

Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 3: Eomysticetidae, a New Family of Primitive Mysticetes (Mammalia: Cetacea)

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ABSTRACT

A new family of relatively large, archaic fossil mysticetes, the Eomysticetidae, is based upon a new genus and new species, *Eomysticetus whitmorei*, from the late Oligocene Chandler Bridge Formation in the vicinity of Charleston, South Carolina, USA. With the exception of the primitive mysticete *Micromysticetus rothauseni* Sanders and Barnes (2002), all previously named Cetacea from these deposits are odontocetes. *Eomysticetus whitmorei*, known by much of an associated skeleton, is a baleen-bearing mysticete having rostral features that are characteristically associated with baleen-whale feeding adaptations. The rostrum is relatively broad and flat, the palate has nutrient foramina associated with baleen development, and the dentaries are elongate, oval in cross section, and edentulous. This whale shares many cranial features with Archaeoceti, e.g., the narrow, elongate intertemporal region, narrow supraorbital processes of the frontals, elongate zygomatic processes of the squamosals, and small cochlear portion and narrow anterior process of the periotic. The numbers and structure of the vertebrae and ribs are intermediate between archaeocetes and cetotheriid mysticetes, and the relative length of the humerus compared with that of the distal limb bones (radius and ulna) is intermediate between those of archaeocetes and Neogene mysticetes.

A second, more highly evolved species, *Eomysticetus carolinensis*, described herein, is represented by a partial skull also from the Chandler Bridge Formation. The osteology of Eomysticetidae strongly reinforces the ancestral-descendant relationship of Archaeoceti to Mysticeti and helps to substantiate the theory of the monophyly of the Cetacea. *Eomysticetus whitmorei* is the most archaic baleen-bearing mysticete yet described and survived into late Oligocene time as a relict form. In its degree of cranial telescoping it is more primitive than the contemporaneous toothed mysticetes of the family Aetiocetidae and contemporaneous baleen-bearing members of the Cetotheriidae. The presence of the second species, *E. carolinensis*, in the same formation demon-

strates the newly recognized evolutionary diversity of the Oligocene Cetacea and the fact that multiple lineages of various groups evolved simultaneously. The family Eomysticetidae is the presumed sister taxon to all of the more-derived baleen-bearing Mysticeti.

Introduction

The Tertiary marine deposits of the South Carolina coastal plain have furnished important fossil cetacean remains since 1845, when Robert W. Gibbes described the archaeocete *Dorudon serratus* from Eocene beds in the vicinity of the Santee River. Subsequent discoveries have included two odontocetes, *Agorophius pygmaeus* (Müller, 1849) and *Xenorophus sloanii* Kellogg, 1923, both of which were described from holotypes found in the Ashley Formation near Charleston. As demonstrated by Whitmore and Sanders (1976), the Ashley Formation is of late Oligocene age, and not Eocene as had been supposed by previous authors. In recent years, studies emanating from the Charleston Museum have disclosed a previously unrecognized formation overlying the Ashley. This rock unit, the Chandler Bridge Formation of Sanders et al. (1982), also is of late Oligocene age (ca. 28 million years ago (Ma)) and has produced a wealth of cetacean material that is providing critical new information about the evolution and systematics of Oligocene Cetacea (Whitmore and Sanders, 1976; Sanders, 1980; Sanders et al., 1982; Weems and Sanders, 1986; Sanders and Barnes, 1989; Barnes and Sanders, 1990).

In October 1975, a Charleston Museum party under Sanders's direction excavated the remains of the first baleen whale to be found in the Oligocene beds around Charleston. The specimen was recovered from the Chandler Bridge Formation in Dorchester County, South Carolina, approximately 20 miles (32.2 km) north of Charleston. Subsequently, another baleen-bearing mysticete was found in this formation, and these two specimens are the subject of this paper. Previously described Oligocene mysticetes from the North Atlantic and Tethys re-

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gions had consisted of two taxa, *Cetotheriopsis lintianus* (von Meyer, 1849) from Linz, Austria, and *Cetotheriopsis tobieni* Rothausen, 1971, from the North Sea Basin near Dusseldorf, Germany. Those taxa and the new form *Micromysticetus rothauseni* are discussed elsewhere in this volume (Sanders and Barnes, 2002).

The first South Carolina specimen is a partial skeleton representing a new genus and new species with cranial characters that are in many ways intermediate between those of previously described members of the suborders Archaeoceti and Mysticeti (Sanders and Barnes, 1989; Barnes and Sanders, 1990). The cranium and dentaries of this specimen are nearly complete and were associated with vertebrae, ribs, and the right forelimb. The second specimen is a partial skull representing another species in the genus.

Two of the most intense subjects of current debate about cetacean evolution are their place of origin and ancestry and whether they are monophyletic, diphyletic, or triphyletic. The descriptions of the new fossil cetaceans in this study shed light on the second of these questions and reinforce the theory that the Cetacea are monophyletic. New morphologic and taxonomic interpretations and subordinal definitions are proposed, and comparisons are made with relevant previously named fossil species.

ACKNOWLEDGMENTS.—Initial thanks must go to Catherine Key, who discovered the holotype of *Eomysticetus whitmorei* and reported it to Sanders. She and Mary Worley contributed many hours of assistance with the excavation work, to which Chaz Duc and Joel Padgett also made valuable contributions. We thank Leroy Blackwell for permission to excavate the holotype on his property and for furnishing a backhoe and operator to remove the Pleistocene overburden from the site. A considerable portion of the preparation work was made possible by a grant from the Charleston Scientific and Cultural Educational Fund; the remainder was funded by the Charleston Museum. For their assistance with the preparation of the holotype we thank Barry Albright, Daniel Davis, Jonathan Geisler, Chester Linder, Aaron Stokes, Mark Taylor, and Robert E. Weems (USGS). Jonathan Durst-Glenn assisted in proofreading the manuscript.

We are particularly grateful to Vance McCollum and Barry Albright, the collectors of the holotype of *Eomysticetus carolinensis*, for their generosity and interest, and we appreciate Mr. McCollum's assistance in the preparation of that specimen. Tanya Elston also aided with the preparation work. Bryan Stone produced all of the photographs except those in Figures 9, 10, 11, 12, and 17C, which were made by the first author with assistance from Aaron Stokes. Chris Olm prepared the drawing for Figure 3B, to which the first author added final details. The remainder of the line drawings were produced by the first author. Peter Laurie made the vertebral measurements for Figure 28, and Clyde White assisted with the tabulations. Milton Rhodes assisted with tabulations for Figure 29. The Charleston Museum and the Natural History Museum of Los

Angeles County and its foundation provided facilities, salaries, and travel funds for the authors that made this study possible. Ewan Fordyce reviewed the manuscript and provided helpful comments. Clayton E. Ray and Frank C. Whitmore, Jr., provided access to fossil cetacean material in the NMNH and were helpful in numerous other ways.

In our description of *Micromysticetus rothauseni* elsewhere in this volume, we have recorded our appreciation of Clayton Ray and his many contributions to vertebrate paleontology. We wish now to acknowledge another long-time friend and colleague, Frank C. Whitmore, Jr., whom we have honored with the patronym *Eomysticetus whitmorei*. We can think of no paleocetologist more deserving of patronymic recognition, but it is at best a very inadequate means of expressing to him our sincere thanks for his friendship and encouragement over the years. We have been the beneficiaries of his wise counseling and sound advice on many occasions, but as much as anything we have appreciated his ever-cheery disposition, even in the face of recent visual difficulties that would have defeated a less courageous person. Admired and respected by all who know him, he is at once an excellent scientist and a valued friend, and we consider it a privilege to have worked with him. Thank you, Frank, for everything.

MATERIAL AND METHODS

Terminology for cranial anatomy follows Kellogg (1927) and Fraser and Purves (1960). With some modifications required by the morphology of the specimen, cranial measurements follow the methodology of Perrin (1975) and of Kellogg (1936, 1965). For the measurements of the mandibles, vertebrae, and forelimb we have followed Kellogg (1936, 1965, 1968, 1969), also with required modifications. The reconstruction of the skull is based upon photographs of the specimen.

Geological interpretations of the unit that produced the holotype specimen are in accordance with the original description of the Chandler Bridge Formation (Sanders et al., 1982) and with subsequent observations about that unit (Weems and Sanders, 1986).

Authorships of modern taxa mentioned in the text follow Rice (1984), and synopses of living species, genera, and suprageneric groups and their authorships may be found there and in Hershkovitz (1966).

ABBREVIATIONS—Institutional abbreviations used in this paper are as follows:

ChM	The Charleston Museum, Charleston, South Carolina
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
USGS	United States Geological Survey
USNM	collections of the National Museum of Natural History, including collections of the former United States National Museum

Anatomical abbreviations used in this paper are as follows:

aon	antorbital notch
bc	basioccipital crest

Boc	basioccipital
ch	cranial hiatus
Eo	exoccipital
fm	foramen magnum
fps	foramen pseudovalle
Fr	frontal
gf	glenoid fossa
hpt	hamular process of pterygoid
jn	jugular notch
lc	lambdoidal crest
Max	maxilla
mea	external auditory meatus
mf	mandibular foramen
mrg	mesorostral groove
Na	nasal
Oc	occipital condyle
Pa	parietal
Pal	palatine
pgl	postglenoid process
Pmx	premaxilla
pop	paroccipital process
Pt	pterygoid
pts	fossa for pterygoid sinus
Soc	supraoccipital
sop	supraorbital process
Sq	squamosal
sqf	squamosal fossa
ssf	secondary squamosal fossa
tf	temporal fossa
Vo	vomer
zps	zygomatic process of squamosal

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758

Order CETACEA Brisson, 1762

Suborder MYSTICETI Flower, 1864

Superfamily EOMYSTICETOIDEA, new superfamily

INCLUDED SUPERFAMILIES.—*Eomysticetoidea*, new superfamily; *Balaenopteroidea* (Gray, 1868) sensu Mitchell, 1989; *Eschrichtioidea* (Ellerman and Morrison-Scott, 1951) sensu Mitchell, 1989; *Balaenoidea* Brandt, 1873 (sensu Mitchell, 1989).

INCLUDED FAMILY.—*Eomysticetidae*, new family, only.

Family EOMYSTICETIDAE, new family

DIAGNOSIS.—The same as for the genus.

TYPE AND ONLY INCLUDED GENUS.—*Eomysticetus*, new genus.

Eomysticetus, new genus

DIAGNOSIS.—A mysticete differing from all other baleen-bearing Mysticeti by having an elongate and narrow intertemporal region and floor of squamosal fossa with small pit-like depressions herein termed “secondary squamosal fossae”; dif-

fering from members of *Aetiocetidae* by the absence of teeth in adulthood; differing from *Cetotheriidae*, *Balaenopteridae*, *Balaenidae*, *Neobalaenidae*, and *Eschrichtiidae* by having elongate anterolateral processes of nasal bones, extremely long zygomatic processes of squamosals, very thin blade-like anterior process of periotic and small posterior process with well-defined facet for articulation with tympanic bulla, and humerus as long as radius and ulna. Differs from *Balaenopteridae*, *Balaenidae*, *Neobalaenidae*, and *Eschrichtiidae* by having naris near mid-length of rostrum, exceptionally elongate nasal bones, parietals exposed along intertemporal region between frontals and apex of supraoccipital, periotic with transversely compressed anterior process and no dorsal process on cochlear portion, and large coronoid process of dentary and posterior edge of coronoid elevated above anterior edge.

The two known species of *Eomysticetus* share the following similarities: exoccipital thick and posteriorly flared; condyles broad and not protruding from skull; basioccipital slightly vaulted transversely; basioccipital crests short anteroposteriorly and wide transversely; large recess for posterior process of periotic; postglenoid process short, thin anteroposteriorly, and continuous with falciform process medially; glenoid fossa with oblique ridge from anteromedial to postlateral; dorsal curvature of zygoma; flattened ventral surface of glenoid fossa; large foramen pseudovalle; wide jugular notch; narrow intercondylar notch; asymmetrical and interfingering frontoparietal suture; sagittal crest present on apex of parietals in intertemporal region; sagittal crest on apex of supraoccipital at right of midline; secondary anteroposterior crest flanking each side of sagittal crest at apex of occiput; paroccipital process not extending laterally as far as lateral edge of zygoma; floor of squamosal fossa with a pit-like depression herein termed the “secondary squamosal fossa.”

TYPE SPECIES.—*Eomysticetus whitmorei*, new species.

INCLUDED SPECIES.—*Eomysticetus whitmorei*, new species, and *Eomysticetus carolinensis*, new species. Late Oligocene, South Carolina, USA.

ETYMOLOGY.—From $\epsilon\omicron\varsigma$ (eos) (Greek), dawn, and $\mu\iota\varsigma\tau\alpha\kappa\omicron$ (mystako) (Greek), whisker or mustache, in reference to the baleen plates in mysticete whales; and from *cetus* or *cete* (Latin, from Greek *ketos*), whale.

Eomysticetus whitmorei, new species

FIGURES 3–17

DIAGNOSIS.—A species of *Eomysticetus* differing from *E. carolinensis*, n. sp., in having transversely thicker basioccipital crests; zygomatic process of squamosal thicker, more nearly parallel to sagittal plane, and extending beyond apex of supraoccipital; a facet on ventral surface of distolateral end of zygoma for articulation with jugal; lambdoidal crests more dorsally directed and not overhanging temporal fossae; parietals nearly vertical on either side of intertemporal region rather than sloping ventrolaterally; sagittal crest on parietals in intertempo-

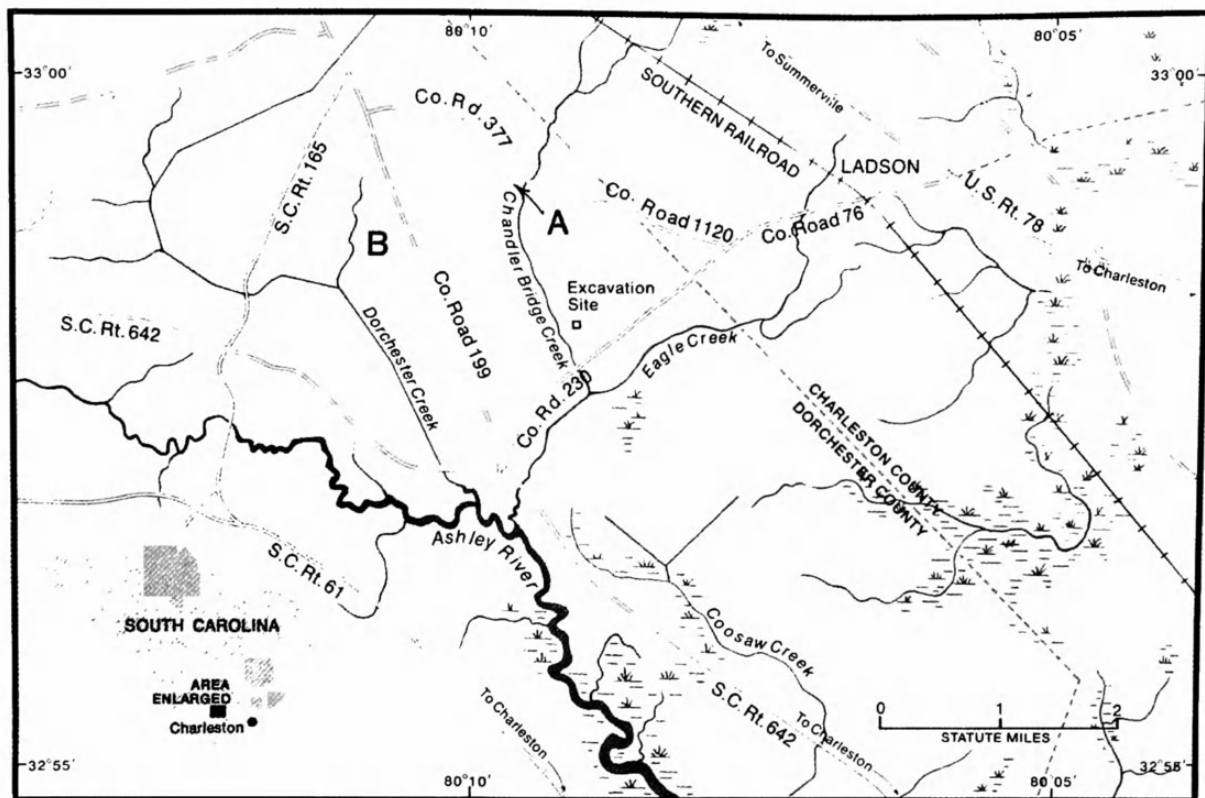


FIGURE 1.—Map showing the type localities of *Eomysticetus whitmorei*, new genus and new species (A), and *Eomysticetus carolinensis*, new species (B), near Charleston, South Carolina. ("Excavation site" on map is location of Charleston Museum excavation of the Chandler Bridge Formation (Sanders, 1980). Base map from Sanders 1980, courtesy of National Geographic Society.)

ral region blade-like posteriorly and not rounded; dorsal exposure of parietal along midline of intertemporal region 50% longer; dorsomedial surface of zygomatic process of squamosal convex rather than flat; deeper supracondylar fossa; articular surfaces of occipital condyles more protuberant posteriorly and more distant from occipital surface.

HOLOTYPE.—ChM PV4253; skull, both periotics, both tympanic bullae, both dentaries; seven cervical vertebrae, seven thoracic vertebrae, two lumbar vertebrae, and one possible caudal vertebra; parts of at least 17 ribs and a possible sternal rib; right scapula, humerus, radius, and ulna; collected by Albert E. Sanders and party, October 1975.

TYPE LOCALITY (Figure 1).—South Carolina, Dorchester County, Greenhurst Subdivision, west bank of drainage ditch at junction with Chandler Bridge Creek, 0.16 km southwest of Jamison Road (County Road 377), approximately 32°52'54"N and 80°09'30"W (USGS, Stallville 7.5' topographic quadrangle). Elevation of dorsal surface of cranium 5.7 m (18.58 ft.) above mean sea level.

FORMATION AND AGE (Figure 2).—Bed 3 of the Chandler Bridge Formation, a late Oligocene (Chattian) marine unit laid down approximately 28 Ma (Sanders et al., 1982). The uppermost portion of the Chandler Bridge Formation, bed 3, is a beach zone from which a large number of marine vertebrate remains were recovered in a major excavation conducted by the

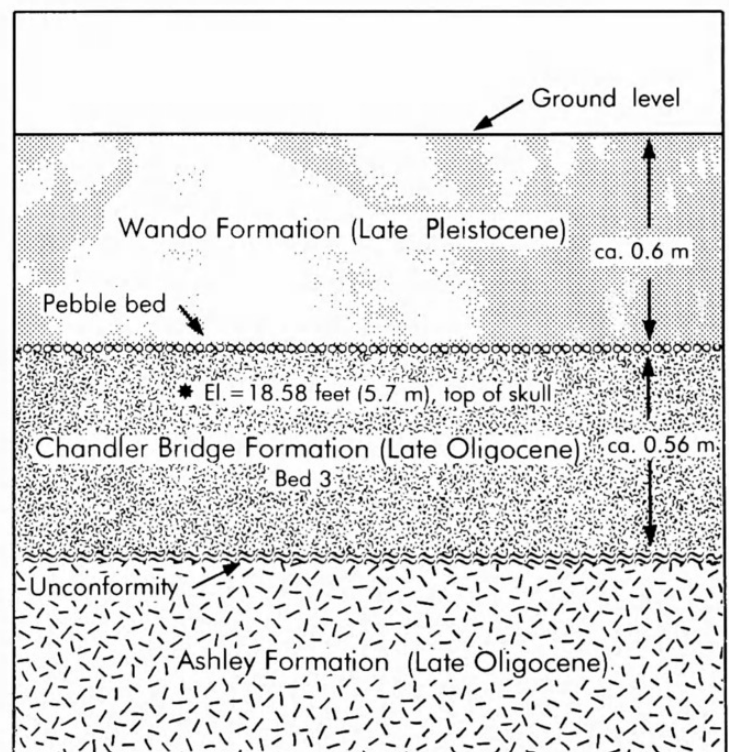


FIGURE 2.—Stratigraphic section at the type locality of *Eomysticetus whitmorei*, new genus and new species, from the Chandler Bridge Formation. (Not to scale.)

Charleston Museum (Sanders, 1980). The site of that excavation is the type locality for the Chandler Bridge Formation and is 2.1 km (1.3 mi.) southeast of the type locality of *Eomysticetus whitmorei*.

The Chandler Bridge Formation unconformably overlies the late Oligocene Ashley Formation (ca. 30 Ma), a calcarenite that underlies the entire Charleston area. Together, these two formations have produced one of the largest and most diverse assemblages of cetacean remains recovered from Oligocene deposits. Squalodontoids and other primitive toothed cetaceans are by far the most numerous, whereas mysticetes are relatively rare. An early Chattian age for the Chandler Bridge Formation is indicated by the presence in this formation of undescribed squalodonts of the same evolutionary grade as *Eosqualodon langewieschei* Rothausen, 1968 (see Whitmore and Sanders, 1976; Sanders, 1980), found in Eochattian sands (Chattian A) at Doberg, Germany, that have been referred to nannoplankton zone NP24 (Martini and Müller, 1975) and are considered to be of early Chattian age (Curry et al., 1978:46). A detailed appraisal of the age of the Chandler Bridge Formation was given by Sanders et al. (1982). As the latter authors have noted, "Because the Chandler Bridge Formation is thin and permeable and thus leached of carbonate, attempts to recover a calcareous microfauna or microflora have been either unsuccessful or equivocal in that the few specimens obtained may represent material reworked from the underlying Ashley Member [now Ashley Formation] . . . into bed 1" (Sanders et al., 1982:H114). E. Martini, however, recently examined the nannoplankton in samples of the Ashley Formation from the type locality of the Chandler Bridge Formation and found the Ashley to be referable to zone NP24 (pers. comm., E. Martini to K. Rothausen, Rothausen to A.E. Sanders, June 1990). Because the same evolutionary grades and many of the same genera are represented in the cetaceans, phocids (Koretsky and Sanders, 2002), sea turtles, a new crocodilian (Erickson and Sawyer, 1996), and other vertebrate faunas of the Ashley and the Chandler Bridge Formations, we consider that these two formations belong to the same biostratigraphic interval (NP24) and that very little time (probably no more than about 2 My) elapsed between the deposition of these two units. The age of the Chandler Bridge Formation is placed at approximately 28 Ma and the underlying Ashley Formation at about 30 Ma. Those estimates are suggested by (1) the primitive aspect of the cetacean fauna of the two units, among which are three undescribed toothed mysticetes with archaeocete-like dentition (Barnes and Sanders, 1996), several relatives of the most-archaic known odontocete, *Xenorophus sloanii* Kellogg (1923), from the Ashley Formation; and the archaic *Eomysticetus whitmorei* and *E. carolinensis* described in this paper; but primarily by (2) biostratigraphic correlation of the Ashley Formation with nannoplankton zone NP24.

ETYMOLOGY.—The species is named in honor of Frank C. Whitmore, Jr., formerly of the USGS, who has contributed

greatly to the study of fossil cetaceans and who has supported us in our efforts in innumerable ways.

DESCRIPTION.—*Skull*: The skull of *Eomysticetus whitmorei* is very long and has a flat, narrow rostrum; a narrow, triangular braincase; large and widely placed zygomatic processes of the squamosals; and an elongate and greatly constricted intertemporal region (Figure 3, Table 1). We have estimated the length of the skull at 1590 mm by articulating the complete right dentary with the right glenoid process and leaving 5 mm clearance for connective tissue.

The rostrum is composed mostly of maxilla on the dorsal surface, as in other mysticetes. The ventral surface of the rostrum lacks development of nutrient grooves, as is typical of other mysticetes. The mesorostral gutter is open dorsally for only a short distance immediately anterior to the narial opening. The premaxillae converge at a point 180 mm anterior to the nasals, and at this location they are a mere 10 mm apart. From that point anteriorly they are closely approximated on the anterior portion of the rostrum, effectively roofing over the mesorostral groove in that region. Anterior to the naris the premaxillae expand anteriorly and are convex transversely, but adjacent to the narial region the premaxillae are narrower and more convex along their midlines. On the right side, adjacent to the narial opening, a piece of the right maxilla attaches to the premaxilla. It laps both dorsally and ventrally to the lateral margin of the premaxilla, and its dorsal surface is convex. Posteriorly, the premaxillae diverge posteriorly at the nares and curve around the lateral margins of the nasal bones, producing a slightly convex surface that slopes ventrolaterally away from the nasals. Adjacent to the anterolateral corner of the naris, the premaxilla is elevated, as in Aetiocetidae, and then slopes anteroventrally (Figure 4). The premaxillae widen posteriorly, extending into the interorbital area and terminating a few millimeters anterior to the posterior tip of the nasals. Breakage of the posterior ends of the premaxillae and nasals prohibits an exact measurement of the latter distance. The posterior termination of each premaxilla appears to have tapered between the ascending process of the frontal and the posterior end of the nasal and probably terminated at the same point as the nasals.

The nasal bone is 300 mm in length, exceeding that of any other described mysticete. It extends posteriorly to a point between the temporal crests and constitutes approximately 18.7% of the estimated total length of the skull. At its midline, the anterior margin of the nasal is virtually straight across transversely, then is slightly concave laterally. Farther laterally, toward the margin of the premaxilla, the anterior edge of the nasal puts forth a small process that is directed farther anteriorly and is sutured into a recess along the medial side of the premaxilla (Figure 3).

The right and left nasals are joined at the midline by an irregular, meandering suture. They are arched transversely, and at the apex of the narial opening they are slightly upturned. From the edge of the narial opening the nasals slope gently downward and backward into a shallow but quite noticeable swale

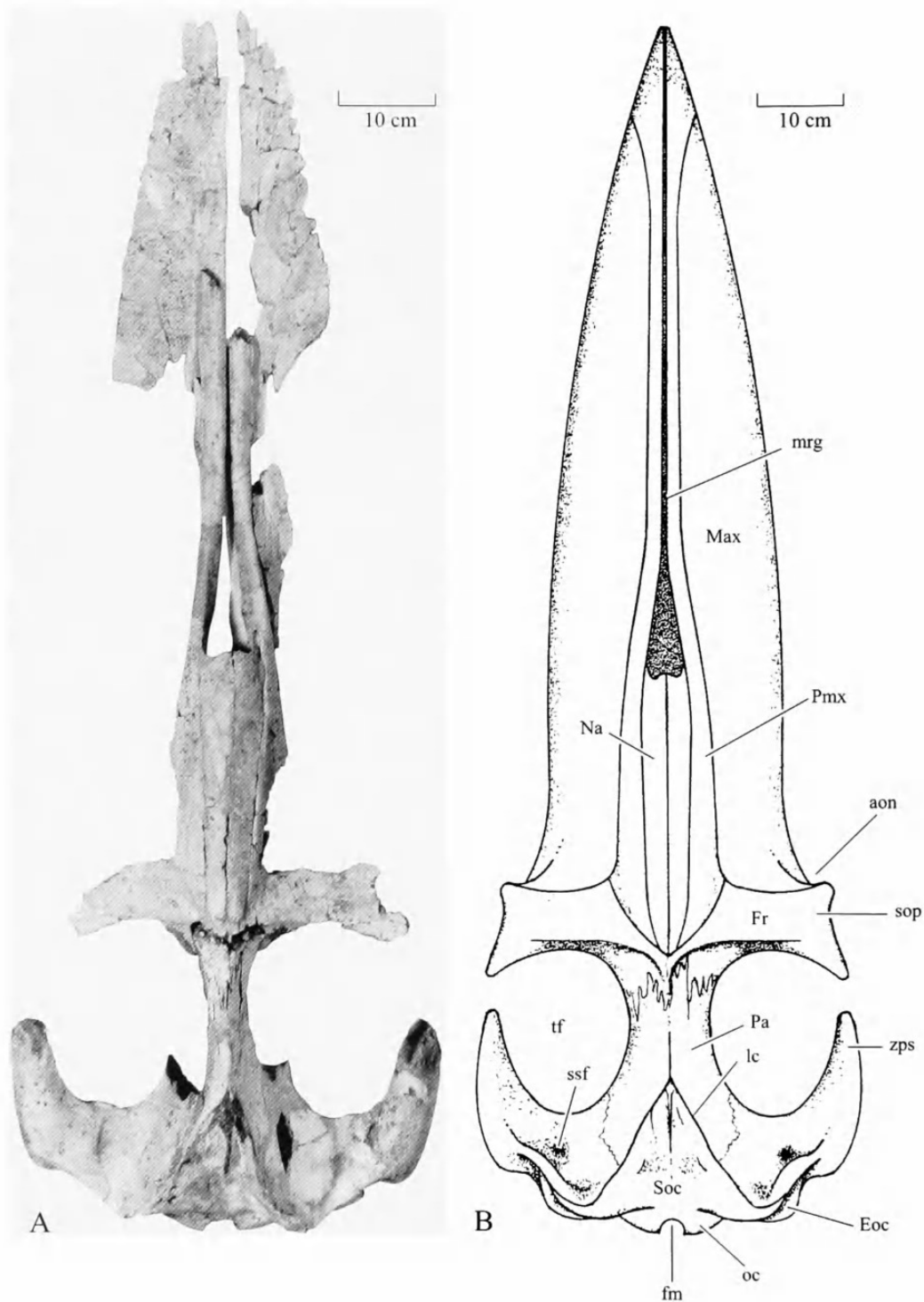


FIGURE 3.—*Eomysticetus whitmorei*, new genus and new species: A, holotype, ChM PV4253, skull, dorsal view; B, reconstruction of skull based upon holotype, dorsal view. (Solid lines in areas of missing bone (see Figure 3A) are hypothetical configurations. Abbreviations are explained in "Material and Methods.")

that extends posteriorly from the anterior margins of the nasals as far as the apex of the supraoccipital (Figure 4). The nasals are widest anteriorly, tapering posteriorly as they overlap the frontals, terminating posteriorly slightly behind the point of the temporal crests.

