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Page(s): Page 229, Page 230, Page 231, Page 232, Page 233, Page 234, Page 235, Page 236,  
Page 237, Page 238

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# Miocene Cetaceans of the Chesapeake Group

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**ABSTRACT.**—The Chesapeake Group of the mid-Atlantic coastal plain of North America consists of nearshore marine sediments that range in age from late Oligocene to Pliocene. The lower to upper Miocene portion of the Chesapeake Group is divided into four formations—in ascending order, the Calvert, Choptank, St. Mary's, and Eastover—which contain a rich and diverse cetacean fauna. General trends within the fauna of these four Miocene formations include the absence of cetotheriid-grade mysticetes in the lower Calvert, absence of squalodontid odontocetes above the Calvert, and an overall reduction in cetacean diversity and total numbers in the post-Calvert formations (possibly associated with environmental changes). Peak diversity and total numbers occur in the upper third of the Calvert, where the dominant forms are long-snouted rhabdosteid odontocetes and cetotheriid-grade mysticetes. Major differences between the cetaceans of the Miocene portion of the Chesapeake Group and the Recent northwestern Atlantic Ocean include the absence of delphinids and large mysticetes and the presence of long-snouted dolphins in the Miocene. Bones of relatively young cetaceans are common in the Miocene Chesapeake Group deposits, probably reflecting the expected high mortality of young individuals, rather than suggesting that the Chesapeake region was a cetacean breeding/calving ground during the Miocene.

## INTRODUCTION

The Chesapeake Group deposits of the mid-Atlantic coastal plain of North America have long been known as one of the world's richest accumulations of late Tertiary marine fossils. Originally called the "Chesapeake Formation" (Darton 1891), the Chesapeake Group (terminology first adopted by Dall and Harris 1892) encompasses upper Oligocene through Pliocene marine claystones, mudstones, siltstones, and sandstones from the Atlantic coastal plain of Delaware, Maryland, Virginia, and North Carolina. According to Ward (1985), the Chesapeake Group consists of the following seven formations (see Fig. 1):

Chowan River Formation .....	upper Pliocene
Yorktown Formation .....	upper to lower Pliocene
Eastover Formation .....	upper Miocene
St. Mary's Formation .....	upper to upper middle Miocene
Choptank Formation .....	middle Miocene
Calvert Formation .....	lower middle to lower Miocene
Old Church Formation .....	lower Miocene to upper Oligocene

Extensive exposures in the Chesapeake Bay region of the Calvert, Choptank, St. Mary's, and Eastover formations, and the abundance of fossil remains, combine to make this part of the Chesapeake Group sequence the best record of Miocene marine life available from eastern North America. Both marine and (less frequently) terrestrial fossils are found, allowing for extraregional correlations with terrestrial and marine sequences from other localities (e.g., Wright and Eshelman 1987). The biota includes palynomorphs, diatoms, terrestrial plants, foraminifers, sponges, annelid worms, corals, abundant and diverse bivalves and gastropods, scaphopods, and a nautiloid, decapod crustaceans, barnacles, an inarticulate brachiopod, echinoderms, abundant sharks and rays, bony fishes, sea turtles and rarer terrestrial turtles, crocodiles, seabirds, occasional land mammals, sirenians, seals, and, rather commonly, cetaceans. General summaries of the geology and paleontology of the Miocene portion of the Chesapeake Group were provided by Clark et al. (1904), Vogt and Eshelman (1987), Ward and Powars (1989), and Ward (1992).

Fossil cetaceans from the Chesapeake Group deposits have been of special interest since the pioneering days of North American paleontology. Explorers and naturalists noted cetacean remains in the Chesapeake region as early as the 17th century (Simpson

1942, Ray 1983). The first formal scientific name assigned to a Chesapeake Group cetacean was *Delphinus calvertensis* Harlan, 1842, among the earliest vertebrate fossils from North America to be formally described (Simpson 1942). Harlan described a specimen (Fig. 2) from the well-known Calvert Cliffs section along the western shore of Chesapeake Bay in southern Maryland. This taxon was later removed from *Delphinus* and placed into *Pontoporia* (Cope 1866) and then *Lophocetus* (Cope 1868c), and was eventually redescribed by Eastman (1907), a history that appropriately symbolizes the taxonomic complications arising from much of the earlier research on Chesapeake Group cetaceans.

Since Harlan's 1842 publication, many prominent paleontologists, including Leidy, Cope, Gill, Eastman, True, Abel, Hay, Case, and most notably Kellogg, have studied Miocene cetaceans from the Chesapeake Group. The bulk of this research has focused on describing new taxa, with comparatively little in the way of more general comparisons and syntheses [see Case in Clark et al. (1904), Kellogg and Whitmore (1957), Kellogg (1957, 1966, 1968), and Whitmore (1971) for earlier general discussions].

This paper enlarges on previous studies of one of the world's richest deposits of fossil cetaceans by providing an overview of Miocene Chesapeake Group cetaceans, including the geologic and paleoenvironmental setting, overall taxonomic diversity, major faunal trends, comparison with modern cetacean assemblages, and aspects of Miocene cetacean paleobiology. We focus on the four formations (see above) that constitute the Miocene portion of the Chesapeake Group; the upper Oligocene to lower Miocene Old Church Formation (named by Ward 1985) is not included because it has not been extensively investigated and to date has not produced significant vertebrate remains. The cetacean fauna of the Pliocene Yorktown Formation is discussed separately (Whitmore 1994, this volume).

## GEOLOGICAL AND PALEOENVIRONMENTAL SETTING

*Geology of the Miocene Chesapeake Group formations.*—The most extensive exposures of the Miocene formations within the Chesapeake Group are found in the Calvert Cliffs (Fig. 3), which extend for approximately 50 km along the western shore of Chesapeake Bay in Calvert and southernmost Anne Arundel counties, southern Maryland; other important localities are found along the

Ma	EPOCH		STAGE	FORMATION	MEMBER	BED	
3.4	PLIOCENE	UPPER	Piacenzian	Chowan River			
				Yorktown	Moore House		
					Morgarts Beach		
					Rushmere		
Sunken Meadow							
5.2		MIOCENE	LOWER	Zanclian			
UPPER				Messinian			
					Eastover	Cobham Bay	
	Claremont Manor						
	Tortonian						
St. Mary's			Windmill Point	24			
	Little Cove Point		21-23				
	Conoy		20				
10.4	MIOCENE	MIDDLE	Serravallian				
Choptank				Boston Cliffs	19		
				St. Leonard	18		
				Drumcliff	17		
Langhian		Calvert Beach	14-16				
		Calvert	Plum Point	4-13			
Burdigalian			Fairhaven	2-3			
			Aquitanian				
21.5	OLIGOCENE		Old Church				
23.3							

Figure 1. Composite stratigraphy of formations constituting the Chesapeake Group, modified after Wright and Eshelman (1987) and Ward (1992). Dates in million years ago (Ma) in left-hand column are at stage boundaries, from Harland et al. (1990). Position of stage boundaries relative to Chesapeake Group formations is approximate; note also that the Eastover Formation extends as far down as 11 Ma according to Ward and Blackwelder (1980) and Andrews (1986).

