

Evolution and Diversification of Antarctic Notothenioid Fishes¹

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SYNOPSIS. Antarctica supported fossil ichthyofaunas during the Devonian, Jurassic, Cretaceous and Eocene/Oligocene. These faunas are not ancestral to each other, nor are they related to any component of the modern fauna. About one hundred species of notothenioids dominate a modern fauna of over 200 species of bottom fishes. This highly endemic perciform suborder is not represented in the fossil record of Antarctica. Notothenioids may have evolved *in situ* on the margins of the Antarctic continent while gradually adapting to cooling conditions during the Tertiary. Cladistic studies indicate that notothenioids are a monophyletic group, but a sister group has not been identified among perciform fishes. With relatively few non-notothenioid fishes in Antarctic waters, notothenioids fill ecological roles normally occupied by taxonomically diverse fishes in temperate waters. There are six notothenioid families: Bovichtidae, Nototheniidae, Harpagiferidae, Artedidraconidae, Bathydraconidae and Channichthyidae. Aspects of their biology are briefly considered with emphasis on the Nototheniidae, the most speciose family. Evolutionary diversification within this family allows recognition of species which are pelagic, cryopelagic, benthopelagic and benthic.

INTRODUCTION

The Antarctic fossil record indicates that fishes inhabited both inland and coastal waters during temperate periods over the past several hundred million years (Grande and Eastman, 1986; Eastman and Grande, 1989). Until about a century ago, most biologists thought that the subzero coastal waters of modern Antarctica were too cold to support a significant fish fauna. Today we recognize over 200 species of fishes comprising an interesting and important component of this unique marine ecosystem. The majority of these fishes are members of the Notothenioidei, a perciform suborder largely confined to the Antarctic Region. They are an indigenous element of the fauna that probably evolved in the shelf waters of the continent 40-60 million years ago (Regan, 1914; Norman, 1938; DeWitt, 1971).

Notothenioids have provided a fascinating glimpse of the wide scope of adaptation and evolution at one extreme of the marine environment. Contributors to this symposium dealt with some of the physiological and biochemical mechanisms enabling fishes to live under Antarctic conditions.

For example, Clarke addressed adaptation to low temperature and DeVries discussed freezing avoidance by means of antifreeze glycopeptides.

I will consider some broader aspects of the biology of Antarctic fishes with emphasis on the notothenioids. My hope is that this treatment will serve the general readership attracted to a symposium on Antarctic marine biology. The scope of this paper includes: 1) a brief history of the fossil ichthyofaunas of Antarctica, 2) recent developments in the taxonomy and systematics of notothenioids and 3) the diversification of notothenioids, especially members of the family Nototheniidae.

GONDWANA AND ANTARCTICA AS BIOTIC ENVIRONMENTS FOR FISHES

While the Antarctic continent with its mile thick icecap does not currently offer a hospitable environment for fishes, the fossil record indicates that the Antarctic component of Gondwana has supported a freshwater fish fauna since the Devonian, 410 million years ago. These Paleozoic fishes include thelodont agnathans, placoderms, acanthodians, xenacanthid elasmobranchs, osteolepid crossopterygians and palaeonisciform actinopterygians (Grande and Eastman, 1986; Eastman and Grande, 1989). Fossils of freshwater fishes are also present in Mesozoic (Lower Juras-

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sic) deposits 179–161 million years old. These fishes are members of the osteichthyan pholidophoriform family Archaeomaenidae (Schaeffer, 1972). Both Devonian and Jurassic fishes show biogeographic affinities with Australian forms, and indicate that, in terms of faunal composition, Antarctica was an integral part of Gondwana (Colbert, 1982).

The first marine fossil fishes from Antarctica were deposited approximately 96 million years ago in Late Cretaceous rocks on Seymour Island. This small island near the tip of the Antarctic Peninsula has been an exceptionally rich locality for Antarctic fossil fishes. Late Cretaceous fossils consist of teeth from lamnid and hexanchiform sharks, and a partial skull of the oldest teleost from Antarctica (Grande and Eastman, 1986; Grande and Chatterjee, 1987). This teleost, *Antarctiberyx seymouri*, is a member of the beryciform family Trachichthyidae, an extant group with a wide marine distribution (Grande and Chatterjee, 1987).

All known Antarctic Cenozoic fishes have also been collected at Seymour Island. These fossils are from the Late Eocene or Early Oligocene La Meseta Formation, a relatively shallow water marine deposit about 40 million years old (Woodburne and Zinsmeister, 1984). This material, deposited under temperate conditions, includes an array of chondrichthyans such as sharks, saw sharks, rays and ratfish. Teleosts are represented in La Meseta Formation by a siluriform pectoral spine, by a variety of fragmentary and unidentifiable vertebral centra and by unidentifiable jaw bones from large and small individuals (Grande and Eastman, 1986).

