

## Quaternary colonization or Paleogene persistence?: historical biogeography of skates (Chondrichthyes: Rajidae) in the Antarctic ichthyofauna

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**Abstract.**—Seven endemic species of skates (Chondrichthyes: Rajidae) represent the only family of elasmobranchs currently known to live in Antarctic continental waters. Many previous authors believed skates colonized Antarctic waters from Patagonia during interglacial periods in the Quaternary. However, recent fossil material collected from the middle Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula, indicates that they may have persisted in Antarctic waters since the Paleogene. Additionally, oceanographic barriers present in the Neogene and Quaternary would have prevented dispersal from southern continents to Antarctica. A revised dispersal scenario, based on skate fossils, biology, paleogeography, and present centers of skate diversity, suggests that skates evolved in the western Tethys and North Boreal seas of western Europe in the Late Cretaceous and early Paleogene and emigrated into Antarctica during the early to middle Eocene via a dispersal corridor along the continental margins of the western Atlantic Ocean. Skates probably populated the Pacific Basin by passing from this dispersal corridor through the Arctic Ocean. Vicariant events, such as opening of the Drake Passage, the development of the Circum-Antarctic Current, and formation of deep and wide basins around Antarctica in the late Paleogene, created barriers that isolated some species of skates in Antarctica and prevented movement of other species of skates into Antarctica from northern areas. Skates are the only group of fishes known to have survived the Oligocene cooling of Antarctica that killed or extirpated the Paleogene ichthyofauna; they persisted by a combination of cold-tolerance, generalized diet, and unspecialized bathymetric and habitat preferences.

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### Introduction

The highly endemic present-day Antarctic ichthyofauna is thought to have evolved since the cooling of coastal waters in the late Oligocene. Ichthyologists presumed that some groups of fishes emigrated to and diversified in Antarctic waters after the Oligocene, and other groups of fishes emigrated into Antarctic waters from South America during Quaternary interglacial periods (Hubbs 1952; Andriashev 1965, 1991; DeWitt 1971; Miller 1987; Eastman and Grande 1989; Anderson 1990; Eastman 1991). Skates, benthic elasmobranchs in the family Rajidae, were suspected by some to be invaders onto the coastal waters of Antarctica from the Patagonian region of South America (fig. 1) (Miller 1987; Anderson 1990; Andriashev 1991). However, neither biogeographic scenario was supported by fossil evidence. The question then arises, are present-day Antarctic skates the sole relicts of the Paleogene ichthyofauna that

persisted until today, or are they South American Quaternary colonists?

The Paleogene ichthyofauna is not believed to be ancestral to the present-day ichthyofauna to the extent that no fossil fish taxa, even on the family level, are currently represented in the waters off continental Antarctica, and none of the current fish fauna has a fossil history in Antarctica (Grande and Eastman 1986; Eastman 1991; Eastman and Grande 1991; Long 1991, 1992a; Ward and Grande 1991). Recently, rajid teeth collected from the middle Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula (fig. 2), mark the first fossil occurrence of skates in Antarctica. These fossils are important because they set a minimum age for the fossil record of skates in Antarctica (*sensu* Grande 1985), and strongly suggest that skates are anachronistic holdovers from the Eocene. Additionally, these fossils, coupled with the known distribution, ecology, behavior, and

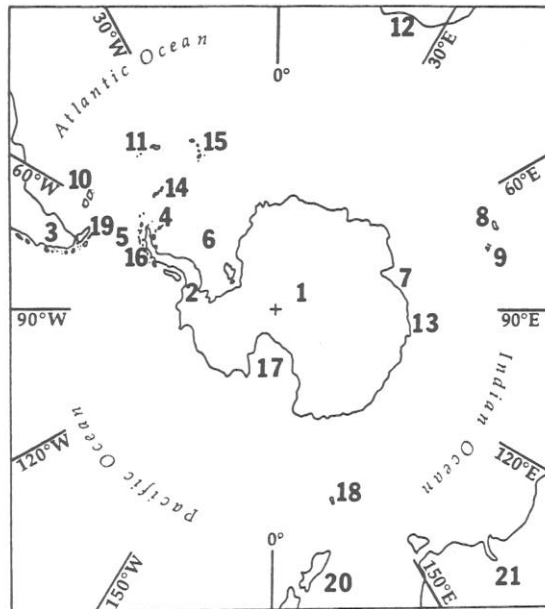


FIGURE 1. Map of the Southern Hemisphere showing localities mentioned in the text: 1, Antarctica; 2, Antarctic Peninsula; 3, southern South America; 4, Seymour Island; 5, Drake Passage; 6, Weddell Sea; 7, Prydz Bay; 8, Kerguelen Island; 9, Heard Island; 10, Falkland Islands; 11, South Georgia Island; 12, southern Africa; 13, Davis Sea; 14, South Orkney Islands; 15, Scotia Arc (South Sandwich Islands); 16, South Shetland Islands; 17, Ross Sea; 18, Macquarie Island; 19, Tierra del Fuego; 20, New Zealand; 21, Australia.

paleontological records of skates, indicate that they are the only member of the Eocene Antarctic ichthyofauna to survive extinctions caused by major climatic and geological changes that occurred since the Oligocene, and are not relatively recent immigrants into Antarctica. For reasons discussed below, it is also improbable that skates lived in Antarctica during the Paleogene, became extinct in the Neogene, and reinvaded Antarctica in the Quaternary.