Maryland and Virginia sides of the Potomac River and in tidewater Virginia (Fig. 4). A newly discovered lower Calvert Formation site in Delaware has produced a more terrestrially influenced fauna than is typical for the Calvert Formation (Ramsey et al. 1992).

Shattuck (1902) subdivided the Chesapeake Group in Maryland into the Calvert, Choptank, and St. Mary's formations; he later (in Clark et al. 1904) divided the three formations into 24 "zones," with "zone" 1 at the base of the Calvert (which lies unconformably above the Eocene Nanjemoy Formation in much of the region) and "zone" 24 at the top of the St. Mary's. Ward (1985) placed

Shattuck's "zone" 1 in the Old Church Formation, but later (Ward 1992) maintained that it was a "distinct unit, younger than the Old Church" (p. 5). In the most recent treatment of these formations the Calvert Formation extends up through "zone" 16, the Choptank includes "zones" 17-19, and the St. Mary's includes "zones" 20-24 (Ward 1992). Shattuck's "zones" are based on changes in lithology, as well as relative abundances—but not unique assemblages—of mollusks; because they are not biostratigraphic zones in the strict sense, we refer to Shattuck's 24 divisions as beds, following Gernant et al. (1971), Wright and Eshelman (1987), and Ward

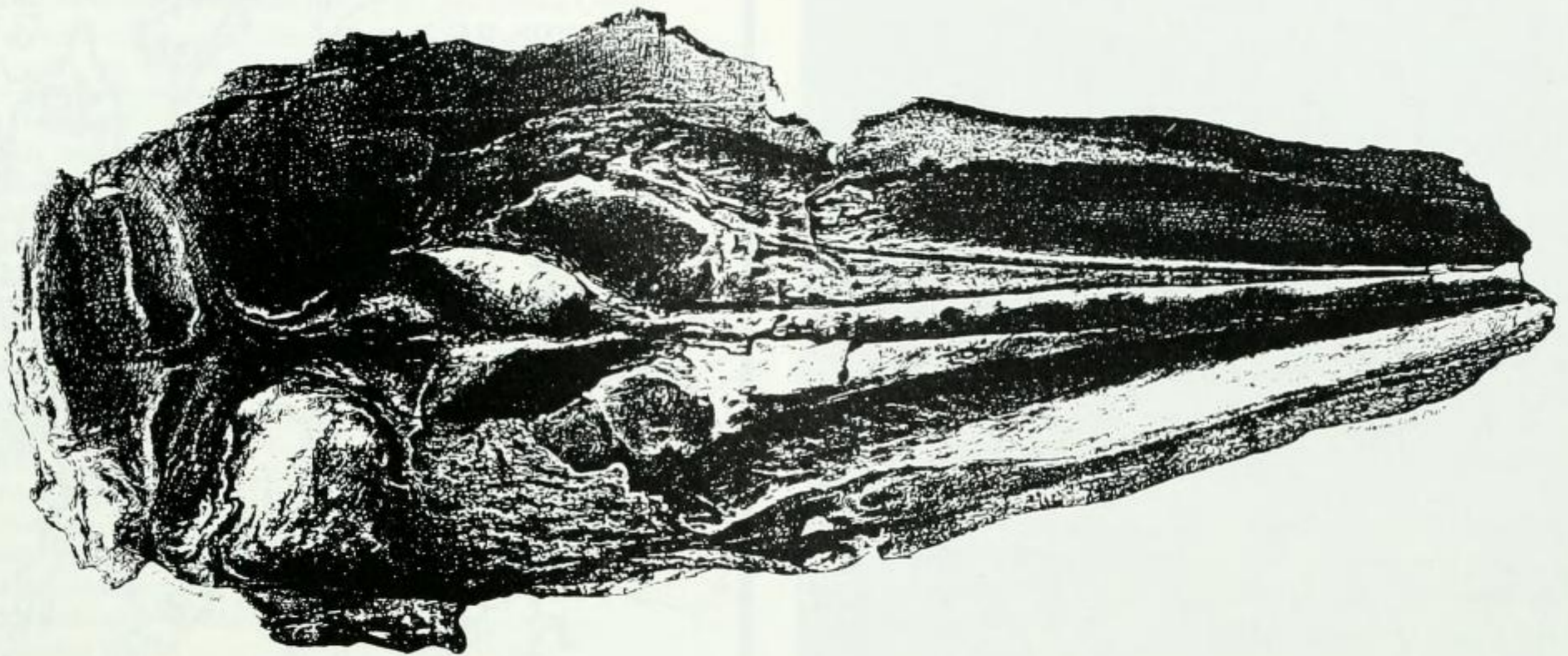


Figure 2. *Lophocetus calvertensis* holotype skull (USNM 16314), in dorsal view. Reproduction of the figure in Harlan's (1842) original description of this specimen as *Delphinus calvertensis*.

(1992). The 24 divisions, however they are referred to, remain useful because they have become the traditional means of indicating relative stratigraphic position within most of the Miocene portion of the Chesapeake Group (Fig. 1). Some of the beds or "zones" have been combined and renamed as members (Fig. 1), as summarized by Ward and Powars (1989) and Ward (1992). Ward (1992) also divided the entire Chesapeake Group into 19 depositional events, with each depositional event representing a unique transgressive depositional episode, and named eight molluscan zones within the Miocene portion of the Chesapeake Group.

The Eastover Formation, the youngest Miocene formation within the Chesapeake Group, was not recognized at the time of Shattuck's 1904 study, and it has not been incorporated into the framework of the 24 divisions first laid out by Shattuck. The Eastover Formation was named by Ward and Blackwelder (1980) and includes beds referred to as the "Virginia St. Mary's" in earlier literature of this century. The formation lies stratigraphically above the St. Mary's and below the Pliocene Yorktown Formation (Fig. 1).

