

A REVIEW OF ANTARCTIC ICHTHYOFAUNAS IN THE LIGHT OF NEW FOSSIL DISCOVERIES

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ABSTRACT. The fossil and Recent fish fauna of the Antarctic region is systematically and biogeographically reviewed. The occurrence of Pristiophoridae, Chimaeriformes, and Siluriformes is reported from the Antarctic region for the first time. The pristiophorids, chimaeriformes, and previously reported Antarctic shark fossils show that although chondrichthyans are a minor component of the Recent Antarctic fauna, they are very diverse in the Lower Tertiary fossil record of the continent. The occurrence of a catfish in Antarctica shows that Siluriformes have been present on all continents of the Southern Hemisphere. The Palaeozoic and early Mesozoic fishes indicate primarily an Australian biogeographic affinity for Antarctica, reflecting the proximity of the two continents to each other during those times. The more recent ichthyofaunas show no particular biogeographic affinity.

FOSSIL fishes from Antarctica are of particular interest to biogeographers because of the lack of diversity in the Recent Antarctic fauna. Biogeographic (area) relationships are usually determined on the basis of relationships of taxa (Nelson and Platnick 1980, 1981; Grande 1985). Areas with relatively few taxa, in general, provide less biogeographic data than areas with many taxa. There are only eighteen families of Recent fishes in the Antarctic region (DeWitt 1971), with most of the species belonging to a single, presumably monophyletic, suborder (Notothenioidei) largely restricted to Antarctica.

Because the Recent environment supports such a sparse fauna, we thought that a search for and description of new fossil fishes from the area would ultimately lead to a better understanding of the biogeography of Antarctica. Fossil fishes have been described from only a few areas of the Antarctic region (text-fig. 1): 1, Cretaceous and Tertiary marine deposits of Seymour Island near the north-eastern tip of the Antarctic Peninsula (Woodward 1908; Elliot *et al.* 1975; de Valle *et al.* 1976; Cione *et al.* 1977; Welton and Zinsmeister 1980; Chatterjee and Zinsmeister 1982); 2, Lower Jurassic freshwater deposits of Southern Queen Alexandra Range of the Transantarctic Mountains in Victoria Land (Schaeffer 1972); 3, Lower Devonian marine deposits of the Horlick Formation, Ohio Range (Doumani *et al.* 1965); and 4, several small Devonian freshwater deposits between the Mulock and Mawson Glaciers, Victoria Land (Woodward 1917, 1921; White 1968; Ritchie 1971; Gunn and Warren 1962a; Young 1982; McKelvey *et al.* 1972). The two major Devonian freshwater fish-producing units are the Lower or Middle Devonian Beacon Sandstone, and the Middle or Upper Devonian (Givetian or Frasnian—Young 1982) Aztec Siltstone, both of which are in the Taylor Group of the Beacon Supergroup (McKelvey *et al.* 1972). References to detailed locality information are given in the text, and only general locality information will be given here.

In this paper we will systematically review the fossil fish fauna of the Antarctic region, including some previously unreported Eocene taxa. For the sake of consistency, all names of implied ordinal rank (including those of placoderms) end in 'formes', as suggested by Nelson (1984) and Berg (1940). After Nelson's (1984) general classification, and Denison's (1978, 1979) placoderm and acanthodian classifications, the fossil fish taxa represented are:

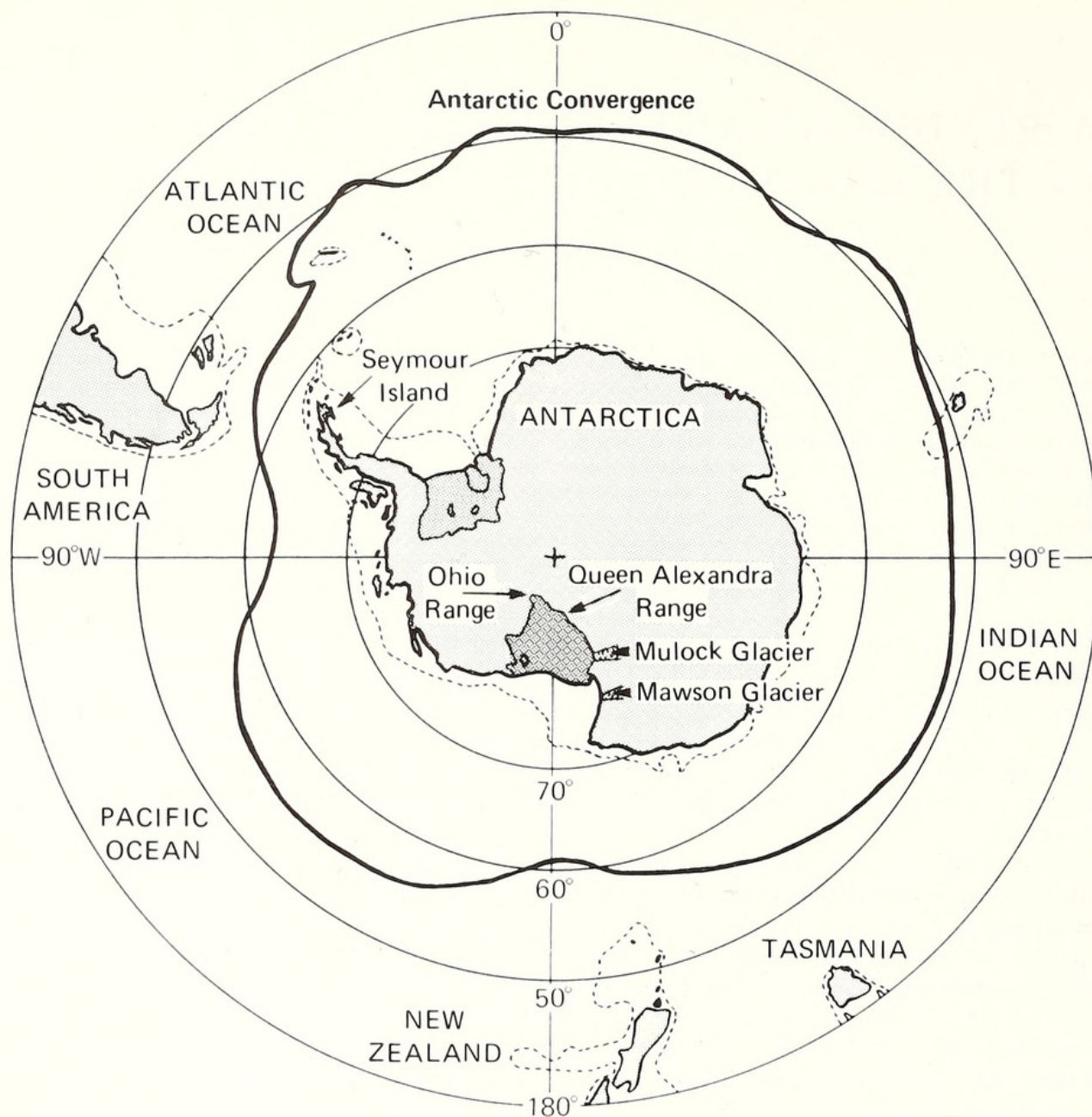
AGNATHA

CLASS *incertae sedis*

Thelodontiformes

Turiniidae

Turinia sp. [Devonian]



TEXT-FIG. 1. Map of the Antarctic region showing localities of the fossils discussed in this paper. Major ice shelves are represented by dense stipple. The narrowness of the continental shelf is indicated by the dashed line of the 1000 m isobath. The heavy line is the Antarctic Convergence, a natural zoogeographic boundary discussed in the paper. Redrawn from DeWitt (1971) with the location of the Antarctic Convergence from Hedgpeth (1969)

GNATHOSTOMATA

CLASS PLACODERMI

Arthrodiriformes

Phlyctaeniidae

unnamed [Lower Devonian]

Holonematidae

Groenlandaspis antarcticus Ritchie 1975 [Middle or Upper Devonian]

Family incertae sedis

Antarctolepis gunni White 1968 [Middle or Upper Devonian]

Family indeterminate

Undetermined remains [Middle to Upper Devonian]

Phyllolepiiformes

Antarctaspidae

Antarctaspis mcmurdoensis White 1968 [Middle or Upper Devonian]

Antiarchiformes

Bothriolepidae

Bothriolepis antarctica Woodward 1921 [Lower or Middle Devonian]

Bothriolepis sp. [Middle to Upper Devonian]

Bothriolepis sp. [Lower to Middle Devonian]

CLASS ACANTHODII

Acanthodiformes

Acanthodidae

?*Cheiracanthus* sp. [Lower or Middle Devonian]

Climatiiformes

Gyracanthidae

Gyracanthides warreni White 1968 [Middle or Upper Devonian]

Order *incertae sedis*

Antarctonchus glacilis White 1968 [Middle or Upper Devonian]

Byssacanthoides debenhami Woodward 1921 [Lower or Middle Devonian]

CLASS CHONDRICHTHYES

Elasmobranchii

Xenacanthiformes

Xenacanthidae

Xenacanthus sp. [Middle or Upper Devonian]

Antarctilamna prisca Young 1982 [Middle or Upper Devonian]

Lamniformes

Odontaspidae

Eugomphodus macrotus (Agassiz 1843) [Late Eocene or Early Oligocene]

