

CALIFORNIA STATE UNIVERSITY NORTHRIDGE

A NEW MIOCENE CETOTHERE (MAMMALIA: CETACEA)
FROM THE MONTEREY FORMATION AT LAGUNA NIGUEL,
ORANGE COUNTY, CALIFORNIA

A thesis submitted in partial fulfillment of the requirements
For the degree of Master of Science
in Geology

By

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DEDICATION

This thesis is affectionately dedicated to my high-school chum

Preston Timothy Landry

...Who I'm sure would not believe a word of it...

And with deepest admiration to my spiritual mentor

Ray Douglas Bradbury

...Whom I suspect would believe most of it.

EPIGRAPH

When I stand among these mighty Leviathan skeletons, skulls, tusks, jaws, ribs, and vertebrae, all characterized by partial resemblances to the existing breeds of sea-monsters; but at the same time bearing on the other hand similar affinities to the annihilated antichronical Leviathans, their incalculable seniors; I am, by a flood, borne back to that wondrous period, ere time itself can be said to have begun....when wedged bastions of ice pressed hard upon what are now the Tropics....Then the whole world was the whale's; and, king of creation, he left his wake along the present lines of the Andes and the Himmalehs. Who can show a pedigree like Leviathan?

From The Fossil Whale (MOBY DICK, Chapter CIV)

By Herman Melville

1851

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INSTITUTIONAL ABBREVIATIONS AND ACRONYMS

CSUN - California State University Northridge

CSULB - California State University Long Beach

GMU - George Mason University, Fairfax, Virginia

LAB - Los Angeles Basin

LACM - Natural History Museum of Los Angeles County

MNB - Museum für Naturkunde, Berlin

MNHN - Muséum National d'Histoire Naturelle, Paris

NALMA - North American Land Mammal Age

NAU - Northern Arizona University, Flagstaff

NMV - Museum Victoria, Melbourne, Australia

RMW - Raschke, Morgan and Weir PaleoAssociates, Los Angeles

SDSNH - San Diego Society of Natural History

SFSU - San Francisco State University, San Francisco

USNM - National Museum of Natural History, Smithsonian Institution

VMNH - Virginia Museum of Natural History

ABSTRACT

A NEW MIOCENE CETOTHERE (MAMMALIA: CETACEA)
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By

Matthew Phillip Ventimiglia

Master of Science in Geology

Phylogenetic relationships among the fossil and living "whalebone" (baleen) whales remain poorly understood. Until recently, the extinct family Cetotheriidae, a former grade taxon of edentulous (toothless) whales of the suborder Mysticeti, was thought to be the evolutionary source of the modern-baleen whales, which include the families Balaenopteridae, Balaenidae, Neobalaenidae, and Eschrichtiidae. Following attempts to identify the most valid "cetotheres" to justifiably include in a strict family clade, the taxon is recognized as a derived group with uncertain relationships to modern taxa. The monophyly of the order Cetacea, suborder Mysticeti, and clade comprised of all edentulous baleen-bearing mysticetes is, nevertheless, assumed to be valid. Fossil baleen-bearing mysticetes commonly exhibit a mosaic of primitive and derived characters, hinting at transitional forms that link them to ancestors among more basal-toothed mysticetes. Furthermore, the toothed mysticetes show affinities with the archaeocetes, the third and most primitive suborder of the cetaceans. The evolutionary chronology of the mysticetes is not transparently linear, but branches stepwise, in radiative spurts. Relict groups commonly survived alongside groups with more derived characters. This thesis involved the preparation and description of a fossil cranium belonging to a new species of cetotherine assigned to the genus *Mixocetus*. The specimen is of late Miocene age and is from the Monterey Formation at Orange County, southern California. The fossil whale is here placed in evolutionary context within the family Cetotheriidae *sensu stricto* (in the strict sense) and suborder Mysticeti.

INTRODUCTION

The baleen “whalebone” whales (order Cetacea, suborder Mysticeti) of both extinct and extant families have dimly understood relationships owing to an incomplete fossil record. The characters that define fossil taxa are subjective, leading to disagreements in classification. Recent fossil finds have started to fill in the branches of the mysticete phylogenetic tree, although transitional fossils are, in some cases, controversially interpreted. The purposes of this study are to 1) review the paleogeography and geologic setting of the site (**Figure 1**) where the fossil bones of a late Miocene baleen-bearing whale (LACM 147795) were found, 2) undertake preparation work on the cranium of this fossil, 3) provide the first formal description of the whale and compare it with related taxa, and 4) provide a general summary of the fossil whale's evolutionary history and

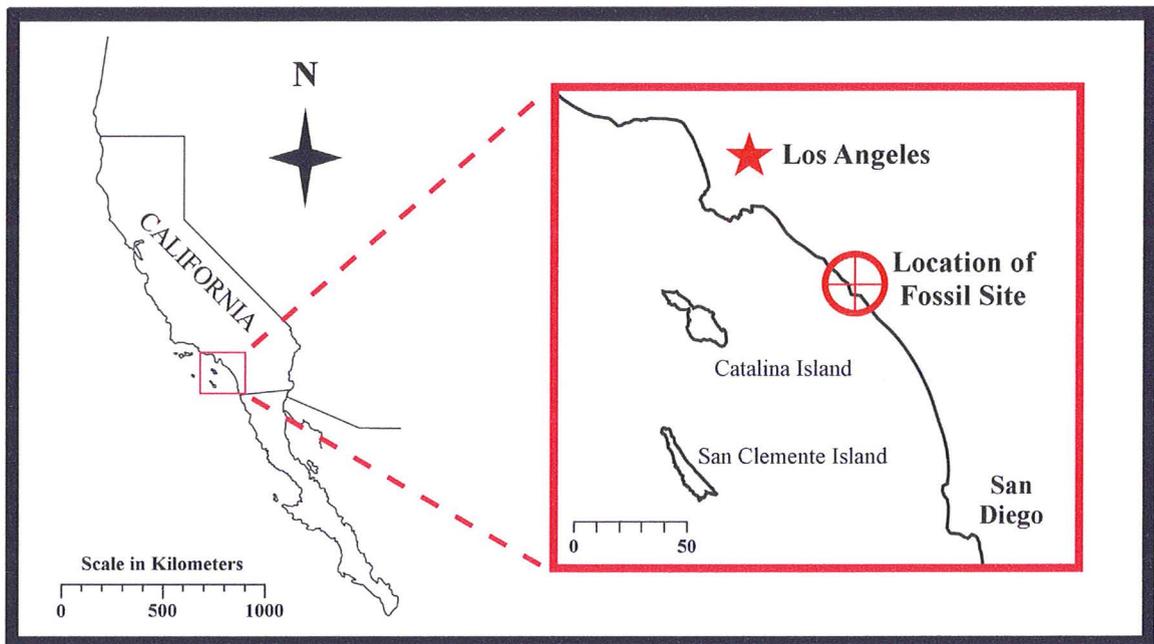


Figure 1. Index map of California showing recovery site of LACM 147795, *Mixocetus* n. sp. in Orange County, less than 7 km north of Dana Point.

phylogenetic placement within the mysticete suborder in relation to both extinct and extant families.

The fossil whale LACM 147795 was recovered from the Monterey Formation in the vicinity of Laguna Niguel, California. The whale is a member of the extinct family Cetotheriidae Brandt, 1872, a former grade taxon recently reorganized by Bouetel and Muizon (2006) into a clade consisting of six genera. Working independently, Whitmore and Barnes (2008) developed a different classification that recognized two subfamilies, Cetotheriinae (consisting of eight genera) and Herpecetinae (consisting of two genera). The fossil cranium LACM 147795 exhibits affinities with the genus *Mixocetus* Kellogg, 1934b, formerly a monotypic taxon represented by *Mixocetus elysius* Kellogg, 1934b (LACM specimen 882), which was discovered in the Lincoln Heights area of Los Angeles, southern California.

MATERIALS AND METHODS

The fossil cranium of *Mixocetus* n. sp., photographs and drawings of related taxa, and other reference materials, were provided by Dr. Lawrence G. Barnes of LACM. The recovered fossil material originally included a partially damaged cranium, mandibles, vertebrae, and ribs, but only the cranium was available for study. Preparation work on dorsal surface of the cranium was done previously by Howell Thomas of LACM. Following this preparation work, the dorsal surface was molded and cast. The exposed dorsal surface was then covered with tissue and newspaper and re-jacketed in burlap cloth reinforced with plaster for safe-keeping during storage.

The jacket was reopened in June of 2009, ventral-side up, to begin preparation of the ventral surface at LACM. This work was performed by me and Tetsuya Sato, a volunteer at LACM. Each worker put in approximately 300 hours of preparation time. The initial matrix removal involved hand tools, such as inch-wide putty knives, smaller palate knives, and some dental tools. Resistant limestone lenses and concretionary layers were removed with electric rotary tools fitted with abrasive stone grinding wheels and diamond burr grinder/cutters. Solutions of acrylic dissolved in acetone ("acryloid") and, less commonly, of white water-soluble glue, were used to stabilize the fragile fossil bone. Photographs were taken to document preparation progress, fossil content of the matrix, and to provide templates for reconstruction drawings initially traced by hand and later modified using "Adobe Illustrator" software. Thin sections of representative samples of matrix were made by R. A. Petrographic (Los Angeles) for petrographic microscope analysis.

Strewn slides, made by pipetting a small amount of matrix material onto a glass

cover slip sandwiched to a slide coated with high-resolution mounting medium, were prepared by Dr. Lisa D. White of SFSU. The material examined was the lightest fraction resulting from a standard acid-bath treatment of hydrogen peroxide and hydrochloric acid, thereby breaking down the organic material and eliminating the carbonate. A centrifuge was used to isolate the lightest fraction. Microfossil identifications were made using a Zeiss Axioskop light microscope at 400X. The purposes of the microfossil work were to refine the geologic age of the fossil setting and estimate its paleobathymetry.

The terminology used for general anatomy of cetacean crania is derived from Mead & Fordyce (2009). Photographs from True (1904) were used for comparison with recent-mysticete crania. The Conventions for anatomical abbreviations are derived from Fordyce (2002a) and Barnes (2008) and listed in **Table 1**. Extent of the rostrum and braincase are indicated in the reference drawing (Kellogg, 1934b) of *Mixocetus elysius* (**Figure 2**). The "rostrum" is defined as the portion of the cranium anterior to the antorbital notch. The "braincase" is defined as the portion posterior to the antorbital notch. The "lambdoid crest" is defined as the crest of the lateral boundary of the occipital shield in dorsal view.

Table 1: Anatomical abbreviations

<i>aon</i>	antorbital notch
<i>apmx</i>	ascending process of maxilla
<i>appmx</i>	ascending process of premaxilla
<i>Boc</i>	basioccipital
<i>bc</i>	basioccipital crest
<i>ch</i>	choanae
<i>Eoc</i>	exoccipital
<i>fm</i>	foramen magnum
<i>fo</i>	foramen ovale
<i>fpo</i>	foramen pseudovale
<i>Fr</i>	frontal
<i>iop</i>	infra-orbital plate of maxilla
<i>Max</i>	maxilla
<i>mea</i>	external auditory meatus
<i>Na</i>	nasal
<i>occ</i>	occipital condyle
<i>Pa</i>	parietal
<i>Pal</i>	palatine
<i>pop</i>	paroccipital process of the occipital
<i>pgl</i>	postglenoid process of squamosal
<i>Pmx</i>	premaxilla
<i>popf</i>	postorbital process of frontal
<i>ppr</i>	posterior process of the periotic
<i>propf</i>	preorbital process of frontal
<i>propmx</i>	preorbital process of maxilla
<i>Pt</i>	pterygoid
<i>pts</i>	pterygoid sinus
<i>Soc</i>	supraoccipital
<i>sop</i>	supraorbital process of frontal
<i>Sq</i>	squamosal
<i>su</i>	sulci of baleen vascular system
<i>stf</i>	sternomastoid fossa
<i>Tb</i>	tympanic bulla
<i>tf</i>	temporal fossa
<i>Vo</i>	vomer
<i>zps</i>	zygomatic process of squamosal

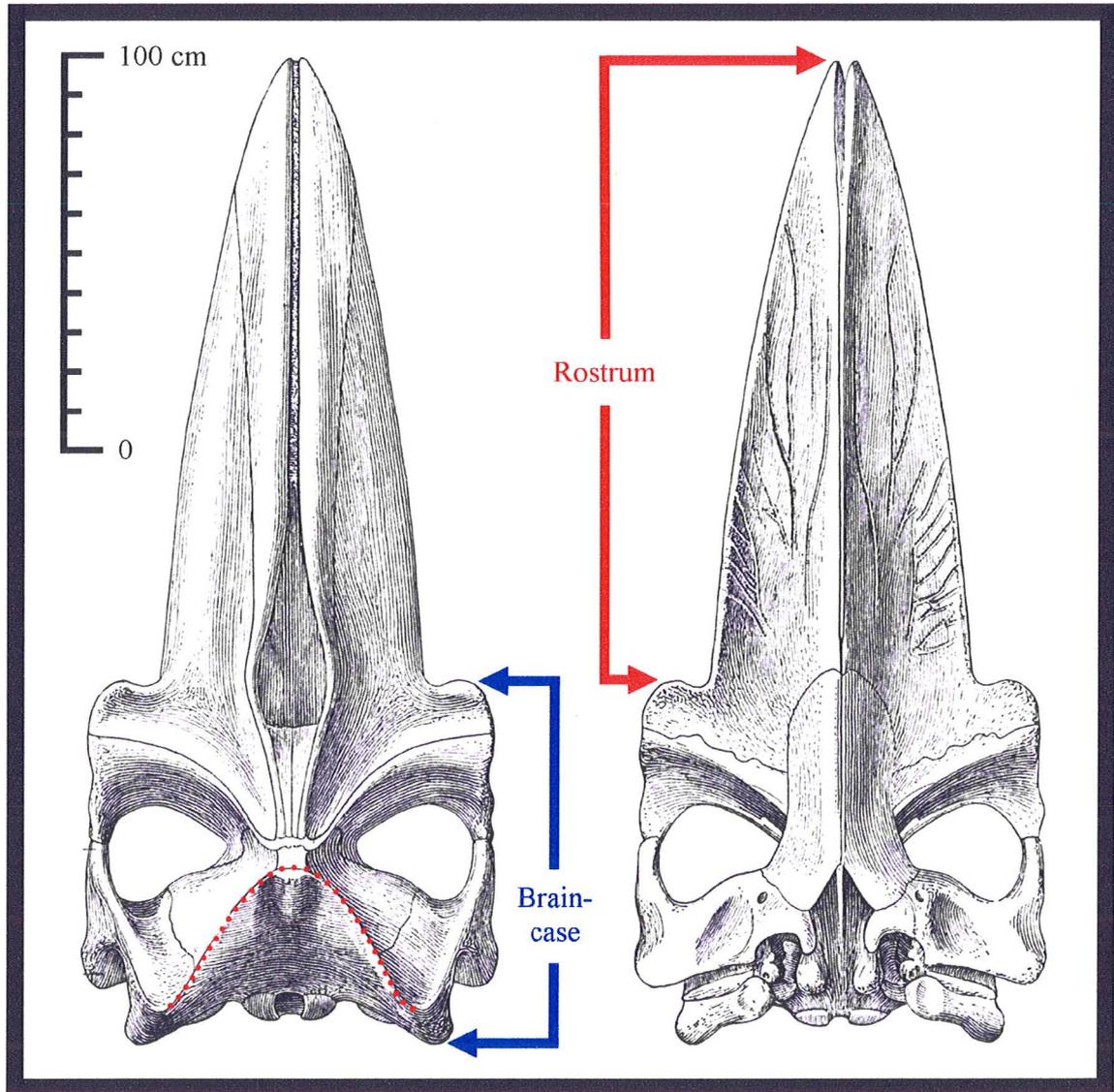


Figure 2. Holotype cranium LACM 882 *Mixocetus elysius*. (Modified from Kellogg, 1934b). The rostrum is defined as the portion from the anterior end of the premaxillae to the antorbital notch. The braincase extends from the antorbital notch to the exoccipital. The lambdoid crest is indicated by the red dotted curve.

GEOLOGIC SETTING

The fossil remains of *Mixocetus* n. sp. were found on July 11, 1989, by Juanita Shinn, a geologist working for the paleo-mitigation company, RMW PaleoAssociates. The discovery was made at a shopping center site being developed immediately east of the "Autonetics plant" (aka, the "Ziggurat," LACM site locality 6906) in the Laguna Niguel area of Orange County, southeast of Los Angeles, California. Field notes by Shinn and Cara Burrus of RMW described the geologic horizon in which *Mixocetus*. n. sp. was preserved as part of the marine Monterey Formation, "diatomaceous earth with brown silt and medium grained sand," deposited during the middle to late Miocene and correlated to the Clarendonian NALMA. The Clarendonian is named for the city of Clarendon in Donley County, Texas, where a rich assemblage of fossil land mammals is found (Wood and Clark, 1941). Plotting field note coordinates on a geologic map (**Figure 3**) confirm placement of *Mixocetus*. n. sp. in the Monterey Formation "shale units" (Vedder et al., 1957). The map legend of Vedder (1957) describes units of Monterey shale in this location as light-gray to gray-brown siliceous shale and siltstone with some limy beds, coquina locally present near the base, thin andesitic tuffs locally present, with interbedded sandstone, breccia, or conglomerate lenses. A generalized stratigraphic column for the San Joaquin Hills is provided in **Figure 4**.

The Monterey Formation of Orange County was deposited in a structural 'pull-apart' deltid basin created by the initiation of both sinistral and dextral displacement and clockwise rotation of rigid land blocks caught between the left-lateral movements of the incipient San Andreas transform fault zone. This same rotation created the Santa Monica Mountains and Channel Islands, both of which began to assume their east-west

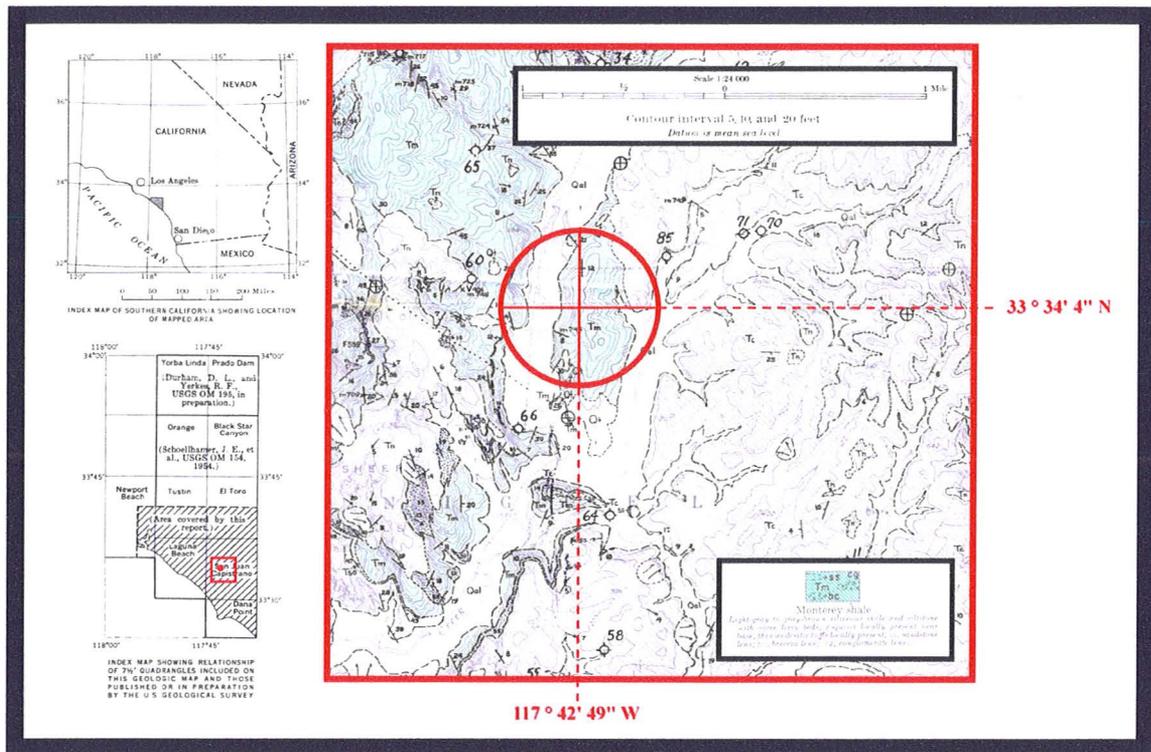


Figure 3. Portion of a geologic map depicting the San Joaquin Hills, San Juan Capistrano Area, in Orange County, California. (Modified from Vedder et al., 1957). Location of fossil site is indicated by red cross-hair circle as determined by Juanita Shinn's field note coordinates.

orientation by the middle to late Miocene (Luyendyk and Hornafius, 1987; Luyendyk, 1991). One of the 'pull-apart' depressions became the LAB. Orange County, including the region of the San Joaquin hills, is considered the southeastern landward part of the LAB. Supporting evidence for this rotation comes from paleomagnetic studies (Kamerling and Luyendyk, 1979) and the distribution of Mesozoic-sourced alluvial remnants, such as those that accumulated in the Eocene Poway fan, later transported to the vicinity of San Miguel Island (Fritsche and Behl, 2008) (**Figure 5**).

During the middle Miocene, a great incursion of marine water, associated with further development of the LAB deepening under sediment loading and the weight of the

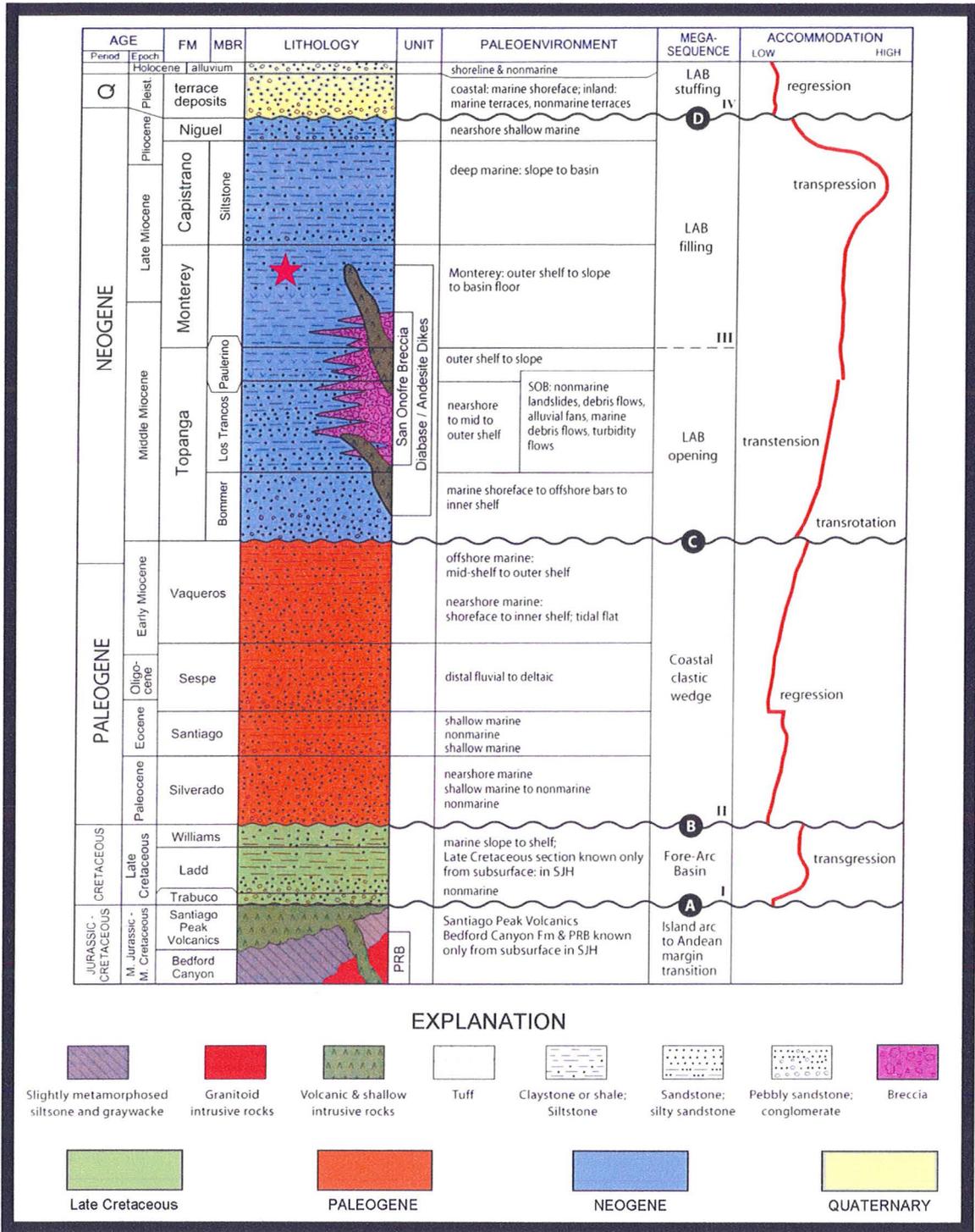


Figure 4. Generalized stratigraphic column in the San Joaquin Hills area showing formations, members, paleoenvironments, megasequences (I-IV) boundaries (A,B,C,D), and accommodation curve as it relates to the development of the LAB. (Modified from Fritsche and Behl, 2008; originally adapted from Vedder, 1979). Star indicates horizon of *Mixocetus* n. sp. at fossil site.