*Geological Setting.*—Seymour Island (fig. 2) lies in the Weddell Sea off the northeast tip of the Antarctic Peninsula. The strata of the island contains marine sequences spanning the Late Cretaceous to the latest Eocene (Welton and Zinsmeister 1980; Sadler 1988). The paleoenvironment of the La Meseta Formation is believed to be a shallow water near-shore marine deposit composed of sands, gravels, and clays interspersed with marine

and terrestrial vertebrate, invertebrate, and plant remains (Woodburne and Zinsmeister 1984; Sadler 1988). The La Meseta Formation is one of the most prolific and diverse Eocene elasmobranch deposits in the Southern Hemisphere. Seventeen species of sharks representing ten families, one family of batoid, and two families of chimaeras have been reported from the La Meseta Formation (Welton and Zinsmeister 1980; Grande and Eastman 1986; Ward and Grande 1991; Long 1992a).

Personnel from the University of California, Riverside (UCR), collected the skate teeth in the 1986–1987 field season at RV-8200 (UCR vertebrate locality), stratigraphically situated in unit 2 of the La Meseta Formation at the base of Telm 4 (Woodburne and Zinsmeister 1984; Sadler 1988; Long 1992a). The specimens were collected by on-site screening of 8 to 10 tons of sediment using fine-mesh mosquito netting, and over 115 kg of concentrated matrix was later sorted under a stereomicroscope at the UCR laboratory. Scanning electron microscope (SEM) photographs were taken on a Phillips 515.

*Material Examined.*—A total of five teeth (UCR 22207 to 22211, fig. 3) were examined. In apical view, the enameloid crowns of the teeth are generally oval to quadrate in shape. In all specimens, there is a lingually inclined cusp that possesses moderately to well-developed transverse cutting edges. UCR 22211 shows a relatively prominent cusp, but the height of the cusp is reduced in UCR 22207, 22208, and 22209. The lingual crown face of the cusp is convex, and the labial crown face (occlusal surface) may be flat (UCR 22207, 22209) or may be slightly convex (UCR 22210, 22208). The perimeter of the crown base, or crown rim, extends both labially and lingually to form a basally-directed lip-like extension of the crown known as an apron. The root extends basally beneath the crown and consists of two bifurcated bony lobes with a foraminal notch between them; the basal surface of the root lobes is flat.

Skates have a tessellate dental pattern consisting of many teeth on the length of the jaw that form a continuous pavement. Near the jaw symphysis, the tooth crowns are high (UCR 22211), but the crown height becomes

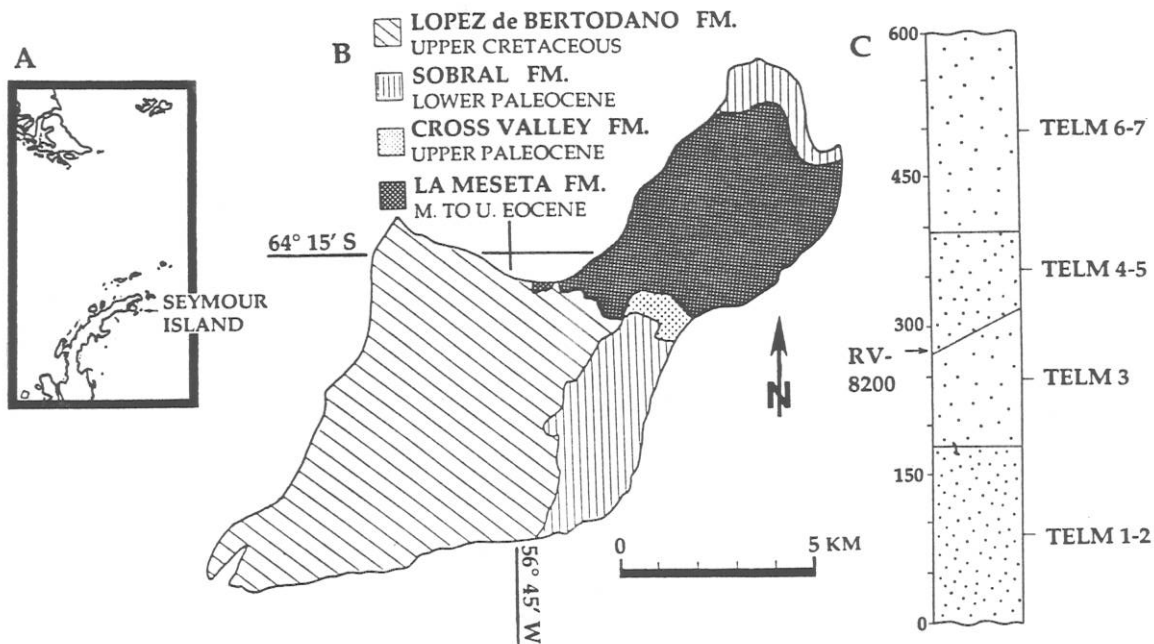


FIGURE 2. Geological map of Seymour Island showing (A) the relationship to South America and the Antarctic Peninsula; (B) the four main fossiliferous deposits, including the Eocene La Meseta Formation; and (C) the stratigraphic sequence of the La Meseta Formation, showing the location of RV-8200.

reduced distally in the jaw, with the posterior teeth showing a very flat crown and a wide occlusal surface (UCR 22209). The mesiodistal shift in tooth morphology is related to diet and feeding behavior; the high crowns of the mesial teeth are used to grasp small prey prior to swallowing, and to rasp flesh from large prey and scavenged food items. The flat distal teeth crush hard food.