Lamnidae

Carcharodon auriculatus (Blainville 1816) [Late Eocene or Early Oligocene]

Isurus sp. [Upper Cretaceous]

Squaliformes

Squalidae

indeterminate [Late Eocene or Early Oligocene]

Pristiophoridae

Pristiophorus sp. [Late Eocene or Early Oligocene]

Squatinae

Squatina sp. [Late Eocene or Early Oligocene]

Rajiformes

Mylobatidae

unnamed [Late Eocene or Early Oligocene]

Order Undetermined

Mcmurdodontidae

Mcmurdodus featherensis White 1968 [Middle to Upper Devonian]

Undetermined Family

Undetermined selachian vertebral centra [Cretaceous]

Holocephali

Chimaeriformes

Chimaeridae

?*Ischyodus* sp. [Late Eocene or Early Oligocene]

INDETERMINATE CHONDRICHTHYAN REMAINS

unnamed [Lower or Middle Devonian]

CLASS OSTEICHTHYES

Crossopterygii

Osteolepiformes

Osteolepidae

Gyroptychius? antarcticus (Woodward 1921) [Lower or Middle Devonian]*Gyroptychius* sp. [Middle or Upper Devonian]

unnamed [Lower or Middle Devonian and Middle or Upper Devonian]

Actinopterygii

Chondrostei

Palaeonisciformes

Undetermined palaeonisciforms [Lower or Middle Devonian and Middle or Upper Devonian]

Neopterygii

Undefined Subdivision

Pholidophoriformes

Archaeomaenidae

Oreochima ellioti Schaeffer 1972 [Lower Jurassic]

Teleostei

Siluriformes

Family *incertae sedis*

unnamed [Late Eocene or Early Oligocene]

Superorder and order *incertae sedis*

unnamed [Late Eocene or Early Oligocene]

INSTITUTIONAL ABBREVIATIONS

AMF = The Australian Museum, Sydney.

AMNH = The American Museum of Natural History, New York, Department of Vertebrate Paleontology.

BMNH = The British Museum (Natural History), London, Department of Palaeontology.

CPC = The Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, Australia.

FMNH = Field Museum of Natural History, Chicago, Vertebrate Paleontology Section, Department of Geology.

NZGS = The New Zealand Geological Survey.

UCMP = Museum of Paleontology of the University of California, Berkeley.

UCR = University of California, Riverside, Department of Earth Sciences.

USNM = United States National Museum of Natural History, Washington.

SYSTEMATIC LIST OF FOSSIL ICHTHYOFAUNA

Superclass AGNATHA

Class *incertae sedis*

Order Thelodontiformes

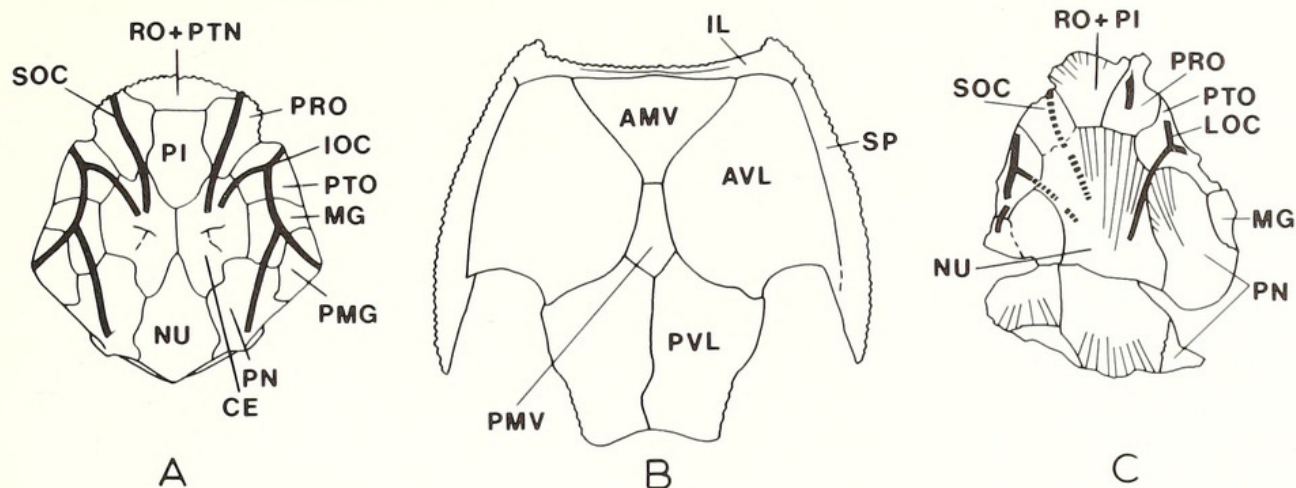
Family TURINIIDAE Obruchev 1964

Turinia sp. (description in preparation by Turner and Young)*Referred material.* FMNH PF 9600 and 9602 (scales).*Geologic age.* Devonian.*Locality.* Mount Fleming, South Victoria land (near Mawson Glacier area), Antarctica. Detailed locality information not available.*Comment.* According to Turner (pers. comm.) this species appears to be closely related to some yet undescribed species from China.

Superclass GNATHOSTOMATA

Class PLACODERMI

Comment. All described placoderm material from the Antarctic Region consists of isolated dermal elements, except for the holonematid *Groenlandaspis antarcticus* Ritchie 1975, which is known



TEXT-FIG. 2. Two Antarctic placoderm species known by articulated material. A, B, *Groenlandaspis antarcticus* Ritchie, 1975, restoration of head shield and ventral trunk shield (after Ritchie 1975); C, *Antartaspis mcmurdoensis* White, 1968 (head shield after White 1968). Abbreviations: AMV = anterior medio-ventral plate, AVL = anterior ventrolateral plate, CE = central plate, IL = interolateral plate, IOC = infraorbital sensory canal, MG = marginal plate, NU = nuchal plate, PI = pineal plate, PMV = posterior medianventral plate, PN = paranuchal plate, PRO = preorbital plate, PTO = postorbital plate, PVL = posterior ventrolateral plate, RO + PI = rostro-pineal plate, RO + PTN = rostro-postnasal plate, SOC = supraorbital sensory line, SP = spinal plate.

by nearly complete head and trunk shields (text-fig. 2A–B), and the arctolepid *Antartaspis mcmurdoensis*, which is known by a partial skull roof (text-fig. 2C). *Byssacanthoides debenhami* Woodward was originally described (1921) as a bothriolepid; but after further preparation, White (1968, p. 12) found this species to be an acanthodian. Woodward (1921, p. 57) also mentions an ‘Undetermined CoccoSTEAN’ based on some poorly preserved fragments (illustrated in Woodward 1921, figs. 23 and 24); White (1968, p. 22) examined this material and determined it was too poorly preserved to be identified as ‘coccoSTEAN’. Ritchie (1971) mentions a large collection of largely undescribed placoderm material at the Australian Museum in Sydney.

Order Arthrodiriformes Family PHLYCTAENIIDAE Fowler 1947

Comment. The family Arctolepidae Heintz 1937 is considered (Denison 1978, p. 54) to be a junior synonym of this family (Miles, 1965, originally referred to this specimen as an ‘arctolepidae plate’). Phlyctaeniidae is also known from Devonian sediments of Europe, Spitsbergen, and North America (Denison 1978). Species in the suborder Phlyctaenioidei have also been reported from South Africa (Chaloner *et al.* 1980, p. 129).

unnamed (described in Miles 1965, p. 273)

Referred material. USNM 145422, a single left anterior lateral plate illustrated in Miles 1965, pl. 18, fig. 5.

Geologic age. Lower Devonian.

Locality. Horlick Formation of the Ohio Range, Antarctica. Additional locality information in Miles 1965, p. 273, and Doumani *et al.* 1965, pp. 243, 245.

Comment. Miles (1965, p. 274) stated, ‘The plate described above certainly belongs to a new species of arctolepid [= phlyctaenid] and, in all probability, to a new genus’. But because of the lack of additional material, he did not erect a new name for the taxon.

Family HOLONEMATIDAE Obruchev 1932
Groenlandaspis antarcticus Ritchie 1975, p. 571

Referred material. Holotype AMF 54334 (text-fig. 2A–B, a nearly complete head shield); several other head and ventral shields deposited at AMF and listed in the type description.

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone at Mount Ritchie and elsewhere between Mulock and Mawson Glaciers, Antarctica (more detailed locality information in type description).

Comment. This is the most complete described fish from the Devonian of Antarctica (text-fig. 2A–B). The genus is also known from Greenland, Ireland, Turkey, England, and New South Wales, Australia. The interrelationships of the *Groenlandaspis* species from these areas are unknown, so the Antarctic species does not yet contribute information on the biogeographic affinity of Antarctica.

Family *incertae sedis*
Antarctolepis gunni White 1968, p. 21

Referred material. Holotype BMNH P.49165 (dermal plate illustrated in White 1968, pl. 3, fig. 1).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone, Boomerang Range, between the Mulock and Mawson Glaciers, Antarctica. More detailed locality information in White 1968, and McKelvey *et al.* 1972.

Comment. Only one specimen (P.49165) was definitely referred to this species, although BMNH P.49165–49166 (White 1968, pl. 3, figs. 1 and 2) were tentatively referred to this species. White (1968, p. 20) put this species questionably in Phlyctaenaspidae, but Denison (1978, p. 102) placed the genus as *Arthrodira incertae sedis*.