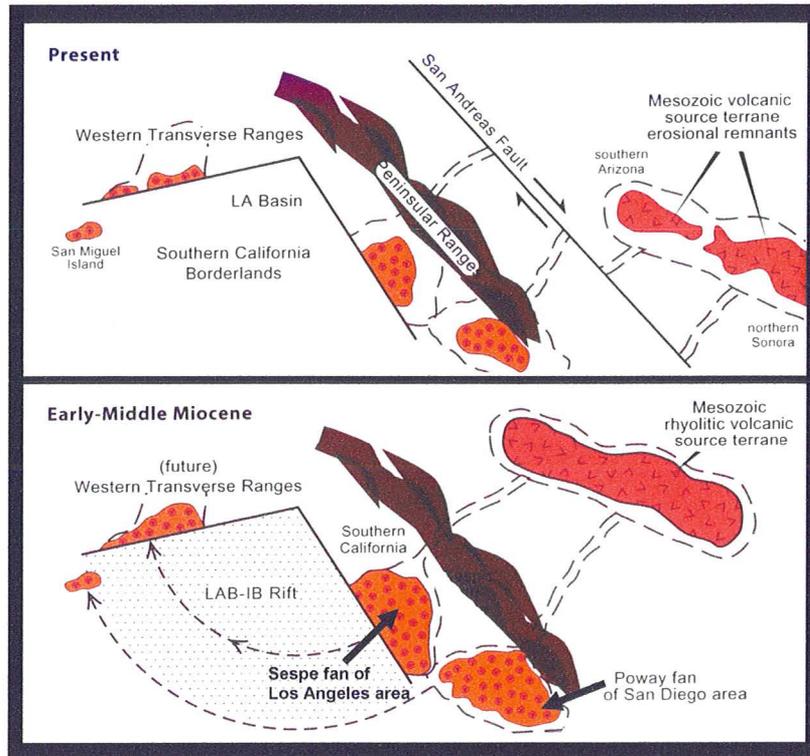


Figure 5. Rotational and transtensional formation of the LAB. (Modified from, Fritsche and Behl, 2008). Note transport pathway of Poway fan material from the mainland to San Miguel Island.

intruding sea, resulted in massive accumulations of the diatomaceous sediments found in the Monterey Formation. White diatomaceous shale cliffs are expressions of the Monterey Formation in the Newport Back Bay location. The paleoenvironment was one of high marine productivity in the photic zone and anoxic conditions in deep water, conducive to the preservation of whale fall carcasses. During the Neogene, the southward-flowing California Current is thought to have controlled upwelling systems along the coast with periods of variable productivity modulated by the paleogeography of the Isthmus of Panama (Barron, 1998). Eustatic sea-level lowstands, associated with glaciations in the north and south during what was otherwise a period of overall diatom-population decline (three-fold following 11.5 Ma and another two-fold following 7.5

Ma), restricted flow due to shoaling through the incipient isthmus. This, in turn, enhanced flow of the California Current and marine productivity in offshore waters during the middle and late Miocene (Barron et al., 2002). The isthmus did not close completely until about 3.5 Ma (Keigwin, 1978; Coates et al., 1992). The fossil remains of *Mixocetus* n. sp. were preserved in the region of the former Capistrano Embayment (Figure 6).

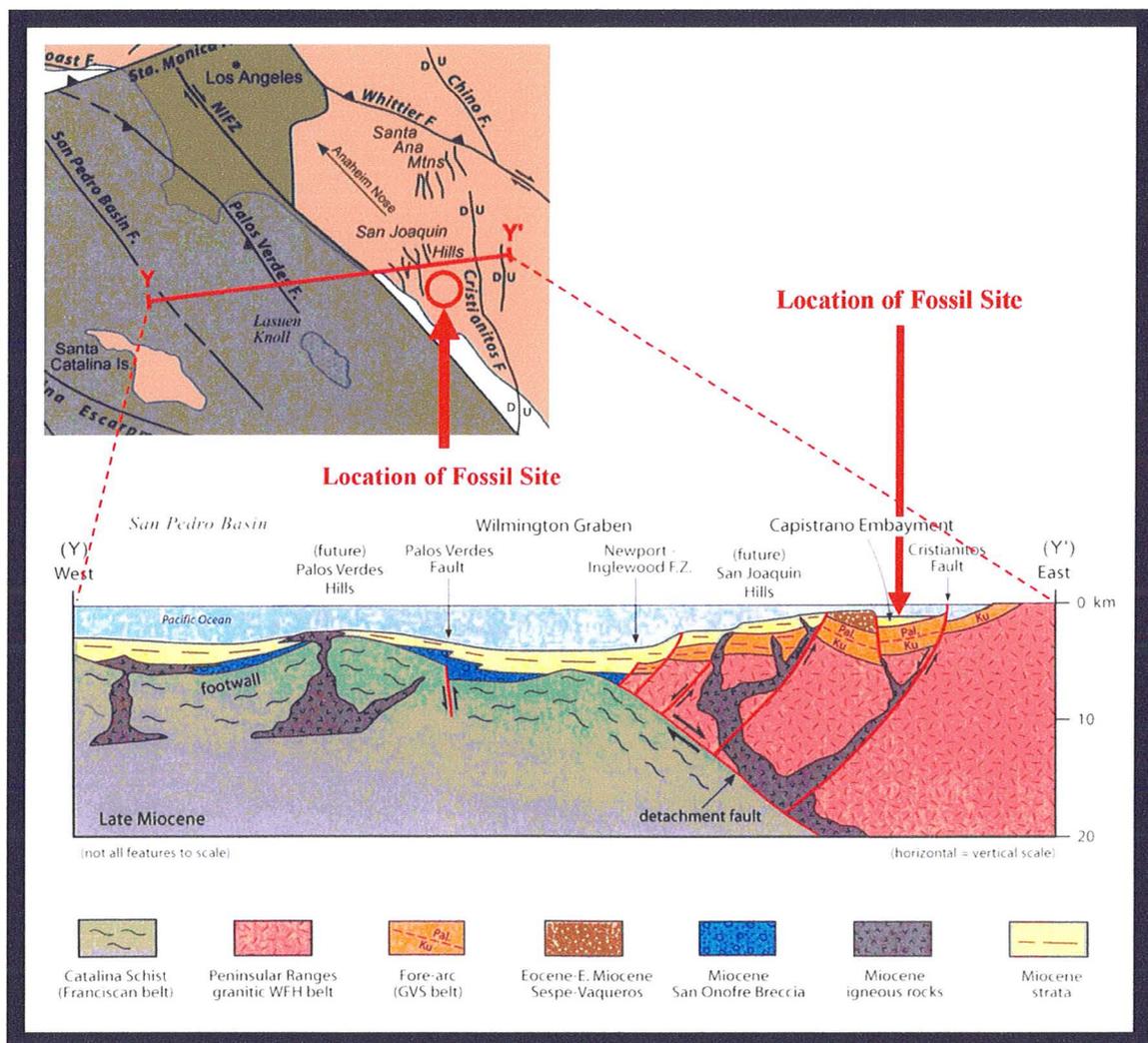


Figure 6. Generalized reconstructed schematic late Miocene cross section. (Modified from Fritsche and Behl, 2008). Section extends from the San Pedro Basin to the future San Joaquin Hills. Fossil recovery site is indicated as shown on the site map and section.

About 6 million years ago to the present, the Baja California Peninsula was transferred to the Pacific Plate, and the bend in the San Andreas Fault, as well as the transpressional phase began (Fritsche and Behl, 2008). The San Joaquin Hills were folded and uplifted, along with many other anticlines and thrust faults in the south basin areas. San Onofre Breccia deposits, which interfinger with the Monterey Formation in these locations, were also uplifted by thrust faulting. This breccia, famously sourced from the Catalina Schist that was unroofed during the earlier extensional phase of basin formation, outcrops in the headland of Dana Point south of the fossil recovery site. For a more complete survey of the geologic history of the region, consult Fritsche and Behl (2008).

During times of lowered-offshore productivity, enclaves of marginally higher diatom blooms occurred closer to shore (Barron et al., 2002). The Capistrano Embayment might have been a feeding ground for baleen whales during this time. Miocene bulk-feeding mysticetes (similar to all baleen-bearing mysticetes today) fed relatively low on the food chain, consuming nekton that thrived on marine microorganisms. Whales are commonly preyed upon by sharks. Bite marks on the bones of fossil whales show clear evidence of predation by giant sharks of the Miocene (Purdy, 1996; Thomas et al., 2008; Ehret et al., 2009). The newly described, large-toothed physterid *Livyatan melvillei* Lambert, Bianucci, Post, Muizon, Salas-Gismondi, Urbina, Reumer, 2010, an extinct Miocene relative of the modern giant sperm whale with the largest biting teeth of any tetrapod in history (including giant Cretaceous crocodylians), might also have preyed on mysticetes (Lambert et al., 2010). Today, even adult blue whales, the largest animal ever to inhabit the Earth, are preyed upon by pods of killer whales (*Orcinus orcas* Linnaeus, 1758) (Slijper, 1958).

TAPHONOMY AND DESCRIPTION OF MATRIX

Fossil remains of *Mixocetus* n. sp. were found in an outcrop with beds trending N-S in strike, and dipping between 8 and 12 degrees to the southeast. The cranium was found dorsal side up, an unusual orientation. The taphonomy of whale falls generally results in a ventral-side-up orientation due to the positive buoyancy of decompositional gases that accumulate in abdominal and throat cavities following death in open water (Fordyce and Barnes, 1994). Shore strandings similar to modern examples are thought to be extremely rare in fossil preservation (Fordyce and Barnes, 1994). In any case, there is no indication that the studied animal died close to shore (see bathymetry results below). It is possible the carcass was rolled onto its ventral side by falling out onto an inclined slope, which caused it to gently roll over. No obvious soft-sediment slump folds were found in the matrix surrounding the cranium. Most of the axial skeleton was missing and no appendicular bones were found.

The bulk lithology surrounding the fossil skull is a friable diatomite, composed of siliceous remains of diatoms in high percentages sufficient for commercial mining (Dr. Lisa White, personal communication). A typical Monterey Formation diatomite ranges from 70-80% silica (opal A composition of diatom frustules), 10-20% detrital components (mostly silt and clay), and up to 10% carbonate (from foraminifera and coccolithophorids) (Chang et al., 1998). Alternating light-and-dark layers (varves) are clearly present and indicate annual to decadal shifts in productivity of the marine environment (**Figure 7**). The prominent rock cleavage along bedding planes permitted easy removal with hand tools. The beds are gently folded around the skull (deformed due to the weight of the carcass) and feature micro-faults, formed after lithification. A few



Figure 7. Fossil matrix cross section showing gently-folded bedding planes, microfaults, and sand-filled trace fossils. Orientation of "stratigraphic up" is down. Small scale bars units in centimeters.

unusual disc-shaped, geode-like voids oriented parallel to bedding planes were found (**Figure 8**). These voids contained radial, drusy, mineralized surfaces that tested negative for calcium carbonate using dilute hydrochloric acid. Extremely hard limy concretionary layers, which tested positive for calcium carbonate, were found in the matrix parallel to bedding planes and, in some cases, directly in contact with the fragile bone of the fossil cranium.

Macrofossil content of the matrix includes small skeletal remains (bony fish) in the form of crania, disarticulated bones, and numerous scales tentatively identified as herring by LACM paleontologist Gary Takeuchi (**Figure 9**). A few trace fossils in the form of sand-filled borrows, likely *Thalassionoides* Seilacher, 1953, a mostly horizontal lattice with vertical access tunnels (Seilacher, 2007) (**Figure 10**), are observed cross-cutting the beds that are otherwise not bioturbated. No coeval bivalves or other colonizing fauna



Figure 8. Hollow, flat, "geode" with friable radial mineralization between bedding planes of matrix. Scale bar units in centimeters.

that are commonly associated elsewhere with whale falls (Squires, et al., 1991) are present. Diatoms in the sample are abundant and well-preserved. Identifiable elements include numerous fragments of bilaterally pennate diatoms, circular or semi-circular "girdle bands" and other mesh-like pieces from disarticulated centric diatoms (**Figures 11-13**), numerous sponge spicules, one near-complete robust radiolarian of unknown species (**Figure 13**), and a pollen grain blown from the western shores of southern California (**Figure 13**). Species found in the sample are typical of a coastal upwelling/high productivity setting overlying a shelf-slope break (Barron, 1985), e.g., the elongate diatom *Denticulopsis dimorpha* (**Figure 11**) and the centric diatom *Thassiosira* sp. (**Figure 12**). Bathymetry based on this assemblage is estimated to be approximately

150-200 m (Maruyama, 2000; Dr. Lisa White, personal communication). The important index taxon *D. dimorpha* (**Figure 11**) constrains the age of the whale- fossil horizon to the North Pacific Diatom Zone NDP 5D, spanning 9.16 to 9.9 Ma (**Figure 14**). This confirms that *Mixocetus* n. sp. is of early late Miocene age and equivalent to the late Clarendonian NALMA as indicated by Woodburne et al. (2004, p. 180, Figure 6.2) and Haq (2007).

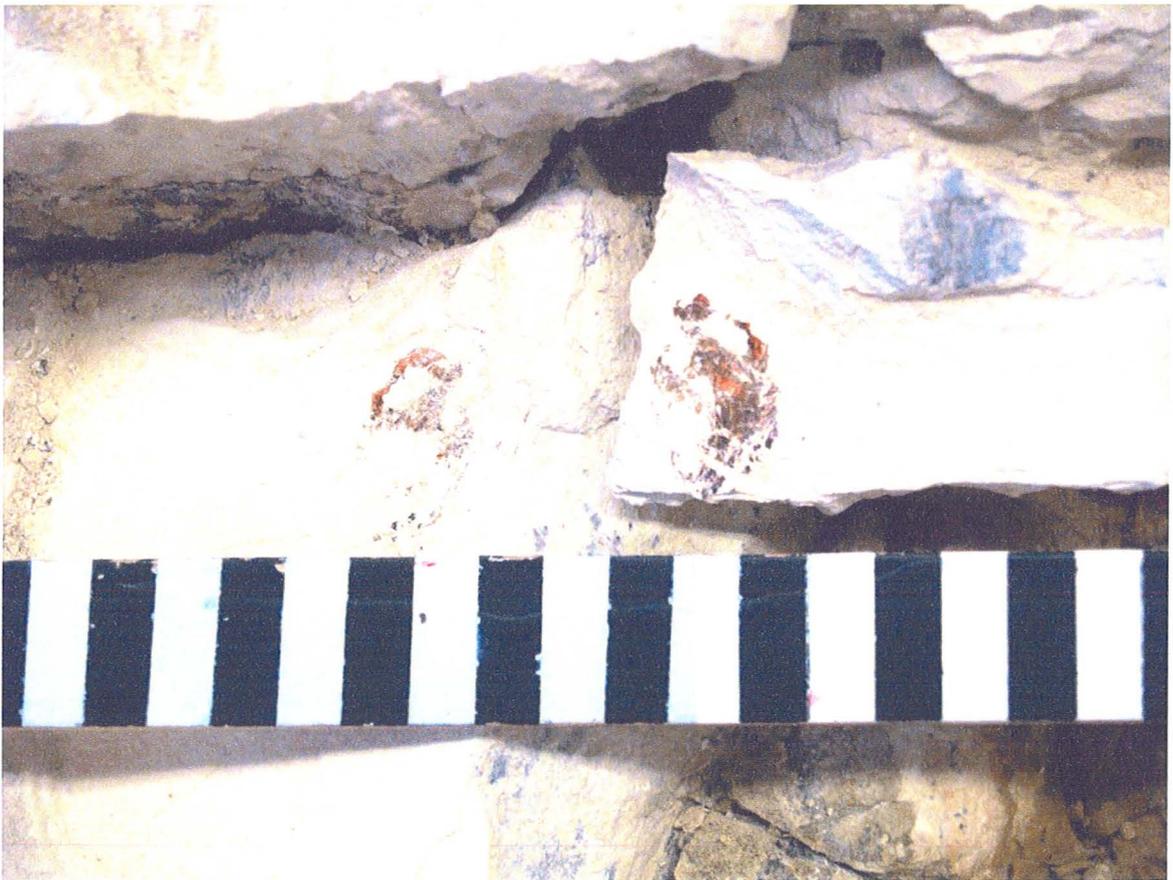


Figure 9. Example of fossil bony fish cranium found in the Pmatrix. Scale bar units in centimeters.



Figure 10. Trace fossils in matrix, likely created by burrowing crustaceans, possibly "mantis shrimp" (Dr. L.G. Barnes, personal communication). A spray-bottle water mist was used to moisten the surface, enhancing contrast. Small scale bar units in centimeters.

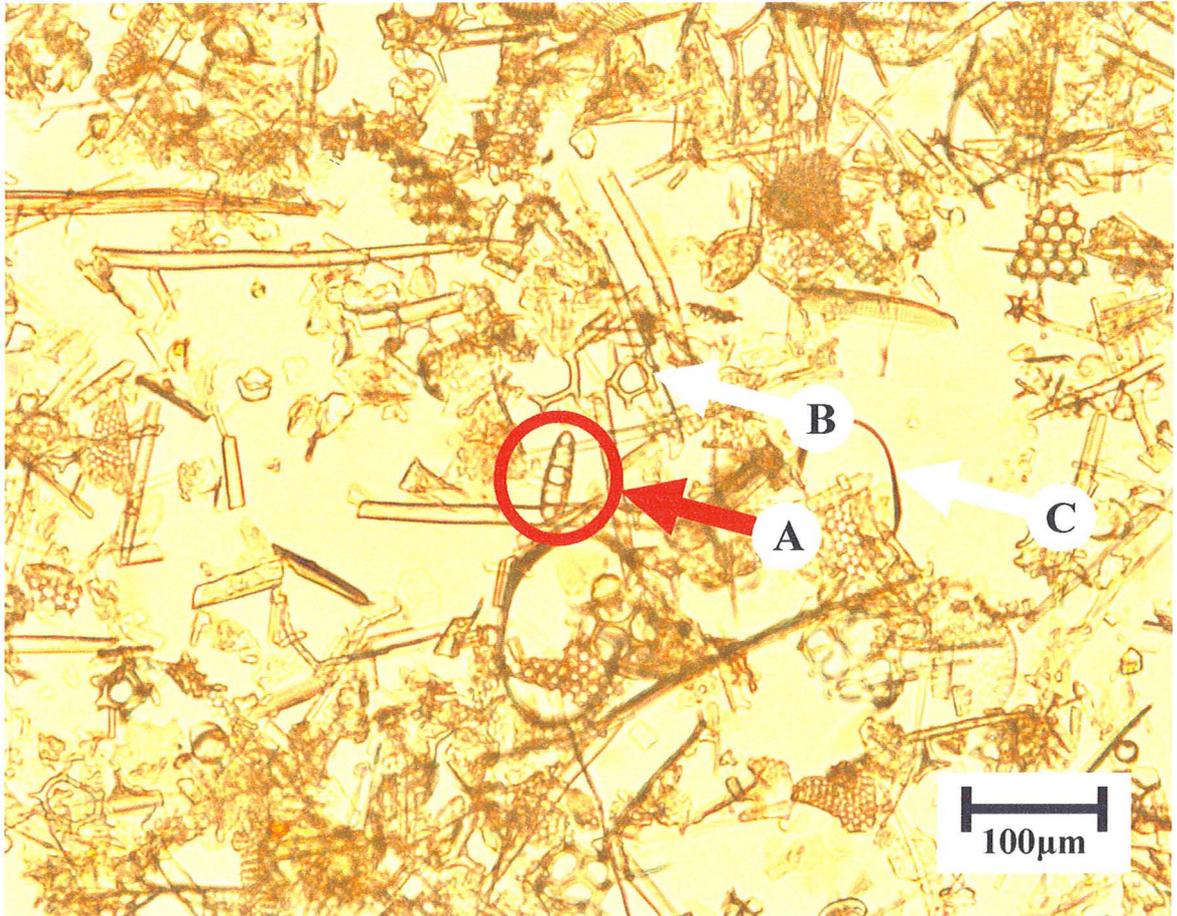


Figure 11. A - *Denticulopsis dimorpha* (in red circle), B - fragment of radiolarian, C - "girdle band" of centric diatom. Also: many fragments of elongate pennate diatoms and sponge spicules. (Micrograph provided by Dr. Lisa White, SFSU).