According to Vogt and Eshelman (1987), the Miocene sediments of the Chesapeake Group were deposited as part of a complex package representing a first-order transgressive/regressive cycle with numerous superimposed smaller-scale perturbations of sea level. The deposits formed in inner shelf to marginal marine conditions associated with the Salisbury Embayment, a Miocene depocenter that was one of a series of embayments along the mid-Atlantic coast of North America during this time (see Ward and Powars 1989). Maximum transgression of the Salisbury Embayment occurred during Calvert time, with the extent of the embayment becoming reduced during deposition of the sediments that constitute the Choptank and St. Mary's formations (Ward and Powars 1989).

Fine sandstones, siltstones, mudstones, claystones, and occasional diatomite beds are represented in the Miocene Chesapeake Group. The thickness and lithic and biotic composition of the beds vary considerably. The reasons for this variation may include a trend toward shoaling and climatic cooling, concurrent uplift of the Atlantic Coastal Plain, uneven subsidence of the Atlantic Coastal Plain, and eustatic changes in sea level (Vogt and Eshelman 1987, and references therein). The highly fossiliferous shell beds have been interpreted variously as being formed by single brief episodes

of rapid accumulation, high natural population levels, or relatively slow sedimentation rates (Kidwell 1982a,b; Kidwell and Jablonski 1983; Vogt and Eshelman 1987).

*Age of the deposits.*—The Miocene age of the portion of the Chesapeake Group we address is well established and has been recognized since the early researches of Rogers (1836) and Lyell (1845). Correlation of the local deposits with other marine sequences is difficult because the Chesapeake Group sediments were deposited in relatively shallow water, so the planktonic foraminifera that are the primary basis for the global marine microfossil zonations are often lacking. Microfossil studies, based on foraminifera and diatoms (summarized by Vogt and Eshelman 1987), corroborate the Miocene age of the formations being considered here. This is further supported by the land mammal fauna, which Wood et al. (1941), Gazin and Collins (1950), Tedford and Hunter (1984), and Wright and Eshelman (1987) all regarded as indicating a Hemingfordian to Barstovian age for the Calvert and Choptank formations. The only three radiometric dates (based on glauconite) obtained for the Miocene of this region (Blackwelder and Ward 1976) suggest late middle and late Miocene ages for the St. Mary's and Eastover formations, respectively. While additional radiometric, microfossil, and land mammal data could prove helpful in refining the formations' ages, enough information is available to bracket the absolute age of the Eastover through Calvert formations as ranging from ca. 6.5 to ca. 20 Ma (see Fig. 1). The duration of possible missing intervals (due to erosion or nondeposition) has not been accurately estimated; according to Vogt and Eshelman (1987) the long-term accumulation rate for the Chesapeake Group in Maryland averages 15 m/Ma.

*Paleoclimate.*—There is general consensus that the Chesapeake Bay region was somewhat warmer during Calvert time than it is presently, and gradually cooled during deposition of the younger Miocene formations. Leopold (1970), as discussed by Whitmore (1971), pointed out that the palynological record of the Chesapeake Group during Calvert time suggests a warm-temperate terrestrial flora with some subtropical elements, similar to the coastal environment of the Carolinas today, succeeded during Choptank time by a slightly cooler warm-temperate climate and a still cooler but temperate regime, similar to the current climate of this region, during deposition of the St. Mary's Formation. A more recent palynologi-



Figure 3. View north along typical Calvert Cliffs exposures through the the Miocene portion of the Chesapeake Group, western shore of Chesapeake Bay, Calvert County, Maryland (locality 1, Fig. 4). Arrows indicate boundary between Choptank (below) and St. Mary's formations.

cal study (de Verteuil 1986) generally agrees with this scenario and found that dinocyst assemblages in the Calvert and Choptank formations were dominated by estuarine and estuarine-neritic taxa indicating a subtropical to warm temperate climate. De Verteuil (1986) also inferred cooling during the late Miocene from the increasing proportion of *Pinus*. The vertebrate fauna is consistent with this interpretation in that indicators of a warm climate—sirenians and a gopher turtle—are found in the Calvert Formation (Whitmore 1971). Müller (1992) postulated a relatively sharp temperature decrease in the late middle Miocene on the basis of a shift to a cooler-water fish fauna during St. Mary's time.

#### DIVERSITY OF CHESAPEAKE GROUP CETACEANS

**Overview.**—The Chesapeake Group deposits contain one of the world's richest and most diverse assemblages of fossil cetaceans. This summary of the Miocene part of that record is based on the extensive holdings of fossil cetaceans at the National Museum of Natural History (USNM) and specimens from the Calvert Marine Museum (CMM) collection. The long history of research on Chesapeake Group cetaceans carries with it a tradition of confusing nomenclatural problems, suspect and erroneous taxonomic assignments, and new taxa erected on the basis of nondiagnostic incomplete specimens. These practices were prevalent during but not exclusive to the time of Leidy, Cope, and their contemporaries and immediate successors. A significant portion of this taxonomic disarray was addressed by Kellogg in a series of papers between 1923 and

