

Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 2: *Micromysticetus rothauseni*, a Primitive Cetotheriid Mysticete (Mammalia: Cetacea)

Albert E. Sanders and Lawrence G. Barnes

ABSTRACT

Previously named fossil mysticete species in the extinct genus *Cetotheriopsis* Brandt, 1871, are *C. lintianus* (von Meyer, 1849), from Austria, and *C. tobieni* Rothausen, 1971, from Germany, both of late Oligocene (lower Chattian) age. Although each species is known only by a single braincase without a rostrum, both have been understood to be baleen-bearing, archaic mysticetes of the extinct family Cetotheriidae. Fossil baleen whales of this age are generally rare worldwide, and no Oligocene cetotheriids have been named previously from the eastern coast of North America. Elsewhere, we have established the family Eomysticetidae to accommodate two very primitive new mysticetes from the late Oligocene Chandler Bridge Formation near Charleston, South Carolina (Sanders and Barnes, 1999, 2002). In addition, two mysticete braincases without rostra from the underlying Ashley Formation near Charleston represent a new genus and new species in the Cetotheriidae. These specimens document a new taxon that is markedly different from *Cetotheriopsis* and is herein named *Micromysticetus rothauseni*, new genus, new species. It is most similar to *Cetotheriopsis tobieni* Rothausen, 1971, which is herein referred to the new genus *Micromysticetus*. *Micromysticetus rothauseni* is a significant addition to the diverse Oligocene marine vertebrate assemblages from the Oligocene beds near Charleston. It constitutes the oldest known western North Atlantic records of the family Cetotheriidae and provides additional evidence of the archaeocete ancestry of the mysticetes.

Introduction

Tertiary marine deposits of South Carolina have yielded 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 (1923b), both of which are known from holotype specimens found in the late Oligocene (ca. 30 Ma) Ashley Formation. In recent years, studies emanating from The Charleston Museum (ChM) have revealed a previously unrecognized rock unit overlying the Ashley Formation. Named the Chandler Bridge Formation by Sanders et al. (1982), this unit is slightly younger than the Ashley Formation, is also of late Oligocene age (ca. 28 Ma), and has yielded a wealth of cetacean material that is providing critical new information about the evolution and systematics of Oligocene whales of the western hemisphere (Whitmore and Sanders, 1976; Sanders, 1980; Sanders et al., 1982; Weems and Sanders, 1986; Sanders and Barnes, 1989, 1991, 1999, 2002; Barnes and Sanders, 1990).

With the exception of the toothed mysticetes of the genera *Aetiocetus* Emlong, 1966, and *Chonecetus* Russell, 1968, from the northwest coast of the United States, Oligocene-age mysticetes from the Northern Hemisphere were formerly known only from Europe. In 1975 the remains of a primitive, archaeocete-like baleen whale were found in the late Oligocene Chandler Bridge Formation near Charleston, South Carolina, and were excavated by the Charleston Museum (Sanders and Barnes, 1989, 1999, 2002; Barnes and Sanders, 1990). We now describe and name an additional mysticete from Oligocene deposits near Charleston, a preliminary report of the holotype (ChM PV4844) having been made by Sanders and Barnes (1991). A partial braincase (ChM PV5933) referable to this taxon also has been found, and both specimens are conserved in the Charleston Museum collections. The purpose of this study is to report this newly recognized whale from South Carolina and to comment on its taxonomic affinities. We recognize that the family Cetotheriidae and the subfamily Cetotheriopsinae are greatly in need of review and definition, but that task is beyond the scope of this paper.

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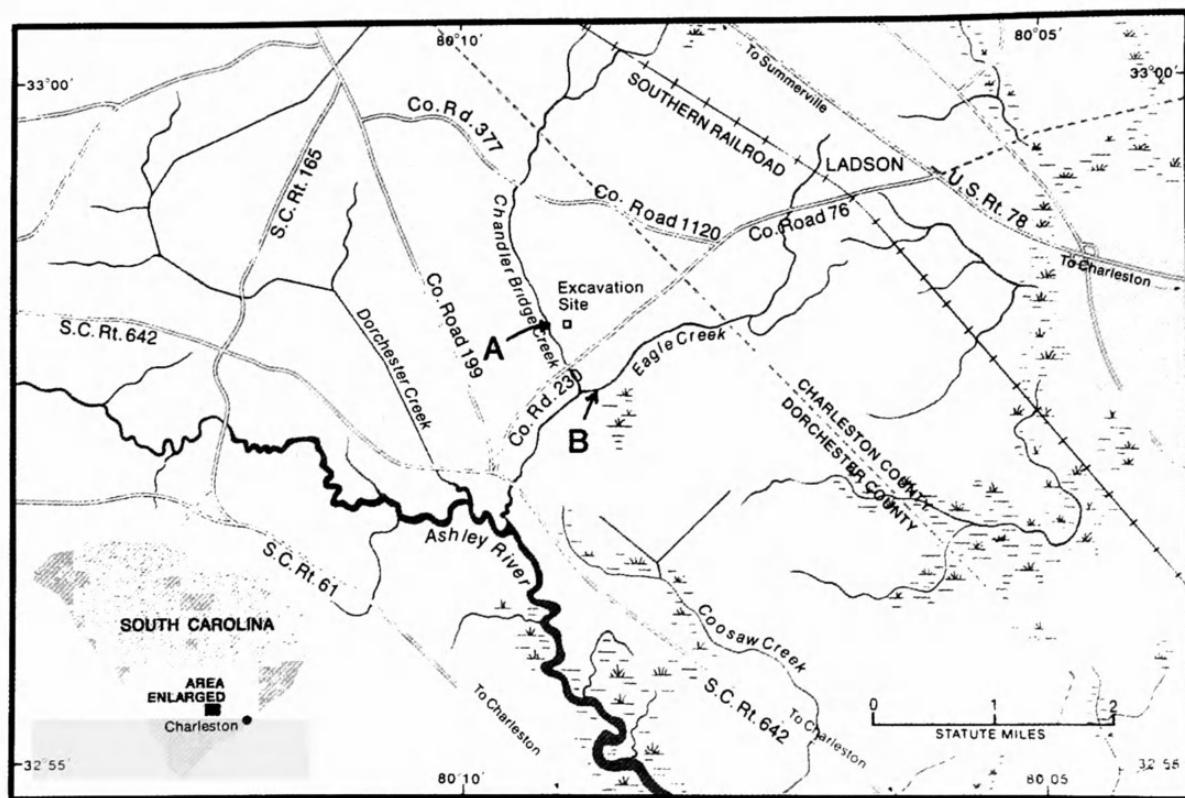


FIGURE 1.—Map showing the localities for the holotype (A) and the paratype (B) of *Micromysticetus rothauseni*, new genus and new species, in Dorchester County, South Carolina, approximately 20 miles north of Charleston. (Base map from Sanders, 1980, courtesy of National Geographic Society.)

ACKNOWLEDGMENTS.—We appreciate this opportunity to recognize the contributions of our longtime friend and colleague Clayton Ray. For more than 25 years he has been ever helpful to us and, in his quiet, tactful manner, has often suggested an alternative answer to a question in such a way that one would wonder why that solution had not seemed evident in the first place. A thorough, meticulous worker, he also is one of the finest writers who has ever graced this profession, having the rare ability to transmit his findings with a lucidity that leaves little doubt about his interpretation of the data that he has presented. A veritable bulldog when in pursuit of an obscure or elusive subject, he leaves virtually no stone unturned until he either has found what he is seeking or is certain that it probably won't be found. One can truly say that if Clayton Ray has been over the ground, there probably isn't much left to find there. More importantly, he is a splendid human being, possessing many of the qualities that distinguished Joseph Leidy. We consider it a privilege to have known him and to have worked with him, for it is doubtful that we will see his like again in our lifetimes.

We thank Vance McCollum, the collector of the holotype of *Micromysticetus rothauseni*, and Billy Palmer, who collected the paratype, for their generosity in making these specimens available to science. We are especially grateful to Karlheinz Rothausen, now retired from the Institut für Geowissen-

schaften-Paläontologie, Johannes Gutenberg-Universität, Mainz, Germany, for the loan of his original drawings, photographs, and negatives of *Micromysticetus (Cetotheriopsis) tobieni*, for his review of our manuscript, and for many other favors. Bernhard Gruber of the Oberösterreichisches Landesmuseum in Linz, Austria, kindly permitted K. Rothausen and the first author to examine the holotype of *Cetotheriopsis lintianus* and other specimens in his care and made arrangements for the excellent photographs of the holotype of *C. lintianus* by the museum photographer Bernhard Ecker. Sanders extends thanks to the Deutsche Forschungsgemeinschaft in Bonn, Germany, for financial assistance in a grant obtained by K. Rothausen to cover lodging expenses incurred in the study of the European material involved in this study and in another study in which he and Rothausen are collaborating. The European segment of this study also was funded in part by a National Geographic Society grant to the first author in connection with his studies of other cetacean specimens at the Oberösterreichisches Landesmuseum in Linz. We also are grateful to the National Geographic Society for permission to use as the base map for our Figure 1 the map published as figure 1 in the first author's report of paleontological excavation activities carried out under the grants (numbers 954 and 1074) from the society (Sanders, 1980:603).

The Charleston Museum and the Natural History Museum of Los Angeles County and its foundation provided facilities, salaries, and travel funds that made this study possible. AES produced the drawings. Bryan Stone produced all of the photographs except Figure 13C, made by Terry Richardson; Figures 11A,B, 12A–C, and 14, made by AES; and Figures 15–17, made by Bernhard Ecker. We thank David P. Whistler for comments on the manuscript and Zhexi Luo for his review of the text and figures of our description of the periotics of *Micromysticetus rothauseni*. Clayton E. Ray and Frank C. Whitmore, Jr., provided access to fossil cetacean material in the National Museum of Natural History and were helpful in numerous other ways.

MATERIAL AND METHODS

Terminology for cranial anatomy follows Kellogg (1938) and Fraser and Purves (1960). With some modifications required by the morphology of the specimens, cranial measurements follow Perrin (1975) and Kellogg (1936, 1965). The cranial reconstructions are in part mirror images of opposite sides of the specimens, and those of the two European taxa are based upon photographs of the holotypes and upon notes made from direct observations by Sanders. Broken lines represent areas of the skull not preserved in the actual specimen and thus are inferred or hypothetical configurations.

Geological interpretations of the rock units that yielded the holotype specimens are in accordance with the original description of the Chandler Bridge Formation (Sanders et al., 1982) and subsequent observations (Weems and Sanders, 1986).

Direct comparison of a cast of the holotype of *Cetotheriopsis tobieni* Rothausen, 1971, with the holotype of *Cetotheriopsis lintianus* (von Meyer, 1849) was made by K. Rothausen and one of us (AES) in July, 1992, and that material was compared with photographs of the holotype of the new taxon from South Carolina described in this paper. Where helpful, the fossils described herein have been compared with specimens of certain extant taxa.

ABBREVIATIONS.—The following abbreviations are used for institutions housing specimens used in this study:

ChM	The Charleston Museum, Charleston, South Carolina
FMNH	Field Museum of Natural History, Chicago, Illinois
JGU	Institut für Geowissenschaften-Paläontologie, Johannes Gutenberg-Universität, Mainz, Germany
LACM	Natural History Museum of Los Angeles County, Los Angeles, California
UCMP	University of California Museum of Paleontology, Berkeley, California
UO	University of Oregon, Eugene, Oregon
USNM	Collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (including the collections of the former United States National Museum)

ABBREVIATIONS.—The following anatomical abbreviations are used in this study:

Al	alisphenoid
bc	basioccipital crest
Boc	basioccipital
Bs	basisphenoid
ch	cranial hiatus
Eoc	exoccipital
fm	foramen magnum
fps	foramen pseudovalve
Fr	frontal bone
gf	glenoid fossa
hpt	hamular process of pterygoid
jn	jugular notch
Me	mesethmoid
mea	external auditory meatus
Na	nasal
Oc	occipital condyle
Pa	parietal
Pal	palatine
pgl	postglenoid process
pop	paroccipital process
Pt	pterygoid
pts	fossa for pterygoid sinus
Soc	supraoccipital
Sq	squamosal
sqf	squamosal fossa
sqp	squamosal prominence
tf	temporal fossa
Vo	vomer
zps	zygomatic process of squamosal

GEOLOGIC SETTING

Throughout the area near Charleston, the Chandler Bridge Formation is underlain by the Ashley Formation (Figure 2). Both formations are late Oligocene (early Chattian) marine units that are rich in fossil vertebrate material. The Chandler Bridge Formation was laid down approximately 28 million years ago (Sanders et al., 1982), and the Ashley Formation is considered to be about 30 million years old.

The holotype material of *Micromysticetus rothauseni*, new genus and new species (ChM PV4844), was found in the Ashley Formation at the bottom of a channelized stream only a few hundred feet west of the type locality of the Chandler Bridge Formation. The other specimen (ChM PV5933) was found relatively nearby, also in the Ashley Formation.

The uppermost portion of the Chandler Bridge Formation (Bed 3) is a beach facies from which a large number of marine vertebrate remains were recovered in a major excavation conducted by the Charleston Museum (Sanders, 1980). The site of that excavation is the type locality for the Chandler Bridge Formation and is 2.1 km southwest of the type locality of another Oligocene mysticete, the archaic *Eomysticetus whitmorei* Sanders and Barnes (2002).