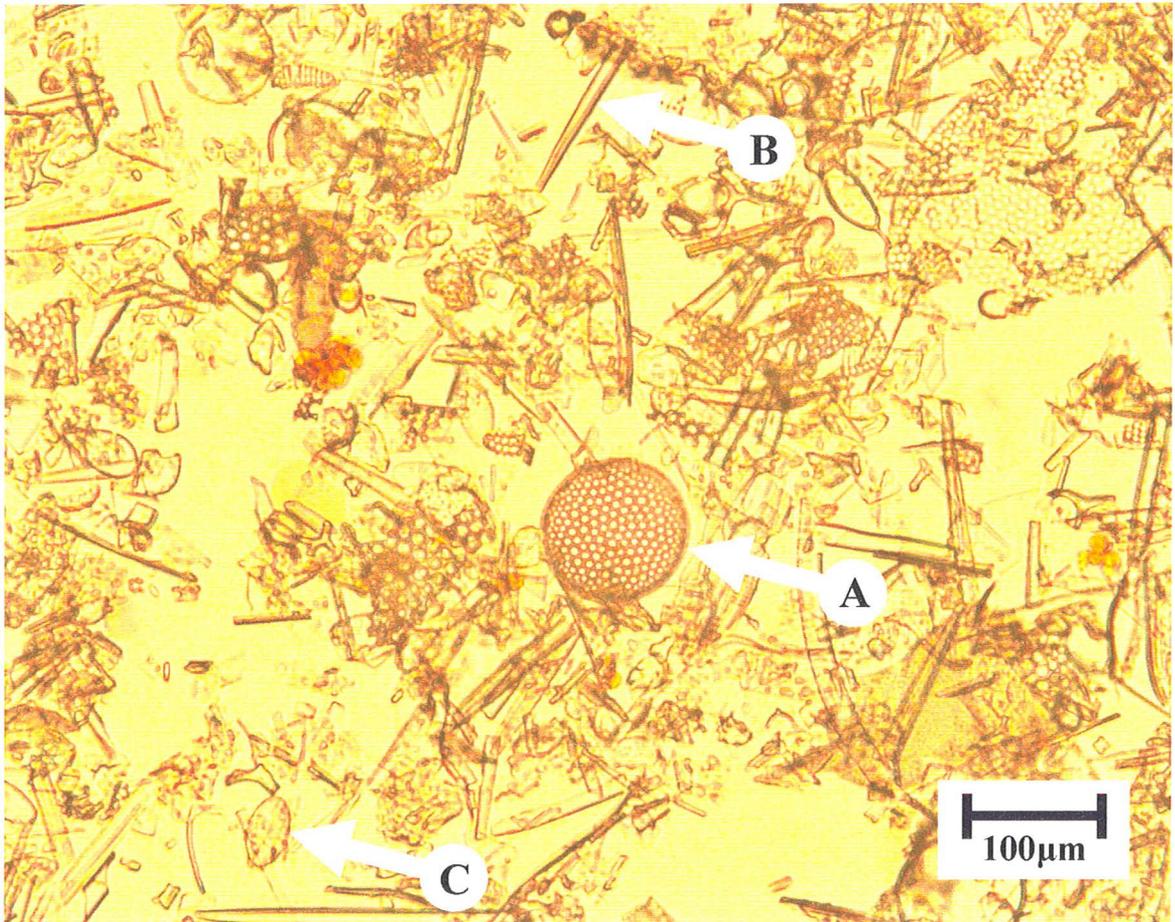


Figure 12. A - Centric diatom *Thassiosira* sp., B - sponge spicule, C - pennate diatom. (Micrograph provided by Dr. Lisa White, SFSU).

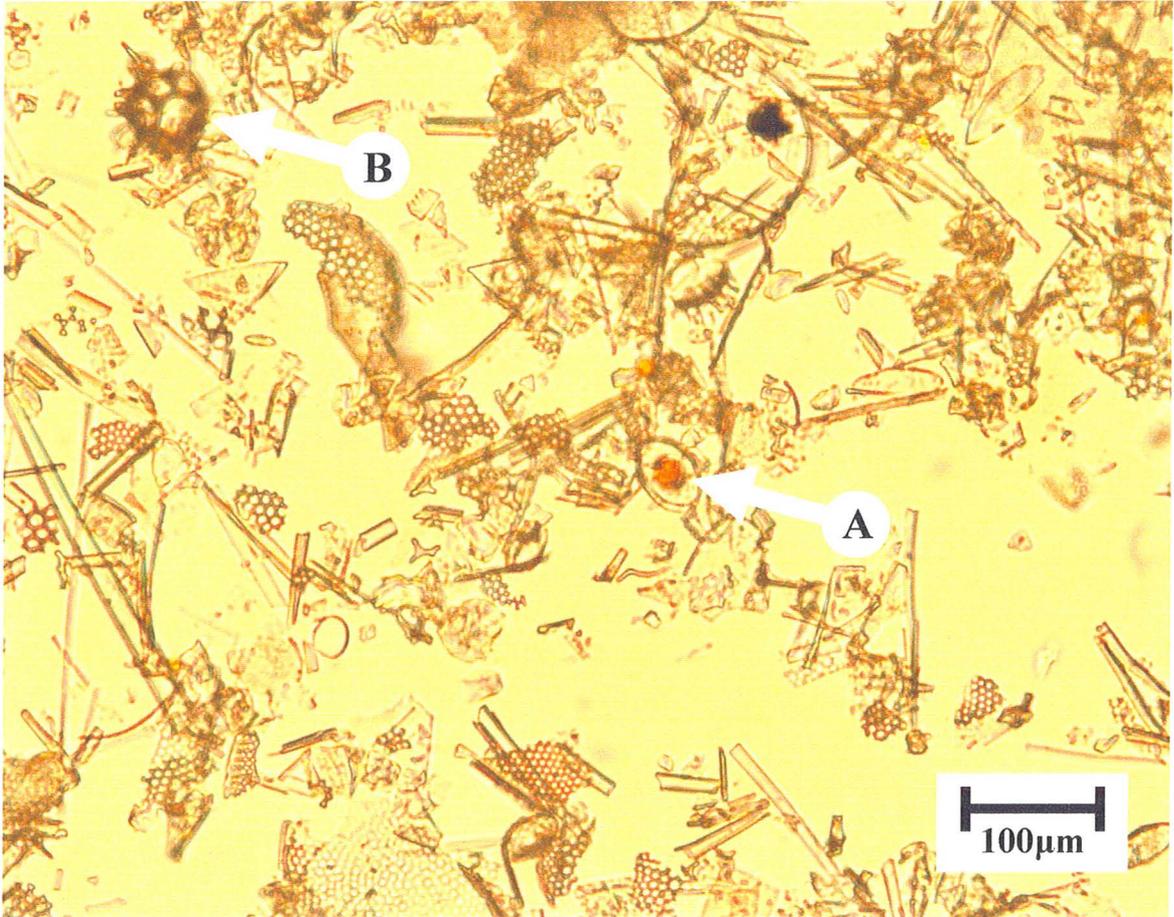


Figure 13. A - Pollen grain, B - radiolarian, slightly out of focus. (Micrograph provided by Dr. Lisa White, SFSU).

Ages (Ma)	Epoch / Subepoch	Chron	Polarity	Zonation	Events	North Pacific Diatom Zone	Boundary ages (Ma)	
1	Quat.	C1	■	<i>N. seminae</i>	LO <i>P. curvirostris</i>	NPD 12	0.30	
				<i>P. curvirostris</i>	LO <i>A. oculatus</i>	NPD 11	1.01-1.46	
2	Pliocene	late	■	<i>A. oculatus</i>	LO <i>N. koizumii</i>	NPD 10	2.0	
3				<i>N. koizumii</i>	LO <i>N. kamtschatica</i>	NPD 9	2.61-2.68	
4		early	■	<i>N. koizumii - N. kamtschatica</i>	FO <i>N. koizumii</i>	NPD 8	3.53-3.59	
5				<i>N. kamtschatica</i>	FO <i>T. oestrupii</i>	NPD 7Bb	5.49	
6	Miocene	late	■	<i>N. kamtschatica</i>	FCO <i>N. kamtschatica</i>	NPD 7Ba	6.65	
7				<i>R. californica</i>	LCO <i>R. californica</i>	NPD 7A	7.6	
8				<i>T. schraderi</i>	LCO <i>T. schraderi</i>	NPD 6B	8.6	
9				<i>D. katayamae</i>	LO <i>D. katayamae</i>	NPD 6A	9.16	
10		middle	■	■	<i>D. dimorpha</i>	LO <i>D. dimorpha</i>	NPD 5D	9.9
11					<i>T. yabei</i>	FO <i>D. dimorpha</i>	NPD 5C	11.5
12					<i>D. praedimorpha</i>	LCO <i>D. praedimorpha</i>	NPD 5B	12.9
13					<i>C. nicobarica</i>	FO <i>D. praedimorpha</i>	NPD 5A	13.1
14	middle	■	■	<i>D. hyalina</i>	LCO <i>D. hyalina</i>	NPD 4Bb	14.4-14.6	
15				<i>D. hyalina</i>	FCO <i>D. simonsenii</i>	NPD 4Ba	14.9	
16				<i>D. lauta</i>	FO <i>D. simonsenii</i>	NPD 4A	15.9	
17				<i>D. praelauta</i>	FO <i>D. lauta</i>	NPD 3B	16.3	
17				<i>C. kanayae</i>	FO <i>D. praelauta</i>	NPD 3A	16.9	

Figure 14. Correlation of diatom zonation, primary zonal markers, and zonal code numbers used on Leg 167 of the Ocean Drilling Program conducted by the *JOIDES Resolution* in 1996. (Modified from Maruyama, 2000). Zone limits have been calibrated to the geochronology of Cande and Kent (1995). LO = last occurrence; FO = first occurrence; FCO = first common occurrence; LCO = last common occurrence. The index fossil *Denticulopsis dimorpha* (range indicated by pink-colored zone) constrains the age of *Mixocetus* n. sp. to 9.16 - 9.9 Ma.

SYSTEMATIC PALEONTOLOGY

Class **Mammalia** Linnaeus, 1758

Superorder **Cetartiodactyla** Montgelard, Catzeflis, Douzery, 1997

Order **Cetacea** Brisson, 1762

Suborder **Mysticeti** Flower, 1864

Diagnosis of Suborder:

- 1) Crania with elongate nasal bones (character shared with Archaeoceti Flower, 1883, primitive suborder of cetacea) (Barnes et al., 1995).
- 2) Anterior bony nares single and continuous with mesorostral groove (character shared with Archaeoceti) (Barnes et al., 1995).
- 3) Maxilla with lateral process appressed to anterolateral surface of antorbital process of frontal (Barnes et al., 1995).
- 4) Maxilla with flat infraorbital plate (Barnes et al., 1995).
- 5) Temporal musculature attaching to temporal crest on posterior part of supraorbital process of frontal (Barnes et al., 1995).
- 6) Basioccipital wide and bulbous (contrasted with odontocetes) (Deméré et al., 2005; Berta et al., 2006; Fitzgerald, 2006).
- 7) Peribullary sinus limited to area anterior to tympanic bulla (Barnes et al., 1994).
- 8) Foramen pseudovale perforating styliform process of squamosal (Barnes et al., 1995).
- 9) Dentary lacking symphyseal articulation, having instead a symphyseal ligament associated with a horizontal groove that curves upward at anterior end (Barnes et al., 1995).
- 10) Thin lateral margin of the maxillae (Deméré et al., 2005; Berta et al., 2006).
- 11) Posterior portion of the vomer exposed on the basicranium and obscuring basiphenoid/basioccipital suture - contrasted with odontocetes (Deméré et al., 2005; Berta et al., 2006).

- 12) Dorsal aspect of mandible curved laterally (Deméré et al., 2005; Berta et al., 2006).
- 13) Sternum consists of a single bone (as compared with three in odontocetes) (Feldhamer, et al. 2004).

Remarks:

The term "diagnosis" used in the preceding and following sections assumes that each taxonomic rank has unequivocal identifiable synapomorphies, or apomorphies for monotypic taxa. This is not easy to determine, particularly for taxa whose diagnosis may be problematic due to poor fossil preservation and/or due to spurious characters erroneously based on symplesiomorphies (shared primitive rather than derived characters) or homoplasy (convergence) (Fitzgerald, 2010).

For example, Bouetel and Muizon (2006) identified 18 synapomorphies of Mysticeti, of which Fitzgerald (2010) asserts that five were symplesiomorphies of Neoceti Fordyce and Muizon, 2001, the clade inclusive of both Odontoceti Flower, 1867 and Mysticeti. Eight other synapomorphies of Mysticeti identified by Bouetel and Muizon (2006) represented potential synapomorphies of less inclusive clades, such as Chaemysticeti Mitchell, 1989, limited to all edentulous baleen-bearing mysticetes. I recognize a ninth in the list of Bouetel and Muizon (2006) which Fitzgerald (2010) seemed to have overlooked: mandible has a constant height along the entire length. This is certainly not true for the archaic mysticetes of family Mammalodontidae Mitchell, 1989 or Aetiocetidae Emlong, 1966 (see **Figure 31**).

For characters 1 and 2 (condition of the nasal bones and nares), it is not known if this condition was different in the earliest odontocetes. For character 6 (the condition of the basioccipital), the term "thick transversely" might be preferable to "wide and

bulbous," and might only apply to families where the basioccipital exhibits a transverse thickening across the entire length (Dr. L. G. Barnes, personal communication). This would include the families Cetotheriidae, Balaenopteridae Gray, 1864, Eschrichtiidae Ellerman and Morrison-Scott, 1951, Balaenidae Gray, 1821, and Neobalaenidae Miller, 1923. In this regard, this character is true only for derived mysticetes of a clade even less inclusive than the Chaemysticeti. For character 9 (lack of symphyseal articulation of the dentary = mandible), this applies unequivocally to all extant families (Balaenidae, Neobalaenidae, Balaenopteridae and Eschrichtiidae), the extinct Aetiocetidae Emlong, 1966, Eomysticetidae Sanders and Barnes, 2002 and Cetotheriidae. Because of poor preservation of fossil anterior mandibles (Fitzgerald, 2006), it is unclear if this character also applies to the most archaic mysticetes of family Llanocetidae Mitchell, 1989, and Mammalodontidae. For character 10 (thin lateral margin of maxillae), this is not true for the Llanocetidae and the Mammalodontidae. Therefore, it would apply only to a clade inclusive of the Aetiocetidae, the Cetotheriidae and the crown group mysticetes. For character 11 (exposure of posterior vomer on basicranium), the legitimacy is questioned by Dr. L. G. Barnes (personal communication). (Character 11 for Llanocetidae is not known due to poor fossil preservation, but is certainly true of the mammalodontid *Janjucetus hunderi* Fitzgerald, 2006). For character 12 (pertaining to mandibles curved laterally), the legitimacy is questioned by Dr. L. G. Barnes who asserts that extinct mysticetes of families Aetiocetidae and Eomysticetidae have straight mandibles. I detected a lateral curve in most of the jaw length of the eomysticetids that exhibits an overall sigmoidal shape when including the posterior end (including the mandibular condyle and coronoid process). By contrast, the mysticete sister taxon Odontoceti

exhibits straight mandibles in dorsal view, but with notable exceptions: the physeterids (sperm whales) and river dolphins (three extant families), which have medially bowed mandibles that meet at a long sutured/bony symphysis. This latter condition is similar to that of the archaeocetes.

The odontocetes developed asymmetries in the narial region of the cranium (derived morphologies enhancing echolocation ability) in all but a few forms, e. g., the earliest known odontocete *Simocetus rayi* Fordyce, 2002a, and the extant South American La Plata river dolphin *Pontoporia blainvillei* Gervais and d'Orbigny, 1844. For this reason, a symmetrical cranium is not considered diagnostic for the suborder Mysticeti (Dr. L. G. Barnes, personal communication). Nevertheless, many textbooks continue to state otherwise (e.g., Feldhamer et al., 2004; Berta et al., 2006) simply because all mysticetes have symmetrical crania as compared with the asymmetrical crania of *most* derived odontocetes. Other odontocete characters differing from mysticetes include isolated periotics and hollow fat-filled lower jaw bones associated with high frequency sensory echolocation. Most odontocetes retained a firmly-articulated (sutured/bony) mandibular symphysis, although *Simocetus*, with its short symphysis, might be an exception in this regard (Fordyce, 2002a; Dr. L. G. Barnes, personal communication). The fact that both the earliest mysticetes and odontocetes appear to have short symphyses with straight mandibles is puzzling in view of the fact that their archaeocete ancestor had a long symphysis with medially bowed mandibles. It is not known if the primitive condition reappeared in an iterative fashion among the physeterids and rivers dolphins, or is symplesiomorphic (Dr, L. G. Barnes, personal communication).

The Latin name "Mysticeti" is derived from Aristotle's *mustoketos* (Greek, "mouse-whale") (Rice, 1998, pg. 59), probably because he intended the name to be a humorous irony, in contrast with the gigantic size of most baleen whales. A once-used Latin variant "Mystacoceti" is translated "moustache whales," referencing the baleen that projects from the upper lip margins of derived mysticetes, but this term was superseded by the former (Rice, 1998, pg. 59).

Infraorder **Chaemysticeti** Mitchell, 1989

Diagnosis of Infraorder:

- 1) Lack of teeth in the mandibulars and maxillary palate as adults.
- 2) Presence of sulce in the ventral maxillary palate.
- 3) Baleen plates numerous and thin (given by 1 and 2).
- 4) Mandible has a generally constant height across entire length.

Remarks:

It is assumed by Mitchell (1989) and Fordyce and Barnes (1994) that baleen evolved only once among mysticetes to satisfy the preference for parsimony, a notion used to justify erection of the infraorder Chaemysticeti, the clade within Mysticeti that includes all baleen-bearing mysticetes both extinct and extant. The name Chaemysticeti is derived from the Greek "chaios" meaning "true" or "genuine," hence "genuine mysticete."

Family **Cetotheriidae** Brandt, 1872 (Whitmore and Barnes, 2008)

Diagnosis of family:

Similarities with modern mysticetes (Fraser and Dooley, 2002):

- 1) Significant "telescoping" of the symmetrical cranium.
- 2) Similar inner ear structure indicating lack of high-frequency hearing ability - no morphologies for echolocation.
- 3) Mandibular symphysis replaced with a ligamentous symphysis.
- 4) Rostrum generally flat, broad and tapering, similar to rorquals (Balaenopteridae), much flatter as compared with gray whales (Eschrichtiidae).
- 5) Sternum reduced.
- 6) Hindlimbs almost totally absent - splint bone homologous with pelvis but no longer articulates with vertebral column.
- 7) Cervical vertebrae typically compressed but not fused.
- 8) Body proportions of most cetotheres similar to *Eschrichtius* which also has somewhat "strong rib-vertebrae articulations" and a relatively long neck.

Dissimilarities with archaic and modern mysticetes (Whitmore and Barnes, 2008, unless otherwise noted):

- 1) Relatively small cranium (less than 25% in proportion to body length) as compared with most modern families (although similar to balaenopterids) (Fraser and Dooley, 2002).
- 2) Generally smaller size compared with most modern taxa (exceptions: minke, pygmy right whales are also small).
- 3) Rib-vertebrae articulations are somewhat reduced but remain strong (modern families have weak to absent articulations) (Fraser and Dooley, 2002).
- 4) Unlike all extant families by having crania with relatively long intertemporal region, orbits far anterior relative to braincase, and posterior extremities of rostral bones (maxillae, premaxillae, and nasals) extending posteriorly on dorsal surface of cranium between paired frontals in a manner forming triangular wedge centered on sagittal axis of cranium.

- 5) Unlike Balaenopteridae and *Eschrichtius* by having supraorbital processes of frontals that descend gradually ventrolaterally from cranial vertex.
- 6) Unlike Balaenopteridae, Neobalaenidae, and Balaenidae by having parietals widely exposed in dorsal and lateral surfaces of intertemporal region, and having temporal fossae open dorsally rather than overhung by margins of occipital shield; the occipital shield does not extend as far anteriorly on the cranium as in modern groups listed, but rostral bones extend much farther, in relatively simple-pointed triangle, of varying width among species, between the frontals – a notably derived character of Cetotheriidae *sensu stricto*.
- 7) The manner in which rostral bones extend posteriorly between frontals towards occipital shield, differing from Balaenidae where posterior margins of rostral bones form a nearly straight line across dorsal surface of cranium at a point anterior to the orbits (eye sockets).
- 8) The manner of interdigitation of rostral bones with frontals differs with all extant mysticetes - a defining character of the Cetotheriidae *sensu stricto*. In Balaenopteridae and Eschrichtiidae rostral bones have broad and complex interdigitation pattern with frontals. In Cetotheriidae *s. s.* the rostral bones (maxillae, premaxillae, and nasals) extend posteriorly in a simple pointed triangle (of varying width among species) between frontals. (Generally speaking, the posterior tapering of rostral bones in Cetotheriidae is symplesiomorphic with the toothed aetiocetids).
- 9) Modern families and genera have many derived features, e.g.:
 - a) Balaenopterids have maxillary spurs extending posteriorly along top of the cranium and supraorbital portions of frontals depressed well below top of cranium
 - b) *Eschrichtius* has enlarged nasals and posterior ends of premaxillae, moderately arched rostrum, posterior maxillary processes similar to balaenopterids, and no coronoid process of the mandible
 - c) Balaenidae have extremely arched narrow rostrum, anteroposteriorly compressed cranium, divergent zygomatic processes, supraoccipital extending to a point anterior to orbit, fused cervical vertebrae.
- 10) Mandibles have uniform height across entire length with a slight distal widening at the anterior end, unlike in rorquals which have a gradual tapering of height anteriorly.

Remarks:

The list of similarities to modern mysticetes is included for completeness but would not be used for a strict diagnosis. For similarity 1 (regarding telescoping of the

cranium), significant rostral bone extension has occurred in at least two mysticete lineages: Aetiocetidae, and Chaeomysticeti. Similarities 2, 5, and 7 (no morphologies for echolocation, sternum reduced, cervical vertebrae compressed but not fused) are symplesiomorphic with the suborder Mysticeti. Similarity 3 (ligamentous mandibular symphysis) is symplesiomorphic with the Chaeomysticeti. Similarity 6 is symplesiomorphic with the order Cetacea. Similarity 8 (comparisons with Eschrichtiidae in terms of body proportions, strong rib articulations, and long neck) questionable since no complete skeletons of Cetotheriidae *sensu stricto* are known. This latter suite of alleged similarities with Eschrichtiidae is probably based on *Parietobalaena palmeri* Kellogg, 1924, which is no longer considered a member of the Cetotheriidae. The authors (Fraser and Dooley, 2002) have also asserted that such similarity as there might be between some "cetotheres" and gray whales represent shared primitive conditions. Only the noted differences from modern families provide unequivocal diagnostic characters for this family.

A few recent attempts have been made to reduce the number of taxa of the former Cetotheriidae *sensu lato* to define Cetotheriidae *sensu stricto*. Bouetel & Muizon (2006) recognized six genera in their Cetotheriidae *sensu stricto*:

- *Cetotherium* Brandt, 1843
- *Mixocetus* Kellogg, 1934
- *Nannocetus* Kellogg, 1929
- *Metopocetus* Cope, 1896
- *Herpetocetus* Van Beneden, 1872
- *Piscobalaena* Pilleri and Siber, 1989

In their study, Bouetel & Muizon (2006) used a matrix with 101 characters and 23 taxa including two archeocetes, two aetiocetids, six genera of Cetotheriidae, five extinct

taxa formerly classified as "cetotheres," and a sampling of modern taxa across the four extant mysticete families. They concluded that a basal "cetother" lineage, Cetotheriidae *s. s.*, and the "crown-group" mysticetes are successive sister taxa. Furthermore, Bouetel and Muizon (2006) recognized relationships among the six genera of cetotheres in terms of successive sister taxa (**Figure 30**), in order of least-to-most derived, as follows: *Mixocetus*, *Nannocetus*, *Cetotherium*, *Metopocetus*, *Herpetocetus*, and *Piscobalaena*. The latter genus is well described and has several specimens including juveniles.

Whitmore and Barnes (2008) expanded the Cetotheriidae *sensu stricto* to ten genera, recognizing two subfamilies, but their work was in press before Bouetel and Muizon (2006) was published and this is why they did not include *Piscobalaena* (Dr. L. G. Barnes, personal communication). It is noteworthy that Bouetel & Muizon (2006) did not recognize subfamilies in the manner of Whitmore and Barnes (2008). I have added *Piscobalaena* to the subfamily Cetotheriinae (new context, Whitmore and Barnes, 2008) based on overall similarity. Bold type shows common genera in both Whitmore and Barnes (2008) and Bouetel and Muizon (2006), with the addition of *Piscobalaena*:

- ***Cetotherium*** Brandt, 1843
- ***Mixocetus*** Kellogg, 1934
- ***Piscobalaena*** Pilleri and Siber, 1989
- ***Metopocetus*** Cope, 1896
- *Amphicetus* Van Beneden, 1880
- *Heterocetus* Capellini, 1877
- *Mesocetus* Van Beneden, 1880
- *Cephalotropis* Cope, 1896
- *Plesiocetopsis* Brandt, 1873

The second subfamily of Cetotheriidae in the taxonomy of Whitmore and Barnes (2008) is Herpetocetinae (sister to Cetotheriinae) and is comprised of two genera: ***Herpetocetus*** and ***Nannocetus***. Both of these taxa were included in the family

Cetotheriidae *sensu stricto* by Bouetel and Muizon (2006).