The supraorbital processes of the frontals are incomplete on the holotype. Their posterior margins are preserved, but the an-

terior and lateral margins are missing on both sides. The right supraorbital process of the frontal is more complete than the left one and seems to have been relatively narrow in comparison with most mysticetes, although that appearance might be an artifact of preservation. The posterior margin is concave, and the anterior margin is mostly incomplete, so that the relationship with the maxilla is not clear. The distal margin of each

TABLE 1.—Measurements (in mm) of the holotype skulls of *Eomysticetus whitmorei*, new genus and new species (ChM PV4253), and *Eomysticetus carolinensis*, new species (ChM PV4845). Parentheses denote estimated measurements.

Character	<i>E. whitmorei</i>	<i>E. carolinensis</i>
Condylobasal length	(1590)*	—
Length of rostrum	(1147)	—
Preserved portion of skull, broken end of left premaxilla to posterior surface of left occipital condyle	1035	—
Anterior end of left premaxilla to apex of supraoccipital	820+	—
Greatest length of left premaxilla	640+	—
Greatest width of right maxilla (preserved portion)	56	—
Anterior end of right premaxilla to anterior end of right nasal bone	350+	—
Anterior end of right nasal bone to apex of supraoccipital	469	—
Deepest point of swale between tip of nasals and apex of supraoccipital	37	—
Greatest length of right nasal bone at midline	(300)	—
Anterior width of right nasal bone	35	—
Combined width of nasal bones, anteriorly	71	—
Combined width of nasal bones, posteriorly	(40)	—
Length of anterolateral extension of left nasal bone from plane of anterior end of nasals	(26)	—
Height of anterior ends of nasal bones above plane of premaxillae at nasal opening	(23)	—
Greatest width of external nares	49	—
Transverse distance between outside margins of premaxillae at level of anterior ends of nasal bones	95+	—
Length of intertemporal region, temporal crest to plane of apex of supraoccipital	192	—
Transverse distance between outside margins of preserved portions of supraorbital processes	373	—
Greatest width across zygomatic processes of squamosals	480	(510)
Maximum length of right zygomatic process, extremity of postglenoid process to anterior end of zygoma	261	233
Length of temporal fossa	357	—
Width of temporal fossa	170	183
Dorsal margin of foramen magnum to apex of supraoccipital	229	236
Transverse diameter of foramen magnum	(32)	43
Vertical diameter of foramen magnum	46.7	44.2
Greatest distance between lateral margins of occipital condyles	142	134.5
Vertical diameter of right occipital condyle	76	84
Greatest transverse diameter of right occipital condyle	58	53
Distance from inner margin of right occipital condyle to outer edge of right exoccipital	163	147.5
Distance between lateral margins of exoccipitals	(350)	(342)
Vertical distance from basisphenoid to apex of supraoccipital	(168)	—
Greatest distance between lateral margins of basioccipital crests	132+	131
Internal length of braincase	(120)	(100)
Internal height of braincase, left cerebral cavity	80	—
Internal height of braincase, right cerebral cavity	81	—
Greatest internal height of braincase at midline	87	87
Greatest internal width of braincase	157	—

*Estimated with complete right dentary articulated

supraorbital process is incomplete but is slightly upturned. A well-defined temporal crest extends transversely across the posterodorsal surface of the supraorbital process and reaches nearly to the midline of the skull, converging with the posterior margin of the supraorbital process and continuing laterally onto the dorsal surface of the process. This crest is highest at its medial part.

The intertemporal region is greatly elongate and narrow and is composed dorsally of a relatively short exposure of the frontals and the anteroposteriorly more elongate parietal bones. The frontals and parietals are joined by irregularly and randomly interdigitating sutures (Figure 5). The intertemporal constriction ascends toward the apex of the occipital shield, and the posterior half of the parietals form a short blade-like sagittal crest

(Figures 6, 7).

The sagittal crest diverges at the juncture with the apex of the supraoccipital, and the remaining bone surface indicates that it was confluent with the lateral margins of the occipital shield. Anteriorly, the supraoccipital is triangular and relatively small and has a prominent sagittal crest beginning approximately at the middle and extending toward the apex. The anterior region of the occipital shield is elevated, but immediately posterior to the sagittal crest it is concavely depressed. Mediolateral to this depression there is a thickened tuberosity on the supraoccipital next to the inner wall of each lambdoidal crest. At that point, the supraoccipital begins to flare outward ventrolaterally. More posteriorly, the surface of the occipital shield is flat to convex dorsal to the foramen magnum, and a condyloid fossa is

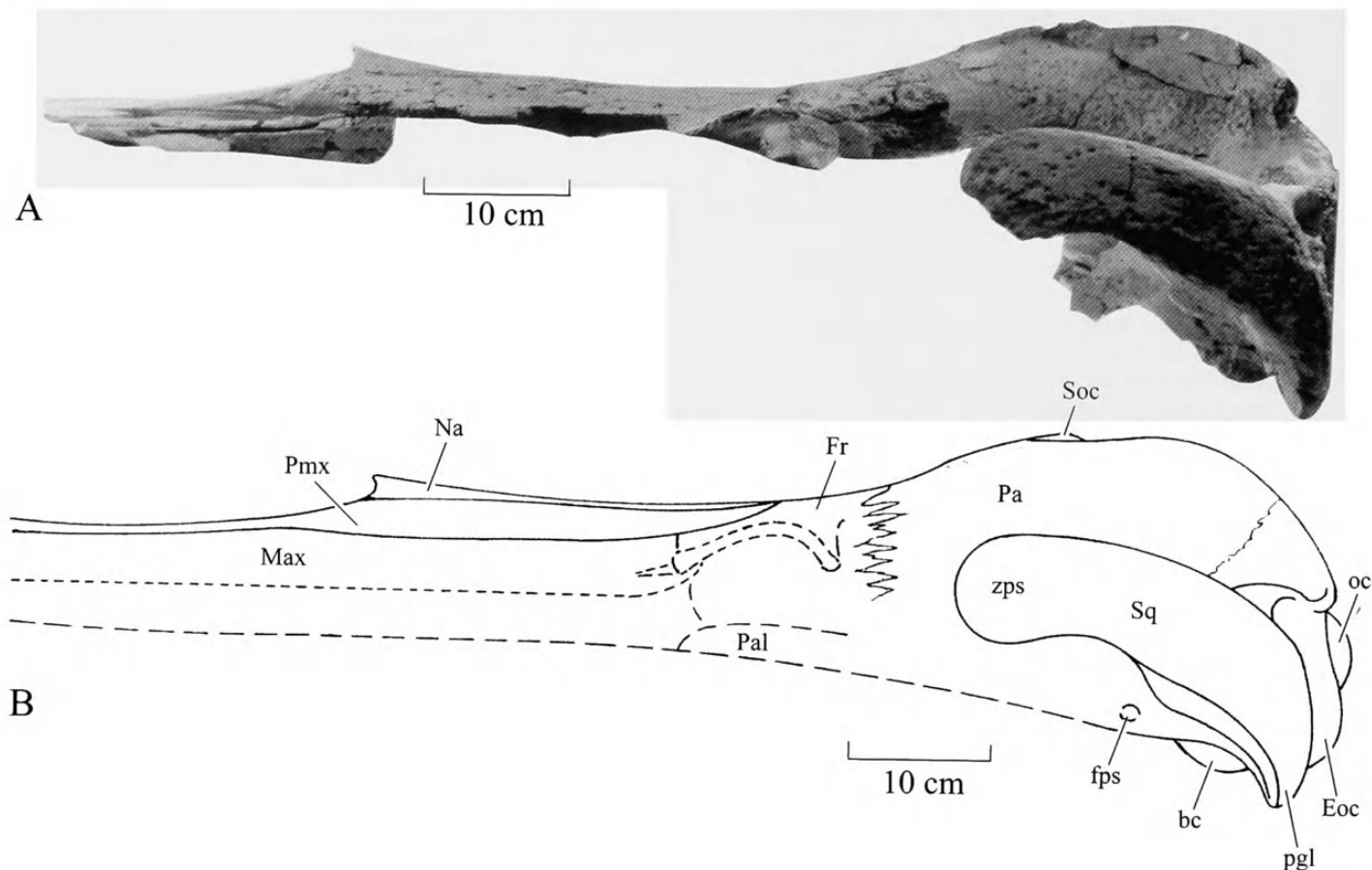


FIGURE 4.—*Eomysticetus whitmorei*, new genus and new species: A, holotype, ChM PV4253, skull, left lateral view; B, reconstruction of skull based upon holotype, left lateral view. (Dashed lines represent hypothetical configurations. Abbreviations are explained in "Material and Methods.")

present above each condyle. The occipital condyles are large, are located relatively low on the occipital shield, and are broad transversely. Lateral to the condyles, the surface of each exoccipital is unusually convex. As in most fossil and extant baleen whales, the exoccipital is mostly thick. In its lateral portion, however, the paraoccipital is thin anteroposteriorly and does not extend laterally farther than the middle of the postglenoid process.

The lambdoidal crest forms the lateral margin of the occipital shield and descends posteriorly and ventrally toward the back of the squamosal fossa. It is continuous with a prominent and narrow ridge-like structure that extends onto the dorsal surface of the zygomatic process of the squamosal. This ridge walls in the posterior end of the squamosal fossa, overhangs the secondary squamosal fossa, and is higher than in later mysticetes. A flexure in this crest is the homologue of the squamosal prominence of *Micromysticetus rothauseni* (Sanders and Barnes, 2002).

Between the braincase and the zygomatic arch, the squamosal fossa is deep, anteroposteriorly elongate, and wide. The posterior end of the fossa ascends steeply to meet the lateral part of the lambdoidal crest. This oblique part of the crest is prominent and spans to the posterior part of the zygomatic process of the squamosal. At the posterior end of the squamosal

fossa, adjacent to the base of the zygomatic process of the squamosal, is a small, circular, pit-like fossa, herein named the secondary squamosal fossa (Figures 3, 5). The lateral wall of the braincase is nearly vertical, is slightly concave near the middle, and is not bowed laterally as in most of the highly evolved taxa of Mysticeti.

The zygomatic process of the squamosal is very large relative to the size of the cranium, is elongate, and diverges only slightly from the midline of the cranium. It arches anterodorsally in a broad curve and bends ventrally at its anterior extremity. The medial face of the process is composed of dense bone and is divided into two planes, one upper and one lower. Its lateral surface is uniformly and smoothly convex and flares slightly ventrolaterally at the ventral margin, especially so at the anterior end of the process. In the ventral tip of the process there is a recess for articulation of the jugal bone (Figure 8). Lateral to this recess, the margin of the zygomatic process flares ventrolaterally. The arch is slightly expanded dorsoventrally at its anterior end and also arches slightly anteroposteriorly to create the large, anterodorsally inclined glenoid fossa.

At the posterior end of the lateral surface of the zygomatic process there is a prominent, transversely oriented sternomastoid fossa. This fossa is inclined anterodorsally and is located immediately lateral to the small paraoccipital process. The latter

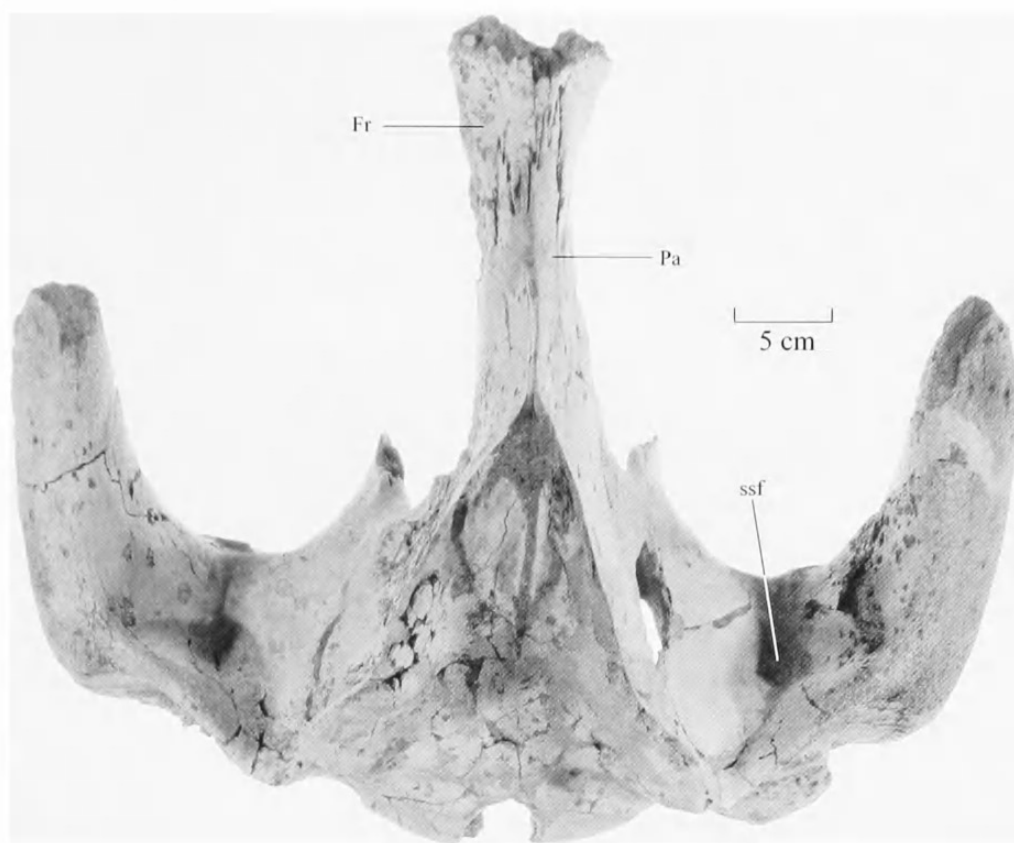


FIGURE 5.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, skull: enlarged view of braincase showing frontoparietal suturing and secondary squamosal fossa. (Abbreviations are explained in "Material and Methods.")

projects slightly ventrally and posteriorly from the occipital shield.

The recess for the external acoustic meatus is deep and is clearly defined between the postglenoid process of the squamosal and the paroccipital process. The mastoid process (posterior process of the bulla) is short and occupies all of the recess.

For a mysticete, *Eomysticetus whitmorei* has a relatively small cranial hiatus, the recess between the squamosal and the basioccipital in which the periotic lies. Lateral to the cranial hiatus and immediately posterior to the large, obliquely oriented foramen pseudovalve is a rather thick falciform process of the squamosal that is bridged to the postglenoid process of the squamosal by a thin wall of bone. This wall of bone is a structure unique to *Eomysticetus* and marks the lateral border of a large peribullary sinus that extends anteriorly from the cranial hiatus, but it is not possible to determine its anterior extent because of breakage of bone in the area. On the lateral wall of the cranial hiatus, dorsal to the medial end of the mastoid process, is an epitympanic recess. As in *Micromysticetus* (Sanders and Barnes, 2002) and other primitive mysticetes, the ventral surface of the basioccipital is arched transversely, a form that is considered to be a primitive character. The basioccipital crests are thick and knob-like.

The glenoid fossa is broad transversely with a nearly square articular surface that is delimited anteriorly by a transverse

margin extending laterally from the anterior edge of the squamosal fossa. The postglenoid process is relatively short and thin and is thickest laterally, where its ventral margin is convex; it then becomes more thin medially, where it terminates at the margin of the peribullary fossa.

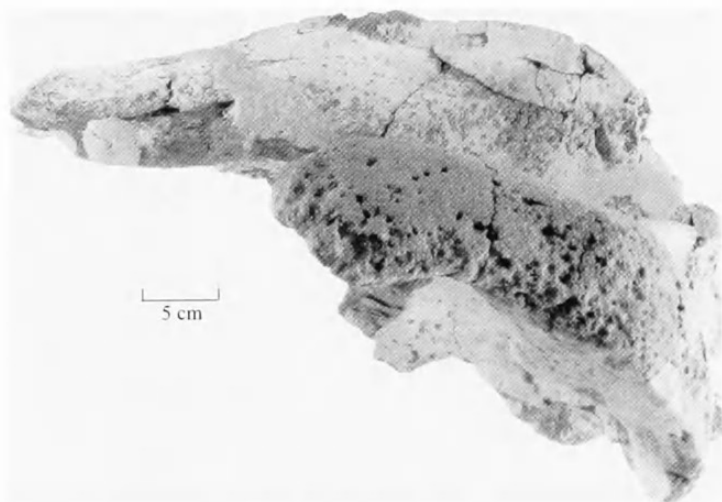


FIGURE 6.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, braincase, left lateral view. (Abbreviations are explained in "Material and Methods.")

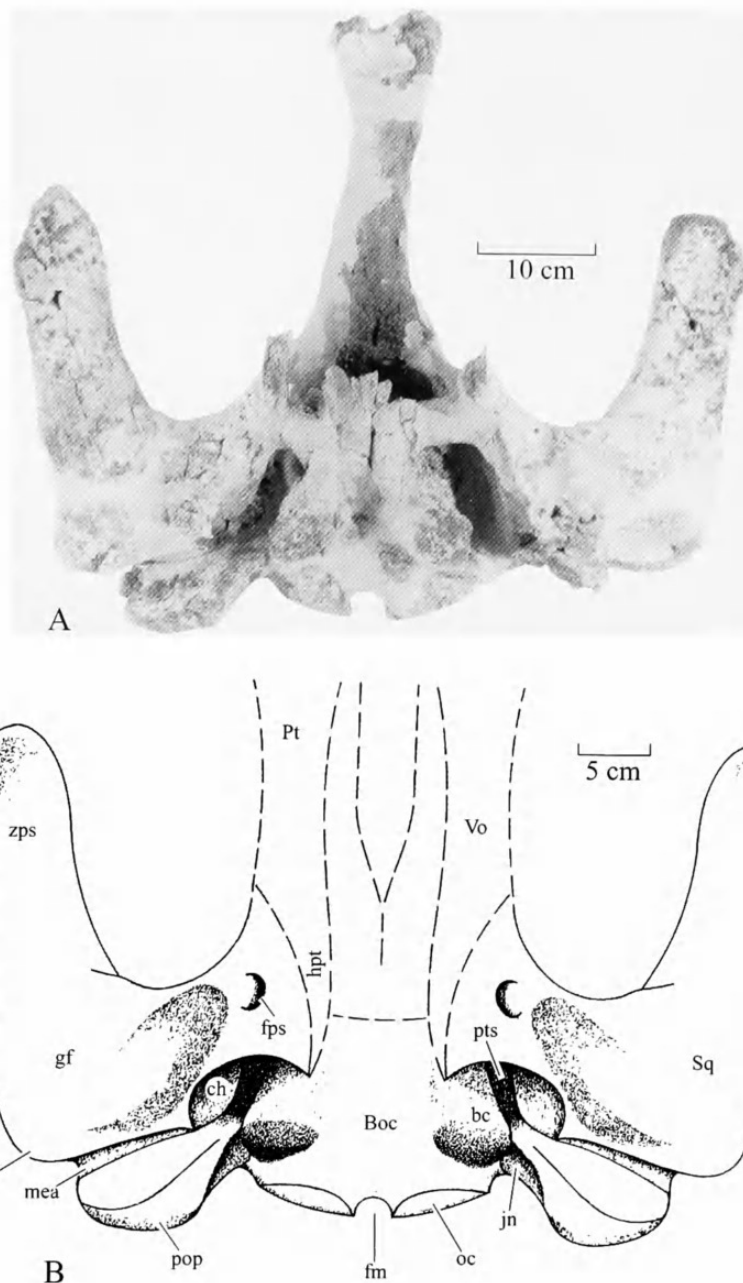


FIGURE 7.—*Eomysticetus whitmorei*, new genus and new species: A, holotype, ChM PV4253, cranium, ventral view; B, reconstruction of holotype cranium, ventral view. (Dashed lines represent hypothetical configurations. Abbreviations are explained in "Material and Methods.")

Periotic: Both of the periotics of *Eomysticetus whitmorei* are preserved and are relatively small for a mysticete (Figure 9). The left one is virtually complete, but the right one is missing approximately one-half of the pars cochlearis. The holotype left periotic measures 78 mm from the anteriormost point of the anterior process to the posteriormost extent of the posterior process. The pars cochlearis is 38 mm in anteroposterior length, 25 mm in dorsoventral diameter, and 31 mm in transverse diameter. At the anterior end of the cochlear portion the bone is deeply incised by the fossa for the tensor tympani muscle.

The anterior process is extremely compressed transversely and broadly expanded dorsoventrally (Figure 10). The poste-

rior process is much shorter and is laterally expanded dorsally but more laterally compressed ventrally. The cochlear portion is relatively small, does not project very far medially from the body of the bone, and is not as globose as that of *Micromysticetus rothauseni* (Figure 10; see also Sanders and Barnes, 2002, fig. 12). A large dorsal process, such as is typical of the more highly evolved mysticetes, is not present, but the bone around the internal acoustic meatus is slightly convex, especially lateral to the meatus. In its overall proportions, the periotic resembles those of the basilosaurid Archaeoceti more than the inflated periotics of the derived Mysticeti (Figure 11).

In the primitive character state (e.g., Basilosauridae such as

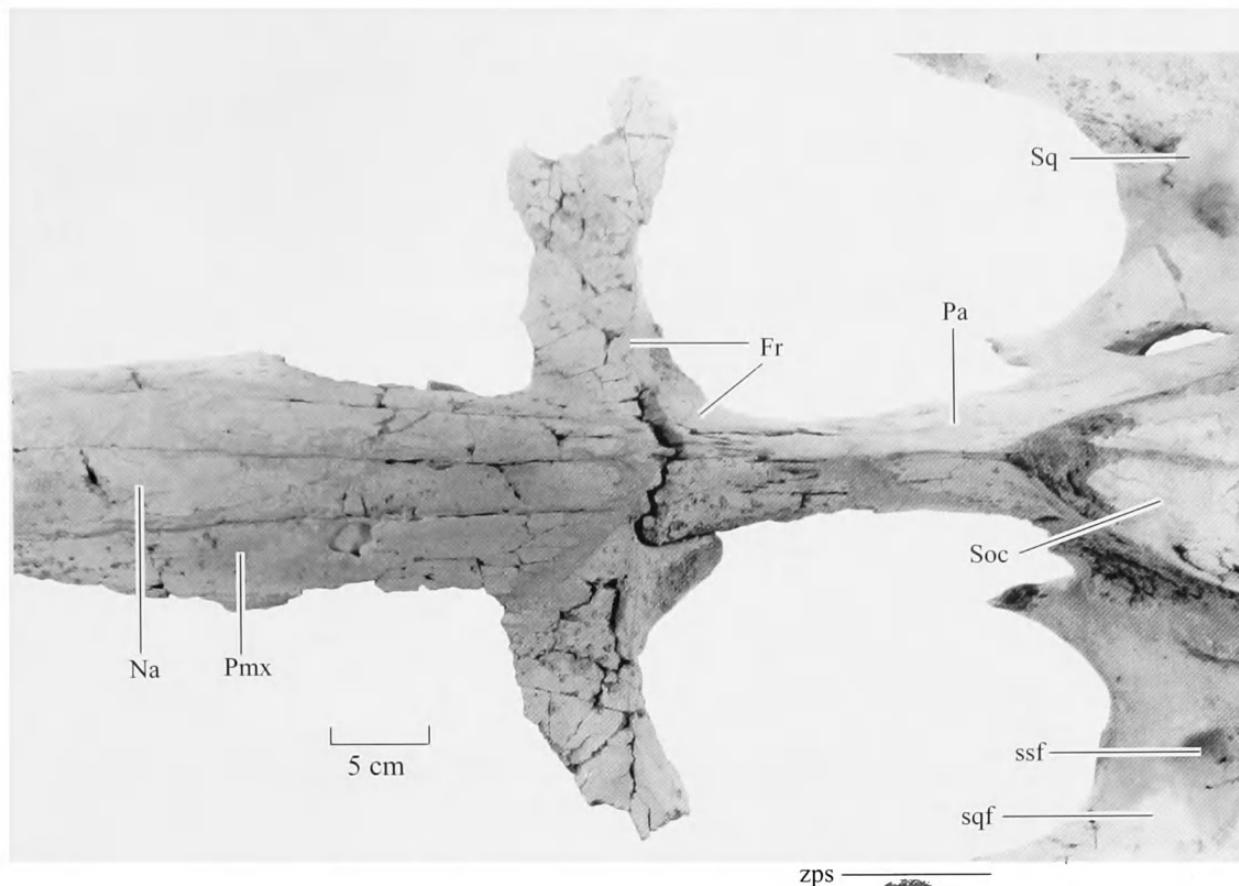


FIGURE 8.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, enlarged view of intertemporal region of cranium, dorsal view. (Abbreviations are explained in "Material and Methods.")

Zygorhiza), the internal acoustic meatus on the cochlear portion of the periotic is a single large aperture, and included within it are the foramina for the facial nerve (VII), the vestibular nerve (=foramen singulare) (VIII), and the cochlear nerve (=tractus spiralis foraminosus) (VIII). This primitive condition also is widespread among the odontocetes.

In *E. whitmorei*, however, the internal acoustic meatus is divided into two parts separated by a thick, dorsally projecting transverse septum of bone that isolates the large foramen for the facial nerve from the foramina for the vestibular nerve and the cochlear nerve (Figure 10C). This situation also is present in such primitive Cetotheriidae as *Herpetocetus* spp., and in the more derived Cetotheriidae. In the Balaenopteridae the same bony septum is very prominent and extends very far cranially, and its extensive development is correlated with the extreme dorsal enlargement of the dorsal tuberosity and the bone around it.