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 a comprehensive assemblage of Oligocene-age marine-associated vertebrates. Included are an extensive fish fauna; five taxa of sea turtles; a large crocodile,

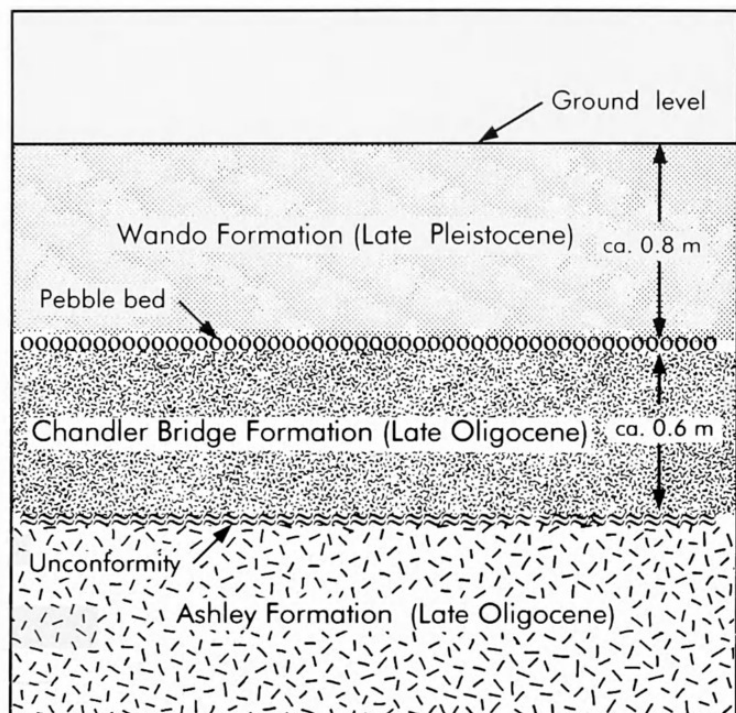


FIGURE 2.—Generalized stratigraphic section of late Oligocene (lower Chattian) beds along Chandler Bridge Creek and Eagle Creek near bridge on Ladson Road (County Road 230) in Dorchester County, South Carolina. Both the holotype and the paratype crania of *Micromysticetus rothauseni*, new genus and new species, were found in the Ashley Formation.

Gavialosuchus carolinensis Erickson and Sawyer (1996); several species of littoral and pelagic birds (including the largest and most nearly complete pseudodontorn yet found); at least two taxa of dugongids; and one of the largest and most diverse assemblages of cetacean remains yet recovered from any Oligocene deposit. Representatives of Mysticeti and Odontoceti have been found in the Chandler Bridge Formation, but squalodontoids and other primitive odontocetes are by far the most numerous, with mysticetes being relatively uncommon. To date, there has been no evidence of faunal assemblages or individual taxa that are positively restricted to either the Chandler Bridge or the Ashley Formation, although *Micromysticetus rothauseni* is presently known only from the Ashley. An early Chattian age for the Chandler Bridge Formation is indicated by the presence of undescribed squalodonts of the same evolutionary grade as *Eosqualodon langewieschei* Rothausen, 1968 (see Whitmore and Sanders, 1976; Sanders, 1980), which is from Eochattian sands (Chattian A) at Doberg, Germany. The Chattian A beds at Doberg 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 is given by Sanders et al. (1982).

E. Martini (pers. comm., June 1990) examined nannoplankton from the underlying Ashley Formation at the type locality of the Chandler Bridge Formation and found the Ashley Formation to be referable to zone NP24. Because the same evolu-

tionary grades and many of the same genera are represented among the cetaceans, sea turtles, and other vertebrate faunas of both 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 (perhaps only about 2 My) elapsed between the deposition of these two units.

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758

Order CETACEA Brisson, 1762

Suborder MYSTICETI Flower, 1864

Superfamily BALAENOPTEROIDEA (Gray, 1868)

Family CETOTHERIIDAE (Brandt, 1872) Miller, 1923

Subfamily CETOTHERIOPSINAE Brandt, 1872

Micromysticetus, new genus

Cetotheriopsis Brandt, 1871 [in part].—Rothausen, 1971:135.

DIAGNOSIS.—A genus of cetotheriopsine cetotheriids differing from *Cetotheriopsis* in the following characteristics: smaller size; cranium with an occipital shield shaped like a broad equilateral triangle, not an anteroposteriorly elongate triangle, medial crest on midline of occipital shield less prominent, squamosal fossa short anteroposteriorly, shallow, and interrupted by a protuberance—herein termed the *squamosal prominence*—extending posterolaterally to its posterior margin; exoccipital thick anteroposteriorly and narrow transversely; zygomatic process of squamosal elongate, deep, arched, and extending beyond apex of supraoccipital; glenoid fossa broad transversely with rounded posterointernal margin; basioccipital between basioccipital crests flat to slightly convex; sulcus for external acoustic meatus short and broad.

Adults with no prominent sulcus dorsal to occipital condyles on occipital shield,

ETYMOLOGY.—From *mikros* (Greek), small, and *mystax* (Greek), moustache, in reference to baleen; and from *ketos* (Greek), whale.

TYPE SPECIES.—*Cetotheriopsis tobieni* Rothausen, 1971.

INCLUDED SPECIES.—*Micromysticetus tobieni* (Rothausen, 1971) and *Micromysticetus rothauseni*, new species.

Micromysticetus tobieni (Rothausen, 1971), new combination

FIGURES 3–6

Cetotheriopsis tobieni Rothausen, 1971:135, figs. 2, 3, plates 1, 2.

EMENDED DIAGNOSIS.—A small species of *Micromysticetus* probably not exceeding 4.5 m in total length, differing from *M. rothauseni*, new species, by having large occipital condyles, occupying more than 45% of distance between outer margins

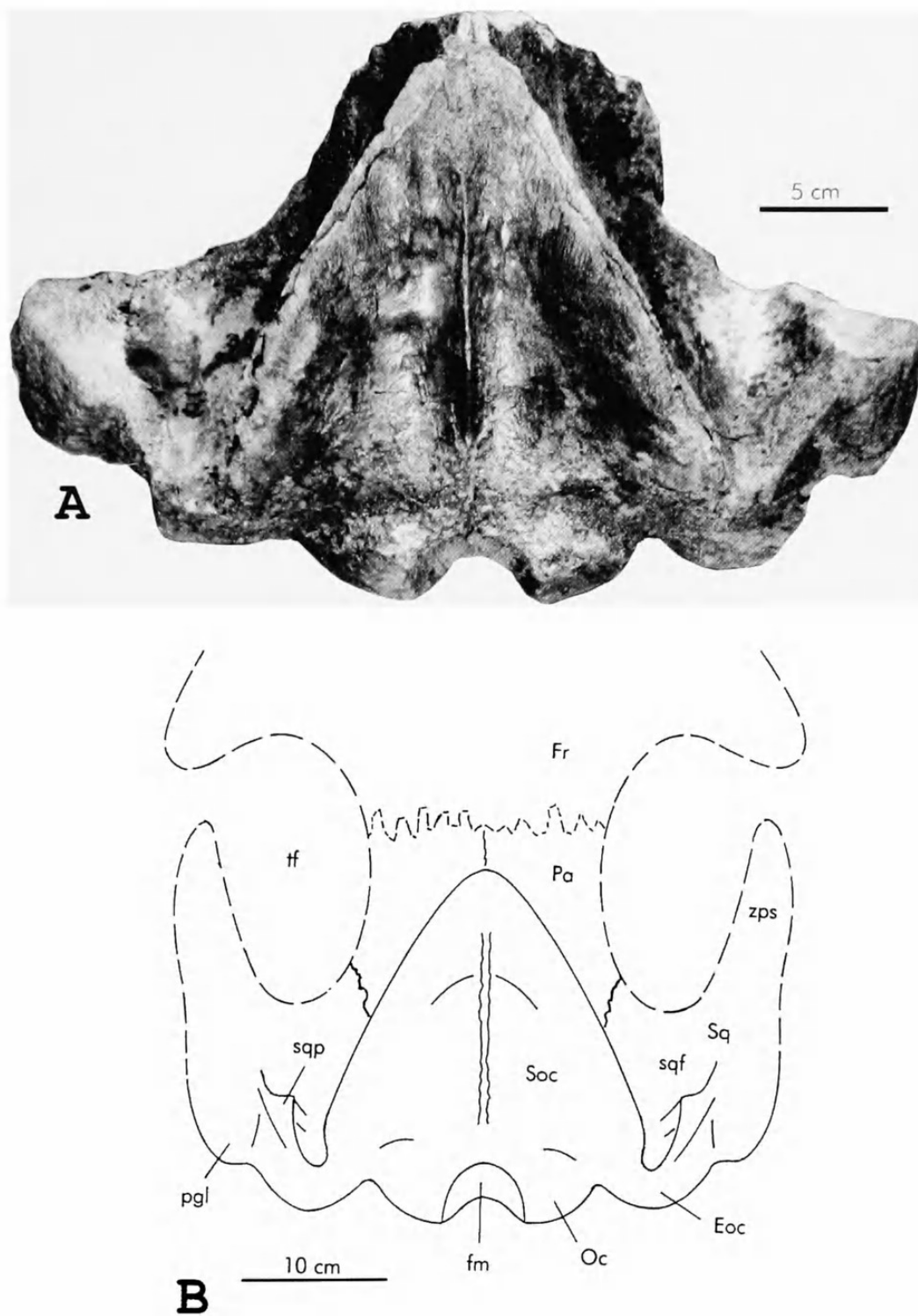


FIGURE 3.—*Micromysticetus tobieni* (Rothausen, 1971): A, holotype braincase (JGU P1289), dorsal view (from original photograph used in Rothausen 1971, table 1: fig. 1; courtesy of K. Rothausen); B, reconstruction. (Dashed lines indicate hypothetical configurations; abbreviations are explained in "Material and Methods.")

of exoccipitals. Lateral margins of supraoccipital almost straight in anterior two-thirds, then forming a slight angle in posterior portion; inner margins of basioccipital crests rounded and curving away from each other posteriorly, the space between them being slightly convex.

HOLOTYPE.—Partial braincase, JGU P1289, collection of Institut für Geowissenschaften-Paläontologie, Johannes Gutenberg-Universität, Mainz, Germany. Previously in the private collection of Fritz von der Hocht, Krefeld, Germany.

TYPE LOCALITY.—Kiesgrube Wilhelm Frangen, Lank-La-

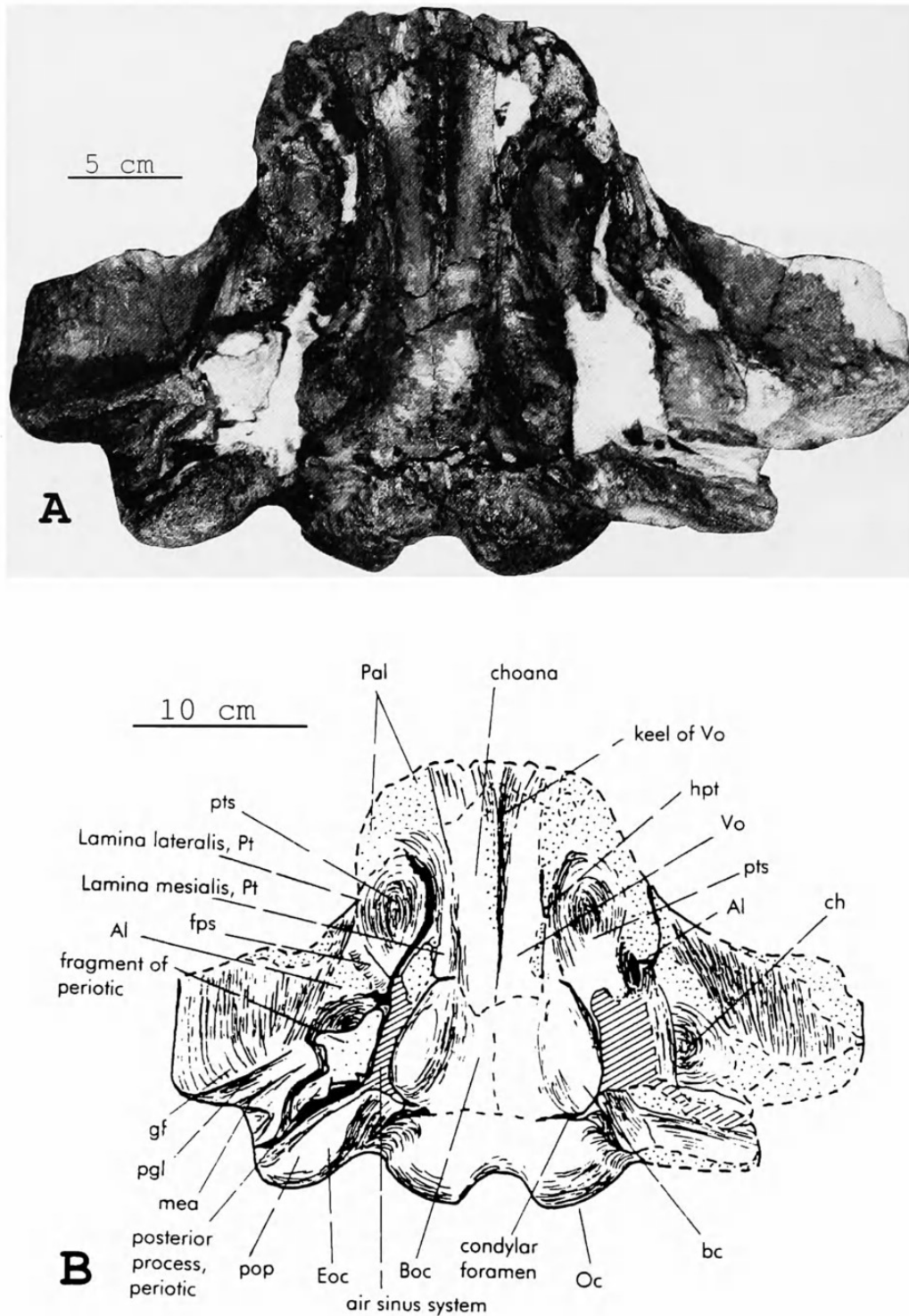


FIGURE 4.—*Micromysticetus tobieni* (Rothausen, 1971), holotype braincase (JGU P1289): A, posterior view (Rothausen 1971, table 1: fig. 3); B, left lateral view (Rothausen 1971, table 2: fig. 4). (From original photographs courtesy of K. Rothausen; abbreviations are explained in "Material and Methods.")

tum, WNW Dusseldorf-Kaiserwerth, Nordrhein-Westfalen, Germany.