A third effort to define Cetotheriidae was undertaken by Steeman (2007), who attempted to combine the interpretations of Bouetel and Muizon (2006) with Whitmore and Barnes (2008). Steeman (2007) recognized two subfamilies but with only two genera in Cetotheriinae (*Cetotherium* and *Piscobalaena*) and four in Herpetocetinae (*Herpetocetus*, *Nannocetus*, *Metopocetus*, *Cephalotropis*). Steeman (2007, pg. 884) considered *Nannocetus* to be a likely synonym for *Herpetocetus*.

Holotype: L'Institut Paris, no. 502, *Cetotherium rathkii* Brandt, 1943

Type Locality:

Ukraine in southeastern Europe; fossil found in steppe district limestone deposited in the Paratethys Sea, the shallow-inland marine waters that covered southern Europe during the Oligocene, Miocene and Pliocene. This limestone is correlated to the Paratethian Sarmatian Stage (11.6 to 12.7 Ma) (Uhen, 2010), which falls within the Mediterranean Serravallian Stage of the late middle Miocene (Haq, 2007).

Remarks:

The family name Cetotheriidae is derived from the name of the type genus *Cetotherium*, from "cetothere" meaning "whale beast" in Latinized Greek. The oldest true cetothere is a partial cranium of *Metopocetus durinasus* Cope, 1896 from the Calvert Hills Formation, Nomini Cliffs area (Kellogg, 1969), in Maryland. The youngest true cetothere is an undescribed *Herpetocetus* sp. from the San Diego Formation in southern California (Barnes, 1977). The fossil includes a left jaw bone fragment (SDSNH 23057)

noteworthy for having pathologies attributed to shark bites (Deméré and Cerutti, 1982). The Calvert Hills Formation is lower to lower middle Miocene, with an age range of 13.8 to 19.2 Ma (Ward and Andrews, 2008). The fossil almost certainly (Dr. Alton Dooley, personal communication) comes from beds 14 and 15 (13.8 - 14.4 Ma) at the top of a unit in the Calvert Hills Formation called the Plum Point Marl (Ward and Andrews, 2008). The San Diego Formation is determined to be early Pliocene to early late Pliocene (3 - 5 Ma), based a correlation with the Wheelerian foraminiferal stage (Haller, 1980), the San Joaquin provincial molluscan stage (Addicott, 1972), and is roughly correlative with the Blancan NALMA. This gives a total range for the family Cetotheriidae *sensu stricto* of no more than 3 to 14.4 million years before present. A comparison of related cetothere crania is presented in **Figure 15**.

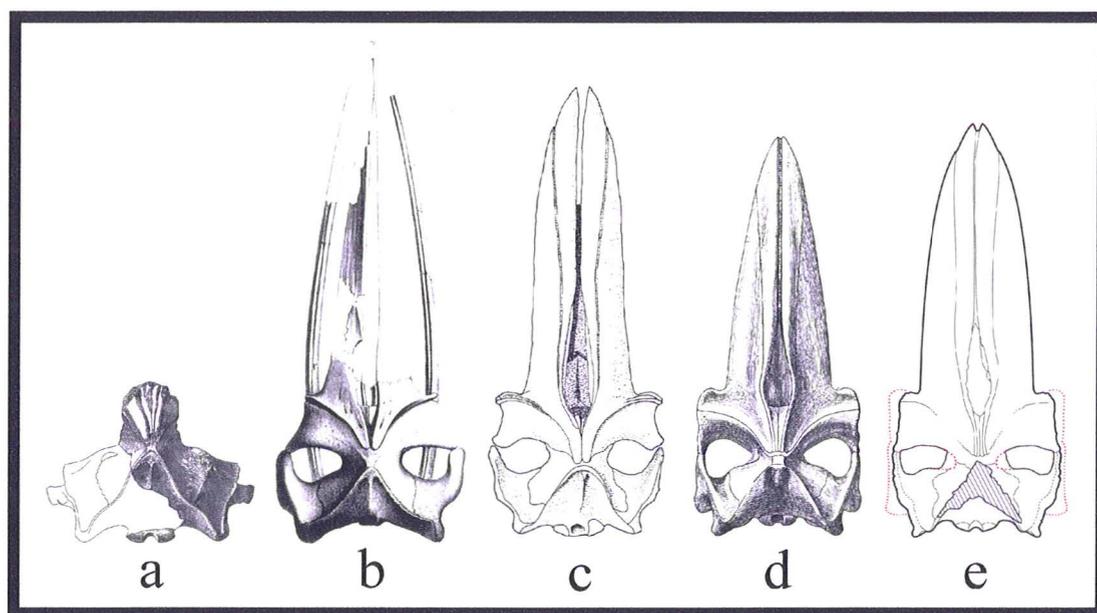


Figure 15. Cetothere crania in dorsal view: **a** - *Metopocetus durinasus* Cope (after Kellogg, 1969), **b** - *Cetotherium rathkii* Brandt (after Van Beneden and Gervais, 1880), **c** - *Piscobalaena nana* Pillari and Siber (after Bouetel and Muizon, 2006), **d** - *Mixocetus elysius* Kellogg (after Kellogg, 1934b), **e** - *Mixocetus* n. sp.), showing the most defining derived character of the family Cetotheriidae: the posterior extension and tapering of maxillary bones towards the cranial vertex. Drawings scaled to same braincase length.

Subfamily **Cetotheriinae** Brandt, 1872 (Whitmore and Barnes, 2008)

Diagnosis of Subfamily:

- 1) Postglenoid process of squamosal directed posteroventrally and expanded in transverse plane.
- 2) Zygomatic process of squamosal positioned laterally on cranium farther than paroccipital process and distal end of posterior process of petrosal.
- 3) Petrosal with anterior process not extremely compressed transversely, with posterior process bearing only a shallow sulcus on ventral surface.
- 4) Posterior process of the periotic either short or long, but not greatly expanded distally (laterally).
- 5) Cranium with posterior ends of maxillae, premaxillae, and nasals penetrating posteriorly as a tapered wedge between frontals.
- 6) Right and left maxillae converging posteriorly toward sagittal midline of cranium thereby constricting posterior ends of nasals and premaxillae

Remarks:

The type genus of the family Cetotheriidae, *Cetotherium*, along with *Metopocetus*, *Mixocetus*, and *Piscobalaena* are grouped within the subfamily Cetotheriinae and share the diagnostic characters outlined above.

Genus *Mixocetus* Kellogg, 1934

Diagnosis of genus:

From Dr. L. G. Barnes (personal communication):

- 1) Bulbous mass in the area of the lateral parietal at the suture of the parietal and squamosal (similar to condition found in extant gray whales of family Eschrichtiidae).

- 2) Large width and anterior extension of the preorbital process of the maxilla.
- 3) Subrectangular braincase contributed to by lateral extension of the preorbital process of the maxilla, postglenoid process of the squamosal and paroccipital process of the exoccipital.
- 4) Prominent dorsal ridge along the zygomatic process of the squamosal reaching to the exoccipital.
- 5) Long posterior process of the petriotic bone.

Remarks:

The genus name refers to its "combination of characters exhibited by the skull" (Kellogg, 1934b, pg. 85), presumably both primitive and derived, although no one is quite sure exactly what Kellogg meant (Dr. L. G. Barnes, personal communication).

Mixocetus elysius Kellogg, 1934

Holotype: LACM 882, *Mixocetus elysius*

Type locality:

Lincoln Heights, southern California, in the northeastern LAB. The "Elysian Park sandstone of the Modelo (Puente) Formation" (Kellogg, 1934b, pg. 86) is given as the fossil horizon. "Elysian Park sandstone" is not a formal rock unit term. Kellogg asserted this sandstone member to be "certainly upper Miocene" (Kellogg, 1934b, p. 87) and correlated it with the Monterey Formation above the *Valvulineria californica* (index foraminifera) zone, based on microfossil identification by Dr. William S. W. Kew (Kellogg, 1934b, p. 86), a petroleum geologist. The Elysian Park sandstone was

identified as a member of the Modelo Formation by Hoots (1930), but Lamar (1970) considered it a middle member of the Puente Formation. The sandstone is temporally equivalent to the provincial benthic foraminifera Mohnian Stage (foraminifera zones D and E) (Lamar, 1970), which correspond to the late middle to early late Miocene (10.5 - 13 Ma) (Repenning and Tedford, 1977).

Description (Kellogg, 1934b):

- 6) Resembling *Mesocetus longirostris* Van Beneden, 1880, and *Metopocetus durinasus* Cope, 1896, in degree of interdigitation of rostral and cranial bones.
- 7) Differing from *Mesocetus longirostris* and *Metopocetus durinasus* in the following ways:
 - a) Cranium with supraorbital processes exhibiting pronounced downward curvature at base.
 - b) Anterior temporal crests less abruptly elevated above level of basal portions of supraorbital processes of frontals.
 - c) Exposure of frontals in median interorbital region reduced to a narrow strip.
 - d) Postglenoid processes quite robust, bulging posteriorly.
 - e) Exoccipitals unusually thickened anteroposteriorly.
- 8) Apex of supraoccipital shield not thrust forward beyond level of hinder parietal margin of temporal fossa.
- 9) Nasals located almost, if not wholly, behind level of preorbital angles of supraorbital process of frontals.
- 10) Thin anterior process of parietal which overrides basal portion of supraorbital process, extended forward beyond level of hinder ends of median rostral elements (ascending processes of maxillaries, premaxillaries, and nasals).
- 11) Backward thrust of rostrum has carried hinder ends of median rostral elements beyond level of anterior-most portion of hinder edge of supraorbital process.
- 12) Rostrum exhibits a rather gradual distal attenuation.

Additional features:

- 13) Apex of supraoccipital shield generally rounded at cranial vertex, similar to *Piscobalaena nana*, rather than pointed as in *Cetotherium rathkii* and *Metopocetus durinasus*.
- 14) Lateral margin of the supraoccipital shield is overthrust such that the medial edge of the parietal at the lambdoid arch curls over itself, although the shield does not cover any part of the temporal fossa opening in dorsal view.
- 15) Temporal fossa opening adjacent to zygomatic arch is wide anteroposteriorly, giving it an overall triangular shape.
- 16) Slight lateral curvature of rostrum, giving it a generally triangular shape.

Remarks:

The species name comes from Kellogg's (1934b) the Elysian Park sandstone in which the fossil was found. Currently, there are two described specimens of genus *Mixocetus*: *Mixocetus elysius* (LACM 882) and *Mixocetus* n. sp. described below. The unique combination of the above diagnostic characters (1 through 5) is shared by both.

***Mixocetus* n. sp.**

Description:

The new species shares all characters noted in the diagnosis of genus *Mixocetus*, but exhibits the following differences:

- 1) Subrectangular shape of the temporal fossa as compared with a more triangular shape in *Mixocetus elysius* (**Figure 22**).
- 2) Shape of the rostrum: width more uniform in posterior 1/4 of length, then margin becomes gradually laterally bowed towards anterior, as compared with subtriangular (less bowed) lateral margins on rostrum of *Mixocetus elysius* (**Figure 22**).
- 3) Unique shape of palatine bones (**Figure 24**)

Holotype: LACM 147795

Type Locality:

San Joaquin Hills of Laguna Niguel, California. The fossil was found in upper Miocene Monterey Formation diatomite correlated to the North Pacific Diatom Zone NDP 5D which has an age range spanning 9.16 to 9.9 Ma (see pp. 16-19 of this thesis). The age of the two described specimens of *Mixocetus* provides the age range of the genus: 13.0 to 9.16 Ma.

Remarks:

The dorsal- and ventral-view photographs with correlating preliminary drawings are shown in **Figures 16** through **19**. Reconstruction drawings adjusted to eliminate cranial asymmetries are shown in **Figures 20** and **21**. The cranium of the specimen is generally well preserved with minimal to moderate asymmetrical distortion due to sediment compaction and tectonic strain. A large portion of the lambdoid crest inclusive of the cranial vertex (crosshatched area in **Figures 17** and **20**) was sheared off by the earth-grading blade that uncovered the fossil during land development/excavation activity. The right fossa was not preserved *in situ* or was damaged during original excavation. The left fossa (the only one preserved in this specimen) is outlined differently in dorsal (laterally narrow and elongate) and ventral view (subrounded to triangular) suggesting that it was misinterpreted in ventral view. The area common in both dorsal and ventral views was used to infer the shape. The same method of inference was used for the lateral extent of the brain case (compare dorsal and ventral views) where it appears in the dorsal-view photograph that matrix was not fully removed to a depth

exposing the postglenoid process of the squamosal and adjacent features. The ventral view should be given more credence when interpreting the lateral posterior cranial extremities.

The specimen is diagnosed as an adult based on the high degree of fusion of cranial bone elements, particularly between temporal, parietal, and supraoccipital. Sex of the animal cannot be determined, because, with a sample of only one member of the species, sexual dimorphism cannot be recognized. Based on the length of the skull (about 2 m), it is estimated that the animal would have had an overall length of about 8 to 10 m. Standard cetacean cranial measurements based on criteria from Perrin (1975) comparing *Mixocetus elysius* with LACM 147795 (*Mixocetus*. n. sp.) are included in **Table 2**.

The shape of the rostrum in modern rorquals of genus *Balaenoptera* Lacépède, 1804, have significant variations across species (**Figure 23**). Some workers (Dr. A. C. Dooley, personal communication) reject this as a diagnostic feature for species, but many modern species of *Balaenoptera* are commonly distinguished by far more subtle soft tissue, behavioral, and genetic differences, as compared with skull morphology (e. g., the northern and southern minke whales).

Differences in the shapes of the palatine bones can separate species. Markedly different shapes are noted in different genera, e. g., between *Mixocetus* and *Piscobalaena* (**Figure 24**). Kellogg (1934b) published retouched photographs of *Mixocetus elysius*, along with drawings that were heavily reconstructed. The shape drawn for the posterior part of the palatine bone (**Figure 24**) is speculative, and Kellogg (1934b, p. 92) admitted that "the hinder ends of the palatine bones are destroyed." This makes it impossible to compare the posterior ends of these bones. But significant differences (lateral indentation

at midlength and a thin medial process extending anteriorly on *Mixocetus* n. sp.) (**Figure 24**) suggests that enough morphology was preserved on the palatine bones of both specimens to argue that these variations represent characters of different species.

Table 2: Cranial measurements (in centimeters).

	<i>Mixocetus elysius</i>	LACM 147795
Overall cranium length	247.2	203.0
Length of rostrum	159.0	135.0
Width of rostrum at base	66.0	54.0
Width of rostrum at midlength	45.7	45.5
Width of premaxillae at midlength of rostrum	22.5	17
Greatest preorbital width	98.8	74.4
Greatest postorbital width	96.4	81.0
Least supraorbital width	92.8	74.6
Greatest width of external nares	15.9	13.5
Greatest width across zygomatic processes of squamosals	102.6	79.8
Greatest width of premaxillae	26	18
Length of temporal fossa (dorsal/left)	21.7	13.1
Width of temporal fossa (ventral left)	29.1	23.2
Length of orbit	20	6.2
Greatest length of premaxilla (dorsal/right)	199.4	161.5
Length of nasal	25.1	19.8
Anterior width of nasal	4.5	3.0
Paroccipital width	78.5	59.8
Width occipital condyle	24.7	20.4
Width of foramen magnum	5.8	6.4
Height of foramen magnum	4.1	7.0

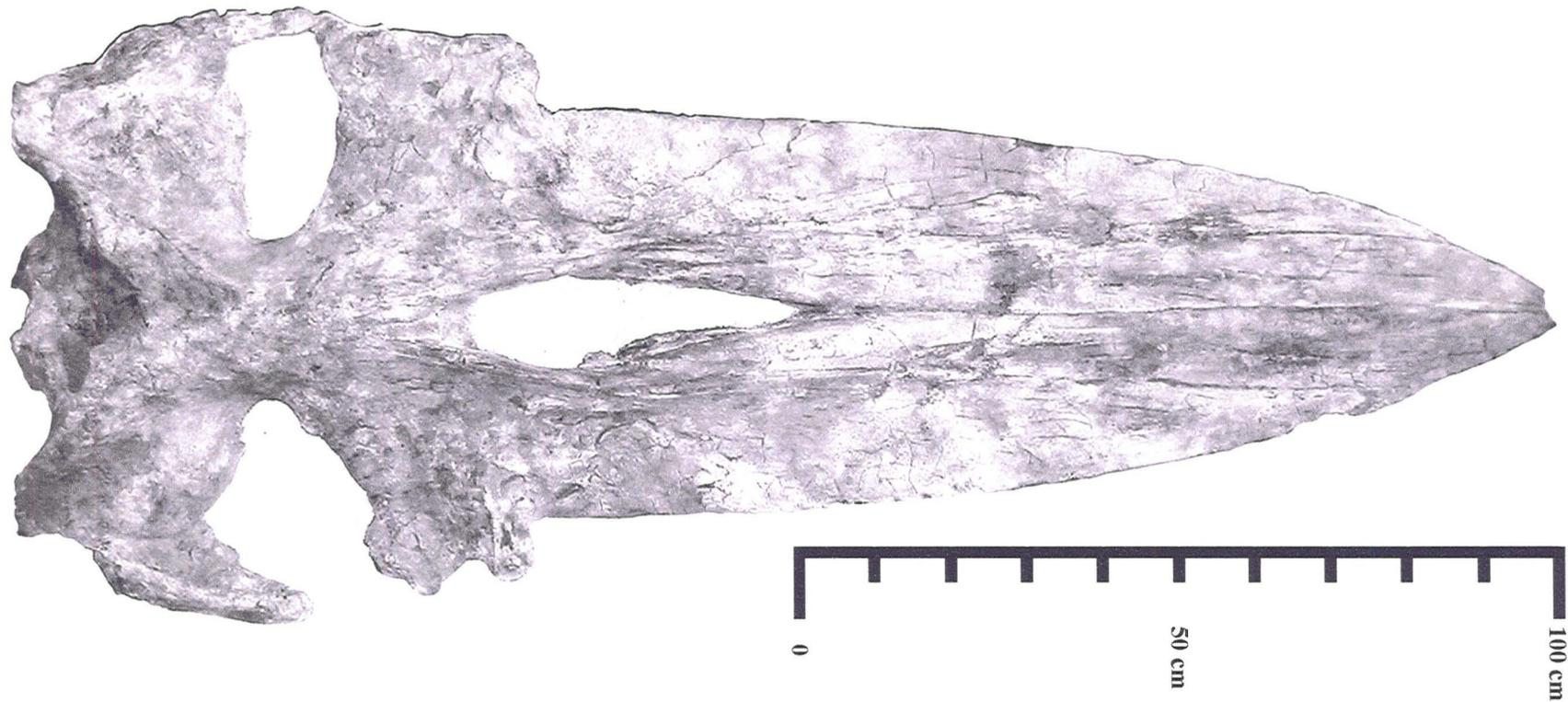


Figure 16: *Mixocetus* n. sp., holotype cranium, LACM 147795. Dorsal view photograph showing preserved laterally elongate left temporal fossa and zygomatic arch. Right zygomatic arch was not preserved in situ or damaged during excavation. The posterior extent of the exoccipitals was inadvertently cropped in this image. (Photograph provided by Dr. L. G. Barnes, LACM).

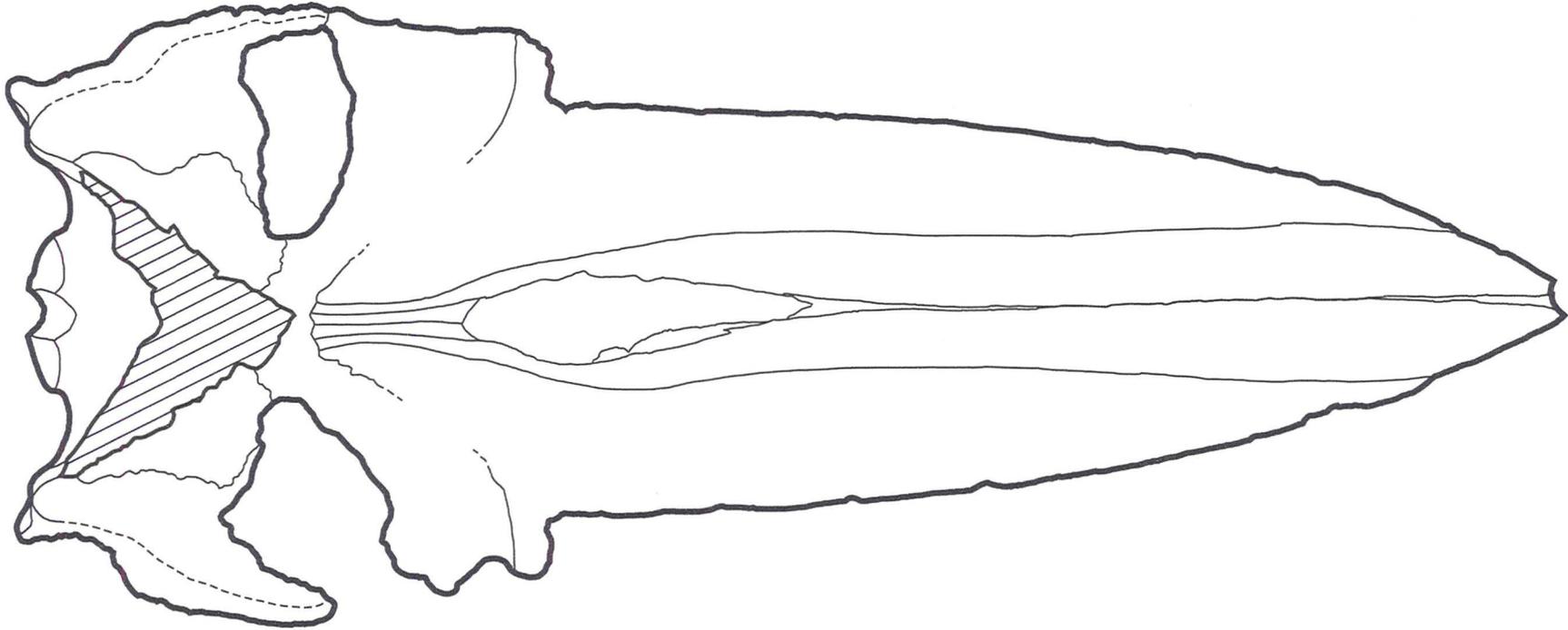


Figure 17: *Mixocetus* n. sp., holotype cranium, LACM 147795. Dorsal view drawing showing crosshatched area where cranial vertex and lamdoid crest were not preserved. Posterior extent of exoccipitals not seen in Figure 16 photograph is restored in this drawing.



Figure 18: *Mixocetus* n. sp., holotype cranium, LACM 147795. Ventral view photograph. Interpretation of the outline of the left temporal fossa (right side in this view) and lateral margin of the zygomatic arch are suspect and will need to be reexamined.

