well as with the pterygoid sinus. The entire medial sides of the tympanic and petrosal are separated from the occipitals by a wide space confluent with the previously-separate basicapsular fissure, jugular foramen and pterygoid sinus. The condition of adult skulls of basilosaurids is designated as "2." Similar ontogenetic modification of the jugular foramen is observed in odontocetes (Pilleri et al., 1986).

53. Postglenoid foramen

Character states: 0 = present (*Heptodon*; *Diacodexis*; *Hapalodectes*); 1 = absent (*Sinonyx*, *Mesonyx*, *Dissacus*; all whales).

The postglenoid foramen is a primitive feature of many basal therian mammals (Archer, 1976; MacPhee, 1981; Novacek, 1986; Wible, 1990). It carries the capsuloparietal emissary vein (variously referred to as the "postglenoid vein" or the petrosquamous vein, Butler, 1967). The presence of the postglenoid foramen is primitive for ungulates, and therefore is regarded as character state 0 (Gazin, 1965; Radinsky, 1965; Coombs and Coombs, 1982; McKenna et al., 1989). The postglenoid foramen within the squamosal is present in *Hapalodectes* (Ting and Li, 1987) but absent in all mesonychids including *Sinonyx* (Zhou et al., 1995) and many archaeocetes (Geisler and Luo, 1998). Absence is a more derived character state 1.

54. Peripetrous vascular groove on the lateral surface of the anterior process (Figs. 1 and 2: vg *and* vf*)*

This is a vascular groove or foramen lying between the squamosal and the petrosal (Geisler and Luo, 1998). Character states: 0 = present (all mesonychids, all archaeocetes including *Pakicetus*, *Ambulocetus*, and the Cross protocetid, but unknown in other protocetids); 1 = absent (mysticetes; *Xenorophus*, delphinoids, and questionable in squalodontoids).

In mesonychids and archaeocetes, there is a transverse groove between the ventrolateral tuberosity and the anterior process on the lateral aspect of the tegmen tympani. The tympanic aperture of this vascular channel is anterior to the ventrolateral tuberosity (Geisler and Luo, 1998). It is most likely to be a vascular channel. Geisler and Luo (1998) interpret that this vascular groove is for the ramus superior of the stapedial artery in mesonychids.

This groove is present in all archaeocetes for which the petrosal could be examined, including: *Basilosaurus* (UM 97507), *Saghacetus* and *Dorudon* (Figs. 2, 6, 7, 14). This groove was illustrated but not identified by Kellogg (1936). The ventral (tympanic) aperture of this vascular channel (but not the channel itself) was identified as the "fossa epitubaria" in *Basilosaurus cetoides* (Kellogg, 1936: fig. 5). It is present in a new (and unnamed) protocetid taxon (Geisler et al., 1996; Geisler and Luo, 1998). Among ungulates, this groove is present in *Mesonyx* (Geisler and Luo, 1998) and *Dissacus* (UM 75501). However, it is absent in taxa with an uninflated tegmen tympani, such as arctocyonids (MacIntyre, 1972; Luo, 1989) and *Heptodon* (text-fig. 2 of Cifelli, 1982), and absent in most other archaic ungulates with a moderately developed tegmen tympani, except *Meniscotherium* (text-fig. 2 in Cifelli, 1982).

Such a vascular groove is absent in all mysticetes (Geisler and Luo, 1996). The majority of odontocetes lack this feature (including *Physeter*, *Mesoplodon*, and *Tursiops*). Several early fossil odontocetes have an anteroexternal sulcus on the dorsal aspect of the petrosal (Fordyce, 1983; 1994; Luo and Eastman, 1995). It has been interpreted as an arterial sulcus for some taxon ("path of a loop of the middle meningeal artery"; Fordyce, 1994: 161). This sulcus is variable in shape from a relatively straight groove (e.g., *Squalodon*, Luo and Eastman, 1995) to a U-shaped loop (rhabdosteids, Fordyce, 1983). It differs from the peripetrous sulcus of mesonychids and basilosaurids in that it does not extend to the tympanic side of the tegmen tympani. We consider this peripetrous sulcus to be absent in odontocetes (character state 0).

SINUS FEATURES

Although cranial pneumatic sinuses are also known from many terrestrial mammals (Paulli, 1900), they are most extensively developed in cetaceans (Fraser and Purves, 1960). The basicranial sinus of extant whales is a fibrovenous plexus interwoven with spongy air sacs. It extensively anastomoses with the endocranial venous system and with the basicranial vasculature (Fraser and Purves, 1960). As the vascular and pneumatic sinus develops, it excavates large spaces in the basicranial bones known as sinus cavities, and forms large gaps and fissures between and within bones.

The osteological structures related to the vascular (and pneumatic) sinuses in fossil mysticetes and odontocetes can provide reliable information on the distribution of the sinuses in their basicrania (Kellogg, 1936; Gingerich et al., 1983; Barnes, 1984). Because archaeocetes have no living representative, identification of a vascular sinus (or air sac) in their skulls is more difficult than in mysticetes and odontocetes. Many skeletal features of archaeocetes, (especially the protocetid archaeocetes) have intermediate conditions between primitive terrestrial mammals and derived extant cetaceans. For these reasons, the anatomical interpretation of these transitional character states in archaeocetes can be ambiguous.

To avoid ambiguity in reconstructing sinuses in archaeocetes, several explicit morphological criteria associated with sinuses in extant cetaceans are necessary to establish the presence of vascular sinuses in extinct archaeocetes:

(1) Existence of open spaces or cavities.

(2) Presence of channels between the putative sinus space or cavity and well established sources of vascular supplies. For the spaces or gaps to be interpreted as sinuses, they must be connected to vascular channels. The vascular plexus is an integral part of the sinus and the vascular supply to the spongy tissue of the sinus is crucial for its function in cetaceans. The presence of a space or a gap in the basicranium does not necessarily indicate the presence of a sinus, if it is not connected to any known vascular structure.

(3) The putative space of a cavity could not be otherwise attributed to non-sinus structures in non-cetacean mammals. The spaces and gaps in the basicranium are interpreted to be sinus structures only if they could not be otherwise correlated to the typical (and non-sinus) structures including the soft tissue features of terrestrial mammals. Presence of a small space (e.g., epitympanic recess) or a gap (e.g., piriform fenestra) does not necessarily indicate that it contained a vascular sinus—for these are common to eutherian mammal skulls with little or no development the vascular and pneumatic sinuses.

(4) For the spaces and gaps to be interpreted as sinuses, they must have a smooth periosteal surface. A smooth periosteal surface is typical of the sinus cavity that contains air sacs in extant cetaceans.

Following these morphological criteria, several sinus features can be recognized in the taxa surveyed here.

55. Anterior pterygoid sinus cavity

Character states: 0 = no ventrally visible sinus cavity anterior to the bulla (all ungulates; *Pakicetus*, *Gaviacetus*, *Indocetus*, and probably all protocetids); 1 = present (all basilosaurids; mysticetes; odontocetes).

As characterized by Fraser and Purves (1960) for odontocetes, the cavity of the anterior pterygoid sinus is bounded by the medial pterygoid lamina, the lateral lamina of the pterygoid, and the anterior falciform process of the squamosal. Its roof is formed mostly by the superior lamina of the pterygoid in mysticetes, or by the superior pterygoid lamina plus contributions from the alisphenoid and basisphenoid in odontocetes (Fraser and Purves, 1960).

The anterior pterygoid sinus is not developed at all in any ungulates (*Hapalodectes*, Fig. 5, and *Dissacus*, Fig. 6). The lack of the anterior pterygoid sinus cavity in ungulates is considered to be character state 0.

In *Pakicetus*, a small open space is present anterior to the bulla. This space has no connection to any vascular channel that may have supported a sinus (against criterion 2). Moreover, the space is in the normal pathway of the eustachian tube and is confluent with the pharynx (against criterion 3). Given these considerations, it is more parsimonious to interpret it as the pathway of the eustachian tube (Figs. 9 and 10: *et*). Thus the absence of the anterior pterygoid sinus cavity in *Pakicetus* is regarded as character state 0.

In *Gaviacetus*, a similar space is present between the bulla and the basioccipital anteromedial to the bulla. This space is more easily interpreted as the groove for the eustachian tube (Figs. 13, 14: *et*; failing criterion 3) and does not seem to have a connection to any vascular channel (failing criterion 2). Even though this space has a smooth periosteal bone surface (criterion 4), we interpret *Gaviacetus* as lacking an anterior pterygoid sinus (character state 0).

Basilosaurids have an anterior pterygoid sinus (Figs. 17-18, 22-23). The sinus is represented by a large cavity between the lateral lamina and the medial lamina of the pterygoid (criterion 1). This cavity is confluent with the basicapsular fissure and thus could have connected to the endocranial vascular rete or the meningeal sinus in the braincase (criterion 2). The pterygoid also forms a roof of this cavity, partially excluding it from the brain cavity (criterion 3). The entire cavity has a periosteal surface typical of the air sac cavity in extant cetaceans (criterion 4). Geisler and Luo (1998) suggested that development of the pterygoid cavity may be a part of a broader change of the vascular pattern involving the enlargement of the endocranial caudal rete mirabile in basilosaurids.

All mysticetes and odontocetes have a fully developed anterior pterygoid sinus (Fraser and Purves, 1960). Basilosaurids, mysticetes, and odontocetes are assigned character state 1.

56. Presence of a sinus under the basal or falcate process of the basioccipital

Character states: 0 = absent (all ungulates; *Pakicetus*); 1 = present (present in most protocetids and *Gaviacetus*, as far as known, and basilosaurids; mysticetes; odontocetes); ? = unknown (*Ambulocetus*). In extant cetaceans, the basioccipital peribullar sinus is the posterior extension of the pterygoid sinus that separates the involucrum (medial rim) of the bulla and the petrosal from the basioccipital (character state 1). In ungulates that lack the pterygoid sinus, the medial rim of the bulla directly contacts the basioccipital, and there is no space between the two structures. The absence of the basioccipital sinus is character state 0.

In *Pakicetus*, medial to the bulla is a space that separates the bulla from the incipient bullar process of the basioccipital. This space between the involucrum and the basicranium is very small and narrow (ambiguous with regard to criterion 1). This space does not have good vascular connection to a venous sinus inside the braincase because the basicapsular fissure is closed between the promontorium and basioccipital. However it would be possible for this space to be supplied by an anastomosis from the tributary of the internal jugular vein near the jugular foramen (ambiguous with regard to criterion 2). The bone around this gap has a smooth periosteal surface (satisfying criterion 3). Because of the limited space and lack of a spacious connection to blood supply, the basioccipital sinus, at the very best, was probably poorly developed in *Pakicetus*. The condition in *Gaviacetus* appears to be similar to *Georgiacetus* (Hulbert et. al., 1998). We tentatively designate both *Georgiacetus* and *Gaviacetus* as character state 1.

In basilosaurids, mysticetes and odontocetes, the basioccipital sinus is fully confluent with the anterior pterygoid sinus cavity. The sinus forms a large space (basicapsular fissure) between the bulla and the basioccipital. This condition is coded state 2.

57. Posterior pterygoid sinus in the exoccipital region (Figs. 22, 23, 24: eos*)*

Character states: 0 = absent (all ungulates; *Pakicetus*); 1= incipient or present but not large enough to separate the bulla from the bullar process of the exoccipital (*Gaviacetus*, *Rodhocetus*, *Indocetus*); 2 = fully developed so that the bulla is separate from the exoccipital (basilosaurids; mysticetes; odontocetes): ? unknown in *Ambulocetus*.

The posterior pterygoid sinus is entirely absent in *Sinonyx* (Zhou et al., 1995) and *Dissacus* (UM 75501). It was not observed in *Diacodexis* (Russell et al., 1983) and other early artiodactyls (Coombs and Coombs, 1982). Absence of the posterior pterygoid sinus in the exoccipital region is designated as state 0.

In the type specimen of *Pakicetus*, the right bulla is tightly articulated with a prominent bullar process on the exoccipital (Gingerich et al., 1983). On the left tympanic cavity, which is exposed and without the bulla, there is no visible development of an open cavity (Figs. 9 and 10). *Pakicetus* does not have a posterior pterygoid sinus, as its exoccipital lacks the necessary space for the sinus (against criterion 1).

As in *Pakicetus*, a large bullar process of the exoccipital is present and articulating with the bulla in *Gaviacetus* (Fig. 13: *eop*). But different from *Pakicetus*, there is a hollow cavity outside the bulla near the bulla-exoccipital articulation and the stylomastoid foramen. This small hollow cavity is visible posterior to the right side of the skull (not illustrated). On the left side where the bulla is detached, it appears that this small hollow space has a channel to the jugular foramen through a small channel anterior (and deep) to the bullar process of the exoccipital, thereby connecting to the internal jugular vein, a known and conservative vascular source in the basicranium. The space is not large enough to separate the bulla from the exoccipital process, but nevertheless qualifies for the criteria of a peribullar sinus (satisfying criteria 1, 2, 3). We interpret that *Gaviacetus* had an incipient exoccipital sinus. *Rodhocetus* appears to have the same condition, although its bulla is slightly crushed. With these justifications and caveats, we designate the small and incomplete sinus in *Gaviacetus* and *Rodhocetus* as "incipient" (character state 1).

The posterior pterygoid sinus separates the tympanic bulla from the exoccipital bone in odontocetes (Fig. 24) and mysticetes (Fig. 2). In basilosaurids, the bulla is articulated with the exoccipital process in subadults (Fig. 21) but this contact is lost in adults as the posterior pterygoid sinus (exoccipital sinus) becomes better developed (see the proportional difference of *eos* in Figs. 18, 22, 23). The condition of mysticetes, odontocetes and adult basilosaurids is designated as character state 2.

58. Middle sinus lateral to the petrotympanic complex

Character states: 0 = absent (all non-odontocetes); 1 = present (most extant odontocetes only).

OTHER BASICRANIAL FEATURES

59. Medial lamina and lateral lamina of the pterygoid

Character states are related to the anterior pterygoid sinus cavity: 0 = no differentiation of separate laminae anterior to the bulla (ungulates; *Ambulocetus* and protocetids including *Gaviacetus* and *Indocetus*); 1 = lateral and medial laminae of the pterygoid differentiated anterior to the bulla (all basilosaurids; mysticetes; odontocetes).

60. Secondary internal foramen for the mandibular branch of the trigeminal nerve

Character states: 0 = absent (ungulates; protocetids except *Indocetus*); 1 = present (basilosaurids; mysticetes; odontocetes); ? = unknown (*Ambulocetus* and *Indocetus*).

In terrestrial mammals, the mandibular branch of the trigeminal nerve exits directly from the cranial cavity via the foramen ovale (= "foramen pseudovale" of Hulbert et al., 1998; also see previous discussion on the variability of basicranial characters in basilosaurids). This is considered to be the primitive characteristic of eutherians (state 0). In various groups of extant cetaceans, the pterygoid, alisphenoid and squamosal form secondary internal bony laminae to shield the anterior pterygoid sinus cavity from the braincase. These internal laminae form an internal foramen through which the mandibular nerve enters the pterygoid sinus cavity. The nerve first enters the anterior pterygoid sinus cavity via the secondary foramen from the braincase, then it exits the anterior pterygoid sinus cavity via the foramen ovale between the squamosal and alisphenoid. This latter condition is present in all adult basilosaurids (Fig. 17B: iof) and extant cetaceans (state 2; Fraser and Purves, 1960; Fordyce, 1994; Geisler, pers. comm.). Presence of this foramen in adult basilosaurids is designated as derived character state 1, for basilosaurids as a group.

61. Basal process of the basioccipital (Figs. 9-10, 13: bp*)*

Character states: 0 = absent, the flat lateral border of the basioccipital serving as the bullar process (ungulates); 1 = incipient, as the basioccipital eminence (*Pakicetus*); 2 = developed into the basal or falcate process (most post-*Pakicetus* cetaceans including *Ambulocetus* and *Indocetus*).