Grande and Chatterjee (1987) indicate that artifactual preservation is probably responsible for the greater diversity of chondrichthyans relative to osteichthyans in the Late Cretaceous/Early Tertiary Seymour Island fauna. Most of the fossil fishes from this locality are preserved as isolated teeth, vertebrae, spines and other fragments. Isolated teeth are diagnostic for both fossil and Recent chondrichthyans, but not for most teleosts. Therefore the teleost fauna appears less diverse as iso-

lated teeth are assigned to indeterminate species.

In conclusion, Gondwana and Antarctica supported fossil fish faunas, both freshwater and marine. The taxonomic composition and biogeographic significance of the faunas have undergone significant change through geological time. The reasonably diverse Late Eocene/Early Oligocene fauna from Seymour Island is not related to any component of the Recent fish fauna. Furthermore, the dominant element of the Recent fauna, the notothenioids, is not represented in the fossil record.

MODERN ANTARCTIC FISHES

The Recent Antarctic fish fauna is exclusively marine and is less diverse than might be expected given the considerable age and large size of the ecosystem. This fauna is also markedly different in composition from the fauna that preceded it in geological time. The Tertiary marine fauna of Australia, for example, is similar to the Recent fish fauna (Long, 1982). This is not true in the Antarctic as formerly diverse and abundant groups such as the Chondrichthyes are represented today by only a few species of rajids (Grande and Eastman, 1986; Eastman and Grande, 1989).

In summarizing information concerning the distribution and endemism of modern Antarctic fishes, DeWitt (1971) notes that the fauna comprises 120 species and is dominated by about 80 species of the perciform suborder Notothenioidei. Since 1971 many new taxa have been described. Over two hundred species of bottom fishes are now recognized (with about 100 notothenioids in the Antarctic Region), and 28 families are represented (Andriashev, 1987). There are an additional 75 mesopelagic species. Both DeWitt and Andriashev also note that endemism is high within the Notothenioidei; 97% for species and 85% for genera. In the forthcoming book *The Fishes of the Southern Ocean*, Gon and Heemstra (personal communication) will recognize about 265 species representing 49 families from waters south of the Antarctic Convergence.

Although the recent discovery of new non-notothenioid species has reduced the numerical dominance of notothenioids in the fauna (Andriashev, 1987), they still constitute about 53% of the species in the Antarctic Region. Thirty-four species of snail fishes (Liparididae) and 19 species of eelpouts (Zoarcidae), families of North Pacific origin, are prominent among non-notothenioids (Andriashev, 1987). Other typical boreal fishes such as cods, herrings, salmons, smelts, sculpins and flatfishes are either absent or poorly represented in the Antarctic Region.

Eastman and Grande (1989) evaluated factors that might have contributed to the paucity of non-notothenioids in the modern fauna. In agreement with Clarke (1983), they concluded that low water temperature was not paramount, and that factors in the realm of ecological constraints were probably at least as important in restricting diversity. They cited limited shallow water habitat on the continental shelf and seasonal oscillation in the food supply as plausible ecological factors.

Since there is no fossil record for the notothenioids, hypotheses pertaining to the origin of the group are speculative. For most of this century Antarctic ichthyologists have suspected that notothenioids evolved *in situ* on the margins of the Antarctic continent while gradually adapting to cooling conditions during the Tertiary (Regan, 1914; Norman, 1938; DeWitt, 1971). With the exception of a time frame for Southern Ocean paleotemperatures (Kennett, 1978; Clarke, 1983 for review) and historical biogeographic scenarios based on plate tectonics (Andersen, 1984; Miller, 1987), no new information has been brought to bear on the origin of notothenioids.

CLASSIFICATION OF NOTOTHENIOIDS

History

Although the first collector of notothenioid fishes is unknown (DeWitt, 1965), Antarctic exploring expeditions provided the initial specimens for scientific investigation during the mid to late nineteenth and early

twentieth centuries. Ichthyologists at European museums, especially Boulenger, Günther, Lönnberg, Regan and Richardson, described many of these species. The classifications of Regan (1914) and Norman (1937, 1938) have persisted largely intact until recently. New species are still being collected and described today, and the systematic relationships of notothenioids is an active area of research (Eakin, 1981a; Andersen, 1984; Balushkin, 1984, 1989a; Iwami, 1985; Voskoboinikova, 1986).