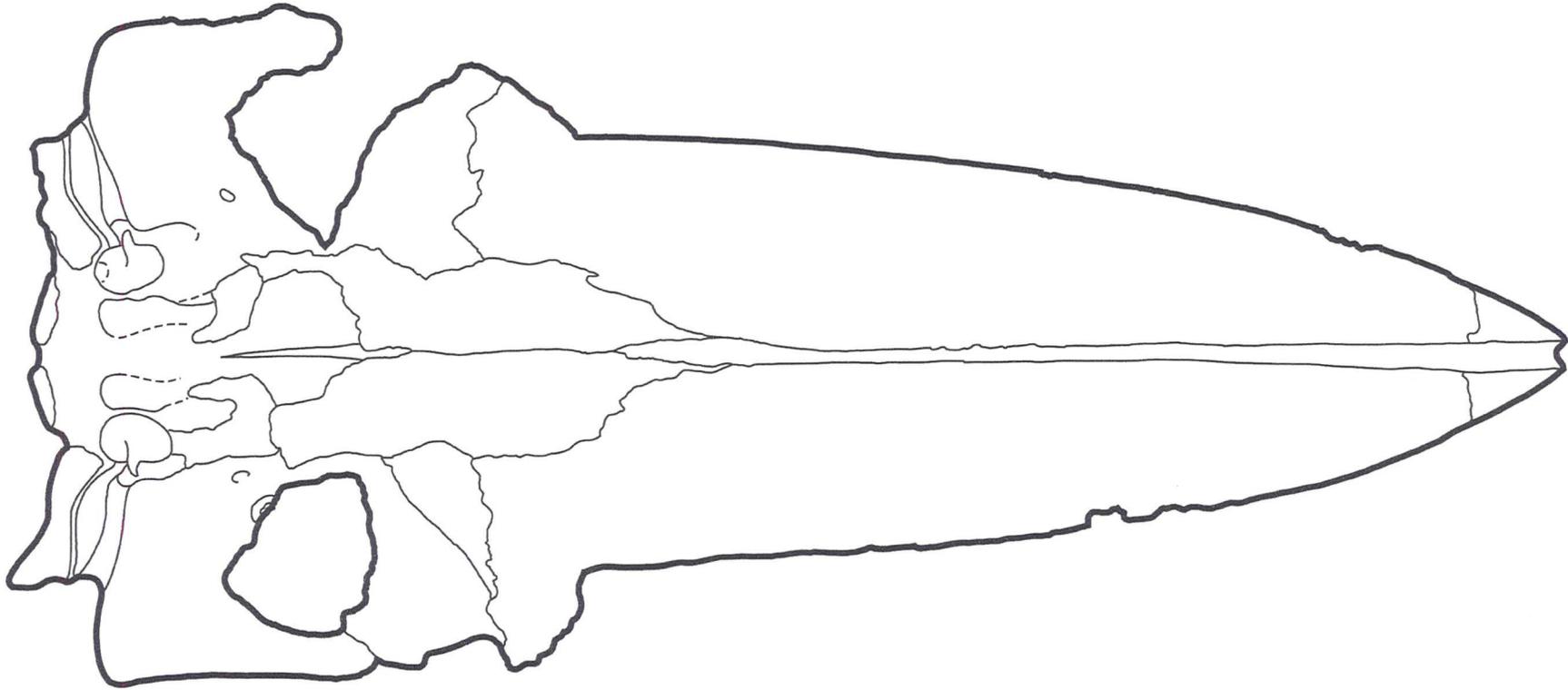


Figure 19: *Mixocetus* n. sp., holotype cranium, LACM, 147795. Ventral view drawing showing outline of the left temporal fossa (right side in this view) to be inaccurately interpreted due to incomplete preparation (see dorsal view for comparison).

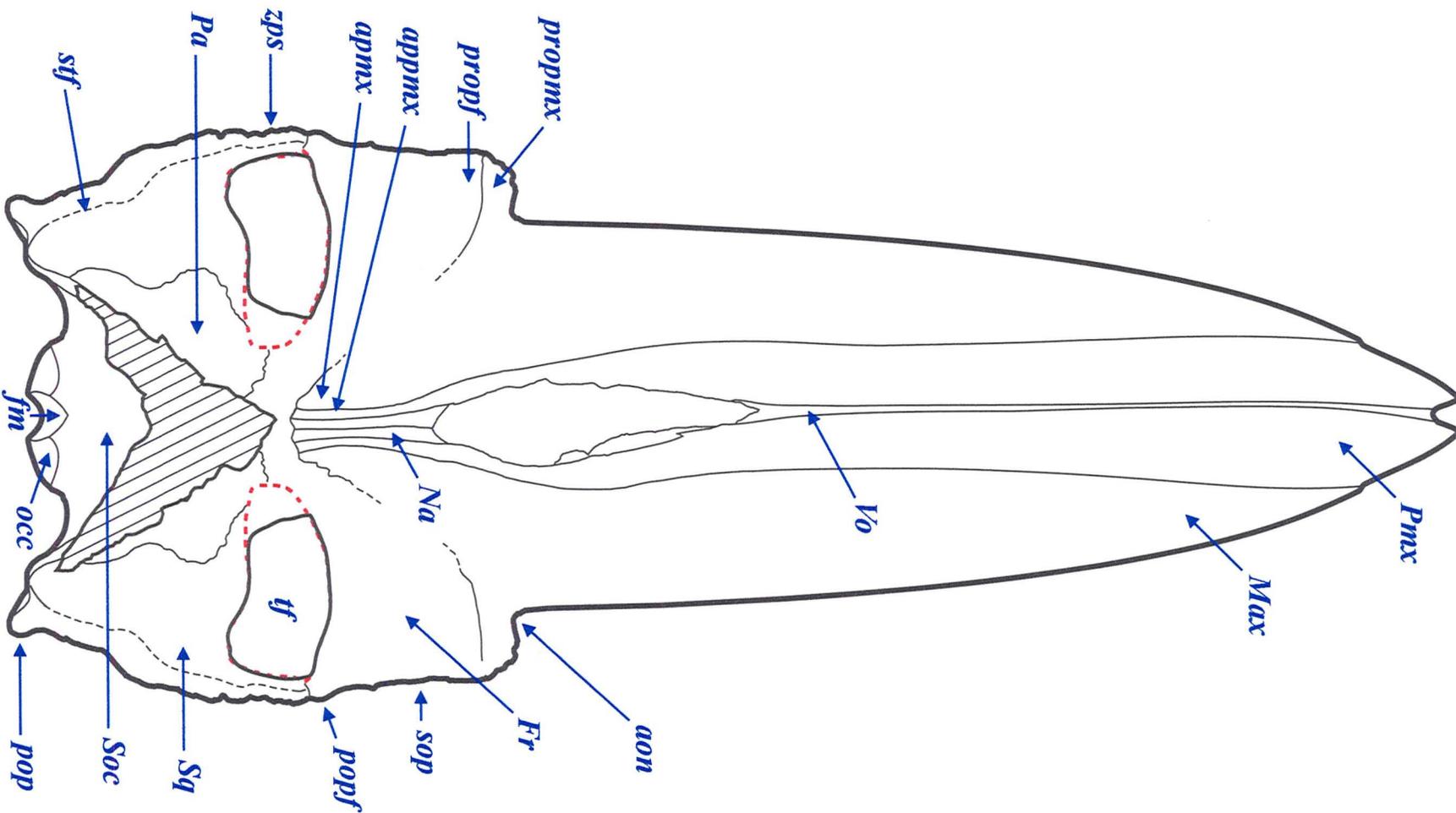


Figure 20: *Mixocetus* n. sp., holotype cranium, LACM 147795. Dorsal view drawing with braincase symmetry restored to correct for distortion. Corrected shape of temporal fossa is inferred from both dorsal and ventral views.

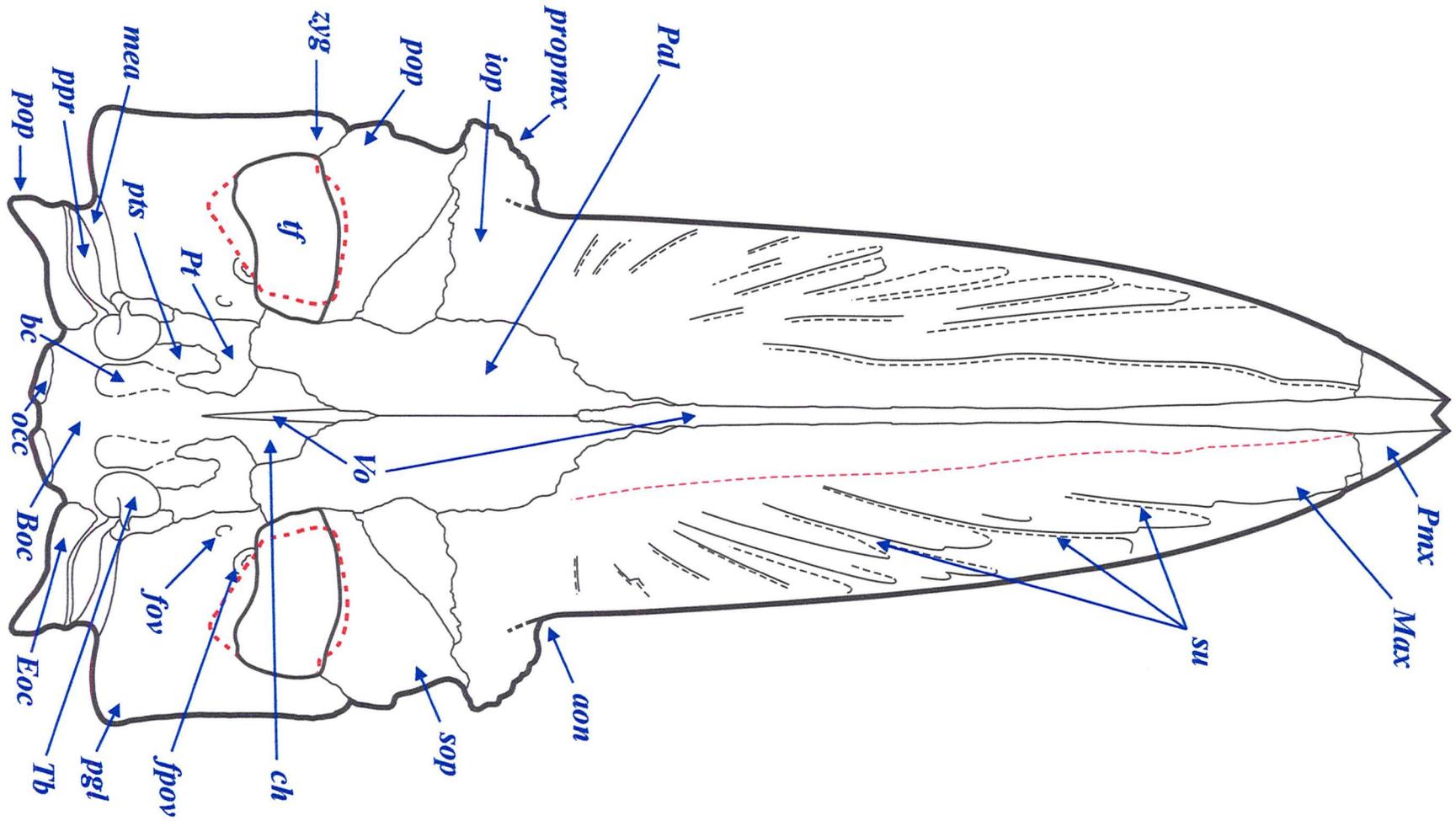


Figure 21: *Mixocetus* n. sp., holotype cranium, LACM 147795. Ventral view drawing with symmetry restored to correct for distortion. Interpreted shape of temporal fossa is inferred from both dorsal and ventral views.

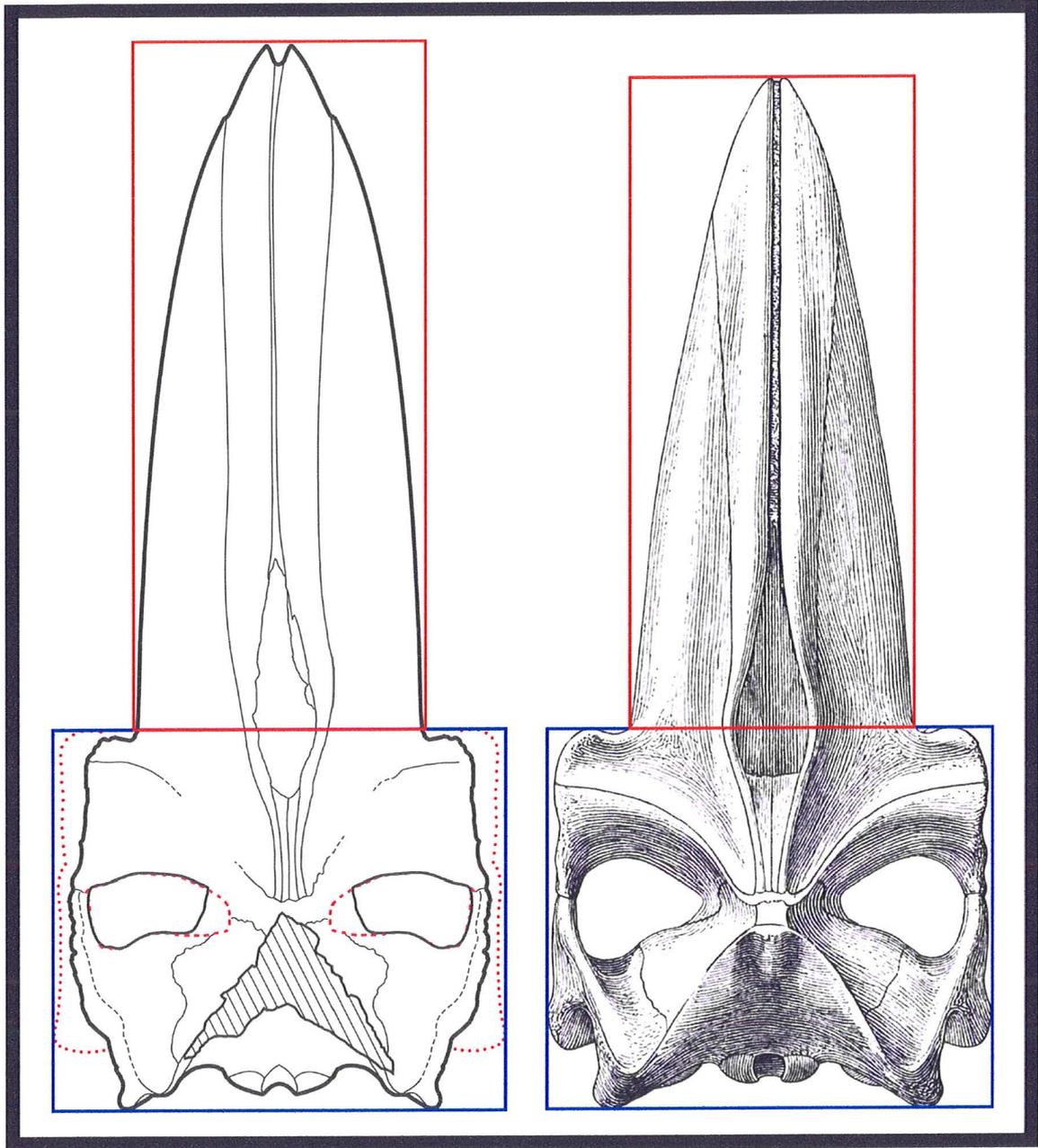


Figure 22. *Mixocetus* n. sp. (left) and holotype cranium LACM 882 *Mixocetus elysius* Kellogg in dorsal view. (Right: modified from Kellogg, 1934b). Braincases (in blue rectangles) scaled to same length. Note more laterally curved dorsal aspect of rostral shape (in red rectangle) for *Mixocetus* n. sp. and comparatively straight aspect for *Mixocetus elysius*. Also note difference in shape of temporal fossa.

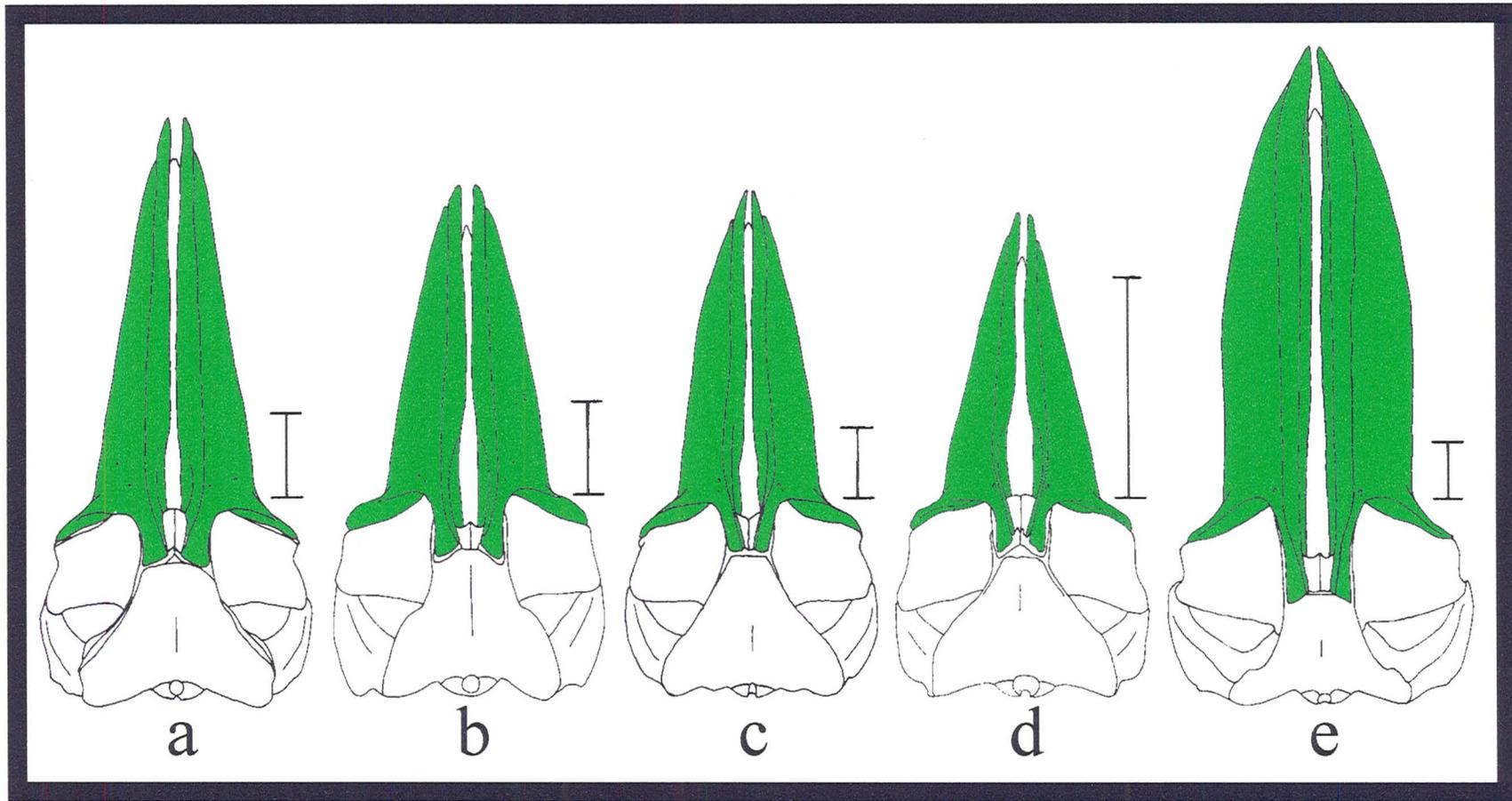


Figure 23. Crania of genus *Balaenoptera*: **a** - *Balaenoptera borealis* Lesson, 1828 (after Miller, 1924b); **b** - *Balaenoptera physalus* Linnaeus, 1758 (after True, 1904); **c** - *Balaenoptera edeni* Anderson, 1879 (after Omura, 1959); **d** - *Balaenoptera acutorostrata* Lacépède, 1804 (after True, 1904); **e** - *Balaenoptera musculus* Linnaeus, 1758 (after Miller, 1924a). Note variations in rostral shape across species. Braincases scaled to same length. Scale bars equal 1 m. (Drawings modified from Barnes and McLeod, 1984).

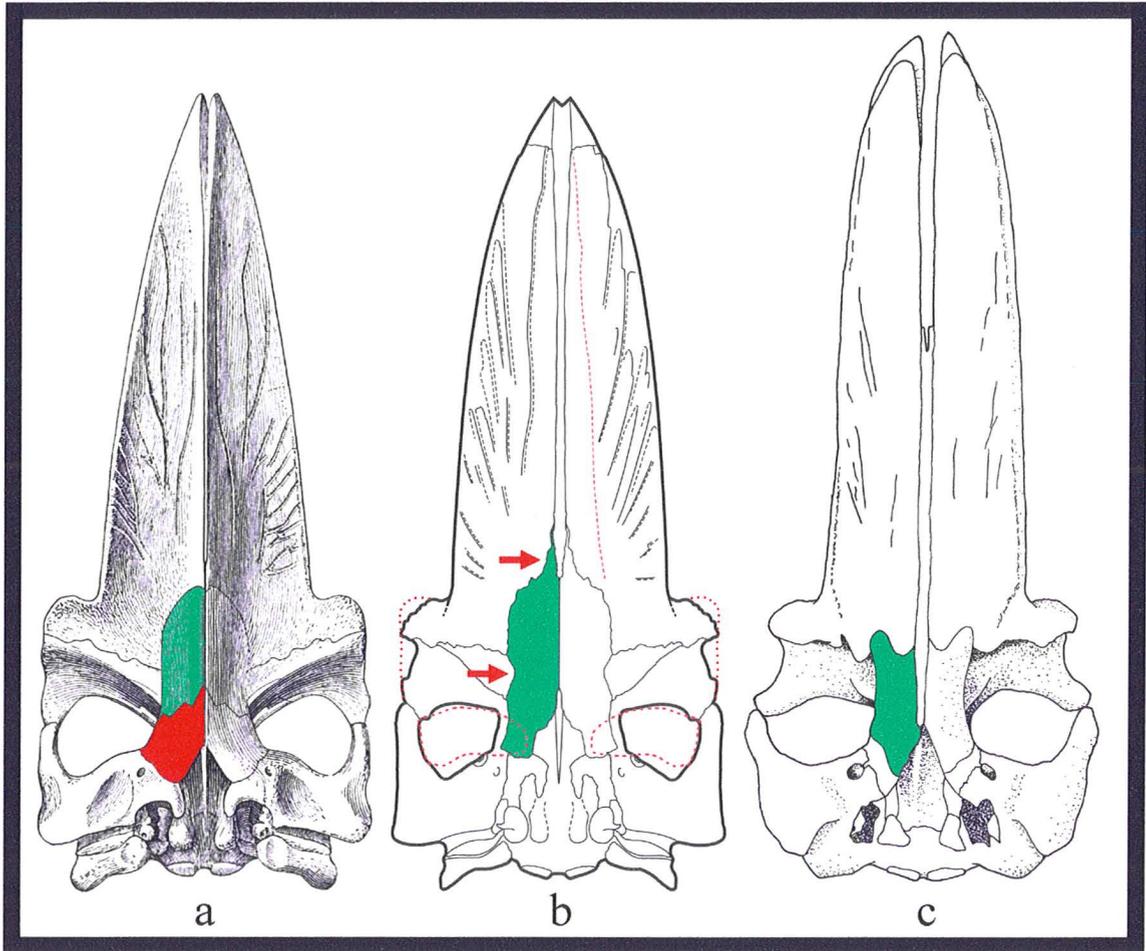


Figure 24. Cetothere crania in ventral view: **a** - *Mixocetus elysius* Kellogg (modified from Kellogg, 1934b), **b** - *Mixocetus* n. sp., **c** - *Piscobalaena nana* Pillari and Siber (modified from Bouetel and Muizon, 2006). Note marked differences in shapes of the palatine bones between different genera (*Mixocetus* and *Piscobalaena*). The red area in image "a" (*Mixocetus elysius*) indicates an unsupported interpretation of the posterior part of the palatine bone which was not preserved in the fossil. Arrows in image "b" (*Mixocetus* n. sp.) indicate morphological differences from *Mixocetus elysius*. All braincases scaled to same length.