The presence of the septum dividing the originally single internal acoustic meatus is an autapomorphy of Eomysticetidae and of most other Mysticeti beyond it.

The loss of a distinct sinuous dorsal crest on the periotic, originally traversing from the center of the cochlear portion to the anterior process, is related to the inflation of the cerebral surface of the periotic and development of a dorsal tuberosity.

More extreme cerebral or dorsal extension of the dorsal tuberosity, associated with dorsal extension of the transverse sep-

tum dividing the internal acoustic meatus and also of other bone surrounding the internal acoustic meatus, is an autapomorphy of the Balaenopteridae.

The septum dividing the internal acoustic meatus in *E. whitmorei* is curiously missing in *Micromysticetus rothauseni*. That taxon has the primitive character state of the single, large, ovoid internal acoustic meatus (Sanders and Barnes, 2002, fig. 12). *Micromysticetus rothauseni* also has a well-defined sinuous dorsal crest that traverses the pars cochlearis, also a primitive character. Only a weak suggestion of that crest is present in *E. whitmorei*. Most likely, these features in *Micromysticetus* are character reversals or relict conditions. Because *Micromysticetus* is otherwise more highly derived than *Eomysticetus whitmorei* (and we have classified it among the Cetotheriidae), and doubtless was a baleen-bearing mysticete, it is very unlikely that *Micromysticetus* represents some different lineage of Mysticeti that evolved separately from archaeocete-like primitive mysticetes and was convergent with the Cetotheriidae.

Tympanic Bulla: Both tympanic bullae are present. The bulla is proportionally small for a mysticete. The involucrum is tapered anteriorly and is not composed of thick bone. As is typical of mysticetes, the sigmoid process is large and convex. In overall shape, the bulla is ovoid and very much like that of archaeocetes of the family Basilosauridae.

Dentaries (Table 2): The virtually complete right dentary is relatively long and slender with a slight lateral curvature, a dis-

TABLE 2.—Measurements (in mm) of the holotype dentaries of *Eomysticetus whitmorei*, new genus and new species, ChM PV4253. Parentheses indicate estimated measurements.

Character	Left	Right
Total length (straight line) as preserved	894	1513
Greatest vertical diameter 100 mm behind anterior end of ramus, as preserved	90	63+
Greatest transverse diameter 100 mm behind anterior end of ramus, as preserved	50	32.5
Greatest transverse diameter 500 mm behind anterior end of ramus (394 mm anterior to posterior face of condyle), as preserved	91	—
Greatest vertical diameter 500 mm behind anterior end of ramus (394 mm anterior to posterior face of condyle), as preserved	45	—
Greatest vertical diameter 500 mm behind anterior end of ramus	—	72.5
Greatest transverse diameter 500 mm behind anterior end of ramus	—	53
Greatest vertical diameter 1000 mm behind anterior end of ramus	—	83+
Greatest transverse diameter 1000 mm behind anterior end of ramus	—	54
Greatest vertical diameter through coronoid process	(200)	—
Horizontal distance from center of coronoid process to posterior face of condyle	(216)	221
Horizontal distance across base of coronoid process	300	—
Horizontal distance from posteriormost extent of condyle to beginning of anterior edge of coronoid	390	389
Horizontal distance from posteriormost extent of condyle to end of posterior edge of coronoid	100	—
Greatest distance from posteriormost extent of condyle to internal margin of orifice for mandibular canal	(210)	(225)
Greatest vertical diameter of posterior end including condyle	(185)	—
Greatest transverse diameter of condyle	46	49
Greatest vertical diameter of condyle	101	—

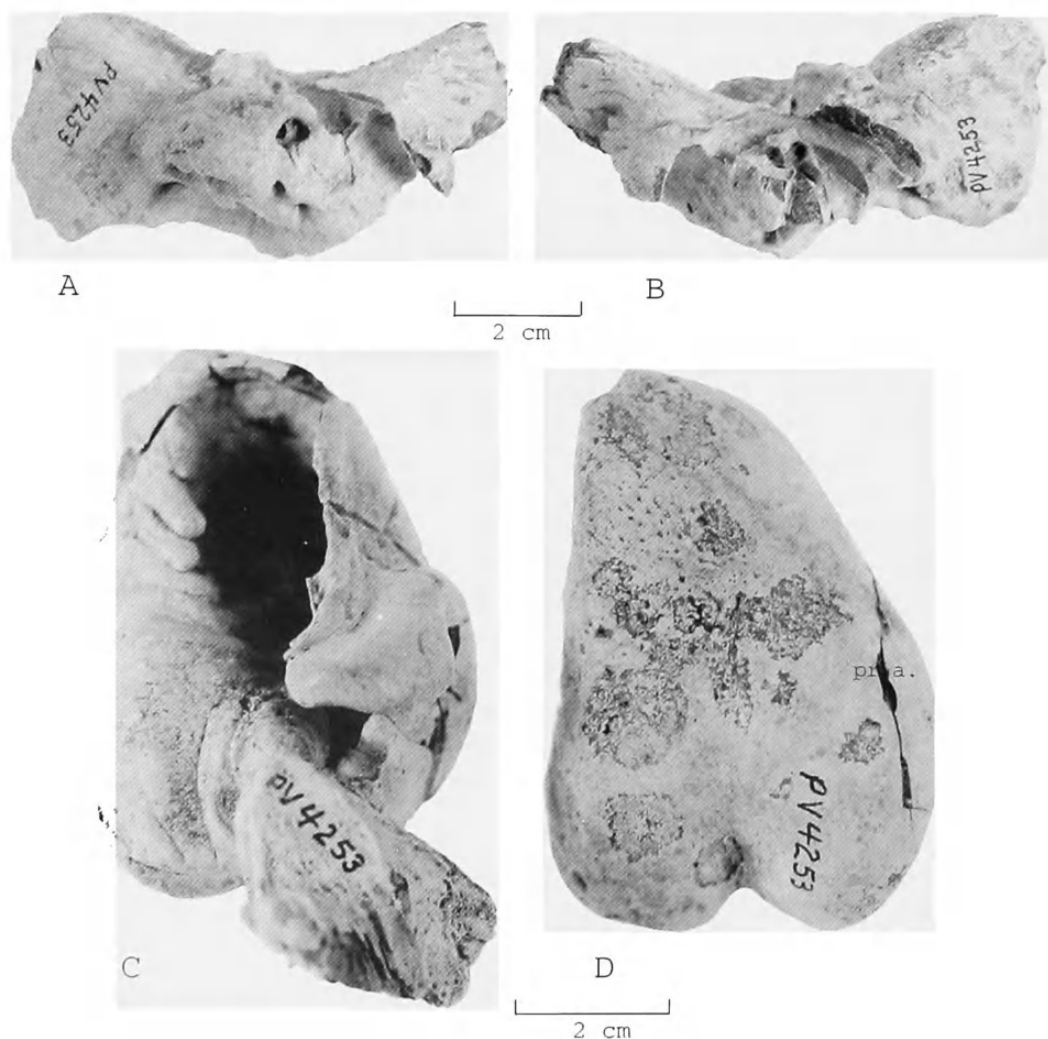


FIGURE 9.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253: A, left periotic; B, right periotic; C, right tympanic bulla in ventral view; D, left tympanic bulla in cerebral or dorsal view.

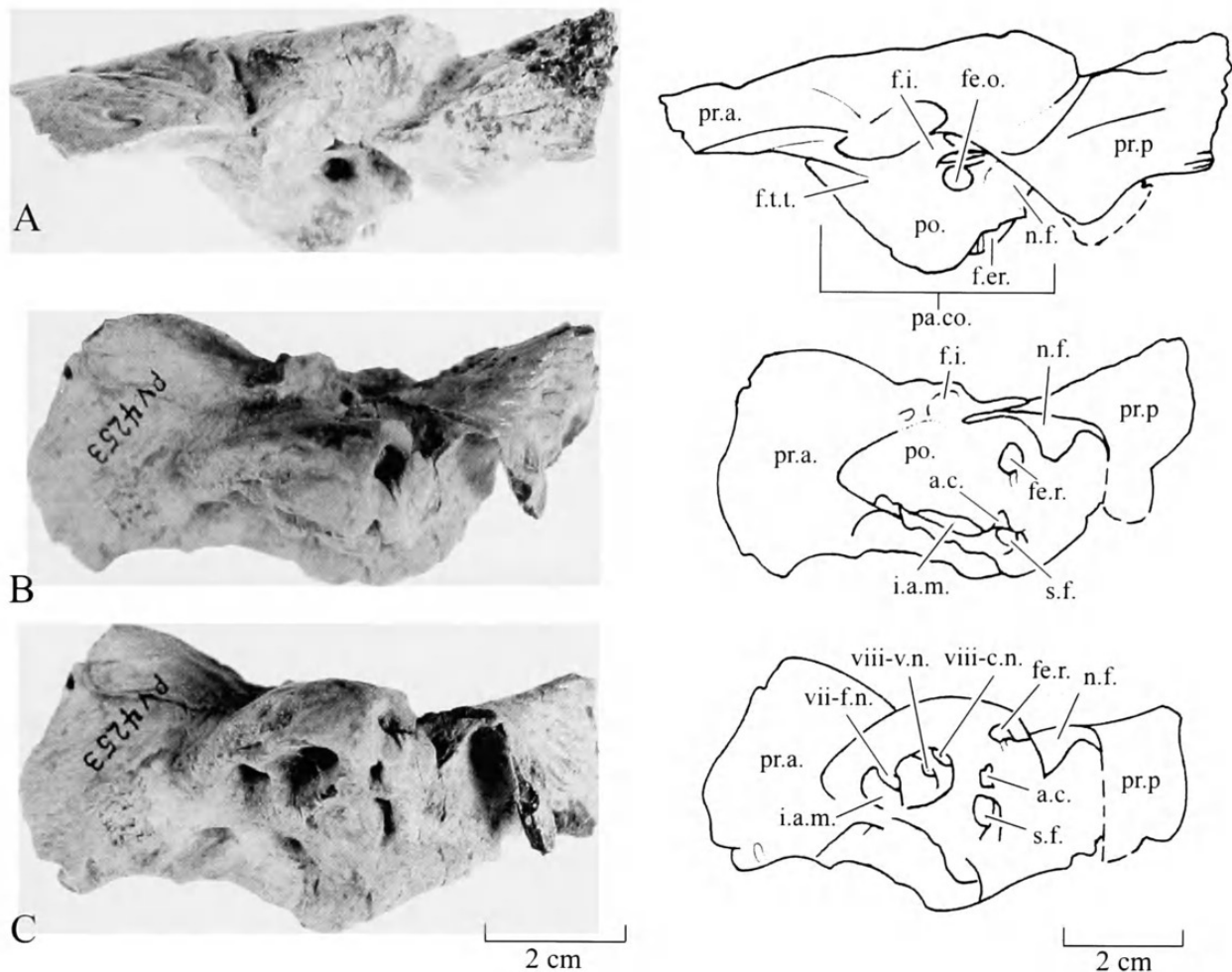


FIGURE 10.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, left periotic: A, ventral view; B, cerebral or dorsal view; C, dorsolateral view. (Dashed lines represent hypothetical configurations; a.c.=aqueductus cochlearis; c.n.=foramen for cochlear nerve (VIII); f.i.=fossa incudis; f.n.=foramen for facial nerve (VII); fe.o.=fenestra ovalis; fe.r.=fenestra rotunda; f.t.t.=fossa for tensor tympani muscle; i.a.m.=internal auditory meatus; n.f.=notch for exit of facial nerve; pa.co.=pars cochlearis; po.=promontorium; pr.a.=anterior process; pr.p.=posterior process; s.f.=subarcuate fossa; v.n.=foramen for vestibular nerve (VIII).)

tinct downward bend anteriorly, a large and laterally deflected coronoid process, and a small posteriorly directed condyle (Figure 12). Approximately 60% (894 mm) of the left dentary is preserved (Figure 13). Most of the posterior end is present in both dentaries, but the anterior end is missing in the left one. The posterior end of the left dentary is complete except for the

lower angle, which is missing in both dentaries. The coronoid process is preserved only on the right side and is relatively large and has a high apex. There is a large mandibular foramen, and, as is typical of mysticetes, the dentary is elongate and lacks alveoli. On the external (labial) surface of the nearly complete right dentary is a series of 10 mental foramina begin-

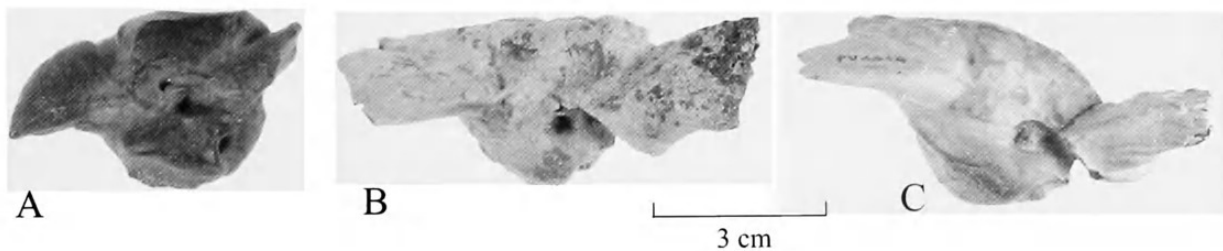


FIGURE 11.—Left periotics: A, *Zygorhiza kochii* (Reichenbach), ChM PV5065; B, *Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253; C, *Micromysticetus rothauseni* Sanders and Barnes, holotype, ChM PV4844.

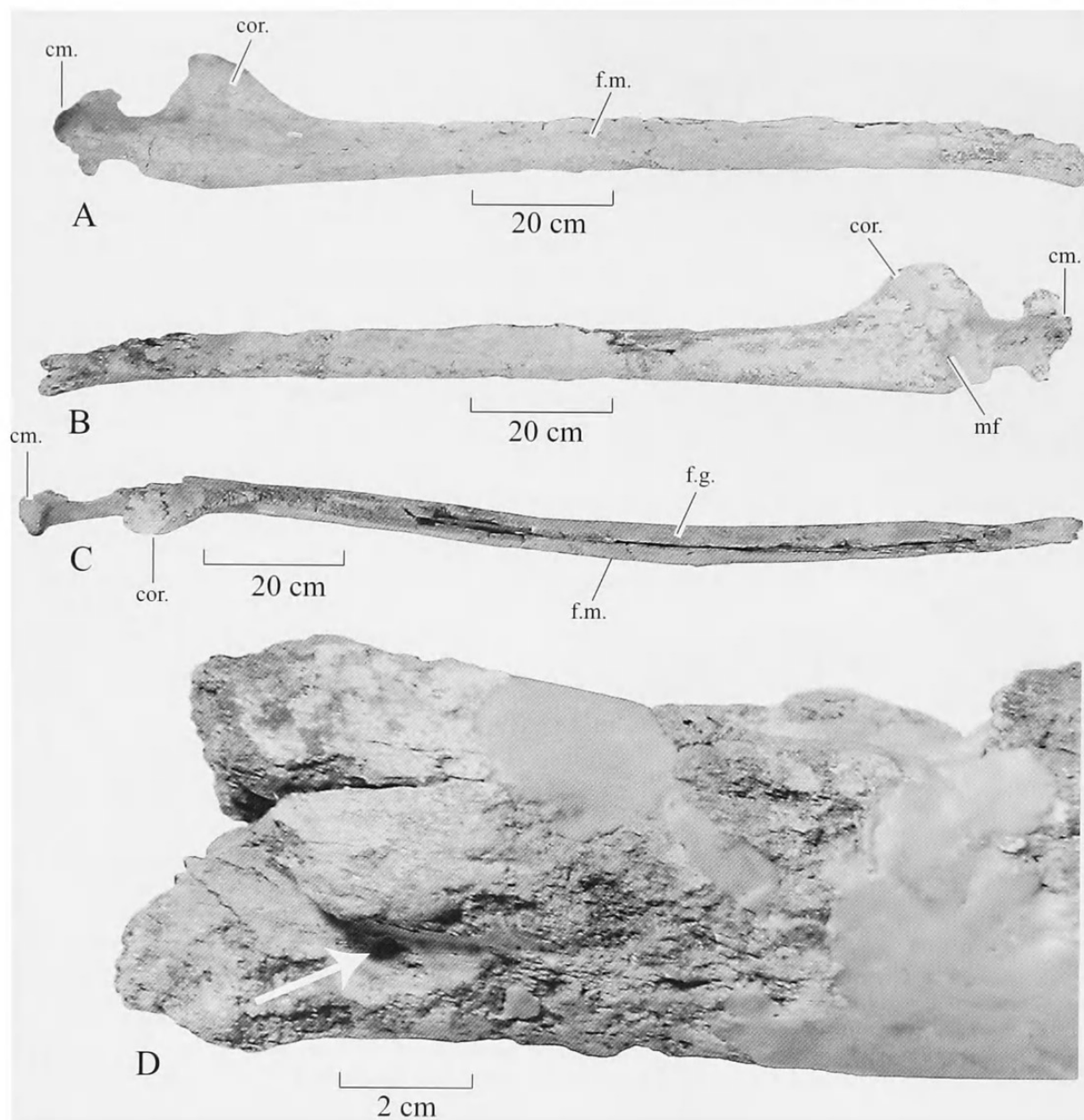


FIGURE 12.—*Eomysticetus whitmorei*, new genus and new species, holotype ChM PV4253, right dentary: A, labial view; B, lingual view; C, dorsal view; D, distal end showing groove for symphyseal ligament. (cm.=mandibular condyle; cor.=coronoid process; f.g.=gingival foramen; f.m.=mental foramen; m.f.=mandibular foramen.)

ning at 95 mm anterior to the anteriormost edge of the coronoid and appearing thereafter at 155, 280, 410, 490, 580, 660, 750, 870, and 940 mm from that point. The posteriormost foramen opens posteriorly. Though badly broken and eroded, a remnant of the gingival groove is preserved on the dorsal margin of the dentary. The groove for the symphyseal ligament begins about 20 mm posterior to the anterior end of the dentary and is approximately 43 mm in anteroposterior length (Figure 12D). It is situated in the ventral one-third of the dentary height and bends slightly dorsally at its anterior end. The ligamentary groove is quite distinct and is indicative of the typical ligamental mandibular symphysis of the more highly evolved mysticetes, such as cetotheriids and balaenopterids.

For approximately 600 mm of its length anterior to the coronoid, the right dentary is almost entirely straight (Figure 12C). From there forward, the anterior part tapers in uniform dorsoventral diameter for the remaining length of the bone. Approximately 600 mm from the anterior end, the horizontal ramus begins to bend noticeably downward and is of almost uniform dorsoventral diameter from that point to its anterior terminus. Unlike the mandibles of most Neogene mysticetes, which are bowed laterally between the level of the coronoid process and the anterior end, the lateral curvature of the dentary in *E. whitmorei* is restricted to the anterior half and forms a much flatter arc than in such forms as *Pelocetus calvertensis* Kellogg (1965, fig. 6), *Mesocetus siphunculus* Cope, 1895 (see

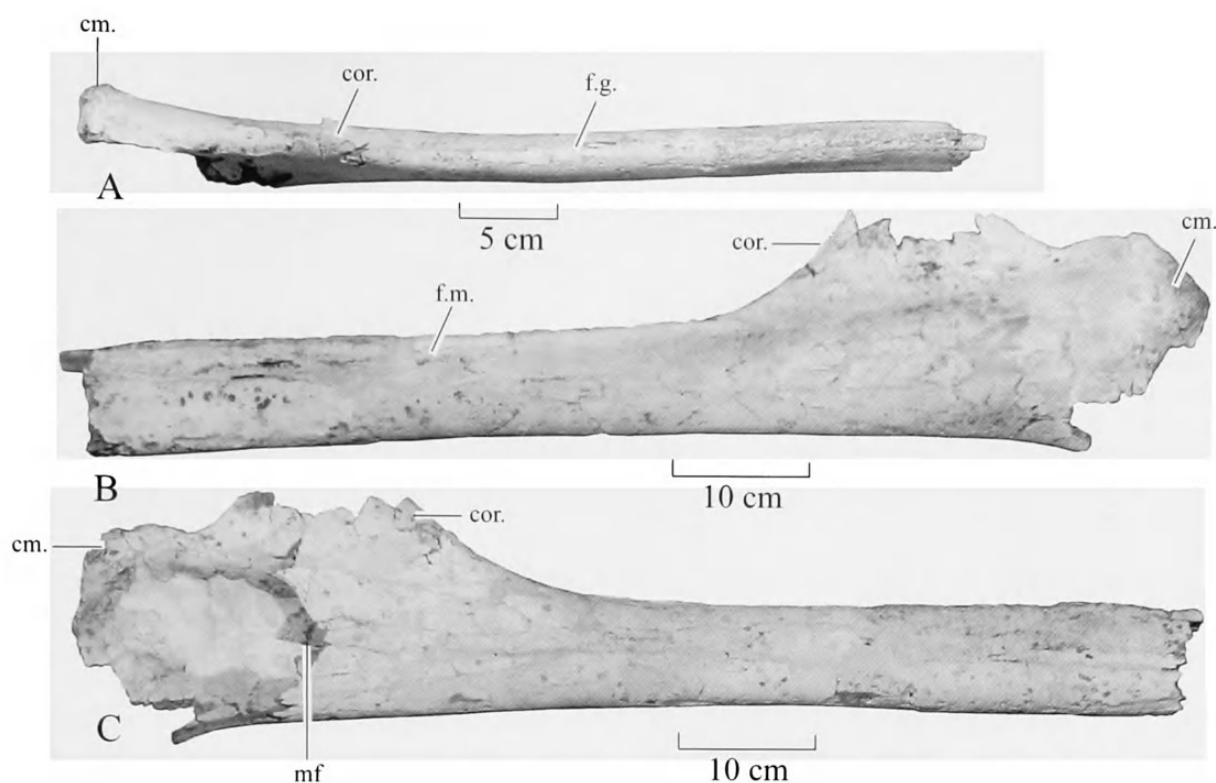


FIGURE 13.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, left dentary: A, dorsal view; B, labial view; C, lingual view. (For abbreviations, see Figure 12.)

Kellogg, 1968, fig. 49), and *Parietobalaena palmeri* Kellogg (1968, fig. 89), all from Miocene deposits of Virginia. The flattened curvature of the mandible of *E. whitmorei* is most nearly like that of *Diorocetus hiatus* Kellogg (1968, fig. 59), in which the curvature is reduced to conform to the narrow, strongly tapered rostrum in that species, which also is from Miocene deposits of Virginia. The length and slight degree of convexity in the mandible of *Eomysticetus* demonstrates the presence of a long, narrow rostrum in this new Oligocene mysticete, as indicated also by the narrowness of two large anterior fragments of the left and right maxillae.

Posteriorly and in dorsal aspect, the external wall of the mandible follows a broad, laterally directed (concave) curve between the level of the anterior end of the coronoid and the posterior edge of the condyle (Figure 12C). To our knowledge, that configuration of the posterior region of the dentary is not known in any other mysticete. In most previously described taxa, the lateral surface follows a convex line and is then sharply recurved in the area between the apex of the coronoid and the condyle, thus placing the posterior edge of the coronoid further medial than the anterior edge. In *E. whitmorei* the posterior edge is on the same long, concave curve as the anterior edge and is not offset medially. Along the base of the coronoid process, the lateral surface of the ramus sweeps dorsally in a broad curve that terminates at the anterior edge of the mandibular condyle, which lies approximately 60 mm above the plane of the dorsal margin (Figures 12A, 13B). Extended posteriorly, the axis of the dorsal margin bisects the condyle approximately

at the center of its vertical diameter. The condyle is thus seated extremely high on the posterior end of the mandible. A similar situation exists in the dentaries of *Mesocetus siphunculus* (see Kellogg, 1968, fig. 49) and *Diorocetus hiatus* (see Kellogg, 1968, fig. 59), but in neither of these forms is the condyle elevated nearly so high as in *A. whitmorei*. In all three taxa, however, the condyle is located much higher than in *Parietobalaena palmeri* and *Pelocetus calvertensis*, the anterior face being only slightly above the plane of the dorsal edge in the latter forms. Of the four Miocene cetotheriids mentioned herein, the mandible of *Diorocetus hiatus* most nearly resembles that of *Eomysticetus whitmorei* in the moderate degree of convexity of the ramus and in the dorsoventral height of the anterior face of the condyle. The mandibular foramen is relatively large and opens posteriorly. Its anteriormost margin is aligned approximately with the apex of the coronoid process, and the anterior margin is a broad curve. The lateral wall within the foramen is thin and dense.

The coronoid process is exceptionally large for a mysticete and more nearly resembles that of the archaeocete *Zygorhiza kochii* (Reichenbach, 1847) (see Kellogg, 1936, fig. 31a). It has a relatively broad base anteroposteriorly and a high, rounded apex. The apex is present on the right dentary of *E. whitmorei* but is missing in the left one (Figures 12, 13). It is thick anteriorly and thinner posteriorly. As seen in Figure 12, the dorsal half of the coronoid is curved laterally in a gentle arc so that it is angled dorsolaterally as in many Neogene mysticetes, but not to such an extreme as in the latter forms (e.g., *Parietobalaena*

TABLE 3.—Measurements (in mm) of the cervical vertebrae of *Eomysticetus whitmorei*, new genus and new species, ChM PV4253. Parentheses indicate estimated measurements.

Character	Atlas	Axis	C.3	C.4	C.5	C.6	C.7
Anteroposterior diameter of centrum	57	66*	39	33	36	40	40
Transverse diameter of centrum, anteriorly	137	127	102	97	(100)	98	95
Vertical diameter of centrum, anteriorly	73	(48)	84	—	(95)	(83)	83
Tip of neural spine to ventral face of centrum, anteriorly	(128)	—	—	—	—	—	(170)
Greatest vertical diameter of neural canal, anteriorly	73	—	—	—	—	(43)	(45)
Greatest transverse diameter of neural canal, anteriorly	46	50	—	—	—	(41)	(89)
Greatest distance between outer ends of diapophyses	—	—	—	—	—	(156)	(196)
Greatest distance between outer ends of parapophyses	—	—	—	—	(186)	(182)	(124)
Least anteroposterior diameter of right pedicle of neural arch	54	15	—	—	—	19	20
Greatest transverse diameter of centrum, posteriorly	(127)	112	105	99	(96)	94	97
Greatest vertical diameter of centrum, posteriorly	(65)	83	92	90	92	(88)	88
Anteroposterior diameter into transverse diameter, centrum (anteriorly)	2.40	1.92	2.62	2.94	2.78	2.45	2.38
Anteroposterior diameter into vertical diameter, centrum (anteriorly)	1.32	0.76	2.15	—	2.64	(2.08)	2.08

*Includes odontoid process.

palmeri Kellogg (1968, fig. 89)). In *E. whitmorei*, there also is a proportionately shorter distance between the anterior edge of the condyle and the terminus of the posterior edge of the coronoid, which also is situated well above the dorsal margin of the ramus.

Cervical Vertebrae. All seven of the cervical vertebrae are preserved (Table 3). None is ankylosed with any of the others in the series; however, the posterior face of the axis vertebra is deeply concave and closely encloses the anterior face of the third cervical, apparently presaging the eventual ankylosis of these two vertebrae in some Neogene mysticetes. The anterior face of the third cervical vertebra is slightly concave transversely, except for its upper portion, which is thickened anteroposteriorly so that it projects anteriorly to fit into a concavity along the dorsal margin of the posterior face of the axis vertebra. In all of the other cervical vertebrae following the axis, the anterior face of the centrum is flat and the posterior face is concave. The epiphyses are firmly ankylosed to the centra in all of the cervical vertebrae, indicating the physical maturity of the specimen.