In terrestrial mammals with a fully developed bulla, the medial rim of the bulla articulates with the lateral edge of the basioccipital, an area called the tympanic process of the basioccipital (MacPhee, 1981). Full contact between the basioccipital and the bulla is a primitive condition (state 0). In *Pakicetus*,

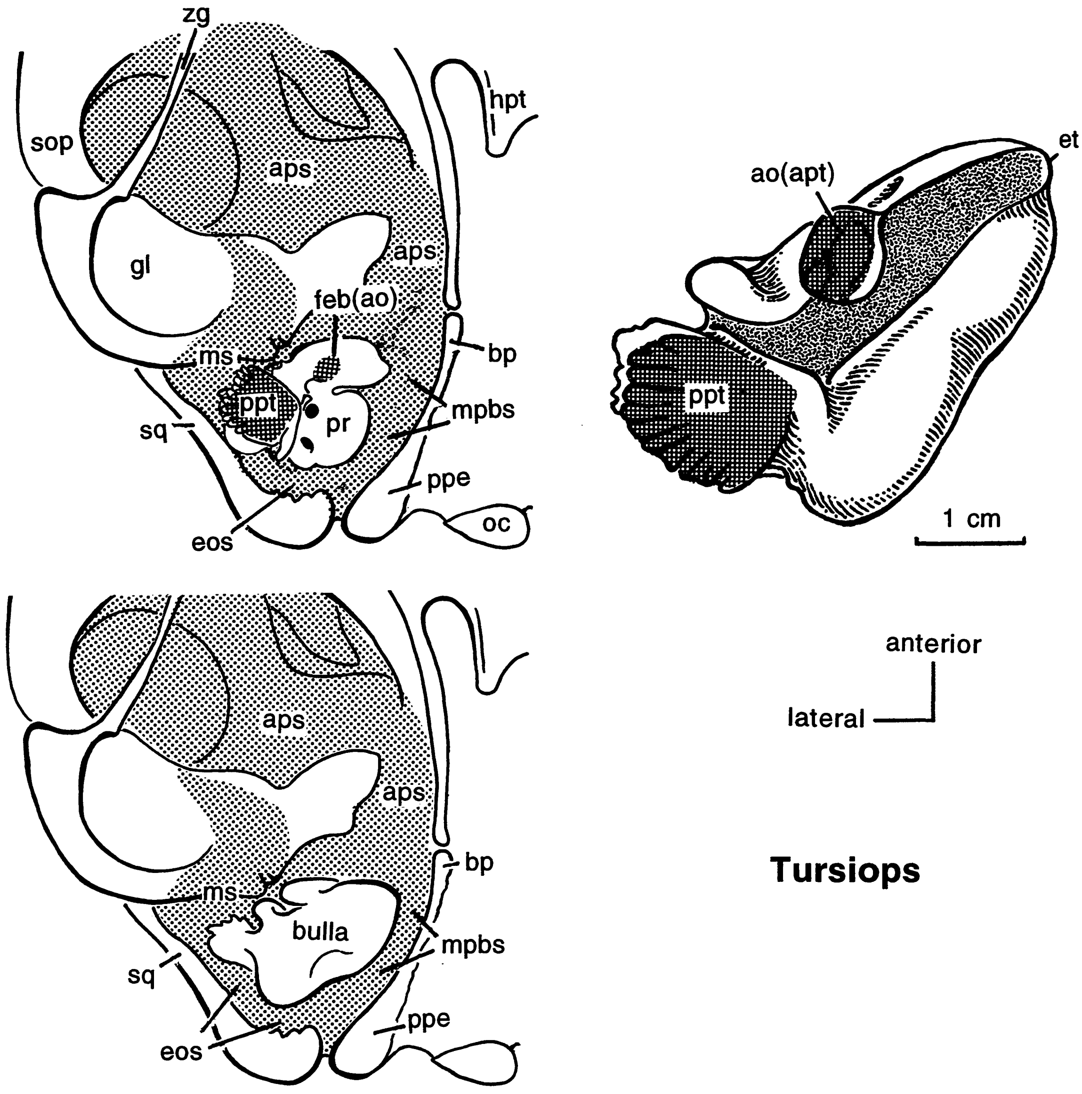


FIGURE 24. Articulation of the petrosal and tympanic in the basicranium of odontocetes, as represented by extant *Tursiops truncatus* (modified from Fraser and Purves, 1960; Oelschläger, 1990). Abbreviations: *ao(apt)*, accessory ossicle (homologous to a part of the anterior process of the tympanic; see Luo, 1998, for discussion of homology); *aps*, pterygoid sinus (anterior portion); *bp*, basal or falcate process of basioccipital; *eos*, posterior pterygoid sinus (exoccipital portion); *et*, eustachian tube; *feb(ao)*, fovea epitubaria on the petrosal to receive accessory ossicle of the ectotympanic; *gl*, glenoid fossa in squamosal; *hpt*, hamulus of pterygoid; *mpbs*, medial peribullar sinus; *ms*, medial ptergygoid sinus; *oc*, occipital condyle; *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of petrosal; *pr*, promontorium; *sop*, supraorbital process; *sq*, squamosal; *zg*, zygoma.

the basioccipital has a longitudinal ridge, which occupies the same position as the basal or falcate process of later cetaceans. Like the basal process, the basioccipital ridge is separated from the bullar rim by a narrow gap. The basioccipital ridge is interpreted as an incipient basal process, and designated as state 1 (Figs. 9, 10: *bp*). In all other cetaceans, the basal process of the basioccipital forms a high crest, separated from the medial bulla rim by a gap. This has been termed the falcate process of the basioccipital. In mysticetes, the basioccipital and the bulla may be linked by dense connective tissue (Fraser and Purves, 1960), but in odontocetes the two are disconnected and separated widely by the basioccipital sinus. The fully developed basal process in protocetids (except *Pakicetus*), basilosaurids and extant whales is designated as character state 2 (e.g., *Gaviacetus*, Fig. 13: *bp*).

62. Paroccipital process of exoccipital

Character states: 0 = short and directed posterolaterally (archaic ungulates including *Heptodon*; *Diacodexis*; *Hapalodectes*); 1 = long and directed laterally (mesonychids;

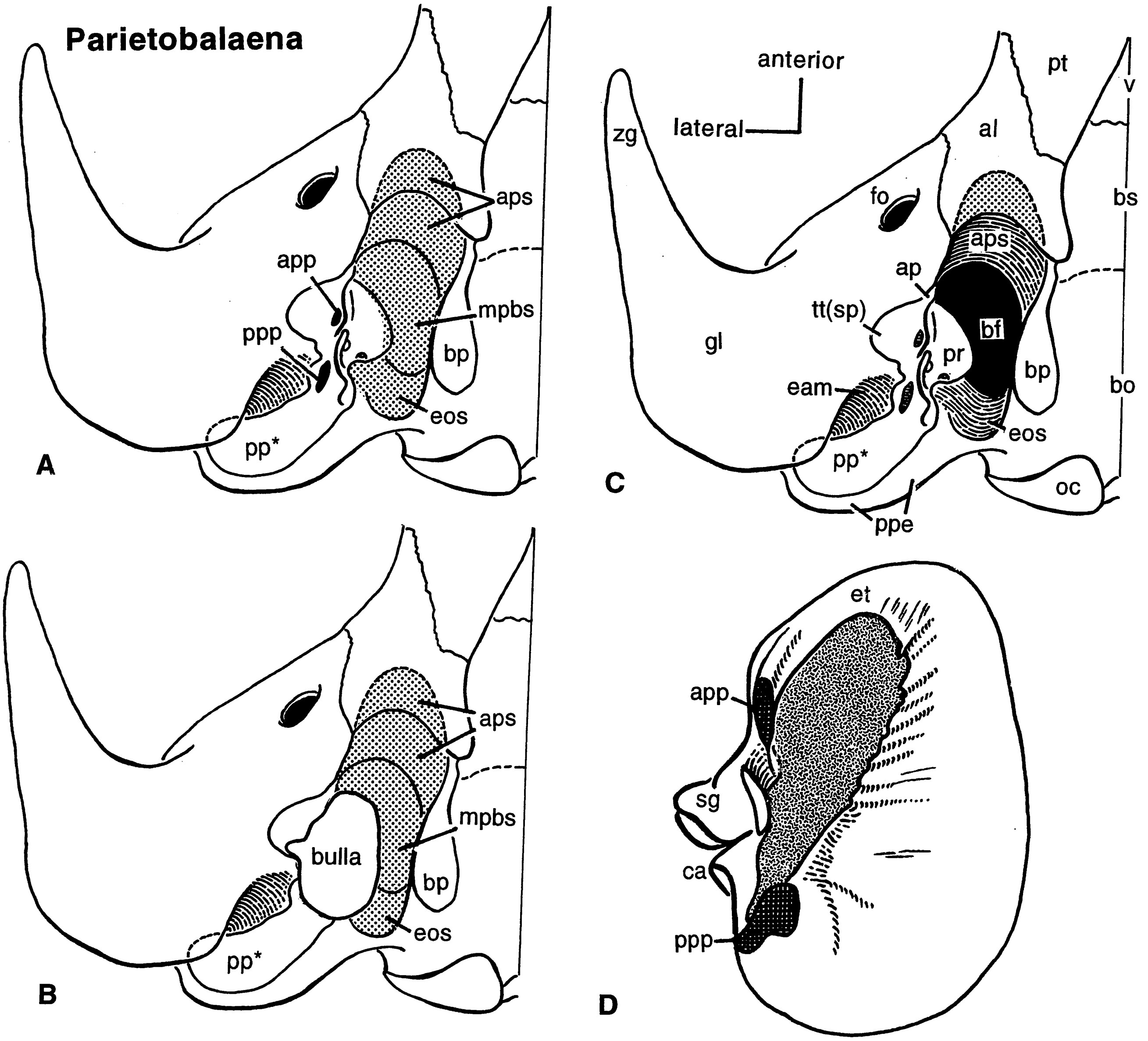


FIGURE 25. Bullar articulation and sinus distribution in mysticetes, as represented by Miocene *Parietobalaena palmeri* (osteological features modified from Kellogg, 1936, 1968; sinus pattern based on extant mysticetes, Fraser and Purves, 1960). Abbreviations: *al*, alisphenoid; *ap*, anterior process of petrosal; *app*, anterior pedicle for the tympanic bulla (= constriction between the bulla and the anterior process of the tympanic); *aps*, anterior pterygoid sinus; *bf*, basicapsular fissure; *bo*, basioccipital; *bp*, falcate process of basioccipital; *bs*, basisphenoid; *ca*, conical apophysis; *eam*, external auditory meatus; *eos*, posterior pterygoid sinus (exoccipital part); *et*, eustachian tube; *fo*, foramen ovale; *gl*, glenoid fossa; *mpbs*, medial peribullar sinus; *oc*, occipital condyle; *pp**, compound posterior processes of the ectotympanic and the petrosal (see Geisler and Luo, 1996 for discussion of homology); *ppe*, paroccipital process of exoccipital; *ppp*, posterior pedicle of the bulla (= constriction between the bulla and the posterior process of the tympanic); *pr*, promontorium; *pt*, pterygoid; *sg*, sigmoid process; *tt(sp)*, tegmen tympani (= superior process); *v*, vomer; *zg*, zygoma. Asterisk indicates that character may be variable.

cetaceans); 2 = hypertrophied paroccipital process contacting the squamosal (most odontocetes).

In archaic ungulates (including *Hapalodectes*), perissodactyls (*Heptodon*, Radinsky, 1966) and artiodactyls (Coombs and Coombs, 1982; Russell et al., 1983), the paroccipital process of the exoccipital is short and bent posteriorly. This is the primitive condition for ungulates. The paroccipital process in mesonychids (such as *Sinonyx* and *Dissacus*) and *Pakicetus* is elongate and directed laterally. The distal end of the paroccipital process is beyond the distal end of the mastoid (posterior) process. This condition is character state 1. In odontocetes, the paroccipital process is hypertrophied such that it meets the squamosal and encloses the mastoid process of the petrosal. This is character state 2.

63. Jugal

Character states: 0 = reaches posteriorly to the glenoid fossa of the squamosal (primitive archaic ungulates; odontocetes), 1 = withdraws anteriorly and terminates in the middle of the zygoma (mesonychids; basilosaurids); 2 = absent (mysticetes); ? = unknown (*Pakicetus*, *Ambulocetus*, *Indocetus*).

The former character state has a widespread distribution not only in all marsupial mammals but also in placental ungulates and odontocetes (Fraser and Purves, 1960). The condition in mesonychids (including *Hapalodectes*, Ting and Li, 1987) is shared with basilosaurids.

The jugal is variable in mysticetes. The jugal is absent in the baleen-bearing taxa considered in this study, including the cetotheriids *Parietobalaena* (Kellogg, 1968) and *Pelocetus* (Kellogg, 1965), as well as the extant mysticete families. However, we note that in the earliest known tooth-bearing mysticete *Aetiocetus* (Emlong, 1966) the jugal is still present. But *Aetiocetus* is not considered here because the detailed features of its basicranium have not been described. For mysticetes as a whole, this character is polymorphic, primitive for the early tooth-bearing taxa but secondarily lost for the more derived baleen-bearing taxa.

64. Hypoglossal nerve (XII) foramen

Character states: 0 = present on the ventral surface of the exoccipital and closer to the occipital condyle than to the jugular foramen (ungulates); 1 = present on the ventral surface of the exoccipital, but closer to the jugular foramen than to the occipital condyle (*Pakicetus* and protocetids); 2 = absent from the ventral surface of the exoccipital—nerve may exit either through a foramen on the tympanic side of the exoccipital falcate or bullar process, or through the cranial hiatus (basilosaurids and odontocetes have a separate foramen; mysticetes exit through the cranial hiatus).

Non-cetacean ungulates are 0, while pakicetids and protocetids have character state 1. Basilosaurids, mysticetes, and odontocetes have character state 2.

CHARACTER STATE MATRIX

A matrix showing the distribution of character states for all 64 morphological characteristics discussed in this chapter and all 23 taxa of interest in this study is listed in Table 6. The matrix was tabulated in MacClade (Maddison and Maddison, 1992), then imported into PAUP (Swofford, 1990, version 3.1.1) for searching the trees. This matrix is the basis for the hypothesis of relationships of ungulates, archaeocetes, and more modern cetaceans developed in Chapter 5 and presented in diagrammatic form there as Figure 26.

TABLE 6 — Matrix of character states for 64 characteristics and 23 taxa analyzed here (see text).