MYSTICETE ORIGINS AND FAMILY RELATIONSHIPS

The suborder that includes the fossil and extant baleen-bearing whales underwent remarkable physiological modifications that spanned 50 million years of evolution. The cetotheres, represented a derived group, evolving in a somewhat parallel fashion with the extant rorquals, but went extinct by the early late Pliocene (Barnes, 1977). The new species of *Mixocetus* is here placed in the context of mysticete evolution. The following is a review of important cetacean and mysticete developments, in order of least to most derived, with the important understanding that a theoretical mysticete phylogeny does not constitute a single unbroken lineage. Most are familiar with the classic but erroneous linear ‘evolutionary progression’ from small mesaxonic perissodactyls such as *Hyracotherium* Owen, 1841, toward the larger, more derived, modern equids. This view of evolution was emended by Simpson (1951) who showed that such progressions involved a complex series of radiative branches, with ‘transitional forms’ representing key innovations within broadly-defined evolutionary trends.

Aristotle (circa 343 BCE) was first in the literature to recognize that cetaceans had close affinities with land mammals, e.g., vivipary and nursing of young. Berta et al. (2006) asserted that Aristotle grouped cetaceans (specifically porpoises) with “fishes,” but Aristotle clearly intended to group cetaceans with “mankind and the viviparous quadrupeds,” although he never explicitly asserted a notion of common ancestry. (Aristotle was also unaware of the primitive egg-laying monotreme mammals, including the platypus and echidna, which would have mystified him as much as they did the first European naturalists to describe them.) By contrast, the Swiss naturalist Linnaeus (1735) *did* initially commit the error of grouping cetaceans with fish, but was allegedly urged by

the British naturalist John Ray to amend his *Systema Naturae* by the 10th edition (1785) (Berta et al., 2006). The French naturalist Brisson (1762) erected the order Cetacea (Latin, *cetus*; Greek, *ketos*, "sea monster" or "whale"), initially to include only extant groups; extinct varieties were not yet known.

All mammals have lower jaws comprised of a left and right mandible, homologous with the dentary bones of reptiles, and commonly well-articulated at an anterior symphysis, or, more rarely, fused by ankylosis. Primitive bones of the ancestral-reptilian jaw became modified as bones of the mammalian middle ear (malleus, incus, stapes) housed in the ectotympanic capsule (homologous with the angular bone of reptiles), whereas the inner ear mechanism is housed in the periotic bone (also called petrosal) formed from the fusion of the pro-otic, epiotic, and opisthotic bones of the ventral cranium. In many derived groups, the middle ear is further enveloped in a neomorph hollow capsule, the tympanic bulla, formed by the tympanic part of the temporal bone (Liem et al, 2001).

Cetaceans exhibit further modifications to their ear structure that are adaptations for hearing underwater. The external auditory meatus (sound pathway of the outer ear) is essentially narrowed to a sigmoidal channel, leading to a modified tympanic membrane whose shape is not like the usual circular disc, but instead like a collapsed umbrella with its top attached to the malleus (Thewissen, 2002). In mysticetes, an added protrusion of the membrane (the "glove finger") extends into the external auditory meatus where it connects to the wide end of a conical "wax" plug. This suggests that some residual-sound reception occurs along this pathway (Slijper, 1958). But for cetaceans generally, and echolocating odontocetes in particular, the isolation of ear bones (and their housings)

from the easily sound-resonating skull are important for directional "stereo" hearing underwater.

The primitive dental condition of mammals is heterodonty, and the earliest mysticetes were no exception. Even before primitive mysticete fossils were recognized, it was surmised that the ancestor of modern-baleen whales must have had teeth, based on the observation (Geoffroy St. Hilaire, 1807) that modern-prenatal bowhead whales possessed rudimentary teeth. By the late 19th century, examination of fetal minke whales revealed that they possessed heterodont buds with multiple-cusped cheek teeth and morphologies later understood to resemble those of the extinct archeocetes (Beddard, 1900). The teeth of fetal-baleen whales are resorbed into soft tissues of the alveolar groove before incipient keratinous baleen plates appear prior to birth (Slijper, 1958).

Flower (1864, 1867, 1883a) erected the currently accepted cetacean suborders, which are: Mysticeti (generally suspension-feeding, baleen-bearing, but now known to include archaic toothed forms), Odontoceti (macrophagous, echolocating, and homodont in more derived forms), and Archaeoceti (basal cetaceans possessing heterodont dentitions, which appeared before mysticetes and odontocetes). Flower (1883b) was also the first to propose a kinship between cetaceans and "ungulates" (phenetic grade taxon comprised of all unguligrade land mammals) and noted close affinities with domestic oxen and cows. Their similarities included lumps of tissue in the female/fetus umbilical cord (called "umbilical pearls") and fibroelastic, rather than spongy tissue characteristic of other mammals, in the external male penis (Flower, 1883b, 1887; Theodor, 2002). Flower's view of cetacean-bovine affinity, although reiterated in the work of Beddard (1900), was slow to earn favor among early 20th century taxonomists. This was in part

due to the influence of Darwin (1859) who speculated that cetaceans and "pinnipeds" (grade taxon including seals, sea lions and the walrus) had evolved from bear-like ancestors. Most biologists in the late 19th and for much of the early 20th century favored a theory of cetacean diphyley (e.g., Beddard, 1900; Slijper, 1958, Yablokov, 1965), with mysticetes sharing a common ancestry close to the "ungulates," but with the raptorial odontocetes descending from a separate lineage among the extinct, flesh-eating, archaic creodonts.

As discussed below, the extinct order Mesonychia Matthew, 1937, a group Van Valen (1966) considered to be the most viable candidate for a cetacean ancestor, was initially thought (Cope, 1881) to be creodont, based on their flesh-eating and bone-crushing dentition. The Eocene mesonychid *Andrewsarchus mongoliensis* Pao, 1923, was the largest predator (or carrion-scavenging) land mammal of all time (Prothero and Schoch, 2002). But Van Valen (1966) refuted its alleged creodont affinities and demonstrated instead an "ungulate connection" based on similarities between auditory bullae and the presence of hooves. The mesonychid dentition was then seen as merely convergent with creodonts (and the more derived carnivorans) simply because many early ungulates, unlike modern groups that are all herbivorous, happened to fill similar predatory and/or carrion-scavenging niches. This insight helped to promote the monophyletic view of cetaceans generally, though it would take the discovery of the middle Eocene archeocete protocetid *Rodhocetus balochistanensis* Gingerich et al., 2001, a whale with well preserved hind flippers, to finally confirm the presence of a double-spoiled trochlea (pulley-like smooth structure in the astragalus = ankle bone), a diagnostic character of the Artiodactyla Owen, 1848. Van Valen's "mesonychid

hypothesis” of cetacean origins has fallen out of favor, and the relationship between mesonychids and basil artiodactyls is now more distant than previously thought (Thewissen, 2007). Nevertheless Flower's early insight (1883b) was vindicated. The erection of the putative monophyletic superorder Cetartiodactyla Montgelard, Catzefflis, Douzery, 1997, had been based on genetic similarities between the artiodactyls and the cetaceans (Montgelard, et al., 1997). In current taxonomy, the order Artiodactyla could be considered paraphyletic if it excluded the cetaceans.

The fossil record records three major adaptive radiations of cetaceans over time (Fordyce and Barnes, 1994; Fordyce, 2002b, 2003) which produced five major lineages (**Figure 25**): 1) the archaeocetes (early Eocene), 2) basal mysticetes (late Eocene), 3) basal odontocetes (late Eocene to early Oligocene), and the appearance of more derived families among 4) the balaenopterids, and 5) delphinoids, the latter two groups, in the Miocene. In a number of geologic ranges, relict taxa with primitive characters survived alongside those with derived characters. The suborder Archeoceti was expanded by many new discoveries during the late 20th and early 21st centuries including noteworthy “transitional forms,” arguable intermediates between terrestrial land-mammal ancestral stock, and more derived marine descendants. Although the monophyly of cetaceans is generally accepted (Fordyce and Barnes, 1994; Fordyce, 2002c), phylogenetic relationships between basal groups and modern taxa are in many cases difficult to resolve. Commonly, “ghost lineages” between basal and more derived forms must be inferred to connect disparate taxa (**Figure 26**).

The first radiation of cetaceans in the early Eocene (Ypresian to earliest Lutetian) covered the initial transition from hoofed-terrestrial-freshwater-semi-aquatic cetaceans in

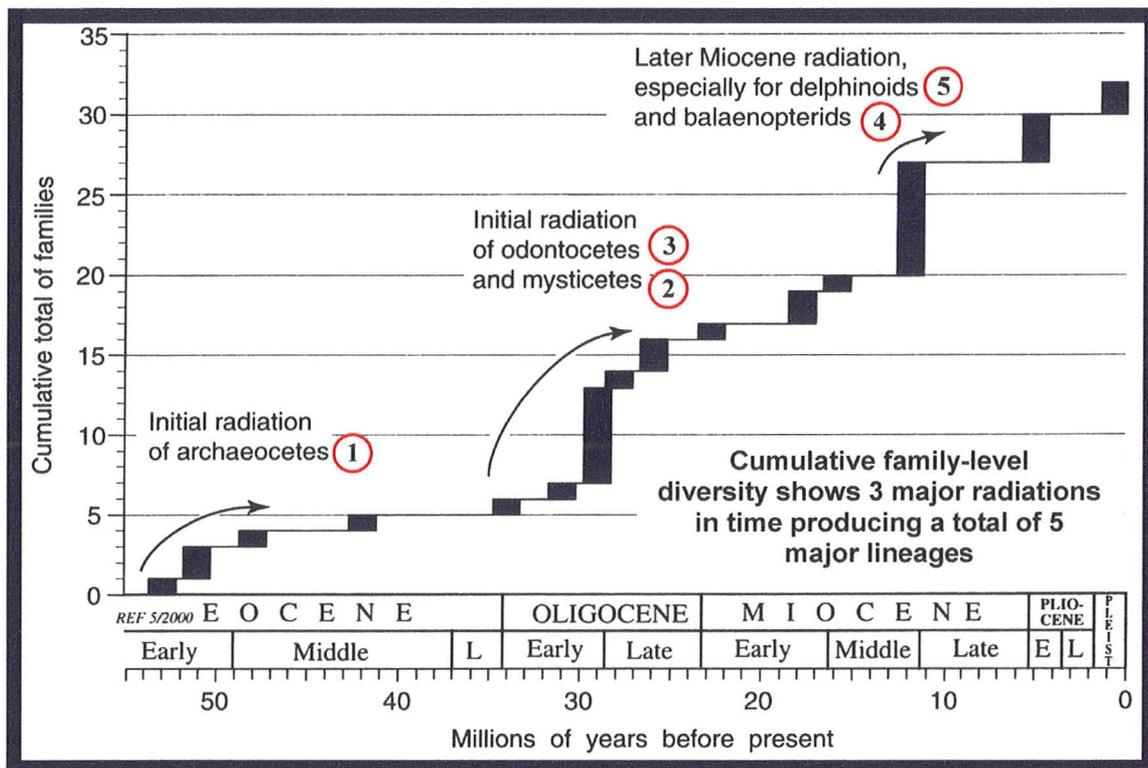


Figure 25: Graph of cetacean family diversity through geologic time. (Modified from Fordyce, 2002b). Three major radiations in time (curved arrows) are noted, the last two are each comprised of two separate radiations into more diverse lineages.

the Indo-Pakistan region, to aquatic-marine mammals located near the warm shores of the ancient Tethys Sea. The first fully marine cetaceans appeared sometime in the middle Eocene. The tectonic arrival of the micro-continent of India, which broke off from Gondwana during the Late Cretaceous and traveled north to Asia, began to restrict the flow of ocean currents into the eastern Tethys by the late Paleocene. The Antarctic Circumpolar Current (ACC) was not yet fully established in the early to middle Oligocene due to insufficient deep water south of Tasmania, and in the narrow gap between the peninsulas of South America and Antarctica following their separation from Gondwana. The eventual formation of the ACC, sometime in the middle Oligocene, is presumed as the cause of Antarctic glaciation (Fordyce, 1992, 2003), although this is

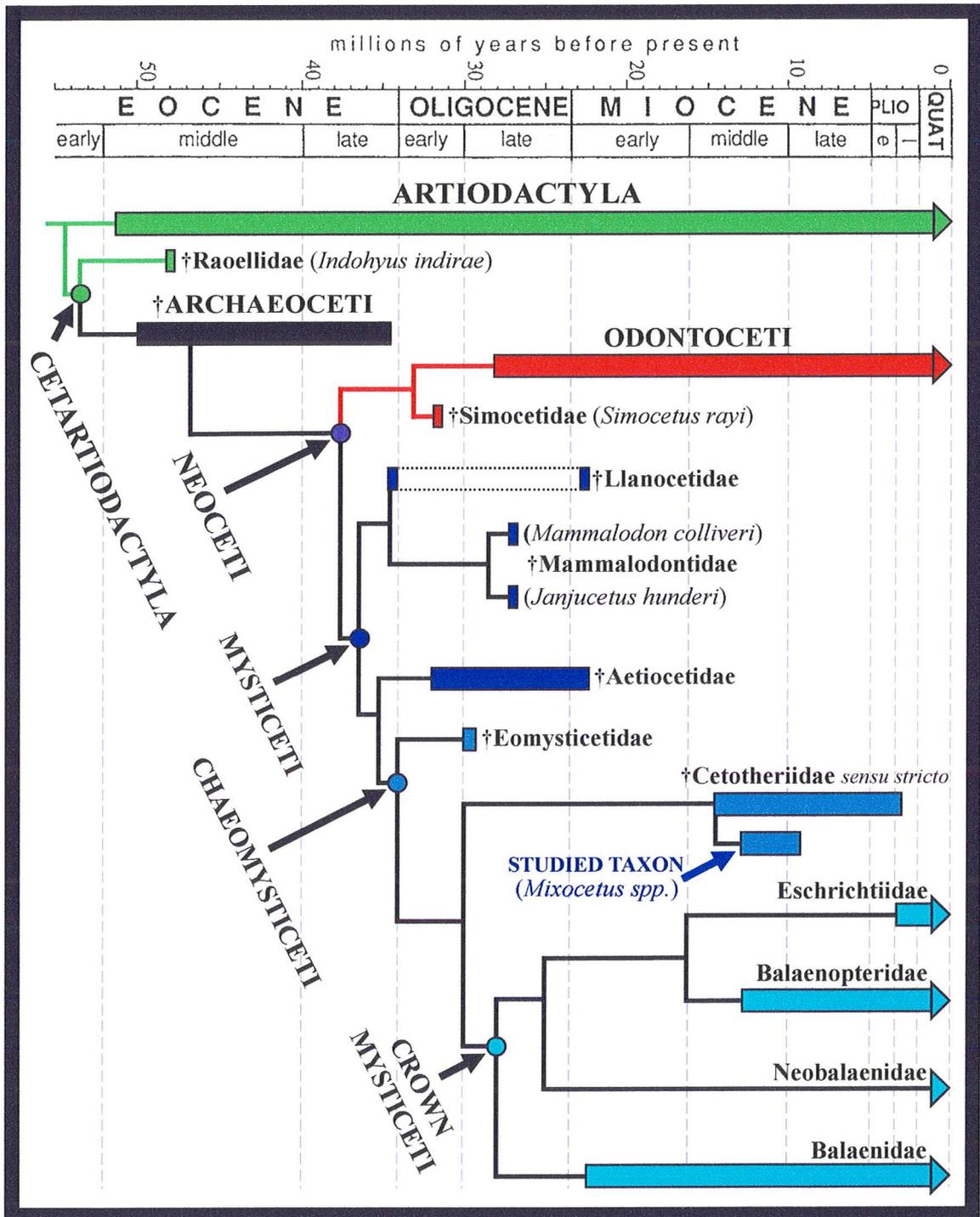


Figure 26: Phylogenetic chart showing geologic ranges and placement of family Cetotheriidae in relation to other taxa. Thin branches are ghost lineages. (Based on Perrin et al., 2002; Rivin, 2010; Dr. L. G. Barnes, personal communication).

controversial. Some workers (Raymo and Ruddiman, 1992; Barker and Thomas, 2004; Ruddiman, 2005) have argued that global cooling during the Oligocene was initiated by the "scrubbing-out" of carbon dioxide from the atmosphere due to chemical weathering associated with rainfall on the uplifting Himalayan mountains. But prior to this time, during the early Eocene, global oceanic circulation was moderate and characterized by the mingling of waters between lower and higher latitudes. A condition termed "Proteus Ocean" (extensive warm saline oxygen-depleted deep water) caused warm climates worldwide (Kennett and Stott, 1995).

The Paleocene-Eocene Thermal Maximum (PETM), a spike in average-global temperatures, was the highest ever recorded as determined by oxygen-isotope ratios in oceanic sediments. It occurred at the boundary between the Paleocene and Eocene and caused a widespread "bottom-up" extinction of benthic foraminifera (Kennett and Stott, 1995). On the continents, high temperatures depleted tropical forests, and these conditions might have driven the extinction of archaic mammalian lineages, perhaps permitting the rise of new orders and families (Janis, 1993). The micro-continent of India might have tectonically transported the land-mammal ancestor of the cetaceans from Gondwana to Asia aboard a biogeographic "Noah's Ark" (Krause et al., 1997).

At the base of the first adaptive radiation of the cetacean lineage is the recently redescribed (Thewissen, 2007) *Indohyus* Rao, 1971, a middle Eocene semi-aquatic wader of the extinct family Raoellidae Sahni et al., 1981. This animal resembled in size and general appearance members of the extant family Tragulidae Milne-Edwards, 1864 ("chevrotains") (Thewissen et al., 2007). Differing from the chevrotains, *Indohyus* was endowed with a large and powerful tail, which might have provided exaptational utility

for later developing an otter-like, dorsal-ventral-flexion swimming behavior. Even so, *Indohyus* is not interpreted (Thewissen et al., 2007) as a strong swimmer, but rather, a wader that may have fled into rivers to avoid predation in the fashion of *Hyemoschus aquaticus* Ogilby, 1841 (the African water chevrotain). A notable degree of limb-bone thickening (osteosclerosis), interpreted as a ballast adaptation (Thewissen et al., 2007), is present in *Indohyus*, thereby suggesting that its ancestral lineage had been adapted to aquatic life for some time. Similar homoplastic bone thickening is noted in sirenians, pinnipeds, sea otters, and Mesozoic marine reptiles. *Indohyus* poses a problem for taxonomists because it exhibits an involucrum, the wrinkled outer flap near the aperture along the dorsal tympanic bulla, a character formerly thought to occur only in cetaceans. This character suggests that *Indohyus* could be included as the most basal cetacean, instead of a putative sister taxon, thereby making the order Artiodactyla unstable (Thewissen et al., 2007). For a review of the first land-to-sea transitional families of archaeocetes, consult works by Gingerich (1998, 2003, 2009), Gingerich et al. (2001), Thewissen (1998), Thewissen and Bajpai (2001), and Thewissen and Williams (2002).

During the middle to late Eocene, cetaceans of the family Basilosauridae Cope, 1868, developed the first fully marine adaptations and were the first to develop gigantism (up to 16 m in length) (Barnes and Mitchell, 1978). It is believed that somewhat smaller animals (about 8 - 10 m in length) of the basilosaurid subfamily Dorudontinae Miller, 1923, produced the common ancestor of the first odontocetes and mysticetes (Fordyce and Barnes, 1994; Gingerich, 1998). The basilosaurids and dorudontines had highly reduced vestigial hind limbs, retained ancestral-heterodont dentition, but lacked the extreme “telescoping” of rostral and cranial bones seen in more derived cetaceans. Even

so, the nares had begun to move back from the ancestral anterior position to that of the dorsal mid-rostrum. Extreme telescoping as exhibited by more derived cetaceans is a condition where: 1) the posterior bones of the cranium are compressed to the point where they overlap each other, and 2) the bones of the rostrum are greatly elongated by extension of the nasal, maxillary, premaxillary, and frontal bones to the point where they overlap the parietal bones (Miller, 1923; Feldhamer et al., 2004). This condition served to accommodate the posterior repositioning of the nares to the top of the skull, an adaptation that enhances energy-efficient breathing while swimming.

Paleogeographic and climatic changes have been implicated in providing selective pressures for the second major cetacean radiation (**Figure 25**) that produced the first Neoceti Fordyce and Muizon, 2001, an unranked taxon commonly called the "crown-group" cetaceans. This group, which includes both extant suborders Mysticeti and Odontoceti and their common ancestor, is considered monophyletic (Fordyce and Barnes, 1994, Fordyce and Muizon, 2001). Mysticetes and odontocetes branched off from the dorudontines sometime in the middle to late Eocene (Fordyce and Barnes, 1994; Gingerich, 1998). During the late Eocene and early Oligocene, in high northern and southern latitudes, glaciations probably began, initiating a higher latitudinal temperature gradient. This gradient, combined with the formation of the gyre of the Southern Ocean, produced global cooling and further changes in ocean circulation. The resulting convergence zones produced conditions where cold, upwelling, oxygenated and nutrient-rich deep waters supported a highly productive photic zone at high latitudes. These environmental changes are commonly assumed to have brought about the radiation of new forms and feeding strategies (Fordyce, 1992, 2003).

Major evolutionary trends among mysticetes include loss of teeth (in more derived forms), development of large body size and large heads, shortening of the intertemporal region, and shortening of the neck (Fordyce and Barnes, 1994). The mysticetes initially lacked baleen and retained many primitive characteristics of the archeocetes including symmetrical skulls and archaic heterodont dentition, but the mysticetes eventually developed a ligamentous mandibular symphysis allowing more kinesis articulation of the lower jaws. The late Oligocene baleen-bearing mysticete *Micromysticetus rothauseni* Sanders and Barnes, 2002, which is similar to the cetotheres (discussed below), also retained primitive characteristics shared with the archaeocete *Zygorhiza kochii* Kellogg, 1936, e. g., similar periotics and a similar axis (no. 2) vertebra.

Three families of archaic-toothed mysticetes are usually recognized: 1) Llanocetidae Mitchell, 1989, from upper Eocene strata in the Antarctic Peninsula, 2) Mammalodontidae Prichard, 1939, from upper Oligocene strata in Australia, and 3) Aetiocetidae Emlong, 1966, from upper Oligocene strata of the North Pacific (western North America and Japan). The evolutionary relationship among the putative archaeocete ancestor and the three archaic-toothed mysticete families is not clear. Some similarities between toothed mysticetes and archeocetes led to a number of the former being initially classified as archaeocetes (Emlong, 1966; Russell, 1968). These diagnoses were later revised after further study (Fordyce, 1982a; Barnes et al., 1994).

Llanocetus denticrenatus Mitchell, 1989, from the late Eocene, was a relatively large archaic-toothed mysticete with a skull length of about 2 meters. It represents the first apparent trend towards gigantism (if one defines "gigantic" as anything over an estimated 10 m for body length) in the Neoceti. Eight such trends in cetacean history

can be recognized, 1) the large serpentine archeocete basilosaurids, 2) the basal mysticete *Llanocetus*, 3) the eomysticetids (discussed below, these might have been too small to qualify), 4) the larger cetotheres (also discussed below), 5) the extant gray whales, 6) the extant family of the bowhead and right whales, 7) the extant rorquals, and 8) the odontocete giant sperm whale.