FORMATION AND AGE.—Meeressande, upper "Chattian A" beds, nannoplankton zone NP24 (Martini and Müller, 1975), lower Chattian, late Oligocene.

REMARKS.—The holotype cranium of *Micromysticetus tobieni* lacks both of the zygomatic processes, but it seems apparent that had the anterior ends of those processes been preserved they would have extended beyond the anteriormost extent of the apex of the supraoccipital, as in *M. rothauseni*, new species,

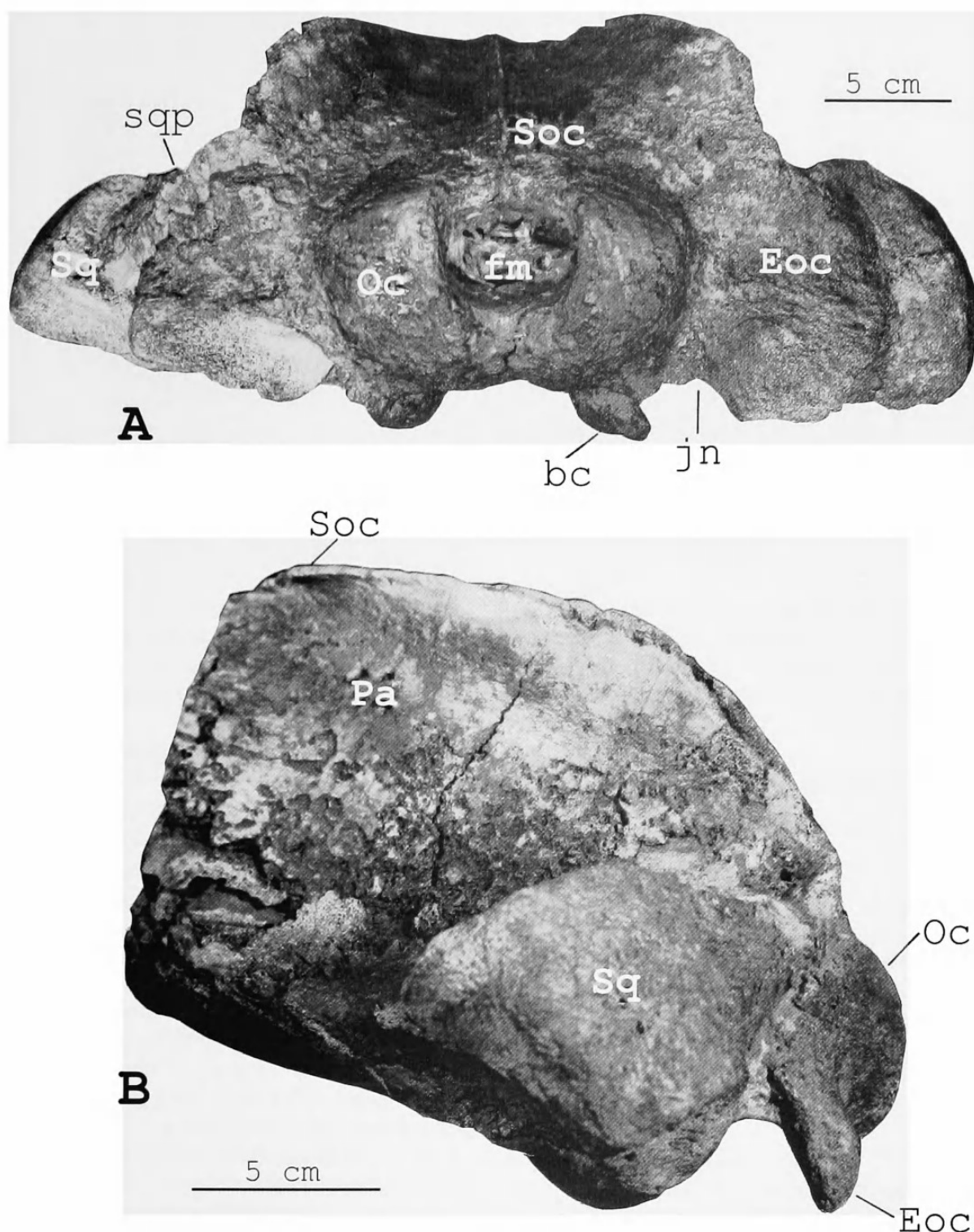


FIGURE 5.—*Micromysticetus tobieni* (Rothausen, 1971), holotype braincase (JGU P1289): A, posterior view (Rothausen 1971, table 1: fig. 3); B, left lateral view (Rothausen 1971, table 2: fig. 4). (From original photographs courtesy of K. Rothausen; abbreviations are explained in "Material and Methods.")

(Figures 3B, 7). The shape of the supraoccipital shield in the holotype is almost that of an equilateral triangle, the axes of the lateral margins intersecting the plane of the posterior margin of the occipital condyles at an angle of approximately 60°. The squamosal prominences are partly eroded but clearly evident

and divide the floor of the squamosal fossa into two levels, as in *M. rothauseni*, new species, but not as conspicuously. The occipital condyles are quite large (Figure 8), occupying 46% of the space between the outer margins of the exoccipitals, but the condyles in *M. rothauseni*, new species, occupy a slightly

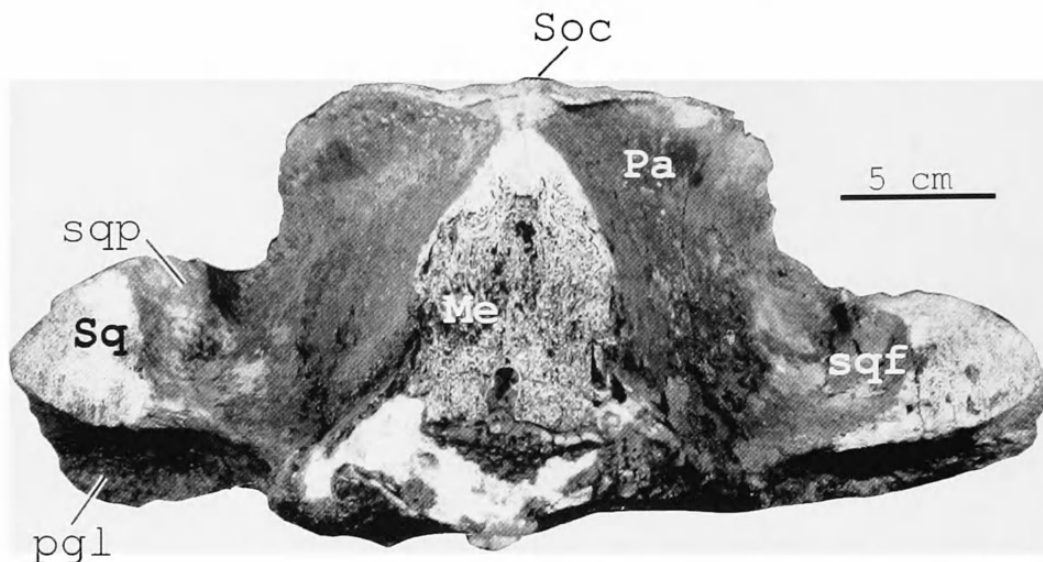


FIGURE 6.—*Micromysticetus tobieni* (Rothausen, 1971), holotype braincase (JGU P1289), anterior view. (Abbreviations are explained in “Material and Methods”; photograph courtesy of K. Rothausen.)

greater portion of the width of the exoccipital region (48% in the holotype skull). Ventrally, the inner margin of the glenoid fossa bordering the cranial hiatus is more rounded than in *Cetotheriopsis lintianus*, in which the corresponding border is sharply angular (Figures 4, 16).

Micromysticetus rothauseni, new species

FIGURES 7–14

Cetothere “possibly related to *Cetotheriopsis*.”—Sanders and Barnes, 1991.

DIAGNOSIS.—A species of *Micromysticetus* differing from *Micromysticetus tobieni* in the following characteristics: cranium with more rounded posterior margin of squamosal fossa; median crest on supraoccipital not extending close to dorsal margin of foramen magnum; lateral margin of occipital shield more convex; exoccipital thicker anteroposteriorly and protruding more posteroventrally; basioccipital crests angular and not rounded as in *M. tobieni*, and with space between them flat and not convex.

HOLOTYPE.—ChM PV4844, braincase lacking the entire rostrum and the right zygomatic process of the squamosal; both periotics; and axis vertebra. Collected by Vance McCollum in March 1986.

TYPE LOCALITY.—South Carolina, Dorchester County; bottom of channelized bed of Chandler Bridge Creek in Hickory Hills housing development, ~0.66 km (0.41 mi.) north of County Road 230 near S.C. Route 642, approximately 32 km (20 mi.) north of Charleston (Figure 1).

FORMATION AND AGE.—Ashley Formation, late Oligocene, early Chattian correlative, nannoplankton zone NP 24, ca. 30 Ma. The skull and related specimens were found in the top of

the Ashley Formation exposed in the streambed, approximately 30 cm below the contact with the overlying Chandler Bridge Formation, and only a few hundred meters west of the type locality of the Chandler Bridge Formation, marked as “Excavation Site” in Figure 1.

ETYMOLOGY.—The specific name is a patronym honoring Karlheinz Rothausen, in recognition of his many contributions to our knowledge of the Oligocene cetaceans of Europe.

PARATYPE.—ChM PV5933, partial braincase missing left side and most of basicranium. South Carolina, Dorchester County; bank of Eagle Creek, ~152 m (500 ft.) northeast of confluence with Chandler Bridge Creek; County Road 230, ~1.04 km (0.65 mi.) southwest of type locality of *Micromysticetus rothauseni*. Collected by Billy Palmer, November 1997.

DESCRIPTION.—*Cranium:* Although missing most of the zygomatic process of the right squamosal and a large section of the supraoccipital (Figure 7A), the holotype cranium of *Micromysticetus rothauseni* is well preserved otherwise, except where some of the dorsal surfaces have been eroded, especially along the lambdoidal crests and portions of the exoccipitals, occipital condyles, and zygomatic processes of the squamosals.

Micromysticetus rothauseni has a broad, triangular braincase; large and widely flaring zygomatic processes of the squamosals; and a narrow squamosal with a well-developed squamosal prominence (Figure 7). The parietals are joined at the midline and form the posterior portion of an intertemporal constriction with a narrowly rounded sagittal crest. This portion of the skull roof is preserved for a distance of 48 mm anterior to the apex of the supraoccipital and shows evidence of interdigitation with the frontals; thus, it is probable that most, if not all, of the parietal portion of the intertemporal region is preserved

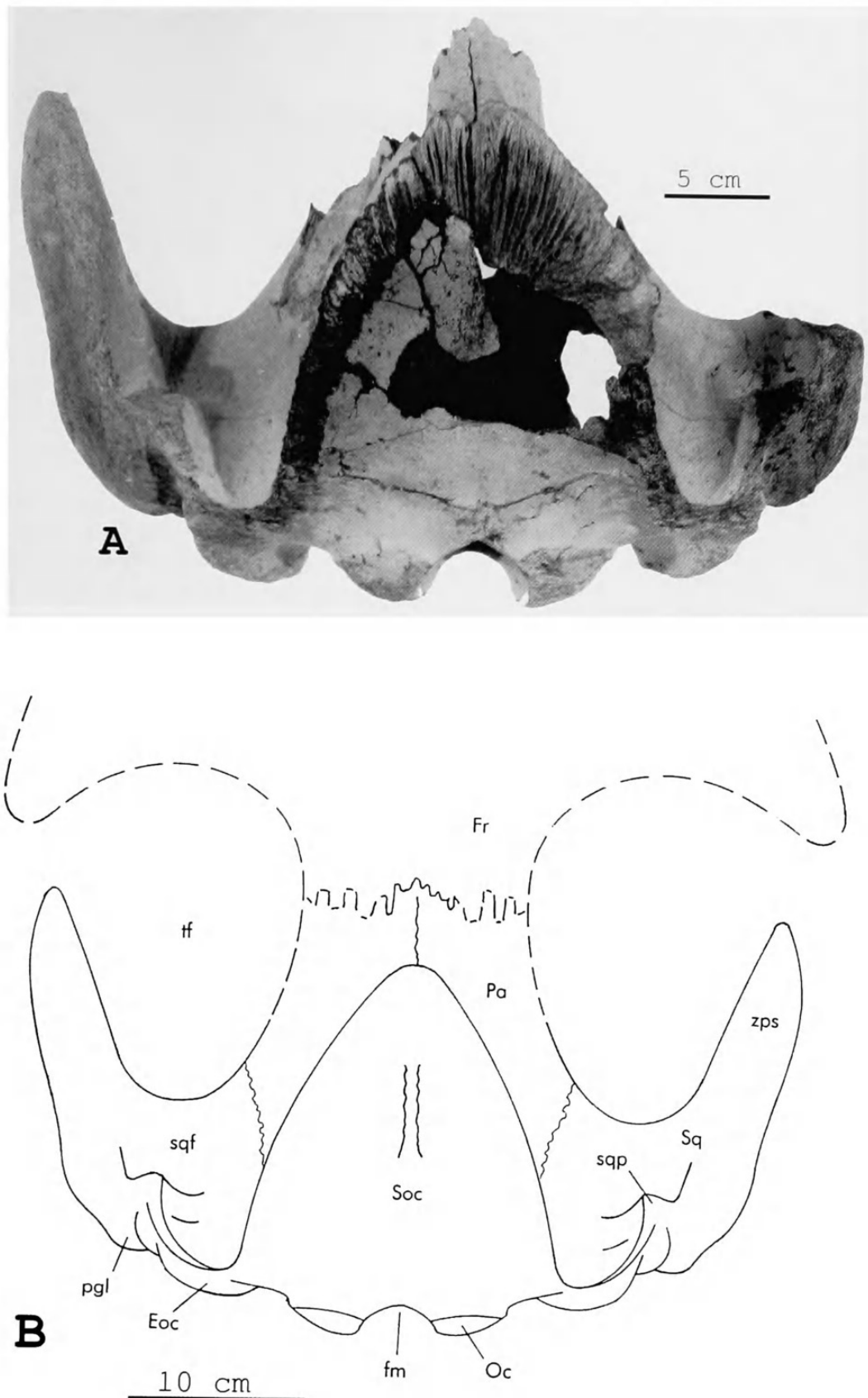


FIGURE 7.—*Micromysticetus rothauseni*, new genus and new species: A, holotype braincase, ChM PV4844, dorsal view; B, reconstruction. (Dashed lines indicate hypothetical configurations; abbreviations are explained in "Material and Methods.")