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
		Outg	Hept	Diac	Hapa	Diss	Sino	Paki	Ambu	Gavi	Rodh	Indo	Habi	Doru	Basi	Zygo	Xeno	Squa	Phys	Meso	Turs	Pari	Euba	Bala
1	Tegmen tympani width	0	0	?	0	1	?	?	?	?	?	?	?	2	2	2	2	?	2	2	2	3	3	3
2	Tegmen tymp. expos.	0	0	0	0	0	0	0	?	?	?	?	?	1	1	1	2	?	2	2	2	2	2	2
3	T.t. dorsolateral edge	0	0	?	0	1	?	?	?	?	?	?	?	1	1	1	2	?	2	2	2	3	3	3
4	Suprameatal fossa	0	?	?	?	1	?	?	?	?	?	?	?	1	1	1	1	2	2	2	2	2	3	3
5	T.t. ventrolat. tuber.	0	0	0	0	1	?	1	2	?	?	?	?	2	2	2	3	3	2	2	2	0	0	0
6	Epitympanic recess	0	0	0	0	0	?	0	1	?	?	?	?	1	1	1	1	1	1	1	1	2	2	2
7	Hiatus epitympanicus	0	?	?	?	0	?	?	1	?	?	?	?	1	1	1	1	1	1	1	1	2	1	2
8	Hiatus fallopi	0	0	?	0	0	?	?	?	?	?	?	?	1	1	1	2	2	2	2	2	1	1	1
9	Ant. process petrosal	0	0	?	0	1	?	1	1	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1
10	Ant. process size	?	?	?	?	0	?	0	?	?	?	?	?	1	1	1	1	1	0	1	0	2	2	2
11	Ant. process apex	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	1	1	1	2	1	3	1
12	Ant. proc. lat. surf.	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	1	1	0	1	0	0
13	Ant. proc.-sq. cont.	?	?	?	?	0	?	0	0	0	0	0	0	1	1	1	2	2	3	3	3	1	1	1
14	Mast. proc. distinct	0	0	0	0	1	1	1	1	1	1	?	?	1	1	1	1	1	1	1	1	2	2	2
15	M.p. with tymp. cov.	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2
16	M.p. rel. length	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	2	2	2
17	M.p. mastoid expos.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	1	1	1
18	Stylomastoid foramen	0	0	1	0	?	1	1	1	2	2	2	?	0	0	0	0	0	0	0	0	0	0	0
19	Hyomand. nerve	0	0	0	1	1	1	1	?	2	2	?	?	2	2	2	0	0	0	0	0	3	3	3
20	Prom.-basiocc. cont.	0	0	0	0	0	0	0	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1
21	Prom. surface	0	0	0	0	1	1	0	?	?	1	?	?	1	1	1	2	2	2	2	2	2	2	2
22	Tensor tym. fossa	0	0	0	0	0	0	1	?	?	?	?	?	1	1	1	1	1	1	1	1	1	2	2
23	Petr. exp. in braincase	0	0	0	0	0	0	0	?	0	0	?	?	0	0	0	2	2	2	2	2	1	1	1
24	Subarcuate fossa	0	0	0	0	0	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1
25	Pole of promontorium	0	0	?	0	0	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1
26	Tymp.-pet. ant. pr. cont.	?	?	?	?	0	0	0	0	0	0	?	?	1	1	1	2	2	2	2	2	3	3	3
27	Tymp. acc. ossicle	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2
28	Tymp.-sq. articulation	?	?	0	?	?	0	1	1	1	1	?	?	2	2	2	3	3	3	3	3	3	3	3
29	Tymp. post. proc. neck	?	0	1	?	0	0	1	1	2	1	1	1	2	2	2	1	1	1	1	1	3	3	3
30	Tymp. post. proc. size	?	?	1	?	0	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3
31	Basiocc.-tymp. contact	2	2	0	?	0	0	0/1	1	1	1	1	?	2	2	2	2	2	2	2	2	2	2	2
32	Exocc.-tymp. contact	?	0	0	?	0	0	1	1	1	1	?	?	2	2	2	2	2	2	2	2	2	2	2
33	Sigmoid process	?	?	1	?	0	0	1	1	1	1	?	2	2	2	2	2	2	2	2	2	2	2	2
34	Sigm.-sq. contact	?	0	0	?	0	0	0	0	0	0	?	0	1	1	1	2	2	2	2	2	2	2	2
35	Sigmoid proc. orient.	?	?	0	?	?	?	0	0	0	0	?	0	1	1	1	1	1	1	1	1	1	1	1
36	Eam-tymp. floor	0	0	0	?	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	Eam on sq.	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	1	0	0	0	0	1	1	1
38	Tympanic annulus	?	0	0	?	0	0	0	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1
39	Mid. conical process	?	?	0	0	0	0	0	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1
40	Lat. bullar furrow	?	0	0	?	?	0	0	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
41	Med. bullar furrow	?	0	0	?	?	0	0	1	1	1	1	1	2	2	2	3	3	3	3	3	0	0	0
42	Interpromint. notch	?	0	0	?	?	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
43	Med. post. prom.	?	0	0	?	?	0	1	?	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
44	Vent. tymp. keel	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
45	Involucrum	?	0	0	?	?	0	2	2	2	2	2	2	2	2	2	1	1	1	1	1	2	2	2
46	Eustachian tube rim	?	?	0	?	?	0	1	?	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1
47	Pos. eust. opening	?	?	0	?	0	0	0	?	1	1	1	?	0	0	0	0	0	0	0	0	0	0	0
48	Int. open. eust. tube	0	0	0	0	0	0	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	1	1
49	Bullar size ratio	?	0	0	?	?	0	0	?	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2
50	Prom. gr. for ica	0	1	0	0	0	0	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1
51	Med. prom. groove	0	?	0	0	0	?	0	?	?	?	?	?	1	1	1	2	2	2	2	1	2	1	1
52	Jugular foramen	0	0	0	0	0	0	1	1	1	1	?	?	2	2	2	2	2	2	2	2	2	2	2
53	Postglenoid foramen	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
54	Peripet. vasc. gr.	0	?	?	?	1	?	1	1	?	?	?	?	1	1	1	0	0	0	0	0	0	0	0
55	Ant. pteryoid sinus	0	0	0	0	0	0	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	1	1
56	Basioccipital sinus	0	0	0	0	0	0	1	?	1	1	?	?	2	2	2	2	2	2	2	2	2	2	2
57	Exoccipital sinus	0	0	0	0	0	0	0	?	1	1	1	?	2	2	2	2	2	2	2	2	2	2	2
58	Middle sinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
59	Divided pter. laminae	0	0	0	0	0	0	0	0	0	0	?	?	1	1	1	1	1	1	1	1	1	1	1
60	Internal V3 foramen	0	0	0	0	0	0	0	?	0	0	?	?	?	1	1	1	1	1	1	1	1	1	1
61	Falcate process	0	0	0	0	0	0	1	1	2	2	?	2	2	2	2	2	2	2	2	2	2	2	2
62	Paroccipital proc.	0	0	0	0	1	1	1	1	1	1	?	?	1	1	1	2	2	2	2	2	1	1	1
63	Jugal or sq glenoid	0	0	0	1	1	1	?	?	?	?	?	1	1	1	1	0	0	0	0	0	2	2	2
64	Hypoglos. for. XII	0	0	0	0	0	0	1	1	1	1	?	?	2	2	2	2	2	2	2	2	2	2	2

V

PHYLOGENETIC RELATIONSHIPS

An hypothesis of relationships of ungulates and cetaceans is presented in Figure 26, based on characteristics of the petrosal, tympanic, squamosal, occipitals, pterygoids, and on other basicranial characteristics related to vasculature and pterygoid sinuses. All 64 basicranial characteristics analyzed here were described in Chapter 4, and character state distributions for the 23 principal taxa are listed in Table 6. Additional archaic ungulate groups, such as *Meniscotherium*, *Hyopsodus*, and arctocyonids (MacIntyre, 1972; Cifelli, 1982; Luo, 1989) were compared to cetaceans in order to achieve a more reliable assessment of character state distributions among early ungulates. Thus, in a general way, basicranial structures of cetaceans were also compared to the basicranial characteristics of non-ungulate eutherians, as established by van Kampen (1905), van der Klaauw (1931), MacPhee (1981), Novacek (1986), and Wible (1990), but these are not listed in our character matrix nor were they incorporated into our analyses explicitly.

Character state distributions were analyzed cladistically using parsimony as implemented by PAUP (Swofford, 1993). These data would also be amenable to a broader stratocladistic analysis incorporating relative ages of taxa (Fisher, 1992, 1994). Multiple character states were treated as unordered to avoid *a priori* bias in interpreting character transformations. Our discussion of phylogenetic relationships is based both on the strict consensus tree and on the bootstrap tree (Fig. 26). Results of cladistic analysis were then compared to the stratigraphic sequence in which major clades emerged in the fossil record as established by Gingerich (1992; Gingerich et al., 1997, 1998).

CETE: RELATIONSHIPS OF MESONYCHIAN FAMILIES TO CETACEANS

A close relationship between cetaceans and mesonychians was first proposed by Van Valen (1966). Since then, the idea that mesonychians are broadly ancestral to cetaceans, has been supported by a long list of later studies (Szalay, 1969; McKenna, 1975, etc.) and the clade combining cetaceans and mesonychians is often called "Cete" (McKenna, 1975; Prothero, 1993; McKenna and Bell, 1997). However, mesonychians are very diverse and there has long been debate as to which mesonychian family is closest to cetaceans among the diverse groups that traditionally have been included in mesonychians, such as triisodontids, hapalodectids, mesonychids, ?wyolestids, and ?andrewsarchids (reviewed by Gingerich and Uhen, 1998; O'Leary, 1998; Gingerich, 1998). For example, Van Valen (1966, 1978) believed that the mesonychid *Dissacus* is a transitional taxon between other mesonychians and cetaceans. This implies that cetaceans are more closely related to *Dissacus* than to other mesonychians. Szalay (1969: fig. 19) implied that hapalodectids are closer to cetacean ancestry than mesonychids are, whereas Prothero et al. (1988) considered andrewsarchids to be closer to cetaceans than either *Mesonyx* (or *Dissacus*) or *Hapalodectes* (Prothero et al., 1988; Prothero, 1993). Ting and Li (1987) suggested that mesonychids are the sister taxon to cetaceans to the exclusion of hapalodectids. Thewissen (1994) suggested that the *Andrewsarchus*-Mesonychidae clade is the sister group of cetaceans to the exclusion of *Dissacus* and Hapalodectidae. In a recent cladistic analysis of dental characters, Zhou et al. (1995) suggested that hapalodectids are more distant from cetacean ancestry, while Mesonychidae (including *Dissacus* and possibly *Andrewsarchus*) is the sister taxon of cetaceans. O'Leary (1998) placed *Hapalodectes* within Mesonychidae and regarded the combined clade to be the sister taxon of cetaceans.

Basicranial characters, which have proven highly useful in the systematics in other mammalian groups, have been underutilized in previous studies of family-level relationships of Cete, with two notable exceptions (Thewissen, 1994; Geisler and Luo, 1998). In this study, we established 64 basicranial features in an effort to expand the representation of basicranial characters available for phylogenetic analysis of mesonychian and cetacean relationships.

Of the limited number of cranial characters that were used previously, some are fairly weak or questionable, as pointed out by Thewissen (1994), Zhou et al. (1995), and Geisler and Luo (1998). Our analysis shows too that some characters cited in previous studies as supporting mesonychid-cetacean relationships are more widely distributed among other ungulate groups. For example, lack of a preglenoid process and presence of an ectotympanic bulla, cited by Van Valen (1966), are widely present in many other ungulate groups. The gap between the promontorium and the basioccipital, cited as a similarity shared by mesonychids and *Protocetus* (Van Valen, 1966), is not present in *Sinonyx* nor in the earliest cetacean *Pakicetus*, a taxon more primitive than *Protocetus* (both, of course, were discovered after Van Valen's study was published).

Our parsimony analysis strongly supports a sister taxon relationship of Mesonychidae and archaeocetes, to the exclusion of Hapalodectidae and other non-mesonychian ungulates. This result is consistent with a phylogeny established on dental characters (Zhou et al., 1995), and with two studies using a broader selection of dental, cranial, postcranial, and soft tissue characters (Thewissen, 1994; Geisler and Luo, 1998).

The first suite of basicranial synapomorphies that unite mesonychids and cetaceans (but are absent or poorly developed in hapalodectids and other ungulates) involve the hypertrophied tegmen tympani. These include: (1) a greater width of the tegmen tympani of mesonychids and cetaceans than in most other ungulates; (2) presence of a distinctive, albeit small, anterior process of the tegmen tympani; (3) presence of an incipient ventrolateral tuberosity on the ventral side of the tegmen tympani (Fig. 2; see also Geisler and Luo, 1998); and (4) presence of the conspicuous suprameatal fossa (Fig. 3). While other ungulates show a moderate amount of inflation of the tegmen tympani (Cifelli, 1982), none has achieved the same degree of hypertrophy as is seen in mesonychids and cetaceans. And few other ungulates have the derived topographic features related to the hypertrophied tegmen tympani, such as the anterior process and the ventrolateral tuberosity.

Another suite of synapomorphies of mesonychids and cetaceans involve the mastoid (posterior) process of the petrosal. These are: (1) elongation of the mastoid process; (2) presence of a distinctive hiatus epitympanicus that separates the mastoid process from the rest of the petrosal (Fig. 2: *het*); (3) development of a long and narrow external auditory meatus (Van Valen, 1966); and (4) elongation of the paroccipital process of the exoccipital. These features are positionally associated with elongation of the mastoid process. The postglenoid foramen in the squamosal is absent in both mesonychids and cetaceans, but present in hapalodectids and other outgroups (Van Valen, 1966; Zhou et al., 1995; Geisler and Luo, 1998).

RELATIONSHIPS OF CETE TO OTHER EUTHERIANS

Several influential morphological studies (Prothero et al., 1988; Novacek, 1992; Prothero, 1993) have suggested that cetaceans are included in a monophyletic group of perissodactyls, hyracoids, and tethytheres (sensu McKenna, 1975), to the exclusion of artiodactyls. Thewissen (1994) proposed that perissodactyls and Cete are closely related to the exclusion of artiodactyls (also see McKenna, 1987). Most immunological studies and molecular studies based on DNA sequences indicate that, among extant eutherian orders, cetaceans are more closely related to artiodactyls to the exclusion of perissodactyls (Boyden and Gemeroy, 1950; Irwin et al., 1991; Irwin and Wilson, 1993; Arnason and Best, 1991; Novacek, 1992; Milinkovitch et al., 1993; Arnason and Gullberg, 1994). Since 1994, several molecular studies support the view that cetaceans and hippopotamids belong to a clade nested within artiodactyls (reviewed by Gatesy, 1998). Other earlier studies would place artiodactyls, perissodactyls, and cetaceans in an unresolved polytomy, without specifically endorsing either of the two alternative arrangements (e.g., see fig. 6 of Goodman et al., 1985; Miyamoto and Goodman, 1986; Novacek et al., 1988; Milinkovitch, 1992).

Two recent papers (Messenger and McGuire, 1998; Luckett and Hong, 1998) reviewed the conflicts of molecular data and morphological characters in phylogenetic studies of artiodactyls and cetaceans, and have pointed out the need to combine molecular data with morphological characters. However, the basicranial features of both fossil mesonychians and archaeocetes, the two crucial transitional groups in ungulate-cetacean evolution, have not been well sampled in previous systematic studies. To date, there has been only one published matrix-based analysis (Geisler and Luo, 1998) that encompassed enough diversity of both mesonychids and fossil cetaceans, as well as other fossil ungulate groups. Our analysis of basicranial characters provides additional characters to test these previous hypotheses.

Our parsimony analysis of the basicrania of the groups involved suggests that artiodactyls and Cete (mesonychids plus cetaceans) are closer to each other than either group is to perissodactyls. This clade of artiodactyls, mesonychians and cetaceans, known as Paraxonia, has also been supported by some previous studies (Geisler and Luo, 1998).

Our analysis of basicrania revealed some incongruence of basicranial characters among paraxonian groups. The earliest artiodactyl *Diacodexis* and archaeocetes are more similar to each other, in derived ectotympanic features, than either taxon is to early perissodactyls. The ectotympanic has a primitive and ringlike structure in the primitive perissodactyl *Heptodon*, one of the earliest and most primitive tapiroids (Radinsky, 1965). This ringlike ectotympanic is characteristic of the entire tapiroid group (van der Klaauw, 1931). Further, the ring-shaped ectotympanic of tapiroids is most likely the primitive condition of perissodactyls. A fully ossified ectotympanic bulla in extant equids appears to have evolved independently among horses because hyracotheriids, the earliest horses, do not have such a structure (van der Klaauw, 1931). Novacek (1977) suggested that a ring-like ectotympanic is a phylogenetic precursor to a fully developed ectotympanic bulla in other eutherians.

The bulla of *Diacodexis* is more similar to bullae of archaeocetes than to the bulla of mesonychids in at least some features. The gracile sigmoid process and the long posterior process of *Diacodexis* are similar to those of archaeocetes (Russell et al., 1983: fig. 4). A more equivocal similarity is that *Diacodexis* and archaeocetes both lack an extrabullar ectotympanic floor of the external auditory meatus, a primitive characteristic of mesonychids.