Taxonomy

Table 1 lists the 127 notothenioid species recognized by Balushkin (1988a). One hundred one of these species are found in the Antarctic Region. The list reflects Balushkin's (1984, 1989a) revision of the subfamily Nototheniinae, based on a detailed study of osteology. The list also includes taxonomic realignments contained in some of his other works that have not been translated into English (*e.g.*, the transfer of all but one species of *Trematomus* to *Pseudotrematomus* and the synonymization of *Pseudotrematomus centronotus* with *P. pennellii*). Although overly split and probably containing some dubious species, Balushkin's (1988a) classification is presented here as a means of introducing it to Western ichthyologists, and with the hope of initiating a discussion of its utility.

A more conservative approach to the classification of the family Nototheniidae will be presented by DeWitt, Heemstra and Gon (personal communication) in the forthcoming book *The Fishes of the Southern Ocean*.

Systematics

There is not a unique osteological feature that characterizes the suborder Notothenioidei. A morphological diagnosis of the Notothenioidei includes (Eakin, 1981a): (1) three flat, platelike pectoral radials, (2) pleural ribs poorly developed and floating or absent, (3) one nostril on each side of the head, (4) nonpungent fin spines, (5) no swimbladder, (6) two or three lateral lines, occasionally one, (7) jugular

TABLE 1. *Notothenioid species.**

Bovichtidae	<i>Nototheniops</i>
<i>Bovichtus</i>	<i>larseni</i> (Lönnberg, 1905)
<i>angustifrons</i> Regan, 1913*	<i>loesha</i> (Balushkin, 1976)
<i>argentinus</i> MacDonagh, 1931*	<i>nybelini</i> (Balushkin, 1976)
<i>chilensis</i> Regan, 1913*	<i>tchizh</i> (Balushkin, 1976)
<i>decepiens</i> Regan, 1913*	<i>Pagothenia</i>
<i>diacanthus</i> (Carmichael, 1818)*	<i>borchgrevinkii</i> (Boulenger, 1902)
<i>effulgens</i> (Waite, 1916)*	<i>phocae</i> (Richardson, 1844)
<i>elongatus</i> Hureau & Tomo, 1977	<i>Paranotothenia</i>
<i>psychrolutes</i> Günther, 1860*	<i>magellanica</i> (Forster in B. & S., 1801)*
<i>roseopictus</i> Hutton, 1903*	<i>Patagonotothen</i>
<i>variegatus</i> Richardson, 1846*	<i>brevicauda</i> (Lönnberg, 1905)*
<i>veneris</i> Sauvage, 1879*	<i>canina</i> (Smitt, 1897)*
<i>Cottoyperca</i>	<i>cornucola</i> (Richardson, 1844)*
<i>gobio</i> (Günther, 1861)	<i>elegans</i> (Günther, 1880)*
<i>Pseudaphritis</i>	<i>guntheri</i> (Norman, 1937)
<i>urvillii</i> (Valenciennes in C. & V., 1832)*	<i>jordani</i> (Thompson, 1916)*
Nototheniidae	<i>longipes</i> (Steindachner, 1876)*
<i>Aethotaxis</i>	<i>ramsayi</i> (Regan, 1913)*
<i>mitopteryx</i> DeWitt, 1962	<i>sima</i> (Richardson, 1844)*
<i>Cryothernia</i>	<i>squamiceps</i> (Peters, 1876)*
<i>peninsulae</i> Daniels, 1981	<i>tessellata</i> (Richardson, 1845)*
<i>Dissostichus</i>	<i>wiltoni</i> (Regan, 1913)*
<i>elegnoides</i> Smitt, 1898	<i>Pleuragramma</i>
<i>mawsoni</i> Norman, 1937	<i>antarcticum</i> Boulenger, 1902
<i>Elegnops</i>	<i>Pseudotrematomus</i>
<i>maclovinus</i> (Valenciennes in C. & V., 1830)*	<i>bernacchii</i> (Boulenger, 1902)
<i>Gobionotothen</i>	<i>eulepidotus</i> (Regan, 1914)
<i>acuta</i> (Günther, 1880)	<i>hansonii</i> (Boulenger, 1902)
<i>angustifrons</i> (Fischer, 1885)	<i>lepidorhinus</i> (Pappenheim, 1912)
<i>gibberifrons</i> (Lönnberg, 1905)	<i>loennbergii</i> (Regan, 1913)
<i>marionensis</i> (Günther, 1880)	<i>nicolai</i> (Boulenger, 1902)
<i>Gvozdarus</i>	<i>pennellii</i> (Regan, 1914)
<i>svetovidovi</i> Balushkin, 1989	<i>scotti</i> (Boulenger, 1907)
<i>Indonotothenia</i>	<i>tokarevi</i> (Andriashev, 1978)
<i>cyanobrancha</i> (Richardson, 1844)	<i>Trematomus</i>
<i>Lepidonotothen</i>	<i>newnesi</i> Boulenger, 1902
<i>kempi</i> (Norman, 1937)	Harpagiferidae
<i>squamifrons</i> (Günther, 1880)	<i>Harpagifer</i>
<i>Lindbergichthys</i>	<i>antarcticus</i> Nybelin, 1947
<i>mizops</i> (Günther, 1880)	<i>bispinus</i> (Forster in B. & S., 1801)
<i>nudifrons</i> (Lönnberg, 1905)	<i>georgianus</i> Nybelin, 1947
<i>Notothenia</i>	<i>marionensis</i> Nybelin, 1947
<i>angustata</i> Hutton, 1875*	<i>kerquelenensis</i> Nybelin, 1947
<i>coriiceps</i> Richardson, 1844	<i>palliolatus</i> Richardson, 1844
<i>microlepidota</i> Hutton, 1875*	<i>spinus</i> Hureau, Louis, Tomo & Ozouf, 1979
<i>neglecta</i> Nybelin, 1951	Artedidraconidae
<i>rossii</i> Richardson, 1844	<i>Artedidraco</i>
	<i>loennbergii</i> Roule, 1913
	<i>mirus</i> Lönnberg, 1905
	<i>orianae</i> Regan, 1914
	<i>shackletoni</i> Waite, 1911
	<i>skottsbergii</i> Lönnberg, 1905