Based on numerous illustrations (Bigelow and Schroeder 1953) of the teeth of rajids, descriptions by Herman (1986), and on fresh and preserved extant skates I examined, the Seymour Island teeth most closely resemble teeth from *Raja* Linnaeus 1758 or *Bathyraja* (Ishiyama 1958). Identifications are based on overall crown and cusp morphology, presence of transverse cutting edges, shape of the bifurcated root, and position of the foramina. The roots show a holaulacorhize condition, characteristic of *Raja*, *Psamnobatis*, *Sympterygia*, and some *Bathyraja*, but lack the completely smooth crowns of *Psamnobatis* and *Sympterygia*. The teeth lack a superficial median groove as in *Dactylobatis*, and the pseudo-grooves seen in *Breviraja*, *Cruriraja*, *Acanthobatis*, *Springeria*,

and *Pseudoraja*. Although *Raja* and *Bathyraja* do not share a close phyletic relationship (McEachran and Miyake 1990a), their teeth are similar in that they both share the same primitive skate dental morphology. The fossil teeth are not sufficiently distinct to give an accurate identification as to which of the two genera (or possibly both) that they belong.

*Fossil Record.*—The fossil record of skates is spotty but widespread through most of the Cenozoic (fig. 4). Skates first appeared in the Tethys Sea during the Late Cretaceous. I agree with Cappetta (1980, 1987) that *Raja daviesi* from the upper Cretaceous (Cenomanian) of Lebanon, believed by many early workers to be the first true rajid, may be instead a highly derived rhinobatid, the sister group of skates (McEachran and Miyake 1990a), or a morphologically transitional form between rhinobatids and rajids. Cappetta (1980, 1987) believed that *Pararaja expansa* from the same age and locality may be the first true rajid. Prasad and Cappetta (1993) recorded a true rajid, *Raja sudhakari* from the Late Cretaceous of India. Contrary to these lines of evidence, McEachran and Miyake (1990b) surmised that

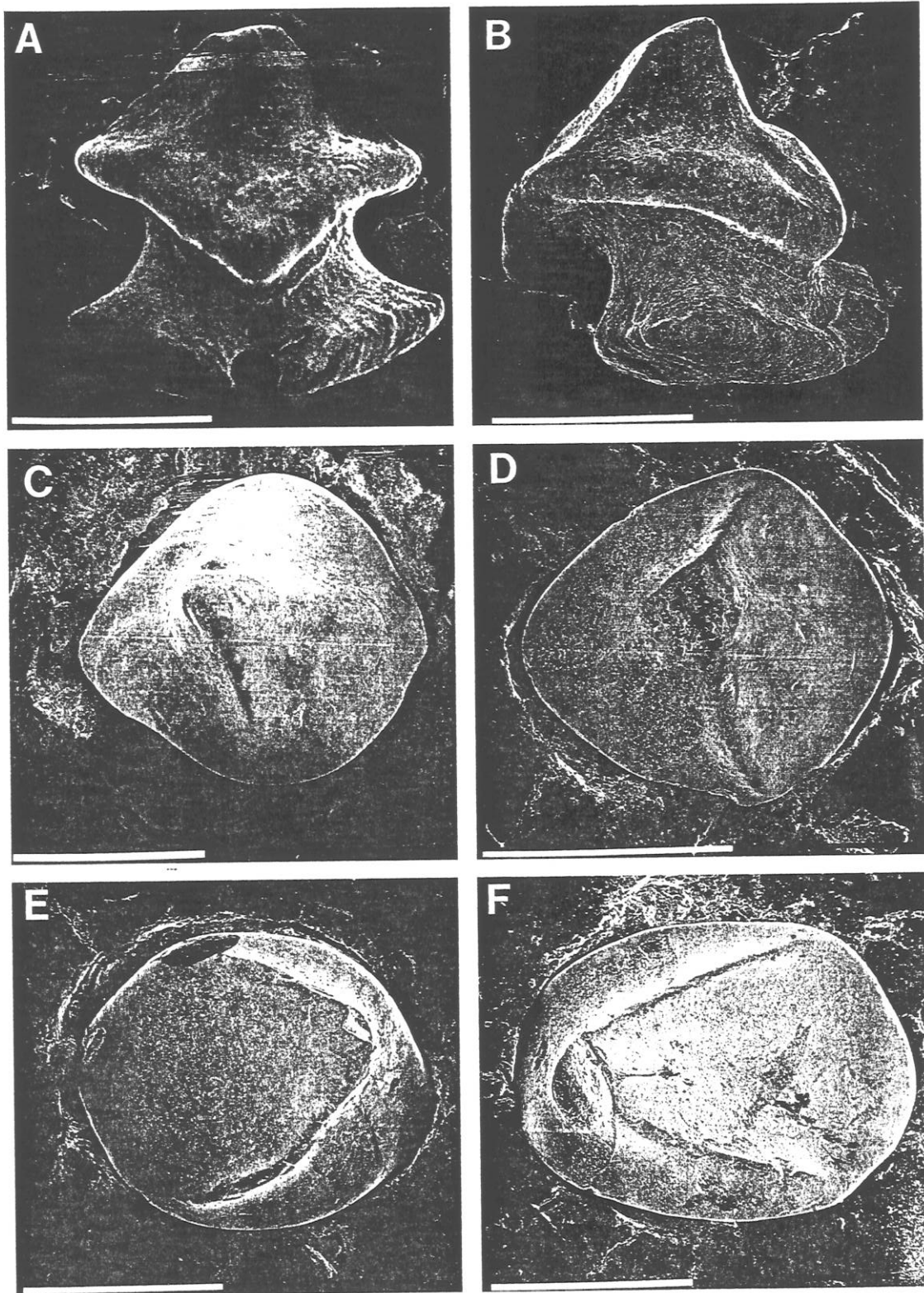


FIGURE 3. Rajid teeth collected from the middle to late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. A-C, Anterior, lateral, and apical views of UCR 22211; D, apical view of UCR 22208; E, apical view of UCR 22207; and F, apical view of UCR 22209. Scale bar, 1 mm.