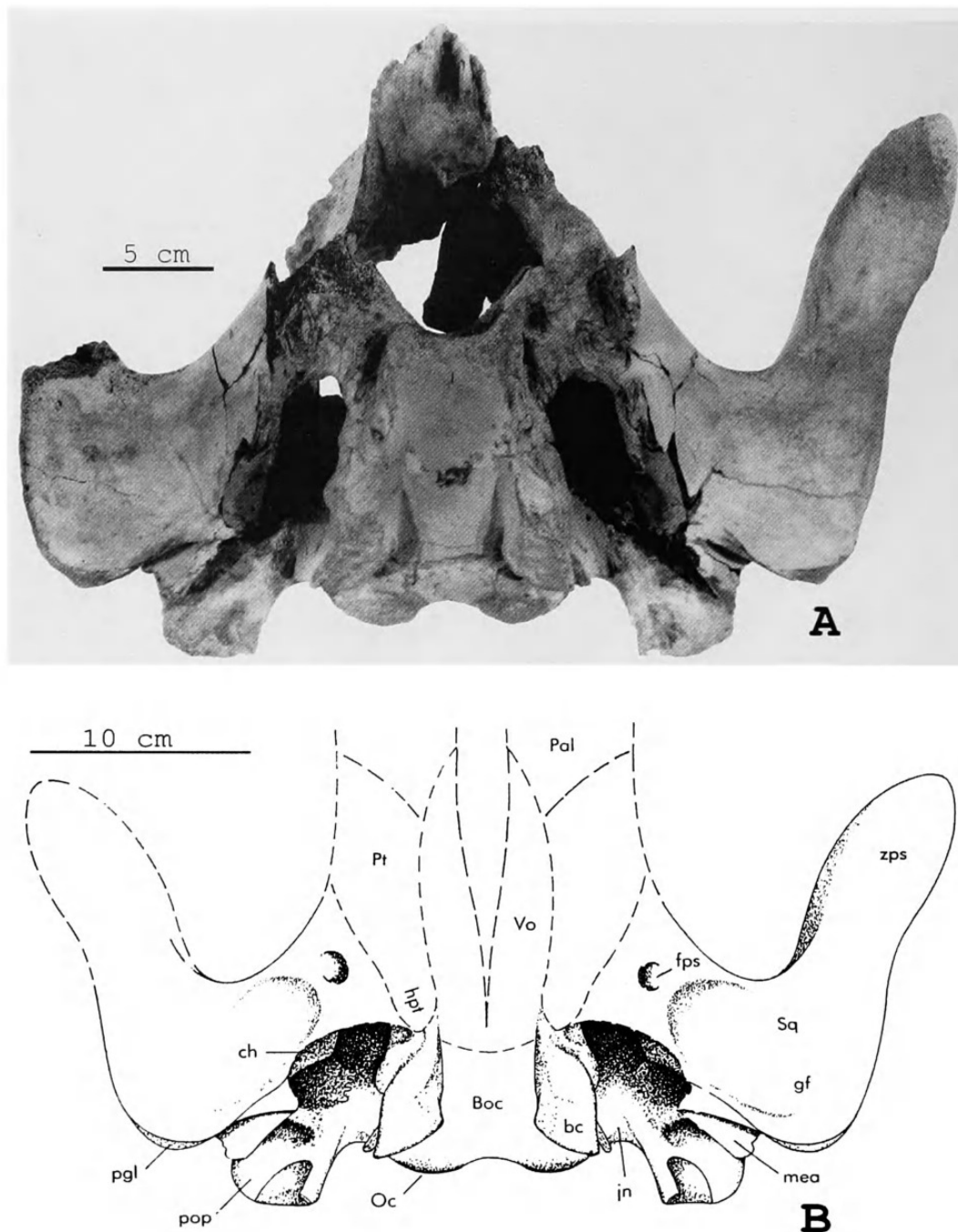


FIGURE 8.—*Micromysticetus rothauseni*, new genus and new species: A, holotype braincase, ChM PV 4844, ventral view; B, reconstruction. (Dashed lines indicate hypothetical configurations; abbreviations are explained in "Material and Methods.")

in the holotype. Details of that region anterior to the parietals are not known, but it seems likely that the frontals would have continued the constriction anteriorly for approximately the same distance as the length of the parietal portion. A moderately long, narrow, intertemporal region in the skull of this animal would have been necessary for the postorbital process of the frontal to clear the anterior tip of the zygoma.

The occipital shield is triangular and relatively broad and is slightly concave anterior to the foramen magnum and medial to the nuchal crest. Dorsal to the occipital condyles the surface of the occipital shield is flat to convex. The lateral and apical mar-

gins of the supraoccipital are missing entirely, but the squamosal and parietal rims of the lambdoidal crests provide the outline of its original form. Laterally, they flare outward and overhang the temporal fossa. The axis of the left lambdoidal crest departs the plane of the posterior margins of the occipital condyles at an angle of approximately 75° (at first nearly 90° in *M. tobieni*, then bending anteriorly at an angle of about 60°). Anterodorsally, the margins of the lambdoidal crests curve inward toward the apex of the supraoccipital. In *M. rothauseni*, therefore, the margins of the supraoccipital are noticeably convex as they approach the apical region, whereas in *M. tobieni*

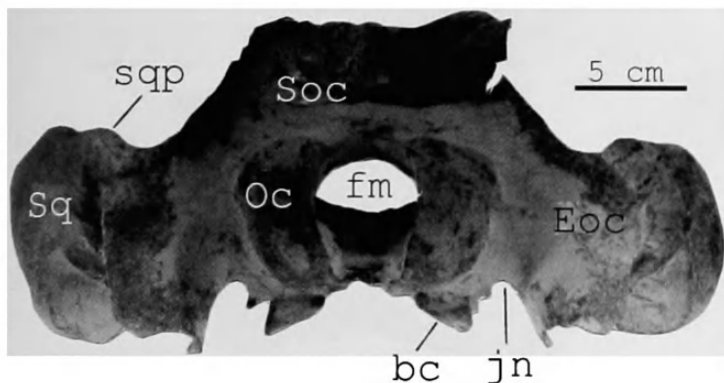


FIGURE 9.—*Micromysticetus rothauseni*, new genus and new species, holotype braincase, ChM PV 4844, posterior view. (Abbreviations are explained in "Material and Methods.")

the marginal curvature is more subtle and much less noticeable. Dorsally, there is a medial crest that extends posteriorly from the apical portion of the supraoccipital for about one-half the distance to the dorsal margin of the foramen magnum. In *M. tobieni* there is a similar crest that extends posteriorly for approximately three-fourths of the distance to the foramen magnum.

The occipital condyles are very large for a skull of such modest dimensions and are exceptionally broad transversely, occupying 48% of the distance (256.6 mm) between the outer margins of the exoccipitals. Despite their massive size, the condyles do not protrude prominently from the occipital shield. The plane of the dorsalmost margins of the condyles is on a level with the posterior margin of the floors of the squamosal fossae. In certain areas where they are least eroded, the articular surfaces of the condyles are punctate, suggesting that the specimen does not represent a fully mature individual. Although there is considerable variation in the amount of hori-

zontal space taken up by the condyles in other species of cetotheres, that variation does not appear to be entirely a function of individual body size. In the holotype skull of the middle Miocene cetother *Cophocetus oregonensis* Packard and Kellogg, 1934 (UO 305), the condyles occupy a mere 28% of the exoccipital region, although the anteroposterior length (1.2 m) of this specimen is only one-half the length (2.5 m) of the holotype skull (LACM 882) of the late Miocene cetotheriid *Mixocetus elysius* Kellogg, 1934a, in which the condyles occupy 34% of the exoccipital region. In the smallest known mysticete, represented by a partial cranium (UCMP 26502) from the late Miocene Towsley Formation (Barnes, 1977:329) of California and described as *Nannocetus eremus* by Kellogg (1929), who considered it to be a small cetother, the condyles take up 49% of the distance between the outer margins of the exoccipitals (182 mm). In the considerably larger form *M. rothauseni*, however, they compose 48% of that distance (256.6 mm), nearly the same as in *Nannocetus*. It thus appears again that larger species do not necessarily have significantly smaller condyles than more diminutive taxa. There may be some ontogenetic variation in the size of the condyles relative to the transverse diameter of the exoccipital region, as suggested by the paratype of *M. rothauseni* (ChM PV5933), in which the condyles occupy 50% of the space between the exoccipital margins. That specimen is decidedly a much younger individual than the holotype. Nevertheless, the exceptionally large condyles of *M. rothauseni* seem to stand alone in comparison with other known cetotheres except *Nannocetus* and thus may be tentatively regarded as diagnostic for this species until proven otherwise by additional material. The condyles of *M. tobieni* also are comparatively large (46% of the width of the exoccipital region), which suggests that large condyles may in fact be characteristic of the genus *Micromysticetus*. Even if an allowance is made for allometric considerations, the condyles of these two

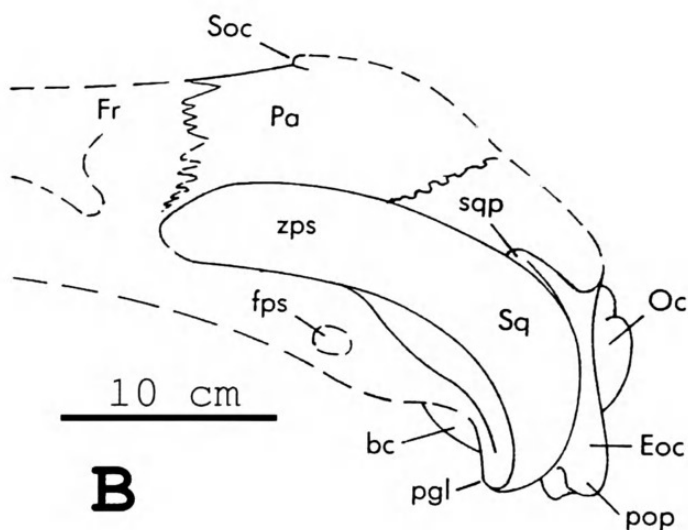
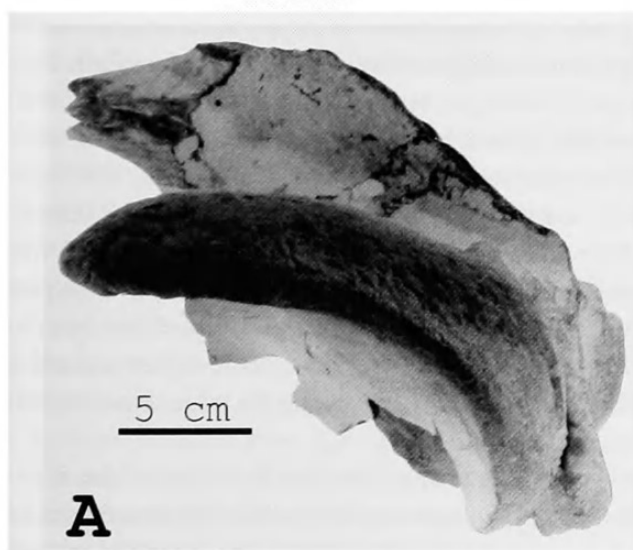


FIGURE 10.—*Micromysticetus rothauseni*, new genus and new species: A, holotype braincase, ChM PV4844, left lateral view; B, reconstruction. (Dashed lines indicate hypothetical configurations; abbreviations are explained in "Material and Methods.")