TABLE 1. *Continued.*

<i>Dolloidraco</i> <i>longedorsalis</i> Roule, 1913	<i>Psilodraco</i> <i>breviceps</i> Norman, 1937
<i>Histiodraco</i> <i>velifer</i> (Regan, 1914)	<i>Racovitzia</i> <i>glacialis</i> Dollo, 1900
<i>Pogonophryne</i> <i>albipinna</i> Eakin, 1981 <i>barsukovi</i> Andriashev, 1967 <i>curtilemma</i> Balushkin, 1988 <i>dewitti</i> Eakin, 1988 <i>dolichobranchiata</i> Andriashev, 1967 <i>immaculata</i> Eakin, 1981 <i>lanceobarbata</i> Eakin, 1987 <i>macropogon</i> Eakin, 1981 <i>marmorata</i> Norman, 1938 <i>mentella</i> Andriashev, 1967 <i>orcadensis</i> Tomo, 1981 <i>permtini</i> Andriashev, 1967 <i>phylopogon</i> Andriashev, 1967 <i>platypogon</i> Eakin, 1988 <i>scotti</i> Regan, 1914 <i>velifera</i> Eakin, 1981 <i>ventrimaculata</i> Eakin, 1987	<i>Vomeridens</i> <i>infuscipinnis</i> (DeWitt, 1964)
	Channichthyidae
	<i>Chaenocephalus</i> <i>aceratus</i> (Lönnerberg, 1906)
	<i>Chaenodraco</i> <i>wilsoni</i> Regan, 1914
	<i>Champscephalus</i> <i>esox</i> (Günther, 1861) <i>gunnari</i> Lönnerberg, 1905
	<i>Channichthys</i> <i>rhinocerotus</i> Richardson, 1844 <i>rugosus</i> Regan, 1913 <i>velifer</i> Meisner, 1974
	<i>Chionobathyscus</i> <i>dewitti</i> Andriashev & Neyelov, 1978
	<i>Chionodraco</i> <i>hamatus</i> (Lönnerberg, 1905) <i>myersi</i> DeWitt & Tyler, 1960 <i>rastrispinosus</i> DeWitt & Hureau, 1979
	<i>Cryodraco</i> <i>antarcticus</i> Dollo, 1900 <i>atkinsoni</i> Regan, 1914
	<i>Dacodraco</i> <i>hunteri</i> Waite, 1916
	<i>Neopagetopsis</i> <i>ionah</i> Nybelin, 1947
	<i>Pagetopsis</i> <i>macropterus</i> (Boulenger, 1907) <i>maculatus</i> Barsukov & Permitin, 1958
	<i>Pseudochaenichthys</i> <i>georgianus</i> Norman, 1937
<i>Bathydraconidae</i>	
<i>Akarotaxis</i> <i>nudiceps</i> (Waite, 1916)	
<i>Bathydraco</i> <i>antarcticus</i> Günther, 1878 <i>joannae</i> DeWitt, 1985 <i>macrolepis</i> Boulenger, 1907 <i>marri</i> Norman, 1938 <i>scotae</i> Dollo, 1906	
<i>Cygnodraco</i> <i>mawsoni</i> Waite, 1916	
<i>Gerlachea</i> <i>australis</i> Dollo, 1900	
<i>Gymnodraco</i> <i>acuticeps</i> Boulenger, 1902	
<i>Parachaenichthys</i> <i>charcoti</i> (Vaillant, 1906) <i>georgianus</i> (Fischer, 1885)	
<i>Prionodraco</i> <i>evansii</i> Regan, 1914	

