

A middle Eocene basking shark (Lamniformes, Cetorhinidae) from Antarctica.

ALBERTO L. CIONE* and M.A. REGUERO

Departamento Científico Paleontología Vertebrados, Museo La Plata, Paseo del Bosque s/n, 1900 - La Plata, Argentina
*Email: museo@isis.unlp.edu.ar

Abstract: A proximal fragment of a gill raker identified as belonging to a shark of the genus *Cetorhinus* was collected from middle Eocene deposits of the La Meseta Formation in the northern part of Seymour Island, Antarctica. This is the first record of a fossil basking shark from Antarctica and one of the earliest records of the genus. The minimum age of Cetorhinidae is middle Eocene. The only living species of the family Cetorhinidae is a very large plankton feeder, *Cetorhinus maximus*. Basking sharks are unknown in subantarctic or Antarctic waters but occur on both South American coasts today. The evolution of filter-feeding vertebrates is discussed.

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Introduction

A diverse ichthyofauna occurs in the Eocene La Meseta Formation of Seymour Island (Cione *et al.* 1977, Welton & Zinsmeister 1980, Grande & Eastman 1986, Long 1992, Cione & Reguero 1994, Marensi *et al.* 1994, Cione *et al.* 1994). While the diversity of teleost fishes appears to be low, the elasmobranch fauna seems to be abundant and quite diverse. However, this is probably the result of taphonomic causes. The bulk of the bearing fossil localities is located in the middle and upper part of the sequence. In the Antarctic summer of 1995–96, one of us (MR) collected a fragmentary proximal gill raker of a shark at the well explored locality IAA 1/90 (Fig. 1). In this paper, the first record of family Cetorhinidae in Antarctica is described and some evolutionary implications are discussed.

Locality and stratigraphical setting

The single specimen described here was collected from the middle–late Eocene La Meseta Formation of Seymour Island. This sequence represents the youngest exposed unit of the sedimentary fill of James Ross Basin and has yielded the best and most diverse ichthyofauna known from Antarctica. Sadler (1988) subdivided La Meseta Formation into seven numbered units (Telm 1 to 7). The La Meseta Formation represents shallow-water marine, nearshore, and paralic environments, and is composed of thick shell beds, sandstones, siltstones, and clays (Marensi *et al.* 1994). Outcrops of La Meseta Formation are exposed on the northern part of Seymour Island.

The fossil was recovered by sieving at locality IAA 1/90 (GPS data: 64°14'4.67"S, 56°39'56.38"W, Fig. 1), which is within Telm 5 and about half way up the section (Fig. 2). The thin horizon that contains the IAA 1/90 vertebrate fauna is a

conglomeratic lens less than 1 m thick composed of bioclasts, gravel and sand. The bioclastic fraction is composed mainly by naticid gastropods; the matrix is made up of fine to coarse sand and contains gravels and cobbles up to 20 cm in size.

Telm 5 includes, by far, the bulk of the fossil shark localities (see Table I). The collecting locality is located within the *Struthiolarella steinmanni* Zone of Stilwell & Zinsmeister (1992); IAA 1/90 has been known since Bond *et al.* (1990) reported the first South American “ungulates” from Antarctica from specimens collected there. The marine vertebrate fauna