	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Recent
Northeast Atlantic		Dark stipling	Dark stipling	Dark stipling	Dark stipling	Dark stipling	Black
Northwest Atlantic		Dark stipling	Dark stipling	Dark stipling	Dark stipling	Dark stipling	Black
Northeast Pacific		Dark stipling	Dark stipling	Dark stipling	Dark stipling	Dark stipling	Black
Southeast Pacific		Dark stipling	Dark stipling	Dark stipling	Dark stipling	Dark stipling	Black
Antarctica		Dark stipling	Dark stipling	Dark stipling	Dark stipling	Dark stipling	Black

FIGURE 4. Known fossil distribution of skates (Rajidae) in the Cenozoic. Black indicates that skates are currently living in these areas; dark stipling indicates areas and periods where skate fossils have been found; medium stipling indicates areas and periods where skates have not yet been collected, but are expected; light stipling indicates a fossil batoid tooth from the Paleocene of eastern North America believed to be a skate; clear areas indicate areas and ages where skates have not been found and are not believed to have lived. Information after Cappetta (1987), Herman (1986), Long (1993a,b, this paper, and unpublished data), Ward (1984), Ward and Weist (1990), Welton (1972).

skates evolved in the Pacific, not in the Tethys or in the North Atlantic, but this view is merely hypothetical and is not supported by any paleontological evidence.

Stehmann (1986), also lacking paleontological information, theorized that an ancestral skate, similar in morphology to *Bathyraja* and the *Raja* subgenus *Dipturus* evolved from a rhinobatid ancestor sometime in the Jurassic, but he does not clearly state where or how. However, *Bathyraja* has the widest global distribution of any rajid genus (Stehmann 1986), suggesting that this may have been one of the first rajid genera to evolve, and hence had the most time to disperse. However, it is more likely that this genus, and possibly other skate taxa, could have evolved and dispersed globally within the Eocene (figs. 4, 5). Rajids became numerous by the early Eocene in western Europe (Ward 1984; Herman 1986), and appeared in the North Pacific by the late Eocene (Welton 1972). Skates are distributed worldwide (McEachran and Miyake 1990b), so they probably emigrated from a center of diversification in the Northeast Atlantic into other coastal areas of the globe during the early Cenozoic.

#### Extant Antarctic Rajids

Batoids are a highly successful group of chondrichthyans, and there are as many as 150 to 220 extant species of skates worldwide (Compagno et al. 1989; Stehmann and Burkel 1990). Skates are benthic fishes that inhabit a variety of habitats including bays and estuaries, tidelines, continental shelves and slopes, and abyssal depths of over 2900 m (Eschmey-

er et al. 1983; Stehmann and Burkel 1990). Rajids have a cosmopolitan marine distribution, but the majority of species are most common in shallow to deep, polar and temperate areas. In the tropics they occur only in deep waters, avoiding tropical carbonate platforms (Bigelow and Schroeder 1953; Eschmeyer et al. 1983; Stehmann and Burkel 1990).

Andriashev (1977) regarded Antarctic skates as inhabitants of the continental slopes, yet Stehmann and Burkel (1990) and McEachran and Miyake (1990b) recorded their occurrence in shallower coastal waters. Seven species of skates in two genera are endemic to waters within the Antarctic Convergence (Stehmann and Burkel 1990). Several species are endemic to the Kerguelen or Macquarie plateaus, while others have been collected from various localities along the mainland coast of continental Antarctica and the Antarctic Peninsula, and from offshore islands (table 1). No other batoids are known from Recent Antarctic waters. Skates are the only remaining group of chondrichthyes that were once part of a diverse elasmobranch fauna in the Eocene (Welton and Zinsmeister 1980; Long 1992a,c). It is therefore interesting to focus on the paleontological aspects of skate biogeography and possible patterns of distribution.

#### Quaternary Colonization or Paleogene Persistence?

Some workers held that skates in present-day Antarctic waters were immigrants from more northern temperate areas, probably South America and Africa, sometime during



FIGURE 5. Map of the Eocene Atlantic Basin and its marginal continental blocks showing hypothetical dispersal route of skates from their origin in western Europe to continental Antarctica. Wide arrows show probable route for the colonization of Antarctica; smaller areas show possible routes for colonization of the Pacific Basin and southern Africa. Skates could have emigrated to Antarctica from western Tethys or the North Boreal Sea along the eastern continental margin of the western Atlantic (1) or followed the western coast of Africa and then crossed over to eastern South America (2A). Some skates followed the eastern coast of Africa to the southern end of that continent (2B), but did not cross over to Antarctica. Skates populated the Pacific Basin by crossing through the Arctic Ocean (3A), or possibly by passing through the Panamic Seaway (3B), or through the Drake Passage (3C).

Pleistocene glacial marine cooling (Hubbs 1952; Kock 1985). However, Antarctic geography, paleontological and geological histories, ocean dynamics, and skate morphology and behavior support the contrary view that Quaternary immigration into Antarctica from outlying areas is unlikely. The occurrence of fossil skate teeth in peninsular Antarctica validates the antiquity of rajids in Antarctica. The teeth, while not numerous, are nevertheless indisputable evidence for the exist-

tence of this family in Antarctica in the Paleogene. The fossil evidence sets a minimum date for skates in Antarctic waters at least as far back as the middle Eocene. Therefore, paleontological evidence refutes previous ideas that skates are relatively recent immigrants into Antarctica from northern waters, and indicates that they are much older components of the Recent fish fauna.