Family indeterminate
Undetermined remains (described by White 1968, pp. 21–22)

Referred material. BMNH P.49167 (White 1968, pl. 3, fig. 3); NZGS 7395/17, 7396/4, 7396/5, 7399/12, 7399/14: all fragments of isolated dermal elements.

Geologic age. Middle or Upper Devonian.

Locality. Various Aztec Siltstone localities between the Mulock and Mawson Glaciers, Antarctica (given in White 1968).

Comment. Identified as 'Undetermined Arthrodire Remains' by White 1968, pp. 21–22.

Order Phyllolepipiformes
Family ANTARCTASPIDAE White 1968

Comment. This monotypic family is known only from Antarctica, and its relationships with other placoderms are not well known. According to Young (1981, fig. 3 and text), *Antarctaspis* is most closely related to Australian species of *Phyllolepis*.

Antarctaspis mcmurdoensis White 1968, p. 18

Type and referred material. Holotype BMNH P.49159 and P.49160 (partial skull-roof, illustrated in text-fig. 2c). Two additional fragments (BMNH P.49161 and P.49162, illustrated in White 1968, figs. 11 and 12) were tentatively referred to the species.

Geologic age. Middle or Upper Devonian.

Locality. In the Aztec Siltstone of the Lashly Mountains of Antarctica, between the Mulock and Mawson Glaciers (see also White 1968).

Order Antiarchiformes
Family BOTHRIOLEPIDAE Cope 1886

Comment. This family is also known from Devonian sediments in North America, Greenland, Europe, USSR, China, and Australia.

Bothriolepis antarctica Woodward 1921, p. 52

Type and referred material. BMNH P.12543–12552 (incomplete isolated plates from the head, trunk, and appendages). Seven of the specimens are illustrated in Woodward 1921, figs. 3–9. BMNH P.12535, 12540, 47824, 49170, 49154.

Geologic age. Lower or Middle Devonian (Beacon Sandstone) and possibly Middle to Upper Devonian (Aztec Siltstone).

Locality. Beacon Sandstone of Granite Harbour, between the Mulock and Mawson Glaciers, Antarctica (see Woodward 1921; McKelvey *et al.* 1972; Debenham 1921). Specimens from the Aztec Siltstone were also referred to this species by White (1968).

Comment. Originally described as an ostracoderm because at the time of description antiarchs were thought to be ostracoderms. Stensiö (1948, p. 521), after reviewing Woodward's material, commented that 'it is most likely . . . referable to *Bothriolepis*, but further material is needed for a definite decision that this is actually true'. The relationships of this species to other bothriolepids are unknown.

Bothriolepis sp. (mentioned in Ritchie 1971)

Referred material. Abundant material deposited in the Australian Museum, Sydney (reported in Ritchie 1971, 1975).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone, several localities between the Mawson and Mulock Glaciers, Antarctica, mentioned in Ritchie (1971, 1975).

Comment. Ritchie (1971) reports that he collected much *Bothriolepis* material including complete articulated head shields, and this material is being described by Young (in prep., citation in Young 1982, p. 820).

Bothriolepis sp. (described by White 1968, p. 15)

Referred material. BMNH P.12535–12542 (dermal plate fragments). Two specimens illustrated in Woodward 1921, figs. 1 and 2.

Geologic age. Lower or Middle Devonian.

Locality. Beacon Sandstone of Granite Harbour, between the Mulock and Mawson Glaciers, Antarctica (see Woodward 1921; McKelvey *et al.* 1972; Debenham 1921).

Comment. Although Woodward (1921, p. 52) did not completely identify this material, he commented that 'several fragments . . . may certainly be referred to [*Bothriolepis*]'. White (1968, p. 15) found, after further preparation of this material, that probably BMNH P.12535 and possibly the rest of the material is referable to Bothriolepidae. White (pp. 16–17) also mentions some additional bothriolepid fragments discovered later.

Class ACANTHODII

Comment. With the exception of ?*Cheiracanthus* sp. the only described acanthodian material from Antarctica consists of partial fin spines. The ?*Cheiracanthus* sp. material includes two scales.

White (1968) identified some Antarctic material as ?*Cosmacanthus* sp., which he included in

Acanthodii. Denison (1979, p. 56) determined that the type species for *Cosmacanthus* is an indeterminate arthrodire, and that later species are presumably elasmobranchs. Therefore, the Antarctic '*Cosmacanthus*' material of White's (BMNH P.49158) is not listed below; it should be re-examined to determine whether it belongs in *Cosmacanthus* or should be placed in some acanthodian taxon.

Order Acanthodiformes
Family ACANTHODIDAE Huxley 1861

Comment. This family is also known from Lower Devonian to Lower Permian sediments in North America, Europe, Siberia, South Africa, and Australia (Denison, 1979).

?*Cheiracanthus* sp. (described in White 1968, p. 25)

Referred material. BMNH P.12559 and 12576 (two scales). Illustrated in Woodward 1921, figs. 12 and 13.

Geologic age. Lower or Middle Devonian.

Locality. Beacon Sandstone of Granite Harbour, between the Mulock and Mawson Glaciers, Antarctica (see Woodward 1921 and Debenham 1921).

Order Climatiformes
Family GYRACANTHIDAE

Comment. The genus *Gyracanthides* has been recorded only from Victoria Land, Antarctica; from near Mansfield in Victoria, Australia; and from South Africa (Chaloner *et al.* 1980). This distribution reflects the geographic continuity of South Africa and Victoria with Antarctica during Devonian times (text-fig. 6). Ritchie (1971, p. 70) mentions the occurrence of *Gyracanthides* also in Devonian deposits of the Lashly Mountains, but Young (1982, p. 822) determined that material belonged to the xenacanth *Antarctilamna*.

Gyracanthides warreni White 1968

Referred material. BMNH P.49156 and 49155 (both external impressions of partial pectoral spines) (illustrated in White 1968, pl. 1, figs. 4 and 5).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone deposits of the Boomerang Range, between the Mulock and Mawson Glaciers, Antarctica (see White 1968).

Order incertae sedis
Antarctonchus glacilis White 1968

Referred material. BMNH P.49164 (holotype) and NZGS 7395/7-7395/8, 7395/12-7395/16, 7395/19 (all fin-spine fragments).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone deposits of the Lashly Mountains and Boomerang Range, between the Mulock and Mawson Glaciers, Antarctica (see White 1968 and Debenham 1921).

Comment. White (1968) did not give an opinion on specific relationships for this species and monotypic genus; Denison (1979, p. 49) placed the genus as Acanthodii, *incertae sedis*.

Byssacanthoides debenhami Woodward 1921

Referred material. BMNH P.12553 (lectotype designated by White 1968, p. 12), P.12554 (illustrated in Woodward 1921, pl. 1, figs. 10 and 11) (both fin-spine fragments).

Geologic age. Lower or Middle Devonian.

Locality. Beacon Sandstone of Granite Harbour, between Mulock and Mawson Glaciers, Antarctica (see Woodward 1921 and McKelvey *et al.* 1972).

Comment. Monotypic genus, originally described as an antiarch placoderm but later placed as *Acanthodii incertae sedis* by White (1968), Denison (1979), and others.

Class CHONDRICHTHYES

Comment. Below is the first report of any holocephalan or pristiophorid from the Antarctic region. Although there is no known articulated fossil chondrichthyan material, some of the holocephalan tooth plates appear to have come from a single individual. Previously, the total recognized fossil chondrichthyan fauna of the region included only *Eugomphodus macrora* (Odontaspidae), *Carcharodon auriculatus* (Lamnidae), and indeterminate species of Lamnidae, Squalidae, Mylobatoidea, and *Squatina*. The only living chondrichthyans reported from the area are five nominal species of skates (Andriashev 1965).

Other fossil chondrichthyan taxa have been erroneously reported from the Antarctic Region (*Ptychodus*, *Scapanorhynchus raphiodon*, *S. subulatus*, *Isurus mantelli*, *Isurus* sp., and *Carcharias* sp. by de Valle *et al.* 1976 and *I. novus?* by Cione *et al.* 1977). These fossils were found by later workers (Welton and Zinsmeister 1980) to have been misidentified (in the case of de Valle *et al.* 1976) or of insufficient completeness to warrant such identification (in the case of Woodward 1908). Below, the taxa recognized by Welton and Zinsmeister (1980) and the new taxa reported here will be listed systematically.

Subclass ELASMOBRANCHII

Comment. It is difficult to derive any significant biogeographical information (other than range extension) based on the Antarctic elasmobranchs because of inadequate preservation. Most of the elasmobranch species are known only from isolated tooth fragments.

Order Xenacanthiformes

Family XENACANTHIDAE Fritsch 1889

Xenacanthus sp. (described in Young 1982 and Ritchie in McKelvey *et al.* 1972, p. 351)

Referred material. CPC 21214–21217, 21228; AMF 54329–54331, 55573 (all isolated teeth, some of which are illustrated in Young 1982, pl. 89, figs. 1–4).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone deposits of Portal Mountain and near Mount Ritchie, near Mawson Glacier (see Young 1982), Antarctica.

Comment. This was the first xenacanthid material reported from Antarctica.