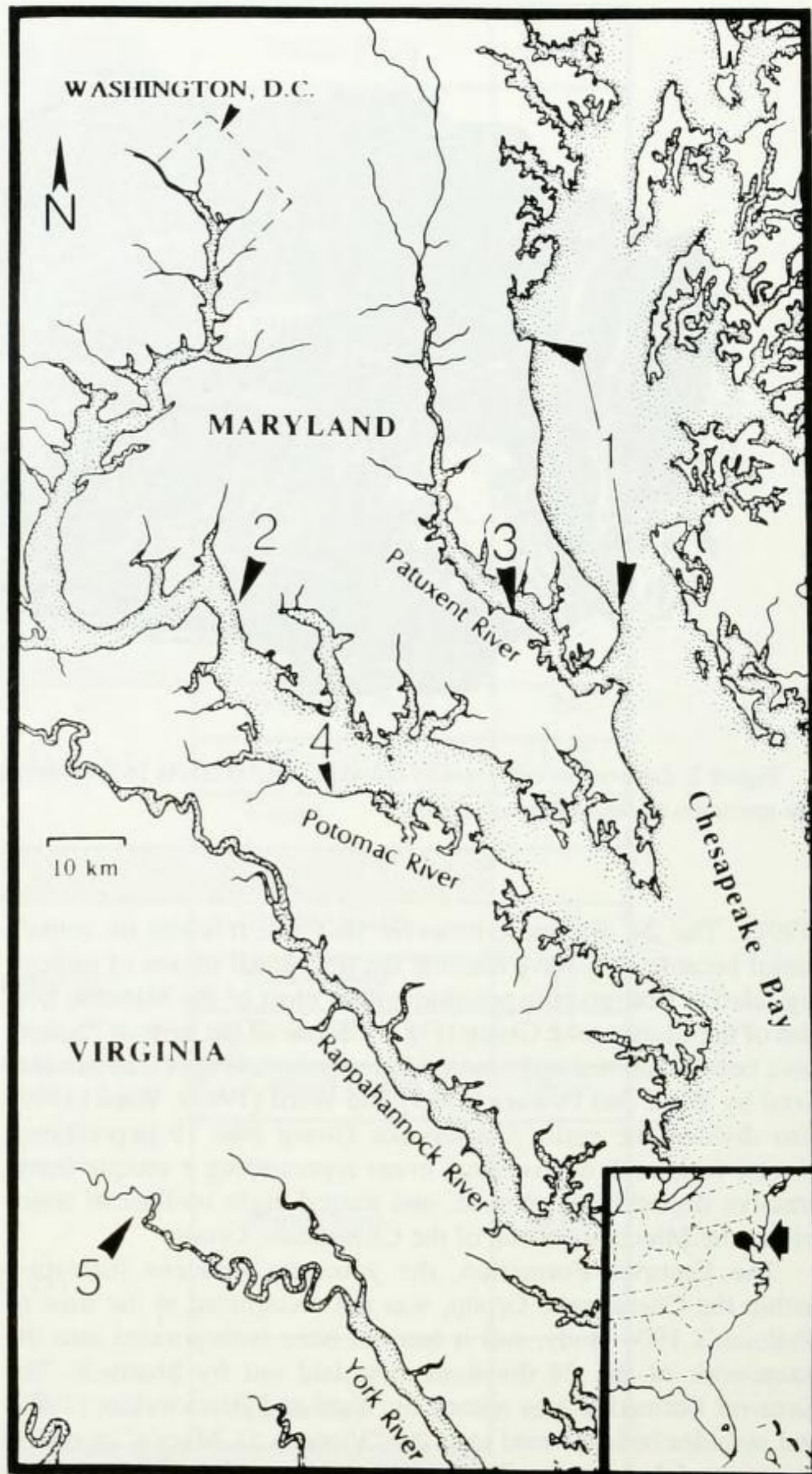


Figure 4. Mid-Chesapeake Bay region of Maryland and Virginia, showing major collecting sites for Miocene Chesapeake Group cetaceans. 1, Calvert Cliffs, Calvert and Anne Arundel counties, Maryland (the cliffs extend between the arrows for ca. 50 km); 2, Popes Creek, Charles County, Maryland; 3, Drum Cliff (and other nearby localities) along the Patuxent River, St. Mary's, Calvert, and Charles counties, Maryland; 4, Stratford and Horsehead cliffs, Westmoreland County, Virginia; 5, Exposures along the upper reaches of the Pamunkey River, Hanover, Caroline, and King William counties, Virginia.

1969; however, many problems still remain. It is not the intent of this paper to undertake a systematic revision of Miocene Chesapeake Group cetaceans—in this review we have focused only on those forms whose taxonomic validity we consider well-established.

To date, some 45 generic names have been applied to Miocene cetaceans from the Chesapeake Group. We provisionally consider 25 of these to be well-substantiated (Table 1); material that is yet assigned only to the families Ziphiidae and Balaenopteridae suggests at least two other genera. These Miocene genera include 16 or 17 odontocetes (about two-thirds of the total) and 9 or 10 mysticetes. The odontocete

Table 1. Miocene Cetaceans from the Chesapeake Group.

Taxon	Occurrence <sup>a</sup>
Order Odontoceti	
Family Squalodontidae	
<i>Squalodon calvertensis</i>	Cal
<i>Squalodon</i> cf. <i>S. tiedemani</i>	Cal
Family Platanistidae	
<i>Zarhachis flagellator</i>	Cal
<i>Zarhachis</i> sp. or <i>Pomatodelphis inaequalis</i>	Cal, Ch
<i>Zarhachis</i> sp.	StM
Family Rhabdosteidae	
<i>Eurhinodelphis bossi</i>	Cal
<i>Rhabdosteus latiradix</i>	Cal
Family Squalodelphidae	
<i>Phocageneus venustus</i>	Cal
<i>Notocetus</i> sp.	Cal
Family Kentriodontidae	
<i>Kentriodon pernix</i>	Cal
" <i>Delphinodon</i> " <i>dividum</i>	Cal
<i>Liolithax pappus</i>	Cal
<i>Hadrodelphis calvertense</i>	Cal, Ch?
<i>Lophocetus calvertensis</i>	StM
Kentriodontid indet.	Ch, StM, Ea
Family Physeteridae	
<i>Orycterocetus crocodilinus</i>	Cal, Ch
<i>Orycterocetus mediatlanticus</i>	StM
Physeterid indet.	StM
Family Ziphiidae	
Ziphiid indet.	Ch?
Odontoceti incertae sedis	
<i>Tretosphys gabbi</i>	Cal
<i>Araeodelphis natator</i>	Cal
<i>Pelodelphis gracilis</i>	Cal
Order Mysticeti	
Family "Cetotheriidae"	
<i>Parietobalaena palmeri</i>	Cal
<i>Mesocetus siphunculus</i>	Cal
<i>Diorocetus hiatus</i>	Cal, Ch
<i>Aglaocetus patulus</i>	Cal, Ch
<i>Pelocetus calvertensis</i>	Cal, Ch
<i>Thinocetus arthritus</i>	Ch
<i>Halicetus ignotus</i>	Ch
<i>Cetotherium</i> sp.	StM
<i>Cephalotropis coronatus</i>	StM
Family Balaenopteridae	
Balaenopterid? indet.	Ea

<sup>a</sup>Cal, Calvert Formation; Ch, Choptank Formation; StM, St. Mary's Formation; Ea, Eastover Formation.

outnumbering the mysticete genera is in keeping with, but not quite as pronounced as, the overall pattern seen in the fossil record and among Recent cetaceans. Worldwide, 76% of all fossil cetacean genera are odontocetes (128 odontocetes vs. 41 mysticetes; Carroll 1988), whereas 84% (32 odontocetes vs. 6 mysticetes) of all living genera are odontocetes (Leatherwood et al. 1983).