*Paleogene Colonization of Antarctica.*—The paleo-Antarctic was populated with a diverse elasmobranch fauna, having their origins in the North Atlantic and North Pacific, by the middle Eocene (Long manuscript). Skates can be considered as slow "diffusion" dispersalists (*sensu* Reif and Saure 1987) along coastal areas and continental shelves. However, they would only have needed to move south 1 km per generation in order to reach Antarctica from the North Atlantic in a relatively short time (>500,000 years). Since Antarctica has been physically isolated since the Oligocene (Kennett and Barker 1990; Lawver et al. 1992), both *Raja* and *Bathyraja* must have entered the area prior to this time. From their probable center of origin in the late Cretaceous and Paleogene European western Tethys Sea and North Boreal seas, skates emigrated to the Southern Hemisphere by the middle Eocene by following the continental margin of the western Atlantic.

Skates probably reached Antarctica from the Northeast Atlantic. In the early Eocene they may have (1) moved south from western Europe to Northeastern Africa where they crossed the Atlantic, at one of its narrowest points, to northeastern South America; or (2) crossed the Atlantic from western Europe to the eastern coast of North America, and then continued south along the eastern edge of the continental shelf of North and South America. Skates then followed the continuous continental shelf on the east coast of South America to Antarctica, as the continental shelves of both were adjacent in the Eocene (Lawver et al. 1992). It seems as likely that one or both genera arrived in this area in the Eocene. The diversity of skates at the southern end of this dispersal pathway supports this theory (Bigelow and Schroeder 1965; Stehmann 1986).

Skates probably migrated from Europe to

TABLE 1. Bathymetric and geographical ranges of skates from Antarctic waters, compiled from Bigelow and Schroeder (1965), DeWitt (1971), Williams (1988), McEachran and Miyake (1990b), and Stehmann and Burkel (1990).

Species	Maximum depth (m)	Range
<i>Bathyraja eatoni</i>	800	Kerguelen Plateau and South Shetland and South Orkney Islands. Possibly circum-Antarctic.
<i>Bathyraja irrasa</i>	1200	Endemic to the Kerguelen Plateau.
<i>Bathyraja maccaini</i>	500	Northern Antarctic Peninsula, South Shetland and South Orkney Islands, Prydz Bay, and the Davis Sea. Probably circum-Antarctic.
<i>Bathyraja meridionalis</i>	800	Endemic to South Georgia Island.
<i>Bathyraja murrayi</i>	650	Endemic to the Kerguelen Plateau.
<i>Raja (Amblyraja) taaf</i>	600	Kerguelen and Macquarie Plateaus.
<i>Raja (Amblyraja) georgiana</i>	1232	South Georgia and South Orkney Islands, and the Ross sea. Possibly circum-Antarctic.

southern Africa by following the coast of western Africa. Hulley (1972) noted that the South African skate fauna shows an affinity with the northeast Atlantic fauna, but he suggests that *Bathyraja* arrived in southern Africa earlier than *Raja*, although he provides no further explanation and no evidence to support this. It is possible that Eocene skates traveled into the Southern Hemisphere along the African continental shelf, but it is unlikely that they migrated to Antarctica from southern Africa. The continental margins of Antarctica and southern Africa are widely separated, and are divided by the deep (over 6000 m) Atlantic-Indian Basin, and these continents have been separated since the Late Cretaceous (Lawver et al. 1990). Skates do not cross deep oceanic basins, and the few pan-oceanic *Raja* and *Bathyraja* cross oceanic basins where coasts are relatively close, and ocean floors are relatively shallow, such as the North Atlantic and North Pacific (Springer 1982; Stehmann and Burkel 1989; Zorzi and Anderson 1990). Therefore, southern Africa is the "dead end" of this dispersal pathway, and it is unlikely that skates colonized Antarctica from there.

Skates could have colonized the Pacific Ocean from three possible points along the western Atlantic dispersal pathway.

1. The most likely route for skate dispersal from North Atlantic to the North Pacific was through the Arctic Ocean. This passageway would have been open in the Eocene before the connection of the Ellsmere Island Land Bridge, and during times of high sea levels when the Bering Land Bridge was submerged. Rajid teeth have been collected from

late Eocene deposits in northwestern North America, confirming that they were in the North Pacific by that time (Welton 1972), and the North Pacific is currently a center of rajid diversity (Stehmann 1986). Berg (1934) suggested this trans-Arctic or "amphiboreal" route for other Northern Hemisphere fishes, and it is also a possible dispersal pathway for skates.

2. Skates may have emigrated into the northern Pacific Basin from the western Atlantic through the Panamic Seaway. At this point, the skates could have headed north along the western coast of North America, and/or south along the western coast of South America, but few rajids, especially *Bathyraja* and the subgenus *Amblyraja* are found along the western coast of Central and South America (Stehmann 1986).

3. Skates may have colonized the eastern Pacific after heading north from Antarctica, following the nearly continuous land mass of the western coasts of North and South America, and then radiating into the North Pacific.

Whichever the dispersal scenario, there is a strong biogeographic connection between the North Pacific and Antarctica. These two areas are centers of skate diversity, and contain many species of *Raja* and *Bathyraja* (Stehmann 1986; McEachran and Miyake 1990b). Anderson (1988, 1990), Andriashev (1965, 1990, 1991), and Briggs (1974) remarked on several families of extant teleosts that share a North Pacific-Antarctic or a North Atlantic-Antarctic distribution, and contend that these groups must have entered Antarctica prior to the opening of the Drake Passage in the late Oligocene. Certain taxa in the teleost families

TABLE 2. Main dietary components of *Bathyraja* and *Raja* (*Amblyraja*). Based on Permitin and Tarverdiyeva (1972), Templeman (1973), Stehman and Burkel (1989), Compagno et al. (1989), Ebert et al. (1991), and Long (unpublished data).