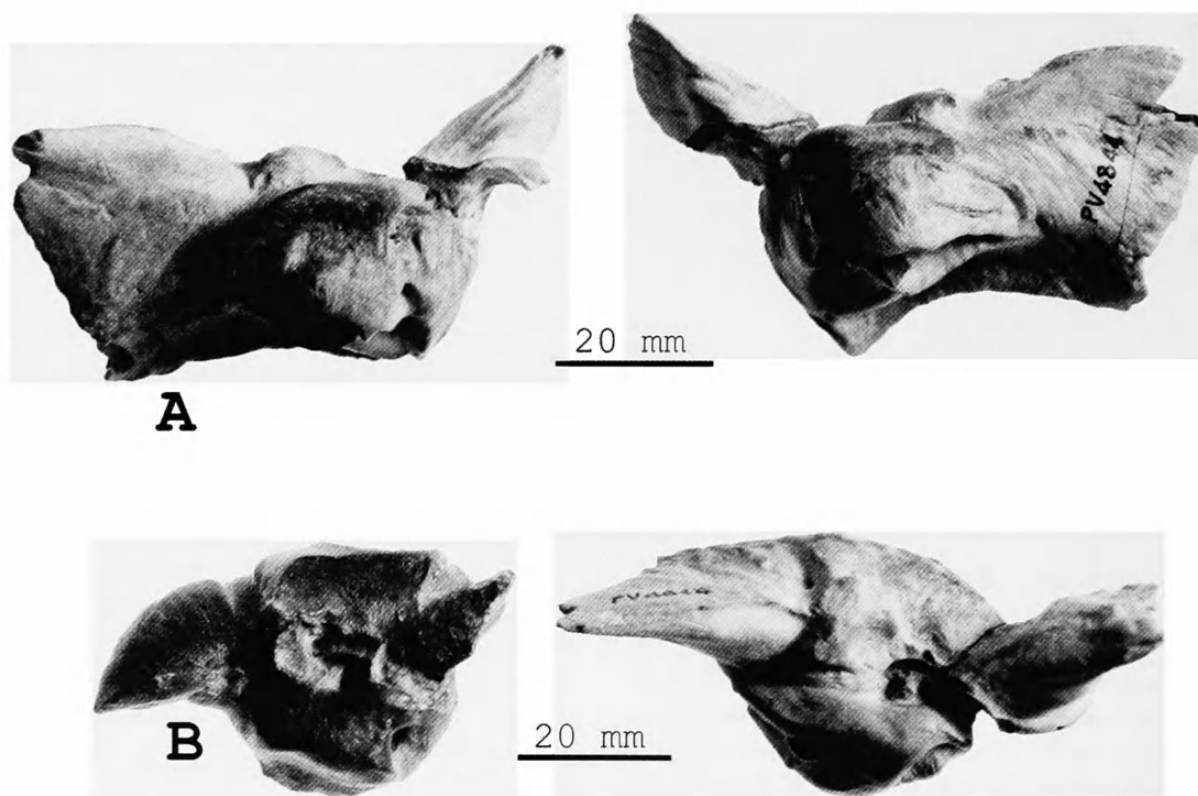


FIGURE 11.—A, *Micromysticetus rothauseni*, new genus and new species, holotype right and left periotics, ChM PV4844; B, left periotic of the archaeocete *Zygorhiza kochii* (ChM PV5065) (missing posterior process) from the late Eocene Harleyville Formation in Dorchester County, South Carolina (left), and the holotype left periotic of *Micromysticetus rothauseni*, new genus and new species (right).

taxa still are proportionately larger than those of most of the other cetotheres noted above.

Lateral to the condyle, the surface of each exoccipital is not concave as in *Cetotheriopsis lintianus*. The exoccipital portion of the occipital shield is thick, as is typical of most fossil and extant baleen whales. In its ventral part, however, the paroccipital process is exceptionally thick, and it extends posteroventrally.

Between the braincase and the zygomatic process, the squamosal fossa is shallow, anteroposteriorly short, and wide. Arising from the center of the floor of the squamosal fossa there is a knobby protuberance that we formally term the “squamosal prominence” (sqp). This prominence forms a scarp-like ridge that divides the floor of the squamosal fossa into two levels, the posterior level being elevated approximately 15 mm above the anterior level. Anteriorly from the anterior margin of the prominence, the floor of the fossa forms a narrow gutter that slopes ventrally to the anterior margin of the squamosal. The posterior level of the fossa is on a plane approximately parallel to the sagittal plane of the skull. A modified extension of the lambdoidal crest, the squamosal prominence is joined to the posterior part of the zygomatic process of the squamosal. The lateral wall of the braincase is nearly vertically oriented and slightly

concave near its middle. It is not bowed laterally as is typical of most balaenopterids.

The zygomatic process of the squamosal is elongate, is very large relative to the size of the cranium, and diverges anterolaterally from the midline of the cranium. It arches anterodorsally in a broad curve and bends ventrally at its anterior extremity. The process is thick dorsoventrally and is of uniform thickness for most of its length, terminating in a rounded point anteriorly. The medial surface is uniformly smooth. The lateral surface is uniformly bowed outward, making its lateral side smoothly convex, and it flares slightly ventrolaterally at the ventral margin, especially so at the posterior end of the process, which is rounded dorsally and flattened ventrally to receive the posterior end of the jugal. The zygomatic process of the squamosal is slightly expanded dorsoventrally at its posterior end and arches slightly anteroposteriorly to create the large, anterodorsally inclined glenoid fossa.

At the posterior end of the lateral surface of the zygomatic process is a prominent, vertically oriented sternomastoid fossa. This fossa is inclined anterodorsally and is located immediately dorsal to the large paroccipital process. The latter is thick anteroposteriorly, is narrow transversely, and projects prominently ventrally and posteriorly from the occipital shield.

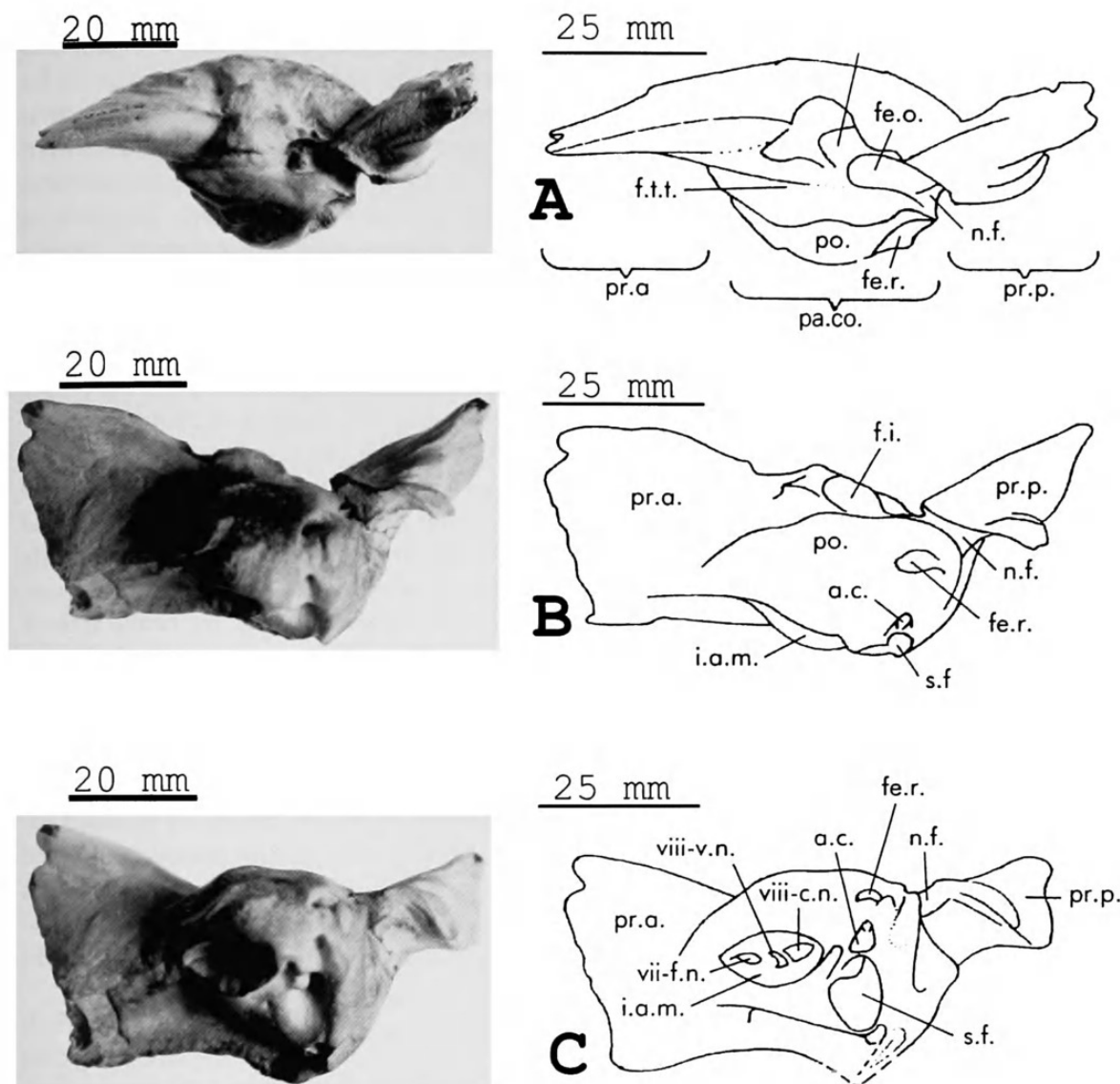


FIGURE 12.—*Micromysticetus rothauseni*, new genus and new species, holotype left periotic, ChM PV4844: A, ventral view; B, cerebral view; C, dorsolateral view. (Abbreviations: a.c.=aqueductus cochlearis; c.n.=foramen for cochlear nerve; f.i.=fossa incudis; f.n.=foramen for facial nerve; fe.o.=fenestra 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.)

The recess for the external auditory meatus is deep, but short transversely and broad anteroposteriorly and is clearly defined between the postglenoid process of the squamosal and the paroccipital process.

The cranial hiatus, the recess between the squamosal and the basioccipital in which the periotic lies, is large and elongated anteroposteriorly. Anterolateral to the cranial hiatus and immediately posterior to the large, obliquely oriented foramen pseudovalve is the falciform process. This process is thick and is connected to the postglenoid process of the squamosal by a very slender and low, transverse crest of bone. This crest marks the lateral border of a large pterygoid sinus extending anteriorly from the cranial hiatus. The ventral surface of the basioccipital is nearly flat. The basioccipital crests are broad, rectangular, and flattened ventrally, their inner margins paralleling the midline axis of the skull before breaking into divergent angles that terminate in narrow, rounded points posteriorly (Figure 7). As depicted by Rothausen (1971:137, pl. 3: fig. 5), the basioccipital crests (*Alae Basioccipitalis* in Rothausen, 1971)

of *Micromysticetus tobieni* are rounded and knob-like, their inner margins curving away from each other posteriorly.

The glenoid fossa is broad transversely, with a nearly square articular surface, which is poorly delimited anteriorly. The innermost margin bordering the cranial hiatus is rounded, as in *Micromysticetus tobieni*. The postglenoid process is canted posterolaterally and is thickest laterally, where its ventral margin is convex, then becomes thinner medially, where it terminates at the margin of the pterygoid sinus.

Periotics: The holotype left and right periotics of *Micromysticetus rothauseni* (ChM PV4844) are well preserved (Figures 11, 12). The left periotic is missing only the dorsalmost extension of the superior process, which is present in the right periotic and has been utilized in the reconstruction of the left one (Figure 12). The right one is chipped in several places. From the anteriormost point on the anterior process to the posteriormost point on the posterior process, the left periotic is 73 mm in length. The pars cochlearis is 28 mm in dorsoventral diameter, 36 mm anteroposteriorly, and 34 mm in transverse diameter. Its external face is strongly rugose. Immediately adja-

cent to the dorsal end of the subarcuate fossa is a much smaller fossa that is reduced to a tiny pit in the right periotic; otherwise, these two bones are mirror images of each other and their measurements do not differ significantly. The anterior process is short, laterally compressed, and broadly expanded dorsoventrally. The posterior process also is short and is much smaller than both the anterior process and the pars cochlearis, quite unlike the periotics of most Miocene cetotheres, in which the posterior process is massive and greatly extended posteriorly (Kellogg, 1934a,b 1965, 1968a,b, 1969; Packard and Kellogg, 1934). The periotic of *M. rothauseni* bears little resemblance to those of Miocene cetotheres, and in ventral aspect it is most similar to the periotic of the late Eocene archaeocete *Zygorhiza kochii* (Reichenbach, 1847) as figured by Kellogg (1936:116, fig. 35a) and as seen in ChM PV5065, a left periotic of *Zygorhiza* (missing the posterior process) from Eocene beds in the Giant Portland Cement quarry near Harleyville, Dorchester County, South Carolina (Figure 11B). The anterior process of the periotic is more laterally compressed in *Micromysticetus* than in *Zygorhiza* and the posterior process is much smaller than in the latter (Kellogg, 1936:116, fig. 35a), but the relative positions of the fossa for the tensor tympani muscle, the fenestra ovalis, the fenestra rotunda, the canal for the facial nerve, the fossa incudis, and the subarcuate fossa are much the same in PV4844 and PV5065. In cerebral (internal) aspect, the anterior process is hatchet-shaped, like that of *Zygorhiza*, and in the left periotic it is 38.8 mm in dorsoventral diameter. The posterior process is small and narrow, measuring only 15.5 mm dorsoventrally. The great disparity in the size of these processes is exactly the opposite of their dimensions in most Miocene cetotheres, in which the anterior process has been drastically reduced and the posterior process greatly expanded.

