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REVIEW OF THE OLIGOCENE CETACEA

FRANK C. WHITMORE, JR. AND ALBERT E. SANDERS

Abstract

Whitmore, F. C., Jr., and Sanders, A. E. (U.S. Geological Survey, National Museum of Natural History, Washington, D.C. 20244 and The Charleston Museum, 121 Rutledge Avenue, Charleston, South Carolina 29401). 1976. Review of the Oligocene Cetacea. *Syst. Zool.* 25:304-320.—Early in the Oligocene Epoch, Cetacea of the primitive suborder Archaeoceti had already declined sharply from their apparent abundance in Eocene seas. By the beginning of the Miocene, archaeocetes are known to have survived only in the northeast Atlantic and southwest Pacific Oceans. Concurrently with this decline, the first members of the suborders Odontoceti and Mysticeti appeared. They are known from only a few specimens, mostly in upper Oligocene deposits, on both coasts of North America, in Germany, Austria, Italy, the Caucasus, Azerbaijan, Australia, and New Zealand. Two important odontocete genera, *Agorophius* and *Xenorophus*, come from beds that are probably no older than late Oligocene and that are certainly not as old as Eocene, where these genera have previously been placed. The wide distribution of known Oligocene Cetacea, especially their presence in Australia and New Zealand, indicates the probable existence of a cosmopolitan cetacean fauna by the end of Oligocene time. The Oligocene Odontoceti are represented by *Agorophius* and related forms and by the Squalodontidae. Several types of skull telescoping are shown by contemporary members of these groups. Recently collected squalodont skulls from the Oligocene of South Carolina show differences in the pattern of cranial bones that may be ontogenetic. Some toothed whales have morphologic features that have led to their being assigned variously to Archaeoceti and Mysticeti because they are regarded as representing a transitional stage between the two suborders. These forms are all of late Oligocene age; they cannot be mysticete ancestors because true Mysticeti are known from middle Oligocene deposits.

Our knowledge of Cetacea that lived during the Oligocene Epoch, extending approximately from 37 million to 22 million years ago (m.y.a.), is less than for any other stage in whale evolution, except for the totally unknown transition from land mammals to whales. From this period of 15 m.y. we know 20 genera of Cetacea (Table 1). Eleven of these are monotypic, and six are known from one specimen each. Sixteen of the genera are found only in rocks of late Oligocene age. Orr and Faulhaber (1975) have discussed possible causes of the low diversity of Oligocene Cetacea. The present study summarizes the state of our knowledge of whale evolution during Oligocene time; it is based upon the published literature and also upon studies in progress of several undescribed specimens recently collected in South Carolina and Oregon.

The sparse Oligocene cetacean discoveries are widespread over the world. Specimens have been collected in Australia, New Zealand, on both coasts of North America,

in Germany, Austria, Italy, the Caucasus, and Azerbaijan. Even allowing for continental drift, this seems to indicate the existence of cosmopolitan cetacean faunas during the Oligocene. An interesting question, and one we cannot yet answer, is whether this fauna was restricted to coastal waters or whether some whales had achieved a pelagic existence.

The first representatives of the two modern suborders of Cetacea, the Odontoceti and Mysticeti, are found in Oligocene rocks. In the preceding Eocene Epoch, all known Cetacea belonged to the extinct suborder Archaeoceti. Strangely, the Eocene Archaeoceti are far better known than are any Oligocene Cetacea.

SUBORDER ARCHAEOCETI

The Archaeoceti were fully aquatic but lacked the drastic skull modifications related to efficient breathing, specialized diet, and echo location, that characterized the modern suborders. Such modifications

began to appear in Oligocene time in the Odontoceti and Mysticeti and were present to a marked degree in the cetacean fauna of Miocene time (about 22 m.y. to 5 m.y.a.). The Archaeoceti survived through the Oligocene and are known from early Miocene rocks of France and New Zealand (Kellogg, 1936:272). Compared with the good Eocene record, that of Oligocene Archaeoceti is sparse: they have been reported from lower Oligocene deposits of the Ukraine and of Vancouver Island (Kellogg, 1936:272; but on page 266 he gives the age, presumably of the same specimen, as late Eocene) and from the middle Oligocene of New Zealand (Keyes, 1973). Russell (1968) has assigned a skull from the Sooke Formation (upper Oligocene) of Vancouver Island to the Archaeoceti. This specimen, the holotype of *Chonecetus sookensis* Russell, 1968, is being restudied by Edward Mitchell, who has expressed doubt (paper presented during the August, 1975, symposium) as to the propriety of its assignment to the Archaeoceti.

Early Oligocene Archaeoceti are known only from vertebrae (Kellogg, 1936:98-99; 269), which indicate a large size. An early Oligocene species, *Platyosphys paulsonii* (Brandt) from the Ukraine, had vertebral centra 190 to 283 mm long. Better known is *Kekenodon onomata* Hector from New Zealand, which Keyes (1973:389) placed in the middle Oligocene. Teeth, parts of the skull, ear bones, and postcranial material of this species have been recovered; they indicate a smaller animal than the early Oligocene forms—about 23 feet (7 m) long (McKay, 1882:104). Kellogg (1936:11) placed *Kekenodon* in the Dorudontidae.

In contrast to the Archaeoceti, the skulls of members of the modern suborders Odontoceti and Mysticeti show a progressive phenomenon called telescoping, marked by backward movement of the nares toward the vertex, or highest point, of the skull. The new location of the nares resulted in more efficient breathing. Telescoping took place, in different ways, in both Odontoceti and Mysticeti (Miller, 1923). It is the most

TABLE 1. GENERA OF OLIGOCENE CETACEA

Late Oligocene
Odontoceti
<i>Incertae sedis</i>
** <i>Agorophius</i> Cope, 1895
<i>Agriocetus</i> Abel, 1914
<i>Patriocetus</i> Abel, 1914
** <i>Xenorophus</i> Kellogg, 1923
Squalodontidae
** <i>Australosqualodon</i> Climo & Baker, 1972
<i>Eosqualodon</i> Rothausen, 1968
<i>Microcetus</i> Kellogg, 1923
* <i>Parasqualodon</i> Hall, 1911
<i>Prosqualodon</i> Lydekker, 1894
<i>Squalodon</i> Grateloup, 1840
** <i>Tangaroasaurus</i> Benham, 1935
Cetacea <i>incertae sedis</i>
* <i>Aetiocetus</i> Emlong, 1966
** <i>Archaeodelphis</i> Allen, 1921
** <i>Chonecetus</i> Russel, 1968
** <i>Fereceterium</i> Mchedlidze, 1970
<i>Mirocetus</i> Mchedlidze, 1970
Mysticeti
Cetotheriidae
Middle Oligocene
Archaeoceti
Dorudontidae
* <i>Kekenodon</i> Hector, 1881
Odontoceti
Squalodontidae
<i>Squalodon</i> ?
Mysticeti
Cetotheriidae
<i>Mauicetus</i> Benham, 1939
Early Oligocene
Archaeoceti
<i>Incertae sedis</i>
<i>Platyosphys</i> Kellogg, 1936

* Monotypic genus.

** Known from only one specimen.

Note: *Uncamentodon hectori* and *Oligosqualodon wingei*, Oligocene species cited by Rothausen (1970:186), are taxa described in a manuscript that has not yet been published (Rothausen, personal communication, January 28, 1975). We have been unable to find the published description of *Oligodelphis azerbaijanicus* Aslanova and Mchedlidze, 1968, an Oligocene species cited by Mchedlidze (1970:20).

striking aquatic adaptation visible in fossil remains and results in drastic modifications related to specialized diet, such as plankton feeding, in the Mysticeti and to echo location in the Odontoceti (Norris, 1968, 1975).