Species	Locality	Diet
<i>B. richardsoni</i>	NW Atlantic	Decapods, gastropods, fishes, alcyonarians
<i>B. pallida</i>	NE Atlantic	Cephalopods
<i>B. kincaidii</i>	NE Pacific	Amphipods, euphausiids, decapods
<i>B. smithi</i>	S Africa	Teleosts, crustaceans, mysids, cephalopods
<i>R. (A.) radiata</i>	N Atlantic	Crustaceans, fishes, polychaetes
<i>R. (A.) georgiana</i>	Antarctica	Mysids, decapods, fishes, polychaetes, euphausiids, amphipods, isopods, cephalopods, echinoderms, cnidarians, ctenophores

Liparididae and Zoarcidae probably emigrated from a center of origin or diversification in the northeast Pacific and traveled south along the continental shelf of western North and South America to Antarctica, where they established a second center of diversification (Anderson 1988; Andriashev 1990, 1991). A similar, but reversed, scenario may hold true for Antarctic skates. Skates may have first appeared in the Antarctic, then spread and diversified into the North Pacific; this model follows the same dispersal pathways suggested by Andriashev (1990, 1991), but the directionality is opposite. Several taxa of sharks in Eocene Antarctic waters also have a disjunct distribution extending into the Northeast Pacific, and into the North Boreal and Tethys Seas (Long 1992a, manuscript). Distributions of both extant and fossil Antarctic fishes emphasize a commonality in biogeographic dispersal pathways among these groups, and reaffirm these pathways as probable dispersal routes for skates between the North Pacific and Antarctica.

*Vicariant Events and Biogeographic Barriers.*—Stehmann and Burkel (1990) showed that all seven species of skates in Antarctic waters are endemic to the area, and none have populations outside of the convergence. Even where Antarctica is closest to South America, species of skates are morphologically distinct and their ranges do not overlap between the Tierra Del Fuego and the Falklands and the Antarctic Peninsula (Bigelow and Schroeder 1965; Stehmann and Burkel 1990). The endemism of Antarctic taxa suggest that these species of skates have been genetically isolated for a fairly long period of time, possibly since the

Oligocene. Skates in Antarctic waters are endemic, but the genera are not, and in fact, have a cosmopolitan distribution in temperate waters (McEachran and Miyake 1990b). A similar biogeographic pattern of low generic diversity but high species endemism in Antarctic waters was noted in the invertebrate shelf fauna by Menzies et al. (1973). They surmised that the invertebrate shelf fauna is a relict dating back at least as far as the Miocene.

Disjunct endemic populations of skates in South American and Antarctic waters suggest there are present-day barriers preventing northward dispersal of the Antarctic species, and preventing northern species from entering Antarctic waters. The most likely isolating mechanisms for these benthic animals are topographic barriers on the seafloor, most likely the deep marine trenches and basins surrounding Antarctica. Lawver et al. (1990, 1992) showed that there was still a relatively shallow connection between southern South America and the Antarctic Peninsula at the end of the Eocene, but by the early Oligocene, these continents rapidly separated as the Drake Passage began to open up and deep trenches between the continents began to develop. Also by this time, Africa, Australia, and New Zealand were separated from continental Antarctica by a wide and deep seafloor; with no continental connections to Antarctica, the cold Antarctic circumpolar current began (Kennett and Barker 1990, Lawver et al. 1992).

Skates do not seem to cross deep ocean basins (Springer 1982), and the deepest recorded capture or observation of a skate is 2904



m (Eschmeyer et al. 1983). Foster (1984) and DeWitt (1971) illustrated the majority of the ocean floor topography encompassing Antarctica is between 3000 m and 6000 m deep. Grover (1972) demonstrated that deep basins are geographical barriers that effectively restrict or prevent movement of some benthic elasmobranchs. More recently, Nakaya and Shirai (1992) showed abyssal depths were effective barriers for many benthic elasmobranchs, especially skates, and that these barriers are the major cause of regional differences in the composition of benthic elasmobranch faunas. Species of *Raja* and *Bathyraja* that cross oceanic basins do so at points where coasts are relatively close, and ocean floors are not very deep, such as the North Atlantic and North Pacific (Stehmann and Burkel 1989; Zorzi and Anderson 1990), so the basins surrounding Antarctica are well beyond the deepest known range of any skate.

Deep basins have a sparse benthic fauna, and may not contain enough food resources to allow some species of benthic fishes, such as slow-moving skates, to successfully cross wide expanses of the seafloor (Anderson et al. 1985). Other physical conditions present in deep basins, such as anoxia and variations in temperature, salinity, and chemistry, may also be barriers preventing dispersal. Thus, any skates attempting to migrate to Antarctica's coastal waters from northern areas face an extremely deep and barren seafloor that is ecologically unfavorable to their survival. In this case, geographic barriers would tend to keep intrusive taxa of skates out of Antarctica's coastal waters and to retain endemic species.

Springer (1971) and Stehmann and Burkel (1990) listed the known maximum depth ranges of Antarctic skates from 500 m to over 1200 m (fig. 4), but all are more common in shallower water. Although Stehmann (1986) listed several Antarctic rajid species as deep-water or transitional, the bathymetric distributions of these species suggest that Antarctic skates do not prefer very deep water and probably do not move into the deeper circum-Antarctic basins.

Skates are usually benthic, and lack the ability to swim over expansive areas of deep

water. All skates lack the large oil-filled liver that provides neutral buoyancy in other free-swimming elasmobranchs; they also lack the powerful tail and fins and the fusiform body shape needed to propel them the great distances necessary to reach Antarctica from the coastal areas of other continents. Rhythmic oscillatory undulations of the pectoral fins are the primary means of locomotion in skates and provide them with slow and limited swimming, and these fins are not employed as sustained flapping "wings" as seen in the more pelagic batoids in the families Myliobatidae and Mobulidae.