The relatively high proportion of mysticete genera in the Chesapeake Group Miocene, as compared to the overall pattern among all fossil cetaceans and Recent forms, has several potential explanations. These include possible collecting bias, environmental bias resulting from ancient habitats that favored mysticetes, or artificially high diversity resulting from taxonomic oversplitting. Another possible factor is the high post-Miocene diversity of odontocetes (at least 10 odontocete genera first appear after the Miocene), whereas Miocene mysticetes were relatively diverse, owing to the early "cetother" radiation.

The Miocene Chesapeake Group mysticetes that have been described in the literature have typically been assigned to the

"Cetotheriidae," a catch-all category into which the majority of primitive and relatively small Tertiary mysticetes have been placed. The forms traditionally classified as "cetotheres" are in serious need of detailed taxonomic revision, and monophyly of the family has yet to be corroborated by shared derived features. The lack of a rigorous phylogenetic analysis that includes cetotheriid-grade mysticetes undermines efforts to study the early evolutionary history of the baleen whales.

The following section summarizes the cetacean fauna known to date from each of the four Miocene formations of the Chesapeake Group. References are given for the original description and subsequent important papers dealing with the named species; catalog numbers from the Calvert Marine Museum and National Museum of Natural History collections are provided for pertinent specimens that have not been published.

*Calvert Formation cetaceans.*—The Calvert Formation has the highest vertebrate diversity as well as the greatest thickness and extent of the formations within the Miocene portion of the Chesapeake Group. The most phylogenetically primitive of the Calvert odontocetes is the squalodontid *Squalodon calvertensis* Kellogg, 1923 (Fig. 5A). An additional larger species referred to *S. tiedemani* Allen, 1887, is also present (A. Dooley, pers. comm.).

The dominant odontocetes in terms of number of specimens are the long-snouted rhabdosteid dolphins *Eurhinodelphis* and *Rhabdosteus*. Kellogg (1955) held that *Rhabdosteus latiradix* Cope, 1868a (also see Cope 1868b; True 1908b), is the most common odontocete in the Calvert; however, computerized records of the USNM collection suggest that *Eurhinodelphis* may be more common, while Myrick (1979) maintained that the two genera are roughly equal in numbers of specimens. *Eurhinodelphis bossi* Kellogg, 1925b, is the only formally described species within the genus from the Calvert; Kellogg originally (1924c) implied the presence of additional taxa, but not in subsequent papers. Myrick (1979) distinguished 10 or 11 rhabdosteid species from the Calvert Formation; however, descriptions of these have not been published.

Muizon (1988) considered *Rhabdosteus* a *nomen dubium* and instead referred specimens from the Maryland Miocene that had been assigned to that genus to the European form *Schizodelphis*, a conclusion he reached after studying the type material of *Schizodelphis*. *Schizodelphis* had been previously reported from the Calvert fauna by True (1908a), who referred *Priscodelphinus crassangulum* Case, 1904, to *Schizodelphis*. Bohaska is currently reinvestigating the issue of whether or not *Schizodelphis* occurs in the Maryland Miocene (and in Florida); until that study is completed we consider North American records of *Schizodelphis* questionable and therefore have not included it on our list of Calvert Formation genera.

In addition to the rhabdosteids, the long-snouted possible platanistoid *Zarhachis* is also present in the Calvert. Kellogg (1924a, 1926) referred specimens from the lower Calvert to *Z. flagellator* Cope, 1868c. A possible second species of this genus, or perhaps the related form *Pomatodelphis inaequalis* Allen, 1921 (see Kellogg 1959), also occurs in the upper Calvert (USNM 11343, 24868, 25168, 205302).

A relatively diverse assemblage of shorter-beaked kentriodontid odontocetes has been reported from the Calvert Formation. The largest of these is *Hadrodelphis calvertense* Kellogg, 1966, originally described on the basis of a single pair of associated partial dentaries and now known from a complete skull, lower jaws, and associated skeleton (CMM-V-11). This large odontocete likely reached a length of over 4 m. Dawson (1992) has been studying the associated CMM material and is preparing a revision of the genus. The rarity of *Hadrodelphis* in the Chesapeake Group may relate to its being a pelagic taxon and therefore not as common in the coastal Salisbury Embayment environments as the more nearshore-adapted long-snouted forms.