SUBORDER ODONTOCETI

The best known Oligocene members of the Odontoceti are the Squalodontidae, a

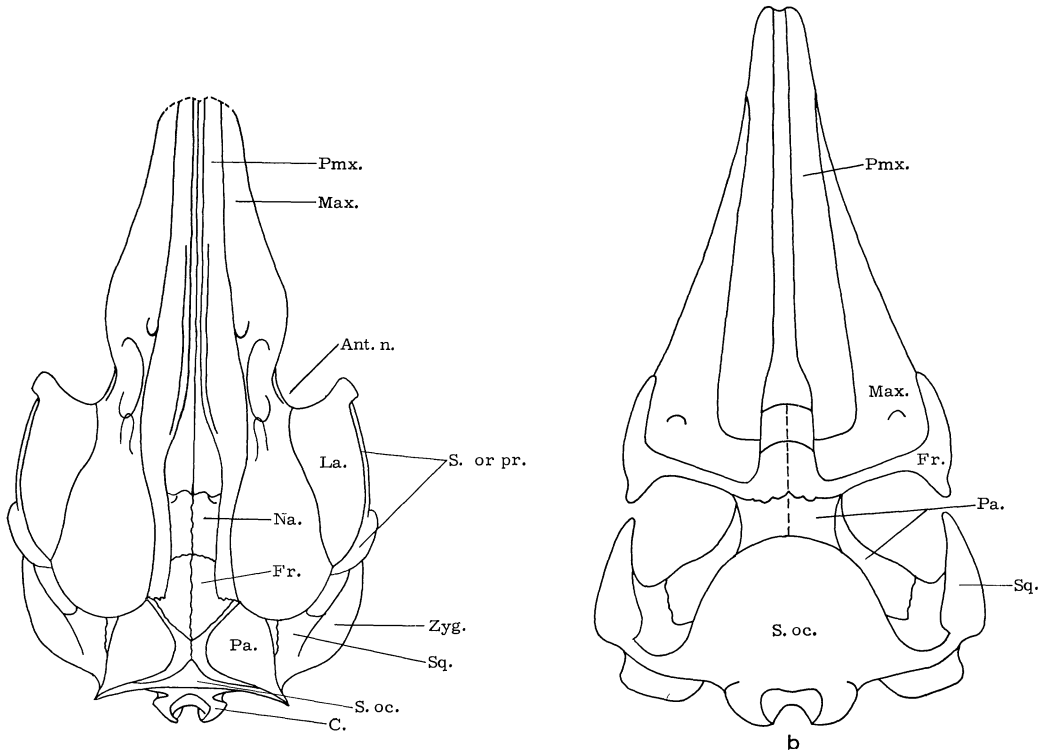


FIG. 1.—a. *Xenorophus sloanii* Kellogg. Reconstruction of skull in dorsal view. b. *Agorophius pygmaeus* (Müller). Dorsal view of skull from Kellogg (1928) and Agassiz *in* True (1907). Key to abbreviations: Ant. n.—Antorbital notch; C.—Occipital condyle; Ex. oc.—Exoccipital; Fr.—Frontal; La.—Lacrimal; Max.—Maxilla; Na.—Nasal; Ol.—Olfactory region; Pa.—Parietal; Pmx.—Premaxilla; Sq.—Squamosal; S. oc.—Supraoccipital; S. or. pr.—Supraorbital process of frontal; Zyg.—Zygomatic process of squamosal.

widespread and successful family first known in early Oligocene deposits of New Zealand (Keyes, 1973). They are known from middle Oligocene rocks of Germany and from late Oligocene deposits of Germany (Rothhausen, 1958, 1968, 1970), Italy (Rothhausen, 1958), U.S.S.R. (Dubrovo and Sharkov, 1971), Australia (Glaessner, 1955), and New Zealand (Benham, 1937a, 1937b, 1942).

Besides the Squalodontidae, other toothed whales, much less well known, showed various degrees of telescoping in Oligocene time. They have been assigned to the families Agorophiidae and Patriocetidae (Romer, 1966:392,393); some have been placed in ?Archaeoceti *incertae sedis* (Simpson, 1945:100). These taxonomically

doubtful genera are listed under *Odontoceti incertae sedis* and *Cetacea incertae sedis* in Table 1. None of them survived into the Miocene. Among these primitive nonsqualodont genera may be the ancestors of modern Odontoceti, and they probably also include structural forms similar to the ancestors of the Mysticeti. However, the taxa that have been suggested as mysticete ancestors are now known only from late Oligocene beds and, as we shall see, the Mysticeti had already evolved by that time.

As can be seen in Table 1, the number of species, and indeed of specimens, of Oligocene Cetacea is so small and their stratigraphic distribution so unbalanced, that taxonomic assignment to family, and in some cases even to suborder, is difficult.

In the case of familial assignments, the small number of species involved makes it hard to settle on definitive characters. In the matter of assigning genera to suborders, there arises, among other questions, that of whether the Mysticeti were descended directly from the Archaeoceti or from Odontoceti. Whichever hypothesis is accepted, there is then the question of whether a whale that has teeth, if it is a mysticete ancestor, should be assigned to the Mysticeti or to the ancestral suborder.

With the exception of *Chonecetus*, the genera listed under Cetacea *incertae sedis* in Table 1 have been advanced as representing the mysticete ancestral type. Most are poorly known; all can be said to be out of context in that they have no known close relatives, and their relationships to each other are unclear. More material must be collected, especially from lower and middle Oligocene rocks, before a valid family structure can be erected for Oligocene Cetacea.

Except for the Squalodontidae, therefore, we will consider the Oligocene Odontoceti without assigning them to families.

Xenorophus

A unique Oligocene odontocete is *Xenorophus sloanii* Kellogg (1923b) (Fig. 1a). *Xenorophus* was placed in the family Agorophiidae by Miller (1923:40), and later authors (Kellogg, 1928:32; Simpson, 1945:100; Romer, 1966:392) have followed this treatment. The genus is founded on a partial skull discovered during phosphate mining operations at Woodstock near Charleston, South Carolina, and sent to Kellogg by Earle Sloan. As reported by Kellogg (1923b:2), Sloan stated that the specimen came from 15 feet (4.6 m) below the upper surface of the "Ashley-Cooper marl," the upper part of which ("Ashley marl") Sloan regarded as "probably Oligocene" and the lower part ("Cooper marl") as Upper Jackson (Eocene). Though now filled in, the marl pit which furnished the holotype of *Xenorophus* was reported to be 76 feet (23.2 m) deep in

1917 (Cooke, 1936:83,85); thus, having been found only 4.6 m below the top of the marl, the specimen obviously came from Sloan's "Ashley marl," which he surmised to be of Oligocene age.

The age of the marl in the Charleston area is of considerable importance in view of the fact that these deposits yielded the holotypes of both *Xenorophus sloanii* and *Agorophius pygmaeus* (Müller, 1849) and, as noted by Kellogg (1923a:27-28), possibly that of *Archaeodelphis patrius* Allen (1921), a form also assigned to the Agorophiidae by Miller (1923:40). *Agorophius* has been suggested as "a somewhat distantly related precursor of the squalodonts" (Kellogg, 1928:49) and *Agorophius* and *Archaeodelphis* have been proposed as "stages of development through which the ancestors of some of the modern toothed Cetacea might have passed" (Miller, 1923:24-25). The Agorophiidae have even been regarded as "the ancestral family" in the Odontoceti (Rothausen, 1968:96; 1970:181-183). These views are based upon the cranial morphology of the forms involved, but assignment of ancestral status to the Agorophiidae hinges upon the age of the deposits which produced the holotypes of at least two of the three agorophiid taxa, i.e. the Charleston marl beds.