The post-canine teeth of *Llanocetus* were molariform with palmate denticles (**Figure 27**) that superficially resembled those of the extant filter-feeding crabeater seal *Lobodon carcinophaga* Hombron and Jacquinot, 1842, although the teeth of *Llanocetus* were much more widely spaced (Mitchell, 1989). Much has been written about a putative bulk/filter-feeding mechanism in *Llanocetus* (Mitchell, 1989; Fordyce, 2003b), but it is not clear how a large diastema could have facilitated this function without 'proto-baleen' or soft tissue morphology in the margins (Mitchell, 1989). In the absence of the latter, the dentition of the crabeater seal, with its much closer lattice-like tooth occlusion,

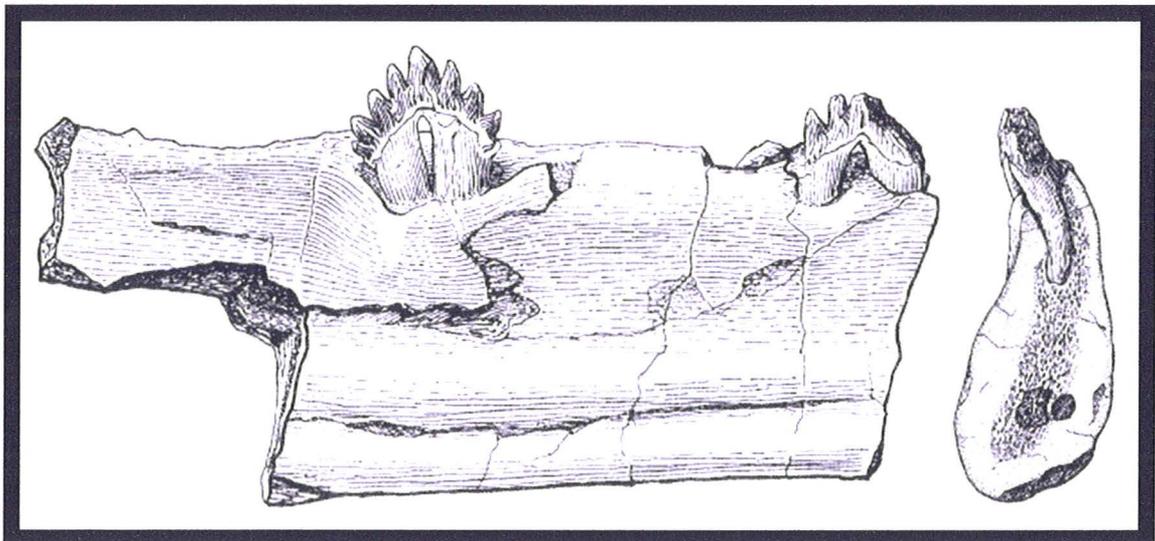


Figure 27: *Llanocetus denticrenatus* Mitchell, portion of right dentary holotype, USNM 183022. Specimen is 32.3 cm long and shows widely spaced palmate teeth (from Mitchell, 1989, Fig. 2).

functions much better as a sieve.

Mitchell's (1989) original placement of *Llanocetus denticrenatus* in the Mysticeti was made from cranial morphologies inferred from an endocast (e.g., slope of an inferred occipital shield). The incomplete mandibular fragments do not preserve the mandibular symphysis region. Therefore, it cannot be determined if *Llanocetus* had a ligamentous symphysis, a morphology interpreted as a condition which developed to facilitate bulk feeding. Although a nearly complete skull of *Llanocetus* exists, it awaits full description by Fordyce (Berta and Deméré, 2009). Although the only confirmed specimens are reported from upper Eocene strata in the Antarctic Peninsula, a recent putative llanocetid fossil from lower Miocene strata in the Vaqueros Formation of southern California (Rivin, 2010) might extend the family's geologic range into the early Miocene.

At first glance, a better candidate for a toothed filter-feeder might seem to be *Janjucetus hunderi* Fitzgerald, 2006, reported from upper Oligocene strata of Victoria Australia. This bizarre small animal (skull length about 50 cm) had large cheek teeth with less splayed, palmate-denticle morphology and more closely spaced tooth occlusion by comparison with *Llanocetus*. But a number of features, including deep double-socketed tooth roots and large orbits positioned to look forward that allowed for keen binocular vision, suggest that *Janjucetus* was a raptorial and sarcophagous animal that grasped relatively large and struggling prey. *Janjucetus* probably hunted by sight, in the same presumed fashion as its archeocete ancestors (Fitzgerald, 2006).

Another strange fossil find from upper Oligocene strata in Victoria Australia that represented an animal of comparable size to *Janjucetus hunderi*, is *Mammalodon colliveri* Prichard, 1939. This animal possessed a short wide rostrum and closely spaced

heterodont teeth not well preserved in specimens. Fordyce (1984) adopted a lunge-feeding/bulk-feeding interpretation for geologically early mysticetes including *Mammalodon*. Reconstructions of *Mammalodon* (e.g., Schouten in Fordyce, 1987; Long in Long and McNamara, 1991), have commonly shown pleated throat grooves similar to modern roquals, such as the blue and humpback whales. Recent work by Fitzgerald (2010) reinterpreted *M. colliveri* as a suction feeder based on its blunt but wide/rounded rostrum and large number of foramina and sulci within the facial fossa of the dorsal anterior maxilla. These morphologies suggest enhanced innervation of powerful upper lip muscles, possibly used in the same fashion as the modern walrus (*Odobenus rosmarus*, Linnaeus, 1758) that feeds individually on medium- to large-sized benthic mollusks and other invertebrates. If this interpretation for *Mammalodon* is correct, this condition would be convergent in at least three lineages of marine mammal, the third being the bizarre extinct odontocete *Odobenocetops* Muizon, 1993. This form of benthic suction feeding should not be confused with the bulk-feeding method of the extant gray whale, which utilizes short and thick baleen racks to sift amphipod crustaceans, polychaete worms, and other invertebrates from benthos scooped from the sea floor and expelled in the water column.

Despite their apparent differences in feeding strategy and rostral/dental morphology, Fitzgerald's (2010) recent reassessment of both *Janjucetus hunderi* and *Mammalodon colliveri* prompted him to consider these sister taxa based on six cranial similarities, and to include *Janjucetus* in the family Mammalodontidae. It is unfortunate that none of the most primitive-toothed mysticete specimens (*Llanocetus*, *Janjucetus* and *Mammalodon*) has well preserved mandibular symphyses. Fitzgerald (2006) originally

identified a shallow groove on the medial anterior side of the *J. hunderi* mandible, which he interpreted as evidence for an incipient ligamentous symphysis, but later retracted this as a misidentification (Fitzgerald, 2010). All that can be said in this regard about the three described genera of basal-toothed mysticetes is that they had short symphyses. Their true condition of articulation would shed light on the transition from the archaeocete-sutured to the mysticete-ligamentous symphysis. Certainly, *J. hunderi* and *M. colliveri* are too young geologically to be ancestors to the edentulous mysticetes and add little to support the notion of the original split between mysticetes and odontocetes being driven by a marked shift to a bulk-feeding strategy for the mysticetes (Fitzgerald, 2010). The feeding strategy of *Janjucetus* is the most primitive and archaeocete-like, whereas that of *Mammalodon* is specialized and more derived.

The aetiocetids were the most diverse group of toothed mysticetes, ranging from more basal forms, such as *Chonecetus sookensis* Russell, 1968 and *Chonecetus goederorum* Barnes and Furusawa, 1994, which exhibit a primitive stage of cranial telescoping, heterodonty, and placental mammalian tooth count (11/11), to the derived *Aetiocetus polydentatus* Sawamura, 1994, with a more highly telescoped cranium, polydont tooth count (13-14/14-15), and homodont dentition (Russell, 1968; Barnes et al, 1994). In this last respect, *A. polydentatus* seems convergent with many odontocetes, but was not necessarily a macrophagous raptorial predator (see further discussion below). All aetiocetids were relatively small (skulls averaging 65 cm, bodies no longer than 2 m), had elongated rostra in comparison with more basal-toothed mysticetes, and unequivocal longitudinal grooves on the medial side of the mandibular apex. These mandibular grooves are interpreted (Barnes, et al., 1995) as attachment points for a ligamentous

symphysis. Whether this latter condition appeared in basal aetiocetids as an adaptation for filter feeding, or was merely exapted from an earlier function, is unclear. There is disagreement on the question of aetiocetid monophyly (Fitzgerald, 2010), but it appears the aetiocetids are closer to the basal filter-feeding edentulous mysticetes than they are to the most primitive tooth mysticetes (Llanocetidae and Mammalodontidae) in relative rostrum length and narrow thickness at the margins. All aetiocetids are reported from the upper Oligocene deposits of the North Pacific across a wide range of longitude (from Japan to North America), but it is expected that southern species will be found (Barnes et al., 1994). Recent findings of aetiocetids in Orange County California might extend the geologic range of the family a bit further into the early Miocene (Riven. 2010).

Deméré et al. (2008) reexamined the skull of *Aetiocetus weltoni* Barnes and Kimura, 1994, and noted palatal features that indicate the presence of baleen. In extant and fossil edentulous mysticetes, the margins of the maxillae are structurally thin. In these animals, the ventral maxillae have extensive radiating sulci (grooves flaring laterally at increasing angles from the sagittal plane toward the posterior), with associated foramina, through which innervations and blood vessels are channeled to nourish the baleen. The maxillary margins of *A. weltoni* are similarly thinned and the lateral area of the ventral rostrum reveals similar foramina and sulci structures, though much less extensive in comparison with edentulous whales. Not all workers (Dr. L. G. Barnes, personal communication) accept the interpretation that the sulci structures in *A. weltoni* nourished baleen. Baleen is a keratinous tissue not generally preserved in the fossil record. A few rare examples have been found, but none are older than late Miocene (Dr. L. G. Barnes, personal communication). Fossil-baleen whales are more commonly

diagnosed from a lack of teeth and the presence of sulci and foramina in palate bones, which represent pathways for blood vessels providing nutrients to baleen-producing tissues.

A baleen-bearing transitional form between archaic-toothed mysticetes and more derived edentulous bulk feeders might be found among the aetiocetids, but the earliest unequivocal baleen-bearing mysticetes *incertae sedis* appear in the geologic record at or before the Eocene/Oligocene boundary, long before the appearance of any aetiocetids (Sanders and Barnes, 2002b, Barnes personal communication). At best, the most basal aetiocetids could represent relictual descendants from a stem sister taxon to the clade comprised of the edentulous baleen-bearing mysticetes. In any case, this does not rule out the possibility of an aetiocetid lineage developing a bulk-feeding strategy that could serve as an analogue for the earlier transition to baleen-bearing lineages. This feeding strategy presumably involved consuming slippery, small- to medium-sized schooling fish or squid, supported by the presence of long and broad rostra with somewhat loosely articulated lower jaws.

It is interesting to note that a few captured rorqual sei whales (*Balaenoptera borealis* Lesson, 1828) have been observed with reduced non-functional baleen, yet appeared to be in seemingly good health with stomachs brimming with anchovies and other small schooling animals (Rice, 1961, Watson, 1981). The baleen on these animals was only seven cm long and had no hairy fringes. This suggests that a bulk-feeding strategy could easily have evolved in early mysticetes before the appearance of functional baleen. Perhaps even the more derived aetiocetid, *Aetiocetus polydentulus* fed in a similar manner with rostral morphologies homoplastic with some of the early as well as

modern baleen-bearing mysticetes.

Another model for this transition might be Dall's porpoise (*Phocoenoides dalli*, True, 1885), an odontocete with a wide rostrum and several prominent maxillary ridges (Heyning and Lento, 2002) in the palate making an angle of 130° to the rostral axis. This animal has numerous highly reduced teeth, many of which do not project far beyond the gum tissue layer (Jefferson, 2002). The gum layer itself is horny and cornified ("gum teeth"), compositionally similar to baleen on a microscopic scale (Miller, 1929; Barnes, 1985), but used to grip small slippery prey rather than sifting. This condition could represent a model for the incipient stage of baleen development which provided the exaptable structures available for later development as sieves for enhanced-bulk feeding. Although it is reasonable to assume piscivory as primitive for all cetaceans, particularly the macrophagous form inherited from the archaeocete tooth morphology (Barnes et al, 1994), the first mysticete bulk feeders may have taken squid and crustaceans as well as small fish.

The most primitive edentulous mysticete in many respects, although not the oldest, is *Eomysticetus whitmorei* Sanders and Barnes, 2002, from upper Oligocene strata of South Carolina. Along with only one other species (*Eomysticetus carolinensis* Sanders and Barnes, 2002), the two comprise the first of only two recognized families of fossil baleen whales, the Eomysticetidae Sanders and Barnes, 2002, and the Cetotheriidae Brandt, 1872 (Miller, 1923; Bouetel and Muizon, 2006; Whitmore and Barnes, 2008). Eomysticetids were moderately sized (skull just over 1.5 m in length) and had very long and relatively narrow rostra. Some features of eomysticetid skulls are similar to those found in archaeocetes, namely, narrow and elongate intertemporal region, narrow

supraorbital process of the frontal, elongate zygomatic process of the squamosal, long nasal bones with nares located more anterior along the rostrum, and small cochlear portion and narrow anterior process of the periotic bone (Sanders and Barnes, 2002b). Other osteological features of importance include number and structure of vertebrae and ribs (intermediate between archeocetes and the edentulous mysticetes loosely classified as "cetotheres") and a relatively long humerus compared with other primary appendicular bones.

The more posterior placement of the nares at mid-rostrum in comparison with the archeocetes, evident in both the toothed aetiocetids and edentulous eomysticetids, suggests homoplasy in the telescoping of the skull. Although this is controversial (Dr. L. G. Barnes, personal communication), the telescoping trend might have developed independently in at least two early mysticete lineages. Some workers (Steeman, 2007) have argued for further examples of independent telescoping among mysticete lineages, e. g., the balaenids, balaenopterids, and cetotheres. Certainly, there are similarities as well as differences in the particular form of rostral-bone-posterior-extension at the genus level, but as to how much these similarities might represent homoplasy vs. genuine common ancestry at higher taxonomic ranks is unclear. (Of course, the differences in telescoping between the odontocetes and mysticetes clearly indicate independent evolutionary trends because the odontocetes lack the anterior extension of the supraoccipital and their rostral bones extend posteriorly much further in a manner totally different from that of the mysticetes.)

The rostrum of the eomysticetids is flat and suggests an active engulfment feeding strategy similar to the extant rorquals (Balaenopteridae), as contrasted with the more

passive ram/sift-feeding method of the extant bowhead and right whales (Balaenidae) or benthic suction/filter-feeding method of the extant gray whales (Eschrichtiidae). However, the amount of vascularization in the palatal surface is small compared to extant mysticetes, suggesting that the baleen of eomysticetids was very short in length compared to modern taxa. Despite the primitive characters of their crania, the fact that eomysticetids were edentulous and possessed baleen suggests that a baleen-bearing lineage branched off from stem mysticetes well before their fossil record first appears (Sanders and Barnes, 2002b, Fitzgerald, 2006, 2010). Transitional mysticetes, from least to most derived, are shown in **Figure 28**.

It is assumed by Mitchell (1989) and Fordyce & Barnes (1994) that baleen evolved only once among mysticetes to satisfy the preference for parsimony, a notion used to justify erection of the infraorder Chaeomysticeti to include all extinct and extant baleen bearing mysticetes (Mitchell, 1989; Fordyce and Barnes, 1994). A sister infraorder Crenaticeti Mitchell, 1989, combining the most basal toothed mysticete families Llanocetidae and Mammalodontidae seems less justified because these taxa do not appear to be closely related. The transitional history from toothed to baleen-bearing mysticetes has a poor fossil record, but toothed mysticetes from upper Oligocene strata of South Carolina (Barnes and Sanders, 1996) might shed some light on this.

The other extinct family of edentulous mysticetes is Cetotheriidae, which includes in its rank the new species studied in this thesis. The family was formerly considered a paraphyletic (and likely polyphyletic) group when including all so-called "cetotheres" *sensu lato*, making it the most diverse taxon among cetacea of any time period with up to 30 genera and 60 species (Kellogg, 1931, Barnes and McLeod, 1984, Fordyce, 1992).

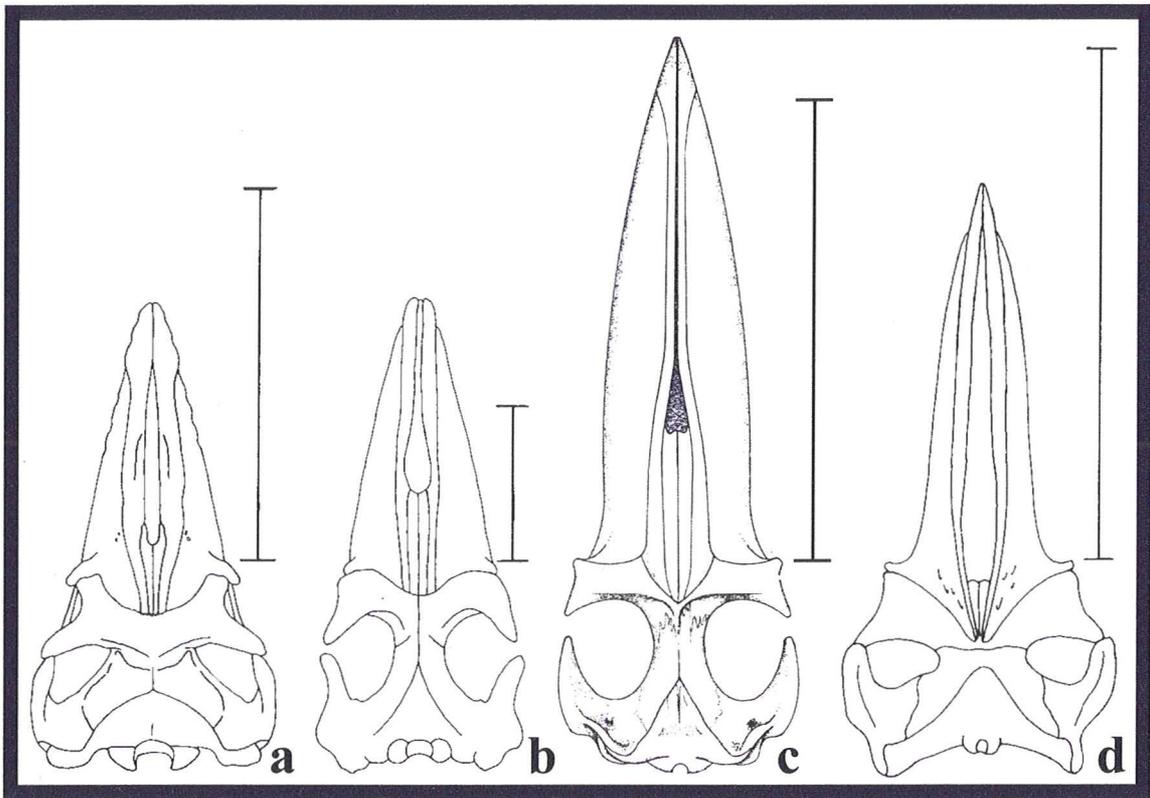


Figure 28. "Transitional" fossil mysticete crania in dorsal view: **a** - *Aetiocetus cotylalveus* Emlong (after Emlong, 1966), **b** - *Mauicetus lophocephalus* Benham, 1939 (after Marples, 1956), **c** - *Eomysticetus whitmorei* Sanders and Barnes (after Sanders and Barnes, 2002b), **d** - *Cetotherium rathkii* Brandt (after Van Beneden and Gervais, 1880). From left to right (least-to-most derived): **a** - toothed mysticete of family Aetiocetidae, **b** - enigmatic baleen-bearing whale *incertae sedis*, **c** - early edentulous whale in family Eomysticetidae (moderately telescoped cranium), **d** - derived edentulous whale in family Cetotheriidae (highly telescoped cranium). (a, b, and d, from Barnes and McLeod, 1984; c, from Sanders and Barnes, 2002b). Braincases scaled to equal length. Scale bars = 1 m.

The revision of this family (see remarks in "Systematic Paleontology") has narrowed the number of taxa to less than a dozen genera. These cetaceans were small to medium sized (3-10 m in overall length) with small heads compared to body length. The family increased in diversity by the early middle Miocene, declined in the middle to late Miocene, and dropped off rapidly in the Plio-Pleistocene (Fordyce, 2002b).

The bloom of diversity recognized as the third major radiation of cetacea is presumed to have been driven by oceanographic and climatic changes which ultimately

led to the "icehouse" conditions of the Plio-Pleistocene (Fordyce, 2002b). The precipitous decline of "cetotheres" occurred concurrently with and following this radiation, a time of greatest diversification of the balaenopterids that began to out-compete and displace other active engulfment feeders. General similarities of skull shape and a putative shared-feeding strategy might have inspired popular reconstructions of *Cetotherium* as a streamlined rorqual-like whale with throat grooves (e.g., Gould in Chadwick, 2001). The term "rorqual" is derived from the Norwegian word for "furrow," referring to grooves in the throat which dilate during feeding, greatly increasing the capacity of the buccal cavity and food intake. The rorqual-like reconstruction of *Cetotherium* is speculative, but certainly more justified than with *Mammalodon*. The "cetotheres" generally exhibit a cosmopolitan distribution with specimens reported from eastern and western North America (including southern California), South America, Europe, New Zealand, and Japan (Barnes, 2002). A map of fossil occurrences with approximate age ranges for genera in the Cetotheriidae *sensu stricto* is shown in **Figure 29**. It is not possible to determine if the cetotheres were partitioned into 'bipolar' taxa seasonally and genetically isolated from each other, in the manner of modern northern and southern minke whales.