The atlas is missing both of its transverse processes, but the size of the broken areas at their bases on the centrum suggests that the processes were of modest size and apparently were not large enough to have enclosed a transverse foramen (Figure 14B). They were situated relatively high on the centrum, directly upon the juncture of the dorsal and lateral surfaces. The transverse diameter of the anterior face is broadest at that point (137 mm) and narrowest across the ventral margin (86 mm). The facets for articulation with the occipital condyles of the cranium are deeply concave and somewhat angular along their lateral margins. Vertically, they are 86 mm in diameter and extend above the level of the dorsal surface of the centrum to a point just below the roof of the neural canal, their dorsal margins forming the anterior edges of the pedicles of the neural arch. The dorsal margins of the facets extend anteriorly beyond the level of the ventral margins. Twelve millimeters behind the anterior margin of the neural arch, each of the pedicles is pierced by a large (13 mm on right, 15 mm on left), laterally di-

rected arterial foramen, or canal, that emerges into a shallow groove on the dorsal surface of the centrum. The spine is missing from the neural arch, but it may not have been much more than an elevated, knob-like continuation of the low, median ridge present on the anterior portion of the arch. The lower portion of the neural canal is deeply concave, the ventral margin being only 44 mm above the ventral surface of the centrum. Anteriorly, its lateral margins are formed entirely by the lateral margins of the articular facets; the transverse diameter of the canal is 42 mm dorsally and 17.5 mm ventrally. The margins of the posterior face of the atlas are not well preserved and provide only an approximate measurement of the transverse diameter, which was at least 127 mm. The facets for articulation with the axis vertebra are much smaller than the anterior facets, their dorsal margins lying well below the dorsal surface of the centrum. The right one is the best preserved of the two and is greater in vertical diameter (~60 mm) than in transverse diameter (~47 mm). The ventral margin of the posterior face is preserved sufficiently to determine that a hyapophysis is not present on the atlas of *E. whitmorei*.

The axis vertebra is missing the neural arch (Figure 14C). The stumps of the pedicles are directed posteriorly at an angle and are flattened anterolaterally. The transverse processes are short and blunt, are imperforate, and are bent posteriorly. The ends are upturned and thus do not project below the level of the ventral surface of the centrum. The anterior face of the axis slopes posteriorly at a slight angle. The anterior facets for articulation with the atlas are concave transversely and are separated above the odontoid process by an interval of approximately 52 mm across the midline of the centrum. The odontoid process is broadly rounded ventrally; dorsally, it is flattened on either side of a median ridge that extends posteriorly onto the dorsal surface of the centrum. Between the pedicles of the neural arch, two foramina are situated on each side of the bony ridge. The posterior face is deeply excavated both transversely and dorsoventrally, but more so in the former direction and especially along the dorsal margin.

The neural arch and most parts of the elements of the trans-

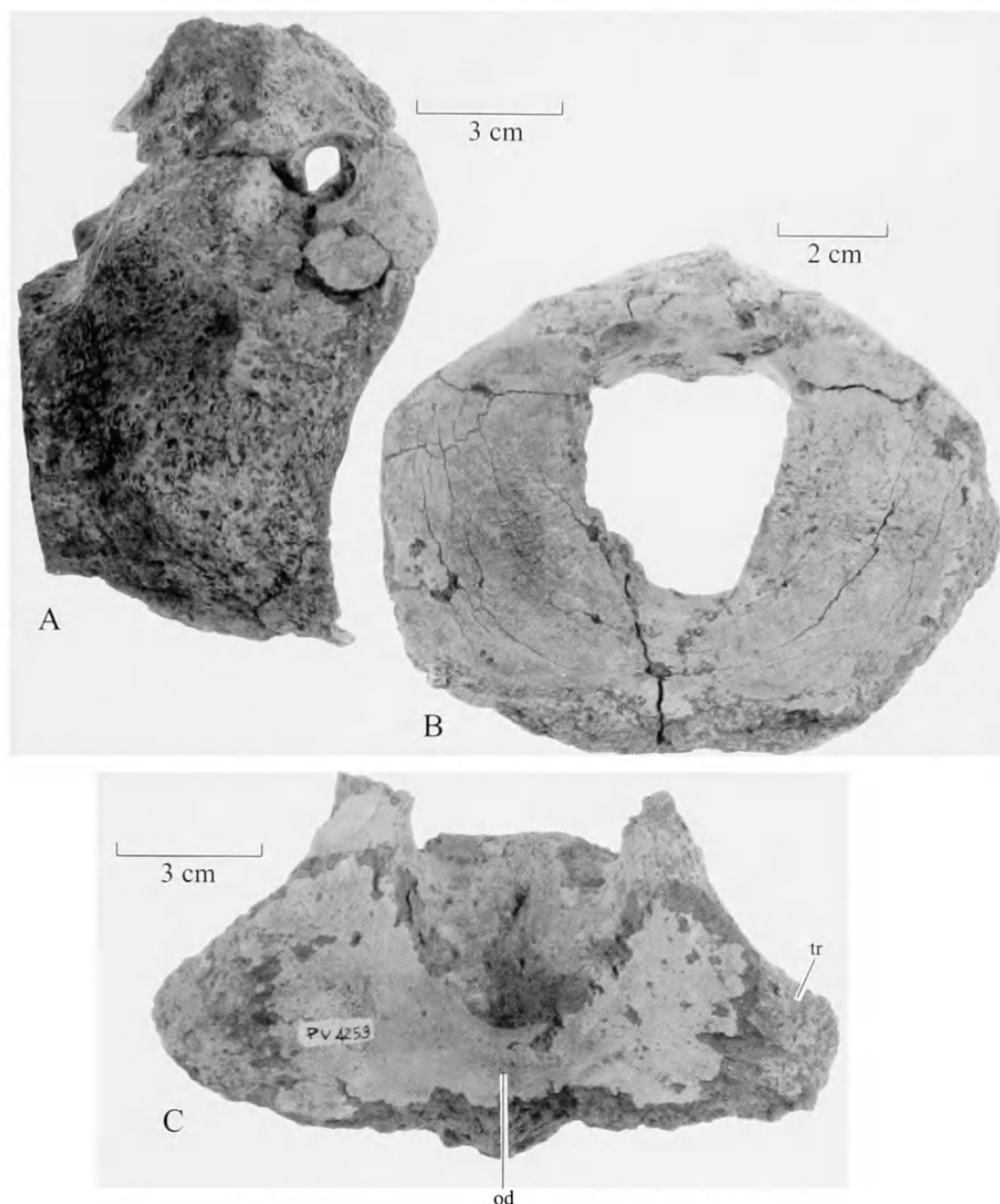


FIGURE 14.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253: A, atlas vertebra in anterior view; B, same, right lateral view; C, axis vertebra, anterior face. (od.=odontoid process; tr.=transverse process.)

verse processes are missing on the third, fourth (Figure 15), and fifth cervical vertebrae. The left lower transverse process is present on the third cervical, and both of the lower processes are preserved on the fourth cervical. On the dorsal surface of the centrum of each of these three vertebrae there is a pair of foramina at the midline. On the third through the seventh cervical vertebrae, the profile of the anterior face of the centrum is approximately that of a flattened circle, the greatest diameter occurring transversely on a level coinciding with the dorsal margin of the base of the parapophyses. The profile of the posterior face is of the same general conformation, with the exception of the third cervical. In that vertebra, the ventral margins of the posterior face assume a triangular shape, sloping sharply

from the widest point of the anterior face to a broadly rounded angle at the edge of the ventral surface of the centrum. This angle projects below the ventral margin of the parapophyses, which extend below the ventral margin of the anterior face.

On the sixth cervical vertebra, the neural spine and the left half of the neural arch are missing (Figure 16A). From the preserved right portion it can be seen that the anterior profile of the neural canal was that of a triangle with rounded angles. The ventral articular facet of the postzygapophysis has the form of a truncated ellipse, is 23×20 mm in dimension, and projects posteriorly 5 mm beyond the centrum. The diapophysis is much more slender than the parapophysis, the base of which is larger in this cervical than in any of the others, extending approxi-

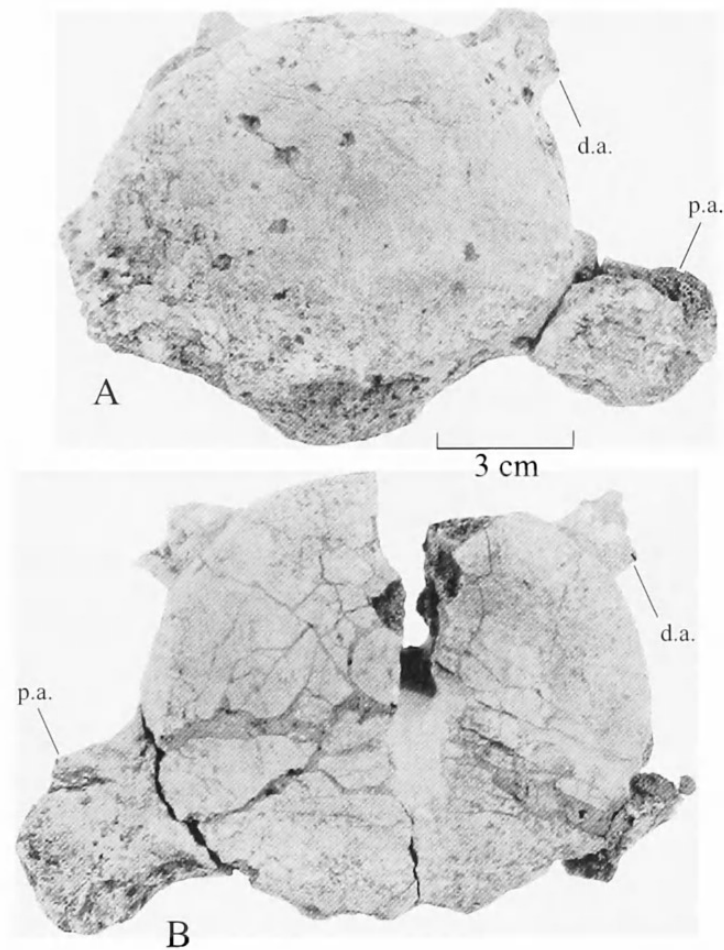


FIGURE 15.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, cervical vertebrae, anterior views: A, third cervical; B, fourth cervical. (d.a.=diapophysis; p.a.=parapophysis.)

mately 17 mm below the ventral surface of the centrum. The vertical diameter of the lateral foramen is 46.6 mm, greater than that of any of the other cervical vertebrae. The articulating portions of the diapophyses and the parapophyses are missing.

On the seventh cervical vertebra, the neural arch is complete and the neural canal is triangular in anterior profile (Figure 16B). The pedicles of the arch are considerably larger than those of the other cervical vertebrae and are noticeably asymmetrical in dorsoventral diameter, the right one being 33 mm and the left one 28 mm. There also is a striking difference in the dimensions of the ventral facets of the postzygapophyses, the right one being approximately 40×16 mm and the left one approximately 31×11 mm. Both are much longer anteroposteriorly and more narrow transversely than corresponding facets of the sixth cervical. The upper and lower transverse processes are more complete on the right side than on the left, the entire right parapophysis being missing. The articulating portions of the right processes are not preserved. In contrast to the sixth cervical, the diapophysis is much larger than the parapophysis, which is greatly reduced from the size of its preceding counterpart. The increased dorsoventral width of the pedicles has de-

creased the size of the lateral foramen; the vertical diameter of the right one is only 36 mm, compared with 46.6 mm on the sixth cervical. At the greatest transverse width of the posterior face of the centrum there are demifacets for the articulation of the first rib. These features are best observed when this vertebra is placed in normal articulating position with the first thoracic vertebra, which has a corresponding demifacet opposite each of those on the last cervical.

Thoracic Vertebrae: Seven thoracic vertebrae are preserved, among them the first three and the fifth, seventh, eighth, and the possible 15th in the thoracic series. Lacking direct evidence of the total number of thoracic vertebrae normally present in *E. whitmorei*, we assume that there were no fewer than 12, based upon Kellogg's (1968:175) comments about the number of dorsal (thoracic) vertebrae in fossil mysticetes from the Miocene Calvert Formation in Maryland and Virginia. *Eomysticetus whitmorei* appears to have had at least 15 pairs of ribs, however, and thus would have had 15 thoracic vertebrae. As shown in Table 4, the anteroposterior diameter of the centrum in the preserved thoracic vertebral series increases from the first through the last, and the transverse diameters are consistently greater than the vertical diameters. Ratios of lengths and widths of the thoracic vertebral centra are diagrammed in Figure 29 and are interpreted in the "Discussion" section below.

The anteroposterior length of the centrum of the first thoracic vertebra (Figure 17A) is only 10 mm greater than that of the seventh cervical vertebra. The spinous process is preserved on the first thoracic vertebra, but the right and left sides of its neural arch are missing. The spinous process slopes anteriorly at an angle of approximately 60° from the plane of the roof of the neural arch, and from that plane to its tip the process is 81 mm in vertical thickness. On the lateral margins of the centrum, the anterior demifacet for the capitulum of the first rib is situated below the level of the posterior demifacet for the capitulum of the second rib.

The second thoracic vertebra (Figure 17B) is essentially complete, with only its left transverse process, the margins of its neural arch, and the posterior edge of its spinous process showing appreciable degrees of erosion. The profile of the neural canal continues the triangular shape that is present on the seventh cervical. The apex of the neural spine is intact, the vertical height of this process being 137 mm, 56 mm greater than that of the first cervical. The pedicles are markedly different in their transverse dimensions, the right one being 33 mm and the left one 29 mm. They are much narrower anteroposteriorly, the right one being 22.5 mm and the left one 20 mm in greatest diameter. Arising from the base of the pedicle, the transverse process projects dorsolaterally at an angle of approximately 35° from the center of the anterior face of the centrum and anteriorly to a point about 40 mm beyond the centrum, placing the articular facet for the tuberculum of the second rib on a level with the roof of the neural arch and well anterior to the anterior face of the centrum. The somewhat elliptical prezygapophysial

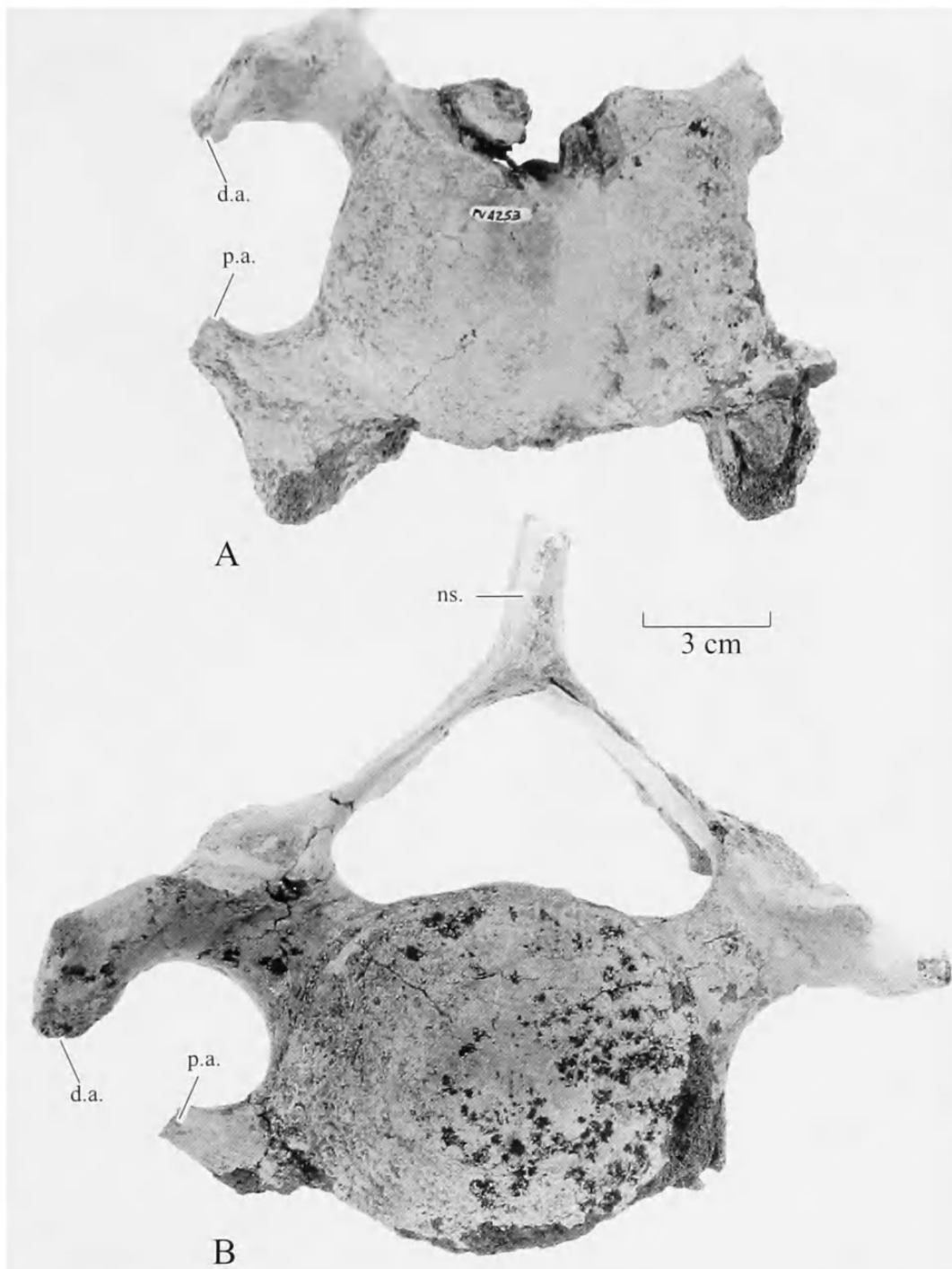


FIGURE 16.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, cervical vertebrae, anterior views: A, sixth cervical; B, seventh cervical. (For abbreviations, see Figure 15.)

facet is situated on the dorsal surface of the diapophysis, forming a shallow depression approximately 37 mm in length. The postzygapophysis extends 9 mm beyond the posterior face of the centrum. Its ventral articular facet is elliptical in form and measures 26×16 mm. On the lateral margins of the centrum,

the anterior facet for the capitulum of the second rib is located slightly ventral to the posterior facet for the capitulum of the third rib.

The third thoracic vertebra (Figure 17C) is similar in form and preservation to the second one, both having a neural spine

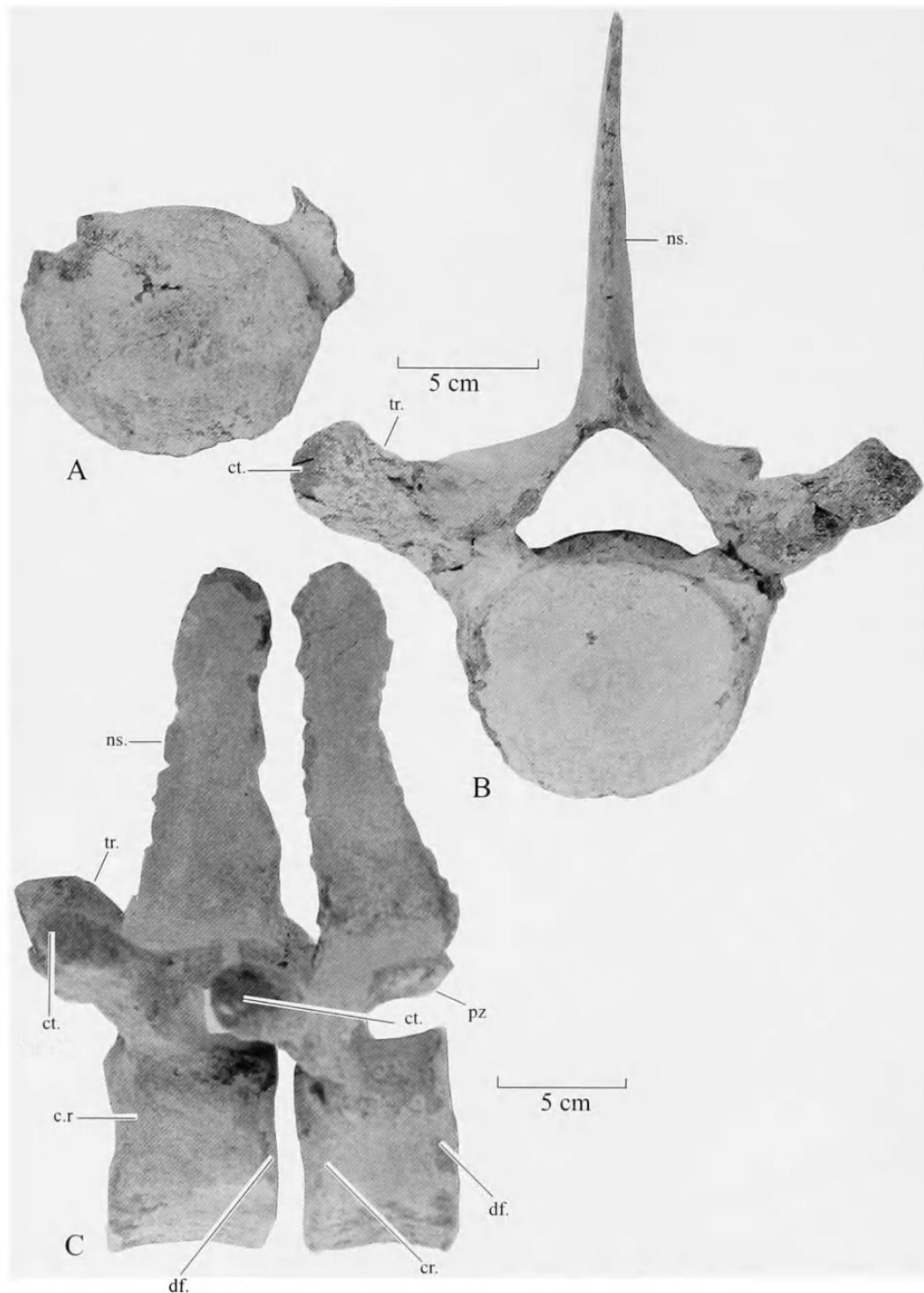


FIGURE 17.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, thoracic vertebrae: A,B, first and second thoracics, respectively, in anterior view; C, second and third thoracics (left to right) in lateral view. (cr.=anterior demifacet for capitulum of rib; ct.=facet for tuberculum of rib; df.=posterior demifacet for capitulum of rib; mp.=metapophysis; ns.=neural spine; pz.=postzygapophysis; tr.=transverse process.)

that is comparatively slender anteroposteriorly. The dorsal tip of the spinous process is missing only a millimeter or two, its vertical dimension being approximately 143 mm with that allowance. Posteriorly, its base has two facets to receive the anterior end of the base of the neural spine of the fourth thoracic. The neural canal is triangular in anterior view, but its apex is not as acute as that of the second thoracic, from which it differs

also by being 3 mm less in vertical diameter. The transverse processes project dorsolaterally, but in this vertebra the axis of each process passes through the ventral margin of the centrum, rather than through the center as in the second thoracic. The right process extends anteriorly approximately 38 mm beyond the anterior face of the centrum. It is the best preserved of the two, the extremity of the left one having been eroded away.

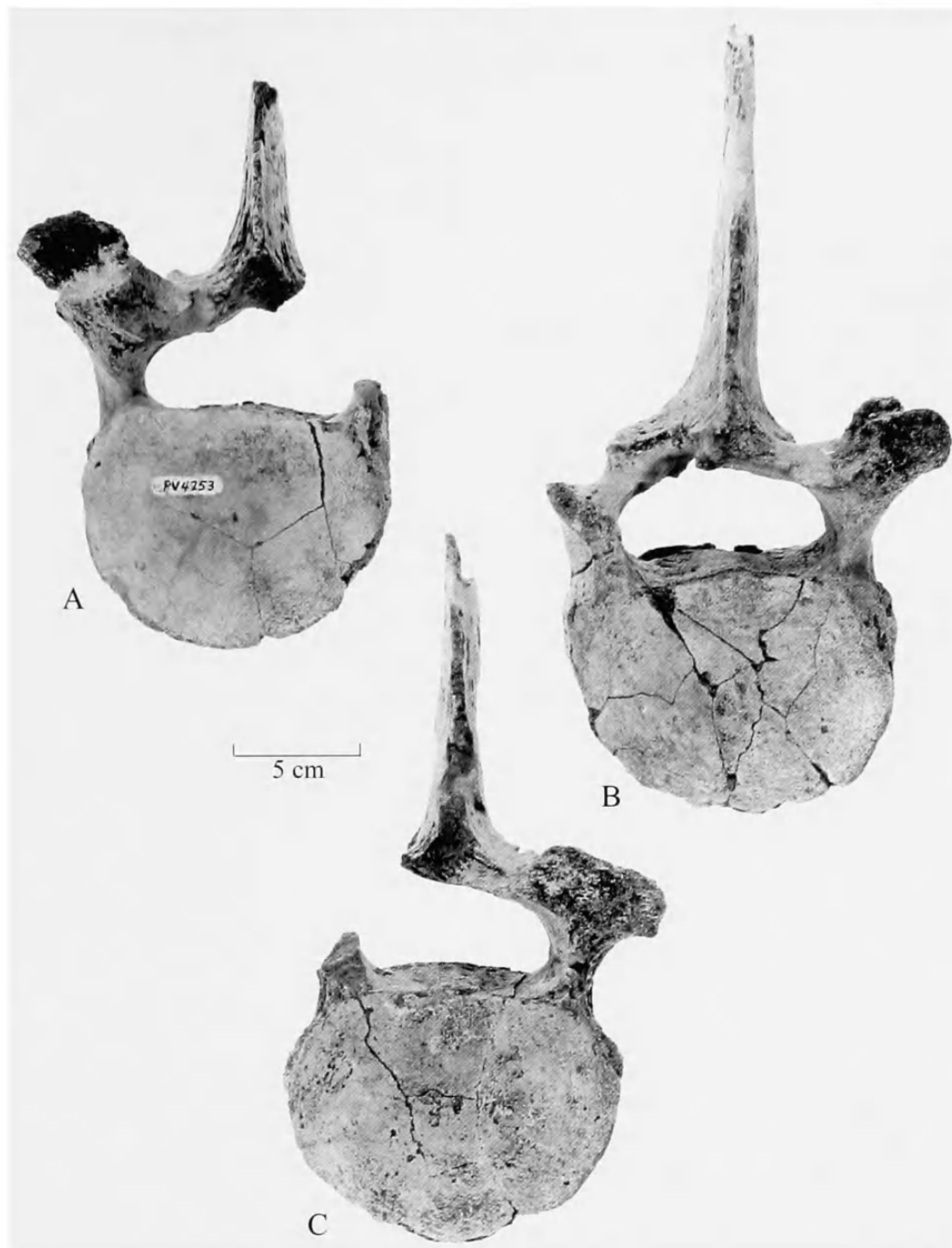


FIGURE 18.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, thoracic vertebrae, anterior views: A, fifth thoracic; B, seventh thoracic; C, eighth thoracic.

The articular facet for the tuberculum of the right third rib is well preserved and measures 32×26 mm. The center of this facet is approximately 6 mm above the level of the roof of the neural canal. On the centrum the anterior facet for the capitulum of the third rib is positioned slightly more ventrally than the posterior facet for the capitulum of the fourth rib. As in the second thoracic, the transverse diameter of the right pedicle of the neural arch exceeds that of the left, the right being 21.5 mm and the left approximately 18 mm, with allowance for erosion of the external surface of the left pedicle. The prezygapophysial facets are not well preserved along their outer edges, but the left one is sufficiently intact to determine its length as 43 mm.

The postzygapophysis extends approximately 4 mm beyond the posterior face of the centrum. Its ventral facet is too badly eroded to yield a measurement.