Antarctilamna prisca Young 1982

Referred material. CPC 21187 (holotype), a partly articulated specimen illustrated in Young 1982, text-figs. 2 and 3a–d, and pl. 89, figs. 5–7; CPC 21188–21190, isolated scales; CPC 21191, teeth; and AMF 55550, 55555, 55617; CPC 21192, fin spines.

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone, near Mawson Glacier (see Young 1982), Antarctica.

Comment. Young (1982) specifies that this Antarctic material belongs to a species most closely related to a Devonian Australian species (he, in fact, considers the Antarctic and Australian material to be conspecific in this monotypic genus).

Although Young (1982, pp. 822–823) does not formally include *Antarctilamna* in Xenacanthidae, he places his monotypic genus as the sister-group of *Xenacanthus* (p. 838). It is therefore included here in Xenacanthidae.

Order Lamniformes

Family ODONTASPIDIDAE Muller and Henle 1839

Eugomphodus macrota (Agassiz 1843)

Referred material. UCMP 116454–116460, incomplete teeth (some illustrated in Welton and Zinsmeister 1980, fig. 4g–p), and 225 broken tooth crowns in the collection of the Ohio State University Institute of Polar Studies. Description of material and locality in Cione *et al.* (1977), and Welton and Zinsmeister (1980, pp. 4–5), with a detailed discussion of the stratigraphy in Woodburne and Zinsmeister (1984).

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island (64° 15' S., 56° 45' W.), Antarctic Peninsula, in a coarse, pebbly, fossiliferous shell bank.

Comment. Cione *et al.* 1977 also referred some material to *Eugomphodus* sp., which Welton and Zinsmeister (1980, p. 7) stated 'are probably *Eugomphodus macrota*'. Teeth reported as belonging to this species are geographically widespread, known from Eocene sediments in North America, Chile, Asia, USSR, and Africa (Welton and Zinsmeister 1980).

Family LAMNIDAE Muller and Henle 1838

Carcharodon auriculatus (Blainville 1816) (= *Procarcharodon auriculatus* of Cione *et al.* 1977)

Referred material. UCMP 116453, a nearly complete anterior tooth lacking one cusplet (illustrated in Welton and Zinsmeister 1980, figs. A–C).

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula.

Comment. Some fragmentary material referred to *Isurus* by Cione *et al.* (1977) was placed in Lamnidae as indeterminate by Welton and Zinsmeister (1980, p. 7). Because this species is based only on teeth, it is difficult to assess its geographic extent. It has been reported from Tertiary sediments of North America, Europe, Africa, South America, Australia, New Zealand, and USSR.

Isurus sp., newly reported Antarctic specimen

Referred material. FMNH PF10294, a nearly complete tooth (text-fig. 3h, i).

Geologic age. Upper Cretaceous.

Locality. Cretaceous–Tertiary boundary, Seymour Island, Antarctic Peninsula (Zinsmeister, pers. comm.).

Comment and description. A single, unicusped, anterior tooth with smooth cutting edges on the lateral margins. The only specimens of *Isurus* sp. previously reported from the Antarctic region were from Late Eocene or Early Oligocene sediments of the La Meseta Formation (Elliot *et al.* 1975; Cione *et al.* 1977). These previously reported specimens were found by Welton and Zinsmeister (1980) to be unassignable to the genus, and are not included in the genus here.

Order Squaliformes

Family SQUALIDAE Leach 1818

indeterminate (described by Welton and Zinsmeister 1980, p. 3)

Comment. Recent squalids have a widespread distribution in marine waters of the Atlantic, Pacific, and Indian Oceans, and fossils are also widespread in marine sediments.



TEXT-FIG. 3. *a-g*, Siluriformes, from early Tertiary deposits of Seymour Island. *a-d*, left pectoral fin spine (FMNH PF10642, coated with ammonium chloride), $\times 2$. *a*, anterior surface. *b*, posterior surface. *c*, dorsal surface. *d*, ventral surface. *e, f*, anterior part of right dentary (FMNH PF10643), anterior pointing down, $\times 2.5$. *e*, view of toothed surface. *f*, medial view. *g*, a single isolated tooth, $\times 2.5$, from another dentigerous bone (FMNH PF10644) associated with dentary in *e* and *f*. *h* and *i*, *Isurus* sp. (FMNH PF10294), $\times 1.6$, from Upper Cretaceous deposits of Seymour Island. Missing part of root. *h*, anterior view. *i*, lateral view. Previously reported specimens identified as *Isurus* sp. from Antarctica have been found to have been incorrectly identified (see text). *j-l*, *Pristiophorus* sp. from early Tertiary deposits of Seymour Island. *j, k*, lateral (anterior facing left) and anterior views of a single rostral tooth (FMNH PF10645c), $\times 2.9$, dashed lines = restored outline. *l*, series of isolated rostral teeth (FMNH PF10645a-l), $\times 0.9$; anterior facing down. This is the first report of a pristiophorid from the Antarctic region. *m-p*, Chimaeridae (?*Ischyodus* sp.) from early Tertiary deposits of Seymour Island. *m, n*, dorsal fin spine, lateral (anterior facing left) and posterior view (FMNH PF10646), $\times 1$. *o, p*, palatine and mandibular tooth (FMNH PF10647a-b), $\times 1.1$; anterior facing left. This is the first report of a holocephalan from the Antarctic region.

Referred material. UCMP 121795, an incomplete tooth (illustrated in Welton and Zinsmeister 1980, fig. 2).

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula (see Welton and Zinsmeister 1980).

Family PRISTIOPHORIDAE Bleeker 1859

Pristiophorus sp., first report

Referred material. FMNH PF10645 (text-fig. 3j-l)—twelve rostral teeth including several nearly complete specimens.

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula.

Comment and description. This is the first report of a saw shark from Antarctica. The blade-like teeth are of orthodentine, with smooth, unbarbed edges, and a root base that is claviform with a distinct anteroposterior groove (for fitting against the lateral margin of rostrum). Because the teeth are smooth (rather than barbed) they are thought to belong to *Pristiophorus* rather than *Pliotrema* or *Ikamaui* (both of which have barbed rostral teeth). It is interesting to note that there are no known fossil or Recent pristiophorids in South America south of northern Ecuador (Keyes 1982). The genus *Pristiophorus* is fairly widespread, today living in Atlantic and Indo-west Pacific waters. Fossils are also known from North America, Europe, South Africa, Asia, and Australia. The biogeography of fossil and Recent pristiophorids was reviewed by Keyes (1982).

Family SQUATINIDAE Muller and Henle 1837

Squatina sp. (described in Welton and Zinsmeister 1980, p. 4)

Referred material. UCMP 121796–121797, two incomplete teeth (one illustrated in Welton and Zinsmeister 1980, fig. 3).

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula (see Welton and Zinsmeister 1980).

Comment. Squatinids are geographically widespread. Recent species (all belonging to a single genus) occur in both Atlantic and Pacific waters, and fossils are 'well represented in most Cenozoic neoselachian assemblages' (Welton and Zinsmeister 1980, p. 8).

Order Rajiformes

Family MYLOBATIDAE Muller and Henle 1837

incertae sedis (described in Welton and Zinsmeister 1980, p. 7)

Referred material. UCMP 116461, an incomplete medial tooth (lacking distal end of crown and one side of root). Illustrated in Welton and Zinsmeister 1980, fig. 4d–f. Also, UCR 21089, 21169, 21170, 21230, and FMNH PF10678–10681 (partial teeth).

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula (see Welton and Zinsmeister 1980).

Comment. Mylobatid rays are geographically widespread. Recent species occur in Atlantic, Pacific, and Indian waters, and the fossils, like *Squatina* fossils, are 'well represented in most Cenozoic neoselachian assemblages' (Welton and Zinsmeister 1980, p. 8). Although mylobatids are unknown in the Recent Antarctic fauna, mylobatid teeth are common in the La Meseta Formation.

Order Undetermined

Family MCMURDODONTIDAE White 1968

Mcmurdodus featherensis White 1968, p. 9

Type specimen. BMNH P.49157, a nearly complete tooth (illustrated in White 1968, fig. 1).

Geologic age. Middle to Upper Devonian.

Locality. Aztec Siltstone deposits at Mount Feather, between the Mulock and Mawson Glaciers, Antarctica (see White 1968).

Comment. Young (1982, p. 835) reported a second specimen of this species (CPC 21229, a tooth from Mount Ritchie, between the Mulock and Mawson Glaciers, Antarctica).

Family indeterminate

Undetermined selachian vertebral centra (described by Woodward 1908, pp. 1-2)

Referred material. Large centra (to 10 cm in diameter) illustrated in Woodward 1908, figs. 1-3.

Geologic age. Cretaceous.

Locality. Seymour Island.

Comment. These vertebrae were originally identified by Woodward (1908) as *Ptychodus* sp., but Welton and Zinsmeister (1980) showed placement in that genus to be tenuous, and they are probably better placed as Elasmobranchii: indeterminate order.

Subclass HOLOCEPHALI

Order Chimaeriformes

Family CHIMAERIDAE Rafinesque 1815

?Ischyodus sp., first report

Referred material. FMNH PF10647a-b (palatine and mandibular tooth illustrated in text-fig. 3o, p); and UCR 21008 (dorsal spine illustrated in text-fig. 3m, n). Also FMNH PF10648-10653 (partial jaw elements).

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula.