Two alternative interpretations are possible with regard to the ectotympanic apomorphies in *Diacodexis* and archaeocetes, and the lack of such in mesonychids. The first is to interpret the bullar similarities of artiodactyls and archaeocetes and their absence in mesonychids as convergences in artiodactyls and archaeocetes but a primitive condition retained in mesonychids. Mesonychids are the best candidates for a sister-group relationship to cetaceans by a large suite of synapomorphies of the dentition (Van Valen, 1966; Zhou et al., 1995; O'Leary, 1998), the petrosal (Fig. 2), the squamosal and exoccipital (Figs. 6

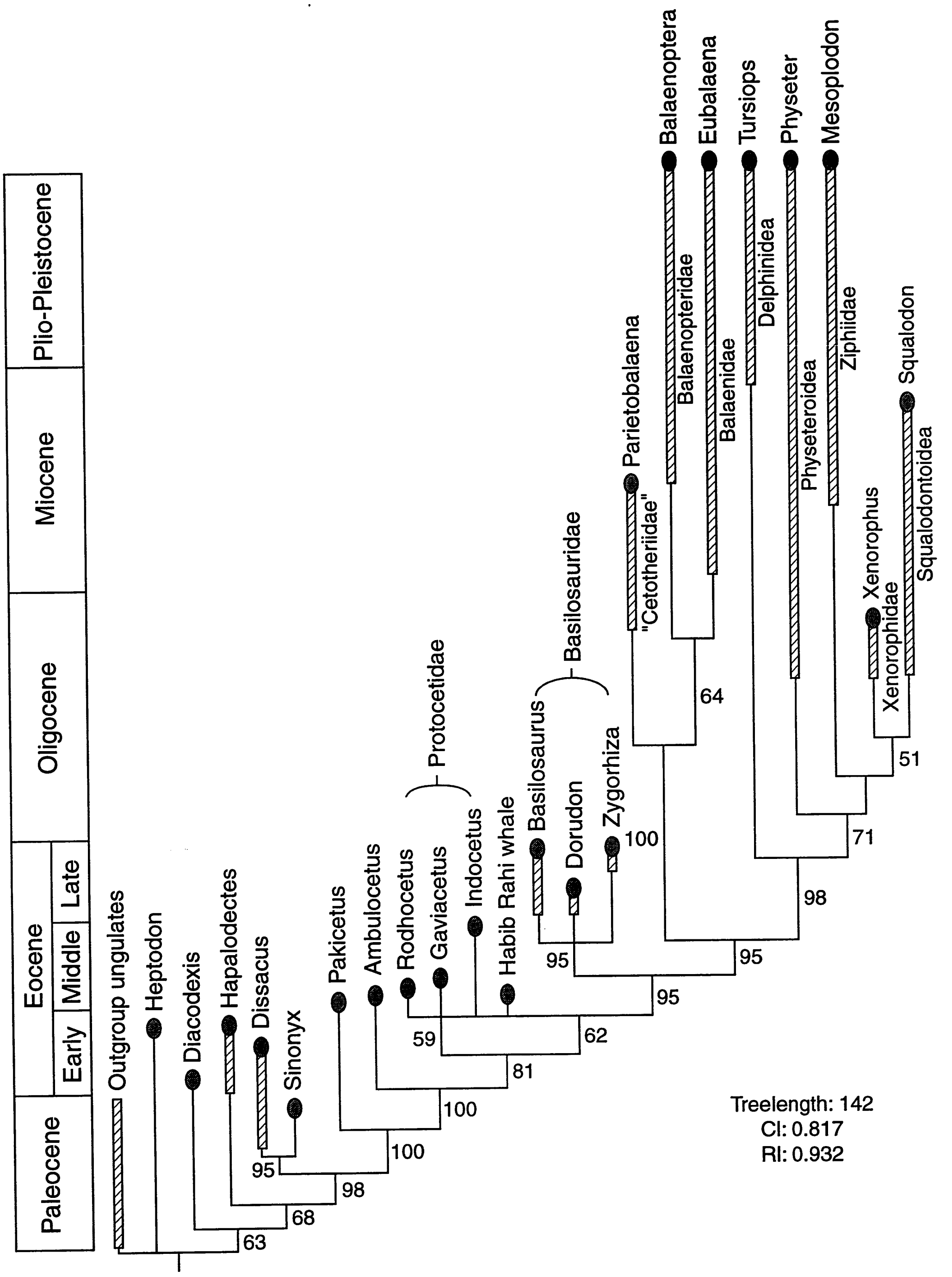


FIGURE 26. Phylogenetic relationships and sequence of appearance of selected ungulate mammals and primitive cetaceans (one most parsimonious tree). Numbers on the branches are scores for 100 bootstrap tests, based on a 50% majority rule consensus tree (the bootstrap 50% majority-rule consensus tree differs from the most parsimonious tree in having an unresolved polytomy of *Tursiops*, *Physeter*, *Mesoplodon* and the clade of [*Xenorophus* + *Squalodon*]). Tree length, CI (consistency index), and RI (retention index) are statistics for the most parsimonious tree. Definitions and descriptions of basicranial characters and character states are summarized in Chapter IV. Character state distributions are shown in Table 6. All character states were regarded as unordered in phylogenetic algorithms. Lengths of the shortest trees were calculated using PAUP and the data matrix in Table 6. Detailed character analysis is presented in the text. Stratigraphic ranges of mesonychians and hapalodectids are summarized in Zhou (1995), Gingerich (1998), and Gingerich and Uhen (1998). Ranges of archaeocetes are from Kellogg (1936), Gingerich (1992), and Gingerich et al. (1997). Ranges of odontocetes and mysticetes are based on Kellogg (1965), Whitmore and Sanders (1976), Barnes (1976, 1984), Barnes and McLeod (1984), Barnes et al. (1985), and Fordyce and Barnes (1994).

and 8), as well as the characters from other areas of the skull (Prothero, 1993; Thewissen, 1994; Geisler and Luo, 1998). Given this very substantial body of evidence that mesonychids and cetaceans are sister groups to the exclusion of artiodactyls, it is more plausible to interpret the presence of a sigmoid-like process and a posterior process in artiodactyls and cetaceans as independently derived. An alternative (more complicated and less plausible) interpretation is that the sigmoid process was present in the common ancestor of artiodactyls, mesonychids, and whales, but was secondarily lost in mesonychids.

MONOPHYLY OF CETACEANS AND DIAGNOSIS OF CETACEA

The monophyly of Cetacea is strongly supported by basicranial apomorphies, most of which are associated either with the involucrum, or with articulation of the ectotympanic bulla with the basicranium. Many other basicranial characteristics of pakicetids described so far are primitive and shared by non-cetacean mammals.

Cetacea, if taken to include the shared common ancestry of *Pakicetus* and living whales, can be diagnosed by four derived basicranial characters:

(1) Presence of the involucrum, the pachyostotic medial rim of the bulla.

(2) Presence of a distally-enlarged posterior process of the tympanic. The distal portion of the posterior process is larger beyond its base than those of mesonychians and artiodactyls. *Diacodexis pakistanensis* (Russell et al., 1983), for example, has a gracile posterior process but lacks the prominent distal enlargement of *Pakicetus*.

(3) Direct articulation of the ectotympanic bulla with the exoccipital. In all archaeocetes including pakicetids, the posterior part of the involucrum sits on the bullar process of the exoccipital. In contrast, *Diacodexis* and mesonychids (except *Harpagolestes*, Geisler, pers. comm.) lack the bullar process of the exoccipital and their bullae do not contact the exoccipital.

(4) Presence of a platform for the bullar process of the squamosal. The contact of the anterior process of the tympanic with the squamosal is also present in mesonychids, although the entoglenoid region of the squamosal lacks the distinctive platform for the bullar articulation (see *Sinonyx*, Fig. 8).

The phylogenetic evolution of cetaceans from a terrestrial ungulate ancestry is documented by an excellent fossil record. The relationships of the transitional groups are well resolved (Fig. 26). Stepwise anatomical evolution through this transition is well established in the early fossil groups, in spite of the enormous anatomical differences between extant cetaceans and other extant ungulates. As a result, the recognition and diagnosis of Cetacea as a taxonomic group has become somewhat arbitrary.

A good case in point is the sigmoid process. The sigmoid ("s-shaped") process is so named because its distal (dorsal) end is slightly twisted from its base and its lateral margin is thick and involuted in modern cetaceans (see Kellogg, 1928, 1936). Because it appears to be so different from the ectotympanic structures of non-cetacean mammals, the sigmoid process has been widely accepted as an important diagnostic characteristic of cetaceans (Kellogg, 1936; Gingerich et al., 1983; Barnes, 1984; Oelschläger, 1990; Lancaster, 1990; Thewissen, 1994; Berta, 1994; Fordyce and Barnes, 1994). However, in view of the new information from *Pakicetus* (Figs. 11-12) and *Ichthyolestes* (Luo, 1998), usefulness of the sigmoid process as a clear-cut diagnostic character is now open to question.

The sigmoid process of *Pakicetus* (Figs. 11, 12) and *Ichthyolestes* (Luo, 1998) is a simple plate. It lacks the "s-shaped twist" and the involuted margin, two very prominent characteristics of the sigmoid process in more derived cetaceans. It has retained the primitive characteristics of a plate-like anterior wall of the ectotympanic meatal tube as in the mesonychids *Mesonyx* (Geisler and Luo, 1998) and *Sinonyx* (Fig. 8; also Zhou et al., 1995) and some other non-cetacean mammals.

In non-cetacean mammals with a fully developed ectotympanic meatal tube, such as ungulates, the extrabullar part of the meatal floor is formed as the embryonic ectotympanic ring grows laterally (Novacek, 1977). The anterior crus gives rise to (and becomes a part of) the anterior wall of the external auditory meatus. Thus the crus does not appear as an independent process in the adults of other mammals.

The main differences can be attributed to an early arrest of lateral growth due to folding in the embryonic ectotympanic ring in cetaceans (Hanke, 1914). Consequently, the sigmoid process remains as independent a process as did the anterior crus, its embryonic precursor (Ridewood, 1922). The sigmoid process of adult cetaceans is a neotenic feature and represents a retention of the embryonic condition of the ectotympanic in non-cetaceans. Therefore, it may be more proper to recognize the sigmoid process as "an enlargement of the anterior crus in the adult bulla" or as the "anterior wall of the external auditory meatus."

The distribution of the sigmoid process among the artiodactyl *Diacodexis*, mesonychids and cetaceans suggests that this character may be homoplastic. A sigmoid process is present in the early artiodactyl *Diacodexis* (Russell et al., 1983) but absent in mesonychids. Because there is a large body of evidence to support the sister group relationship of mesonychids and cetaceans to the exclusion of artiodactyls (Prothero, 1993; Thewissen, 1994; Geisler and Luo, 1998), the sigmoid process in *Diacodexis* could be considered to be a "convergence" to cetaceans. Alternatively, the presence of an independent sigmoid process can be interpreted as a synapomorphy of Paraxonia (a clade including artiodactyls, mesonychids, and cetaceans). Absence of the sigmoid process in mesonychids could be considered to be a secondary loss within Paraxonia. Either way, it is clear that this character (an independent and enlarged projection derived from the embryonic anterior crus) has some degree of homoplasy. It is also possible (although not probable) to consider the sigmoid process to be a shared derived character of *Diacodexis* and cetaceans.

Other bullar features of pakicetids are plesiomorphies with wide distributions among non-cetacean mammals. These plesiomorphous characters are: (1) presence of an annulus for a fully developed tympanic membrane; (2) presence of an intrabullar meatus in the tympanic cavity, (3) presence of a large aperture for the eustachian tube, and (4) presence of a hollowed processus tubarius. These primitive characters are conspicuously absent in all whales more derived than *Pakicetus*, which are discussed below.

MONOPHYLY OF ALL POST-*PAKICETUS* CETACEANS

Rodhocetus, *Gaviacetus* and other cetaceans form a monophyletic group to the exclusion of *Pakicetus*. The taxa of this clade, collectively referred to as "post-pakicetid cetaceans," share a large number of derived basicranial characteristics. These include the absence of the tympanic annulus and the formation of a conical process in the ectotympanic bulla—features present in all protocetids for which the relevant parts of the skull are preserved, all basilosaurids, and extant cetaceans (Pompeckj, 1922; Lancaster, 1990; Luo, 1998). Both features are very significant as they are related to development of the conical tympanic ligament in extant cetaceans (Purves, 1966; Fleischer, 1978; Lancaster, 1990).

Post-*Pakicetus* cetaceans are diagnosed also by a median furrow and a more inflated medial rim of the bulla, both correlated with greater inflation of the involucrum than is seen in *Pakicetus*, and by a more enlarged posterior process of the tympanic that covers the full length of the mastoid process of the petrosal. The external auditory meatus is much broader than the narrow groove in mesonychids and *Pakicetus*.

All post-*Pakicetus* cetaceans have developed a well-defined falcate process in the basioccipital, and an incipient sinus in the exoccipital region. This exoccipital sinus expands slightly to invade the area of the stylomastoid foramen, forming a large space next to the stylomastoid foramen in both *Rodhocetus* and *Gaviacetus*. The sinus is large enough to make the jugular foramen and basicapsular fissure confluent with each other, as in *Georgiacetus* (Hulbert et al., 1998). However it is not so large as to separate the medial prominence of the bulla (Fig. 12: *eoc*) from the bullar process of the exoccipital (Fig. 12: *eop*).

An apomorphy corroborating the monophyly of post-*Pakicetus* cetaceans comes from the large size of the mandibular canal. The mandibular canal is greatly enlarged in *Rodhocetus* (Gingerich et al., 1994) and other protocetids (Hulbert, 1993; Geisler et al., 1996), where it approaches the size of the mandibular canal in the more derived basilosaurids. In contrast, the mandibular canal is small in *Pakicetus*, where it is about the same size as in terrestrial ungulates (Thewissen and Hussain, 1993).

The opening for the eustachian tube (Figs. 12, 13: *et*) is positioned on the medial side of the tympanic bulla in *Gaviacetus* (Figs. 12, 13: *mn*), instead of the anterior end of the bulla as in *Pakicetus* and basilosaurids. The orientation of the eustachian opening (on the medial side of the bulla) is also present in *Rodhocetus* (GSP-UM 3012) and *Protocetus* (fig. 2 of Fraas, 1904). Pending verification of the distribution of this character, it may be a synapomorphy that unites protocetids as a group.

MONOPHYLY OF BASILOSAURIDS, MYSTICETES, AND ODONTOCETES

Several hypotheses were proposed with regard to relationships of mysticetes and odontocetes to archaeocetes (see review by Barnes and Mitchell, 1978). One hypothesis among these was brought forth by Van Valen (1968), who postulated that both mysticetes and odontocetes originated from *Protocetus* because the Protocetidae "is beautifully intermediate between primitive mesonychids and recent whales." However, Van Valen (1968) did not provide specific anatomical characters for this idea except for the general resemblance of the bullae.

Barnes and Mitchell (1978) and Barnes (1984) suggested that mysticetes and odontocetes originated from dorudontine basilosaurids. They offered several derived characters to support the affinities of dorudontines to extant cetaceans: (1) cheek teeth with two roots (instead of three roots as in protocetids), closer to those of later odontocetes and "tooth-bearing" mysticetes; (2) teeth with serrated accessory denticles; (3) elongated mandibles; (4) an "enlarged air sinus around the ear;" and (5) more posteriorly positioned narial openings (Barnes and Mitchell, 1978: 595; Barnes, 1984: 146). This hypothesis has been widely accepted by other workers (Fordyce, 1980; Fordyce and Barnes, 1994; Berta, 1994; Luo and Marsh, 1996; Geisler and Luo, 1996; Uhen, 1998).