The vertebra that we have identified as the fifth thoracic (Figure 18A) qualifies for that position by virtue of the antero-posterior length of its centrum (76 mm) compared with that of the other thoracics (see Table 4). In this specimen, the right side of the neural arch and approximately one-half of the vertical diameter of the spinous process are preserved. The anterior profile of the neural canal is not so triangular as it is on the second and third thoracic vertebrae, the vertical diameter being 4 mm less than that of the third thoracic (see Table 4). The right

TABLE 4.—Measurements (in mm) of the thoracic vertebrae of *Eomysticetus whitmorei*, new genus and new species, ChM PV4253. (Parentheses indicate estimated measurements.)

Character	T.1	T.2	T.3	T.5	T.7	T.8	T.15(?)
Anteroposterior length of centrum	49	56	63	76	81	84	93
Transverse diameter of centrum, anteriorly	96	90	91	93	96	102.6	(101)
Vertical diameter of centrum, anteriorly	82	78	81	76	(79)	81	87
Minimum anteroposterior length of pedicle of neural arch	19	20	27	—	42	49	—
Transverse diameter of neural canal, anteriorly	—	63	72	(64)	67	(59)	—
Vertical diameter of neural canal, anteriorly	—	40	37	33	32	32	—
Distance between ends of transverse processes	—	190	(176)	—	(162)	—	—
Dorsal edge of metapophysis to ventral face of centrum, anteriorly	—	27	30	—	31	—	—
Tip of neural spine to ventral face of centrum, anteriorly	—	176	(177)	—	(190)	—	—
Transverse diameter of centrum, posteriorly	92	94	94	—	(106)	102	110
Vertical diameter of centrum, posteriorly	82	82	83	(84)	(84)	(85)	94
Anteroposterior length into transverse diameter of centrum, anteriorly	1.97	1.55	1.52	1.22	1.19	1.22	1.09
Anteroposterior length into vertical diameter of centrum, anteriorly	1.68	1.39	1.35	1.00	(0.98)	0.96	0.94

transverse process projects dorsolaterally, but not at as great an angle as those of the second and third thoracic vertebrae. Unlike the latter vertebrae, the pedicles are not angled outward with the transverse process but instead arise almost directly vertical to the plane of the dorsal surface of the centrum. The end of the transverse process is badly eroded, but it is clear that the articular facet for the tuberculum of the fifth rib is well above the roof of the neural canal. The anterior end of the prezygapophysis is broken off, its preserved portion extending approximately 15 mm beyond the anterior face of the centrum. The posterior end of the postzygapophysis also is missing, but apparently it did not project much beyond the posterior face of the centrum. Its ventral facet is canted ventrolaterally and appears to have been more rounded than its counterparts on the second and third thoracic vertebrae.

The seventh thoracic vertebra (Figure 18B) continues a trend of progressive increase in the anteroposterior diameter of the centrum in the thoracic series (see Table 4). Concomitantly, it continues a gradational trend in the decrease in the vertical diameter of the neural canal. Much of the spinous process is preserved, but it lacks the dorsal tip and portions of the anterior and posterior edges. The left transverse process is badly eroded but extends at least 9 mm beyond the anterior face of the cen-

trum. The right transverse process is entirely missing. The postzygapophysis extends only slightly beyond the posterior face of the centrum.

The eighth thoracic vertebra (Figure 18C) has most of its spinous process but lacks the tip and sections of the anterior and posterior margins. The left transverse process is preserved but is badly eroded and is incomplete anteriorly. Both the right transverse process and its pedicle are absent. At this position in the thoracic series, the transverse processes are still situated high on the flanks of the neural arch, the articular facet for the tuberculum of the rib being about level with the roof of the neural canal. As seen in Table 4, this vertebra reflects three progressive anterior-to-posterior trends in certain dimensions of the thoracic vertebrae: (1) a progressive increase in the anteroposterior length of the centrum; (2) a corresponding increase in the anteroposterior dimension of the pedicles of the neural arch; and (3) a reduction in the height of the neural canal. Commonly seen in cetacean vertebral columns, these trends are nothing more than accommodations for the disparate sizes of the cervical and lumbar series.

On the probable 15th thoracic vertebra (Figure 19) the transverse processes are located at a midlateral position on the centrum, clearly indicating that it is one of the last in the thoracic

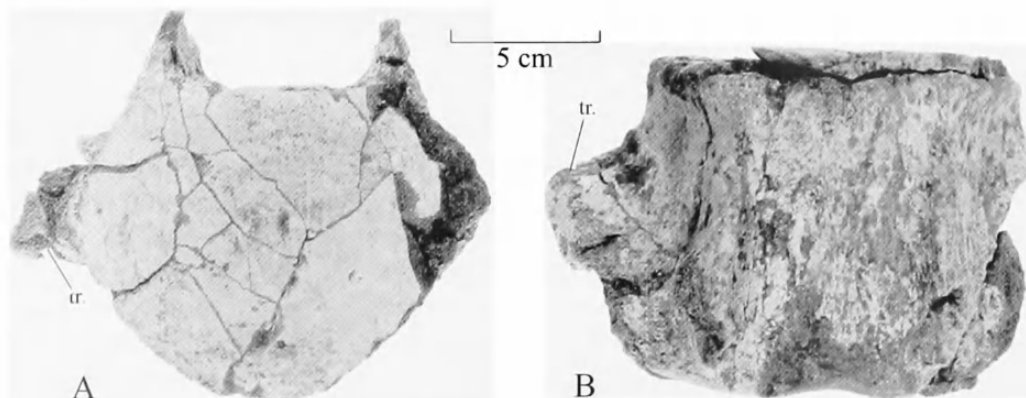


FIGURE 19.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, probable fifteenth thoracic vertebra: A, anterior view; B, dorsal view. (tr.=transverse process.)

TABLE 5.—Measurements (in mm) of the lumbar vertebrae and probable first caudal vertebra of *Eomysticetus whitmorei*, new genus and new species, ChM PV4253. Parentheses indicate estimated measurements.

Character	Lumbar A	Lumbar B	First caudal (?)
Anteroposterior length of centrum	126	(127)	125
Transverse diameter of centrum, anteriorly	118	(128)	(115)
Vertical diameter of centrum, anteriorly	(119)	(114)	(114)
Minimum anteroposterior length of pedicle of neural arch	76	(73)	61
Transverse diameter of neural canal, anteriorly	31	(20)	21
Vertical diameter of neural canal, anteriorly	—	—	36
Distance across ends of transverse processes	(330)	—	(258)
Dorsal edge of metapophysis to ventral face of centrum, anteriorly	—	—	195
Tip of neural spine to ventral face of centrum, anteriorly	—	—	(252)
Transverse diameter of centrum, posteriorly	(114)	(127)	(123)
Vertical diameter of centrum posteriorly	(108)	(128)	(110)
Anteroposterior length into transverse diameter of centrum, anteriorly	0.94	(1.01)	0.92
Anteroposterior length into vertical diameter of centrum, anteriorly	(0.94)	(0.90)	0.92

series. Furthermore, its very short and blunt transverse process is additional evidence that this vertebra is the last thoracic. This vertebra exemplifies the archaeocete-like characters that are evident in the thoracic vertebrae of *E. whitmorei*. The entire neural arch, including the spinous process, is missing, as is the left transverse process. Only the posterior half of the right transverse process is preserved, but that portion is sufficient to demonstrate that the transverse processes on this vertebra are short and are positioned midlaterally on the centrum, as in the last seven thoracic vertebrae of the archaeocete *Zygorhiza kochii* (see Kellogg, 1936:139–142). In the Miocene cetotheres *Pelocetus calvertensis* (see Kellogg, 1965, pl. 12), *Diorocetus hiatus* (see Kellogg, 1968, pl. 54), and *Thinocetus arthritus* (see Kellogg, 1969, pl. 6), the transverse processes of the last three or four thoracic vertebrae extend from the centrum, but they are much more elongate than in either *Eomysticetus whitmorei* or *Zygorhiza kochii*. These latter species also differ from the aforementioned cetotheres by having the articular facet for the tuberculum of the ribs positioned above the level of the roof of the neural canal on the third through the seventh thoracics. In *Pelocetus calvertensis* and *Thinocetus arthritus*, two species of cetotheriids for which there is sufficient material for comparison, the facet for the tuberculum does not extend dorsal to that level and is usually situated ventral to it (Kellogg, 1965, pls. 5–9; 1969, pl. 6).

Lumbar Vertebrae: Only two lumbar vertebrae were found with the holotype skeleton of *Eomysticetus whitmorei*. Both are missing the neural arch, and in the absence of other lumbar vertebrae, it is difficult to place these vertebrae in their exact positions in the vertebral column. We therefore believe it best to refer to these vertebrae only as lumbar “A” and lumbar “B.”

Lumbar vertebra “A” (Figure 20A) is the anteriormost of the two and seems clearly referable to the anterior one-third of the series, judging from the length and form of the right transverse process, the only one preserved on this specimen (see Table 5). The transverse process is elongate and flattened, with a slightly expanded and dorsally curved distal extremity, showing that it did not articulate with a rib. As in vertebrae of the Archaeoceti, the transverse processes of this vertebra are directed ventrolat-

erally, not horizontally as in typical Mysticeti. The centrum is nearly cylindrical, its height and width being nearly equal. Compared with more highly evolved Mysticeti, such as Cetotheriidae (e.g., *Thinocetus arthritus*), the centrum is relatively more elongate, and in this regard it is reminiscent of the lumbar vertebrae of basilosaurine archaeocetes. It is relatively shorter than in dorudontines, its length being somewhat intermediate between basilosaurines and dorudontines. The base of the pedicle is elongate anteroposteriorly and narrow transversely, indicating that the pedicle was typical of the condition in Mysticeti.

Lumbar vertebra “B” (Figure 20B) is from a more posterior location in the vertebral column than the one that we have labeled as lumbar vertebra “A.” Judging by the disparity in size and shape between it and lumbar vertebra “A,” several vertebrae undoubtedly separated the two. It also suffered from severe weathering and is fractured and lacks its processes. It has a longer centrum, of greater diameter, and this is typical of the more posterior lumbar vertebrae in species of Mysticeti. Its neural canal also is of smaller diameter, in agreement with a narrower nerve cord posteriorly in the body. Also, as with lumbar vertebra “A,” the centrum is relatively more elongate than is typical in species of Mysticeti.

Possible Caudal Vertebra: The posteriormost vertebra of the holotype skeleton is possibly a caudal vertebra (Figure 20C). It is definitely from a position more posterior in the body than any of the aforementioned vertebrae. Its centrum is larger, its neural process shorter, its transverse processes shorter and more ventrally directed, and its neural canal narrower (Table 5). The parts of the ventral surface of the centrum that would have borne facets for articulation with chevron bones have been abraded away; therefore, we cannot definitely place this bone in the caudal series, but it could be either a posteriormost lumbar or an anterior caudal. In its overall morphology, this vertebra resembles posterior lumbar and anterior caudal vertebrae of archaeocetes (see Kellogg, 1936, fig. 60 for *Zygorhiza kochii*, and pl. 5 for *Basilosaurus cetoides*).

The dorsal process is longer than those in this part of the column in *B. cetoides*, but the metapophyses extend dorsolaterally as in the same species. The distal end of the intact left trans-

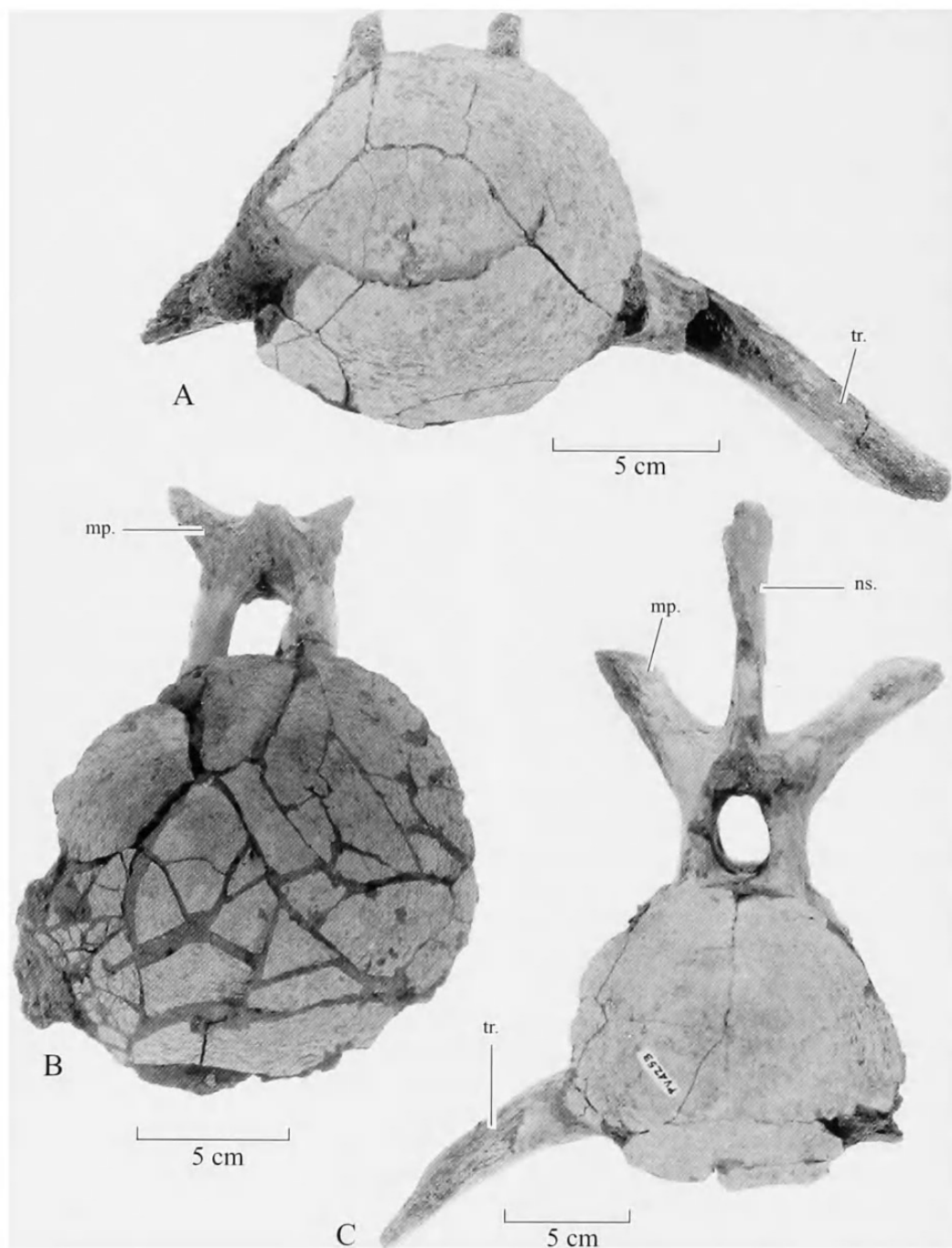


FIGURE 20.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, lumbar and caudal (?) vertebrae in anterior view: A, lumbar “A”; B, lumbar “B”; C, probable anterior caudal vertebra. (For other abbreviations see Figure 17.)

verse process bends ventrally at its extremity, not dorsally as in the lumbar vertebra “A” described above. On the dorsal surface of the transverse process is an oblique crest of bone, representing a muscle scar, that is typically seen on vertebrae in the anterior part of the caudal series in species of modern Cetacea.

Ribs: The ribs of the holotype as they were found in the excavation were not in anatomical position, and the field occurrence did not therefore indicate the sequence in life. We have

determined the apparent positions of the ribs using comparisons with other fossil and extant Cetacea (see Figure 21). Because it is typically short and broad in cetaceans, the first rib is the only one that is definitely identifiable. All the other positions that we indicate are approximations and might be inaccurate by one or two positions. The ribs that have both the tuberculum and the capitulum are identifiable as right or left by the posteroventral slope of the facet on the tuberculum, by the an-

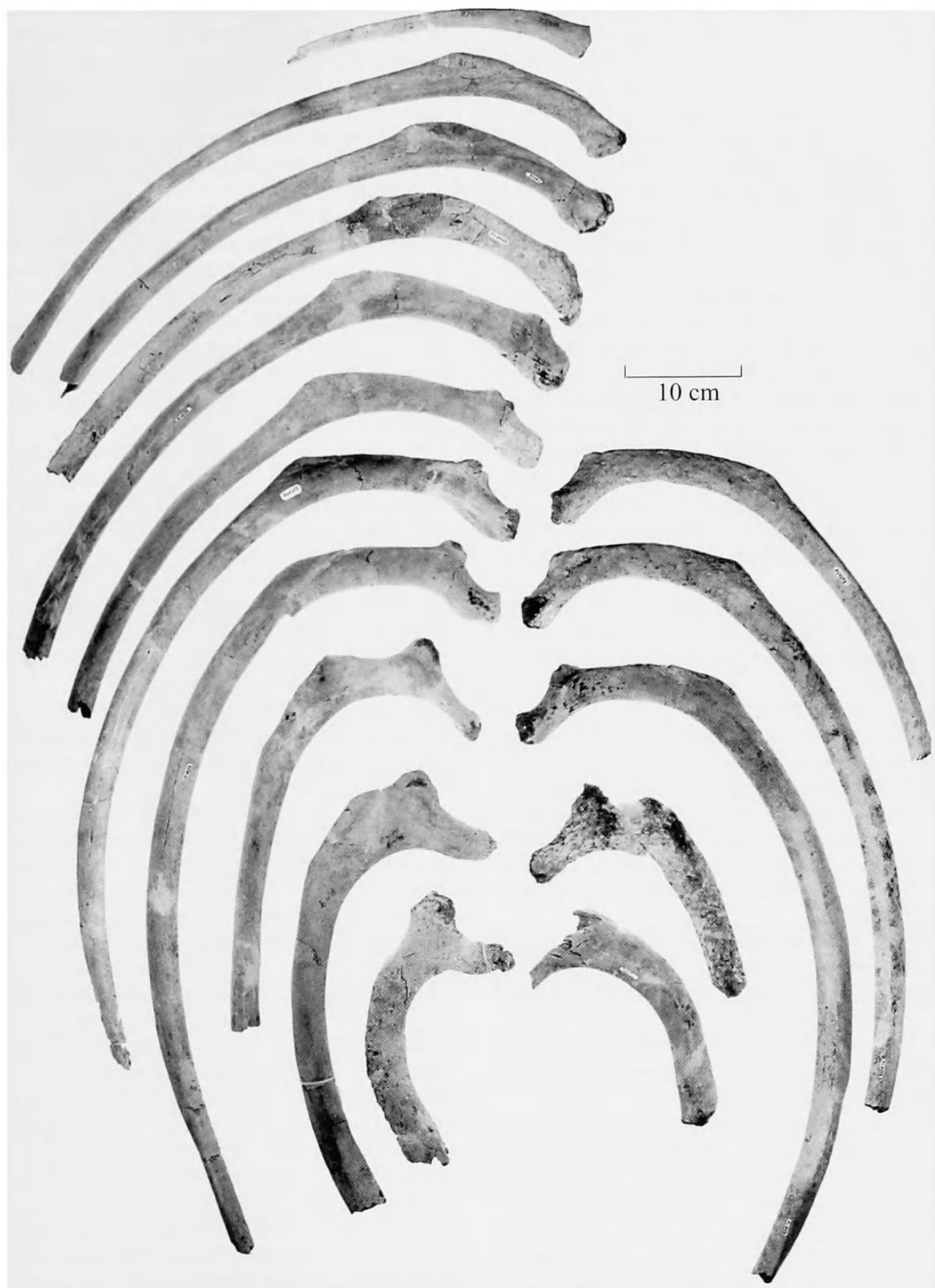


FIGURE 21.—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253; ribs in anterior view.

terior twist of the neck and capitulum, and by the direction of the prominence and strut at the change in angle of the shaft of the rib. The posterior ribs, which lack the capitulum and terminate proximally in only an irregular facet, are less certainly identified as right or left; however, except for the posteriormost one, the ribs from the right and left sides are probably identified correctly. The determination of the sequence of the ribs after the first rib on each side was based upon (1) progressive lengthening and thickening of the shaft toward the middle of the series, (2) progressive shortening of the neck and reduction in size of the capitulum posteriorly, and (3) loss of head and reduction in overall size of the posteriormost ribs.

According to these generalizations, there are at least 15 different rib positions among the bones of the skeleton. This judgment assumes that the smallest rib, which is not complete, is a posteriormost rib, and that the slightly mismatched pair that we have identified as the right and left seventh ribs are in fact a pair. This number is equal to the 15 ribs that are present in species of Archaeoceti and is more than the typical 12 of cetotheriids (see Kellogg, 1968:175). If the mismatched ribs we identify as the right and left seventh ribs in fact represent different positions, then the holotype of *Eomysticetus whitmorei* may have had 16 ribs on each side.

Only the first rib on the left side is present, and it is missing part of its head. It is short, broad, and flat, its proximal end is strongly curved, and the shaft is short with a definite rugose articular facet distally.

The probable right second rib is not complete. It is not as broad and flat as the first, and it is definitely longer than that rib, even though it is broken distally.

The probable right and left third ribs are not complete. The one from the right side is the better preserved of the two and is longer. The left one seems to match it well, but its surface is badly eroded. Each of these ribs is not so curved as the previous one, and each has a prominent angle, a prominent tuberculum, and a long head.

The possible fourth rib, represented only in the right series, is less curved proximally, is more slender, and has a shorter neck between the tuberculum and capitulum compared with the previous rib.

The probable fifth rib, present only in the right series, is more elongate and has a more cylindrical cross section and a shorter neck than the previous rib.

Both the right and left probable sixth ribs are present, and they differ from the previous one in the following ways: they are more elongate, the head is smaller, the neck is shorter and more slender, and the tuberosity at the change in angle is located farther distally on the shaft of the rib. We are cautious about the assignment of both ribs to the same location, because the left one has a slightly more slender head.

The possible left seventh rib is slightly thicker than the previous one at the proximal end.

The probable left eighth rib differs from the previous one by having a shorter neck.

The probable ninth rib is represented on the right side only. It has a shorter neck, and the tuberosity at the change in angle is located farther distally on the shaft of the rib.

The rib that we believe to be the 10th is represented on the right side only. Compared with the previous rib, the neck is much shorter, the head has a large and flat articulation, and the tuberosity at the change in angle is located farther distally on the shaft of the rib.

The possible 11th rib is represented on the right side only. Compared with the previous rib, it has a less prominent tuberosity at the change in angle of the shaft, a very short neck, and barely separate tuberculum and capitulum.

The possible 12th rib also is represented on the right side only. Compared with the previous rib, the tuberosity at the change in angle of the shaft is less prominent. It is the first rib without a capitulum, and the tuberculum has a rounded, blunt articulation.

The possible 13th rib also is represented on the right side only. Compared with the previous rib, it is more slender and has a less prominent tuberosity at the change in angle of the shaft. It also lacks a capitulum, and the tuberculum has a smaller, blunt articulation.

The possible 14th rib is represented on the left side only. It is more slender than the previous rib and has a less prominent tuberosity at the change in angle of the shaft. Like the previous two ribs, it lacks a capitulum and the tuberculum has even a smaller articulation.

The presumed 15th is the smallest of the preserved ribs. It appears to be from the right side, and it is missing the proximal end. By its curvature, it appears similar to the posteriormost ribs of extant Cetacea.

Forelimb: The anterior limb in *Eomysticetus whitmorei* is represented by a partial right scapula, the right humerus, the right ulna, and the right radius (Figure 22). The scapula is preserved only in the area immediately above the glenoid cavity and for a distance of 200 mm along the posterior edge. Although lacking its anterior external and internal edges, the glenoid cavity is subovate (60×90 mm), shallow, and somewhat flattened transversely. The articular head and glenoid cavity are distinctly elongate rather than ovoid, as in the Miocene cetotheres *Pelocetus calvertensis*, *Diorocetus hiatus*, and *Thi-nocetus arthritus*, for example. Anteriorly, the articular head extends well forward of the base of the anterior edge and acromion and curves sharply inward. The posterior edge of the scapula rises directly from the posterior end of the articular head and projects backward in a low arc for a distance of 122 mm along the plane from the head to the terminus of the arc. Midway along that distance the edge is 33 mm thick, but in the space of only 40 mm above the edge, the scapula thins to 9 mm in transverse diameter. A similar but more concave arc is described by the posterior edge of the scapula of the late Oligocene odontocete *Sulakocetus dagestanicus* Mchedlidze, 1976 (see Mchedlidze, 1976, fig. 1, table 16) from the northern Caucasus region of Dagestan.

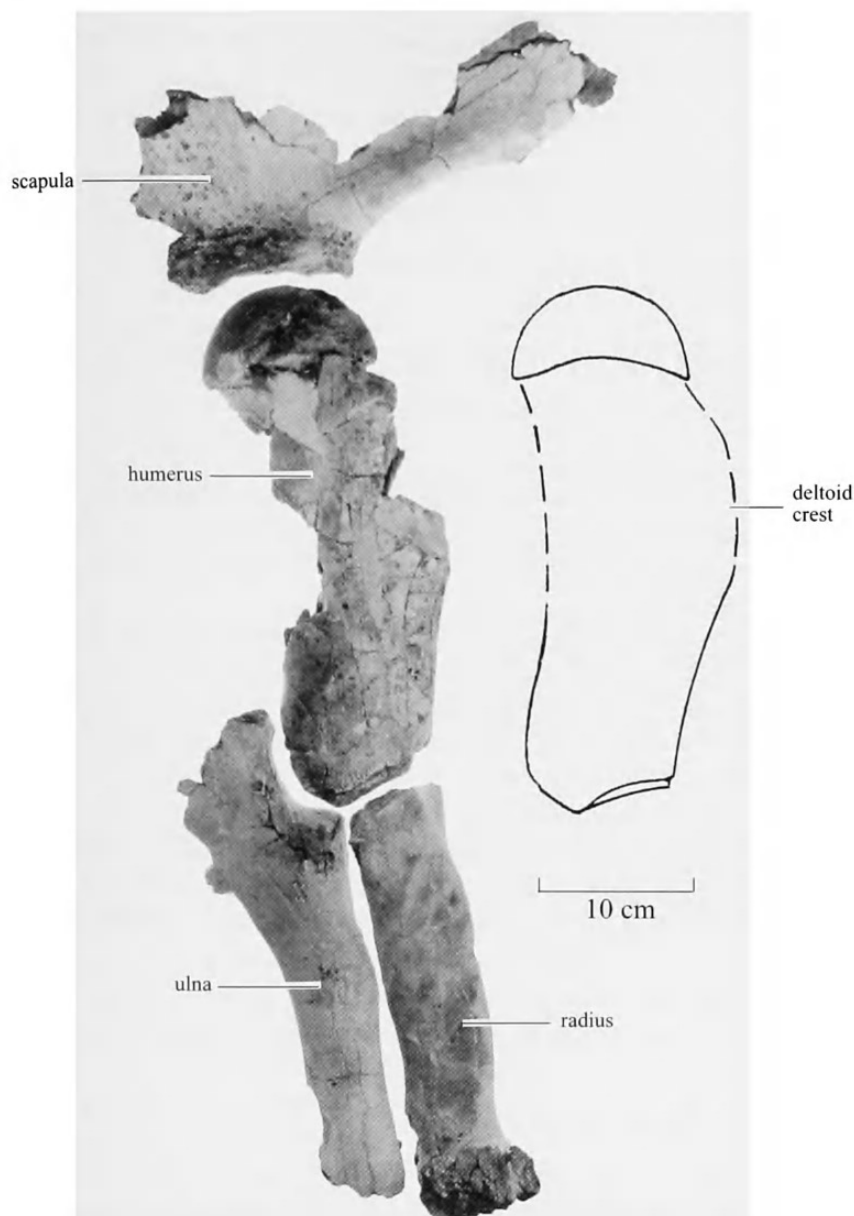


FIGURE 22 (left).—*Eomysticetus whitmorei*, new genus and new species, holotype, ChM PV4253, right forelimb in lateral view, with reconstruction of humerus at right. (Dashed lines represent hypothetical configurations.)