Comment. This is the first report of a holocephalan from Antarctica. A description of this new species is currently in progress (Maisey and Grande). This material is extremely abundant in the La Meseta Formation of Seymour Island.

INDETERMINATE CHONDRICHTHYAN REMAINS

unnamed (described in Woodward 1921, p. 56)

Referred material. BMNH P.12561-12563, 12589, 12590 (minute fragments of dermal armour and shagreen-granules).

Geologic age. Lower to Middle Devonian.

Locality. Beacon Sandstone of Granite Harbour, between the Mulock and Mawson Glaciers, Antarctica (see Woodward 1921 and Debenham 1921).

Comment. Woodward (1921) stated that the fragments were referable to a primitive ostracoderm or elasmobranch group, possibly even to Cladoselachiformes. Gross (1950) and Tarlo (1966) suggested that they might be referable to Psammosteidae (Heterostraci).

Class OSTEICHTHYES
Subclass CROSSOPTERYGII
Order Osteolepiformes

Family OSTEOLEPIDAE Cope 1889

Gyroptychius? antarcticus (Woodward 1921, p. 58)

Holoptychius antarcticus Woodward 1921, pp. 58–59, pl. 1, figs. 25–29

Type and referred material. BMNH P.12573, lectotype designated by White (1968, p. 22), consisting of the impression of a flank scale (illustrated in White 1968, fig. 14); and numerous other BMNH and NZGS specimens, including a few teeth, part of a lower jaw, imperfect branchiostegal rays, a suboperculum, and a gular plate (all disassociated).

Geologic age. Lower or Middle Devonian (Beacon Sandstone) and possibly also Middle or Upper Devonian (Aztec Siltstone).

Locality. Originally described from the Beacon Sandstone of Granite Harbour, between the Mulock and Mawson Glaciers, Antarctica. Specimens from the Aztec Siltstone were also referred to this species by White (1968).

Comment. Woodward described this species in the porolepiform genus *Holoptychius* based mainly on a scale and a supposed clavicle fragment. White (1968, p. 22) further prepared and re-examined this material and found the scales to be those of an osteolepid, and the 'clavicle' to be a small dorsal central plate of an antiarch pectoral limb. White also added some osteolepid material from the Aztec Siltstone (the teeth, suboperculum, gular plate, and branchiostegal rays) to Woodward's original material. White (1968, p. 25) admitted that his placement of this fragmentary material into the genus *Gyroptychius* was tenuous. This material should, at best, probably be *incertae sedis* under Osteolepiformes (a widespread order found also in Devonian sediments of North America, Europe, Australia, and Asia).

Gyroptychius sp. (mentioned in Ritchie 1971, pp. 69–70)

Referred material. Some undescribed AMF material including a lower jaw (Ritchie 1971, fig. p. 70), and possibly a nearly complete anterior half of a fish (mentioned in Ritchie 1971, p. 69).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone deposits between the Mulock and Mawson Glaciers, Antarctica (see Ritchie 1971).

Comment. *Gyroptychius* is also reported from Australia (Young and Gorter 1981), and Europe and Greenland (Thompson 1964), but the monophyly of the genus as currently defined is doubtful (Young and Gorter 1981).

unnamed (described by Woodward 1921, p. 59)

Type and referred material. BMNH P.12576, 12579, 12581, 12583, 12588 (scales and incomplete operculum, illustrated in Woodward 1921, figs. 27–29).

Geologic age. Lower or Middle Devonian.

Locality. Beacon Sandstone of Granite Harbour, between the Mulock and Mawson Glaciers, Antarctica (see Woodward 1921 and Debenham 1921).

unnamed (illustrated in McKelvey 1972, fig. 4)

Type and referred material. NZGS 234 (a disarticulated skull).

Geologic age. Middle or Upper Devonian.

Locality. Aztec Siltstone deposits between Mulock and Mawson Glaciers, Antarctica.

Comment. This specimen has not yet been described.

Subclass ACTINOPTERYGII

Infraclass CHONDROSTEI

Order Palaeonisciformes

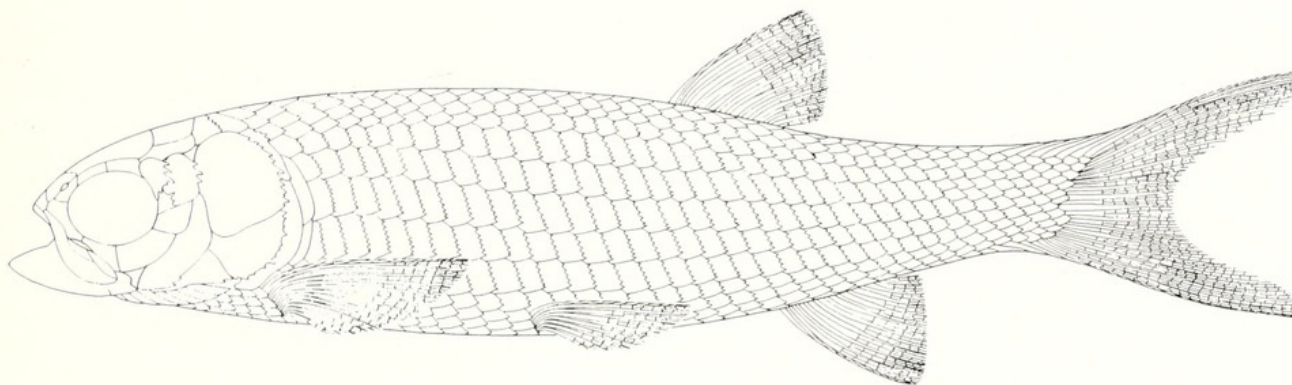
Undet. palaeonisciforms (described by Woodward 1921 and White 1968)

Referred material. Many BMNH and NZGS scales listed in Woodward 1921, p. 601 and White 1968, p. 24. Woodward (1908, figs. 30–34) illustrates some of them.

Geologic age. Lower or Middle Devonian, and Middle or Upper Devonian.

Locality. Various Aztec Siltstone and Beacon Sandstone localities between the Mulock and Mawson Glaciers.

Comment. Woodward (1921, p. 601) tentatively suggested a resemblance of some of these to *Rhadinichthys*, but White (1968, p. 24) pointed out that they also resembled several other genera. White (1968, p. 24) determined that there were at least three palaeoniscoid taxa represented, but found none of the material of sufficient preservation for more specific identification or description.



TEXT-FIG. 4. *Oreochima ellioti* Schaeffer. The only described fossil fish species from the Antarctic region that is known by nearly complete articulated specimens. Restored line drawing taken from Schaeffer 1972, with permission of the author.

Infraclass NEOPTERYGII

Subdivision Undefined

Order 'Pholidophoriformes'

Family ARCHAEOMAENIDAE Goodrich 1909

Oreochima ellioti Schaeffer 1972, p. 3

Type and referred material. AMNH 9910A–B (holotype—a complete fish, part and counterpart illustrated in Schaeffer 1972, fig. 1) and AMNH 9922–9971 (partial to nearly complete fish, some illustrated in Schaeffer 1972, figs. 4–8).

Geologic age. Lower Jurassic.

Locality. Sedimentary interbeds (freshwater deposits) of the Kirkpatrick Basalt, Ferrar Group, Queen Alexandra Range, Antarctica (see Schaeffer 1972 and Grindley 1963).

Comment. Because the 'Pholidophoriformes' is probably a non-monophyletic group (Patterson 1977) and the interrelationships of its members are poorly known, this species and family is placed in an undefined subdivision of Neopterygii. This freshwater species is the only described fossil vertebrate which is represented in Antarctica by nearly complete articulated skeletons (reconstruction in text-fig. 4). It appears to be most clearly related to Australian species, because the family Archaeomaenidae are restricted to Australia (Schaeffer 1972).

Subdivision TELEOSTEI
Superorder OSTARIOPHYSI
Order Siluriformes
Family *incertae sedis*
unnamed, first report

Referred material. A single pectoral spine (text-fig. 3a–d), FMNH PF10642; and a partial dentary (text-fig. 3e–g), FMNH PF10643.

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula.

Description. Nearly complete left pectoral spine (33 mm in length) missing only distal tip and part of dorsal surface of main shaft. Posterior dentitions (serrae) very strong, few in number (nine or ten), retrose, evenly spaced, and single cusped. No well-developed anterior serrae. Main shaft with weakly developed subparallel ridges, and at anterior-proximal end there are a few small tubercles.

A lower jaw (text-fig. 3e, f) and another toothed element associated with the jaw also appear to be catfish bones. Specimen FMNH PF10643 is the anterior portion of a right dentary which is relatively massive (text-fig. 3f) for a catfish, and bears a broad band of closely and uniformly spaced teeth (text-fig. 3e). The teeth are all hollow and broken off at the base, as is common in fossil catfish jaw elements (e.g. Lundberg 1975, figs. 1D, 5D, F). One nearly complete villiform tooth (text-fig. 3g) is preserved on another toothed catfish element (FMNH PF10644) associated with the dentary. The tooth is detached and lying on its side on the dentigerous surface of the bone.

Comment. This is the first catfish reported from the Antarctic region. The lower jaw elements were not associated closely enough with the pectoral spine to indicate with certainty that these bones belonged to the same individual or even the same species, although they all belonged at least to individuals of similar size. The spine (text-fig. 3a–d) appears to have a fairly primitive morphology most similar to ictalurids, bagrids, and diplomystids. It does not resemble any Recent marine catfishes (i.e. ariids, plotosids). We therefore leave the spine and lower jaw as Siluriformes *incertae sedis*, and belonging to one or possibly two different species.