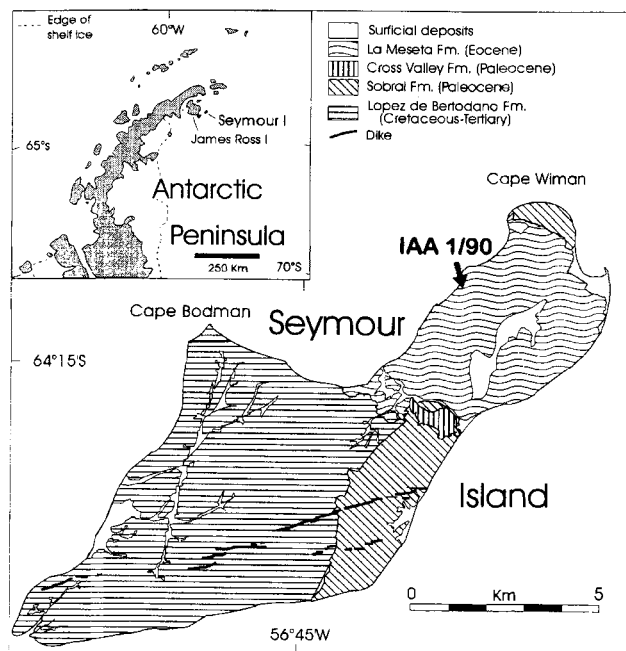


Fig. 1. Map to show the collecting locality (arrowed) of the basking shark on Seymour Island.

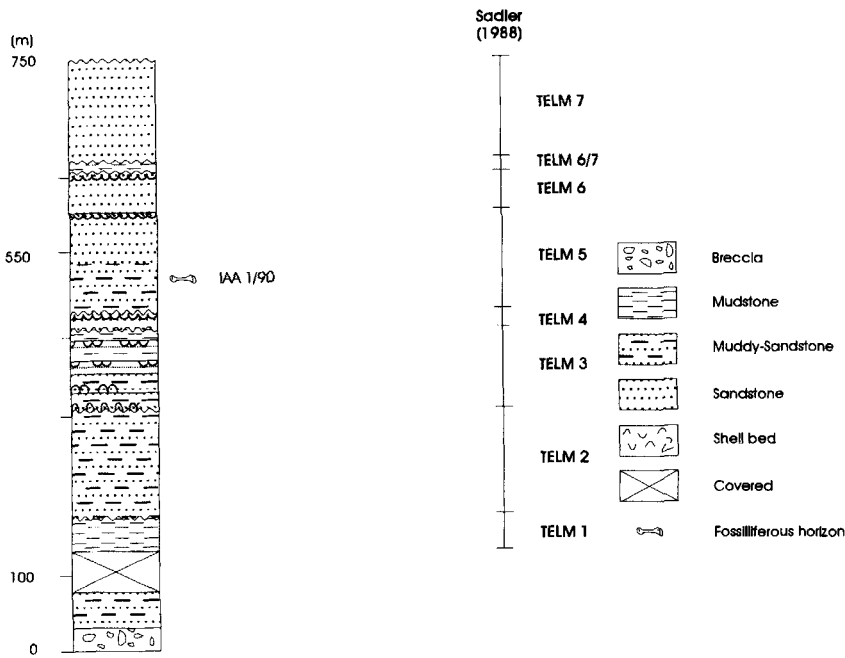


Fig. 2. Simplified stratigraphical section of the collecting locality (modified from Sadler 1988).

Table 1. Elasmobranchs reported from Telm 5 of the Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula.

Hexanchidae	
	<i>Hexanchus</i> sp.
	<i>Hepranchias howelli</i>
Squalidae	
	<i>Squalus weltoni</i>
	<i>Squalus woodburnei</i>
	<i>Centrophorus</i> sp.
	<i>Deania</i> sp.
	<i>Dalatis licha</i>
Pristiophoridae	
	<i>Pristiophorus lanceolatus</i>
Cetorhinidae	
	<i>Cetorhinus</i> sp.
Squatinae	
	<i>Squatina</i> sp.
Stegostomatidae	
	<i>Stegostoma</i> cf. <i>S. fasciatum</i>
Ginglymostomatidae	
	<i>Pseudoginglymostoma</i> cf. <i>P. brevicaudatum</i>
Odontaspidae	
	<i>Carcharias macrotia</i>
	<i>Odontaspis rutoti</i>
	<i>Odontaspis winkleri</i>
Mitsukurinidae	
	<i>Anomotodon multidenticulata</i>
Lamnae	
	<i>Isurus praecursor</i>
	<i>Lamna nasus</i>
Carcharhinidae	
	<i>Scollodon</i> sp.
Myliobatidae	
	<i>Myliobatis</i> sp.
Rajidae	
	Rajidae indet.