The sister group relationship of basilosaurids and crown group cetaceans is strongly supported by additional basicranial apomorphies from this study. Basilosaurids, extant mysticetes, and extant odontocetes share three suites of interrelated apomorphies:

(1) The greatly expanded pterygoid sinus with divided medial and lateral pterygoid laminae. The pterygoid sinus cavity is absent in *Pakicetus*. It is very limited in *Rodhocetus, Gaviacetus*, and *Georgiacetus*. Although the basicapsular fissure is enlarged in these protocetids, the sinus is not visible anterior to the tympanic bulla in ventral view, and does not spread to the outside of the bulla. In contrast, basilosaurids developed a deep sinus cavity anterior to the tympanic bulla between the medial lamina and the lateral lamina of the pterygoid. The cavity has an internal wall (the superior pterygoid lamina) that partially separates the anterior pterygoid sinus from the brain cavity. In adult skulls of basilosaurids (e.g., UM 97507), this internal wall to the sinus cavity has come to partially encircle the mandibular branch of the trigeminal nerve (Fig. 18B: *iof*). These derived characters are related to expansion of the anterior pterygoid sinus.

(2) Reduced contact between the anterior process of the tympanic and the entoglenoid process of the squamosal. In *Pakicetus* and *Gaviacetus*, there is an elevated and round platform on the entoglenoid process of the squamosal (Figs. 10 and 11: *sqc*). The anterior process of the ectotympanic (*apt*) forms extensive contact with this elevated stage, but little or no contact with the anterior process of the petrosal. This condi-

tion is retained, although showing some variability in protocetids, such as *Protocetus* and a new protocetid from South Carolina (Geisler, pers. comm.). In contrast, this articulation between the ectotympanic and the squamosal is greatly reduced to a thin edge of the squamosal in basilosaurids (Fig. 21: *sqc*). The contact between the anterior process of the tympanic and the petrosal is developed at the expense of the tympanic-squamosal articulation (more developed than in any protocetid). In mysticetes and odontocetes, the articulation of the anterior process of the tympanic with the squamosal is entirely absent.

(3) Detachment of the bulla from the bullar process of the exoccipital and presence of the peribullar sinus medial to the involucrum in larger basilosaurid taxa and in extant cetaceans, as a result of further expansion of the sinuses.

MONOPHYLY OF THE CETACEAN CROWN GROUP

The distribution of basicranial characters supports the monophyly of mysticetes and odontocetes. Both groups share the following basicranial synapomorphies:

(1) The anterior process of the ectotympanic and its derivatives are completely detached from the squamosal and fully attached to the anterior process of the petrosal. In several protocetids (but not *Gaviacetus*) and basilosaurids, the anterolateral rim of the bulla still retains its articulation (at least in part) with the squamosal. In contrast, the direct articulation of the anterior process of the tympanic is lost in the crown group of cetaceans, although in very different ways in mysticetes and odontocetes. The accessory ossicle on the anterior rim of the bulla in odontocetes has little or no articulation with the squamosal (Kasuya, 1973; de Muizon, 1987; Fordyce, 1994; Luo and Marsh, 1996). In mysticetes, the anterior process of the tympanic is fused to the petrosal and has little or no contact with the squamosal, even though the lateral aspect of the tegmen tympani of the petrosal still has a substantial contact with the squamosal. The sigmoid process, which usually articulates with the entoglenoid process in archaeocetes, is withdrawn from the squamosal in both mysticetes and odontocetes.

(2) Loss of the inner posterior pedicle of the posterior process of the tympanic. In basilosaurids there are two pedicles for the posterior process of the tympanic. This is a primitive feature of *Gaviacetus* and *Georgiacetus*. In contrast, there is only one pedicle in odontocetes and mysticetes. Ridewood (1922) speculated that the double posterior pedicles of basilosaurids may be fused in the ontogeny of more derived extant whales.

(3) The epitympanic recess area, which partially overlaps the squamosal in all archaeocetes, is completely detached from the squamosal in odontocetes and mysticetes (de Muizon, 1987; Fordyce, 1994; Luo and Eastman, 1995; Luo and Marsh, 1996; Geisler and Luo, 1996; Fig. 27). This allows full exposure of the ventrolateral tuberosity in tympanic view in odontocetes, and full exposure of the entire flat epitympanic area in mysticetes.

(4) The suprameatal fossa is fully concave in archaeocetes, but nearly flat or even slightly convex in most odontocetes (except *Xenorophus*) and in mysticetes. This is a direct result of hypertrophy of the tegmen tympani beyond the extent seen in basilosaurids.

(5) Much larger pterygoid vascular sinus on the medial side of the petrotympanic complex in extant cetaceans than in archaeocetes (Fig. 28).

MONOPHYLY OF ODONTOCETES

Finally, the monophyly of Odontoceti is supported by several apomorphies. The hiatus fallopii, located in front of the pars cochlearis and between the anterior process and the pars cochlearis in basilosaurids and mysticetes, is shifted to the medial side of the pars cochlearis in odontocetes. The posterior process of the tympanic and mastoid process of the petrosal are relatively short, in contrast to the condition in archaeocetes and mysticetes. The distal ends of both processes are enclosed by the squamosal and exoccipital. They are not exposed on the outer surface of the skull. This is convergent with the "amastoid condition" in some derived artiodactyls. The external auditory meatus is absent in extant odontocetes. Most of the lateral side of the petrosal is detached from the squamosal except for a small area near the hiatus epitympanicus (Figs. 24, 27).

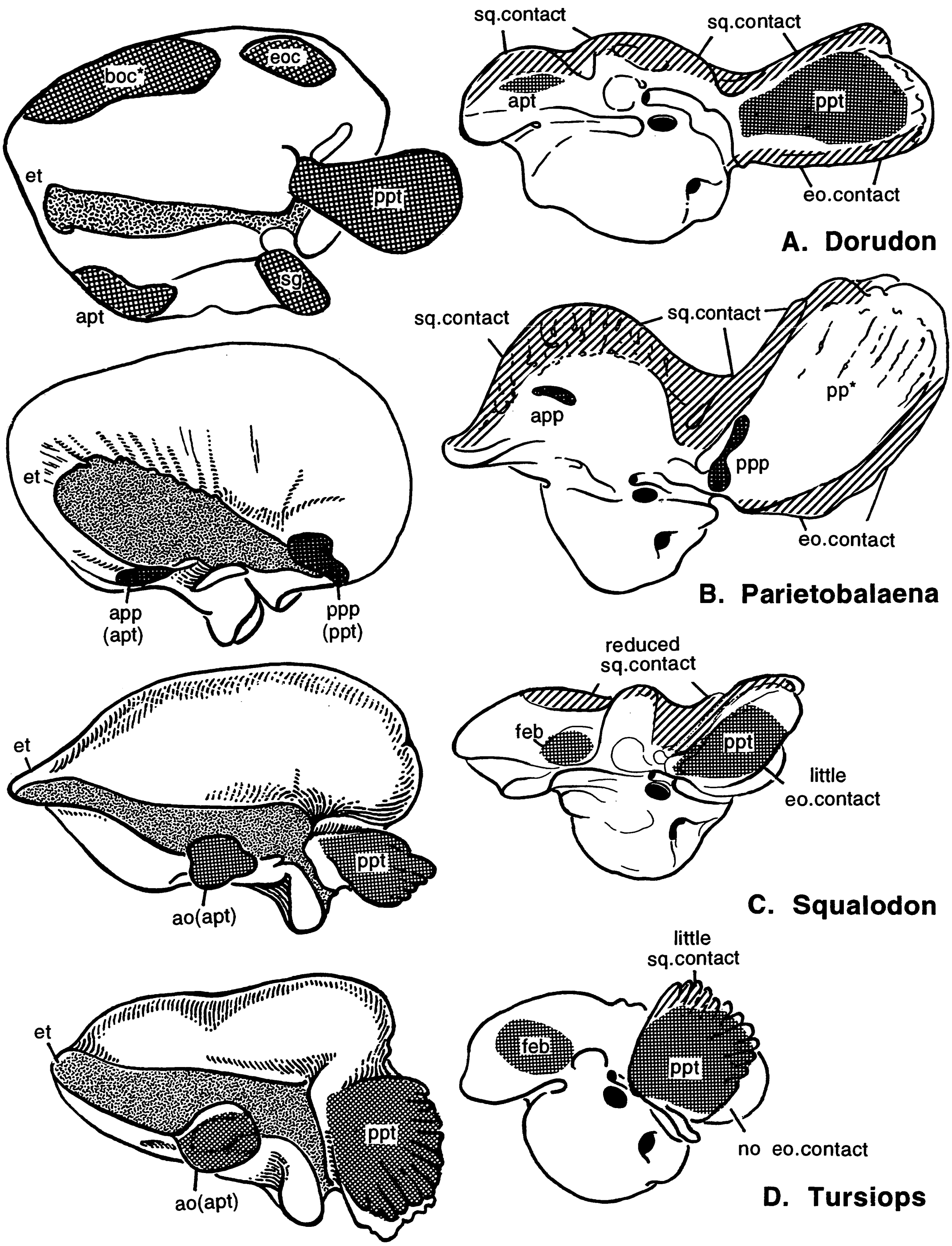
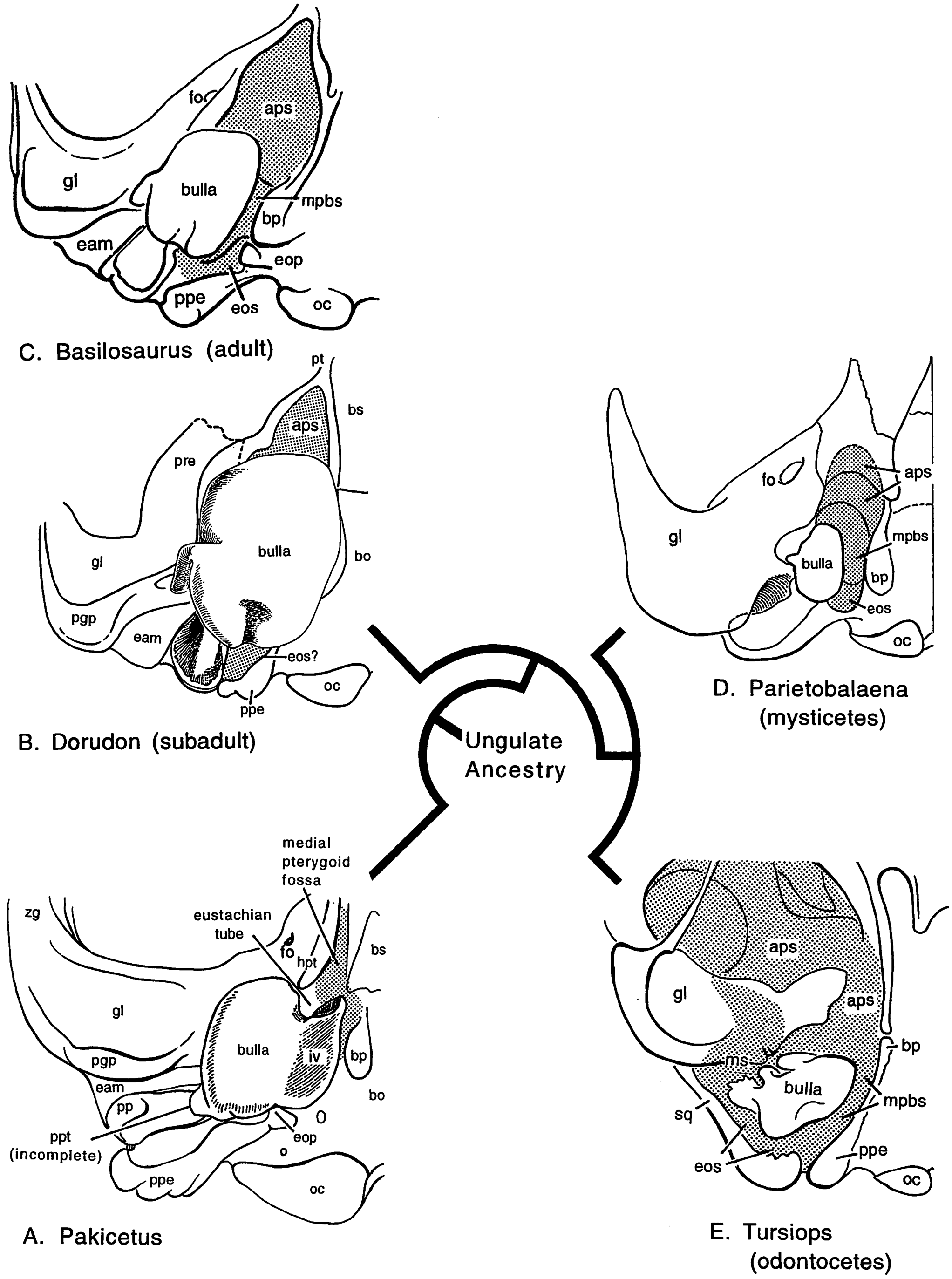


FIGURE 27. Hypothesized stages in the transformation of articulation of the petrosal and tympanic in cetaceans. A, *Dorudon*. B, *Parietobalaena*. C, *Squalodon*. D, *Tursiops*. Petrosals at right are shown in ventral view. Tympanic bullae at left are shown in dorsal view. Darker cross-hatching shows articulations of the petrosal and bulla. Slanted hatching shows articulation of the petrosal with surrounding bones of the basicranium. Abbreviations: *ao(apt)*, accessory ossicle (= related to anterior process of tympanic); *app*, anterior pedicle of bulla; *apt*, anterior process of tympanic; *boc**, contact of the bulla to the basal or falcate process of basioccipital (variable with skull size and present only in smaller skulls); *eoc*, bullar contact to exoccipital (variable); *eo.contact*, contact of petrosal with exoccipital; *et*, eustachian tube; *feb*, fovea epitubaria; *ppp*, pedicle for the posterior process of tympanic; *ppt*, posterior process of tympanic; *sg*, sigmoid process; *sq.contact*, contact of petrosal with squamosal.



C. Basilosaurus (adult)

B. Dorudon (subadult)

D. Parietobalaena (mysticetes)

A. Pakicetus

E. Tursiops (odontocetes)

FIGURE 28. Pattern of evolution of sinuses in the basicranium of cetaceans. A, *Pakicetus*. B, *Dorudon*. C, *Basilosaurus*. D, *Parietobalaena*. E, *Tursiops*. Abbreviations: *aps*, anterior pterygoid sinus; *bo*, basioccipital; *bp*, basal or falcate process of basioccipital; *bs*, basisphenoid; *eam*, external auditory meatus; *eop*, bullar process of the exoccipital; *eos*, pterygoid sinus (posterior or exoccipital part); *fo*, foramen ovale; *gl*, glenoid fossa of squamosal; *hpt*, base for the hamulus of pterygoid; *mpbs*, medial peribullar sinus; *ms*, middle sinus; *oc*, occipital condyle; *pgp*, postglenoid process; *pp*, posterior process of petrosal; *ppe*, paroccipital process of exoccipital; *ppt*, posterior process of tympanic; *pre*, preglenoid process of squamosal; *pt*, ptergygoid; *sq*, squamosal; *zg*, zygoma. The branching sequence shown here is based on basicranial characters, but is fully consistent with the pattern of reduction of the hind limbs (see Chapter VI).

VI

STAGES OF BASICRANIAL EVOLUTION

We recognize six distinct stages in the evolution of auditory morphology and hearing that are part of the transition from land-living ungulates to aquatic whales. The primitive condition is regarded as stage 0, and remaining stages are numbered from 1 to 5. Important changes in the transformation of bullar articulation with the petrosal are summarized in Figure 27, and changes in the evolutionary development of sinuses are shown in Figure 28. Interestingly, these stages correspond for the most part to similar stages recognized in the postcranial skeleton that involve shortening of the neck and alignment of the head with the rest of the body, simplification of the forelimb, and reduction of the sacrum and hind limbs, which are all adaptations to life in an aquatic environment.