Skates do not have a planktonic larval stage; the young are relatively large and are also benthic, so unlike many other species of fishes, there is no oceanic dispersal during the juvenile stage. Permitin (1970) found krill in 23% of juvenile *Raja georgiana* stomachs, and DeWitt (1971) inferred this finding to indicate that juvenile skates have the ability to occasionally swim off the bottom and feed on krill in the midwater. He stretched this observation into the possibility that skates may have extended their ranges into Antarctica from South America by long-distance movement of these periodically free-swimming juveniles. However, he apparently never observed this behavior, and the skates in Permitin's study were probably feeding on dead or moribund krill lying on the bottom, or on krill that swam near the bottom. Additionally, the system of oceanic currents off Antarctica would carry juvenile skates north and east of the Falkland Islands area and away from peninsular Antarctica where they are found today (Foster 1984). Also, as noted above, skates do not have the necessary morphologic adaptations that would allow for sustained swimming (for hundreds of miles in this case), and this lengthy journey would be even more difficult for young skates.

#### Eocene Extinction in Antarctica and Survival of Skates

In the late Eocene when the La Meseta Formation was deposited, the marine climate was far more temperate than at present, and had more expansive shallow-water and shelf areas compared to today (Zinsmeister 1982). This

provided more suitable habitats for skates and other species of fishes. The diversity of the Eocene ichthyofauna in Antarctica is well demonstrated by abundant fossils from the La Meseta Formation on Seymour Island. The elasmobranch fauna is particularly diverse; seventeen species of sharks in eight families, two species of chimaeras representing two families, and one other family of batoid have been recorded so far (Welton and Zinsmeister 1980; Ward and Grande 1991; Long 1992a). Rajids are the only reported group of elasmobranchs that are currently resident in coastal waters of the Antarctic continent. Three species of sharks, *Etmopterus lucifer*, *Somniosus microcephalus*, and *Lamna nasus*, are rare in the sub-Antarctic, and may only be occasional vagrants into pelagic Antarctic waters from northern latitudes (Compagno 1990). (Compagno 1990).

Five major groups of teleosts (Siluriformes, Gadiformes, clupeoids, trichiurids, and labrids) have also been recovered from the La Meseta Formation (Grande and Eastman 1986; Eastman and Grande 1991; Jerzemska 1991; Long 1991, 1992b). The impact on the ichthyofauna of coastal Antarctica and the extent of extinctions due to late Paleogene-early Tertiary climatic change appears to have been great. Virtually the entire Eocene ichthyofauna seems to have become extinct or regionally extirpated to more northern waters by the end of the Paleogene, and there are few Eocene components in the current Antarctic ichthyofauna. The only exceptions are the shark genus *Lamna* that occasionally strays into sub-Antarctic waters (Compagno 1990; Long 1992a), and skates, the only true continental Antarctic elasmobranch.

Through tectonism and an overall cooling trend that began in the late Oligocene, Antarctica became isolated from the other southern continents because of the emergence of deep-water trenches and the increased cooling of marine temperatures (Kennett and Barker 1990; Lawver et al. 1990, 1992). By the Miocene, the waters off coastal Antarctica may have been too cold to support the once diverse Eocene elasmobranch fauna, and these taxa gradually emigrated out of Antarctica by following the receding temperate areas, or

were extirpated in the area as the temperatures in the Neogene cooled and their marine ecosystems changed. The skates found suitable habitat in only a few areas, and exist there today as relict populations from the late Eocene. The endemism of certain insular Antarctic skates may be due to their inability to escape their refugia in the isolated Kerguelen, Heard, and South Shetland islands where adjacent deep waters around these areas now serve as geographical barriers to dispersal. The maximum depth ranges of these species is 1232 m, and the depth zones of the areas surrounding their coastal habitats may exceed 6000 m (DeWitt 1971; Kock 1985), preventing dispersal into other areas.

The physical boundaries retaining the endemic population of skates within Antarctica were present since the early Neogene. Thus, there was no possible way of recolonization after the climatic and geographical changes that would have initially caused the extinctions. Rather, skates undoubtedly withstood these physical and ecological changes, and represent the only surviving Eocene component in the Recent Antarctic ichthyofauna known so far.

The advent of climatic deterioration and changes in the topography and ecology of coastal Antarctic waters altered suitable habitats for Eocene fishes, and extirpated most of the genera of fishes from the La Meseta Formation (Eastman and Grande 1989; Long 1991, 1992b). However, skates persisted in the coastal waters off continental Antarctica into the present day. Causes of regional extinction in the temperate Eocene fauna from Antarctica include thermal decline, reduction of marine shelf habitats, and changes in the trophic structure and disruption of Antarctic food chains (Eastman and Grande 1989). Skates seem to have escaped these proposed causes of extinction.

*Thermal Decline.*—In the late Oligocene or Early Miocene, the opening of the Drake Passage between Antarctica and South America initiated the flow of the Circum-Antarctic current, which effectively isolated the Antarctic Ocean from the adjacent Pacific, Atlantic, and Indian oceans. Once the waters around Antarctica became isolated, the marine tem-

perature dropped dramatically (Kennett and Barker 1990). Average sea surface temperatures for Antarctic waters is about  $-1^{\circ}\text{C}$  to  $6^{\circ}\text{C}$  in the austral summer and  $-1^{\circ}\text{C}$  to  $4^{\circ}\text{C}$  in the austral winter (Lutjeharms 1990). The Eocene fish fauna of the Antarctic Weddell Sea was temperate (Long 1992c), so the sudden drop in water temperature may have caused a regional extinction or forced them to northern latitudes as warmer waters receded northwards. Yet, the distribution of skates into cold and deep northern polar waters indicates they are a cold-tolerant group (Bigelow and Schroeder 1953; Stehmann and Burkel 1989; McEachran and Miyake 1990b). Therefore, skates may have been pre-adapted to withstand the cooling of Antarctic waters that had such a major impact on the rest of the Eocene fish fauna, and are able to live in the extremely cold Antarctic seas.