Sloan's (1908:463-464) division of the marl into two separately-named units ("Ashley marl" and "Cooper marl") was a variation of previous concepts proposed by Ruffin (1843), Tuomey (1848), Holmes (1870) and Clark (1891), all of whom except Ruffin (1843:7) referred these beds to the Eocene along with the underlying "Santee white limestone" of Lyell (1845:434). Dall (1898:330,341) retained the limestone in the Eocene but assigned the marl to the lower Oligocene. Stephenson (1914:85) applied the name "Cooper marl" to the Charleston marl deposits and regarded them as a single formation "referable to the uppermost Eocene or Oligocene," as did Rogers (1914:186), who also employed the name "Cooper marl."

Miller (1923:23) may have followed

Stephenson's (*op. cit.*) or Rogers' (*op. cit.*) determination of the age of the Cooper Marl in noting that *Agorophius* and *Xenorophus* were from "the Eocene or Oligocene of South Carolina." Kellogg (1924:758) placed *Xenorophus* in the upper Eocene, stating that it came from the Cooper Marl "which is correlated with the Jackson group." In his well-known history of the whales Kellogg (1928:32) continued to regard *Xenorophus* and *Agorophius* as being of upper Eocene age. Most subsequent authors followed Kellogg's appraisal of the age of these forms, and their status as upper Eocene taxa was perpetuated in the literature until Rothausen (1968:96; 1970:183) assigned them to the lower Oligocene in accordance with Cooke and MacNeil's (1952:27) referral of the Cooper Marl to the early Oligocene. But Cooke and MacNeil (1952) did not remove the Jackson group from the upper Eocene, as interpreted by Rothausen (1968:96); instead, they removed the Cooper Marl from the Jackson, suggesting that the Cooper "is really one stage younger, early Oligocene (?), and is equivalent to the Red Bluff Formation of Alabama and Mississippi."

However, recent investigations indicate that part of the Cooper Marl is even younger than early Oligocene. Malde (1959:25-26) presented evidence that the Cooper Marl in the vicinity of Charleston is of late Oligocene age, and studies in progress by the United States Geological Survey infer that the portion of the Cooper Marl outcropping in the area where the holotype of *Xenorophus* was collected is no older than late Oligocene.

Until 1970 only the holotype of *Xenorophus* was known; then Sanders collected six additional specimens near Eagle Creek in Dorchester County, South Carolina, about 30 km north of Charleston and only 6.4 km from the type locality.

The cranium of the holotype of *Xenorophus*, posterior to the frontals, is missing, but the new material includes a skull with an essentially complete cranium which shows the postorbital region of *Xenorophus*

to be unlike that of any other known odontocete. In both shape and construction, the braincase is more nearly like that of a typical land mammal than that of a cetacean. The parietals meet at the middle and produce a pronounced sagittal crest (Fig. 1a). The supraoccipital plate of *Xenorophus* is almost vertical, as in land mammals, archaeocetes and pinnipeds. A well-developed nuchal crest projects forward from the supraoccipital and overhangs the sagittal crest.

Although the postorbital region of the skull of *Xenorophus* has not undergone the telescoping process, telescoping of the rostral elements is well advanced. The maxillae and even the premaxillae extend backward over and posterior to the orbital region and overhang the temporal fossae. Though visible only as narrow strips paralleling the nasals and the frontals, the posterior extensions of the premaxillae actually spread outward beneath the maxillae. The extraordinary widening of the proximal end of the premaxillary and the overspreading of the supraorbital process by the lacrimal (Fig. 1a) are not duplicated in any other known odontocete. The nasals in *Xenorophus* are situated on a level with the postorbital extension of the supraorbital process, and, as observed by Miller (1923:24), the nasal passages slope backward as in *Archaeodelphis* (Allen, 1921:5). Although the nasals are missing in the holotype of *Agorophius* (True, 1907:Pl. 1), it is probably safe to assume that the nares opened forward in this form as well, inasmuch as the nasal opening in *Agorophius* occupies about the same relative position as that of *Archaeodelphis* (Kellogg, 1928: fig. 4).

Agorophius

The only species in the genus *Agorophius* Cope, 1895, is *A. pygmaeus* (Müller, 1849) (Fig. 1b), described from a partial skull collected in South Carolina in 1847 and now lost (True, 1907:3,4). The specimen was first reported by Tuomey (1847) as "a cranium of the Zeuglodon" and shortly

thereafter was assigned to the archaeocete genus *Basilosaurus* by Gibbes (1847:6, Pl. 5). Subsequent taxonomic allocations of this specimen have been reviewed by True (1907).

Tuomey (1847:152) stated that the "Zeuglodon" (= *Agorophius*) skull was found by F. S. Holmes in "the Eocene beds of Ashley River, about ten miles from Charleston," but he did not give the exact location of its discovery. Later, in a detailed account of the "Eocene" marl beds along the Ashley River, Tuomey (1848:166) remarked that "Greer's Landing is noted as the Zeuglodon locality." Consequently, "Greer's Landing" has long been accepted as the type locality of *Agorophius pygmaeus* (e.g. True, 1907; Kellogg, 1923a:29). We have been unable to find the exact location of Greer's Landing, but it was certainly in the general vicinity of Middleton Place Gardens (USGS Stallville 7.5 quadrangle), which is situated on the west bank of the Ashley River approximately 20.2 km (12.5 miles) upriver from Charleston. The topography along the river marshes both upstream and downstream from Middleton Place Gardens closely corresponds to Tuomey's (1848:166) brief description of the area in which the skull of *Agorophius* was found: "It is a long, low bluff, extending from the landing to Middleton Place." It is not clear whether Tuomey was referring to the bluff above Middleton or the one below it, but the latter seems to be the more likely of the two.

The stratigraphic origin of *Agorophius* is more firmly based. Tuomey's (1847:152) statement that the specimen came from "the Eocene beds of Ashley River" leaves no doubt that it was found in the Cooper Marl, which provides the only exposures on the Ashley River that were considered to be of Eocene age during the time of Tuomey. The collector, Francis S. Holmes, was one of the pioneers of South Carolina paleontology and was thoroughly familiar with the stratigraphic units along the Ashley River (Holmes, 1870). Thus, there is virtually no chance that the holotype of *Agor-*

ophius came from deposits other than the Cooper Marl.

Agorophius is the basis of the widely accepted family Agorophiidae Abel, 1913, generally regarded as the most primitive of the true Odontoceti. As defined by Kellogg (1923a:44) and Miller (1923:33), the Agorophiidae are characterized by a well-defined intertemporal constriction formed by the parietals (Fig. 1b). The presence of this feature in *Archaeodelphis patrius* Allen (1921:figs. 1-2) and the assumption of its presence in *Xenorophus sloanii* led Miller (1923:23-24) to assign these two forms to the Agorophiidae along with the nominative genus *Agorophius*. Kellogg (1928:32,34) retained *Xenorophus* and *Agorophius* in this group but placed *Archaeodelphis* in *incertae sedis*. More recently, Rothausen (1968:97,98) included *Archaeodelphis* in the Agorophiidae and added *Microzeuglodon* aff. *causasicum* (Lydekker, 1892) from the upper Oligocene of Azerbaijan, a form which Mchedlidze (1970:47-48,77) redescribed as *Mirocetus riabinini* and referred to the *Patriocetidae* (see below). From this brief synopsis it is evident that the taxonomic structure of the Agorophiidae has never been entirely sound.