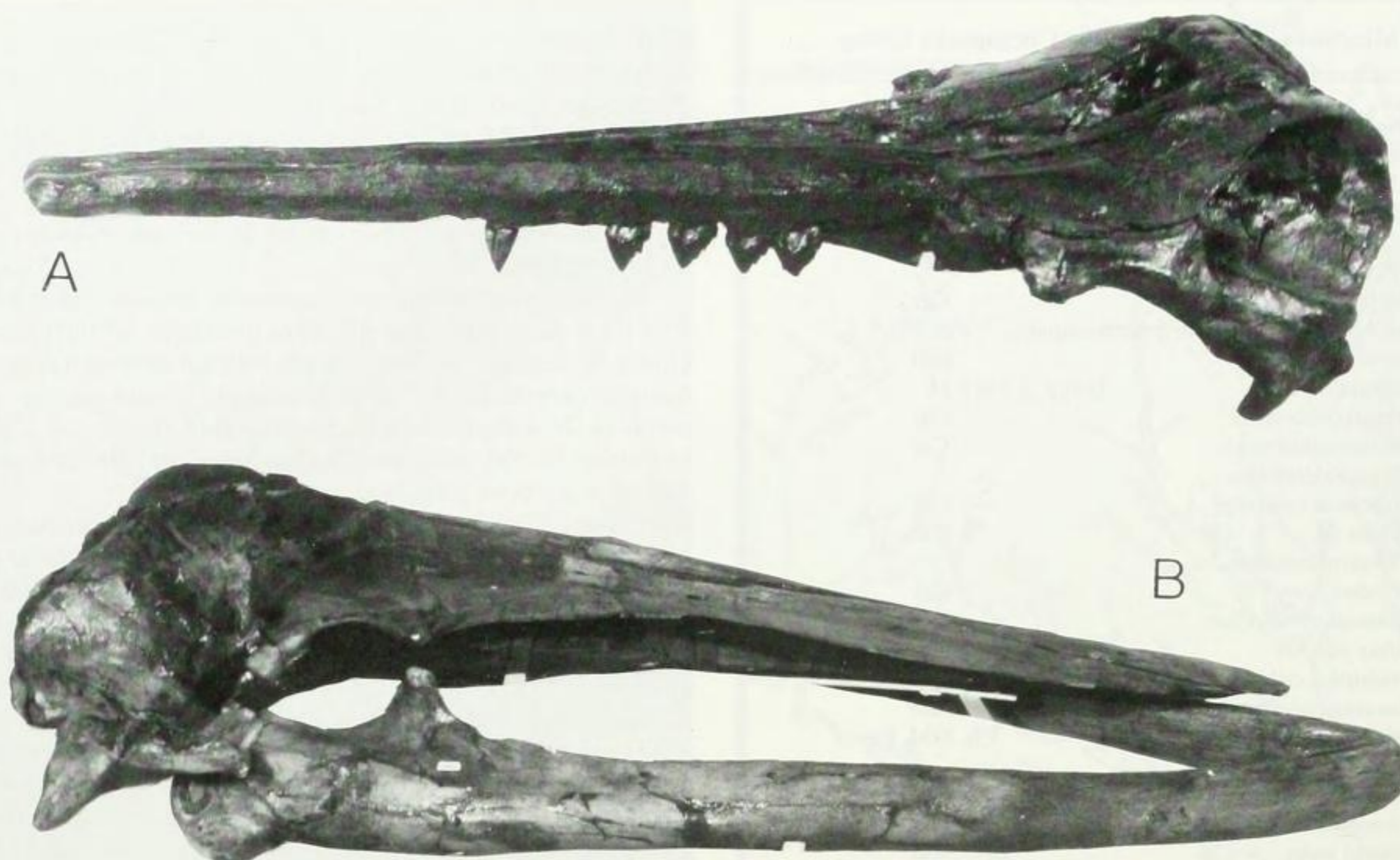


Figure 5. A, Squalodontid odontocete *Squalodon calvertensis*, cast of skull of USNM 206288,  $\times 0.20$ . (B) Cetotheriid-grade mysticete *Parietobalaena palmeri*, USNM 24883, skull and lower jaws,  $\times 0.15$ . Both specimens on exhibit at the Calvert Marine Museum.

Smaller kentriodontids in the Calvert include *Delphinodon dividum* True, 1912, and *Kentriodon pernix* Kellogg, 1927, each well-represented by fairly complete specimens; Kellogg (1957) questioned whether "*D.*" *dividum* was properly assigned to that genus. Somewhat rarer than these is a medium-sized form originally named *Lophocetus pappus* Kellogg, 1955, which was revised and placed into the genus *Liolithax* by Barnes (1978).

The largest odontocete, and the largest cetacean recorded from the Calvert Formation, is the physeterid *Orycterocetus crocodilinus* Cope, 1868b (discussed in some detail by Kellogg, 1965). Unlike Recent sperm whales, this Miocene form retained functional teeth in its upper jaws.

Other, relatively poorly known Calvert Formation odontocetes have been assigned to the Squalodelphidae, including *Phocageneus venustus* Leidy, 1869 (more complete material of this taxon was discussed by Kellogg in 1957), and *Notocetus* sp. (Muizon 1987). Three additional forms have to date been placed only as *Odontoceti incertae sedis*: *Tretosphys gabbi* Cope, 1868c (restudied from additional remains by Kellogg, 1955), *Pelodelphis gracilis* Kellogg, 1955; and *Araeodelphis natator* Kellogg, 1957. These species are all represented by relatively limited material with no well-preserved skulls known.

Nominal mysticetes from the Calvert Formation have almost all been placed in the "Cetotheriidae," which as previously discussed is a problematic grade-level assemblage. The most common Calvert mysticete is *Parietobalaena palmeri* Kellogg, 1924b (see Fig. 5B and Kellogg 1968), which is the smallest of the Maryland Miocene baleen whales (adult length approximately 4 to 5 m). Other "cetotheres" from the Calvert include *Diorocetus hiatus* Kellogg, 1968, *Aglaocetus patulus* Kellogg, 1968, *Mesocetus siphunculus* Cope, 1895 (redescribed by Kellogg 1968), and *Pelocetus calvertensis* Kellogg, 1965 (the largest form, length 7–8 m).

Although no non-cetotheriid-grade mysticetes have been definitively reported from the Calvert Formation, *Eschrichtius cephalum* Cope, 1868a (which is not a gray whale, despite Cope's assigning it to what is now considered the proper genus for gray whales; see Barnes and MacLeod 1984) is a large, possibly balaenopterid mysticete represented by a single partial skeleton (Kellogg 1968) that has been considered Miocene in age. However, the stratigraphic position of this material is unclear, and Cope's precise locality is uncertain. It is possible that the specimen was collected from a Pliocene deposit, which would be more consistent with the relative abundance of balaenopterids in the Pliocene Yorktown Formation exposures of Virginia and North Carolina. In addition, a typically Pliocene mustelid was apparently collected at the same site (Ray et al. 1981). For these reasons we continue to regard the occurrence of balaenopterid mysticetes in the Calvert Formation as unsubstantiated.

*Choptank Formation cetaceans.*—The Choptank Formation is not as thick or extensive as the Calvert and cetacean (and other vertebrate) specimens are markedly fewer and less diverse than in the Calvert Formation. In Shattuck's original division (in Clark et al. 1904), the Choptank included beds (or "zones") 15 through 20, but more recently beds 15 and 16 have been placed in the Calvert Formation, and bed 20 has been transferred to the St. Mary's (Ward and Strickland 1985; Ward 1992). Beds 17, 18, and 19, currently considered to constitute the Choptank Formation, are sandier than the underlying Calvert Formation and may represent a shallow-shelf open-marine setting rather than the nearshore depositional setting proposed for the Calvert (Ward and Powars 1989). This environmental shift may be at least partially responsible for the decrease in number and diversity of cetacean specimens in the Choptank.

Choptank odontocetes include a long-snouted taxon (or taxa) identifiable as either *Zarhachis* sp. or *Pomatodelphis inaequalis*.



This long-snouted material has been recovered from bed 17 of the Choptank (USNM 13768, 187414, 206000), and the same form may also occur in beds 10 and 12 of the Calvert Formation. The two most conspicuous long-snouted genera in the Calvert Formation, *Eurhinodelphis* and *Rhabdosteus*, have not been recovered from the Choptank.