STAGES OF BASICRANIAL EVOLUTION

Stage 0.—Mesonychians of the late Paleocene to middle Eocene have an ectotympanic bulla with an extrabullar meatal floor. The bulla is fully articulated with the squamosal and basioccipital bones of the basicranium, having little contact with the exoccipital or with the mastoid or posterior process of the petrosal. This condition is shared by artiodactyls.

Stage 1.—The earliest known cetacean with the basicranium preserved, the early-to-middle Eocene pakicetid *Pakicetus inachus*, represents a more advanced stage 1. *Pakicetus* has a tympanic involucrum. The presence of an involucrum represents the beginning of pachyostosis and osteosclerosis of the bulla, making it denser than surrounding bones and much denser than surrounding soft tissues or water. The primary contacts of the bulla are now with the mastoid process of the petrosal, the squamosal, the exoccipital, and possibly the basioccipital. Thus the bulla maintains solid contacts with most surrounding basicranial bones (Gingerich et al., 1983). The external auditory meatus retains an annulus for a fully functional tympanic membrane. The tympanic cavity has several internal septa. All of these characteristics taken together indicate that *Pakicetus* had more-or-less normal hearing capability for a land-living mammal, with its hearing involving low frequency sound.

Stage 2.—Protocetid whales, such as middle Eocene *Rodhocetus*, *Gaviacetus*, *Indocetus*, and *Georgiacetus*, represent stage 2 in the basicranial evolution of cetaceans. An important apomorphy is the conical apophysis or middle process (as found in *Georgiacetus*, Hulbert et al., 1998). The conical apophysis is developed by the folding of the embryonic tympanic ring (Hanke, 1914; Luo, 1998). Its presence in modern cetaceans is correlated with development of the conical tympanic ligament from an embryonic precursor tympanic membrane. Thus we infer that protocetid whales had a conical tympanic ligament instead of a tympanic membrane. Protocetids like *Georgiacetus* have incipient pterygoid sinuses in the basicapsular fissure (Hulbert et al., 1998). These are much smaller than the sinus cavities of basilosaurids, and they are never fully developed anterior to or outside the bulla.

Stage 3.—Basilosaurids of middle-to-late and late Eocene age represent stage 3 in the evolution of the ear region of cetaceans. These have a well-developed pterygoid sinus that extends into the exoccipital region, and also extends in front of the bulla. Larger skulls have developed a medial peribullar sinus too, outside and medial to the involucrum (Figs. 22-23). Bullar articulation with the basioccipital and exoccipital is completely lost in adults. The bullar contact with the squamosal is partially replaced by contact with the petrosal. The petrosal is pachyostotic (hypertrophied), in addition to being osteosclerotic (dense). The petrosal remains firmly ankylosed with the surrounding squamosal and exoccipital (Pompeckj, 1922; Fordyce, 1994; Luo and Marsh, 1996).

Stage 4.—Modern mysticetes and odontocetes, both of which originated in the Oligocene, represent stage 4 in the evolution of the auditory region of cetaceans. The sigmoid process of the bulla is detached from the squamosal. The petrosal is at least partially excluded from the braincase and isolated in a peribullar cavity.

Stage 5.—In odontocetes, which represent evolutionary stage 5, the petrotympanic complex is completely enclosed in a peribullar cavity and isolated from the rest of the cranium. The pterygoid sinus has spread to the lateral side of the petrotympanic complex, to form a well-developed middle sinus that separates the petrotympanic complex from the squamosal to various degrees in extant odontocetes (Fig. 24: *ms*).

STAGES OF LOCOMOTOR EVOLUTION

Stages of basicranial evolution in the transition from land-living ungulates to aquatic whales parallel a corresponding series of stages in the evolution of the postcranial skeleton.

Stage 0.—Paleocene-Eocene mesonychians are always found in continental depositional environments, and we know from virtually complete skeletons that they were hoofed, cursorial land mammals (Zhou et al., 1992; O'Leary and Rose, 1995).

Stage 1.—Early middle Eocene pakicetid archaeocetes are generally found with land mammals in continental red bed deposits (e.g., *Ichthyolestes*, Dehm and Oettingen-Spielberg, 1958; *Pakicetus*, Gingerich et al., 1983; and *Nalacetus*, Thewissen and Hussain, 1998). The one exception is *Himalayacetus* (Bajpai and Gingerich, 1998), which was found in shallow marine deposits. Postcranial remains of pakicetids are almost completely unknown, but an atlas vertebra suggests that the head was held at an angle to a neck of presumably moderate length (as in mesonychians). An astragalus referred to Pakicetidae indicates that at least one genus was still capable of terrestrial locomotion (Thewissen et al., 1998). Associated faunas and sediments suggest that pakicetids might have been largely terrestrial (Gingerich et al., 1983; Thewissen, 1998), and it is reasonable to infer that pakicetids, by analogy with *Ambulocetus* (Thewissen et al., 1996), were as terrestrial as they were aquatic.

Stage 2.—Middle Eocene protocetid archaeocetes are all found in shallow marine deposits. Where known, the atlas vertebra indicates that the head was positioned anterior to the skeleton, while cervical vertebrae are clearly shorter than those of mesonychians. Forelimb elements are known in several protocetid specimens, but these have not yet been described. Protocetids range from early forms with a solidly fused three or four-centrum sacrum (e.g., *Takracetus*; Gingerich et al., 1995; in prep.) to intermediate forms with a four-centrum sacrum lacking fusion (*Rodhocetus*; Gingerich et al., 1994), to later forms with a single-centrum sacrum (*Protocetus*; Fraas, 1904), or possibly no distinct sacrum (*Georgiacetus*; Hulbert et al., 1998) for attachment of pelves and hind limbs. Pelves of two have been described (*Rodhocetus* and *Georgiacetus*) and these are both large, with a long ilium, large obturator foramen, and large well-formed acetabulum for articulation with the femur. The only described femur (of *Rodhocetus*) is robust, but short for the size of the skeleton. Protocetids are known from virtually the beginning to end of the middle Eocene, a long interval of some 10-12 million years, during which the vertebral column can be seen to have lost the rigid sacrum that anchors pelves and hind limbs in land mammals but would interfere with the caudal undulation of efficient cetacean swimmers. Thus protocetids represent a shifting balance of terrestrial and aquatic locomotor specializations. In the most advanced of described protocetids, *Georgiacetus*, the pelves no longer articulated with the vertebral column, making it doubtful that *Georgiacetus* could support its weight on land (though it apparently retained a relatively large and functional hind limb).

Stage 3.—Middle-to-late and late Eocene basilosaurid archaeocetes have long been known from excellent, if incomplete, skeletons. Kellogg (1936) described good skeletons of *Basilosaurus* and *Zygorhiza*. New specimens of *Basilosaurus* and *Dorudon* are virtually complete (Gingerich et al., 1990; Uhen, 1996). Atlas vertebrae show that the skull was positioned anterior to the postcranial skeleton and cervical vertebrae are shorter than those of Protocetidae—indicating greater hydrodynamic streamlining. Virtually complete forelimbs and hands are known for *Basilosaurus* (Gingerich and Smith, 1990) and *Dorudon* (Uhen, 1996, 1998). These retain mobility in a more or less horizontal plane at the elbow joint, but are otherwise advanced in having fixed carpals, metacarpals, and phalanges forming a broad and flat flipper-like hand functioning as a hydrofoil. The new specimens of *Basilosaurus* and *Dorudon* show that there was no sacrum of any kind in either genus (although vertebrae preceding the tail are undoubtedly homologous with elements that were formerly part of a sacrum), and both had greatly reduced pelves and hind limbs. Left and right pelves joined at the midline, but these were enveloped in muscles of the ventral body wall far from the vertebral column. Hind limbs were too small to be used in locomotion, and there is no possibility of basilosaurids supporting their weight on land. Basilosaurids as a group were the first archaeocetes to be fully aquatic.

Stage 4.—Crown group cetaceans (mysticetes plus odontocetes) have skulls directly in front of the postcranial skeleton, with very short necks (cervicals may be paper-thin, and are often fused to each other), enhancing their hydrodynamic streamlining. Modern whales have no muscles and no flexion or extension in forelimb joints below the shoulder, while the hands are broad, flat, and function as hydrofoils. Mysticetes and odontocetes retain pelvic bones and sometimes femora, but have no external hind limbs.

Stage 5.—Finally, odontocetes are similar to mysticetes in body form and forelimb structure. Odontocetes generally lack femora, indicating a further stage of hind limb reduction over mysticetes.

STAGES OF AQUATIC ADAPTATION

The easiest way to reconcile these two series of stages is to regard them as parallel manifestations of increasing adaptation to life in an aquatic medium. Stage 0 in both series involves no aquatic adaptation at all. Stage 1 in basicranial evolution involves little more than the beginning of pachyostosis and osteosclerosis of the bulla, making it denser than surrounding bones, tissues, and water. Little can be said about Stage 1 in locomotor evolution because so little is known. It is possible that pakicetids were largely terrestrial, but the presence of long, narrow, almost needle-like anterior teeth in some, the presence of premolars specialized like those of later aquatic archaeocetes, and recovery of *Himalayacetus* from a marine deposit are all consistent with pachyostosis and osteosclerosis of the bulla in suggesting some aquatic adaptation.

Stage 2 in basicranial evolution involves conversion of the tympanic membrane into a tympanic ligament, with loss of the ability to hear in air, and development of incipient pterygoid sinuses. Both are characteristic of the late protocetid *Georgiacetus*, which is also the most fully aquatic protocetid in terms of sacral and pelvic modifications. We predict that the middle ear of primitive protocetids like *Takracetus*, when known, might retain a tympanic membrane and lack pterygoid sinuses.

Stage 3 involves further hypertrophy of the tympanic bulla, acquisition of a well developed pterygoid sinus flanking and partially surrounding the petrosal, and reduction in the number and size of bullar contacts with other bones. Comparison with the corresponding stage of locomotor evolution indicates that basilosaurids were fully aquatic. Changes in the middle ear were sufficient to enable hearing in water.

Stage 4 in basicranial evolution involves restriction of articulation of the bulla to two sites on the petrosal, a site on the anterior process of the petrosal, and a site on the mastoid or posterior process of the petrosal. The petrosal itself is at least partially excluded from the braincase and isolated in a peribullar cavity. These can be regarded as the culmination of a trend toward isolation of the petrosal and bulla that started in stage 2, and was already well developed in stage 3 in whales that are fully aquatic.

Stage 5 involves full separation of the petrotympanic complex in a peribullar cavity isolated from the rest of the cranium. This is a further development of a trend toward isolation that started in stage 2 and continued through stages 3 and 4. Stage 5 has to be regarded as something more than satisfying requirements of specialized hearing in water. It is found only in odontocetes, and undoubtedly represents a highly specialized apparatus for hearing high frequency sound associated with development of sophisticated sonar in this group.

VII

CHARACTER EVOLUTION

Several character complexes can be traced as they change through time in the transition of archaeocetes from life on land to life in water. Here we consider change in the tegmen tympani and anterior process of the petrosal, articulation of the petrosal, articulation of the ectotympanic, origin of the sigmoid process of the ectotympanic, pachyosteosclerosis of the petrotympanic complex, and change in the pterygoid sinus.

TEGMEN TYMPANI AND THE ANTERIOR PROCESS OF THE PETROSAL

The tegmen tympani is present, but small, in the earliest ungulate petrosals (MacIntyre, 1972; Luo 1989). The structure is enlarged in some eutherian mammals of the Eocene. Slight enlargement of the tegmen is not only present in ungulates, such as *Hyopsodus*, *Meniscotherium*, and *Phenacodus* (Gazin, 1965; Cifelli, 1982), but it is also present in bats and primates (MacPhee and Cartmill, 1986; Wible and Novacek, 1988; Wible and Martin, 1993). A slightly enlarged tegmen tympani, such as is seen in *Hyopsodus* (Cifelli, 1982), is not an apomorphy for ungulates, as evidenced by the wider distribution of this feature in other eutherians.

Hyperinflation of the tegmen tympani in mesonychids and cetaceans provides a very prominent contrast with some archaic ungulates (Fig. 2). The hypertrophied tegmen tympani in cetaceans (previously known as the "superior process") was considered to be "unique" to cetaceans (see Pompeckj, 1922; Kellogg, 1936). This study shows that it is a shared derived character of both cetaceans and mesonychids.

Given the phylogenetic framework established by independent evidence (Fig. 26), it is reasonable to interpret the hypertrophied tegmen tympani of mesonychids and cetaceans as being derived from the precursor condition of a moderately enlarged tegmen tympani, which is present in most archaic ungulates and other eutherians. Hyperinflation of the tegmen tympani is a key character that further modifies articulation of the petrosal with the rest of the basicranium. It is also correlated with differentiation of a very large suite of neomorphic topographic structures in neighboring areas, especially the epitympanic recess (see the chapter on character analysis).

The most noticeable apomorphic feature derived from the inflated tegmen tympani is the anterior process of the petrosal in both mesonychids and cetaceans. The anterior process provides additional contact surface between the petrosal and the squamosal in archaeocetes, and between the petrosal and anterior process of the tympanic in mysticetes and odontocetes. However, the squamosal is secondarily withdrawn from the anterior process of the petrosal in odontocetes, with only ligamentous connection between the two (Fig. 27). All articulating structures on the anterior process of the petrosal, as seen in modern cetaceans, can be attributed to the inflated tegmen tympani because the tegmen gives rise to the anterior process. Thus hypertrophy of the tegmen tympani is a necessary structural precursor to the anterior process, and an essential part of the neomorphic petrotympanic complex of cetaceans.

ARTICULATION OF THE PETROSAL

The primary transformation of the articulation of the petrosal is a shift of articulation from the medial side of the petrosal to the lateral side in the course of ungulate-to-cetacean evolution. In addition, there is loss of almost all bony articulation in the later evolution of odontocetes (Fig. 27). The primitive condition of eutherians involves a primary articulation of the petrosal with other bones of the basicranium through the mastoid process to the squamosal and the exoccipital. The pars cochlearis contacts the basioccipital. The tegmen tympani is small, and does not provide much surface for articulation with the squamosal.

In archaic ungulates, such as *Hyopsodus*, *Meniscotherium*, *Phenacodus*, and extant ungulates (Fig. 1), the tegmen tympani articulates with the squamosal. This articulation is further developed in mesonychids and cetaceans, and culminates in extant mysticetes in which the rugose surface of the hypertrophied tegmen tympani and the anterior process have extensive contact with the squamosal (Fig. 27). In comparison, the contact between the pars cochlearis and the basioccipital is retained in *Pakicetus* but completely lost in most protocetids, basilosaurids, mysticetes and odontocetes. As a result, the primary articulation of the petrosal with the basicranium shifted from its medial side (with the basioccipital) to the lateral side (with the squamosal).

Odontocetes are the only group in which much of the anterior process and tegmen tympani became detached from the squamosal by intervention of the anterior pterygoid sinus (Fig. 27D). This detachment from the squamosal is a secondary reversal or convergence to the condition of primitive ungulates (such as *Hapalodectes*) where there is relatively little articulation of the tegmen and the squamosal. It is a clear case of convergence, because the detachment differs among primitive eutherians and highly derived odontocetes. In the former it is due to weak development of the tegmen tympani. In the latter the tegmen and the anterior process are well developed, and detachment occurred as the pterygoid sinus eroded into the adjacent squamosal.

ARTICULATION OF THE TYMPANIC

The primary transformation seen in articulation of the tympanic bulla is one of reduction. The bulla initially articulates around most of its periphery (*Pakicetus*) but ends up articulating at only two isolated points—the anterior and posterior bullar processes (Fig. 27). The ectotympanic ring is the primitive condition of the ectotympanic bulla in eutherians (van der Klaauw, 1931; Novacek, 1977; MacPhee, 1981). In basal eutherians with an ectotympanic ring, the anterior crus of the ring either articulates with or is bound by ligamentous tissue to the entoglenoid process of the squamosal. The anterior crus rarely articulates with the tegmen tympani of the petrosal except in some edentates (Wible, pers. comm.). The posterior crus of the tympanic ring almost always attaches to the tympanohyal (Fig. 1: see the interlocking of the tympanohyal to the tympanohyal sulcus at the base of the posterior crus in *Ovis*).