Of the various genera which have at times been assigned to the Agorophiidae only *Xenorophus* and *Agorophius* have endured as traditional members of this family, the latter for obvious reasons. But now that the morphology of the postorbital region of *Xenorophus* is known in full detail the stability of this group has been even further eroded.

When the skulls of *Xenorophus* (Fig. 1a) and *Agorophius* (Fig. 1b) are compared it becomes apparent that the cranial structure in these two genera is so different that there can be little justification for retaining them in the same family. Although the parietals are exposed on the skull roof in both animals, those of *Xenorophus* form part of a transversely curved braincase while those of *Agorophius* form a prominent intertemporal constriction, the roof

of the braincase being narrow and tabular instead of broadly rounded as in *Xenorophus*. *Xenorophus* has a sagittal crest; *Agorophius* has none. In contrast to the vertical occiput of *Xenorophus*, the supraoccipital of *Agorophius* is thrust forward to a point beyond the center of the post-orbital region. Clearly, *Agorophius* and *Xenorophus* represent two separate lines of evolution.

In our opinion, no useful purpose would be served by erecting a new family to accommodate *Xenorophus*, especially since its relationships to other odontocetes are unknown at this time. Therefore, we place *Xenorophus sloanii* Kellogg in *incertae sedis*.

With the removal of *Xenorophus* the Agorophiidae becomes a monotypic family, unless one chooses to include *Archaeodelphis*. Since there is some division of opinion as to whether *Archaeodelphis* is more closely allied to the Odontoceti (Allen, 1921:13; Kellogg, 1923a:28; Miller, 1923:40; Rothausen, 1968:97) or to the Mysticeti (Kellogg, 1928:180; Dechaseaux, 1961:881-886), we prefer to place *Archaeodelphis patrius* Allen in *incertae sedis* pending further study of the cranial morphology of this interesting cetacean.

Believing that the preservation of the Agorophiidae as a monotypic family would be of no real systematic value, we also place *Agorophius pygmaeus* (Müller) in *incertae sedis*. However, we do not reject the possibility that *Agorophius* and *Archaeodelphis* are familially related, in which case a revival of the family Agorophiidae would be appropriate.

Two important factors now preclude further consideration of *Agorophius* as an ancestral form. If recent determinations indicating the Cooper Marl to be of late Oligocene age in the Charleston, South Carolina, area are correct, as they appear to be, *Agorophius* can no longer be entertained as a possible ancestor of the squalodonts (Kellogg, 1928:49) or any other odontocete group. Secondly, there is conclusive evidence that forms representing

more advanced stages of telescoping were contemporaneous with *Agorophius*, as demonstrated by a skull fragment recently found in the Cooper Marl only 9.6 km southeast of the *Agorophius* type locality (see Fig. 9 and discussion below). Nevertheless, the stage of telescoping manifested in *Agorophius* does seem to have been a part of the general evolutionary sequence, or sequences, which led to the more advanced stages seen in the squalodonts and certain nonsqualodontid odontocetes (e.g. Fig. 9). Hence, Miller (1923:24) was probably correct in suggesting that *Agorophius* merely exemplifies an evolutionary stage "through which the ancestors of some of the modern toothed cetacea might have passed."

Late Oligocene Odontoceti from Oregon

Two skulls, recently collected by Douglas Emlong from the late Oligocene part of the Alsea Formation of Oregon, represent primitive nonsqualodontid forms showing two quite different types of telescoping.

In one of these skulls (Fig. 2a), the nares face forward in land-mammal (or archaeocete) fashion and there is a strong intertemporal constriction with a sagittal crest, yet the triangular occiput is thrust forward in a manner reminiscent of the Mysticeti. The long, narrow premaxillae extend posteriorly to the level of the anterior edge of the orbit. Because of flaws in the preservation of the skull, the posterior extent of the ascending process of the maxilla cannot be determined. This specimen has small triangular teeth.

Another skull (Fig. 2b), found by Emlong less than 30 m from the previous one in the Alsea Formation, differs from it in having a tabular parietal region, much more cetacean-like, and no trace of a sagittal crest. The supraoccipital plate is thrust forward to the middle of the postorbital region. The nares face forward, and there is abrupt narrowing and lowering of the rostrum anterior to the orbital region. The ascending plate of the maxilla is vertical, as in land mammals, anterior to the antorbi-

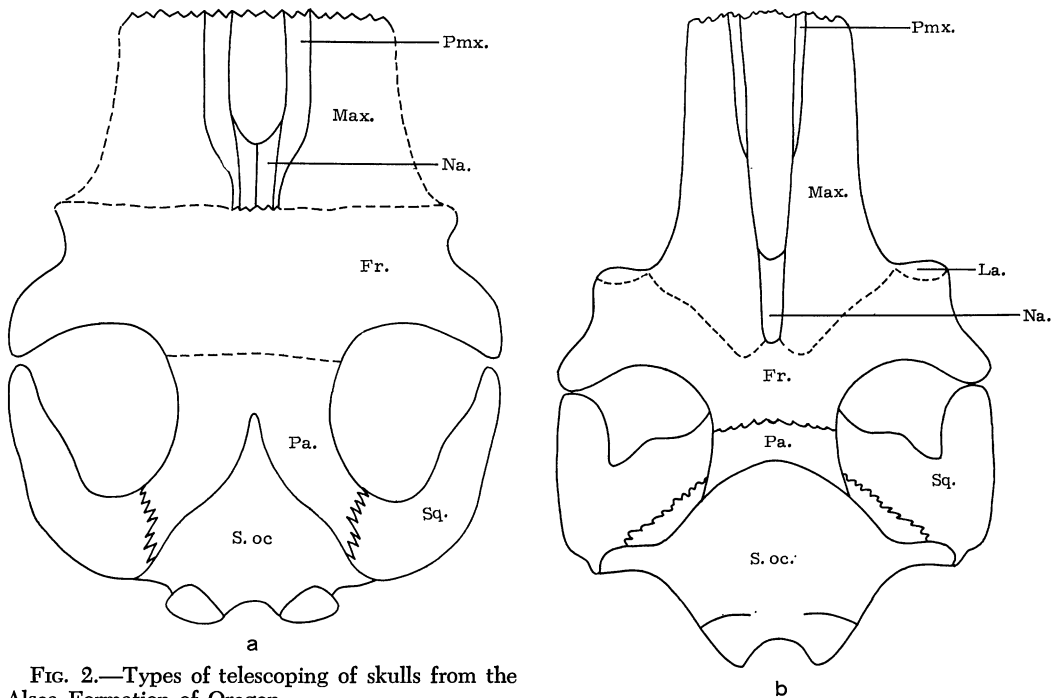


FIG. 2.—Types of telescoping of skulls from the Alsea Formation of Oregon.

tal notch. The ascending process of the maxilla is not preserved on the supraorbital process of the frontal, but striations in this region, indicating a squamous articulation on the frontal, show that such a part of the maxilla, composed of very thin bone, may originally have been present. The braincase of this skull closely resembles that of *Agorophius*, but the rostrum is much narrower.