The humerus is incomplete, lacking the lateral edges of the head, the region of the radial tuberosity, most of the posterior face, and approximately 80 mm of the proximal portion of the medial side. The head is smooth and is directed obliquely laterally and posteriorly, the greater portion of it being positioned posterior to the long axis of the bone, which passes through the convergence of the radial and ulnar facets. It is flattened along its external side and is decidedly less globose than the heads of the humeri of *Pelocetus calvertensis*, *Diorocetus hiatus*, and *Thinocetus arthritus*. At the distal end of the humerus, the lateral portion of the juncture of the radial and ulnar facets is preserved, permitting an accurate measurement of the length of this bone at its greatest distal extent. As in all non-archaeocete Cetacea, the radial and ulnar facets converge to form an obtuse angle, approximately 125° in this individual. The shaft of the humerus is quite different from those of Neogene mysticetes, being considerably longer, more robust, and of an entirely different configuration. The preserved portion above the ulnar

facet is rounded, and immediately above the proximal margin of that facet there is a shallow gutter, above which the bone begins to widen transversely. Anteriorly, the lateral and medial sides of the shaft are greatly flattened distally and converge to form a narrow keel for a distance of approximately 90 mm along the preserved portion of the anterior face. The keel arises from the proximal border of the radial facet and angles upward along a tangent of approximately 55° from the axis of the radial facet, a line approximately paralleling the anterodistal angle from the lower end of the deltoid crest in archaeocete humeri. This feature can thus be termed the anterodistal angle of the humerus in *E. whitmorei*. Although the region above it is missing in the holotype, the slope of this angle suggests the presence of a prominent deltoid crest in humeri of Eomysticetidae (Figure 22). At a point approximately 148 mm from the distal end of the humerus, the anterior face begins to broaden proximally toward the head.

TABLE 6.—Measurements (in mm) of the holotype right humerus of *Eomysticetus whitmorei*, new genus and new species, ChM PV4253. Parentheses indicate estimated measurements.

Greatest length	329
Anteroposterior diameter of head	110+
Transverse diameter of head	93+
Anteroposterior diameter of shaft in valley above ulnar facet	95
Anteroposterior diameter of shaft, 120 mm above distal tip	103
Transverse diameter of shaft at same level	63
Transverse diameter of anterior face of shaft at same level	16
Transverse diameter of posterior face of shaft at same level	47
Anteroposterior diameter of external portion of radial facet	54
Anteroposterior diameter of distal end at level of anterior margin of radial facet	77
Transverse diameter of distal end	(84)

The humerus of *E. whitmorei* displays a remarkable combination of archaeocete and mysticete characters but is most similar to humeri of Archaeoceti (e.g., *Basilosaurus cetoides* and *Zygorhiza kochii* (see Kellogg, 1936:65–66, 161–162)) in three major respects: (1) the greatest anteroposterior diameter of the shaft exceeds that of the distal end; (2) there is a pronounced anterodistal angle characteristic of archaeocetes but unknown in previously described mysticete humeri; and (3) the extreme length of the shaft, compared with humeri in Neogene mysticetes (Table 6). The most distinctive non-archaeocete character is the presence of separate, flattened radial and ulnar facets, instead of the rounded trochlea and capitulum that are typical of humeri of archaeocetes and other mammals. That is the difference between the rotational elbow joint of archaeocetes and the nonrotational joint of the modernized Cetacea.

The radius was badly shattered by compaction of sediments but has been restored closely enough to its proper form to yield a reasonably accurate measurement of its greatest length, which is 268 mm. Proximodistally, the anterior and posterior margins of the shaft do not appear to have been as strongly curved as those of the radii of archaeocetes and of Miocene cetotheriids (see Kellogg, 1936, fig. 72; 1965, fig. 23; 1968, fig. 73; 1969, pl. 3). Although the distal end of the radius is badly crushed and incomplete, the preserved portion shows that it was expanded both transversely and anteroposteriorly. The distal epiphysis is missing. The proximal end is bent posteriorly to articulate with the radial facet of the humerus. The facet for articulation with the ulna was not preserved, and the medial face immediately below the radial facet also is missing. Approximately 50 mm below the anterior edge of the proximal end, the transverse diameter of the shaft abruptly increases, marking the proximal termination of a broad, flat area that extends proximodistally along the anterior face for a distance of about 65 mm, at which point it diminishes into the normal transverse diameter and rounded form of this face of the shaft. This feature seems to be homologous with the “elliptical rugose area” noted by Kellogg (1936:162) in his description of the radius of *Zygorhiza kochii*. Kellogg (1936:162) presumed it to be the area for the insertion of the pronator teres muscle, which may still have been slightly functional in *Z. kochii*, considering the prim-

TABLE 7.—Measurements (in mm) of the holotype right ulna of *Eomysticetus whitmorei*, new genus and new species, ChM PV4253.

Length of preserved portion (from 13 mm above proximal portion of greater sigmoid cavity to distal end)	327
Greatest diameter of greater sigmoid cavity	51+
Greatest transverse diameter of proximal portion of greater sigmoid cavity	38.5
Greatest transverse diameter of distal portion of greater sigmoid cavity	51+
Greatest length of anterior face of shaft below greater sigmoid cavity	246
Anteroposterior diameter of shaft at 85 mm below greater sigmoid cavity	61
Transverse diameter of shaft at same level	31

itive structure of its elbow joint. If present in *Eomysticetus*, it is doubtful that that muscle would have been functional at all in view of the more highly specialized, nonrotational elbow joint in this form.

The ulna (Table 7) is missing the posterior portion of the olecranon process and a large area of its internal side proximal to the shaft. Also missing are the distal sections of the anterior and posterior faces and the distal sections of the medial face. The shaft is transversely compressed and is broadly curved proximodistally. It is transversely expanded at both the distal and the proximal ends. The proximal portion of the greater sigmoid cavity is slightly concave, the distal portion being broadly convex transversely. As with the radius, the distal epiphysis is not present.

Eomysticetus carolinensis, new species

FIGURES 24–28

Cetothere “similar to *C. tobieni*.”—Sanders and Barnes, 1991.

DIAGNOSIS.—A species of *Eomysticetus* separated from *E. whitmorei* by the following characters: intertemporal region shorter; parietals one-third less in length along midline; apex of supraoccipital extending farther anteriorly (by approximately 38 mm); anterior portion of supraoccipital heavily corrugated; lambdoidal crests more laterally oriented and overhanging temporal fossa; parietals sloping from intertemporal region more laterally and not so vertically directed; sagittal crest of parietals in intertemporal region rounded, not blade-like; squamosal fossa narrower; zygomatic process of squamosa thinner and more divergent from sagittal plane; distal end of zygoma extending to or slightly behind plane of apex of supraoccipital and lacking a prominent ventral facet for articulation with jugal; dorsomedial side of zygoma not convex but flat to slightly concave; basioccipital crests transversely thinner, more ventrally extended, and more knob-like; foramen ovale of larger diameter and more elongate; anterior border of glenoid fossa broadly curving, not angular; glenoid fossa more square and deeper anteroposteriorly; postglenoid process thicker and deeper; supracondylar fossae shallower; intercondylar notch (between occipital condyles) shallower; jugular notch bilobed (not preserved in *E. whitmorei*).

HOLOTYPE.—ChM PV4845, braincase lacking the entire rostrum and missing the left exoccipital and squamosal. Collected by Barry Albright and Vance McCollum during the summer of 1988.

TYPE LOCALITY.—Found in a ditch in the Irongate subdivision, Dorchester County, South Carolina, approximately 33.8 km (21 mi.) north of Charleston and about 2.6 km (1.6 mi.) northwest of the type locality of *Micromysticetus rothauseni* Sanders and Barnes (2002).

FORMATION AND AGE.—Chandler Bridge Formation, bed 2, lower Chattian correlative, late Oligocene, nannoplankton zone NP24 (by inference), ca. 28 Ma (Figure 23).

ETYMOLOGY.—The specific name recognizes South Carolina as the origin of the holotype.

DESCRIPTION.—Lacking the left squamosal and exoccipital regions and all of the ventral portion of the postorbital region anterior to the basisphenoid, the holotype cranium of *Eomysticetus carolinensis* is not as complete as the holotype of *E. whitmorei*, but the surfaces are well preserved and the basicranium and most of the dorsal surface of the intertemporal region are present (Figures 24–26).

The lambdoidal crests are incompletely preserved in the apical region and elsewhere are missing altogether, making it difficult to determine the original shape of the supraoccipital. Nonetheless, the curvature and angle at which the preserved remnant of the left lambdoidal crest extends posteriorly from the apex of the supraoccipital permit a reasonably close approximation of the shape of the occipital shield (Figure 24B), which evidently is narrow and elongate, more so than in *E. whitmorei*. Also unlike the condition in *E. whitmorei*, the supraoccipital extends beyond the plane of the anterior tips of the zygomae. The dorsal surface of the supraoccipital in *E. carolinensis* is divided into two elevations, the posterior portion being a shallow depression beginning approximately 40 mm anterior to the posterior margin of the supraoccipital and extending forward to the posterior margin of the parietals. At that point the supraoccipital abruptly ascends the parietals to a plateau formed by the parietals and slopes upward and forward to the apex, a distance of approximately 130 mm. A conspicuous rounded eminence on each side of the midline marks the point of contact between the supraoccipital and the parietals during an earlier stage of ontogeny when the bone of the supraoccipital was thinner and more plastic. A prominent medial crest traverses virtually the entire length of the supraoccipital, extending from a point near the apex to the posterior margin of the lower, excavated area, dividing that area into two sections. The crest achieves its maximum height on the plateau formed by the parietals, where it rises almost to the height of the adjacent lambdoidal crests. In this region the crest is flanked by two short crests, each of which is bordered on both sides by an elongate gully-like depression. The resulting pattern of alternating ridges and grooves produces a corrugated effect over most of the elevated portion of the supraoccipital (Figure 24).

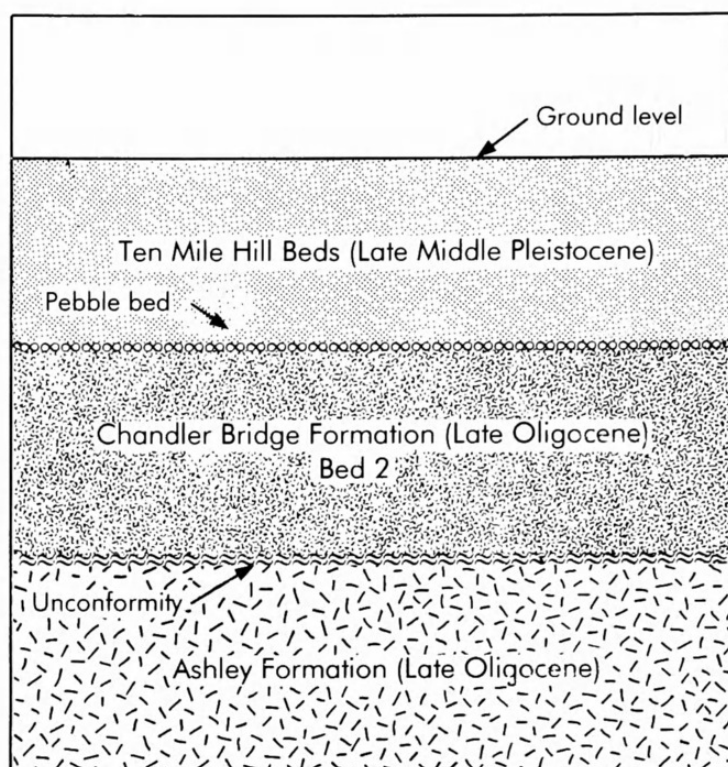
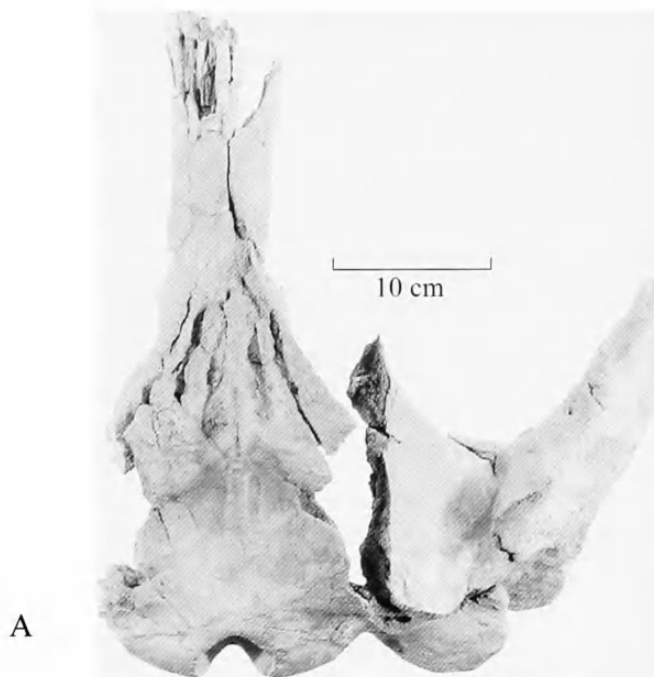


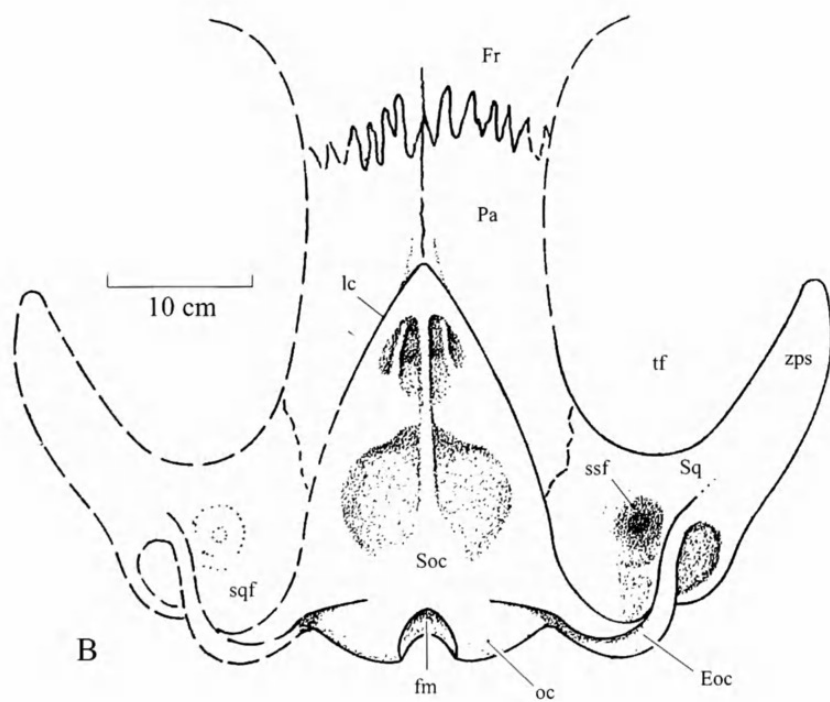
FIGURE 23.—Stratigraphic section at type locality of *Eomysticetus carolinensis*, new species, ChM PV4845. (Not to scale.)

The holotype of *E. carolinensis* represents a mature individual, as indicated by the smooth articular surfaces of the occipital condyles. The dorsal margins of the condyles of *E. carolinensis* lie only slightly below the level of the floors of the squamosal fossae (Figure 27). The vertical diameter of the foramen magnum exceeds the transverse diameter. The exoccipital is broad and does not extend very far posteroventrally, and most of the paroccipital process is missing. The lateral wall of the braincase is concave, the squamosal inclining posteriorly to the posterior margin of the lambdoidal crest along the inner flank of the squamosal fossa. The floor of the squamosal fossa is interrupted by the secondary squamosal fossa, a deep, circular, pit-like depression approximately 18 mm in diameter at its deepest point. The posterior wall of this pit receives a narrow gutter that steeply ascends to the floor of the squamosal fossa and extends to its posteriormost margin. Anterior to the pit, the floor of the fossa is broadly concave. The zygomatic process of the squamosal diverges more abruptly from the sagittal plane, is rather long, is tapered anteriorly, and is not so strongly arched as that of *E. whitmorei*. It is angled sharply outward from the long axis of the skull and extends forward to a point slightly behind the plane of the apex of the supraoccipital. A relatively small, shallow, and anterodorsally inclined sternomastoid fossa occupies the posterior face of the squamosal near the suture with the exoccipital.

On the ventral side of the cranium the basioccipital is well preserved. It is dorsally arched transversely and has large,



A



B

FIGURE 24 (left).—*Eomysticetus carolinensis*, new species, holotype, ChM PV4845: A, cranium, dorsal view; B, reconstruction of cranium based upon holotype, dorsal view. (Dashed lines and solid lines in areas of missing bone (see Figure 24A) represent hypothetical configurations. Abbreviations are explained in "Material and Methods.")

somewhat rounded basioccipital crests that are sharply divergent posteriorly and descend prominently from the basicranium. Extending forward from the anterior slope of the basioccipital crest and along the lateral margin of the basisphenoid there are large, elongate, and obliquely oriented interdigitations that form the suture for the hamular process of the pterygoid. The glenoid fossa is large and almost rectangular in form, its transverse width (102.7 mm) nearly equaling its anteroposterior length (106 mm). Slightly posterior to the cranial hiatus, the innermost margin of this fossa forms an acute angle. The glenoid process is elongate transversely and is very narrow anteroposteriorly. There is a correspondingly long external auditory meatus.

The most noticeable features of the holotype cranium of *E.*

carolinensis are the elongate supraoccipital shield and the long intertemporal region. The preserved portion of this region is 135 mm in length anterior to the apex of the supraoccipital and consists primarily of the parietals, which interdigitate with a narrow posterior extension of the frontals over a broad area anteroposteriorly. Dorsally, a finger of the frontals extends backward to within 60 mm of the apex of the supraoccipital. Laterally, the parietals project forward for a distance of at least 110 mm anterior to the apex, overlapping the posterior end of the frontals for a distance of at least 50 mm. Although only a 78 mm portion of the frontals is preserved, the degree to which the left side of this section has begun to flare outward anteriorly indicates that a forward extension of approximately 50 mm along a line of intensifying outward curvature would bring it into

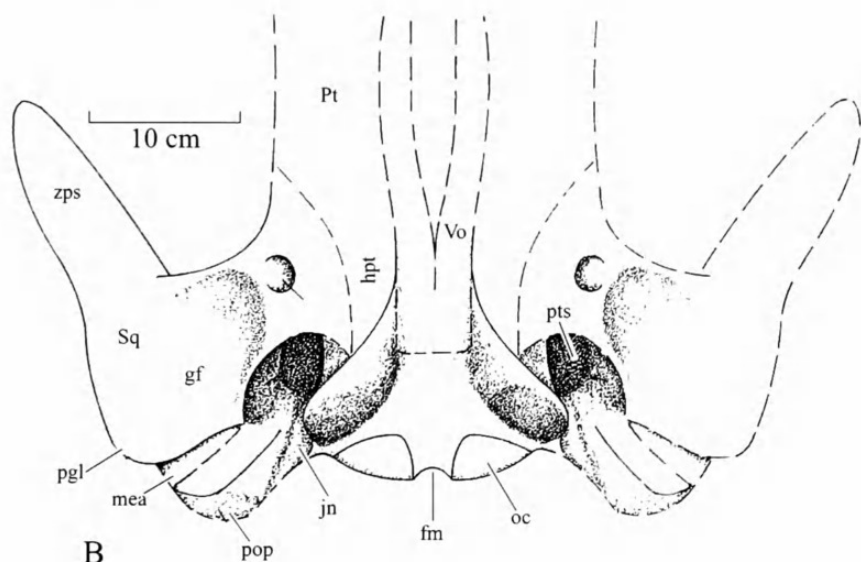
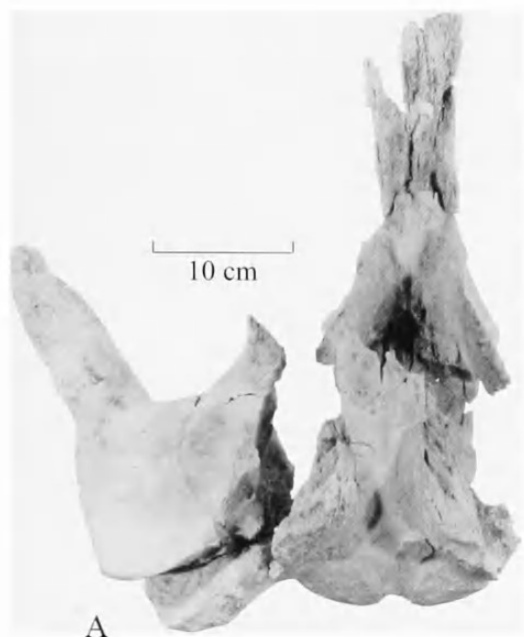


FIGURE 25 (left).—*Eomysticetus carolinensis*, new species, holotype, ChM PV4845: A, cranium, ventral view; B, reconstruction of skull based upon holotype, ventral view. (Dashed lines and solid lines in areas of missing bone (see Figure 24A) represent hypothetical configurations. Abbreviations are explained in "Material and Methods.")

contact with the posterior margin of the supraorbital processes of the frontal. We estimate that the distance between the apex of the supraoccipital and the level of the posterior edges of the supraorbital process was approximately 165 mm. The distance from the posterior margin of the temporal fossa to the apex of the supraoccipital is about 195 mm; thus, the anteroposterior length of the temporal fossa in this specimen can be conservatively estimated as approximately 360 mm.

Although no portion of the rostrum was preserved, we believe that the nasals of *E. carolinensis* must have been elongated as in *E. whitmorei*, and it is not unreasonable to think that the rostrum was long and narrow like that of *E. whitmorei*.

Discussion

COMPARISONS WITH OTHER CETACEAN TAXA

General evolutionary trends within the suborder Mysticeti are toward progressively large body size, relatively large heads,

short necks, grooves in the throat region, and telescoping of the cranial elements with an emphasis on movement of occipital bones anteriorly over the braincase. In its forward progress through the various grades of telescoping (Miller, 1923), the acute anterior margin of the supraoccipital shield seems to have wedged between the parietals and gradually forced them apart, producing well-developed lambdoidal crests that usually overhang the temporal fossae in Oligocene and primitive mysticetes. In most later mysticetes of Neogene time the dorsal portion of the parietals has been reduced to a small area in the anterior region of the skull roof. In *Eomysticetus whitmorei* and *E. carolinensis* the parietals occupy a prominent portion of the intertemporal region of the skull.

The braincase of *E. whitmorei* shares more characters with archaeocetes than does any other described mysticete skull. The same could probably be said for *E. carolinensis* were more of the skull preserved. Comparison of the skulls of the late Eocene archaeocete *Zygorhiza kochii*, the late Oligocene *Eomysticetus whitmorei*, the late Oligocene "*Mauicetus*" *lopho-*

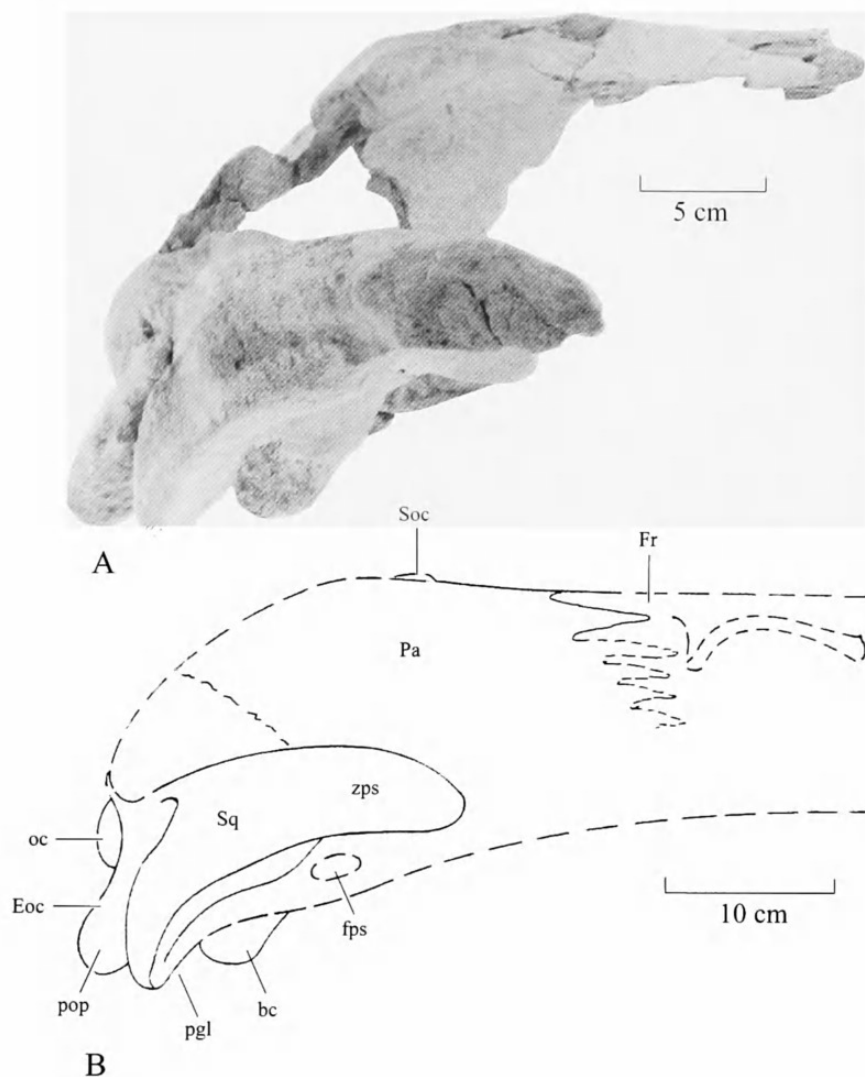


FIGURE 26 (left).—*Eomysticetus carolinensis*, new species, holotype, ChM PV4845: A, cranium, right lateral view; B, reconstruction of skull based upon holotype, right lateral view. (Dashed lines represent hypothetical configurations. Abbreviations are explained in "Material and Methods.")

cephalus Marples, 1956, the early Miocene *Aglaocetus moreni* (Lydekker, 1894), the late Miocene *Cetotherium rathkii* (Brandt, 1873), and the late Oligocene toothed mysticete *Aetiocetus cotylalveus* Emlong, 1966, shows a general progression from the non-telescoped archaeocete skull represented by *Zygorhiza kochii* through the telescoping of the cranial elements in the grades represented by *Eomysticetus*, "*Mauicetus lophocephalus*," *Aglaocetus*, and *Cetotherium*. The most striking evolutionary changes in the crania of those four taxa are the shortening of the intertemporal region and a corresponding reduction in the length of the nasal bones. Although more primitive in rostral characters and presence of teeth, *Aetiocetus cotylalveus* actually has a more highly telescoped cranium than does either *Eomysticetus* or *Mauicetus*, and it really does not fit into the progression of telescoping in the mysticetes. That observation lends strong support to Kellogg's (1969:1) doubt that *Aetiocetus* was an antecedent of the baleen-bearing whales and to the suggestions of Barnes (1987, 1989) and Barnes et al. (1995) that it is unlikely that any of the aetiocetid mysticetes were involved with the ancestry of modern mysticetes. True baleen-bearing Mysticeti were contemporaneous with the Aetiocetidae and in fact occur even earlier in the fossil record than

any known aetiocetid. Those facts, coupled with the presence of autapomorphies in aetiocetids that are not shared with the earliest baleen-bearing Mysticeti (for example the comparatively shorter and wider intertemporal region of the Aetiocetidae), confirm that all known Aetiocetidae were relict taxa. Likewise, *Eomysticetus whitmorei* and *E. carolinensis* were in their time also relict taxa, for they have cranial characters that are more primitive than some earlier-occurring baleen-bearing mysticetes. It seems most probable that the Aetiocetidae and the Mammalodontidae are side branches of Mysticeti in which baleen was never developed, the retention of teeth into adulthood perhaps being a paedomorphic character that became firmly entrenched. Whether the same can be suggested for the third family of toothed mysticetes, the Llanocetidae, is a question that must await knowledge of the cranial characters of species in that group.