Axis Vertebra: The holotype axis vertebra of *Micromysticetus rothauseni* (ChM PV4844, Figure 13, Table 1) is essentially complete, with only minor erosion of certain surfaces. Like the periotic, the axis vertebra most closely resembles its counterpart in the archaeocete *Zygorhiza kochii*, as figured by Kellogg (1936:133, fig. 41) from USNM 4679. The transverse processes are extremely short and, like those of the axis in *Z. kochii*, are "directed more backward than forward" (Kellogg 1936:132). They are extremely narrow anteroposteriorly and thus lack the vertebral arterial canal present in the axis of *Zygorhiza*. The anterior face of the axis slopes upward and posteriorly at a very slight angle. The anterior facets for articulation with the atlas vertebra are flat along their outer portions but curve upward onto the odontoid process. They are separated above the odontoid process by an interval of approximately 40 mm. The odontoid process is broadly rounded ventrolaterally and slopes upward from the centrum to its anteriormost extent, where it abruptly assumes a vertical face 16.5 mm in width that ascends to the level of the dorsal surface of the centrum. On either side of the narrow rectangular vertical face there is a

curvilinear excavation extending laterally to the inner margin of the articulating facets. In the upper inner corner of this excavation there is a declivity that notches out the area directly behind the anterior face. Both the dorsal surface of the centrum and the roof of the neural canal slope upward and backward. The neural canal is circular in profile, and in vertical diameter it is 35.3 mm anteriorly and 36.7 mm posteriorly. The posterior face of the centrum is 74.5 mm in transverse diameter and 60.6 mm in vertical diameter and is slightly concave. The epiphysis is well ankylosed to the centrum, but its outer margins have not yet reached the outer margins of the centrum. On the ventral face of the centrum there is a rectangular, tab-like prominence measuring 29.2 mm transversely and 22.4 mm anteroposteriorly. The neural spine is short, low, and conspicuously thickened at its base, which is anteroposteriorly elongated so that it overhangs the odontoid process, as in *Zygorhiza kochii* (Kellogg, 1936:133, fig. 41b). Its posterior face is vertically inclined, does not extend beyond the posterior face of the centrum, and bears a medial carina. Dorsally, the neural spine is divided medially by a sulcus that is narrow anteriorly but becomes increasingly wider and deeper posteriorly until it has divided the posteriormost portion of the dorsal surface of the spine into two low, knob-like prominences. The pedicles of the neural arch are thinnest anterolaterally and are flattened posteriorly below the postzygapophyses, which are inclined obliquely upward and have circular ventral postzygapophysial facets. The punctate surfaces of the anterior articular facets and the failure of the epiphysis to reach the margins of the posterior face indicate that this specimen was not a mature individual.

PARATYPE.—The paratype partial cranium (ChM PV5933, Figure 14) is missing virtually the entire left side except the condyle and upper portion of the parietal and the anterior margin of the supraoccipital. All of the basioccipital is missing except for the badly eroded remnant of the right basioccipital crest and the posterior portion of the pterygoid.

This specimen duplicates all of the characters of the holotype except in one regard. Approximately 37 mm anterior to the dorsal margin of the foramen magnum, a small sulcus about 5 mm in transverse diameter begins to traverse the surface of the supraoccipital posteriorly along the midline until it reaches a foramen that penetrates the occipital shield about 13 mm anterior to the dorsal edge of the foramen magnum. This feature is completely absent in the holotype braincase (obviously that of an older individual); the only trace of it is a small, shallow, almost unnoticeable depression at the midline.

DISCUSSION.—The archaeocete-like periotic and axis vertebra of *Micromysticetus rothauseni* suggest that it and *M. tobi- eni* are more primitive than the preserved elements of their cranial architecture might indicate. As previously noted, the length of the preserved portion of the intertemporal region in *M. rothauseni* is almost certainly only half of its original

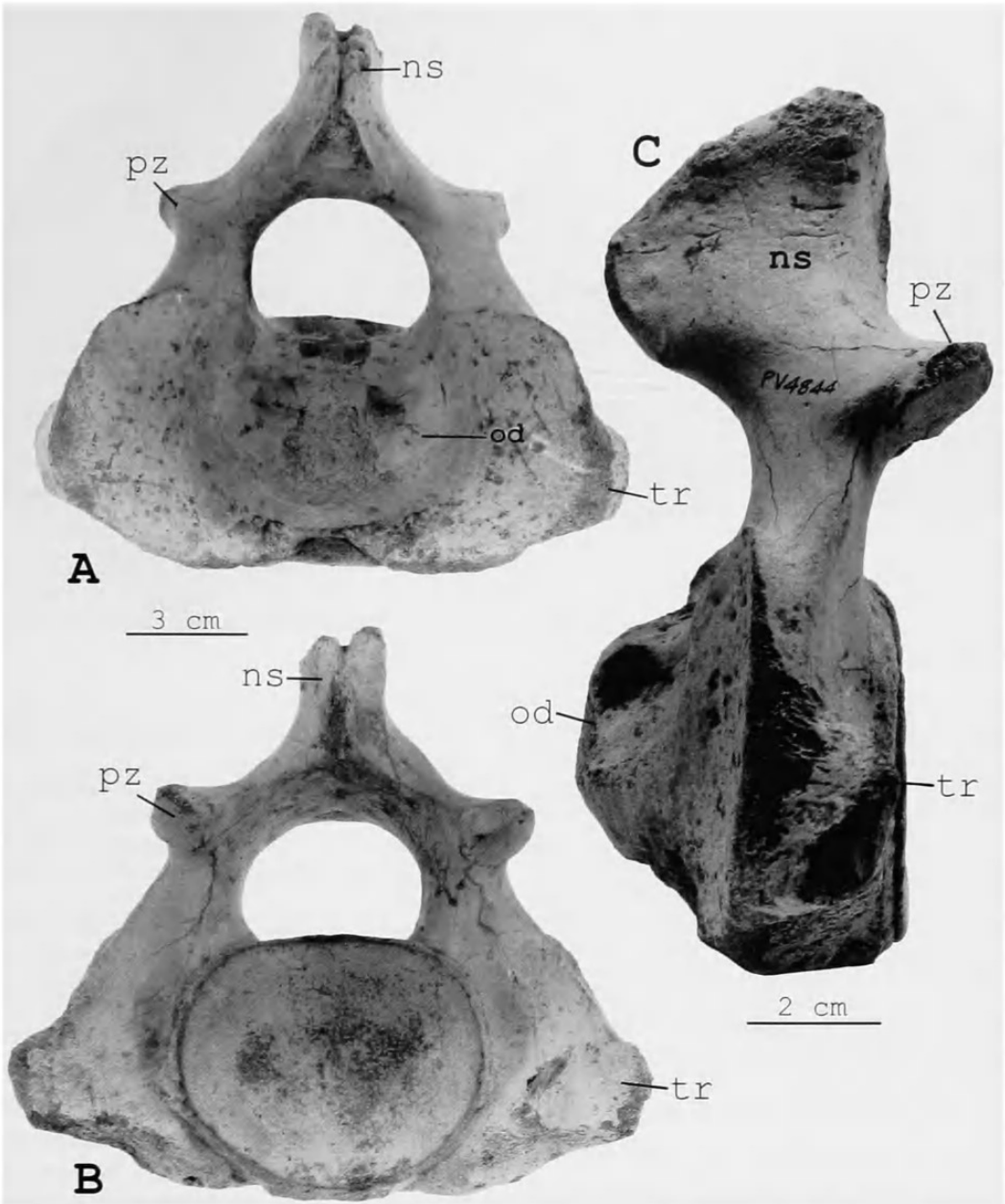


FIGURE 13.—*Micromysticetus rothauseni*, new genus and new species, holotype axis vertebra, ChM PV4844: A, left lateral view; B, anterior view; C, posterior view. (Abbreviations: ns.=neural spine; od.=odontoid process; pz.=postzygapophysis; tr.=transverse process.)

length, estimated to be approximately 95 mm, and it seems probable that *M. tobieni* had an intertemporal constriction of similar length proportionate to its size. An intertemporal region of even greater proportionate length is present in the primitive Oligocene baleen whale family Eomysticetidae (Sanders and Barnes, 2002), a group that firmly establishes Archaeoceti as ancestors of Mysticeti. The striking similarities between the periotic and axis vertebra of *M. rothauseni* and those of *Zygorhiza kochii* provide additional evidence of archaeocete-mysticete relationships and argue strongly in favor of a dorudontine archaeocete ancestry of the Mysticeti.

TABLE 1.—Measurements (in mm) of the holotype axis vertebra of *Micromysticetus rothauseni*, new genus and new species (ChM PV4844), from the late Oligocene of South Carolina. (*=measurement is an estimate).

Anteroposterior diameter of centrum	49*
Transverse diameter of centrum, anteriorly	132
Vertical diameter of centrum, anteriorly	66
Tip of neural spine to ventral face of centrum, anteriorly	134
Greatest vertical diameter of neural canal, anteriorly	35
Greatest transverse diameter of neural canal, anteriorly	42
Greatest distance between outer margins of transverse processes	147
Least anteroposterior diameter of right pedicle of neural arch	13
Greatest transverse diameter of centrum, posteriorly	76
Greatest vertical diameter of centrum, posteriorly	59

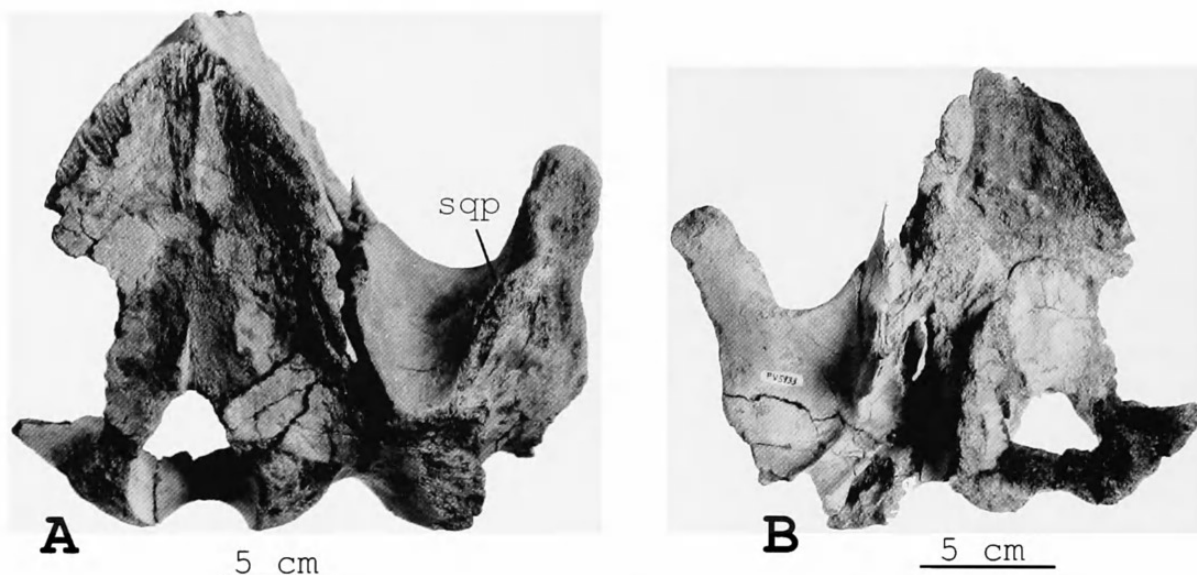


FIGURE 14.—*Micromysticetus rothauseni*, new genus and new species, paratype braincase, ChM PV5933: A, dorsal view; B, ventral view.

Cetotheriopsis Brandt, 1871

Balaenodon Owen, 1846 [in part].—Von Meyer, 1849:550; 1850:201.

Stenodon Van Beneden, 1865 [based upon composite assemblage of specimens belonging to one or more unrelated animals].

Cetotheriopsis Brandt, 1871:566.—Brandt, 1873:40, pl. 19: figs. 1–4; 1874: 6–11, pl. 1: figs. 1–16.—Winge, 1910:17–19.—Kellogg, 1923a:22–23; 1931: 307; 1934a:81.—Rothausen, 1971:131, 135, etc.—Whitmore and Sanders, 1976:318.—Fordyce, 1977:265; 1984, fig. 5b.

Aulocetus Van Beneden, 1875:537–539. [First latinized use of the name. “Aulocete” was used previously by Van Beneden (1861; see Kellogg, 1923a: 22–23). It is a junior synonym of *Cetotheriopsis* Brandt, 1871, because it has as its type species *Balaenodon lintianus* (see Winge, 1910:17–18; Kellogg, 1923a: 22–23); therefore, both genera, *Aulocetus* and *Cetotheriopsis*, have the same type species (see Kellogg, 1923a:22–23; 1931:307).]

DIAGNOSIS.—A genus of the subfamily Cetotheriopsinae differing from *Micromysticetus* in the following characteristics: larger size; cranium with occipital shield shaped like an antero-posteriorly elongate triangle; exoccipital broad transversely; glenoid fossa elongate anteroposteriorly and with an angular posterointerior margin; sulcus for external acoustic meatus long; zygomatic processes of squamosals not extending beyond apex of supraoccipital.

TYPE SPECIES.—*Balaenodon lintianus* von Meyer, 1849.

INCLUDED SPECIES.—*Cetotheriopsis lintianus* (von Meyer, 1849), late Oligocene, Austria.

Cetotheriopsis lintianus (von Meyer, 1849)

FIGURES 15–17

Balaenodon lintianus von Meyer, 1849:550.—Von Meyer, 1850:201.

“Aulocete” Van Beneden, 1861.

Stenodon lintianus Van Beneden, 1865:73–79, text fig. 2 [see Kellogg, 1923a: 22–23].

Cetotheriopsis lintianus Brandt, 1871:196.—Brandt, 1873:40, pl. 19: figs. 1–4; 1874:6–11, pl. 1: figs. 1–16.—Kellogg, 1923a:22–23; 1928:185–187, fig. 18; 1931:307; 1934a:81; 1969:1.—Slijper, 1936:209.—Rothausen, 1971:132.—

Whitmore and Sanders, 1977:314.—Fordyce, 1984, fig. 5b [photo of dorsal view of holotype].

Cetotheriopsis linziana Brandt, 1873 [in part, based upon the holotype of *Cetotheriopsis lintianus* and other specimens].—Brandt, 1874.

Squalodon linzianus Brandt, 1871. [A tympanic bulla that Brandt (1873) reasigned to *Squalodon ehrlichii* and Abel (1913) referred to *Patriocetus ehrlichii*.]