Two fundamental problems associated with the taxon Cetotheriidae remain unresolved in modern study: 1) the relationship of cetotheres to the extant crown group (Balaenopteridae, Eschrichiidae, Balaenidae, and Neobalaenidae) and 2) the relationships among genera of cetotheres within a meaningfully narrowed family clade. A large percentage of "cetothere" *sensu lato* taxa are probably not related, and the group was considered a "waste basket" in which historically any edentulous fossil mysticete not

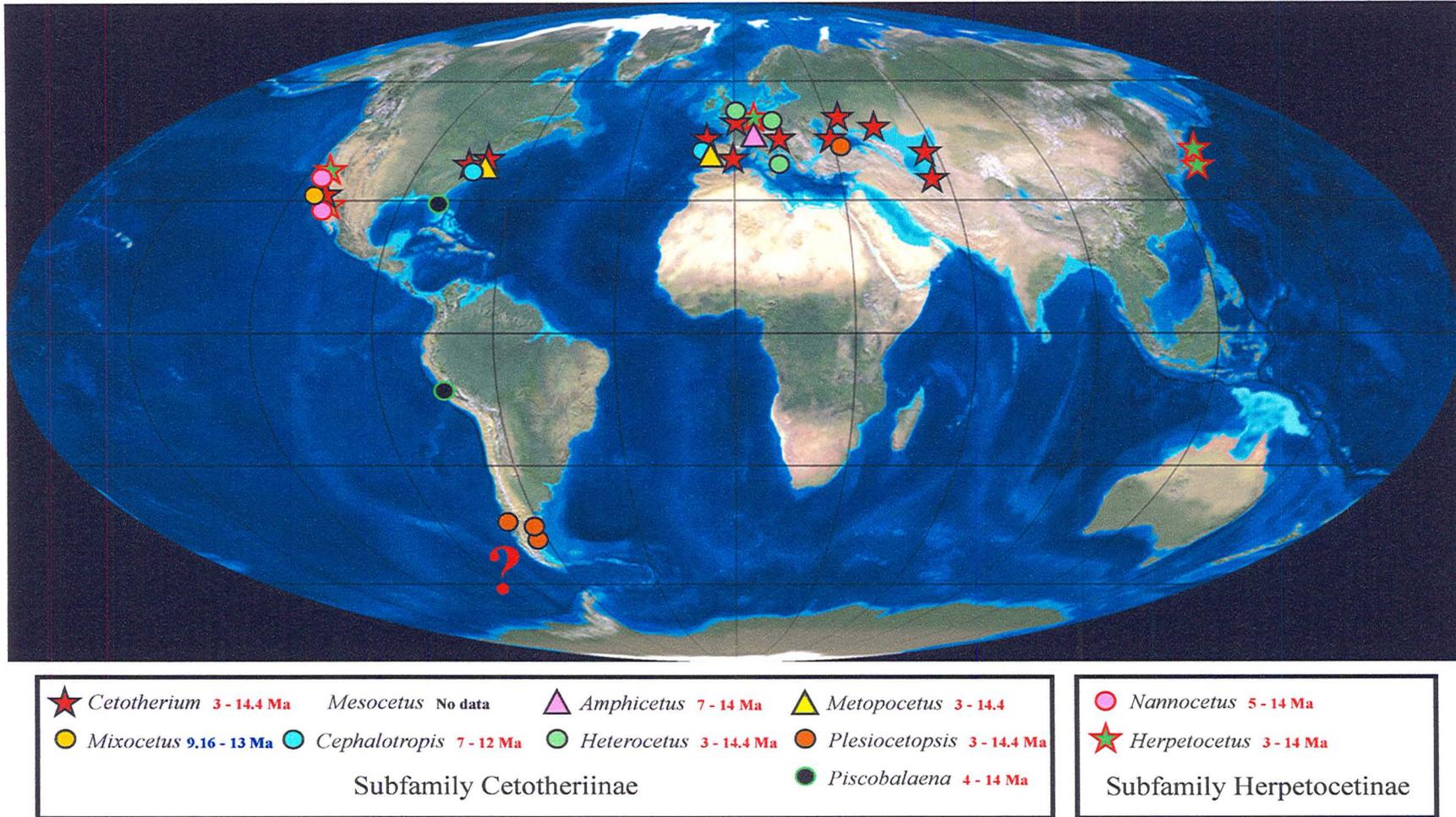


Figure 29. General paleogeographic distribution of genera in the family Cetotheriidae, early middle Miocene to early late Pliocene. Age ranges in red are suspect and need to be refined. Occurrences of *Plesiocetopsis* in the Patagonian region are suspect due to possible synonymy with *Plesiocetus*, a taxon not included in Cetotheriidae *sensu stricto*. (Background Miocene mollweide map from Blakey, R., <http://jan.ucc.nau.edu/~rcb7/20moll.jpg>, accessed on November 11, 2010; Age and distribution date from Uhen, M., <http://paleodb.org/cgi-bin/bridge.pl>, accessed on November 11, 2010.

considered a member of extant groups has been lumped. It has become somewhat of a flippant cliché to suggest that any newly discovered, well-preserved "cetotheres" skull should automatically be assigned to a new genus (Dr. A. Dooley, personal communication). Some new genera assigned to this family, such as *Isanacetus* Kimura and Ozawa, 2002, have closer affinities with stem balaenopterids and might not belong to the Cetotheriidae *sensu stricto* (Dr. L. G. Barnes, personal communication).

Historically the relationship of the cetotheres to the "crown-group" mysticetes has been confusing. In the 19th century, all baleen whales were assigned to one of two families (Brandt, 1873; Cope, 1896), the Balaenidae (right and bowhead whales) and Balaenopteridae (rorquals), or to a single family only (Flower, 1883a, 1883b), the Balaenidae. Brandt (1872) initially erected Cetotheriinae as an extinct subfamily within the extant Balaenopteridae based on the similarity of flattened rostra and interdigitation of rostral and cranial bones. Brandt (1873) later elevated the cetotheres to family rank and Miller (1923) offered the first significant character rediagnosis.

Eventually it was recognized that the "cetotheres" were somewhat more primitive based on the temporal-fossa area being generally exposed in dorsal view, rather than being overthrust by margins of the supraoccipital shield (Miller, 1923). But cetotheres do share some features with extant mysticetes (e. g., the posterior ascending process of the maxillary bones), thus the cetotheres display an intermediate mosaic of relatively primitive with derived characters. For most of the early and middle 20th century, it was assumed that the extant mysticetes arose from ancestors among the "cetotheres" (Kellogg 1928; Slijper, 1958). Cabrera (1926) and Kellogg (1934a) proposed that a clade of Cetotheriidae *sensu stricto* surrounding the type genus *Cetotherium* had provided the

ancestor of the rorquals. According to Bouetel (2005), there are three characters shared among *Cetotherium rathkii*, *Herpetocetus sendaicus*, *Metopocetus durinasus*, *Nannocetus emerus*, *Piscobalaena nana*, *Mixocetus elysius*, and the extant rorquals. These shared characters are: 1) the interdigitation of rostral and cranial bones, 2) a massive posteriorly developed angular process of the dentary, and 3) a long hook-like outwardly bent coronoid process of the mandible. These features, combined with a short ligamentous symphysis, provide control of longitudinal rotation and widening of the lower jaws associated with active engulfment feeding. This similarity could either represent a simple homoplasy resulting from similar selective pressures giving rise to the same engulfment feeding strategy, or a genuine and relatively recent common ancestry (Bouetel, 2005).

Miller (1923) suggested that a taxon including *Cetotherium* and related genera, combined with the gray whales (Eschrichtiidae), would be the sister to a rorqual clade based on two shared characters: manner of telescoping inducing the interdigitation of rostral and cranial bones, and the nasals and posterior process of the premaxillae extend to a line joining the preorbital process of the frontals. Andrews (1914) also saw close similarities between the crania of cetotheres and gray whales, e. g., the thick and protruding exoccipitals onto which the lambdoid crest does not encroach. A similar view based on more numerous characters is echoed in the recent work of Bisconti (2007b) and Steeman (2007). Others (Dooley et al., 2004) have argued for a clade uniting Balaenoptera and Eschrichtiidae with the cetotheres more distant. Molecular studies show a closer affinity between gray whales and rorquals as compared with other extant mysticete families (Jones and Swartz, 2002). Bouetel and Muizon (2006) also placed the cetotheres as distant to the crown-group mysticetes, but placed Eschrichtiidae as sister to

the superfamily Balaenoidea (combining Balaenidae and Neobalaenidae) based on a shared dorsal curvature of the rostrum. This curvature is less so in the gray whale, as compared with the bowhead and right whales, but nevertheless distinct from the flattened rostra of the rorquals.

The family Balaenidae (bowhead and right whales) is generally considered more primitive than either rorquals or gray whales, with the pygmy right whales, being even more primitive, as indicated in the ghost lineage branching depicted in Perrin et al. (2002, inside cover) (**Figure 29**). The pygmy right whale has one prominent similarity with the Balaenidae (e. g., the arching rostrum), but its massive jaw, the most disproportionately large compared with all other mysticetes, looks nothing like that of the balaenids, and much more like that of the gray whale (Eschrichtiidae) (Watson, 1981, pp. 75 and 77). The pygmy right whale also shares with the gray whale a pair of throat grooves, although homology for this feature is difficult to argue, given that sperm whales also exhibit them, and the more numerous throat grooves of the rorquals have a more functional aspect. But the pygmy right whale shares with the rorquals a similarly placed and shaped dorsal fin (absent in the gray whales) and a similar fusiform body (Watson, 1981). As to which of these similarities (between pygmy right whales and gray whales, or between pygmy right whales and rorquals) represent true homologies vs. simple convergences, is not well understood. Genetic studies (Árnason and Best, 1991, Adegoke et al., 1993, Árnason and Gillberg, 1994) have suggested that the pygmy right whale is the remnant of an ancient sister group to a rorqual - gray whale clade. Clearly, relationships among some modern taxa, and among modern and fossil taxa, have not been fully resolved. A comparison of two contrasting views on mysticete family relationships and the placement of the

cetotheres is shown in **Figure 30**.

Some workers (Kimura and Ozawa, 2002; Bisconti, 2008; Barnes, personal communication) have concluded that *Cetotherium* (type genus of family Cetotheriidae) and *Mixocetus* (type species *M. elysius*) are sister genera. But others workers have reached different conclusions. Kellogg (1934b) saw closer affinities among *Mixocetus*, *Mesocetus*, and *Metopocetus*. Bouetel and Muizon (2006), Steeman (2007), and Dr. A. Dooley (personal communication) have asserted that *Cetotherium* has more affinities with *Piscobalaena*. Furthermore, Bouetel and Muizon (2006), Drs. A. Dooley (personal communication,) and L. G. Barnes (personal communication) have asserted that *Mixocetus* is most basal in the family as a whole, based on the longer posterior process of the periotic bone as compared with either *Cetotherium* or *Herpetocetus*.

Bouetel and Muizon (2006) have asserted that *Cetotherium*, *Mixocetus*, and *Piscobalaena* share at least three significant characters: 1) the narial opening extends posterior to a transverse line drawn through the anterior extent of the preorbital processes of the maxilla, 2) lateral margin of the zygomatic process is slightly concave, and 3) a sigmoid morphology of the frontal/parietal suture (concaved anteriorly in dorsal extent and convex anteriorly in ventral extent that borders the posterior portion of the temporal crest). This latter character is difficult to assess because the holotype skull of *M. elysius* at LACM is heavily reconstructed with plaster, the result of an early unfortunate attempt to make a display specimen out of the fossil. Indeed, there are not many studies that include *Mixocetus* in a polarized-character matrix. The ones that do (e.g., Kimura and Ozawa, 2002, using 77 generalized characters; Bouetel and Muizon, 2006, using the aforementioned 101 characters split into categories for skull, tympanic, and dentary; and

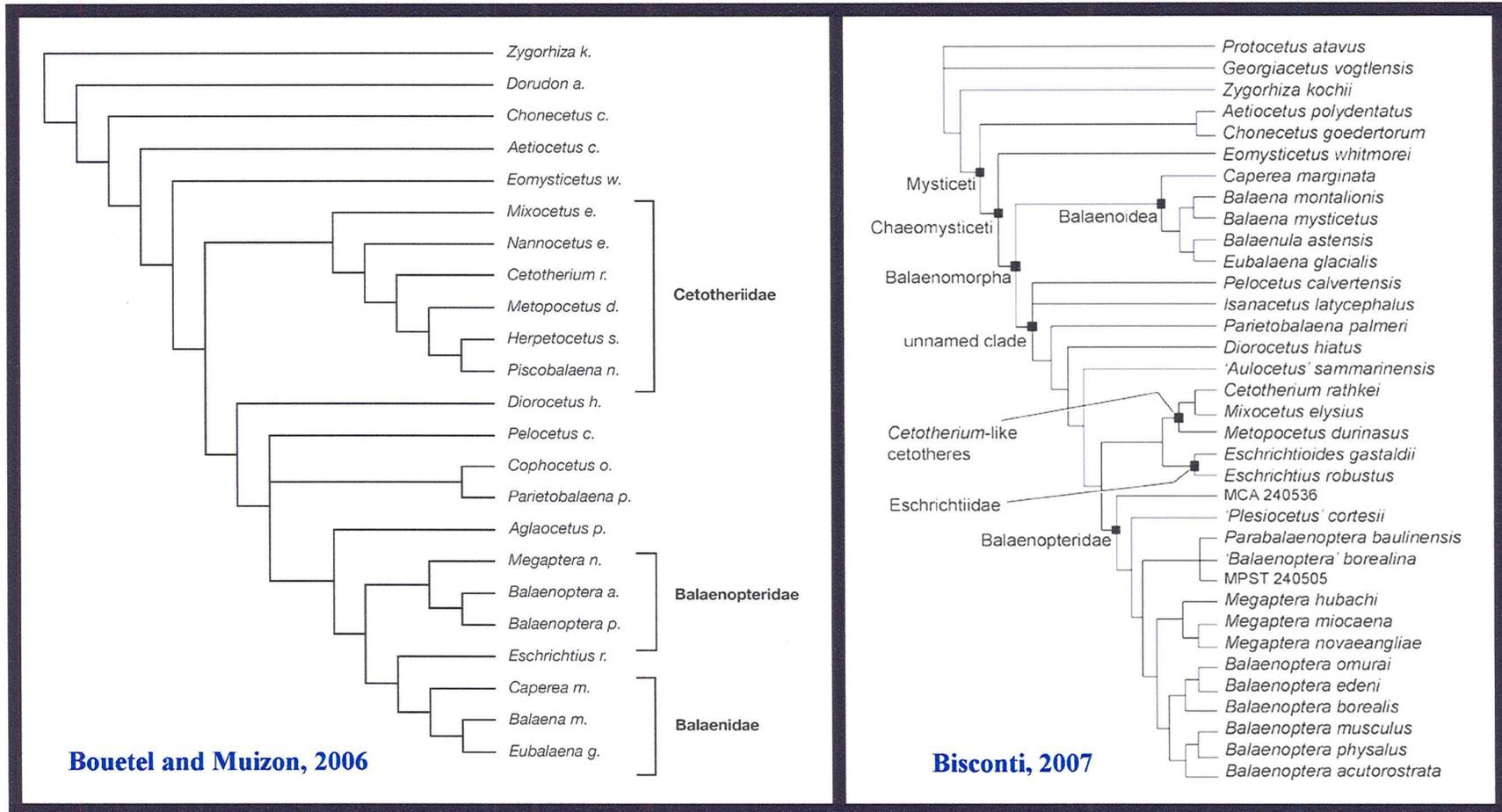


Figure 30. Comparison of contrasting views on mysticete family relationships. Bouetel and Muizon (2006) regard Cetotheriidae as sister to a clade comprised of some stem balaenopterids and the crown group mysticetes. They also recognize an order of least-to-most derived among the Cetotheriidae *sensu stricto*. By contrast, Bisconti (2007) recognizes the “Cetotherium-like cetotheres” as sister to the Eschrichtiidae (gray whales), effectively adding Cetotheriidae into the “crown group” mysticete clade.

Bisconti, 2008, using 165 characters) have many question marks assigned to numerous characters instead of unequivocal numerical values. Steeman (2007, p. 880) regarded *Mixocetus* as *incertae sedis* (of unknown placement) due to its condition of reconstruction and did not include it in a polarized-character matrix. Many of the other taxa in Cetotheriidae are known only from fragmentary remains. Not surprisingly, resolving the relationships among the members of Cetotheriidae, and between the Cetotheriidae and the "crown group," are considered among of the most difficult taxonomic problems in cetacean paleontology (Dr. E. D. Mitchell, personal communication).

Cetotherium is from the Ukraine, whereas both *Mixocetus* and *Piscobalaena* are from the eastern Pacific Basin. This should not be surprising because whales are potentially cosmopolitan and, as previously mentioned, the Isthmus of Panama was still open at the time of the late Miocene and early Pliocene, not closing completely until the late Pliocene, about 3.6 Ma. Except for the questionable case of *Plesiocetopsis*, putatively found at intermediate-to-high southern latitudes of the Patagonian peninsula, possibly misreported due to synonymy with *Plesiocetus* according to Dr. Mark Uhen, (personal communication), and *Piscobalaena* of Peru, all fossils of Cetotheriidae *sensu stricto* have so far been found at what would have been subtropical to temperate locations of the north (**Figure 29**). The cetotheres were a derived group, but were apparently unable to adapt to the climate change and/or competition with other suspension-feeding whales that rapidly diversified during the cooling late Miocene and early Pliocene.

The history of mysticete evolution can be summarized in part by looking at the morphological modifications of the jaw (**Figure 31**) and how these changes relate to

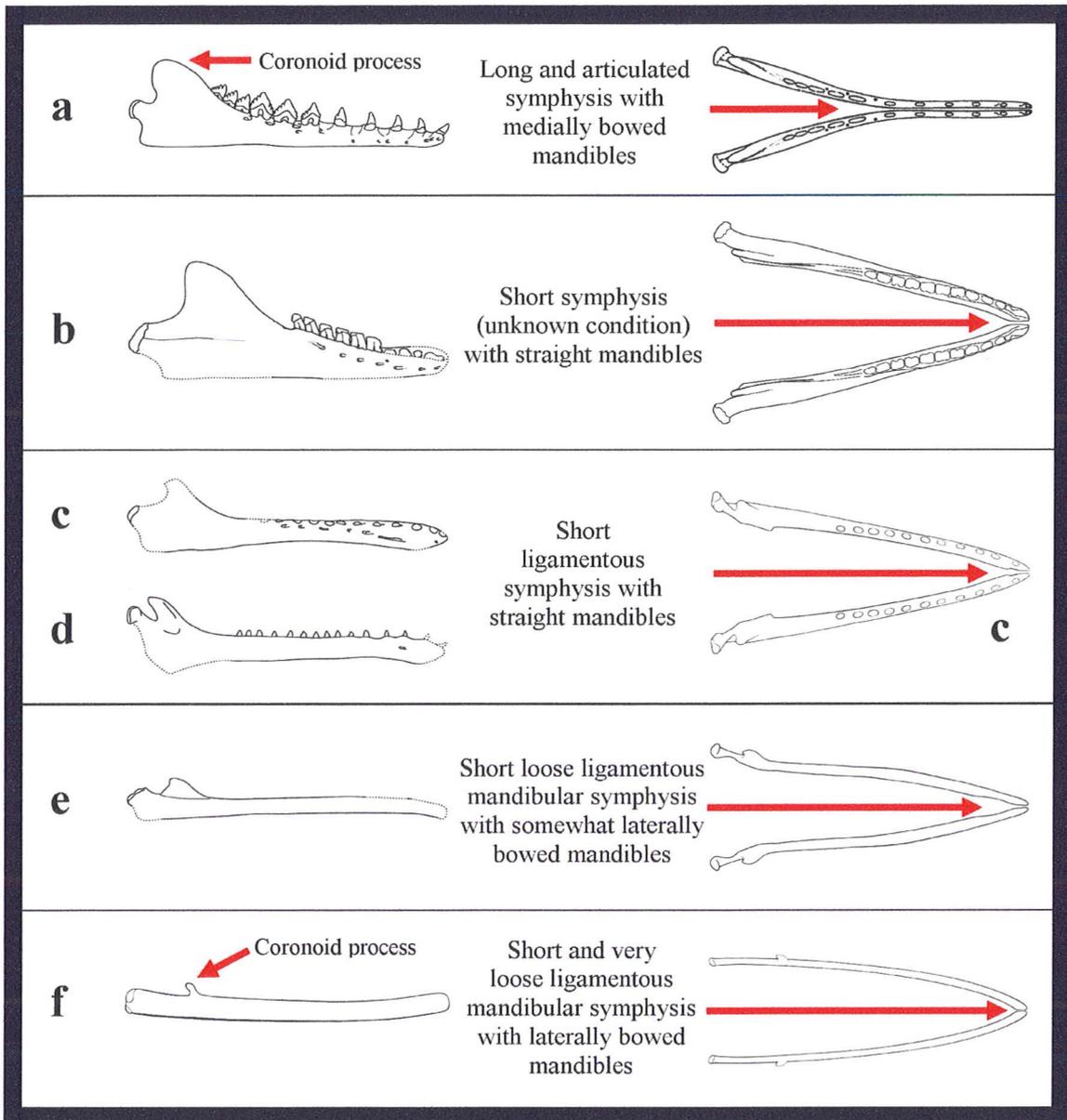


Figure 31: The evolution of the mysticete jaw.

a - *Zygorhiza kochii* Kellogg (ARCHAEOCETI - BASILOSURIDAE),

b - *Mammalodon colliveri* Prichard (MYSTICETI - MAMMALODONTIDAE),

c - *Chonecetus goedertorum* Barnes and Furusawa (MYSTICETI - AETIOCETIDAE)

d - *Aetiocetus polydentatus* Sawamura (MYSTICETI - AETIOCETIDAE)

e - *Eomysticetus whitmorei* Sanders and Barnes (MYSTICETI—EOMYSTICETIDAE)

f - *Mixocetus elysius* Kellogg (MYSTICETI—CETOTHERIIDAE)

(**a** - modified from Kellogg, 1936; **b** - modified from Fitzgerald, 2010; **c** & **d** modified from Barnes, et al., 1995; **e** - modified from Sanders and Barnes, 2002b). Diagram shows changes in symphysis and reduction of coronoid process from least (**a**) to most (**f**) derived. All jaws scaled to same length.

feeding behavior. The most dramatic transition occurred between the archaeocetes and the first mysticetes when the jaw shifted rather suddenly from the condition of a long articulated symphysis to a short symphysis that might have been ligamentous at a very early stage. Unless the first mysticete was a "hopeful monster" (Goldschmidt, 1940), there must have been a gradual shift to this condition represented by some 'missing link' not yet found in the fossil record. The selective pressures that originally produced the short-ligamentous symphysis are difficult to imagine. But once established, it might have been quickly exapted towards a bulk-feeding function. The demands for strong struggling-prey-grasping jaws diminished, leading passively to derived morphologies adapted for specialized forms of filter-feeding including active engulfment for eomysticetids, cetotheres, and the extant rorquals.

SUMMARY AND CONCLUSIONS

The studied fossil whale cranium came to rest in diatomite of the Upper Monterey Formation that accumulated in late Miocene waters of the Capistrano embayment adjacent to the deepening southern Los Angeles Basin. The lithology of the fossil site is typical of a coastal-upwelling high-productivity setting overlying a shelf-slope break with bathymetry approximately 150 to 200 m. The age of the fossil horizon was determined by the presence of the index fossil diatom *Denticulopsis dimorpha* to be 9.16 - 9.9 Ma, a range equivalent to the late Clarendonian NALMA. Despite damage to the skull during excavation, a symmetrical reconstruction of cranial morphology shows that the fossil whale is *Mixocetus* n. sp. and belongs to the extinct family Cetotheriidae Brandt, 1872 (new context, Whitmore and Barnes, 2008). The fossil is nested in the genus *Mixocetus* based on a comparison with *Mixocetus elysius*, a similar fossil cetothere of late Miocene age found in the northeastern LAB. The unique laterally elongate shape of the temporal fossa, unique shape of the rostrum, and unique palatine bones, all support recognition of a new species.

The geologic range of genus *Mixocetus* must be determined from a limited sampling of two fossils. *Mixocetus elysius* was found in upper middle Miocene Mohnian Stage sandstone determined to be 10.5 to 13.0 Ma. Combining this range with the results for *Mixocetus* n. sp. (9.16 to 9.9 Ma) gives a total range of no less than 9.16 to 13 Ma. The range of the family Cetotheriidae *sensu stricto* is given from the age of the oldest and youngest reported members: about 3 to 14.4 million years before present.

The cetotheres were part of a culminating evolutionary process that produced edentulous baleen-bearing whales, in no less than six separate family lineages. The

cetotheres appeared earlier in the fossil record than the extant crown-group mysticetes but the cetotheres might be their sister group. Both the cetotheres and the crown-group mysticetes were derived baleen whales, but the former group apparently could not compete during the early appearance and radiation of modern families and did not survive into the Pleistocene. The study of a new species of *Mixocetus* has hopefully contributed a part to this story. At the very least, it strengthens the diagnosis of the genus. Recent discoveries have filled in many branches of the mysticete phylogenetic tree, but ghost lineages must be inferred to connect disparate fossil taxa. Intermediate forms must be inferred from relict groups that lived along side more derived forms. Only future discoveries will determine how the earliest suspension-feeding Chaeomysticeti, possessing straight or laterally bowed jaws and a short, loose ligamentous mandibular symphysis, suddenly appeared in the fossil record after descending from macrophagous archaic whales with medially bowed mandibles sutured in a long symphysis.

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