Both the skulls from Oregon differ markedly from *Xenorophus* in mode of telescoping (cf. Fig. 1) but share with it a considerable exposure of the parietal on the roof of the braincase. In this they differ from the Squalodontidae.

Squalodontidae

Among the Oligocene Odontoceti, the Squalodontidae are represented by the largest number of specimens. Recently collected squalodont specimens from the Oligocene of South Carolina well illustrate the way in which the telescoping process re-

sulted in the elimination of the parietals from the surface of the skull roof. Heretofore, this aspect of telescoping has not been clearly understood. Miller (1923:5-7) and Kellogg (1928:44-46) discussed the reduction of the parietals in general terms but lacked the fossil material necessary for a detailed treatment. Mchedlidze (1970:71) postulated that "in the toothed cetaceans the displacement of the parietals is probably caused by the intensive expansion of the maxillae," but we are unaware of any evidence that supports this premise.

As shown by the South Carolina material and certain other Oligocene odontocetes, two of the most important steps in telescoping in the Squalodontidae were: 1) covering of the parietals by a forward thrust of the supraoccipital and 2) progressive posterior extension of the maxillae until, in *Squalodon* (Fig. 3c) and *Prosqualodon*, they are in broad contact with the anterior margin of the supraoccipital. These stages are observable in Charleston Mu-

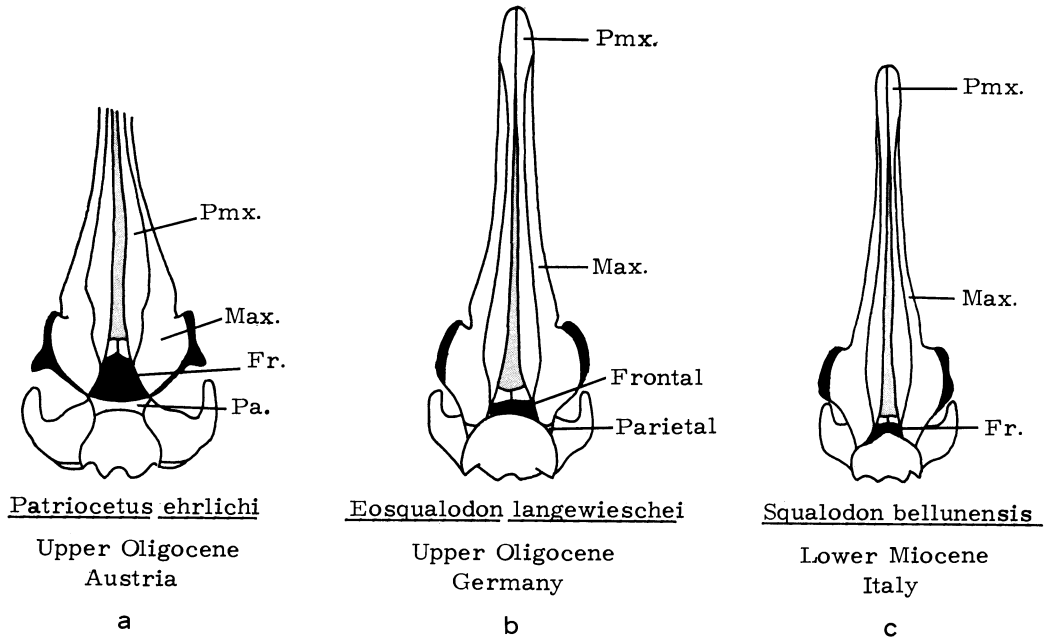


FIG. 3.—Stages in skull telescoping in European Odontoceti. From Rothausen (1968), with modifications in parietal region of *Patriocetus*.

seum specimens collected by Sanders during three summers of excavation near Eagle Creek in Dorchester County, South Carolina. The specimens were associated with *Xenorophus sloanii* (see above) in deposits that appear to be of late Oligocene age.

In skulls of two new squalodonts from Eagle Creek, temporarily designated as Genus Y and Genus Z, the parietals participate in the structure of the skull roof and form a prominent intertemporal constriction. The supraoccipital is thrust forward to meet the frontals, covering the parietals along the midline but leaving them exposed at the edges of the skull roof, where they are seen as small triangles.

Three ontogenetic stages are represented in the specimens of Genus Y. In a fragment of the skull of a juvenile individual, the anterior margin of the supraoccipital reaches the frontoparietal suture at the midline but does not come in contact with the frontals. In a virtually complete skull of a much larger individual, evidently a young adult (Fig. 4a), the apex of the

supraoccipital has grown over the frontoparietal suture and has established sutural contact with the frontals. A surprising development is seen in a well-preserved skull of a much older adult (Fig. 4b). Adjacent to the posteriormost end of the maxilla, the frontal projects backward to meet the supraoccipital, covering about half of the parietal triangle. All of the anterior margin of the supraoccipital is now in contact with the frontals.

Genus Y and Genus Z (not figured) represent a stage of telescoping in which the supraoccipital and the frontals have achieved contact, but the maxillae cannot reach the supraoccipital because the parietal region is too narrow to accommodate them.

A more advanced stage of telescoping is seen in another new squalodont from Eagle Creek, which we have temporarily designated as Genus X. In this stage, as in the two forms discussed above, the parietals are covered by the supraoccipital on the midline but are exposed as triangu-

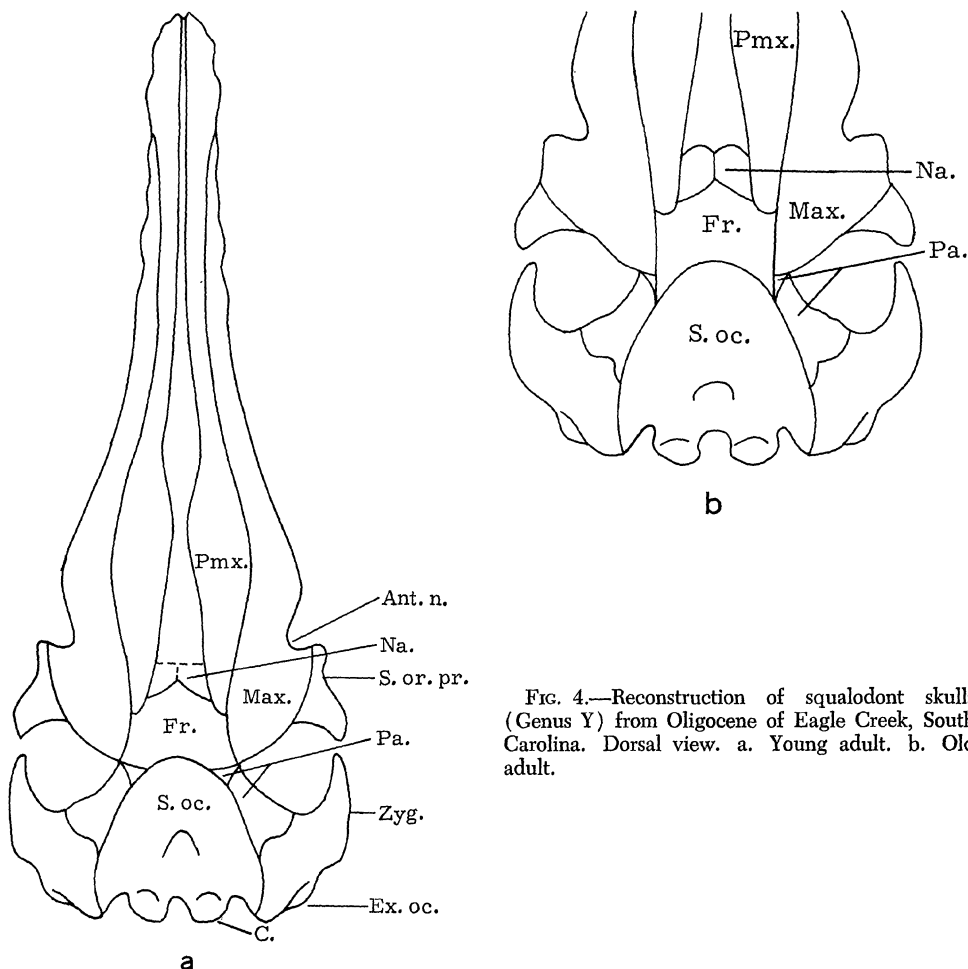


FIG. 4.—Reconstruction of squalodont skulls (Genus Y) from Oligocene of Eagle Creek, South Carolina. Dorsal view. a. Young adult. b. Old adult.