*Loss of Habitat.*—Eastman and Grande (1989) also proposed that extinction of the Eocene Antarctic fish fauna may have also been caused by loss of shallow-water shelf habitat. The Weddellian Province during the Eocene had extensive shallow, coastal habitats (Zinsmeister 1982; Long 1992c). When the Antarctic climate cooled and continental glaciers formed, the majority of these shallow, near-shore habitats were lost. Present-day Antarctica has a very narrow continental shelf. Loss of shallow water areas may have been an important factor in the extinction of some groups of fishes that needed such areas for living or breeding (Long 1991, 1992b,c). Skates, however, do not live exclusively in shallow water, and frequently occur on the outer shelf, continental slopes, and in deep-water continental troughs (McEachran and Miyake 1990b; Stehmann and Burkel 1990; Andriashev 1977). Because skates are not dependent on shallow-water habitats, loss of these areas probably did not greatly impact their populations.

*Disruption of Trophic Structure.*—Grande and Eastman (1986) presumed that low rajid diversity in Antarctica is primarily because mollusks, suggested as an important prey of rajids, are poorly represented in the present Antarctic marine biota. This assumption is invalid for at least three reasons:

1. The Antarctic skate fauna may not be

particularly diverse, but it is not especially depauperate. Stehmann (1986) believed that Antarctica is a center of skate diversity, at least for *Bathyraja*; the two other major areas of *Bathyraja* diversity are in the north Pacific and in the coastal Patagonian region of South America. The subgenus *Amblyraja*, while having a global distribution, is neither speciose nor abundant anywhere (McEachran and Miyake 1990b), so its lack of diversity in Antarctica is not unusual.

2. Not all molluscan groups are poorly represented in present-day Antarctic seas. Cephalopods are a diverse and numerous molluscan group in Antarctic waters; species of several genera are common in waters around coastal Antarctica and several more species also live in the waters around the Antarctic Convergence (Roper et al. 1984; Rodhouse 1990). Cephalopods are important prey items of many species of skates, including those species from Antarctica (Permitin and Tarverdiyeva 1972; McEachran et al. 1976; Ebert et al. 1991).

3. Some areas of Antarctica actually have a rich and diverse molluscan fauna (Arnaud and Hain 1992), and although abundance of mollusks may not be evenly distributed in respect to locality or depth, they would be an abundant potential food resource. Most skates, however, seem to be opportunistic feeders on a wide range of vertebrates and invertebrates, not just mollusks. Diets of Atlantic skates listed by Bigelow and Schroeder (1953) and McEachran et al. (1976) include crabs, shrimps, amphipods, isopods, mysids, copepods, gastropods, echinoderms, bryozoans, cnidarians, ascidians, anemones, polychaete and annelid worms, bivalves, cephalopods, and a variety of fishes, including other skates. Both *Bathyraja* and *Raja* (*Amblyraja*) exploit a wide range of prey types (table 2).

Because skates have a generalized diet, and feed on organisms that also survived the late Paleogene extinction, the likelihood of extinction due to trophic change is minimal. Dietary studies of skates from the northeast Atlantic (Ajayi 1982; Gordon and Duncan 1989; total of 7 species), northwest Atlantic (McEachran et al. 1976; Hacunda 1981; Robichaud et al. 1991; total of 4 species), and

southern Africa (Ebert et al. 1991; total of 13 species) demonstrate that gastropods and bivalves are relatively insignificant dietary components of all species investigated, so the paucity of shelled mollusks in Antarctic waters is not crucial to the survival of skates. Rather, the diverse benthic community of many areas in Antarctica (Richardson and Hedgepeth 1977) offers most prey items preferred by skates.

Eastman and Grande (1989) also surmised that abrupt cooling in the marine climate of the Antarctic Ocean may have caused extinctions in the Eocene fish fauna because of changes in the marine food webs. For specialized feeders, sudden changes in the trophic structure or in the availability of certain food items would increase the likelihood of extinction. For taxa with a generalized diet, such as skates, the likelihood of extinction is diminished. The Paleogene extinctions in Antarctica affected many invertebrate groups, but not to the extent it affected fishes. Bivalves, gastropods, cephalopods, isopods, decapods, echinoderms, and other invertebrate groups still live in Antarctic waters today, as they did in the Eocene, although with different representative taxa.

### Summary

Seven endemic species of skates in two families represent the only elasmobranch family currently living in the waters around continental Antarctica. Some authors have proposed that skates may have colonized Antarctic waters by crossing the Drake Passage from southern South America. However, the presence of deep basins and the skate's physical inability to cross these barriers invalidates that assumption. Additionally, teeth of fossil skates (from either *Raja* or *Bathyraja*) have recently been collected in middle Eocene marine sediments from the La Meseta Formation, Seymour Island, Antarctic Peninsula. Fossil evidence and examination of the present distribution of *Raja* and *Bathyraja* support a revised scenario of skate dispersal: they evolved in the Late Cretaceous and early Paleogene in the north Atlantic of western Europe, and emigrated to the Southern Hemisphere by following a dispersal corridor along

the continental margins of the western Atlantic. They may have then entered the Pacific Basin through either the Arctic Ocean, the Panamic Seaway, or the early opening of the Drake Passage.

Skates persisted in Antarctic waters from the Paleogene until today; they are the only family of fish that survived the abrupt and severe cooling period and geographical isolation that killed or extirpated the Paleogene Antarctic ichthyofauna. They survived this event because they are cold-tolerant, they live at a wide range of depths and so were not affected by loss of shallow-water areas, and they have a generalized diet and feed on a variety of invertebrates that also survived the cooling.

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