Data from Cione *et al.* 1977, Tonni & Cione 1978, Welton & Zinsmeister 1980, Long 1992, 1994, Cione & Reguero 1994, this paper).

consists of sharks, rays, chimaeroids, bony fishes, whales, turtles, and birds (mainly penguins); the marine invertebrate macrofauna is numerically dominated by naticid gastropods together with bivalves, brachiopods, crinoids, nautiloids, sand crabs, and asteroids. Many trace fossils were found in this horizon including *Ophiomorpha*, *Scoyenia*, *Diplocraterion*, and *Skolithos*.

Over 9000 teeth from about 20 different shark taxa have been collected at locality IAA 1/90 by Argentine expeditions by intensive and careful sieving.

Systematic description

Class CHONDRICHTHYES Huxley 1880

Order LAMNIFORMES Compagno 1973

Family CETORHINIDAE Gill 1862

Genus CETORHINUS Blainville 1816

Cetorhinus sp.

Fig. 3

Material

MLP 96-I-5-42, a proximal part of a gill raker (or branchiotechna; see Cappetta 1987) from Telm 5 of La Meseta Formation, Seymour Island (Isla Marambio), Antarctica; middle Eocene.

Description

The fragment is 6.1 mm long. The complete gill rakers are composed by a long, slender rod and a flattened, broad proximal expanded region (Fig. 4). In MLP 96-I-5-42, the slender rod is broken away almost at the base. The proximal

part is made up of rugose dentine. The distal region is covered with smooth enameloid. The sinuous proximal boundary of enameloid is clearly shown in Fig. 3. A longitudinal cavity is observed in the broken distal end.

Discussion

The gill raker from Seymour Island is very close in morphology to those of *Cetorhinus* and clearly differs from those of other filter-feeding sharks and rays such as the whale sharks of the family Rhiniodontidae, the megamouth *Megachasma pelagios*, or the mobulid batoids. The specialized denticle gill rakers of *Cetorhinus* are unique among Chondrichthyes, and resembles the bony gill rakers and slender gill arches in many filter feeding teleosts (Compagno 1990). The gill rakers of *Cetorhinus* are modified, elongated dermal denticles, which are attached to the branchial arches and form filter webs to catch plankton (Cappetta 1987, Fig. 4). *Rhiniodon typus* has laminar gill rakers covered with denticles and *Megachasma pelagios* has unique gill rakers, formed as elongated, slender, cartilage-filled dermal papillae covered by imbricated denticles (Taylor *et al.* 1983).

Fossil remains assignable to *Cetorhinus* have been recovered from the Eocene of North America; the Oligocene of Netherlands, Germany, Belgium, Roumania, and France; the Miocene of France, Austria, Switzerland, Japan, and United States; the Pliocene of Belgium, Italy, and Chile; and the Pleistocene of Japan (Herman 1975, 1979, Cappetta 1987, Bellwood & Schultz 1991, Bault 1993, Génault 1993, Long 1993, Yabumoto & Uyeno 1994, Gottfried 1995).

Undetermined remains assigned to the genus *Cetorhinus*



Fig. 3. Lateral view of the proximal part of a gill raker of *Cetorhinus* from La Meseta Formation. MLP 96-I-5-42. Scale bar is 0.5 mm long.