lar areas at the edges of the skull roof. However, the parietal region is proportionately broader than in forms Y and Z; hence, there is only a slight intertemporal constriction. The additional width of the parietal region in Genus X allows the posterior tips of the maxillae to come in contact with the supraoccipital (Fig. 5).

Two ontogenetic stages are manifested in the specimens of Genus X. In a partial skull of a subadult, apparently a very young animal, the parietals are exposed across the entire width of the skull roof (Fig. 6), and in sagittal section (Fig. 7) they are seen to extend backward beneath the supraoc-

cipital. In adults of this form, the supraoccipital has grown over the parietals in the vicinity of the midline (Fig. 8), concealing them from dorsal view except for the triangular areas at the edges of the skull roof.

Sagittal sections of skulls of Genus Y and Genus Z have shown that the parietals in these squalodonts are covered by the supraoccipital in the same fashion as in Genus X, and the presence of triangular exposures of the parietals at the edge of the skull roof in *Eosqualodon* (Fig. 3b) indicates that a similar situation exists in that form.

While providing new data about the telescoping process, the Eagle Creek speci-

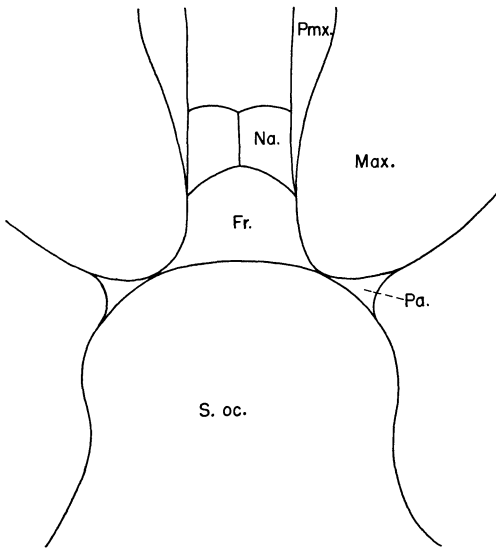


FIG. 5.—Adult squalodont (Genus X) from Oligocene of Eagle Creek, South Carolina. Dorsal view of cranial region.

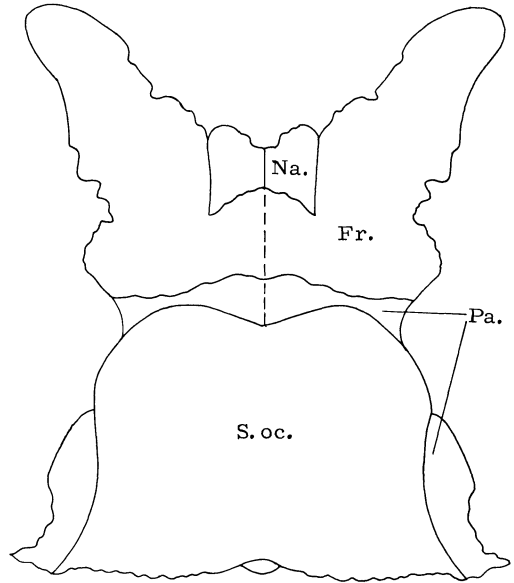


FIG. 6.—Subadult squalodont (Genus X) from Oligocene of Eagle Creek, South Carolina. Dorsal view of cranial region.

mens also emphasize the importance of considering ontogenetic stages in studies of fossil Cetacea.

Patriocetus and Agriocetus

Knowledge of the manner in which the parietals were crowded out of the skull roof in the odontocetes makes it possible to re-examine certain Oligocene taxa with a better understanding of structural details which have not been altogether clear in these forms. Of considerable importance in this respect is the skull of *Patriocetus ehrlichi* (Van Beneden, 1865) from Upper Oligocene sands near Linz, Austria. Rabeder (1975) places the Linz sands in the Chattian (late Oligocene) on the basis of the presence of the anthracothere *Microbunodon minus* (Cuvier). Besides *Patriocetus ehrlichi*, these sands are also the source of *Agriocetus incertus* (Brandt), *Squalodon* sp., and *Cetotheriopsis lintianus* (von Meyer). *Patriocetus* is the basis for the family Patriocetidae Abel, 1913, in which Abel also placed *Agriocetus incertus* (Brandt, 1874). Abel (1913:64) contended

that the baleen whales are descended from the Patriocetidae, but Kellogg (1928:182) pointed out that *Patriocetus* could not be an ancestor of the Mysticeti, since it was contemporaneous with *Cetotheriopsis*, a true mysticete.

As noted by Kellogg (1928:181), the two known skulls of *Patriocetus* are covered with grains of sand which obscure the su-

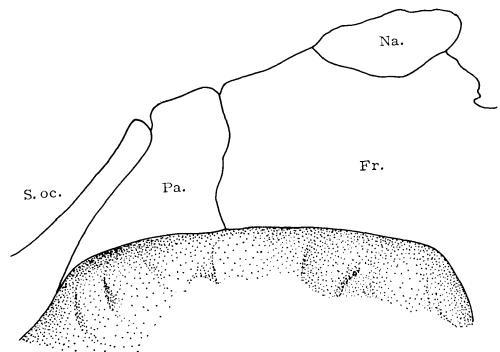


FIG. 7.—Subadult squalodont (Genus X) from Oligocene of Eagle Creek, South Carolina. Sagittal section of skull roof.

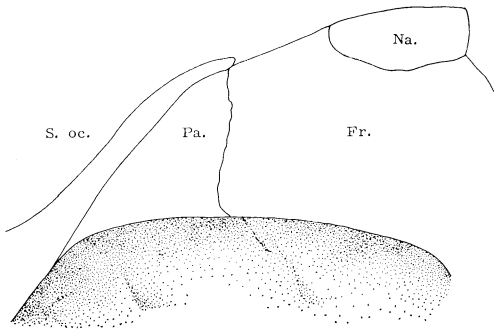


FIG. 8.—Adult squalodont (Genus X) from Oligocene of Eagle Creek, South Carolina. Sagittal section of skull roof.

tures, making it difficult to determine the boundaries of the bones in the skull roof. In Abel's (1913) reconstruction of the skull of *Patriocetus* the parietals occupy all of the skull roof between the supraoccipital and the posterior ends of the premaxillae. Kellogg (1928:181–183) did not comment on this interpretation but called attention to other questionable aspects of Abel's reconstruction, notably the abrupt termination of the maxilla at the anterior margin of the frontal, an arrangement that Kellogg considered to be improbable because of its structural defectiveness. Rothausen (1968:88) also disagreed with Abel's version, stating that the supraorbital plates of the maxillae are shoved up on the cranium in the normal odontocete manner. He reduced the Patriocetidae to subfamilial level (Patriocetinae) within the Squalodontidae (Rothausen, 1968:88).