A large kentriodontid is known from one skull (CMM-V-15) found in bed 17 of the Choptank. A small as yet undescribed kentriodontid, probably *Kentriodon pernix*, is also present in bed 17, on the basis of a periotic (CMM-V-239). A section of a large physeterid mandible has also been collected from the Choptank (USNM 16552).

The only ziphiids known from the Chesapeake Group are three partial rostra (USNM 412120, 412124, 425487), presumably all from the Choptank Formation. None of these ziphiid specimens were found *in situ*, but all were collected along the southern (geologically younger) end of Calvert Cliffs in Calvert County, Maryland, several kilometers from any Calvert Formation outcrops, and vertebrates are quite rare in the overlying St. Mary's Formation in this area. It is likely therefore that the ziphiid specimens are out of the Choptank Formation. Whitmore et al. (1986) discussed the association of ziphiids with offshore upwelling zones, phosphorites, and large squid populations (a primary food source for extant ziphiids). The absence of ziphiids in the Calvert and their scarcity in the Choptank may be an environmental artifact in that the Salisbury Embayment was not an environment pelagic enough to support a substantial ziphiid population.

The mysticete record of the Choptank Formation includes two forms not known from the Calvert, *Thinocetus arthritus* Kellogg, 1969, and *Halicetus ignotus* Kellogg, 1969. Other cetotheres from the Choptank include the genera *Pelocetus*, *Diorocetus*, and *Aglaocetus* (all also known from the Calvert). Although the number of specimens is smaller, the diversity of mysticetes in the Choptank Formation is about the same as in the Calvert (see Table 1).

*St. Mary's Formation cetaceans.*—The St. Mary's Formation is now considered to include beds 20 through 24 from Shattuck's original division of the Chesapeake Group (Ward 1992). Outcrops referred to in the older literature as the "Virginia St. Mary's" pertain mainly to the Eastover Formation (Blackwelder and Ward 1976, and below), although there are St. Mary's sites along the rivers of the coastal plain of Virginia. Exposures of the St. Mary's are not as extensive as those of either the Calvert or Choptank and are poorer in vertebrate remains.

St. Mary's Formation cetaceans are relatively scarce and not as diverse as those from the Calvert or the Choptank. Long-snouted dolphins are represented by a possible third Chesapeake Group Miocene species of *Zarhachis* or a related form, based on four specimens (USNM 22500, 214759, 447490, 464067). The only kentriodontid described from the St. Mary's is the historically important *Lophocetus calvertensis* (Harlan, 1842) (Fig. 2), still known only from the holotype specimen. Much of the material of the relatively small odontocetes from the St. Mary's Formation is incomplete and relatively undiagnostic, and probably includes specimens of kentriodontid and/or delphinoid affinities.

Physeterids from the St. Mary's include a skull of *Orycterocetus mediatlanticus* Cope, 1895, restudied by Kellogg (1925a). Isolated sperm whale teeth include a specimen (USNM 464139) with an enamel crown similar to that seen on the European and Australian genus *Scaldicetus*. One additional very large tooth (USNM 167608) is comparable in size but not in morphology to teeth of the extant sperm whale, *Physeter catodon*. Clearly, significantly more attention needs to be paid to fossil physeterids from the Miocene Chesapeake Group.

"Cetotheres" have also been recovered from the St. Mary's Formation. A number of undescribed skulls have been collected by

watermen dredging for oysters in Chesapeake Bay—such specimens often include enough adhering matrix to reveal their geologic context. Baum and Wheeler (1977) assigned vertebrae and a mandible from the St. Mary's in Virginia to Cope's (1895) "cetothere" genus *Siphonocetus*; Kellogg (1968) implied that material assigned to this genus actually pertains to *Cetotherium*. An additional "cetothere," *Cephalotropis coronatus* Cope, 1896, is known from a skull out of the St. Mary's Formation.

*Eastover Formation cetaceans.*—The Eastover Formation was named by Ward and Blackwelder (1980) and includes upper Miocene beds overlying the St. Mary's and underlying the Pliocene Yorktown Formation. The molluscan fauna of the Eastover indicates a temperate climate cooler than the warm-temperate conditions that predominated lower in the Chesapeake Group section.

The Eastover Formation is not as well exposed as the formations lower in the section. In addition, relatively little attention has been paid to this formation, with the result that our knowledge of the Eastover fauna is still inadequate. Whitmore (1984) noted a large kentriodontid, which he considered close to *Kentriodon*, from an Eastover exposure near the Pamunkey River in Caroline County, Virginia. Whitmore also mentioned that bones of a "large mysticete" had been collected out of the Eastover along the Pamunkey River in New Kent County, Virginia. It has yet to be determined if these latter remains are from a large "cetothere" or if they represent a relatively early record of a balaenopterid mysticete.

## DISCUSSION

*Major temporal trends.*—Several trends in the pattern of cetacean diversity and distribution through the Miocene portion of the Chesapeake Group are apparent. First, squalodontid odontocetes (represented by *Squalodon calvertensis* and *S. cf. S. tiedemani*), the most phylogenetically primitive odontocetes in the Chesapeake Group, persist only through the upper part of the lower-to-middle Miocene Calvert Formation. This is in keeping with the worldwide pattern of squalodontids becoming extinct partway through the Miocene as more derived odontocetes appear (Barnes et al. 1985).

A somewhat unexpected situation exists with regard to the first appearance of "cetotheres" in the Calvert Formation. The oldest known "cetotheres" from the Calvert were collected from bed 8; no specimens are known from the lower part (beds 1–7) of the Calvert, which is late early to early middle Miocene and contains several species of odontocetes. "Cetotheres" are known from lower Miocene and Oligocene deposits in Europe, New Zealand, and South America (Barnes et al. 1985), so their absence from a richly fossiliferous lower-to-middle Miocene marine deposit is somewhat surprising. It is not possible to determine whether this reflects collecting bias, environmental bias, or an actual pattern of Miocene mysticete distribution, but it would not be surprising if "cetothere" remains were eventually found in the lower beds of the Calvert Formation.

Perhaps the most striking pattern observed is the decline in diversity (see Table 1) and number of specimens above the Calvert Formation. Maximum diversity is reached in the upper part of the Calvert Formation, centered around beds 12 to 14, which together contain 17 genera. In comparison, the most diverse post-Calvert assemblage is bed 17 of the Choptank Formation, which has produced about seven genera to date. This decline in diversity may be connected to cooling and general climatic deterioration, or it may be an artifact of facies changes, the post-Calvert sediments apparently being deposited in somewhat more open marine settings, with a less diverse cetacean fauna, than those of the Calvert Formation. It may also reflect a real change in the diversity of cetaceans along the mid-Atlantic coast of North America during the latter half of the Miocene.