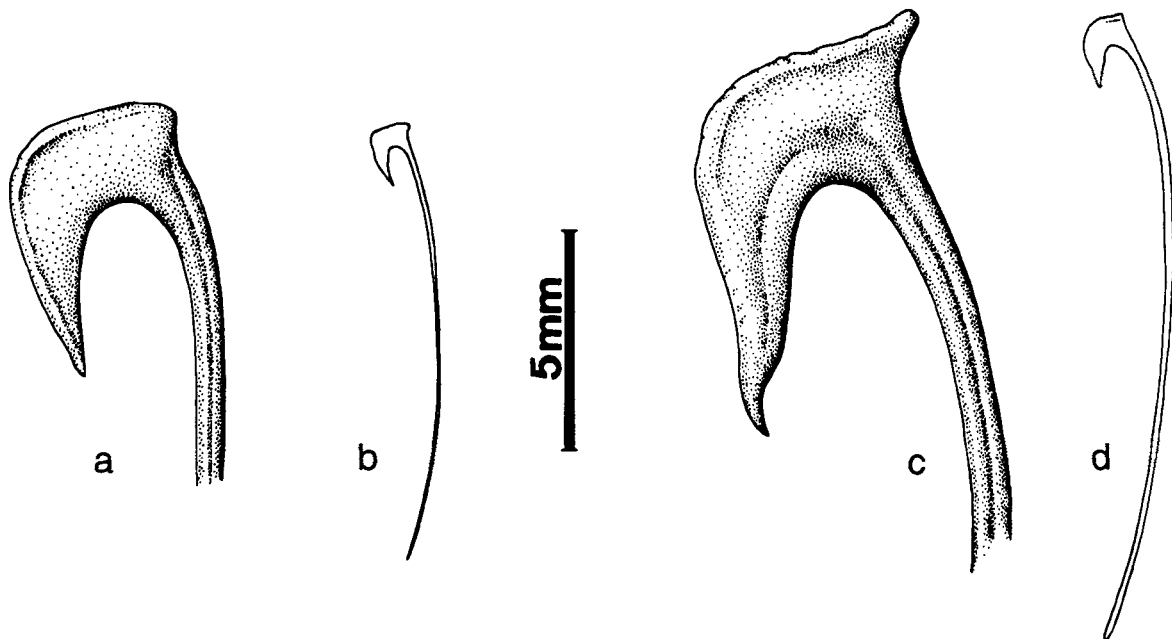


Fig. 4. Two gill rakers of a specimen of the extant *Cetorhinus maximus* (modified from Siccardi 1960). a, c. Enlargements of the proximal part. The scale corresponds to a and c.

were mentioned from unidentified Eocene beds in North America (B. Welton in Cappetta 1987, D. Long, personal communication 1997). The oldest described and figured specimens came from the lower Oligocene of Europe (Leriche 1910, Cappetta 1987, Bault 1993, Génault 1993). Thus, the present is the first description and illustration of an Eocene specimen assignable to *Cetorhinus*.

Oligocene and Miocene basking sharks have been referred to the extinct species *C. parvus* Leriche 1908. Teeth of that species are different to those of *C. maximus* (Gunner 1765) but its gill rakers seem to be similar although smaller (Herman 1979). Pliocene and Pleistocene records have been assigned to the recent *C. maximus* (see Cappetta 1987, Long 1993).

Cetorhinus maximus is an amphitemperate species that reaches cold waters in north-eastern Atlantic and Barents Sea during the summer (Bigelow & Schroeder 1948, Compagno 1984, Fig. 5). In contrast with the whale shark *R. typus*, where the basic planktonic diet is often supplemented by fish, *C. maximus* appears to subsist on plankton alone; the temperate waters inhabited by *C. maximus* probably always

contain sufficient plankton to satisfy its requirements. The relatively sterile tropical seas where *R. typus* is found generally have low concentrations of plankton, making some form of supplement necessary (Taylor *et al.* 1983).