* From Balushkin, 1988a.
(Asterisk indicates non-Antarctic species)

pelvic fins and (8) usually fewer than 15 principal caudal rays (10–19). Individually none of these characters is unique to notothenioids and therefore as characters they are ambiguous. The group is diag-

nosed by a proposed unique combination of characters rather than by one or more synapomorphies. If suspected notothenioid fossils are eventually discovered, it will be difficult to recognize as a notothenioid

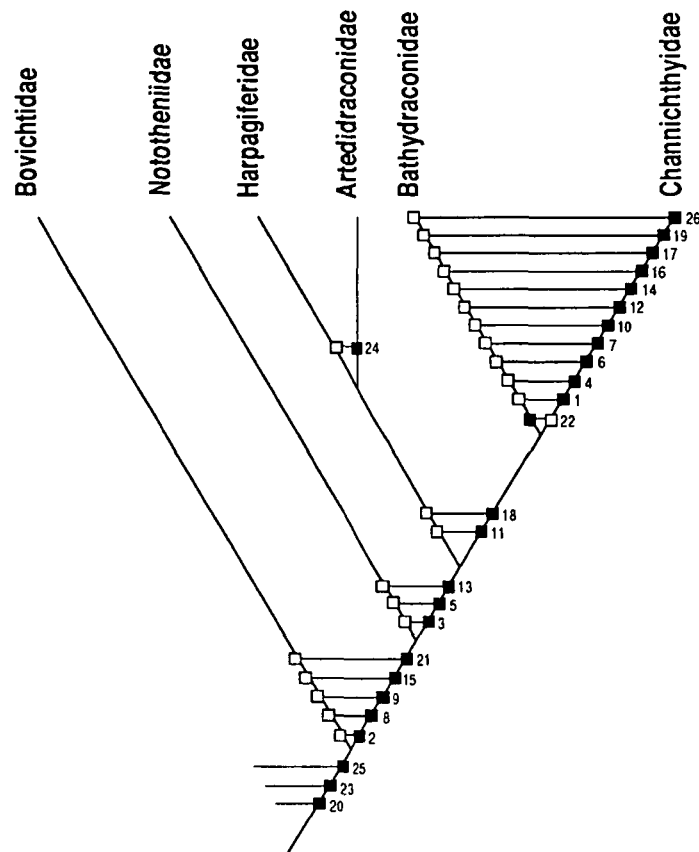


FIG. 1. Cladogram for the suborder Notothenioidei. Character information supporting cladogram is given in Table 2. White squares, primitive character states; black squares, derived character states. Modified and redrawn from Iwami (1985).

any specimen not possessing the entire suite of characters. Also some are features of the soft anatomy that may not be preserved.

Monophyly had been assumed but not proven until Iwami (1985) used cladistic methodology to evaluate phylogenetic relationships among notothenioids (Table 2, Fig. 1). Iwami's conclusions are similar to Eakin's (1981a) hypothesized relationships among notothenioid families. The notothenioid sister group has not been definitely identified among the Perciformes, although blennioids are generally thought to be a likely candidate (Gosline, 1968; Eakin, 1981a). However, there is no unambiguous character evidence that clearly establishes blennioids or any other perciform subgroup as the sister group. Eakin (1981a) has a good analysis of the problems

encountered in separating convergences from true relationships and of the difficulty in recognizing a notothenioid sister group.

I have modified Iwami's (1985) cladogram to reflect the practice of treating the Harpagiferidae (*sensu lato*) as two families (Fischer and Hureau, 1985) instead of two subfamilies (Andriashev, 1967; Eakin, 1981a). The presence of a mental barbel in artedidraconids is a derived state clearly separating them from harpagiferids.

Because our knowledge of intra- and interspecific variation in notothenioid osteology is incomplete, the polarity of some character states in Table 2 should be considered provisional. I have not attempted to resolve these anatomical details here, although character 18 in the caudal skeleton serves as a case in point.

TABLE 2. Characters used by Iwami (1985) in establishing cladogram for notothenioids (Fig. 1).*