*Comparison with Recent cetacean assemblages.*—Chesapeake Group cetaceans reach their highest diversity in the upper Calvert Formation, where they are comparable to modern cetaceans in total diversity and in the variety of forms represented. The upper Calvert includes at least 5 mysticete and 12 odontocete genera; in comparison, the Recent cetacean assemblage in the northwest Atlantic Ocean consists of 4 mysticete and 20 odontocete genera (Leatherwood et al. 1976). The total number of genera (17 in the upper Calvert versus 24 Recent) suggests that the cetacean record from this interval of the Chesapeake Group provides a reasonable approximation of cetacean diversity in the northwestern Atlantic Ocean during the middle Miocene.

Among the major size classes of cetaceans, only large mysticetes of modern aspect are missing from the Miocene portion of the Chesapeake Group. It is possible that balaenopterids first appeared in the region near the end of the Miocene, as suggested by the Eastover Formation material discussed by Whitmore (1984), but they have yet to be identified definitively, and it is clear that relatively small and primitive cetotheriid-grade mysticetes were the dominant baleen whales in the Chesapeake region during the Miocene. Balaenopterids did not become well-established in the northwest Atlantic until the Pliocene (see Whitmore 1994, this volume). Also missing from the Miocene Chesapeake Group deposits are delphinids, the open-ocean dolphins that today constitute the most diverse and abundant group of odontocetes, and phocoenids, the porpoises.

*Paleobiological considerations.*—Past authors, including Kellogg (1966, 1968), Whitmore (1971), and Vogt and Eshelman (1987), have speculated that the relative abundance in the Chesapeake Group of cetacean bones with unfused epiphyses and of skulls with incompletely closed sutures indicates that the Salisbury Embayment was the site of a breeding and/or calving ground for Miocene cetaceans. Kellogg (1966:67) summarized this view as follows: "The presence of such a preponderance of immature or young marine mammals suggests that this region was the calving ground for the mysticetes, the sperm whales and probably some of the smaller odontocetes." This idea has become firmly entrenched in the popular literature and among fossil collectors active in the Chesapeake Group.

We find several problems with this scenario. First, skeletal fusion of the cetaceans studied to date is not completed until after sexual maturity. Mead and Potter (1990) provided evidence that bottlenose dolphins become reproductively active at six to eight years of age, whereas the epiphyses in their forelimb bones do not completely fuse until several years later. This suggests that lack of skeletal fusion is not a reliable indicator of a specimen's being a neonate or even a juvenile. Incompletely fused skeletons might well represent cetaceans that had reached sexual but not complete physical maturity.

Furthermore, thousands of stranding records compiled over many years show that the majority of stranded cetaceans are relatively young animals (up to two years old, J. G. Mead, pers. comm.) whose skeletons are not completely fused. Thus the apparent demographic skew of Chesapeake Group cetaceans may in fact reflect the normal mammalian pattern of high mortality rates in the younger age classes (as expected in a random sample) and is not an unusual or unexpected phenomenon requiring a special explanation.

Finally, there are no modern instances of several cetacean species breeding or calving in the same nearshore habitat. The only comparable modern example is the gray whale *Eschrichtius robustus*, which breeds in protected lagoons along the Pacific coast of Baja California, Mexico. However, this apparently specialized behavior is unique to gray whales among Recent cetaceans. It may be that the breeding/calving scenario concerning the Miocene Chesapeake Group cetaceans arose at least in part out of the earlier

idea that "cetotheres" are ancestral to gray whales (as implied by Kellogg 1928) and therefore similar in certain habits. Barnes and MacLeod (1984) argued against a close gray whale—"cetotheres" relationship and maintained that the evolutionary history of gray whales can be traced back only as far as the Pleistocene.

One well-substantiated aspect of Chesapeake Group cetacean paleobiology is that both mysticetes and odontocetes were preyed upon and/or scavenged by sharks. Cetacean bones regularly show linear grooves and gouges caused by shark bites during attacks and/or scavenging on carcasses. Deméré and Cerutti (1982) demonstrated that similar grooves on the mandible of a late Pliocene "cetotheres" from San Diego, California, resulted from a shark attack or scavenging, probably by the Pliocene great white shark *Carcharodon sulcidens* Agassiz, 1843. More recently, Cigala-Fulgosi (1990) described and figured bite marks of a great white shark on the skeleton of a Pliocene dolphin from Italy. Similar grooves and gouges seen on Miocene cetacean bones from the Chesapeake Group can also be ascribed to sharks, whose teeth are common fossils in the region and which include the giant megatooth shark *Carcharodon* [= *Carcharocles* of some authors] *megalodon* (Charlesworth, 1837). *Carcharodon carcharias* (Linnaeus, 1758), the Recent species of great white shark, and other large sharks are also known to prey on marine mammals (Ames and Morejohn 1980; Leatherwood et al. 1983; Corkeron et al. 1987; Cigala-Fulgosi 1990).

#### FUTURE RESEARCH

This overview of Miocene Chesapeake Group cetaceans leads to some suggestions on where future research efforts might be concentrated to address problems that have not been resolved.

(1) More effort should go into elucidating phylogenetic interrelationships and classification of the mysticetes. The lack of any testable phylogenetic hypothesis of mysticete interrelationships that includes fossil taxa makes it difficult to discuss baleen whale evolution meaningfully and leaves unresolved the question of what, if anything, is a "cetotheres."

(2) More collecting and research attention should be paid to cetaceans from the upper Miocene St. Mary's and Eastover formations to yield a better understanding of the transition from the mid-Miocene cetacean faunas, which include relatively primitive forms, to the Pliocene assemblages (discussed by Whitmore 1994, this volume), in which the modern families of cetaceans begin to dominate.

(3) The interrelationships of fossil and living long-snouted dolphins remain unclear despite a recent increase in attention (Muizon 1990, 1991; Messenger 1991). A better understanding of the phylogeny of these taxa is necessary for the relationship between living and fossil long-snouted dolphins to be assessed and for the position within the Odontoceti of the Miocene long-snouted forms to be resolved.

(4) Alpha-level taxonomic problems remain to be addressed. These include questionable species named by Cope that are overdue for reexamination and complicated synonymies that require unraveling. A stable classification and more firmly established phylogenetic hypotheses will be possible when these problems are better resolved.

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