Evolutionary considerations

Herman (1979) suggested that *Alopias* should be related to *Cetorhinus*. Certainly, some oral teeth of the fossil species *C. parvus* recall those of *Alopias* (Cappetta 1987). However, Maisey (1985) suggested that *Cetorhinus* and *Megachasma* were sister groups, a view that was championed by Compagno (1990), who considered that *Megachasma* was the sister group of *Alopias* plus *Cetorhinus*, *Isurus*, *Carcharodon*, and *Lamna*. According to Compagno (1990), *Megachasma pelagios* could have evolved its feeding apparatus from an odontaspid-like primitive jaw mechanism by exaggerating its jaw size and acquiring papillose gill rakers, while harnessing and modifying the primitive lamnoid mode of jaw protrusion for suction-feeding. By contrast, basking sharks would have

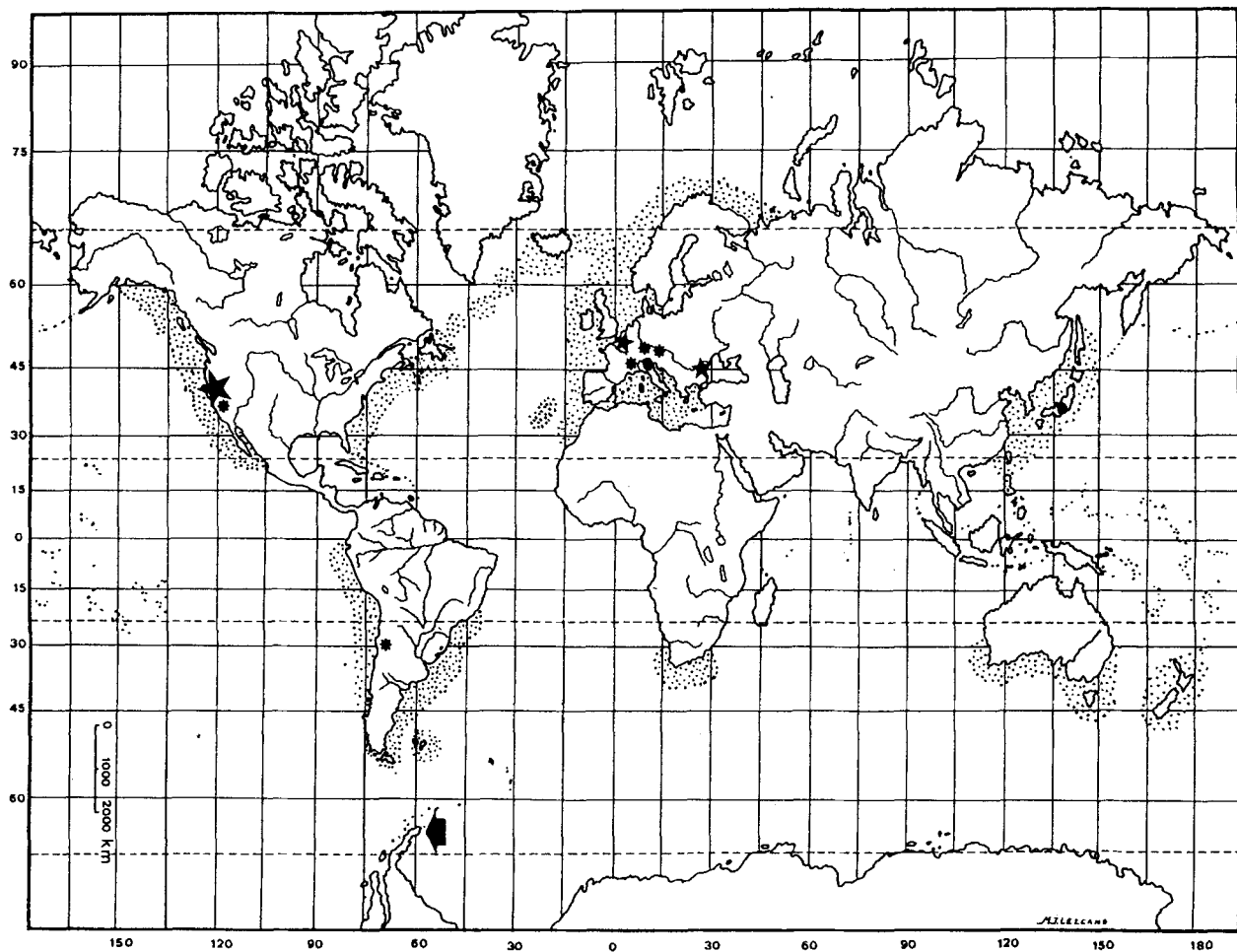


Fig. 5. Distribution of the extant species *Cetorhinus maximus* (stippled areas) and the fossil records of *Cetorhinus*. The arrow indicates Seymour Island. Other fossil records are indicated by large stars (Eocene), little stars (Oligocene), asterisks (Miocene), and points (Pliocene-Pleistocene).

evolved their feeding apparatus from a lamnid-like antecedent with restricted protrusion, but virtually eliminated protrusion in favour of jaw distension and teleost-like method of filter feeding that is unparalleled amongst elasmobranchs (Compagno 1990). Consequently, it appears that not only the orectolobiform *Rhiniodon* but also the lamniforms *Cetorhinus* and *Megachasma* evolved convergently to a filter-feeding mode of life.

The oldest putative filter-feeding sharks are known from the early Palaeogene (Rhincodontidae, *Palaeorhincodon*, late Palaeocene, Herman 1975, Cappetta 1987, Kemp *et al.* 1990; *Eorhincodon*, late Eocene, Li 1996; *Cetorhinus*, middle Eocene, this paper, undetermined Eocene, D. Long personal communication).

The filter-feeding mode of life, characteristic of large, nectonic coastal and oceanic vertebrates, was also developed by the Mysticeti in the late Palaeogene (Mammalia, Cetacea). Many Oligocene, Neogene, and recent whales and sharks are filter feeders. In contrast, during the Mesozoic, this niche was occupied by very few vertebrates such as the large teleost *Leedsichthys problematicus*. This pachycormid surpassed 10 m in total length and lived in England during the middle-late Jurassic (Martill 1991). When filter-feeding sharks appeared in the Palaeogene this niche had apparently been unoccupied for many million years.