Aulocetus lintianus Van Beneden, 1861, 1875. [= *Balaenodon lintianus*; see Winge, 1909:17–18; Kellogg, 1923a:22–23; 1931:307.]

Aulocetus linzianum Van Beneden, 1875 [see Kellogg, 1923a:22–23].

HOLOTYPE.—Cranium missing the entire rostrum; possibly associated atlas and another vertebra (see Kellogg, 1923a:22–23). The tooth and tympanic bulla that were originally included in the type material by von Meyer (1849) were later removed from it (von Meyer, 1850:202; Kellogg, 1923a:22–23); they were thought by Van Beneden (1865) to belong to a squalodont and subsequently were referred to “*Squalodon*” *ehrlichii* by Brandt (1873, 1874). Oberösterreichisches Landesmuseum, Linz/Donau, Austria.

TYPE LOCALITY.—The holotype was found in the Sandgrube Bauernberg near Linz, Austria (Rothausen, 1971:140).

FORMATION AND AGE.—Linz Sands, upper Chattian, uppermost Oligocene, nannoplankton zone NP25 (Rabeder and Steininger, 1975:177).

EMENDED DIAGNOSIS.—A relatively small mysticete probably not exceeding 5 m; supraoccipital with well-developed medial crest on anterior half and deep, basin-like depression in posterior half; apex narrow and acute. Crest lying below level of adjacent lambdoidal crests in medial trough extending from depressed center of supraoccipital anteriorly almost to apex; apex elevated slightly above posterior portion of supraoccipital (Figure 16B). In posterior view, vertex of braincase strongly depressed below lambdoidal crests (Kellogg, 1928:187); lambdoidal crests prominently developed and overhanging temporal

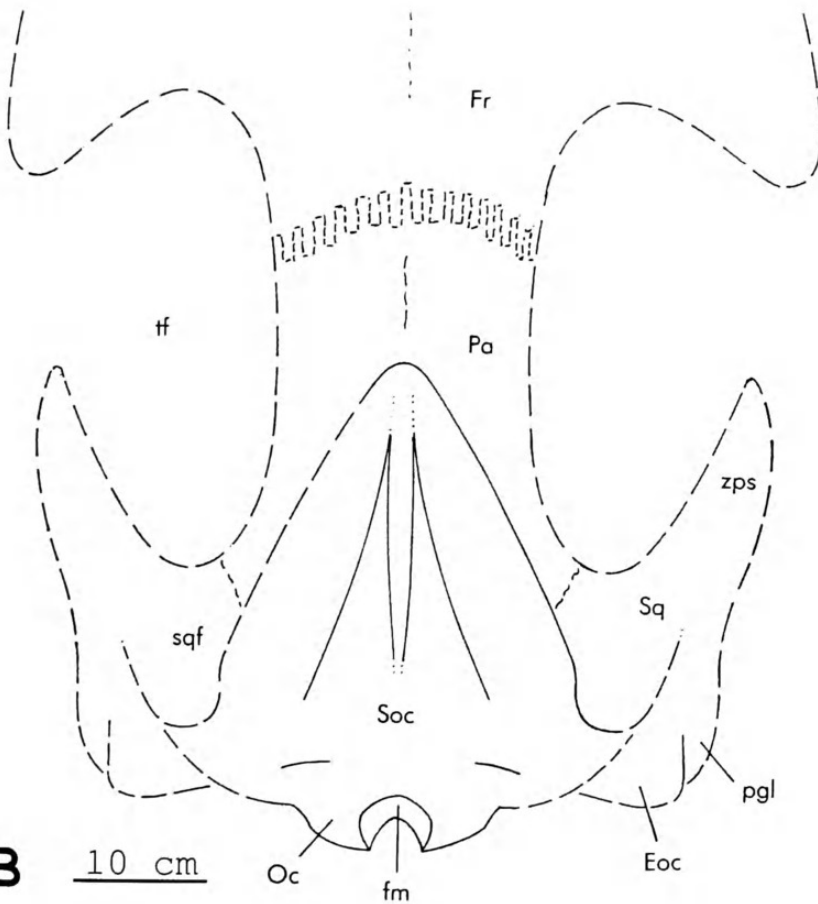
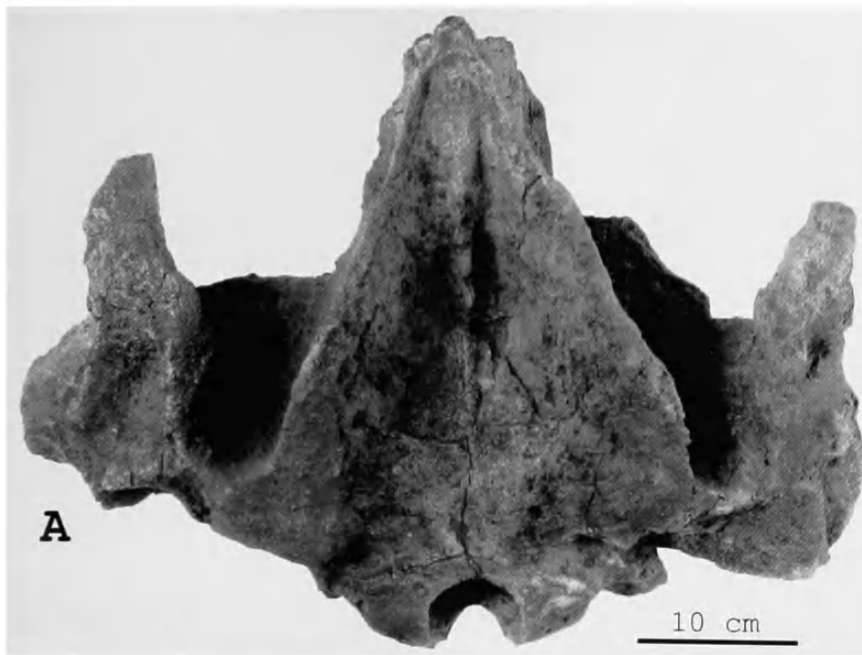


FIGURE 15.—*Cetotheriopsis lintianus* (von Meyer, 1849): A, holotype braincase, dorsal view (Oberösterreichisches Landesmuseum photograph by B. Ecker); B, reconstruction. (Dashed lines indicate hypothetical configurations; abbreviations are explained in "Material and Methods.")

fossae. Exoccipitals broadly rounded and sloping posteroventrally from posterior margin of squamosal fossae, but outer margins too badly eroded to permit reliable transverse measurement. Occipital condyles massive and with dorsal margins situated well below level of floors of squamosal fossae; squamosal fossae elongate and deeply excavated. Zygomatic pro-

cesses of squamosal roughly parallel to axis of skull midline and not conspicuously directed outward.

REMARKS.—The holotype skull is so badly eroded in the squamosal and exoccipital regions that it is difficult to determine their details. The ventral side of the skull (Figure 16A) has not been prepared, and virtually the entire basicranium is

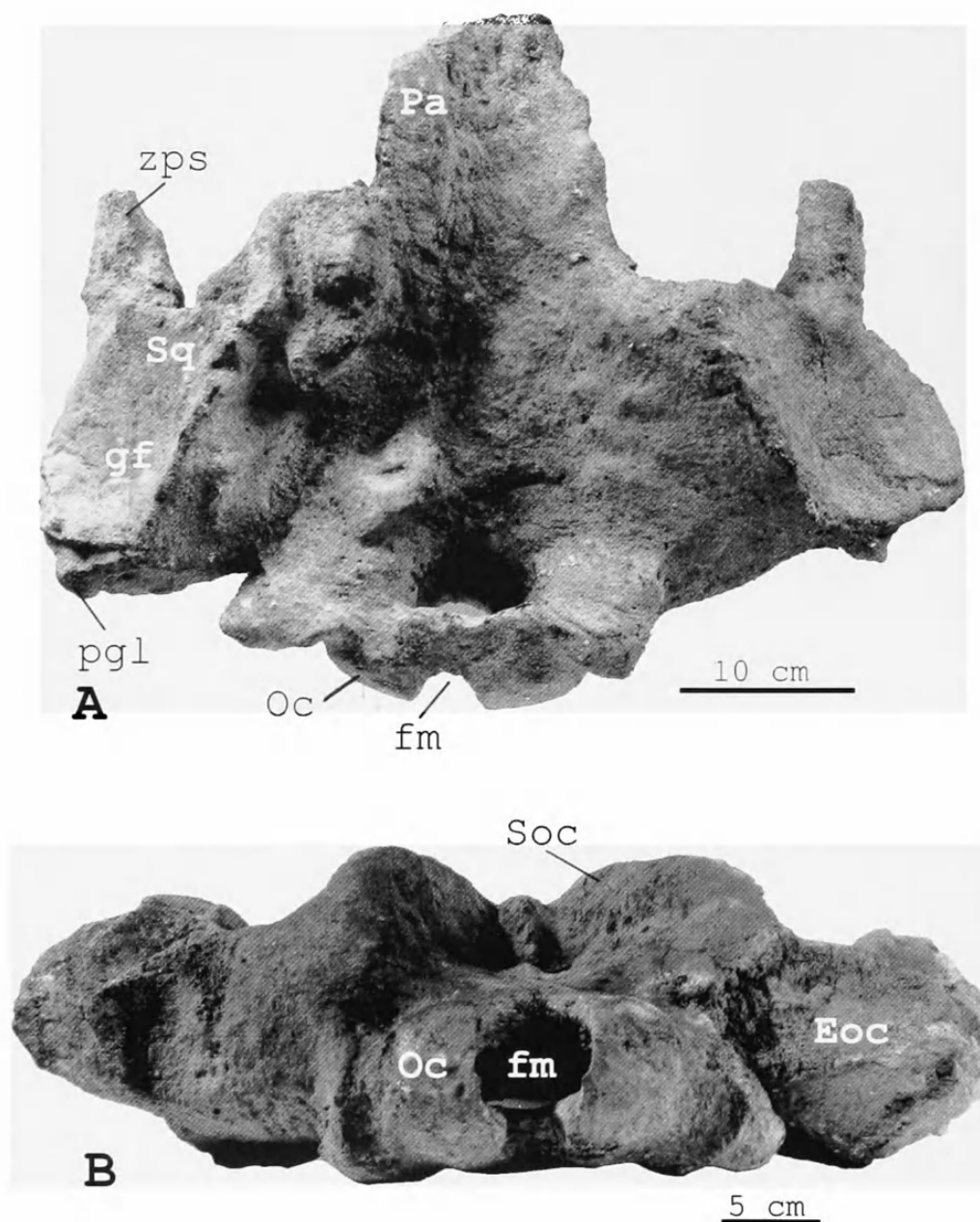
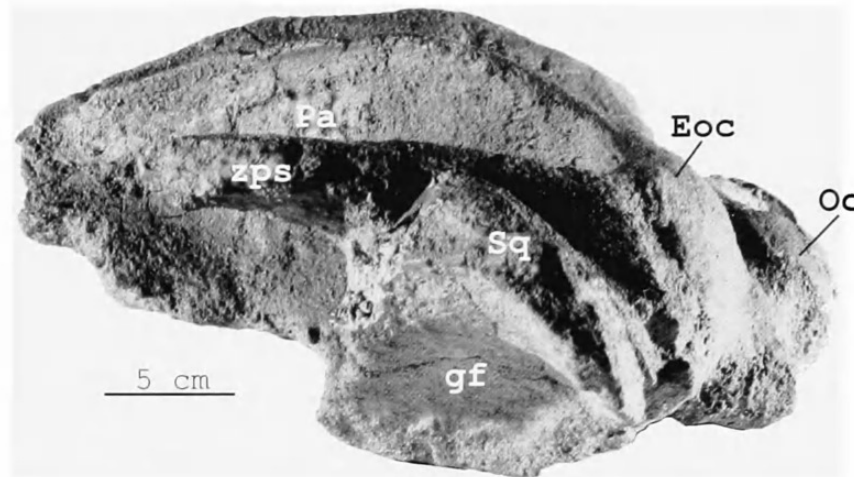


FIGURE 16.—*Cetotheriopsis lintianus* (von Meyer, 1849), holotype braincase: A, ventral view; B, posterior view (Oberösterreichisches Landesmuseum photographs by B. Ecker). (Abbreviations are explained in “Material and Methods.”)

missing. The specimen is covered with fine quartz sand grains like those that have long hindered studies of the odontocetes *Patriocetus ehrlichi* (Van Beneden, 1865) and *Agriocetus incertus* (Brandt, 1874), also from the Linz Sands. Kellogg (1928:187) noted that this species has “elongate zygomatic processes, that do not reach forward to the level of the apex of the supraoccipital shield.” These processes are so badly eroded that it is difficult to be certain about their original length, but in view of the greatly elongated supraoccipital and relative length of the zygomatic processes in *Eomysticetus* (Sanders and Barnes, 2002), it seems highly unlikely that the zygomata of *C. lintianus* extended beyond the apex of the supraoccipital, if in

fact they even reached that point. Probably through deformation by the weight of overlying sediments, the left squamosal has been twisted out of its proper orientation, the lateral face having been turned upward into the dorsal plane of the skull, thus causing the glenoid fossa to be abnormally visible in lateral aspect (Figure 17). In our reconstruction of this specimen (Figure 15B), we have followed the orientation suggested by the right squamosal and the remains of its zygomatic process; the form and lateral angle of the left squamosal in the actual specimen and the reconstruction are therefore noticeably different (Figure 15A,B). Our reconstruction of the portion of the skull anterior to the apex of the supraoccipital is based upon

FIGURE 17.—*Cetotheropsis lintianus* (von Meyer, 1849), holotype braincase, left lateral view (Oberösterreichisches Landesmuseum photograph by B. Ecker).



features manifested in the holotype cranium of the archaic mysticete *Eomyticetus whitmorei* (Sanders and Barnes, 2002), which has an elongate intertemporal region and a supraoccipital thrust strongly forward like that of *C. lintianus*.