Characters	Derived state																									
	Primitive state													Derived state												
1. Frontal	Convex dorsally													Flat, elongate												
2. Vomerine teeth	Present													Absent												
3. Prootics	Attached													Separated												
4. Sphenotic-pterosphenoid	Bordered													Separated												
5. Basisphenoid	Present													Absent												
6. Premaxillary process	Present													Absent												
7. Mesopterygoid	Developed													Filamentous												
8. Ectopterygoid teeth	Present													Absent												
9. Palatine teeth	Present													Absent												
10. Dorsal hypohyal	Ossified													Cartilaginous												
11. Epi-ceratothal junction	L-shaped													I-shaped												
12. 1st basibranchial	Ossified													Cartilaginous												
13. 2nd basibranchial	Ossified													Cartilaginous												
14. 3rd hypobranchial	Triangular													Rod-like												
15. Epibranchial teeth	Present													Absent												
16. Pharyngobranchials	3													2												
17. 5th hypural	Separated													Fused												
18. Uroneural	Separated													Fused												
19. Forked depression on cleithrum	Present													Absent												
20. Pectoral radials	4													3												
21. Coracoid-uppermost radial	Separated													Bordered												
22. 1st dorsal fin	Present													Absent												
23. Nostril	2 pairs													1 pair												
24. Mental barbel	Absent													Present												
25. Swim bladder	Present													Absent												
26. Hemoglobin	Present													Absent												

Families	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23	24	25	26	
Bovichtidae	-	-	-	-	-	-	-	±	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nototheniidae	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Harpagiferidae	-	+	+	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Artedidraconidae	-	+	+	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bathydraconidae	-	+	+	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Channichthyidae	+	+	+	±	+	+	+	+	±	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

- Primitive state, + derived state.
* Lower portion of table indicates character states for the six notothenioid families.

Iwami (1985) indicates that in harpagiferids (*s. l.*), the uroneural is a distinct bone, unfused to other components of the caudal skeleton. I have retained this polarity for this character in the cladogram. However, Eakin's (1981a) work indicates that there is variability in the extent of fusion in the caudal skeleton. Harpagiferids (*sensu stricto*) generally have the uroneural fused to the urostyle. Artedidraconids have an autogenous uroneural. Normally the fusion exhibited by harpagiferids (*s. s.*) would be considered a derived character state. Eakin suggests that this and other fusions in the caudal skeleton of harpagiferids have adaptive value for a sluggish, benthic mode of life. Therefore they do not accurately reflect the phylogeny of the group. However, Eakin provides a great deal of other osteological evidence supporting the phylogenetically derived condition of the artedidraconids. For example, artedidraconids are more advanced than harpagiferids in having five instead of six branchiostegals, two rather than three basibranchials and reduced or absent pleural ribs.

DIVERSIFICATION OF NOTOTHENIOIDS

The Antarctic continental shelf is 400–500 m deep at the edge and also contains innershelf depressions 1,000 m deep (Andriashev, 1965). When compared to the depth distribution of temperate fishes, species diversity among notothenioids is greatest at 300–600 m rather than 100–200 m (Andriashev, 1965, 1987; DeWitt, 1971). This pattern of distribution, known as glacial submergence, may be attributable to destruction of bottom habitat by continental glaciers and ice shelves (Andriashev, 1987). This habitat and faunal destruction may have caused the local extinction of most of the Tertiary fish fauna, leaving an ecological void which was filled by a notothenioid fauna tolerant of deep water conditions.

Most notothenioids are bottom fishes confined to waters less than 1,000 m deep, although the depth range of individual species may be considerable (DeWitt, 1971). They lack swim bladders, are usually denser than seawater and commonly feed and reproduce on the substrate. There is no

reason to suspect that the ancestral notothenioid stock lived in deep water because closely related perciform groups like blennies are coastal fishes.

The Southern Ocean is underutilized by fishes, in an ecological sense, and could theoretically support more species. The waters south of the Antarctic Convergence are productive during the summer, but contain relatively few non-notothenioid fishes. Thus reduced competition and the isolation of Antarctica have provided the opportunity for speciation within this group. Notothenioids fill ecological roles normally occupied by taxonomically diverse fishes in temperate waters.

In the following sections I will introduce aspects of the biology of the six notothenioid families, with emphasis on the Nototheniidae.

Bovichtidae—temperate icefishes

Bovichtids (Figs. 2A, 3A) have long been regarded as the most primitive notothenioid family (Regan, 1914). This view has been sustained by modern systematic (Eakin, 1981a; Iwami, 1985; Balushkin, 1989a) and karyological (Prirodina, 1986) work. Although the physiology of bovichtids has not been studied in detail, they are known to possess glomerular kidneys and to lack antifreeze glycopeptides (Eastman and DeVries, 1986b).

Bovichtids have a non-Antarctic distribution including southeastern Australia, New Zealand and South America, although *Bovichtus elongatus* inhabits waters near the Antarctic Peninsula. Most species have heavy bodies with bony and spiny heads. As adults they are bottom dwellers in shallow coastal or intertidal habitats. The young of *Bovichtus variegatus*, however, pass through a pelagic, distributive phase when they may be captured near the surface in the outer shelf waters off New Zealand (Robertson and Mito, 1979). This life history pattern may be common to other bovichtids, as it is for notothenioids in general. Pelagic larvae enhance the possibility of dispersal.