The Mysticeti whales appear in rocks close to the Eocene/Oligocene boundary in middle and high latitudes of the Southern Hemisphere (e.g. Telm 7 of La Meseta Formation; Fordyce 1992). Thus, the putative filter-feeding sharks assigned to the family Rhiniodontidae apparently preceded the filter-feeder cetaceans by perhaps 25 million years. However, these old rhinodontids are only known from isolated teeth.

The appearance of the first representatives of the family Rhiniodontidae coincides with a remarkable increase in species diversity of many oceanic organisms (e.g. planktic foraminifera, dinoflagellates, teleost and elasmobranch fishes) during the late Palaeocene (a "polytaxic" period, see Fisher & Arthur 1977). It should also be noted that a temperature peak occurred in the early Paleogene (at 63–52 Ma; Clarke & Crame 1992). The extant *Rhiniodon typus* inhabits warm seas. The ecologic structure of marine communities alters as diversity increases and the increased species packing within communities is accompanied by a broader utilization of ecospace (Bambach 1985). In this context, new adaptive types could appear and utilize available resources. Generally, an increase in effectiveness of resource utilization occurs only by the development of new groups (Bambach 1993).

A long-term cooling trend was established during the middle-late Eocene, with abrupt drops in sea temperatures near the early and middle Eocene boundary and in the late middle Eocene (Frakes *et al.* 1992). The "Terminal Eocene Event" in the marine realm was comprised of a sequence of geological events that registered the climatic transition from a warm peak in the early Eocene to cold Oligocene conditions

(Miller 1992). Cetacean, and perhaps cethorhinid evolution, during the earlier Oligocene seems to have been linked to progressive cooling and, by inference, to new feeding opportunities offered by increased vertical and horizontal diversification of the oceans (Fordyce 1992).

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