Discussion

Until recently, *Micromysticetus tobieni* (Rothausen, 1971), from lower Chattian beds near Dusseldorf, Germany (Figures 3–6), and *Cetotheriopsis lintianus* (von Meyer, 1849), from uppermost Oligocene sands at Linz, Austria (Figures 15–17), represented the only toothless baleen-bearing, fossil mysticete specimens reported from Oligocene beds in the Northern Hemisphere. Despite the absence of rostra on these specimens, they have been accepted as true, baleen-bearing mysticetes and have been classified in the family Cetotheriidae Brandt, 1872. The family Cetotheriidae differs from the families Balaenopteridae, Eschrichtiidae, and Balaenidae by having a skull with an elongate intertemporal region formed by the parietals and a gradual lateral slope from the cranial vertex to the dorsal surface of the supraorbital process. The laterally projecting zygomatic processes in all three of the species of the subfamily Cetotheriopsinae discussed herein suggests the presence in each of a wide supraorbital process and a broad rostrum consistent with the development of baleen and the filter-feeding method used by the true mysticetes. In view of the elongate intertemporal region in all four specimens, their assignment to the family Cetotheriidae corresponds with previous classifications of such animals and is supported by our present, although somewhat limited, knowledge of the group.

A comparison of the measurements of the holotype skulls of *Micromysticetus tobieni* and *Cetotheriopsis lintianus* with those of *Micromysticetus rothauseni* (Table 2) reveals three principal points about these three species. First, *Micromysticetus tobieni* and *Micromysticetus rothauseni* are approximately comparable in size, *M. tobieni* being slightly larger, and both are smaller than the holotype of *Cetotheriopsis lintianus*. Second, the skull of *C. lintianus* is the largest of all three of the ho-

lotypes. Third, and most important, the anteroposterior lengths of the supraoccipitals separate the three specimens into two sets, one in which the supraoccipital is narrow and greatly elongated (*C. lintianus*) and the other in which it is considerably shorter anteroposteriorly (*M. tobieni* and *M. rothauseni*).

The set of curves in Figure 18 graphically demonstrates the morphometric separation between the two groups of speci-

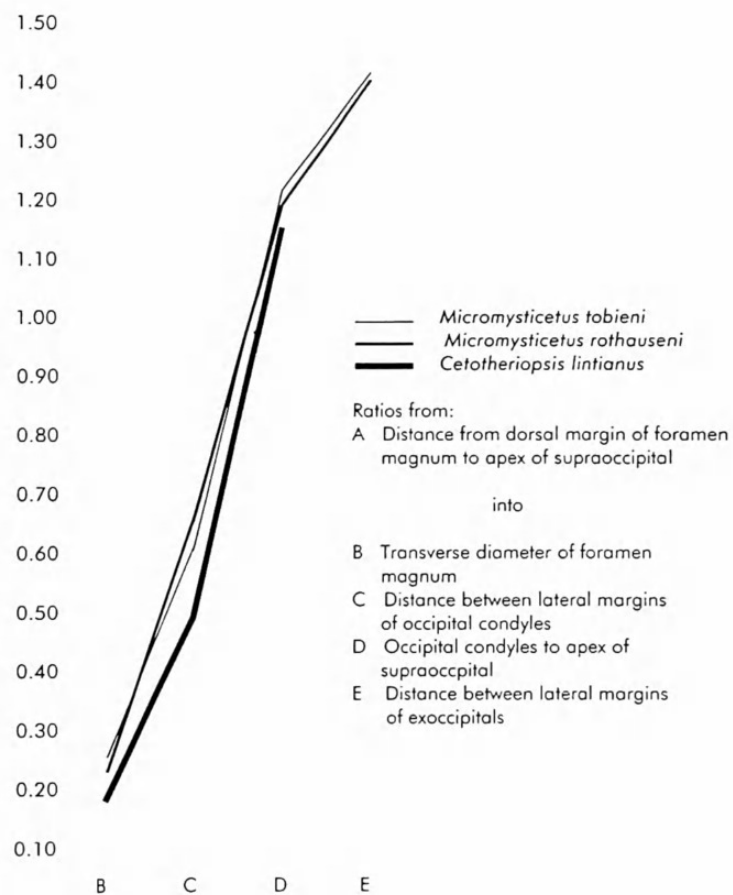


FIGURE 18.—Morphometric comparison of the holotype crania of *Micromysticetus tobieni* (Rothausen, 1971), *Micromysticetus rothauseni*, new genus and new species, and *Cetotheriopsis lintianus* (von Meyer, 1849), using ratios derived from five selected cranial measurements.

TABLE 2.—Measurements (in mm) of the holotype (ChM PV4844) and paratype (ChM PV5933) skulls of *Micromysticetus rothauseni*, n. gen. n. sp., from the late Oligocene of South Carolina, and of the holotype skulls of *Micromysticetus tobieni* (Rothausen) (JGU P1289) and *Cetotheriopsis lintianus* (von Meyer) from the late Oligocene of Europe. Except as noted below, measurements of *M. tobieni* and *C. lintianus* are from Rothausen (1971, table 1). (Measurements in parentheses are estimates; * = measurement from cast of *Micromysticetus tobieni*; † = measurement from holotype of *Cetotheriopsis lintianus*; — = no data.)

Character	<i>M. rothauseni</i> (holotype)	<i>M. rothauseni</i> (paratype)	<i>M. tobieni</i> (P1289)	<i>C. lintianus</i>
Occipital condyles to plane of anteriormost end of specimen, as preserved	256.4	214.2	267	340
Dorsal edge of foramen magnum to apex of supraoccipital	182.5	(156)	199	287†
Occipital condyles to apex of supraoccipital	224.5	200.2	247	325
Occipital condyles to posterior end of vomer	—	—	110	—
Greatest width across zygomatic processes of squamosals	(398)	(370)	403	505
Distance between lateral margins of exoccipitals	256.6	(230)	278*	—
Distance between lateral margins of occipital condyles	124.4	115	126*	145
Greatest distance between lateral margins of basioccipital processes (Alae Basioccipitalis in Rothausen, 1971)	94.7	—	116	—
Transverse diameter of foramen magnum	44.4	(43)	54	55.5†
Vertical diameter of foramen magnum	36.3	—	45	41†
Vertical diameter of right occipital condyle	67	(54)	78.5*	84†
Greatest transverse diameter of right occipital condyle	41	(37)	49*	55†
Distance from inner margin of right occipital condyle to outer edge of right exoccipital	109.6	(97)	112	—
Maximum length of left zygomatic process, extremity of postglenoid process to anterior end of zygoma	192	—	—	—
Width of temporal fossa	122	(103)	—	—
Greatest internal height of braincase at midline	82	(70)	—	—

mens. To obtain these ratios, we divided measurement A, the distance from the dorsal margin of the foramen magnum to the apex of the supraoccipital, into four other measurements: B, the transverse diameter of the foramen magnum; C, the distance between the lateral margins of the occipital condyles; D, the distance from the occipital condyles to the apex of the supraoccipital; and E, the distance between the lateral margins of the exoccipitals. Although poor preservation prevents the taking of measurement E in the holotype of *Cetotheriopsis lintianus*, measurements of B, C, and D place the curve for that species well away from those for *Micromysticetus tobieni* and *Micromysticetus rothauseni*.

Although *M. rothauseni* and *M. tobieni* are similar in general appearance, there is considerable difference in the shape of the basioccipital crests in these two specimens. In *M. tobieni* the basioccipital crests have rounded margins, whereas in *M. rothauseni* the margins of these processes are decidedly angular, their inner margins paralleling each other before breaking into divergent angles that terminate in narrow, rounded points posteriorly. *Micromysticetus rothauseni* thus represents a species that is distinct from *M. tobieni*, but the variability between other species in polytypic mysticete genera and particularly the presence of squamosal prominences in both forms support their referral to the same genus.

Conclusions

Two mysticete braincases without rostra, from the late Oligocene Ashley Formation (lower Chattian) near Charleston,

South Carolina, represent a new genus and new species herein named *Micromysticetus rothauseni*. *Micromysticetus rothauseni* is distinct from the European *Cetotheriopsis tobieni* at the specific level, but the presence of a previously unrecognized character uniting these two species requires that *C. tobieni* be reassigned to the new genus *Micromysticetus*.

Micromysticetus tobieni (Rothausen, 1971) and *M. rothauseni* differ from *Cetotheriopsis lintianus* (von Meyer, 1849) principally in having an anteroposteriorly shorter supraoccipital, the apex of which terminates behind the anteriormost extent of the zygomatic process of the squamosal. That feature is in contrast with the condition in the skull of *C. lintianus*, in which the apex of the supraoccipital seems almost certainly to have reached the level of the anterior tip of the zygoma. *Micromysticetus* also is characterized by the presence of a knob-like eminence (the squamosal prominence) on the squamosal. Both genera are classified in the family Cetotheriidae.

Micromysticetus rothauseni constitutes the oldest western North Atlantic records of the family Cetotheriidae; previous specimens of cetotheres from this region were found in Miocene sediments (Kellogg, 1924, 1965, 1968a–c, 1969). It further documents that this genus of cetotheriids was present on both sides of the North Atlantic during late Oligocene time. In their archaeocete-like morphologies, the periotic and axis vertebra of *Micromysticetus rothauseni* greatly resemble those structures in the Eocene archaeocete *Zygorhiza kochii* (Reichenbach, 1847), lending further support to the idea that the ancestry of the suborder Mysticeti is tied to the subfamily Dorudontinae of the archaeocete family Basilosauridae.

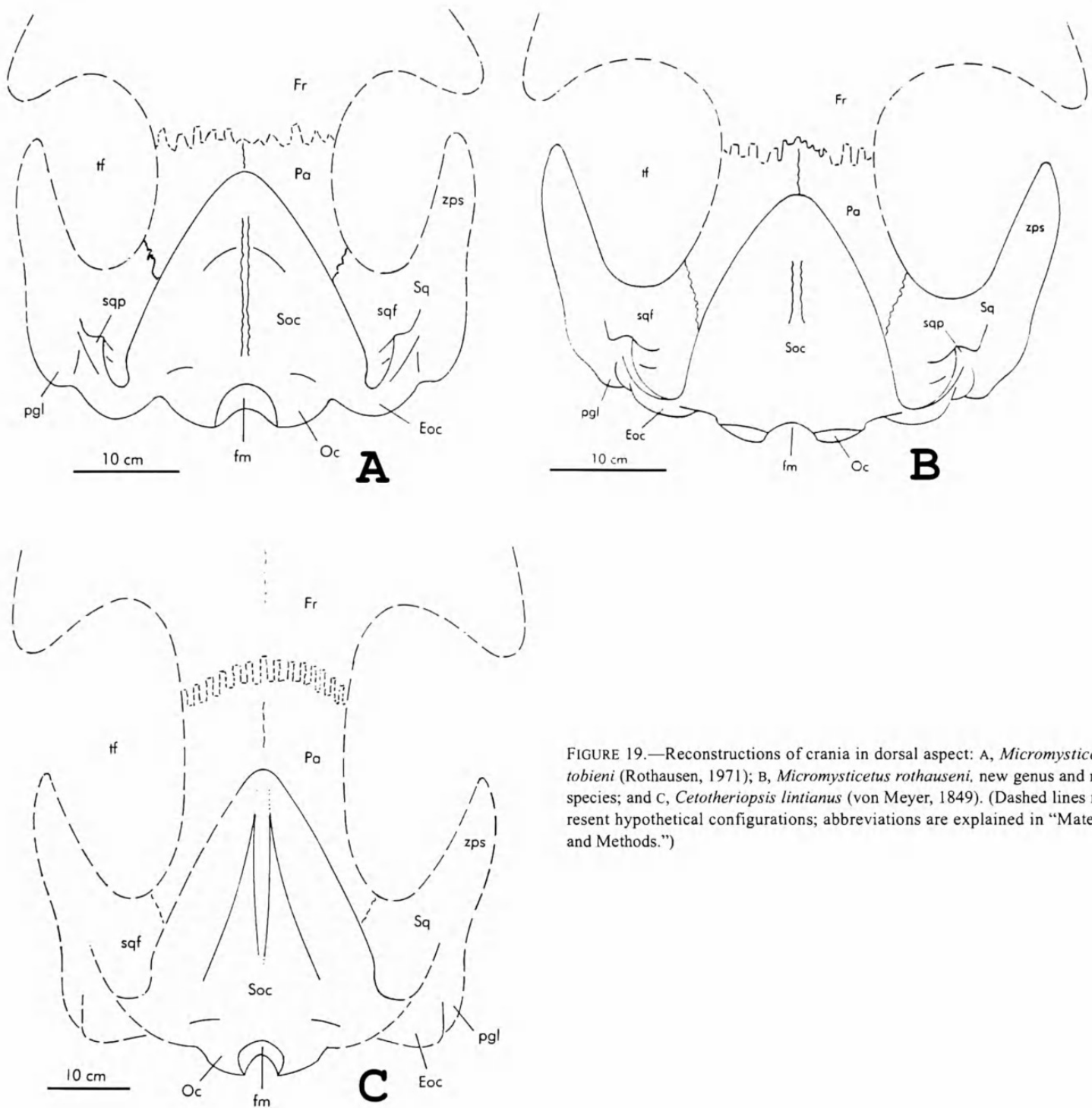


FIGURE 19.—Reconstructions of crania in dorsal aspect: A, *Micromysticetus tobieni* (Rothausen, 1971); B, *Micromysticetus rothauseni*, new genus and new species; and C, *Cetotheriopsis lintianus* (von Meyer, 1849). (Dashed lines represent hypothetical configurations; abbreviations are explained in "Material and Methods.")

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