Subdivision TELEOSTEI
Superorder *incertae sedis*
unnamed, newly reported Antarctic material

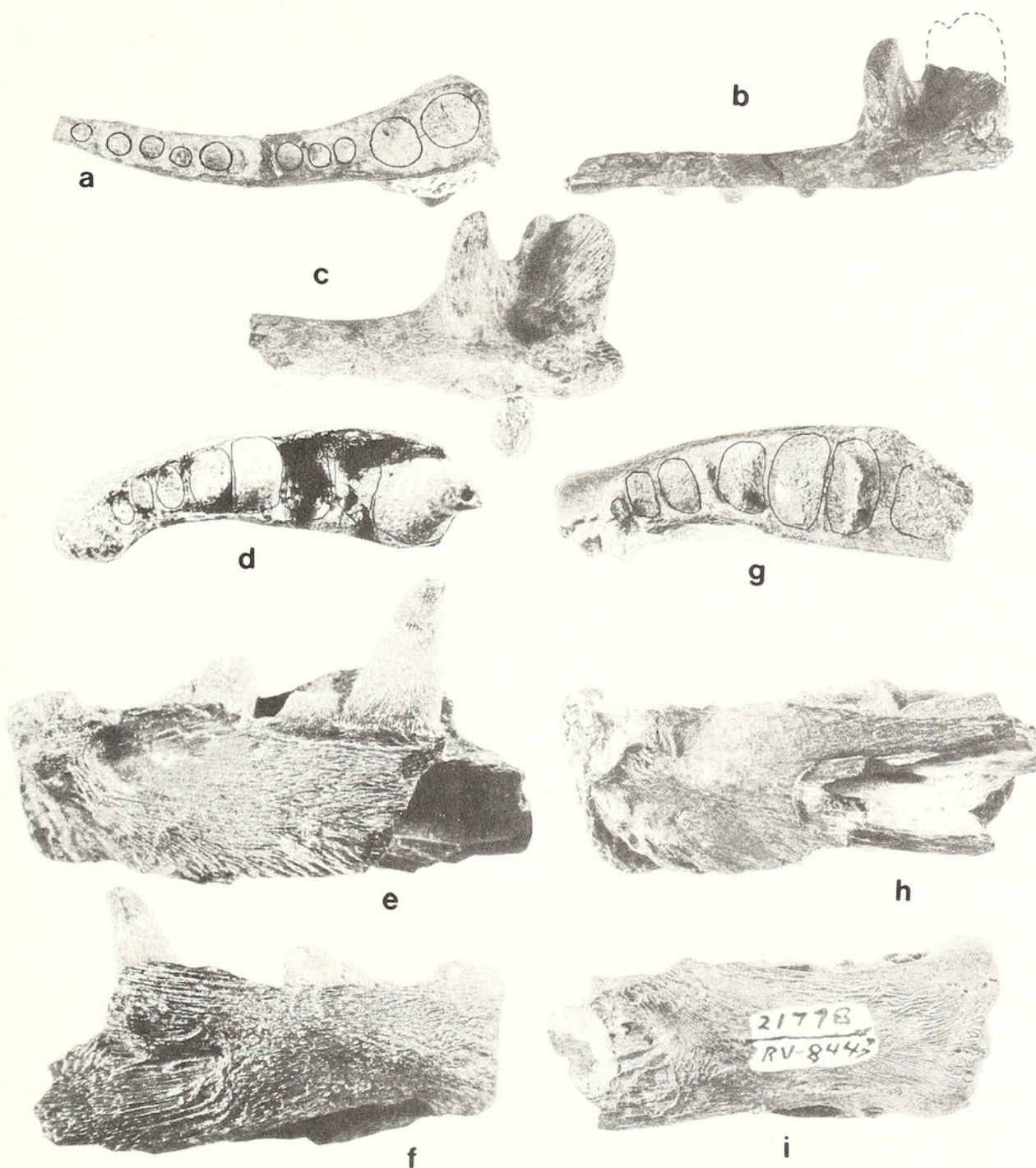
Referred material. Disarticulated and fragmented skeletal material including a variety of vertebral centra of various sizes (specimens FMNH PF10658–10669 each with 1 to 5 centra for a total of twenty-one vertebrae); basioccipital (FMNH PF10670); dentaries, some with conical teeth (FMNH PF10656–10657, 10671–10672); premaxillae with conical teeth (FMNH PF10654–10655); maxillae (FMNH PF10674–10675); unidentified jaw fragment with conical teeth (FMNH PF10676); pharyngeal tooth plate or part of fifth ceratobranchial containing bases of small conical teeth (FMNH PF10677). Some of the jaw elements are illustrated in text-fig. 5.

Geologic age. Late Eocene or Early Oligocene.

Locality. The La Meseta Formation, Seymour Island, Antarctic Peninsula.

Comment. This material is a significant addition in quantity to the teleost fossils from Antarctica. It contributes some insights into the biology of these fishes, but unfortunately offers no systematic information. While it is reasonable to expect that ancestral notothenioids might be represented in this material, there is nothing that allows a definitive diagnosis of this group. A morphological diagnosis of the Notothenioidei includes (Eakin 1976) 33 flat, plate-like pectoral radials; pleural ribs poorly developed and floating or absent; one nostril on each side of the head; non-pungent fin spines; usually two or three lateral lines; no swim bladder; 10–19 principal caudal rays and 5–9 branchiostegals. None of these features is evident in the fragmentary material from Seymour Island.

Although some of the fossilized vertebral centra are similar to those of some Recent notothenioids



TEXT-FIG. 5. *a-c*. Indeterminate teleost premaxilla from early Tertiary deposits of Seymour Island (resembling a gadiform type, but specimens are too incomplete to make a positive assignment); in all three specimens, anterior faces right. *a, b* (FMNH PF10654). *a* shows tooth surface (tooth bases outlined with black lines) and *b* is the medial surface (anterior processes restored with dashed lines, based on *c*), posterior end and teeth broken off, $\times 1$. *c* (FMNH PF10655) anterior end of a premaxilla, probably belonging to the same species as the specimens in *a* and *b*, $\times 2$. *d-i*. Indeterminate teleost partial dentaries from early Tertiary deposits of Seymour Island. These dentaries are peculiar in that they are extremely massive, and they have teeth that increase greatly in base width posteriorly (most teeth were broken off near base so the tooth morphology is unknown). Tooth bases outlined with black lines (*d, g*). *d-f*, FMNH PF10656, $\times 6$. *g-i*, FMNH PF10657, $\times 1.3$.

the material is not distinctive enough for a positive identification. The vertebrae are, however, from at least two different kinds of fishes and from fishes of greatly different sizes.

A large caudal vertebra (FMNH PF10667; maximum diameter of centrum = 4.7 cm) is generally similar to those of the Recent nototheniid *Dissostichus mawsoni*. As in *Dissostichus* the centrum contains deep fossae: two on each lateral aspect, one mid-dorsally and one mid-ventrally. This, however, is not a characteristic unique to notothenioids. The fossil centrum is not as cancellous as those of *Dissostichus*.

Casteel (1976) discusses a proportional method for estimating the size of a fish from the dimensions of one of its bones by comparison with the bones of a type specimen of known size. We applied this method to vertebra FMNH PF10667. The centrum measures 3.27 cm anteroposteriorly. The centrum of the first caudal vertebra of an 88 cm SL *Dissostichus* measures 1.43 cm. Solving for the unknown the proportion yields 201 cm as the standard length of the specimen. *D. mawsoni* is both the largest teleost and the largest Recent nototheniid in Antarctic waters. The largest specimen captured by Eastman and DeVries (1981) measured 163 cm TL and weighed 60.3 kg. This is probably close to maximum size for the species. The late Eocene fauna from Seymour Island thus contained fishes considerably larger than those of the Recent fauna.

The centra of many of the smaller vertebrae in the sample resembled the large specimen FMNH PF10667. For example, the arrangement and relative depth of the fossae was similar in most centra that were not badly weathered. Of the twenty-one vertebrae in the sample, most were typically amphicoelous with no evidence of a notochordal foramen (19%) or with a pin-hole sized foramen (71%). Among Recent notothenioids, a pin-hole sized foramen is characteristic of *D. mawsoni*, *Notothenia angustata*, and *Bovichthys variegatus*.

Buoyancy specializations among some Recent notothenioids include reduction in the extent of skeletal ossification. Some species exhibit diminished vertebral amphicoely with persistence of a partial or complete notochord in a foramen traversing the middle of the centrum (Eastman and DeVries 1982; DeVries and Eastman 1978, 1981). Thus the size of the notochordal foramen is related to the degree of constriction of the notochord by the centra such that large foramina are present in species with unconstricted (*Pleuragramma*) or slightly constricted (*Aethotaxis*) centra. Many Recent notothenioids have moderately large notochordal foramina. When expressed as a relative measurement the notochordal foramina are 20–38% of the diameter of the centra at the intervertebral joint. Included in this group are species from the genera *Trematomus*, *Notothenia*, *Gymnodraco*, *Pagetopsis*, *Champscephalus*, and *Chionodraco*. Two (10%) of the teleost fossils from Seymour Island have notochordal foramina similar in size to those of many Recent notothenioids. However, this character is probably not unique to notothenioids.