In our reconstruction of the skull of *Patriocetus* (Fig. 3a) the parietals meet at the midline and are exposed in a narrow space across the entire width of the skull roof. We considered it to be the most likely arrangement of the parietals in *Patriocetus* as indicated by photographs of the holotype made for us by Mr. Michael N. Cohen and by our evidence of the manner in which the parietals were eliminated from the skull roof in the odontocetes. For reasons which will be discussed below, the intertemporal constriction in *Patriocetus*

implied that the parietals are in contact at the midline, and the extreme length of the constriction suggested that the supraoccipital did not cover the parietalia in the stage of telescoping represented by *Patriocetus*. However, Figure 3a was prepared more than a year in advance of publication and does not coincide with our recent observations of the holotype of *Patriocetus* at the Oberösterreichisches Landesmuseum in Linz, Austria. From direct examinations of the holotype and a second, less complete skull of this form, it now seems quite evident that the frontals are in contact with the supraoccipital at the midline and that the parietals are not exposed across the entire width of the skull roof as shown in Figure 3a, although these bones are in place in the skull roof as we had anticipated. We regret that this detail could not be corrected before publication, the engravings for the figures having already been made.

Rothausen's (1968:89, fig. 2a) reconstruction of the skull of *Patriocetus* has been a major contribution to studies of this form. We concur with his interpretation of the original form of the skull and with all of his sutural delineations except those of the parietals. Rothausen shows the parietals in *Patriocetus* as two disjunct rectangles at the edges of the skull roof, an arrangement which infers that in forms ancestral to *Patriocetus* the parietals were progressively wedged apart by the frontals. However, the existence of such an evolutionary sequence has not been demonstrated elsewhere and is not reflected in the cranial morphology of *Patriocetus*.

Though it has received far less attention than the holotype, the more fragmentary second skull of *Patriocetus* is highly informative. In this specimen the right side of the skull roof is broken away, providing an excellent sagittal view in which the left parietal can be seen beneath the anterior portion of the supraoccipital. Thus, the parietals are in place across the width of the skull roof in *Patriocetus* but are concealed from dorsal view by the supraoccipi-

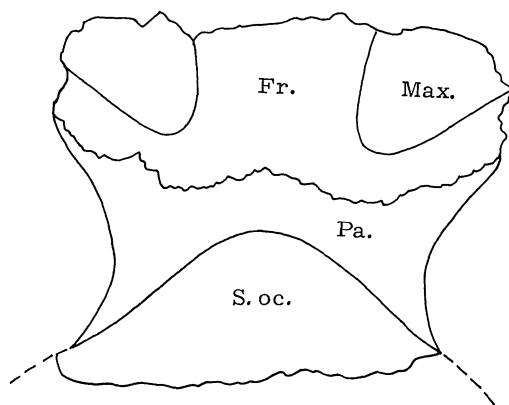


FIG. 9.—Fragment of squalodont skull (Genus A) from Oligocene of Charleston County, South Carolina. Dorsal view.

tal except at the very edge of the skull roof between the anterior margin of the supraoccipital and the posteriormost extent of the maxillae.

Since there is a pronounced intertemporal constriction in the skull of *Patriocetus*, it is not at all surprising to find that the parietals participate in the formation of the skull roof. As demonstrated in the archaeocetes, in *Agorophius* (Fig. 1b) and *Archaeodelphis* (Allen, 1921:figs. 1-2), and in our new forms from Oregon (Fig. 2b) and South Carolina (Figs. 4-9), the intertemporal constriction is always formed by the parietals. Therefore, it is possible to predict their presence in the roof of any odontocete skull in which there is an intertemporal constriction, even though these bones may not be completely visible in dorsal aspect. As we have shown, it is essential to employ this knowledge in the diagnosis of odontocete cranial material from the Oligocene. Specimens from this period of intense evolutionary activity often display external features which can be quite deceiving. Here it is appropriate to mention a recently discovered cranial fragment (Fig. 9) demonstrating an undescribed stage of telescoping.

The new specimen is the parietal region of the skull of a squalodontoid odontocete

apparently comparable in size to modern *Tursiops*. Morphological details of this specimen indicate that it represents a previously unknown form, which we have temporarily designated as Genus A. The fragment was found in early 1975 by Albert C. Duc in spoil material removed during channelization of a small stream in Charleston County, South Carolina, approximately 13 km northwest of the city of Charleston and about 17 km southeast of the Eagle Creek locality. Sediments adhering to the specimen confirm that it came from the Cooper Marl, previously noted as being of Oligocene age.

Structural details are well preserved in this specimen. As seen in Fig. 9, the parietals are visible across the entire width of the skull roof between the supraoccipital and the frontals. In dorsal aspect, the frontals and the parietals appear to share an equal role in the formation of the skull roof, but in reality they do not. Ventrally, the parietals extend the entire length of the specimen, showing anteriorly the cavity that accommodated the olfactory lobes of the brain. Thus, in Genus A, the parietals form the roof of the braincase and are overridden not only by the supraoccipital but by the frontals as well, suggesting that sutural contact between the frontals and the supraoccipital was accomplished in this fashion in some odontocete lines.

The preserved parts of the maxillae in Genus A infer that, in a complete state, the shape of these bones may have been similar to that of the maxillae of *Agorophius* (Fig. 1b). These two animals also appear to have been of about the same size. Tuomey (1847:153) reported the preserved part of the skull of *Agorophius* to be 14½ inches (368 mm) in length and 7½ inches (190.5 mm) in greatest width. Applying these dimensions to the scale of Agassiz's figure of "*phocodon*" (= *Agorophius*) in True (1907), we find that the parietal region in the missing holotype of *Agorophius* apparently was of about the same width as that of Genus A, i.e. 57 mm. However, the anteroposterior length of the dorsal side of

the parietal region in Genus A is only about half that of *Agorophius*. On the basis of this character alone, Genus A seems to represent a stage of telescoping intermediate between the stages exemplified by *Agorophius* and by Genus Y.

Although the maximum adult size of *Agorophius* and Genus A may never be known, it seems clear that they probably did not exceed the dimensions of individuals in coastal populations of modern *Tursiops*. The presence of such diminutive forms, seemingly ill-suited for the demands of a pelagic existence, lends weight to speculations that most of the more primitive odontocetes of Oligocene times were moderate-sized inhabitants of coastal waters.

CETACEA INCERTAE SEDIS

A superb specimen of a whale having a triangular rostrum and diverging rows of small leaf-shaped teeth was collected and described as *Aetiocetus* by Emlong (1966) from the late Oligocene part of the Yaquina Formation of Oregon. At least two other skulls of the genus have been collected from the same formation. The diverging tooth rows and anterior-facing nares are reminiscent of *Patriocetus*, but the almost vertical supraoccipital is concave posteriorly like those of the Archaeoceti, in which Emlong placed this genus. The parietals are visible in the skull roof, which is transversely rounded, as in primitive Cetacea, rather than tabular, as in more advanced forms. There is no sagittal crest. The cheek teeth are leaf shaped, similar to those of *Patriocetus*, but smaller and with the roots coalesced.