The family includes three genera and 13 species. Eleven species of *Bovichtus* are currently recognized; however, additional

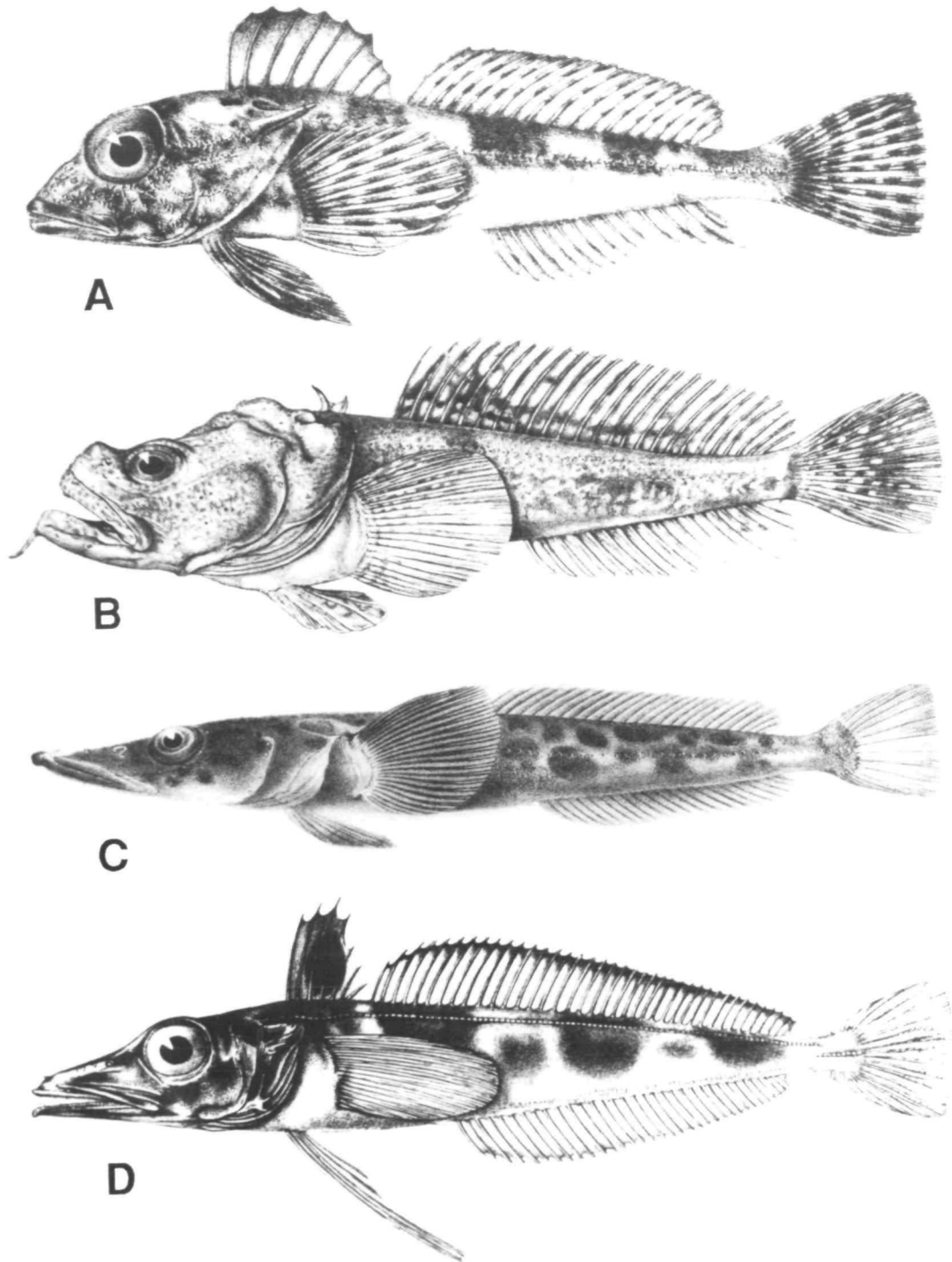


FIG. 2. Representative notothenioid fishes. A) Bovichtidae—*Bovichtus angustifrons* (from Regan, 1913). B) Artedidraconidae—*Pogonophryne scotti* (from Regan, 1914). C) Bathydraconidae—*Gymnodraco acuticeps* (from Boulenger, 1902). D) Channichthyidae—*Chaenodraco wilsoni* (from Regan, 1914).