Other teleost skeletal material from the La Meseta Formation comprises mainly jaw fragments. The material is too incomplete to allow taxonomic identification, but it also indicates that some specimens were larger than the Recent specimen of *D. mawsoni* mentioned above. The teeth of these specimens are heavy and conical with both large and small series on a single jaw element. Teeth of *D. mawsoni* are smaller, sharper, and curved posteriorly.

DISCUSSION

Although chondrichthyans are a minor component of the Recent Antarctic fauna, they are more diverse in the fossil record of the continent. The three to five species of Recent rajids are most numerous near the Antarctic Peninsula, South Georgia, and Kerguelen (Andriashev 1965; Bigelow and Schroeder 1965; DeWitt 1971; Springer 1971).

There are several factors that may have contributed to the restriction of Recent chondrichthyans from Antarctic waters. More than half of the living chondrichthyans are batoids (Compagno 1977), and they are generally most abundant in waters less than 1000 metres deep (Moyle and Cech 1982). Shallow benthic continental shelf habitat is limited in Antarctica (text-fig. 1 and see below). Furthermore, the benthos consists largely of sessile filter-feeding invertebrates (Hedgpeth 1969) that are mainly inedible (sponges, sea urchins, sea stars, sea spiders, and brittle stars). In addition,

molluscs, an important food group for many rajids, are poorly represented in the Antarctic fauna (Dell 1969). It is possible that these circumstances, along with cold water temperatures, may have served to eliminate many chondrichthyans from Antarctic waters during the late Tertiary.

This is the first report of Holocephali, Pristiophoridae, or Ostariophysii from the Antarctic region, thus adding two more families to the chondrichthyan faunal list and a teleostean order (Siluriformes). Previously, the only known chondrichthyan families represented were Odontaspidae, Lamnidae, Squalidae, Squatinidae, and Myliobatidae (all represented by fossils only) and rajidae. Previously known fossil teleosts were all Teleostei *incertae sedis*; and known Recent teleosts are discussed below.

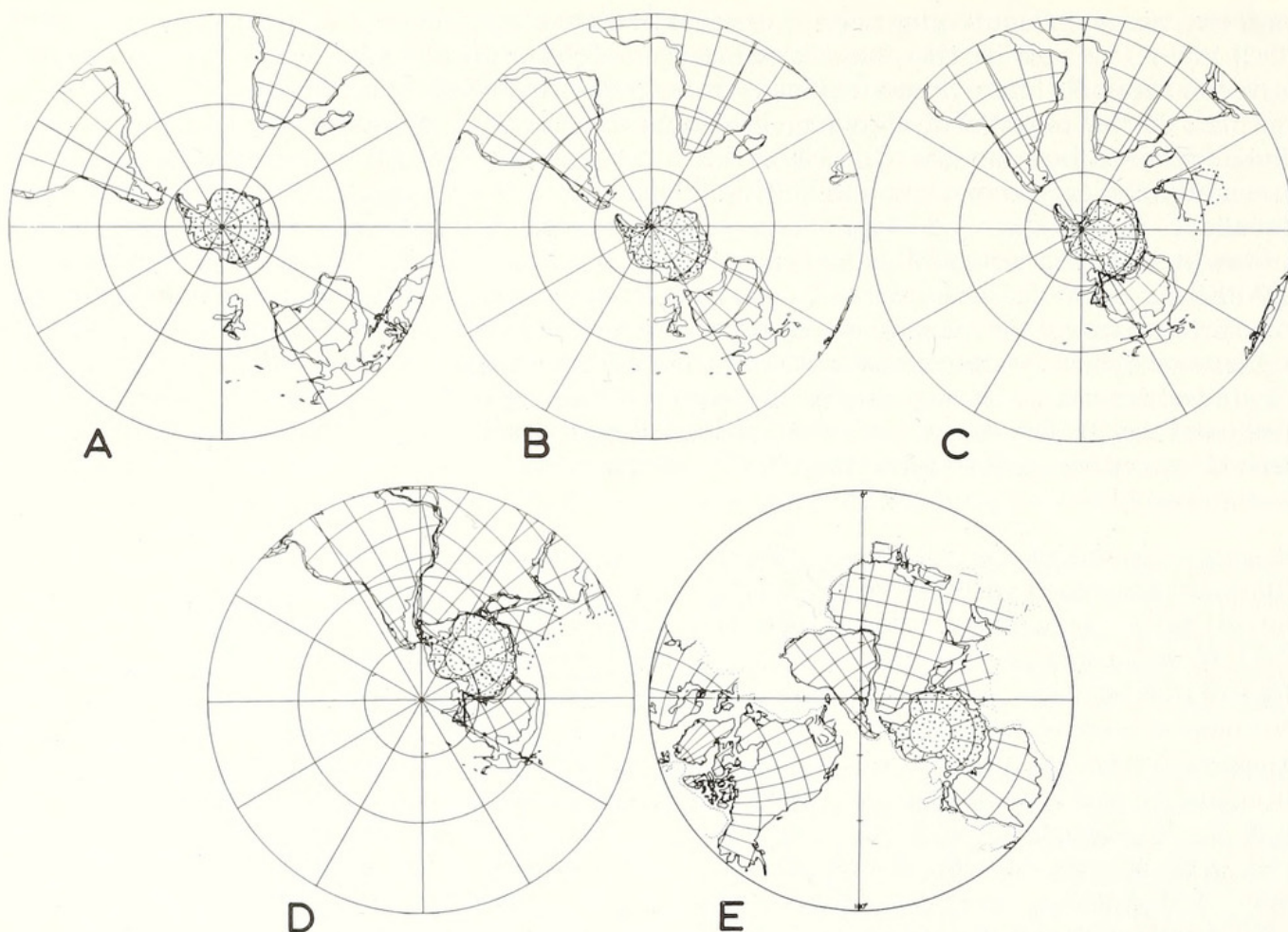
Although fossil fishes have been described from several localities in the Antarctic Region (text-fig. 1), most of the material is very poorly preserved. Only one described species (text-fig. 4) is represented by nearly complete articulated skeletons (the Jurassic *Oreochima ellioti* Schaeffer 1972). The only other reasonably articulated specimen is a skull roof of *Antarctaspis mcmurdoensis* White 1968 (text-fig. 2). The rest of the known fossil fish material consists mostly of incomplete isolated dermal head plates, scales, teeth, and other fragments, much of which cannot be accurately assigned even to family.

Biogeographic Significance of the Fish Fauna. The evolution and biogeography of the Antarctic fish fauna are associated with the break-up of Gondwana and subsequent development of the ocean current pattern around Antarctica. These events may be briefly summarized as follows (Craddock 1982; Woodburne and Zinsmeister 1984). Gondwana was intact throughout the Palaeozoic (text-fig. 6E) and into the early Jurassic 195 ma (text-fig. 6D). Antarctica has been in a south polar position throughout most of the Mesozoic (text-fig. 6C). During the Late Cretaceous (text-fig. 6C), South America, Antarctica, and Australia were continuous, although there were prominent breaks between all crustal blocks. Separation of Australia from East Antarctica may have begun in the Late Jurassic, with the development of deep-sea conditions in this narrow trough about 80 ma. Final separation took place between the Late Eocene and Early Oligocene (38 ma). Separation of West Antarctica from South America was the last major event in the break-up of Gondwana and occurred between the Early Cretaceous and the Late Eocene (text-fig. 6B). Deep-water conditions have prevailed in the Drake Passage since at least 20 ma. Once Antarctica was isolated the unrestricted circum-Antarctic current reached full development. By decoupling warm subtropical gyres from the continent the circum-Antarctic current served as a barrier to heat flow and thermally isolated Antarctica. Subsequently glaciers developed and the polar ice cap began to form (Kennett 1978, 1980).

The biogeographic significance of the Antarctic fauna is variable through geologic time, so it will be discussed below by era.

Palaeozoic. All known Palaeozoic fishes from the Antarctic region are from Devonian rocks. The Devonian is well before the break-up of Gondwanaland (text-fig. 6E), so the occurrence of the widespread family Bothriolepidae is not too surprising. Few of the Devonian fish taxa are well enough preserved to be included in phylogenetic studies of relationship and biogeography at the species level (i.e. What other species of *Bothriolepis* is *B. antarctica* most closely related to, and where did that sister species live?). In most cases preservation of the described Devonian fishes from Antarctica is inadequate to enable positive assignment even to family, but there are exceptions. Of the two described well-preserved Devonian species (both placoderms), one (*Groenlandaspis antarcticus*) is insufficiently known to yield any particular biogeographic affinity for Antarctica, and the other (*A. mcmurdoensis*) is thought by Young (1981, fig. 3C) to indicate a biogeographic relationship between Antarctica and Australia. The presence of *Antarctilamna* (Xenacanthidae) also indicates an Australian biogeographic affinity for Antarctica during Devonian time. The genera are both represented only in Devonian deposits of Antarctica and Australia. The Antarctic-Australian biogeographic relationship of the placoderms and xenacanth reflects the proximity of Australia to Antarctica during Devonian time (text-fig. 6).