Among currently known fossil and living mysticetes, the extremely long nasal bones in *Eomysticetus whitmorei* are approached in length by those of "*Mauicetus*" *lophocephalus* (see Crowley and Barnes, 1996). A comparison of the measurements of the nasals of *E. whitmorei* with those of the holotype of "*M.*" *lophocephalus* (see Marples, 1956:568) can be decep-

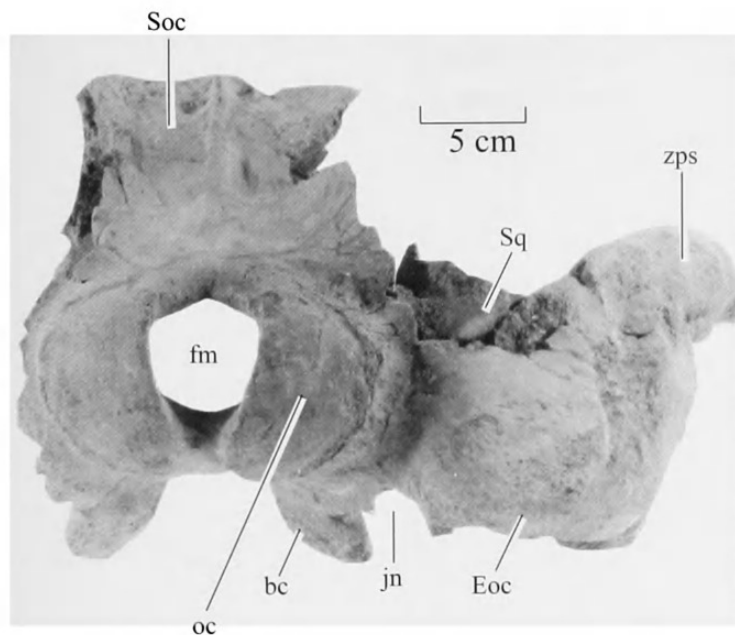


FIGURE 27.—*Eomysticetus carolinensis*, new species, holotype, ChM PV4845, cranium, posterior view. (Abbreviations are explained in "Material and Methods.")

tive if the differences in sizes between the respective skulls are not taken into account. The nasal bones in *E. whitmorei* are approximately 300 mm long, whereas those of the holotype of "*M.*" *lophocephalus* are given (by Marples) as 350+ mm in length. The distance between the lateral margins of the exoccipitals is 495 mm in "*M.*" *lophocephalus* but only 340 mm in *E. whitmorei*, demonstrating that the holotype skull of "*M.*" *lophocephalus* is approximately 30% larger. Consequently, if the skull of *Eomysticetus whitmorei* were as large as the New Zealand specimen, the nasals would measure about 393 mm, exceeding those of the latter. Compared directly, the length of the nasals is 88% of the distance between the lateral margins of the supraoccipitals of *Eomysticetus whitmorei*, but only 71% of the same distance in the holotype skull of "*M.*" *lophocephalus*. Unfortunately, we find that comparisons of the nasal bones of these two specimens based upon the original description of "*M.*" *lophocephalus* seem uncertain at best because of the discrepancy between the figured length of the nasals in Marples's (1956:567, fig. 1c) reconstruction and their apparent length in photographs A and B of his plate 1. In the reconstruction, the nasals and the premaxillae are shown to terminate at the anterior edge of the frontals, whereas in both of the two published photographs (A, the prepared specimen, and B, the skull in place) the nasals appear to extend posteriorly onto the frontals as in *Eomysticetus* and other, more typical baleen whales. Not having seen the holotype of "*M.*" *lophocephalus*, we cannot venture a qualified opinion as to which of the two alternatives is correct. Apparently that question will never be settled, because the holotype cranium of "*M.*" *lophocephalus* has been lost (E. Fordyce, pers. comm., July 1994). Among other cetaceans, the length of the nasal in *Eomysticetus whitmorei* appar-

ently is matched by that of *Remingtonocetus harudiensis* (Kumar and Sahni, 1986:331–332, figs. 3, 4). The anterior portion of the nasals are missing in the figured paratype of the latter taxon, but their length was estimated as 310 mm (Kumar and Sahni, 1986:333, table 1).

The presence of a temporal crest on the dorsal surface of the supraorbital process is one of the defining features of mysticetes. In Odontoceti, the temporal line is at the posterior margin of the process. The fact that the temporal crest in *E. whitmorei* merges with the middle part of the posterior margin of the supraorbital process indicates that this is a very primitive position for the structure. The intertemporal region is elongate and narrow, exceedingly so in comparison with most other fossil and extant Cetacea. The structure of the intertemporal region of *E. whitmorei* is a primitive condition for a cetacean, especially for a baleen whale. The prominent sagittal crest on the upper part of the occipital shield also is present in some species of the family Cetotheriidae (e.g., *Micromysticetus rothauseni* Sanders and Barnes, 2002). The condition of the paroccipital process—being thin laterally and only extending laterally as far as the middle part of the postglenoid process—is primitive among Cetacea and also is present in extant gray whales (*Eschrichtius robustus*). The pit-like secondary squamosal fossa, described above, is known to occur only in *E. whitmorei* and *E. carolinensis*. For a mysticete, *Eomysticetus whitmorei* has a relatively small cranial hiatus, another primitive character.

The periotic of *E. whitmorei* closely resembles that of *Micromysticetus rothauseni* (Sanders and Barnes, 2002, figs. 12, 13) in having a large, flattened, hatchet-shaped anterior process and a short, stubby posterior process. That form is very similar to the configuration of the periotic of the archaeocete *Zygorhiza kochii*. The dentary of *Eomysticetus whitmorei* is unique among known mysticetes, the posterior end being massive in size compared with Neogene forms. In its shape, dorsoventral height, anteroposterior length, and elevation of the end of the posterior edge above the anterior edge, the coronoid process of *E. whitmorei* is more nearly like that of an archaeocete than a mysticete and thus appears to represent a transitional stage between the configuration of the coronoid in Eocene archaeocetes, such as *Zygorhiza kochii*, and that of the Miocene cetotheres, such as *Parietobalaena palmeri*. In lateral aspect, the dentary displays the parallel dorsal/ventral profiles characteristic of Mysticeti.

The vertebral column of *E. whitmorei* also exhibits features intermediate between archaeocetes and mysticetes. Interestingly, the vertebrae are more like those of the archaeocete *Zygorhiza kochii* than their counterparts in other baleen whales. In the third through the seventh thoracic vertebrae the articular facet for the tuberculum is situated above the level of the roof of the neural canal, as in *Z. kochii*. The transverse processes of the lumbar and caudal vertebrae bend ventrolaterally as in Archaeoceti, rather than extending horizontally as in more highly evolved Mysticeti. In size and relative length/width ratios of their centra, the thoracic, lumbar, and caudal vertebrae of *E.*

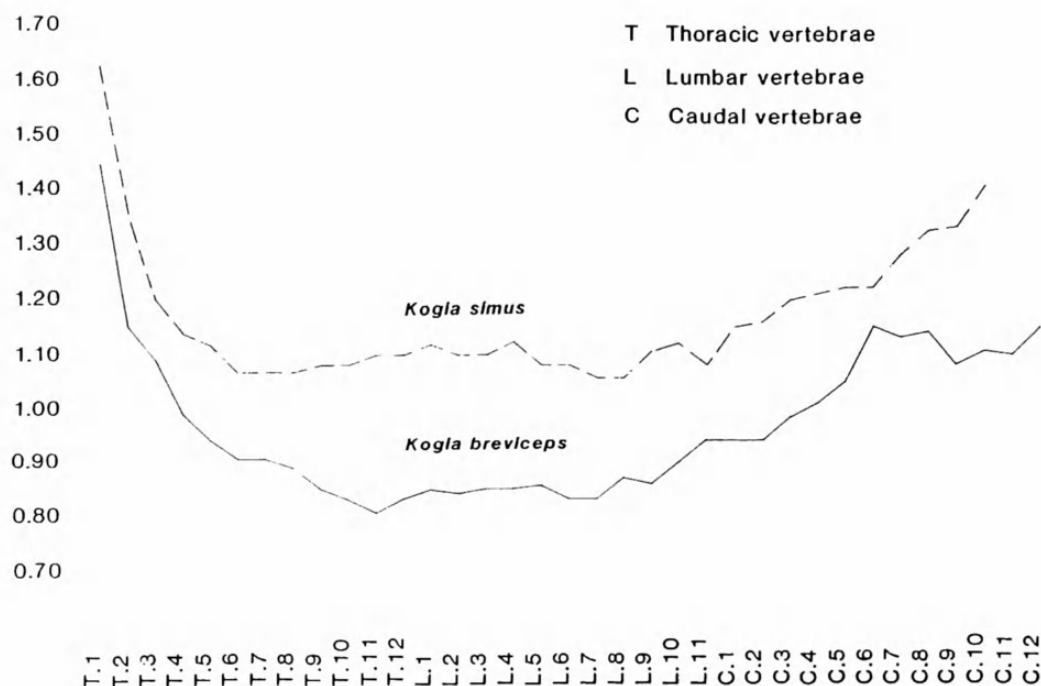


FIGURE 28.—Curves of mean values of vertebral width/length ratios of five specimens of extant *Kogia breviceps* and four specimens of extant *Kogia simus*.

whitmorei are intermediate between those of dorudontine archaeocetes and cetotheriid mysticetes (Figure 29).

Unpublished studies initiated by Sanders have shown that the two living species of the odontocete genus *Kogia* (*K. breviceps* and *K. simus*) have distinctly different vertebral length/width ratios (Figure 28), making it possible to identify isolated vertebrae of these two taxa. We have used this method in comparisons of the vertebrae of *Eomysticetus whitmorei* with those of selected archaeocetes and mysticetes to see how those forms might be sorted out on the basis of vertebral ratios. In Figure 29 we compare the curves of ratios obtained by dividing the transverse width of the anterior end of the centrum by the anteroposterior length of the centrum in the thoracic vertebrae of *E. whitmorei*, three Eocene archaeocetes (*Zygorhiza kochii* (Reichenbach, 1847), *Dorudon stromeri* Kellogg, 1936, *Basilosaurus cetoides* (Harlan, 1845)), and three Miocene cetotheres (*Pelocetus calvertensis* Kellogg, 1965, *Thinocetus arthritus* Kellogg, 1969, and *Halicetus ignotus* Kellogg, 1969). The thoracic vertebrae were selected because only two lumbar vertebrae and one caudal vertebra are available for *Eomysticetus*. As illustrated by the curve for the thoracics of *Basilosaurus cetoides*, lower ratios reflect elongate centra; thus, the low range of the extremely elongate vertebrae of that taxon does not permit plotting of the entire thoracic series within the vertical limits of Figure 29, the ratio for the 15th thoracic vertebra being 0.49.

As seen in Figure 29, the anterior portion of the curve for the thoracic vertebrae of *Eomysticetus whitmorei* falls between those of the archaeocetes *Zygorhiza kochii* and *Basilosaurus cetoides* below it, and those of the three cetotheriids above it. From the fifth thoracic vertebra posteriorly through the sev-

enth, eighth, and 15th (?), the *Eomysticetus whitmorei* curve most closely follows the curves of the two specimens of *Zygorhiza kochii* (USNM 4679, USNM 11962) for which measurements of thoracic vertebra were available (Kellogg, 1936: 143). Noting that the anterior portions of the curves of the three cetotheres form a discrete group separate from the curves of *Eomysticetus whitmorei*, *Zygorhiza kochii*, and *Basilosaurus cetoides*, we suggest that vertebral width/length ratios may be useful as indicators of broad phenetic relationships.

In Figure 29 the first six thoracic vertebrae furnish the best indices for comparison of the taxa shown. Of the eight individuals represented, the curves of three of them (*Pelocetus*, *Halicetus*, and one of the *Zygorhiza* specimens) converge within the range of 1.34 and 1.37 at the seventh thoracic vertebra. At the eighth thoracic all but three of the curves (*Basilosaurus cetoides*, *Thinocetus arthritus*, and *Dorudon stromeri*) converge between 1.20 and 1.26. Thereafter, the curves diverge again as they approach the lumbar vertebrae. The position of the eighth thoracic as the focal point for five of the eight curves shown indicates that it is in this vertebra that dramatic increases in the anteroposterior length of the centrum begin to take place. In the series of 15 thoracic vertebrae that is characteristic of the archaeocetes reviewed by Kellogg (1936), the eighth one is at the direct numerical center of the series. Anterior to that point, the first seven thoracics tend to reflect the shorter anteroposterior lengths of the cervical vertebrae, whereas those posterior to the eighth thoracic reflect the proportionately greater lengths of the lumbar centra. Recognition of the eighth thoracic vertebra as the commencement point of anteroposterior lengthening of the centra in the thoracic vertebrae of ancestral cetaceans (i.e., the Archaeoceti) suggests that the reduction in the number of tho-

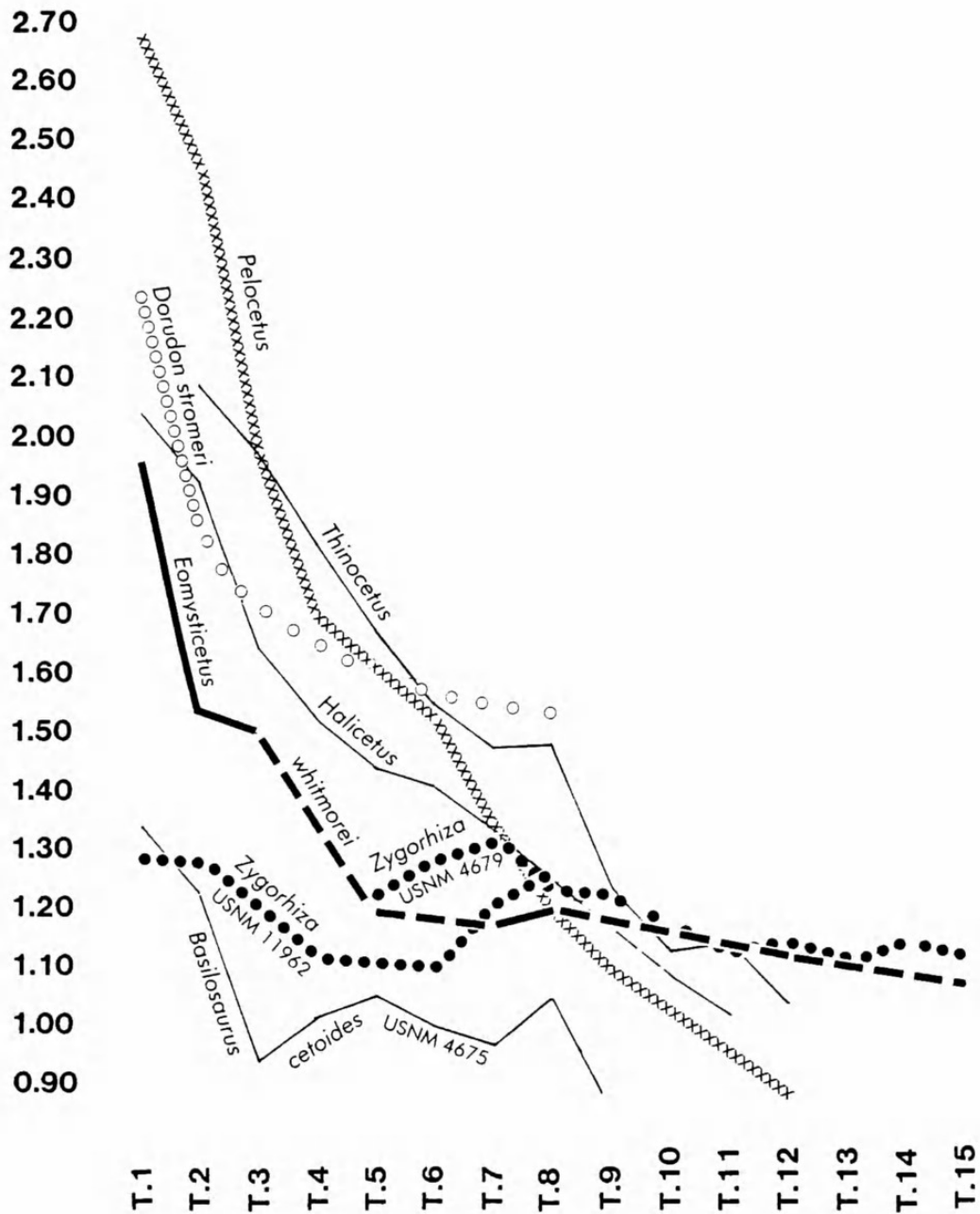


FIGURE 29.—Curves of width/length ratios of holotype thoracic vertebrae of *Eomysticetus whitmorei*, new genus and new species (late Oligocene); the late Eocene archaeocetes *Basilosaurus cetoides*, *Dorudon stromeri*, and *Zygorhiza kochii*; and the middle Miocene cetotheres *Halicetus ignotus*, *Pelocetus calvertensis*, and *Thinocetus arthritus*. (Lower values reflect more elongate vertebrae. Dashed lines and widely separated symbols indicate absence of specimens at those points in the column. See “Discussion” for sources of measurements used in these curves.)

racic vertebrae from 15 in archaeocetes to 12 in cetotheres took place in the posterior region of the thoracic series. The reason for that reduction is probably rooted in the adaptive economics of cetacean evolution.

Among modern mysticete taxa, *Balaenoptera musculus* and *B. physalus* have 15 thoracic vertebrae, *B. borealis* has 13–14, *B. acutorostrata* has 11, and *Eschrichtius robustus*, *Megaptera novaeangliae*, and *Eubalaena glacialis* all have 14 thoracic vertebrae (Kellogg, 1968:175). Kellogg (1968:175) also noted that “skeletons of adult Recent mysticetes are not only larger,

with one exception, but are also comprised of more vertebrae than the Calvert Miocene cetotheres. This increase in the number of vertebrae occurs notably in the caudal series.” In view of the numerous affinities that *Eomysticetus whitmorei* shares with archaeocetes, including certain morphological features of the thoracic vertebrae, it is not entirely surprising to find that this animal apparently carried a higher complement of thoracic vertebrae than the Miocene cetotheres that it preceded, and that they would be closer in number to the 15 thoracic vertebrae present in both *Basilosaurus cetoides* and *Zygorhiza kochii*

(Kellogg, 1936:46, 143). The presence of 15 thoracic vertebrae in this archaic Oligocene mysticete seems almost certainly to be a primitive character, quite unrelated to the increased number of thoracic vertebrae in extant mysticetes as discussed by Kellogg (1968:175).

That premise is supported by the fact that the heads of the ribs of *Eomysticetus* have capitular articulations with the centra in the first through the ninth thoracic vertebrae, whereas capitular articulation among the extant balaenopterids has been reduced to the first three or four pairs of anterior ribs (Kellogg, 1968:175). In the late Eocene dorudontine archaeocete *Zygorhiza kochii*, 10 of the anterior ribs have both the capitular and tubercular articulations (Kellogg, 1936:167), and in the Calvert cetotheres the heads of only seven or eight of the anterior ribs have the two articular surfaces (Kellogg, 1968:175).

The ribs of *Eomysticetus whitmorei* are of a normal cetacean type. They are neither pachyostotic nor osteosclerotic. They bow strongly laterally, indicating a full-bodied animal. The anteriormost rib is short and broad as is typical of derived Cetacea.

The most striking feature of the forelimb in *Eomysticetus whitmorei* is the large size of the humerus in comparison with the radius and the ulna, a condition more characteristic of Archaeoceti than of either the Mysticeti or the Odontoceti, the humerus in archaeocetes being considerably longer and more robust than the radius and the ulna. In all known Neogene Cetacea, the humerus is much shorter than the radius and the ulna, reflecting evolutionary trends toward the shortening of the humerus as the forelimb becomes more highly specialized as a flipper-like structure. As seen in Table 8, the relative proportions of the humerus and the radius and ulna in *Eomysticetus whitmorei* are intermediate between those of the middle Eocene archaeocete *Basilosaurus cetoides* (USNM 4675; Kellogg, 1936) and the middle Miocene cetothere *Thinocetus arthritus* (USNM 23794; Kellogg, 1969). Archaic limb proportions apparently were characteristic of many late Oligocene odontocetes as well. The humerus is longer than the radius and ulna (130|100,102) in the primitive odontocete *Sulakocetus dagestanicus* Mchedlidze, 1976 (see Mchedlidze, 1976:50–51) and greatly exceeds the length of the lower arm bones in the squalodontid *Kelloggia barbarus* Mchedlidze, 1976 (see Mchedlidze, 1976, pl. 26) from Azerbaijan. More-advanced trends are seen in two other late Oligocene odontocetes from the Caucasus region. The humerus and radius-ulna complex are about equal in length in *Ferecetotherium kelloggi* Mchedlidze, 1970 (Mchedlidze, 1976:15, pl. 5), a sperm whale (see Barnes, 1985), and the humerus is slightly shorter in *Oligodelphis azerbaidzanicus* Mchedlidze and Aslanova, 1968 (Mchedlidze, 1976, pl. 11), a probable kentriodontid dolphin (see Barnes, 1985). In both Mysticeti and Odontoceti, therefore, late Oligocene time appears to have been a period of transition between the archaeocete type of forelimb and the various kinds of more highly adapted limb structure of Neogene Cetacea, the

TABLE 8.—Greatest proximodistal lengths of humerus, radius, and ulna in the late Eocene archaeocete *Basilosaurus cetoides* (USNM 4675; Kellogg, 1936:64, 67, 68, tables 13–15), the late Oligocene mysticete *Eomysticetus whitmorei* (holotype, ChM 4253), and the middle Miocene mysticete *Thinocetus arthritus* (USNM 23794; Kellogg, 1969:9, 10, tables 9–11), all from North America.

Specimen	Humerus	Radius	Ulna
<i>Basilosaurus cetoides</i> (USNM 4675)	490±	250	334
<i>Eomysticetus whitmorei</i> (holotype, ChM PV4253)	329	268	327
<i>Thinocetus arthritus</i> (USNM 23794)	260	385	398

shortened humerus having evolved convergently in the two extant groups.

Eomysticetus whitmorei exemplifies a more primitive grade of telescoping than the late Oligocene species of *Mauicetus* of New Zealand. Apparently, it was one of the last members of a line that preceded *Mauicetus*, and it probably demonstrates the general appearance of the skull in the earliest baleen-bearing mysticetes. The progenitors of the line that it represents would seem quite evidently to have been forms that were in evolutionary transition from Archaeoceti to Mysticeti.

The Archaeoceti is the most archaic suborder of Cetacea and includes three families, ranging from the most primitive Protocetidae through the more highly evolved Remingtonocetidae and Basilosauridae. Typical Eocene forms are characterized principally by nontelescoped skulls, the nares being situated anteriorly on the anterior part of the rostrum, and by a distinctive dental formula and morphology. The Protocetidae are the oldest and most primitive archaeocetes and include early and middle Eocene animals from North Africa, India, and Pakistan in the Tethys region (e.g., Gingerich et al., 1983, 1990, 1995) and two new protocetids from Georgia (Hulbert et al., 1998) and South Carolina (Geisler et al., 1996). The South Carolina animal is currently under study at The Charleston Museum. All were less than 4 m long, had the normal mammalian dental formula, had fully movable (but reduced) hind limbs, and had the petrosal still located within the braincase. The Basilosauridae include the medium-sized, generalized Dorudontinae and the more divergent, large Basilosaurinae. Species in this family have been discovered around the world, but no unquestionable basilosaurid represented by a skull has been recorded in rocks younger than late Eocene age. Like the Protocetidae, their skulls were not telescoped, but their molars and premolars were more highly evolved because none were three-rooted, there were accessory denticles on the anterior and posterior edges, and because M3 was lost. Generalized dorudontines may have been the ancestors of the mysticetes and the odontocetes (Barnes and Mitchell, 1978; Fordyce, 1980; Barnes and Sanders, 1996).

Although most of the major steps in cetacean evolution are represented in the fossil record, previously described material has not included skulls evincing transitional grades between archaeocetes and mysticetes or between archaeocetes and odontocetes. Characters derived from archaeocetes are evident in

early members of both of the modern suborders (e.g., Barnes and Mitchell, 1978), but the long absence of skulls of advanced archaeocetes showing trends toward specific odontocete or mysticete characters has led some authors to dismiss the Archaeoceti as being the possible ancestors of the living Cetacea.

Kleinenberg and Yablokov (Kleinenberg, 1958, 1959; Kleinenberg and Yablokov, 1958; Yablokov, 1964) have argued that modern baleen and toothed whales must have had separate origins because they are such dissimilar animals now and because they both differ so greatly from archaeocetes. Rice (1966, 1984) and some authors of other general works have accepted such arguments and have classified the archaeocetes, odontocetes, and mysticetes as separate mammalian orders. Van Valen (1968) rebutted the arguments for triphyly by Yablokov, Kleinenberg, and others, and his conclusion that archaeocetes should be accepted as the ancestors of modern whales has been supported by statements by Fordyce (1980), Gaskin (1982), and Rothausen (1985).

Proponents of the theory of polyphyletic origin of cetaceans have unknowingly rested much of their case upon unsound stratigraphic ground. Yablokov and others have argued that the "earliest" odontocetes from Charleston, South Carolina, i.e., *Agorophius pygmaeus* (Müller, 1849) and *Xenorophus sloanii* Kellogg, 1923, which had figured prominently in paleontological analyses, were late Eocene in age, contemporaries of the archaeocetes, and therefore could not possibly be considered as their descendants; however, the deposits that produced these early odontocetes have now been reinterpreted as late Oligocene in age (Whitmore and Sanders, 1976), which makes them millions of years younger than ancestral Eocene archaeocetes and places them in an intermediate position both chronologically and anatomically. Unfortunately, few summary articles have incorporated that information.

One of the major shortcomings of Yablokov and Kleinenberg's triphyletic argument is that the extremely different characters of modern mysticetes and odontocetes show only that they have diverged in their evolutionary history, not necessarily that they had separate origins. Additionally, many of those authors' arguments are simply based upon incorrect or incomplete data. Because archaeocetes are known only as fossils, skeletal structures are the only presently available characters that are useful when comparing them with living odontocetes and mysticetes. The early, primitive odontocetes and mysticetes have few of the skeletal features that some mammalogists, working only with living taxa, often consider to be important and/or diagnostic for the living groups. When considering only the cetaceans of the Oligocene, however, we find odontocetes and mysticetes that are remarkably similar to one another as well as to archaeocetes, and that, in fact, have many osteological characters that are intermediate between archaeocetes and primitive members of the other two suborders. Of these, *Eomysticetus whitmorei* provides the most dramatic example of shared archaeocete and mysticete characters and should put to rest any further claims of polyphyly in cetacean phylogeny.