The triangular rostrum, reduced dentition, and the conformation of the posterior ends of the maxillae, premaxillae, and nasals (Emlong, 1966:5) are characters that would be expected in the ancestor of the mysticetes. Thenius (1969:489) stated: "Even if *Aetiocetus*, because of its geologic age (upper Oligocene) cannot be a direct stem form of the cetotheres, yet this genus documents that a specific family (Aetiocetidae) must be classified as ancestor, the link be-

tween ancient and baleen whales. Considering the combination of characters it is a matter of convention whether one classifies Aetiocetidae as evolved Archaeoceti or as primitive, toothed Mysticoceti."

G. G. Mchedlidze (written commun., April 21, 1975) regards *Aetiocetus*, together with *Ferecetotherium* and *Mirocetus*, as standing on the Archaeoceti-Mysticeti evolutionary line, and as not to be included in the Odontoceti. With regard to *Mirocetus*, Mchedlidze points out that this represents a change in opinion from that expressed by him previously (Mchedlidze, 1970:47) when he placed the genus in the Patriocetidae.

We place the above genera, together with *Agriocetus* and *Archaeodelphis*, in *incertae sedis* (Table 1). *Archaeodelphis* has also been advanced as representing the structure of mysticete ancestors (Kellogg, 1928:180; Dechaseaux, 1961), as has *Patriocetus* (Abel, 1913:214-218). All these genera are younger than known true Mysticeti.

MYSTICETI

Among the few Cetacea known from deposits of middle Oligocene age are two occurrences of unmistakable Mysticeti. One of these, *Mauicetus* Benham, 1939 (Fig. 10), from New Zealand, has long nasals embraced by premaxillae and maxillae which extend posteriorly to the level of the supra-orbital process of the frontal, together with an anteriorly thrusting triangular supra-occipital (Marples, 1956). This structure is typical of the Cetotheriidae, the oldest family of baleen whales, which became common in Miocene time. The intertemporal area of *Mauicetus* is, expectably, longer than in Miocene cetotheres. It resembles that of the archaeocetes.

Recently, Frank Climo (written commun., January 1975) has discovered, in middle Oligocene rocks of New Zealand, a skull and mandible of a mysticete, probably a cetotheres. The mandibles are toothless, elongate, with a low coronoid process

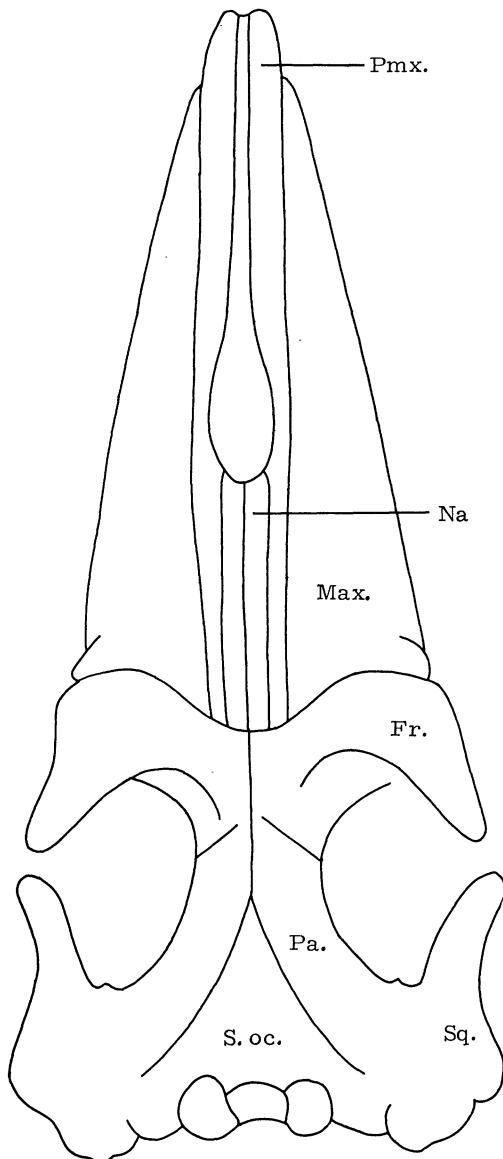


FIG. 10.—*Mauicetus lophocephalus* Marples. Skull in dorsal view. From Marples (1956).

and backward-facing condyles; they are fully developed mysticete jaws.

Further evidence of the development of Mysticeti in the Oligocene, and of their wide distribution, is *Cetotheriopsis* Brandt, 1871, from the late Oligocene of Austria and Germany (Rothausen, 1971).

SUMMARY

Oligocene cetacean assemblages consisted of the following elements:

1. Surviving archaeocetes, probably representing at least two families. They were apparently still widespread, although fossils are rare.

2. Squalodonts: the best known Oligocene Cetacea, known from New Zealand, North America, and Europe.

3. Other primitive toothed whales, represented by few and usually poor specimens. They are characterized by triangular teeth, similar to but much smaller than those of archaeocetes and squalodonts. Contemporary members of this loosely defined group had widely varying types of telescoping, leading to the conclusion that many phylogenetic lines are represented. Differences in width of rostrum probably indicate different diets and may bear on relationship with the Mysticeti.

4. Mysticeti. The baleen whale mode of feeding had fully evolved by middle Oligocene time. Although few specimens have been found, their occurrence in Europe and New Zealand makes it likely that Mysticeti had cosmopolitan distribution at that time.

CONCLUSIONS

In comparison with the modern fauna, the Oligocene Mysticeti are more advanced than the Oligocene Odontoceti. The latter showed no sign of the asymmetry that is now the hallmark of the odontocete, or of the basining of the facial region that, in some Odontoceti, indicates the presence of the melon, the bulbous "forehead" structure that plays an important part in echo location. Both these phenomena appear, in muted form, in the Miocene. Gerald Fleischer (written commun., May 17, 1974), in studying the periotic of the squalodont Genus Z from the Eagle Creek locality in South Carolina, has determined that the basal half of the cochlea is of the right dimensions to receive high-frequency sound. He concludes that, although not all details are preserved, this squalodont seems

to be some sort of an intermediate stage between a cetacean able to hear only low frequencies and a typical modern dolphin.

The Oligocene Mysticeti, on the other hand, had already evolved the elongated, edentulous rostrum, constituting $\frac{3}{4}$ to $\frac{1}{2}$ of total skull length, that typifies the modern baleen whales. The mandible of Oligocene Mysticeti was also edentulous and, like those of modern baleen whales, was long and slim.

In the Oligocene, the dietary contrast between Mysticeti and Odontoceti was well established. How much variety existed in the diet of the Odontoceti is hard to say, but variety in type and size of teeth was far less than that existing in the Miocene.

As to phylogeny, we can only say that the Mysticeti must have had a considerable independent history before middle Oligocene time. The presence in late Oligocene deposits of toothed whales with broad rostra suggests that such a form, in late Eocene or very early Oligocene time, may have been ancestral to the Mysticeti. The ancestor of the modern Odontoceti probably resembled one of the narrow-snouted primitive odontocetes discussed above: it had undergone less telescoping than even the most primitive Squalodontidae and had smaller, although triangular, teeth. It is probably this type of animal that Rothausen (1968:99) had in mind for his "Agorophiide Stufe," an early Oligocene evolutionary stage which he postulated as ancestral to the Squalodontoidea, Platanistoidea, and Delphinoidea. However, until we have good collections from lower Oligocene deposits, we will be unable to do more than speculate about the phylogenetic pattern that produced the many different forms of Cetacea that we know from the Miocene.

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