In ungulates with a fully developed ectotympanic bulla, the anterolateral rim of the bulla overlaps extensively with the entoglenoid process of the squamosal. The meatal part of the bulla has a full contact with both the postglenoid process and the postmeatal crest of the squamosal. The medial rim of the bulla contacts the basioccipital bone. In summary, the bulla has extensive contact with the squamosal and the basioccipital, but relatively limited contact with the petrosal except through the tympanohyal, and almost no contact with the exoccipital (see for example *Sinonyx* in Fig. 8).

In pakicetids and protocetids, three neomorphic features appear in the bullar articulation: (1) The primary contact of the bulla to the petrosal is through the large mastoid process of the latter, although the posterior process of the tympanic only covers half of the mastoid process in *Pakicetus* (Figs. 10-11; also see Luo, 1998). (2) The posterior medial prominence of the bulla has developed a new articulation with the bullar process of the exoccipital. (3) A platform appears on the entoglenoid part of the squamosal for articulation with the bulla in pakicetids and some protocetids. In contrast, none of these neomorphic articulations were present in either *Diacodexis* or mesonychids.

The main transformation of the ectotympanic articulation in basilosaurids is loss of contact of the medial posterior prominence of the bulla with the bullar process of the exoccipital in larger basilosaurid taxa. The shift of the anterior process of the tympanic to the anterior process of the petrosal is incipient in some protocetids and most basilosaurids. In odontocetes and mysticetes, articulation of the ectotympanic with the anterior process of the petrosal is established at the expense of tympanic articulation with the squamosal.

ORIGIN OF THE SIGMOID PROCESS OF THE ECTOTYMPANIC

There are two prominent differences in the basicranium between mesonychids and cetaceans. In mesonychids the external auditory meatus of the squamosal is covered ventrally by an extrabullar floor of ectotympanic. In contrast, the meatus does not have such an extrabullar floor in all cetaceans including *Pakicetus*. The bulla of cetaceans has a sigmoid process, but this structure has been considered to be absent in all non-cetacean ungulates (except *Diacodexis*). An hypothesis of homology of the sigmoid process and its evolutionary origins must account for both differences.

As discussed in the chapter on character analysis, the sigmoid process of cetaceans has three putative precursor structures in the ectotympanic of non-cetacean ungulate mammals. The first hypothesis suggests homology of the sigmoid process to the anterior crus of the ectotympanic (or the anterior wall of the extrabullar meatus that is ontogenetically derived from the crus). If the sigmoid process is homologous with the anterior crus of the ring-shaped ectotympanic, then the absence of the extrabullar part of the ectotympanic floor for the squamosal meatus in cetaceans must be interpreted as a secondary loss from the ancestral condition (presence of the floor) in the common ancestor of mesonychids and cetaceans.

The second alternative hypothesis is that the sigmoid process of cetaceans is homologous with fusion of the folian process (a membranous ossification usually associated with the malleus), the anterior process of the malleus, and the anterior crus of the tympanic of non-cetacean mammals (van der Klaauw, 1931). Under this hypothesis, the sigmoid process of cetaceans is a compound structure formed from several elements that have independent origins in early embryogenesis in non-cetaceans.

The third alternative is that the sigmoid process is homologous to the entire extrabullar meatal floor of the ectotympanic (instead of the anterior crus or the anterior meatal wall of ectotympanic ring) in non-cetacean ungulates. This is supported by similarities in the inner surface of the sigmoid process of cetaceans and the meatal tube of the bulla in ungulates. The internal surface of the extant cetacean sigmoid process is a groove with an involuted rim, very similar to the inner surface of the tubelike ectotympanic floor of the external auditory meatus in terrestrial mammals. Rotation and simultaneous reduction in size would remove the meatal floor of the ectotympanic from the external auditory meatus of the squamosal. It requires only minimal morphological change for the extrabullar meatus of the ectotympanic of ungulates to be modified into a ventrally-open meatus in cetaceans. This hypothesis does not require postulating loss of any major bony element through the ungulate-cetacean transition, but it lacks support from embryonic evidence.

These competing hypotheses are testable. If the sigmoid process is a neomorphic structure made prominent by the lack of an extrabullar meatal floor of the ectotympanic due to early developmental arrest of the meatal floor, then the homology of the sigmoid process with the anterior crus of the tympanic ring would be supported. If the sigmoid process shows an anterior rotation during its embryonic development, then the homology of the sigmoid process of cetaceans to the extrabullar meatal process of terrestrial mammals would be supported.

We endorse the hypothesis of homology of the sigmoid process and the anterior crus (or the anterior wall of the extrabullar meatus) of the tympanic ring, as it is best supported by available embryological evidence. Homology of the anterior crus with the sigmoid process is plausible for two reasons: (1) Development of the sigmoid process from the anterior crus of the embryonic tympanic ring— in embryogenesis of the bulla, the anterior crus of the ectotympanic ring has remained as an independent process throughout later development. The only modification of the adult sigmoid process from the embryonic anterior crus is its slightly larger size (Ridewood, 1922). (2) Topographical relationships of the malleus, the conical apophysis, and the sigmoid process in cetaceans are almost identical to relationships of the malleus and the anterior crus of the ectotympanic in non-cetacean mammals (Fig. 1).

Moreover, the sigmoid process is a plate-like structure in pakicetids, representing a good structural intermediate between the flaring sigmoid process of more derived cetaceans and the anterior wall of the extrabullar meatal tube of the ectotympanic of mesonychids, which would have presumably developed from the embryonic anterior crus.

The second hypothesis, that the sigmoid process was a compound structure of the folian process and anterior process of malleus (van der Klaauw, 1931), lacks support from the well established embryological observation that the folian process is homologous to the gonial element (both being membranous ossifications), which becomes the malleolar ridge for attachment of the malleus (Ridewood, 1922; de Beer, 1937). The malleolar ridge (or process) is topographically separated from the base of the sigmoid by the chorda tympani sulcus in the adult bulla of basilosaurids (Fig. 21), indicating that the embryonic precursor to the "folian process" does not contribute to the sigmoid process.

The third hypothesis, that the sigmoid process is equivalent to the entire extrabullar meatal floor in extant non-cetacean mammals, is also contradicted by embryological evidence. Hanke (1914) shows that, in early cetacean development, the middle portion of the embryonic ectotympanic ring develops into a "W-shaped" folding. This folding becomes the conical apophysis of the bulla, a structure posterior to (and clearly separated from) the sigmoid process (see discussion in Luo, 1998). In contrast, this middle portion of the embryonic ectotympanic ring would develop into the ventral floor of the meatal tube in non-cetaceans.

Development of the conical apophysis in cetaceans suggests that the extrabullar meatus floor of non-cetaceans simply does not develop in cetaceans. Absence of the extrabullar meatal floor in cetaceans discounts the postulation that the sigmoid process would be equivalent to a twisted extrabullar meatus of the ectotympanic in non-cetaceans.

We propose the following series of transformations for the sigmoid process of the ectotympanic: the fully developed extrabullar tube in mesonychids represents the precursor condition (stage 0); the plate-like sigmoid process in pakicetids (stage 1) corresponds to a part of the anterior wall of the extrabullar meatus, and this in turn is intermediate to the twisted and flared sigmoid of the more derived cetaceans (stages 2 to 3).

PACHYOSTEOSCLEROSIS OF THE PETROTYMPANIC COMPLEX

Development of skeletal pachyostosis and osteosclerosis is common in marine mammals (Domning and de Buffrénil, 1991). The petrosal is usually osteosclerotic (dense and more heavily mineralized) in extant odontocetes, and pachyosteosclerotic (massive and hypertrophied, in addition to being dense and more mineralized) in extant mysticetes. The ectotympanic bullae of both odontocetes and mysticetes are not only pachyostotic (hypertrophied and massive) but also osteosclerotic (very dense). The cetacean tympanic bulla is better mineralized than the long bones of the mammalian skeleton (Currey, 1979). Increased mineralization of the tympanic bulla increases its density and stiffness, resulting in a high modulus of elasticity (Currey, 1979, 1984). The microstructure of the bulla is more randomly arranged than other types of bone (Currey, 1979), and the bone of the bulla is more isotropic, a property for transmitting sound vibration without distortion (J. Rensberger, pers. comm.). The hardness of the bulla borders on the lower range of enamel. The bone structure of the bulla is second only to dental enamel in density and stiffness among all vertebrate skeletal tissues (J. Rensberger, pers. comm.).

Pachyosteosclerosis of the petrotympanic complex in cetaceans increases the density differential between the middle ear bones and their surrounding soft tissues and vascular sinuses. The greater the differential, the more effective is sound deflection at the interface between the petrotympanic complex and surrounding soft tissues. The greater the contrast in density between the petrotympanic complex and the surrounding soft tissues, the less acoustic interference via conduction is possible from the rest of the cranium. In addition to their (very limited) utility for counteracting buoyancy (Domning and de Buffrénil, 1991), pachyosteosclerosis of the ear bones is almost certainly correlated with the origin of underwater hearing in different groups of vertebrates.

Massive and very dense (pachyosteosclerotic) ear bones are convergent adaptations to aquatic life that occurred independently in several unrelated groups of vertebrates that returned from land to an aquatic environment. In mosasaurs, a group of marine lizards of the Cretaceous, the quadrate bone is pachyostotic in comparison with terrestrial relatives (Pompeckj, 1922; Bell, pers. comm.). Similar pachyostosis of the ear region also occurs in aquatic ichthyosaurs (Pompeckj, 1922). The petrosal and the tympanic in sirenians have developed pachyostosis. Although to a lesser extent than in cetaceans, the tympanic ring is massive, and the mastoid process of the petrosal is hypertrophied in sirenians in contrast to that of terrestrial mammals (Ketten et al., 1992). Pachyosteosclerosis of the petrosal and tympanic is probably a prerequisite for all specialization for underwater hearing of both low frequencies and high frequencies.

Although animals with pachyostotic petrosals and tympanics always have pachyostotic middle ear ossicles (cetaceans and sirenians), animals with pachyostotic middle ear ossicles may not have massive petrosal or tympanics (pinnipeds, chrysochlorids, and palaeanodonts). Pachyostotic middle ear ossicles have a broader distribution in several unrelated groups of marine mammals (sirenians, Doran, 1878; Ketten et al., 1992; seals, Repenning, 1972; sea lions, Thewissen, 1994; walruses, Wyss, 1987) than pachyostotic petrosals and tympanics. Moreover, pachyostotic ossicles occur in several unrelated terrestrial fossorial mammals (Rose and Emry, 1983).

Living reptiles do not have the inner ear structures specialized for high frequency hearing, such as the organ of Corti, nor the bony structure associated with the organ of Corti (Wever, 1978). Nonetheless, dense and massive middle ear bones, such as the hypertrophied quadrate, occurred twice in convergent evolution in fossil reptiles, in mosasaurs and ichthyosaurs.

Pachyosteosclerosis of middle ear ossicles (the malleus, incus, and stapes) can be interpreted as an adaptation to hearing either airborne sound or waterborne sound in both high and low frequencies. But, by itself, pachyosteosclerosis is not sufficient for inferring high-frequency underwater hearing in an extinct marine mammal. Corroborating evidence from the inner ear is required. Pachyostosis of middle ear elements in stem groups of whales could be an adaptation for underwater hearing of all frequency ranges, but not necessarily a specialization for high frequency hearing. By the same principle, pachyostosis of the petrosal and the tympanic by itself may not be sufficient for inferring high frequency hearing in extinct whales.

Through the ungulate-cetacean transition, pachyosteosclerosis of the petrotympanic complex has been built up in three evolutionary steps.

(1) Inflation (pachyostosis) of the tegmen tympani in the common ancestor to mesonychids and cetaceans (stage 0). This initiates the pachyostosis (hypertrophy) of the petrosal above and beyond the generalized pachyosclerotic (dense) condition of the petrosal in most early mammals. The inflated tegmen tympani in amphibious protocetids is a primitive feature inherited from terrestrial ungulates. It is a structural precursor to a greater degree of pachyostosis in extant whales. The tegmen is tightly sutured to the squamosal in all archaeocetes, therefore its pachyostosis does not have any immediate effect for acoustic isolation of the ear.

(2) Formation of the ectotympanic involucrum in the common ancestor to all cetaceans including *Pakicetus* (stage 1). The pachyosteosclerosis of the involucrum begins with *Pakicetus*, and becomes more massive in *Protocetus* (Fraas, 1904; Kellogg, 1936), *Gaviacetus* (Figs. 11-12: *in*) and *Georgiacetus* (Hulbert et al., 1998; stage 2). Coupled with an incipient vascular sinus in the basicapsular fissure, it could serve as a crude sound barrier to acoustic interference between the left and right ears, however ineffectively. It is noteworthy that the promontorium of the petrosal of protocetids has not yet developed pachyostosis, whereas the bulla is already pachyosteosclerotic.

(3) Pachyosteosclerosis of the pars cochlearis and rotation of the promontorium occurred in the shared common ancestor of basilosaurids and extant cetaceans (stage 3 and beyond). The pars cochlearis is heavier and denser in basilosaurids than in more primitive protocetids. Coupled with the increase in density and mass, the pars cochlearis has rotated dorsally (Pompeckj, 1922; Fordyce, 1994; Thewissen, 1994).

PTERYGOID SINUS

The pterygoid sinus in extant cetaceans is filled with a fibrovenous plexus interwoven with air sacs (see Fraser and Purves, 1960: 29). The pterygoid sinus is primarily supplied by the pterygoid vein, but it also anastomoses with derivatives of the external carotid artery (Fraser and Purves, 1960; Vogl and Fisher, 1981, 1982). The sinus cavity is most prominent in the pterygoid region, and it is thus termed the pterygoid sinus (Fraser and Purves, 1960). Expansion of this vascular and pneumatic sinus into other parts of the basicranium has modified different basicranial characters in cetaceans. The pneumatic air space associated with the spongy sinus tissue is directly responsible for acoustic isolation of the petrotympanic complex. A vascular sinus can regulate pressure in the basicranium during diving. Pterygoid sinus cavities in the fossil taxa of either mysticetes or odontocetes can be identified according to their extant phylogenetic relatives (Witmer, 1994). However, for extinct archaeocetes that are outside the crown group of cetaceans, the task of interpreting the pterygoid sinus cavities is more difficult.

In discussing the pterygoid sinus (see chapter on character analysis), we established several osteological criteria. For a space or cavity to be interpreted as a pterygoid sinus in extinct archaeocetes, it must: (1) be open, (2) connect to a vascular structure for supply, (3) not be otherwise interpreted as some common non-sinus structure in non-cetacean mammals, and (4) have a smoothly periosteal surface.

It is widely accepted that sinus cavities are crucial for acoustical isolation of the ears (see reviews by Fleischer, 1978; Oelschläger, 1986a). However, for the sinus cavities to be effective in acoustic isolation, the sinus must be peribullar—the sinus must be large enough to surround and envelop the petrotympanic complex (Fleischer, 1978; Oelschläger, 1986a). It would be ambiguous whether a sinus functioned to isolate ears acoustically if the sinus were restricted to the tympanic space enclosed by the petrosal and the ectotympanic.

To identify a space or a gap as part of a peribullar sinus or peribullar air sac, it must be both outside the cranial cavity and outside the petrotympanic complex. Extant odontocetes have developed internal laminae or septa of the ptergyoid, the squamosal, the basioccipital, and the parietal. These secondary internal laminae exclude the petrotympanic complex from the cranial cavity. The petrotympanic complex does not participate in the braincase, and the sinus enveloping the petrotympanic complex is extracranial in extant odontocetes. It must be noted that these structures may be developed to some extant in mysticetes, but they are far from complete.