THE PRIMITIVE PHYLOGENETIC POSITION OF *Eomysticetus whitmorei*

Eomysticetus whitmorei was demonstrably a baleen-bearing mysticete. There are no dental alveoli on its palate nor on its dentaries, the palatal surface of its maxilla has sulci that indicate the presence in life of blood vessels that would have nourished baleen, the horizontal rami of the dentaries are elongate and parallel-sided, and a line of nutrient foramina along the dorsal (gingival) border of each dentary marks the former row of mandibular dental alveoli and their associated nutrient foramina. All of these features are typical of baleen-bearing mysticetes that use a bulk-feeding mode.

Eomysticetus whitmorei represents a previously undocumented stage in the evolutionary history of baleen-bearing mysticetes, and at present it and *E. carolinensis* are the only named members of a previously unreported clade of Mysticeti recognized herein as the family Eomysticetidae. Other primitive baleen-bearing mysticetes of a similar, but slightly more derived grade of evolution have been reported, but as yet most of them are either unnamed and/or uncertainly assigned to a family. Some or all of these may, upon future study, be determined to belong as well to the family Eomysticetidae.

Autapomorphies that define *Eomysticetus whitmorei* and the family Eomysticetidae (Figure 30) include (1) the extremely narrow intertemporal region (not to be confused with the anteroposteriorly elongate intertemporal, a primitive character retained from Archaeoceti); (2) the narrow, elongate rostrum; (3) the elongate nasal bones; (4) the small, pit-like secondary squamosal fossae; (5) the elongate zygomatic processes of the squamosals diverging anterolaterally from the sagittal plane of the skull (*E. carolinensis*); (6) the spatulate anterior end of the zygomatic process of the squamosal (*E. whitmorei*); (7) the blade-like anterior process of the periotic that is compressed transversely and expanded dorsoventrally (*E. whitmorei* and probably *E. carolinensis* as well); and (8) the length of the humerus, which equals the length of the radius and ulna.

Otherwise, *Eomysticetus whitmorei* has the most primitive cranial morphology of any named primitive baleen-bearing mysticete. The morphologic sequence arranged from *E. whitmorei* to *Eomysticetus carolinensis* to *Micromysticetus rothauseni* to Cetotheriidae to Balaenopteridae, in general demonstrates development or enhancement of the following derived character states among Mysticeti: anteroposterior shortening of the frontal and parietal in the intertemporal region, anteroposterior shortening and concomitant transverse widening of the occipital shield, more horizontal extension of the lambdoidal crests, loss of the secondary squamosal fossa, increase in size of the squamosal prominence, shortening of the zygomatic process of the squamosal, increase in lateral displacement of the anterior end of the zygomatic process of the squamosal, widening of the intercondylar notch, and more ventrolateral flaring of the lateral wall of the braincase.

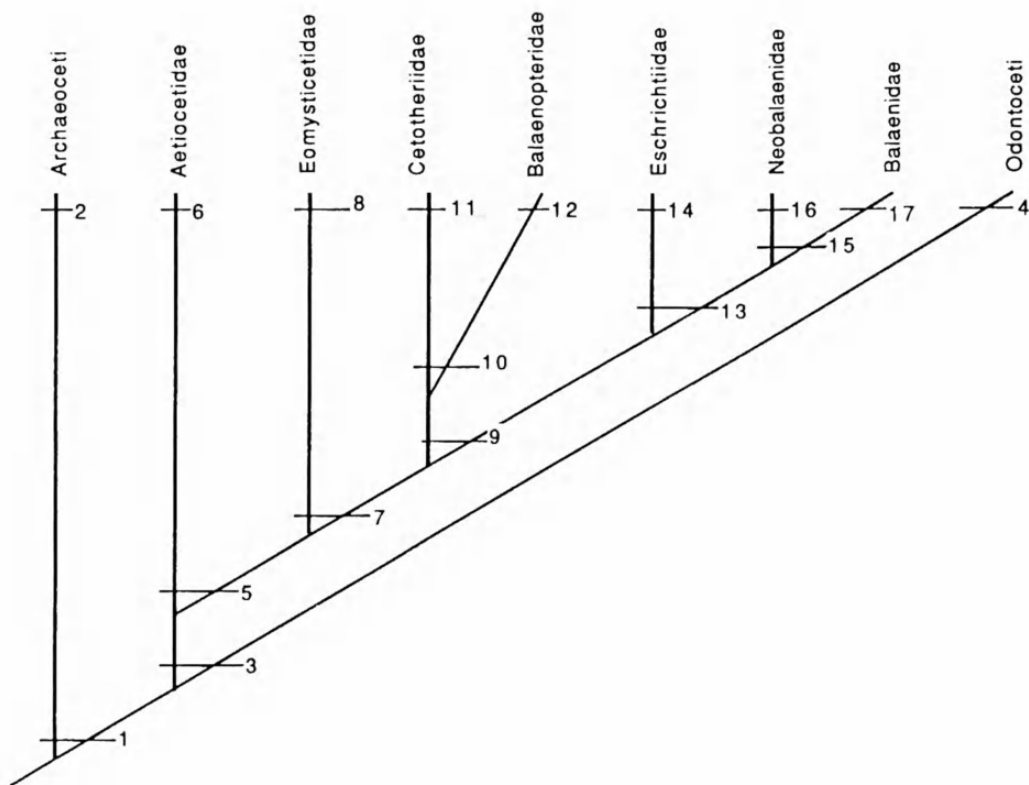


FIGURE 30.—Cladogram showing relationships of *Eomysticetus whitmorei* to other Cetacea. In part from Barnes, 1990; Barnes and McLeod, 1984; McLeod et al., 1989, 1992. The nominal families Llanocetidae and Mammalodontidae are omitted because their characters are poorly known. Characters at dichotomies are as follows:

Node 1=Order Cetacea: 1, Facial region of skull elongated; 2, Intertemporal region narrow and elongated; 3, Sagittal and lambdoidal crests high; 4, Incisive (anterior palatine) foramina lost; 5, Tympanic bulla involutioned and inflated; 6, Supraorbital process of frontal enlarged; 7, Basioccipital crest enlarged; 8, Falciform process of squamosal present lateral to anterior process of periotic; 9, Periotic and tympanic bulla separated on their medial sides from the basioccipital; 10, Tympanic bulla separated posteriorly from the exoccipital; 11, Hypoglossal foramen in basioccipital located either at the apex of or inside the jugular notch; 12, Peribullary sinus and pterygoid sinus present as diverticula of middle ear sinus; 13, Incisors and canines not transverse, but aligned anteroposteriorly with the cheek-tooth row; 14, Central cusp of both upper and lower cheek teeth transversely compressed; 15, Mandibular foramen enlarged; 16, Scapula with suprascapular fossa reduced and with acromion and coracoid processes parallel and directed anteriorly; 17, Postzygapophyses on thoracic and lumbar vertebrae reduced.

Point 2=Archaeoceti: Apparently paraphyletic; defined primarily by primitive characters.

Node 3=Mysticeti plus Odontoceti: 1, Bones of cranium telescoped; 2, Multiple maxillary foramina derived from infraorbital foramen; 3, Elongate (laterally) supraorbital process of frontal; 4, Vomer exposed on basicranium and extending posteriorly to cover basisphenoid/basioccipital suture; 5, Zygomatic process of the squamosal contacting postorbital process of frontal and/or connected to it by a ligament; 6, Posterior part of dentary thin and dense in area of mandibular foramen (the "pan bone"); 7, Monophyodonty; 8, Elbow joint nonrotational, with anteroposterior position of radius and ulna and formation of discrete flattened articular facets on distal end of humerus (one for radius, two for ulna); 9, Olecranon fossa of humerus lost; 10, Hyperphalangy.

Point 4=Odontoceti: 1, Premaxillary foramen present (as an aperture of infraorbital foramen complex) with anteromedial, posteromedial and posterolateral sulci emanating from it; 2, Spiracular plate present on premaxilla anterolateral to nares (for premaxillary sac, a diverticulum of the narial passage); 3, Ascending process of maxilla expanding posteriorly over supraorbital process of frontal; 4, Antorbital notch present; 5, Pterygoid sinus extending anteriorly and around lateral side of narial passage; 6, Middle sinus present; 7, Lachrymal and jugal bones fused.

Node 5=Mysticeti: 1, Flat (tabular) supraorbital process of frontal with knob-like postorbital process; 2, Antorbital process of maxilla present (antorbital process extending posterolaterally from dorsal surface of rostrum along anterior margin of supraorbital process); 3, Maxilla extending posteriorly ventral to supraorbital process of frontal; 4, Lateral margin of maxilla becoming thin; 5, Temporal crest moved to dorsal surface of supraorbital process of frontal; 6, Basioccipital and basisphenoid becoming thickened dorsoventrally; 7, Mandibular symphysis loose, with elongate ligamental groove at symphysis; 8, Atlas with single transverse process.

- Point 6=Family Aetiocetidae: 1, Intertemporal region shortened anteroposteriorly and widened transversely; 2, Protuberance present on premaxilla at anterolateral corner of nasal bone; 3, Squamosal fossa shortened anteroposteriorly; 4, Elongate notch present in posterior border of palatine at posterior end of palate.
- Node 7=Family Eomysticetidae plus all other Mysticeti: 1, Functional teeth lost in adult; 2, Baleen present in postfetal stage; 3, Gingival foramina present and enlarged along dorsal margin of horizontal ramus of dentary; 4, Sulci present on palatal surface of maxillae marking paths of nutrient vessels that nourish baleen plates; 5, Vomer forming a prominent ventral keel along midline of palate.
- Point 8=*Eomysticetus* (=Family Eomysticetidae): 1, Intertemporal region extremely narrowed; 2, Nasal bones elongated; 3, Zygomatic process of squamosal elongated; 4, Zygomatic process of squamosal diverging anterolaterally from sagittal plane of skull; 5, Anterior process of periotic compressed transversely and expanded dorsoventrally ("blade-like").
- Node 9=All Mysticeti beyond Family Eomysticetidae: 1, Nasal bones shortened anteroposteriorly; 2, Supraorbital process of frontal widened anteroposteriorly; 3, Intertemporal region shortened anteroposteriorly so that zygomatic process of squamosal contacts postorbital process of frontal; 4, Anterior process of periotic thickened transversely; 5, Posterior process of periotic fused to posterior (mastoid) process of tympanic bulla; 6, Humerus shorter than radius or ulna.
- Node 10=Family Cetotheriidae plus Family Balaenopteridae (=Superfamily Balaenopteroidea): 1, Transversely aligned gap present between posterior margin of ascending process of maxilla and anterior margin of supraorbital process of frontal; 2, Ascending process of premaxilla tapered between posterior ends of nasal and maxilla; 3, Zygomatic process of squamosal relatively shortened and blunt; 4, Postglenoid process globose.
- Point 11=Cetotheriidae: 1, Ascending process of maxilla tapered posteriorly between frontal and ascending process of premaxilla.
- Point 12=Family Balaenopteridae: 1, Cleft present along alisphenoid/squamosal suture in lateral wall of braincase; 2, Dorsal surface of supraorbital process of frontal depressed ventrally relative to intertemporal region; 3, Rostral bones (maxillae, premaxillae, nasals) extending posteriorly toward occipital shield anteroposteriorly compressing frontals and parietals; 4, Mandibular canal and mandibular foramen reduced in diameter; 5, Bone of mandible porous and inflated; 6, Numerous throat grooves present; 7, Four digits in manus.
- Node 13=Family Eschrichtiidae plus Superfamily Balaenoidea: 1, Rostrum arched dorsally (at least 10°) (from Barnes and McLeod, 1984); 2, Nasal bones wide and "blocky"; 3, Bones around narial region of skull elevated; 4, Horizontal ramus of dentary torsioned in anterior part; 5, Mandibular condyle enlarged and nearly spherical; 6, Horizontal ramus of dentary expanded and arched dorsoventrally; 7, Coronoid process of dentary reduced.
- Point 14=Family Eschrichtiidae: 1, Premaxillary foramen present on either or both premaxillae lateral to narial opening (convergence with Odontoceti); 2, Premaxillae wide posteriorly and excluding maxillae from exposure on cranial vertex; 3, Nasal bones large and forming highest part of skull; 4, Tubercles for muscle attachment present on both sides of occipital shield; 5, Baleen plates thick anteroposteriorly; 6, Baleen plates cream in color; 7, Dorsal fin lost.
- Node 15=Superfamily Balaenoidea: 1, Zygomatic process of squamosal and glenoid fossa positioned far ventrally on the skull; 2, Pterygoids extending far posteriorly beneath basicranium; 3, Baleen plates numerous and thin; 4, Cervical vertebrae fused.
- Point 16=Family Neobalaenidae: 1, Body size reduced; 2, Rostrum arched about 17 degrees; 3, Occipital shield extended anteriorly; 4, Zygomatic process of squamosal short; 5, Nasal bones small; 6, Horizontal ramus of dentary deep dorsoventrally; 7, Humerus shortened.
- Point 17=Family Balaenidae: 1, Head greatly enlarged, approximately one-third of body length; 2, Rostrum transversely compressed; 3, Rostrum greatly arched dorsally, premaxillae forming highest part of skull; 4, Baleen plates greatly elongated; 5, Supraorbital process of frontal sloping and greatly elongate (extended laterally); 6, Zygomatic process of squamosal flaring anterolaterally; 7, Involucrum of tympanic bulla flattened dorsoventrally; 8, Dorsal fin lost.

OTHER PRIMITIVE BALEEN-BEARING MYSTICETES

A primitive baleen-bearing mysticete, represented by a remarkably complete skull and skeleton, was preliminarily reported by Okazaki (1995) from a late Oligocene deposit on the island of Kyushu in Japan. This unnamed whale is quite similar to *Eomysticetus whitmorei* but is more highly derived. The two species share similar overall size, a narrow and elongate intertemporal region capped by a narrow sagittal crest, elongate and

narrow nasal bones, a secondary fossa within the squamosal fossa, a relatively small but transversely expanded postglenoid process, a relatively small occipital shield, elongate and anterolaterally flaring zygomatic processes of the squamosals, a tubercle-like posterior end of the basioccipital crest, an anteroposteriorly thick exoccipital, elongate and relatively flat rostrum, relatively straight horizontal ramus of the dentary, and a large and dorsally lobate coronoid process of the dentary. The

unnamed Oligocene mysticete from Kyushu differs from *Eomysticetus whitmorei* by having the following derived character states (derived polarity determined in relation to the condition in Archaeoceti): a wider rostrum, an anteroposteriorly wider supraorbital process of the frontal, an anteroposteriorly shorter intertemporal region, larger and wider occipital shield that flares laterally over the temporal fossa rather than flaring dorsally, transversely narrower but more anteroposteriorly extensive squamosal fossa, and a relatively deeper horizontal ramus of the dentary. The unnamed mysticete from Kyushu also differs from *E. whitmorei* by having more convex occipital condyles. Although this might be a primitive character state, because it is shared with the Archaeoceti, we interpret it as a derived character state in comparison with *E. whitmorei* and, therefore, as a reversal. The elongate intertemporal region of *E. whitmorei* is a primitive character state that is shared with archaeocetes, and for this reason (as with the archaeocetes) the zygomatic process of the squamosal makes no contact with the postorbital process of the frontal. In the Kyushu specimen, with its anteroposteriorly shorter intertemporal region, the zygomatic process of the squamosal contacts the postorbital process of the frontal (see Okazaki, 1995, fig. 1b), and this is the derived character state. That derived condition exists as well in all other (more derived) mysticetes, except in "*M.*" *lophocephalus*, as illustrated by Marples (1956, fig. 1c; see also Barnes and McLeod, 1984, fig. 3c). The gap between the anterior tip of the zygomatic process and the squamosal and the postorbital process of the frontal is smaller in "*M.*" *lophocephalus* than it is in *E. whitmorei*. In that regard, among the Mysticeti *E. whitmorei* is the form most like the Archaeoceti, and "*M.*" *lophocephalus* approaches the condition in various derived groups of mysticetes, such as the Cetotheriidae, Balaenopteridae, Eschrichtiidae, Neobalaenidae, and Balaenidae.

Late Oligocene *Mauicetus* is a problematic taxon. It is usually classified in the family Cetotheriidae, although Barnes and McLeod (1984:16) noted that it does not have autapomorphic characters that distinguish the type genus of the family Cetotheriidae, the late Miocene genus *Cetotherium*. Of the nominal species in the genus *Mauicetus*, only "*M.*" *lophocephalus* is known by a relatively complete skull, and the illustrations of this skull (e.g., Marples, 1956, fig. 1c; Barnes and McLeod, 1984, fig. 3c) are based upon interpretations of its morphology prior to its being completely removed from sediment. If we restrict our interpretation of the skull morphology to the specimen illustrated by Marples (1956), it is clear that "*M.*" *lophocephalus* is a relatively primitive baleen-bearing mysticete, although it is not nearly so primitive as *Eomysticetus whitmorei*. In some characters (e.g., zygomatic process of squamosal not contacting postorbital process of the frontal, smaller supraoccipital shield) "*M.*" *lophocephalus* is more primitive than the unnamed baleen-bearing mysticete reported by Okazaki (1995) from Kyushu. It does not have the elongate and flaring zygomatic process of the squamosal that the unnamed mysticete from Kyushu shares with *E. whitmorei*, and it is not so

closely related to either of these taxa as they are to each other. Whether "*M.*" *lophocephalus* is ultimately determined to belong to the Cetotheriidae or to some other clade, it is not inclusive within the clade containing *Eomysticetus whitmorei* and the unnamed mysticete from Kyushu.

Crowley and Barnes (1996) reported yet another type of unnamed primitive baleen-bearing mysticete of late Oligocene age from the Olympic Peninsula of Washington. This whale is not closely related to "*M.*" *lophocephalus*, nor does it belong to the family Eomysticetidae. Although that specimen, *Eomysticetus whitmorei*, and the unnamed mysticete from Kyushu all have a sagittal crest and an extensive exposure of the parietals in the intertemporal region, as well as a large and dorsally lobate coronoid process of the dentary, these are shared primitive characters and do not necessarily indicate close relationship. The late Oligocene mysticete from Washington has autapomorphic characters—such as a short and medially curved zygomatic process of the squamosal, a relatively anteroposteriorly shorter and wider intertemporal region, and a shorter rostrum—that serve to distinguish it from *Eomysticetus whitmorei*.

From late Oligocene deposits in southern Baja California Sur, Mexico, have been reported other primitive baleen-bearing mysticetes (Barnes, 1998) that appear to share characters with *Eomysticetus whitmorei*: elongate nasal bones, elongate and divergent zygomatic process of the squamosal, and a small supraoccipital shield whose margins flare dorsally rather than laterally. These specimens have not yet been completely cleaned from their enclosing matrix, and only preliminary studies of them have been made.

The specimens from Baja California Sur, along with the unnamed mysticete reported from Kyushu by Okazaki (1995), demonstrate that primitive baleen-bearing mysticetes of the *Eomysticetus* grade, and possibly belonging to the family Eomysticetidae, were widespread in late Oligocene time. With apparent records of this group in the western North Atlantic, the eastern North Pacific, and the western North Pacific, the group might have been essentially cosmopolitan in late Oligocene time.

CLASSIFICATION

Within the classification of mysticetes we recognize the families Aetiocetidae, Eomysticetidae, Cetotheriidae, Balaenidae, Neobalaenidae, Balaenopteridae, and Eschrichtiidae. Barnes (1984) and Barnes et al. (1985) proposed classifications of Cetacea that embraced both fossil and extant taxa, and Mitchell (1989) offered a new arrangement of Archaeoceti and Mysticeti accompanying his description of *Llanocetus denticrenatus*, an enigmatic, primitive late Eocene toothed mysticete from Antarctica. Our establishment of the new taxon *Eomysticetus whitmorei* necessitates further reappraisal of mysticete systematics. In the revised classification of Mysticeti presented below, subfamilies are used where they have become commonly recognized. In instances where the family group name is not used

at the same rank as originally proposed, the original author is listed in parentheses followed by the author(s) who used the emended rank. Our classification differs from Mitchell's (1989) arrangement principally in our avoidance of the use of infraorders to group primitive, toothed mysticetes (i.e., *Llanocetus*, *Aetiocetus*, *Mammalodon*) about which too little is known to warrant such definitive hierarchical assignments, especially in the case of *Llanocetus denticrenatus*, which Mitchell (1989) described from only a fragment of the right dentary and a cranial endocast.

The two archaeocete-like teeth preserved in the mandibular fragment of *Llanocetus denticrenatus* and the wide diastema between them differ considerably from dental morphology and tooth spacing in *Aetiocetus cotylalveus* Emlong, 1966, and *Mammalodon colliveri* Pritchard, 1939, but these differences do not necessarily indicate the absence of shared similarities in cranial morphology. We therefore propose the new superfamily Aetiocetoidea as a group to accommodate all of the few known Paleogene toothed mysticetes, and we accordingly refer the Llanocetidae of Mitchell (1989) to that superfamily pending knowledge of the cranial anatomy of Llanocetids.

In the following classification, a † in front of a taxonomic group indicates that it is extinct.

Order Cetacea Brisson, 1762

Suborder Mysticeti Flower, 1864

†Superfamily Aetiocetoidea, new superfamily

†Family Aetiocetidae Emlong, 1966

†Subfamily Chonecetinae Barnes, Kimura, Furusawa, and Sawamura, 1995

†Family Llanocetidae Mitchell, 1989

†Family Mammalodontidae Mitchell, 1989

†Superfamily Eomysticetoidea, new superfamily

†Family Eomysticetidae, new family

Superfamily Balaenopteroidea (Gray, 1868) Mitchell, 1989

†Family Cetotheriidae (Brandt, 1872) Miller, 1923

†Subfamily Cetotheriopsinae Brandt, 1872

†Subfamily Cetotheriinae Brandt, 1872

Family Balaenopteridae Gray, 1864

Subfamily Megapterinae (Gray, 1866) Gray, 1868

Subfamily Balaenopterinae (Gray, 1864) Brandt, 1872

Superfamily Eschrichtioidea (Ellerman and Morrison-Scott, 1951) Mitchell, 1989

Family Eschrichtiidae Ellerman and Morrison-Scott, 1951

Superfamily Balaenoidea (Brandt, 1873) Mitchell, 1989

Family Neobalaenidae Gray, 1874

Family Balaenidae Gray, 1825

Absent from the foregoing arrangement and from most of the recent classifications of the Mysticeti are several taxa once thought to be mysticetes or to be mysticete ancestors. Commenting on the primitive late Oligocene cetacean *Squalodon pygmaeus* (Müller, 1849) from South Carolina, Gervais (1871:138) proposed that *S. pygmaeus* actually belonged among the rorquals. In erecting the new genus *Agorophius* for *S. pygmaeus*, Cope (1895:139) noted that "the form of the skull in this genus approaches distinctly that of *Cetotherium* ... and the permanent loss of the teeth would probably render it necessary to refer it to a Mysticocete." Subsequent authors (e.g.,

True, 1907, 1908; Abel, 1913; Miller, 1923; Kellogg, 1928) correctly placed *Agorophius pygmaeus* in the Odontoceti. *Patriocetus ehrlichi* (Van Beneden, 1865), from the late Oligocene sands at Linz, Austria, was figured incorrectly by Abel (1913; see also Kellogg, 1928), who suggested that it was a primitive toothed mysticete. Miller (1923:44) recognized its true affinities with the Odontoceti, and Rothausen (1968) illustrated the correct form of the rostrum and referred *Patriocetus* to the Squalodontidae.

Archaeodelphis patrius Allen, 1921, known by a partial cranium without locality data but thought to be of late Eocene age (Allen, 1921), was assigned to the odontocete family Agorophiidae by Miller (1923:40). Kellogg (1928) placed *Archaeodelphis* in Odontoceti incertae sedis, but suggested it as a possible mysticete ancestor, as did Dechaseaux (1961:881). Rothausen (1968:97–98) included *Archaeodelphis* in the Agorophiidae, but Whitmore and Sanders (1976) returned it to incertae sedis. We have considered the morphology of the holotype (MCZ 15749) of *Archaeodelphis patrius* in some detail and agree with Fordyce (1981:1042) that it is clearly an odontocete and had nothing whatsoever to do with the ancestry of the mysticetes.

Following Emlong (1966) in regarding *Aetiocetus cotylalveus* as a member of the Archaeoceti, Mchedlidze (1976) suggested that *Ferecetotherium kelloggi* Mchedlidze, 1970, and *Mirocetus rjabini* Mchedlidze, 1970, belonged with *Aetiocetus* in the family Aetiocetidae, which he concluded was the archaeocete family that gave rise to the Mysticeti. Many authors (e.g., Barnes and Mitchell, 1978; Fordyce, 1980; Barnes, 1985, 1987, 1989; Barnes et al., 1995; Evans, 1987; Sanders and Barnes, 1989), however, agree with Van Valen's (1968) interpretation of *Aetiocetus cotylalveus* as a primitive toothed mysticete, thus leaving in question the other two taxa assigned to the Aetiocetidae by Mchedlidze. Barnes (1985) proposed that *Ferecetotherium kelloggi* is actually a primitive sperm whale, its slender, conical teeth constituting a homodont dentition quite unlike the dental characteristics of Archaeoceti. As for *Mirocetus rjabini*, independent examinations of its holotype by Sanders and by Rothausen produced concurrent opinions: that the maxillae ascend well onto the frontals and probably overspread most of the supraorbital processes, and that *Mirocetus rjabini* therefore belongs in the Odontoceti (Rothausen to Sanders, pers. comm., 1976, 1990).

In summary, our opinions regarding the subordinal positions of the genera discussed above are as follows:

Suborder Mysticeti

Aetiocetus

Llanocetus

Mammalodon

Suborder Odontoceti

Agorophius

Archaeodelphis

Ferecetotherium

Mirocetus

Patriocetus

Conclusions

Eomysticetus whitmorei is an archaic, baleen-bearing mysticete of late Oligocene age. The length of the skull and the size of the vertebrae indicate that it was of moderate size (~8 m long) in life, and although its rostrum and mandibles are edentulous as in other mysticetes, it has a braincase very much like that of an archaeocete. The stage of its cranial telescoping is unlike that of any other mysticete yet described. The palatal surface of its maxilla has sulci that indicate the presence in life of blood vessels that would have nourished baleen, but the palatal surface was not highly vascularized, as is typical of highly evolved mysticetes, so the baleen probably was not very long. The coronoid process of the dentary is very large, and the temporal musculature was extensive.

In many characters, *E. whitmorei* is morphologically transitional between archaeocetes and mysticetes, which demonstrates clearly the direct ancestral-descendant relationship between the two groups and helps to refute the arguments for cetacean polyphyly.

Eomysticetus whitmorei is a relict taxon, however, because baleen-bearing mysticetes with a higher degree of cranial telescoping are known earlier in the Oligocene and also were contemporaneous with *A. whitmorei* in Chandler Bridge (lower

Chattian) time. Its morphology demonstrates the stage of cranial telescoping that was probably achieved in the early Oligocene by other lineages of mysticetes. The species was contemporaneous with, and perhaps sympatric with, at least two other species of mysticetes (cetotheriopsine cetotheriids; Sanders and Barnes, 2002), a diversity of primitive odontocetes, and some new and as-yet-undescribed toothed mysticetes from South Carolina (Barnes and Sanders, 1996). It also is broadly contemporaneous with relict tooth-bearing aetiocetid mysticetes and with several other lineages of primitive mysticetes that existed elsewhere in the world in late Oligocene time. Some of these other mysticetes had teeth, some had baleen, some had highly evolved crania, and some had primitive crania.

The skull of *Eomysticetus whitmorei* exhibits the most primitive cranial features known in a fossil baleen-bearing mysticete whale. Its prominent archaeocete-like characters—such as the location of the nasal opening far anterior to the vertex of the skull—provide new insights into the origin of baleen whales and suggest that a presently unknown line of Archaeoceti branched directly toward Mysticeti and that Odontoceti evolved from Archaeoceti along an entirely separate evolutionary pathway.

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