Mesozoic. Antarctic fossil fish material is described from two periods of the Mesozoic: the Cretaceous (Woodward 1908, pp. 1–3) and the Lower Jurassic (Schaeffer 1972). Woodward's (1908) Cretaceous



TEXT-FIG. 6. South polar stereographic projection maps showing the position of Antarctica relative to other continents during Recent (A), Late Eocene (B), Late Cretaceous (C), Early Jurassic (D), and Lower Devonian (E) time. A–D are after Smith and Briden (1977); E is after Smith *et al.* (1973). Fishes described in this paper lived during these geologic times.

material consists only of a few isolated scales, and poorly preserved tooth and vertebral fragments, which are indeterminate to order. Our Cretaceous material consists of only a single well-preserved tooth (reported as *Isurus* sp.). Some additional unidentified Jurassic actinopterygian fragments are illustrated in Tasch and Gafford (1984, figs. 2–6). Zinsmeister (1982) and Chatterjee and Zinsmeister (1982) mention their discovery of some ‘Holosteans’ and other ‘bony fishes’ from Cretaceous deposits, but this material has yet to be described, and was unavailable for this study. These Cretaceous bony fishes (probably belonging to only two identifiable teleost species) will be described later by Grande and Chatterjee.

Of the described Mesozoic material the Jurassic species appears to be the most informative. It is known by several nearly complete individuals and is reconstructed in text-fig. 4. This species belongs to a freshwater family, Archaeomaenidae, which was previously confined to Australia (*Archaeomaena*, *Madariscus*, and *Wadeichthys*). According to Schaeffer (pers. comm.) the Antarctic species is most closely related to *W. oxyops* Waldman (1971) from the Lower Cretaceous of Victoria. Thus, as during Devonian time, the Mesozoic material indicates an Australian biogeographic affinity for Antarctica.

Cenozoic. All known Cenozoic fish fossils from Antarctica are from Seymour Island. The sediments which contain these fossils are probably of Eocene age (Welton and Zinsmeister 1980, p. 2; Woodburne and Zinsmeister 1984), although they were previously (Wilckens 1911) thought to be

Miocene. According to Welton and Zinsmeister (1980) and Woodburne and Zinsmeister (1984), Tertiary rocks on the Island appear to range in age from Palaeocene (Cross Valley Formation) to Late Eocene or Early Oligocene (La Meseta Formation). The fish fossils are from the La Meseta Formation. Eocene fishes were first reported by Woodward (1908) and later by Elliot *et al.* (1977), de Valle *et al.* (1976), Cione *et al.* (1977), and Welton and Zinsmeister (1980). Woodward (1908) reported both teleost and shark material, and the rest of the papers cited above reported only shark material.

The Eocene teleost material reported by Woodward (1908, pp. 3–4 and fig. 5) consisted only of isolated partial centra, which he attributed to *Nototheniidae* because 'they very closely resemble the corresponding vertebrae of a large existing species of *Notothenia*'. It would not be surprising to find notothenioid fossils in the area, because they dominate the Recent Antarctic fish fauna. However, as mentioned previously, such an assignment based only on isolated centra seems somewhat tenuous. The report of *Notothenia* from the middle-late Miocene of New Zealand (Stinton 1957) has since been shown to be a misidentification (Fordyce 1982).

The fossil shark and catfish material reported contributes little biogeographic information other than range extensions of already widespread taxa.

Recent. DeWitt (1971) summarized information concerning the distribution and endemism of the Recent Antarctic fish fauna. The fauna comprises 120 species including one geotriid, one myxinid, and four rajids. Among the teleosts, DeWitt notes that there are 4 families (with 10 species) of deep sea fishes representing the orders Anguilliformes, Notacanthiformes, and Gadiformes. The remaining 14 families of fishes are coastal. Within this group and excluding the notothenioids, zoarcids and liparids are most numerous, with 11 and 5 species, respectively. However, these two families as well as the four deep sea families provide no biogeographic information as they are found in all deep, cold oceanic areas.

Among the remaining coastal groups, there are 3 families of Gadiformes (6 species), one family of Scorpaeniformes (one species), and one family of Pleuronectiformes (2 species). McGinnis (1982) indicates that there are also 14 species of myctophids found south of the Antarctic Convergence and that some of these species probably evolved in Antarctic waters in the Tertiary.

DeWitt's (1971) compilation clearly indicates that 4 families of the suborder Notothenioidei dominate the Recent fauna. With more than 80 species, this group includes at least 67% of the species and 90% of the individuals in the Antarctic region. The incidence of endemism is 86% at the species level. A few species from these families are found in New Zealand, southern South America, and the Falkland Islands (Andriashev 1965). A fifth notothenioid family, the Bovichthyidae (6 species), is distributed outside the Antarctic region in New Zealand, Australia, and southern South America (Nelson 1984).

The Antarctic fish fauna is considerably less diverse than the Recent Arctic fauna. Although the number of species in the two regions is not greatly disparate (120 for the Antarctic, 180 for the Arctic), there are 32 families in the Arctic and only 18 in the Antarctic (Llano 1978). Furthermore, 21 of these 32 Arctic families are not present in the Antarctic. The Arctic fauna is dominated by cod, herring, salmon, smelt, sculpin, and flatfish—groups that are either absent or poorly represented in the Antarctic. The Arctic fauna does not contain a unique endemic group equivalent to the notothenioids, and it consists, for the most part, of typical North Atlantic and North Pacific species. The Arctic region is geologically younger and less isolated than the Antarctic, and these aspects of biogeography are reflected in the composition of the Recent fauna.

While the Tertiary marine fauna of Australia is similar to the Recent fish fauna (Long 1982), this is certainly not true of the Antarctic. As indicated previously, there have been marked reductions in formerly diverse and abundant groups such as the Chondrichthyes. Moreover, the Recent fauna is dominated by a single perciform suborder, the Notothenioidei. There are a number of factors responsible for the unique and endemic Recent fauna:

1. *Geographic isolation.* The break-up of Gondwanaland and northward movement of other southern continents left Antarctica isolated in a south polar position for most of the Tertiary. It is

separated from other southern continents by great distance, deep expanses of cold ocean, and unfavourable surface currents. Colonization from the north is therefore difficult. The only shallow-water migration route into Antarctic waters is through the islands of the Scotia Ridge that connect southern South America with the Antarctic Peninsula.

2. *Ocean current pattern.* The circum-Antarctic current probably developed in the Late Oligocene (22 ma), and it contributed to the thermal isolation of Antarctica with subsequent formation of glaciers and ice sheets (Kennett 1978, 1980). Shortly thereafter the Antarctic Convergence (text-fig. 1) began to develop and expand northward. The Convergence, located between 50 and 60° S., represents the northern limit of the Antarctic Ocean and delimits a natural biogeographic province. The Convergence is characterized by a sharp change in water temperature as well as in a number of other oceanographic parameters. At the Convergence, northward moving Antarctic surface water (temperature in winter less than 1 °C) sinks below the warmer less dense water to the north (Hedgpeth 1969). This region of abrupt thermal change has had a marked effect on the shallow-water fauna by preventing southern migration and colonization of Antarctic waters by most pelagic fishes.

3. *Age of the ecosystem as reflected in the extent and duration of glaciation.* As indicated by the palaeontological study of planktonic foraminiferal assemblages (Kennett 1978, 1980) the endemic fish fauna has evolved under the influence of cold temperatures and sea ice since the Eocene–Oligocene boundary 38 ma. Most of the non-notothenioid Cenozoic fauna probably died out as the climate became colder. Glaciation was initiated about 25 ma in the Antarctic compared with 5 ma in the Arctic (Johnson *et al.* 1982). The ecosystem and endemic fish fauna are thus specialized, having evolved for a considerable period of time under cold conditions.

4. *Depth and narrowness of the continental shelf.* As a result of isostatic depression of the Antarctic continent by the ice sheet, the depth of the continental shelf is four times greater than that of other continents, and twice as great as that of the Arctic (Johnson *et al.* 1982). The shelf is also steep and narrow, and Antarctica lacks the extensive archipelagos characteristic of the Arctic. Thus with deep water close to the continental margin (text-fig. 1), the prime habitat, the continental shelf, for fish diversity is very small in Antarctica.

It has been hypothesized that the ancestral notothenioid stock has been associated with Antarctica at least since the waters began to cool down 38 ma (Regan 1914; Norman 1938; DeWitt 1971). Low water temperatures, limited and deep continental shelf habitat, extreme geographic isolation, and the absence of south-flowing surface currents have all probably contributed to the paucity of non-notothenioid fish groups in Antarctic waters. Recent notothenioids are a diverse group of fishes that have filled ecological roles normally occupied by other fishes in temperate oceans (Eastman and DeVries 1981, 1982).

Summary of Biogeographic Significance. The Antarctic ichthyofauna shows an Australian affinity during the Palaeocene and early Mesozoic that is not so visible in the Recent Antarctic ichthyofauna. The apparent disappearance of this Antarctic–Australia pattern through time is probably due to extinction (i.e. of Archaeomaenidae, Xenacanthidae, and Placodermi). The phylogenetically younger groups (e.g. Teleostei) in the Recent fauna may reflect younger geographic patterns (text-fig. 6) than were evident by the phylogenetically older group (e.g. Acanthodii). Changing patterns of biogeographic affinity through time are probably not unusual, and have been documented elsewhere (Grande 1985).

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