If bony grooves and sulci are located inside the braincase and not in the excluded peribullar cavity, then they are more likely to be a part of the dural vasculature associated with the meningeal tissue or the endocranial rete mirabiles around the brain (Bajpai et al., 1996; Geisler and Luo, 1998), and not part of the peribullar sinus in the basicranium.

These morphological criteria provide a basis for establishing the taxonomic distribution of sinuses among archaeocetes. The homology, ontogenetic variation, and phylogenetic evolution of these characters will be discussed as follows.

Homology.—The expanded pterygoid sinus is mostly extracranial in extant mysticetes. However, it is confluent with the endocranial cavernous sinus through the basicapsular fissure. The tympanic and peribullar parts of the extracranial pterygoid sinus are an extension of the endocranial cavernous sinus in the cranial cavity (Fraser and Purves, 1960). The extended cavernous sinus may have incorporated the inferior petrosal sinus that is a common feature in the tympanic region of noncetacean mammals. The endocranial sinus cavernosus in ungulates and its tympanic (extracranial) extension in cetaceans can be interpreted to be homologous.

This postulation is supported by two observations: (1) Fraser and Purves (1960) observed that the internal carotid artery traverses the tympanic part of the sinus in early embryogenesis before the artery degenerates in later development. The ephemeral internal carotid artery also traverses the cavernous sinus upon entering the cranial cavity (Fraser and Purves, 1960). The tympanic sinus anastomoses extensively with the endocranial cavernous sinus to such an extent that the two structures are confluent with each other in adult extant mysticetes. (2) In both terrestrial mammals and in cetaceans, the internal carotid artery passes through the cavernous sinus after it enters the cranial cavity.

It is possible to hypothesize that the extracranial sinus in the basicapsular fissure formed by an extension of the dural cavernous sinus since both structures have a common embryonic association with the internal carotid artery. Using the embryonic internal carotid artery as a criterion for homology, it can be argued that the confluent tympanic sinus and endocranial cavernous sinus of cetaceans are enlarged versions of the endocranial cavernous sinus of terrestrial mammals. The primitive endocranial cavernous sinus has a broad phylogenetic distribution among mammals and a more ancient phylogenetic origin. Therefore it is a reasonable candidate as a precursor to the extracranial sinus in cetaceans. If the peribullar part of the pterygoid sinus (largely extracranial) and the cavernous sinus (endocranial and associated with meninges and endocranial retes) are associated, then the cavernous sinus can be considered a plesiomorphic precursor to the derived condition of the peribullar sinus in cetaceans. We adopt this as a working hypothesis for interpreting the tympanic portion of the pterygoid sinus.

In adult odontocetes, the tympanic and peribullar sinuses are completely excluded from the endocranial (dural) sinuses by secondary bony septa or laminae of the peribullar cavity that form in late embryogenesis and/or in subadult stage. The vascular supplies for the peribullar cavity in the adult have switched to the external carotid artery and pterygoid vein (figs. 7 to 10 of Fraser and Purves, 1960; Vogl and Fisher, 1981, 1982).

During ontogeny in odontocetes, there was a transient stage at which the basicapsular fissure was open and the tympanic cavity was confluent with the cranial cavity (Eales, 1951; Pilleri et al., 1986) before the internal laminae develop in subadults. In mysticetes, this embryonic condition is retained in adults (Ridewood, 1922). Therefore, we hypothesize the absence of any direct connection between endocranial sinuses and peribullar sinuses in odontocetes to be a secondary reversal for this most-derived group of all cetaceans.

Ontogenetic Variation.—There is a clear difference in the size of the pterygoid sinus between subadult and adult skulls of basilosaurid archaeocetes. In subadult specimens (e.g., UM 94812), the bulla rests on the basal process of the basioccipital, and on the bullar process of the exoccipital. In contrast, in adults (UM 97507), the bulla is separated from the basal process of the basioccipital and the bullar process of the exoccipital by a wide gap. This difference in the size of the sinus between the subadult and adult skulls is also reported in *Balaenoptera* (Hanke, 1914; Fraser and Purves, 1960). In *Balaenoptera* the pterygoid bone contacts the bulla in early development, whereas there is a 10 cm gap between the two bones in adults, indicating dramatic growth of the sinus surrounding the bulla late in ontogenetic development (Fraser and Purves, 1960: 17).

Endocranial sinuses also increase in size during ontogeny (Fig. 23). As described earlier, grooves for the superior petrosal sinus and sigmoid sinus between the dorsal edge of the tegmen tympani and the adjacent squamosal are nonexistent in smaller (or subadult) basilosaurid skulls (UM 94812 *Dorudon atrox*; Kellogg, 1936: fig 6), but become a very conspicuous trough in larger (and presumably older) specimens (UM 97507 *Basilosaurus isis*).

We hypothesize that the extracranial pterygoid sinus was first developed by outward expansion of the endocranial (and dural) cavernous sinus into the extracranial space in the tympanic region. The expanding cavernous sinus probably annexed the inferior petrosal sinus. This occurred to some limited and variable degrees in protocetids (Stage 2; Thewissen et al., 1996; Geisler and Luo, 1998; Hulbert et al., 1998). Upon entering the tympanic region, the sinus expanded posteriorly to form the sinus on the exoccipital. However, the larger anterior ptergyoid sinus and medial peribullar sinus were only developed in more derived basilosaurids (stage 3), and more or less retained in mysticetes (stage 4). It is only in odontocetes that the peribullar sinus cavity begins to develop fully and expands to surround the lateral side of the petrotympanic complex (stage 5). This evolutionary scenario is justified on the following grounds.

The promontorium has some contact with the basioccipital in *Pakicetus*, thus blocking the pathway by which the endocranial cavernous sinus could have expanded extracranially into the tympanic area. This indicates that the extracranial sinus did not develop in the most primitive cetaceans.

The open space in the basicranium of protocetids appeared with development of the basicapsular fissure and the petrotympanic fissure in some protocetid whales. This suggests an extracranial expansion of the cavernous sinus into the tympanic cavity, possibly by annexing the inferior petrosal sinus. Some protocetids developed a small sinus area near the exoccipital and stylomastoid foramen (e. g., *Gaviacetus*), but no protocetids developed any anterior pterygoid sinus cavity as in more derived basilosaurids (Figs. 18, 22).

Further expansion of the sinus occurred in more derived basilosaurids. The sinus space is present in the basicapsular fissure, in the pterygoid (anterior to the bulla), and in the exoccipital region of smaller skulls. In larger adult skulls of basilosaurids, the pterygoid sinus is also on the medial side of (and external to) the petrotympanic complex, so that it is truly peribullar (Figs. 22C, 23B: *mpbs*).

The posterior (exoccipital) portion of the pterygoid sinus is also more enlarged in basilosaurids than in protocetids. This expansion of the sinus in the exoccipital region is correlated with the shift of location of the hypoglossal foramen. The hypoglossal foramen is on the ventral surface of the exoccipital and external to the tympanic cavity in protocetids, a primitive condition shared by pakicetids and ungulates. In contrast, basilosaurids have a more derived condition, in which the hypoglossal foramen is located in the sinus space on the tympanic side of the bullar (or falcate) process of the exoccipital. If the exit of the hypoglossal nerve (XII) on the exoccipital is regarded as an anatomical landmark, then the shift of its location is a reflection of the extent to which the pterygoid sinus has grown posteriorly in the exoccipital region.

It must be noted that the size of the medial peribullar sinus in adult skulls of basilosaurids is still much smaller than those of baleen-bearing mysticetes (Fig. 27). Geisler and Luo (1998) hypothesize that expansion of the peribullar sinus in basilosaurids is correlated with development of the caudal endocranial rete and reorganization of the cranial circulation.

Vascular sinuses in baleen-bearing mysticetes are larger in proportion to the skull and in absolute size than those of basilosaurids (Figs. 25, 28). Although the extracranial and peribullar sinuses are present in basilosaurids and mysticetes, neither group has developed internal walls to the peribullar sinus cavity like those of odontocetes.

A true peribullar sinus cavity with an internal wall formed by secondary laminae of cranial bones is an apomorphic structure of odontocetes that is absent in all archaeocetes and very incomplete in mysticetes. Upon exclusion of the tympanic sinus from the dural sinus by a bony wall of the peribullar cavity in odontocetes, the main vascular supply to the sinus came from anastomoses with the external carotid artery connected to the pterygoid vein (Walmsley, 1937; Fraser and Purves, 1960; Vogl and Fisher, 1981, 1982; Geisler and Luo, 1998).

VIII

EVOLUTION OF DIRECTIONAL HEARING IN WATER

Pachyosteosclerosis and vascular sinuses are two important anatomical characteristics of cetaceans facilitating directional hearing in water. The density of water is much greater than that of air, and it is close to the density of most mammalian tissues. Waterborne sound causes greater interference between left and right ears in a mammal than does airborne sound. Therefore, acoustic isolation of the two ears is crucial for maintaining directional hearing in aquatic mammals, regardless of whether they are specialized for high frequency or low frequency hearing.

In extant cetaceans, acoustic isolation of left and right ears is mostly effected by vascular sinuses between the petrotympanic complex and the rest of the basicranium, and, to a lesser extent, also by pachyosteosclerosis of the ear bones. Both vascular sinuses and pachyosteosclerosis serve the same function—to increase the density contrast between the middle ear bones and the surrounding bone and soft tissues. The greater the difference in density between the ears and the rest of cranium, the more effective is reflection of interfering sound through surrounding tissues.

Development of pachyostosis and pachyosteosclerosis precedes development of pneumatized vascular sinuses in the phylogenetic evolution of whales. Pachyosteosclerosis and vascular sinuses achieve density contrasts in different ways: the former by increasing the density of ear bones relative to a more or less constant density of surrounding soft tissues, while the latter decrease the density of soft tissues enveloping the ear bones relative to the density of surrounding bone. The earliest archaeocetes have only pachyostosis-osteosclerosis whereas the more derived archaeocetes have both pachyosteosclerosis and vascular sinuses.

PAKICETIDAE

Pachyostosis of the involucrum in pakicetids represents the initial evolution of increasingly greater pachyosteosclerosis in the petrotympanic complex. However, pakicetids retained the intrabullar part of the auditory meatus and the annulus for a tympanic membrane. Both indicate that these earliest cetaceans were fully capable of hearing airborne sound. As discussed above, some pakicetids may have been predominantly terrestrial, yet these terrestrial pakicetids have an interesting mosaic of pachyosteosclerosis of the involucrum (a derived character for underwater hearing) with the annulus of the tympanic membrane (a primitive, yet functionally significant character for hearing airborne sound). Pachyosteosclerosis in *Pakicetus* is restricted to the involucrum and does not develop in other parts of the ear region, such as the promontorium. We note that pakicetids have no extracranial vascular sinuses (at least according to our anatomical criteria for identifying such sinuses in stem groups). In summary, if pachyostosis in *Pakicetus* can be interpreted as evidence for hearing in water, then its ability to hear in water must have been very limited.

PROTOCETIDAE

In protocetids like *Gaviacetus* and *Georgiacetus* for which we have well preserved tympanics (Hulbert et al., 1998; Geisler and Luo, 1998; this study), the annulus for suspension of a planar tympanic membrane is lost. In its place a conical apophysis or middle conical process has developed from folding of the ectotympanic. Both indicate that archaeocetes lost the tympanic membrane early in their evolution. Pachyosteosclerosis has developed in the pars cochlearis of the petrosal. The basicapsular fissure is expanded to accommodate larger vascular sinuses. Hence, by inference, protocetids were more capable of hearing waterborne sound than airborne sound.

Nevertheless the pterygoid sinuses are poorly developed in protocetids, and they are not well enough developed to separate the tympanic bulla from the exoccipital. The sinuses did not surround the bulla. We infer that acoustic isolation of the two ears was very limited in protocetids. Thus these amphibious cetaceans had very limited ability for directional hearing in water.

BASILOSAURIDAE

Sinus cavities in the petrotympanic complex are much better developed in basilosaurids than in pakicetids or protocetids. The degrees of sinus development and dissociation of the petrotympanic complex from the cranium along much of its medial side indicate that basilosaurids probably had some degree of directional hearing.

The tightly coupled petrosal and tympanic bones of crown group cetaceans were lacking in basilosaurids. Unlike basilosaurids, mysticetes and odontocetes have the anterior process of the bulla withdrawn completely from the falciform (entoglenoid) process of the squamosal and this articulates exclusively with the anterior process of the petrosal. The sigmoid process has some contact with the squamosal. These characteristics suggest that underwater hearing in basilosaurids was not as highly developed as it became in later mysticetes.

HIGH-FREQUENCY HEARING

Pachyosteosclerosis of the middle ear bones, by itself, does not necessarily indicate an archaeocete was capable of high frequency hearing or echolocation. It is rather common for other aquatic vertebrates known to lack high frequency hearing and echolocation to have pachyosteosclerotic ear bones, and, as pointed out earlier, all vertebrates secondarily adapted to aquatic life show a greater degree of pachyosteosclerosis in the ear structures than their terrestrial relatives.

Ichthyosaurs and mosasaurs are two well known non-mammalian aquatic vertebrates. Both groups have some pachyosteosclerosis in the quadrate and in the stapes, while at the same time their reptilian inner ear lacks the structures required for high frequency hearing. Without corroboration from the inner ear structures known to be associated with high frequency hearing in extant mammals, pachyosteosclerosis of the ear bones can be only regarded as a general adaptation to directional hearing in water. Pachyosteosclerosis, by itself, is not sufficient to support an inference of specialized high frequency hearing in an extinct aquatic mammal. Thus there is no evidence that archaeocetes were capable of high frequency hearing.

IX

CONCLUSIONS

(1) Basicranial characters suggest that Mesonychidae and Cetacea are sister groups. Phylogenetic relatives of the mesonychid-cetacean clade are, successively: hapalodectids, artiodactyls, and other extant ungulates. Within Cetacea, all post-*Pakicetus* whales form a monophyletic group. Basilosaurids and crown group cetaceans are sister groups.

(2) The directional hearing of cetaceans, as correlated with pachyosteosclerosis and isolation of the petrotympanic complex by sinuses, evolved through four major steps in the ungulate-cetacean transition. First, in the common ancestor of all cetaceans, the tympanic bulla became enlarged and developed a thickened involucrum, while the middle ear was still fully capable of hearing airborne sound. Second, in the common ancestor of protocetids and more derived cetaceans, or possibly within protocetids and their descendants, the middle conical process of the bulla developed, indicating the presence of a conical tympanic ligament as in modern whales. The ectotympanic and petrosal had reduced contact to the basicranium because of the presence of an incipient sinus. Third, in basilosaurids and modern whales, the anterior process of the tympanic began to lose contact with the squamosal and exoccipital as the pterygoid sinus expanded both anteriorly and posteriorly external to the bulla. Fourth, in odontocetes, the tympanic is suspended primarily by the petrosal and to lesser extent by the squamosal, with a peribullar cavity completely surrounding the petrotympanic complex. Complete isolation of the petrotympanic complex occurred in a stepwise transformation in the evolution of cetaceans.

(3) Finally, study of basicranial characters in archaeocetes that are morphologically and temporally intermediate between land mammals and extant whales indicates that the highly specialized acute directional underwater hearing that we associate with modern cetaceans evolved gradually through a series of steps. Pakicetids retained the ability to hear in air but had little ability to hear in water. Protocetids had little ability to hear in air, and limited ability to hear directionally under water. The more derived basilosaurids had some ability for directional hearing, but less than that in modern mysticetes. There is no evidence in the petrotympanic complex to indicate that any archaeocetes were capable of high frequency hearing, which would be a prerequisite for echolocation. High frequency hearing and echolocation are innovations of odontocetes.

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