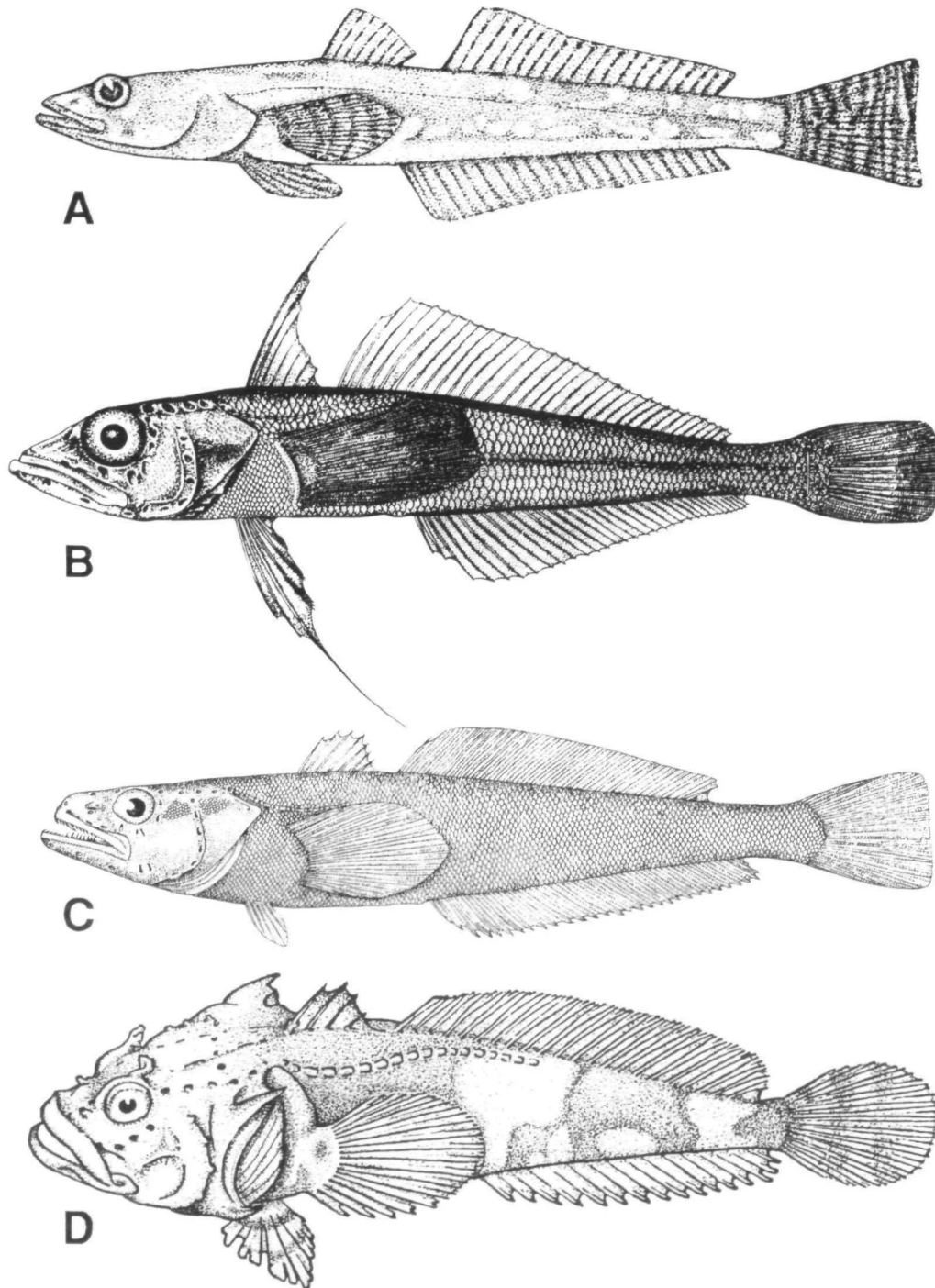


FIG. 3. Representative notothenioid fishes. A) Bovichtidae—*Pseudaphritis urvillii* (from McDowall, 1980). B) Nototheniidae—*Aethotaxis mitopteryx* (from Andriashev, 1986). C) Nototheniidae—*Guozdarus svetovidovi* (from Balushkin, 1989b). D) Harpagiferidae—*Harpagifer bispinis* (modified from Norman, 1938).

study will probably show that some are not valid species. Hardy (1988) reported that *Aurion effulgens* Waite (1916) is a junior synonym of *Bovichtus psychrolutes*. Balushkin (1988a) refers to *Aurion* as *Bovichtus effulgens*. Unfortunately the holotype and only specimen of *Aurion* has been lost. Dr. P. R. Last (personal communication) and colleagues at the CSIRO Marine Laboratories in Hobart, Tasmania are describing a new species of bovichtid from coastal waters of Tasmania and Victoria. *Pseudaphritis urvillii* (Fig. 3A), a catadromous species with a similar distribution, is the only notothenioid inhabiting freshwater. *Pseudaphritis* may be either a Gondwanian form that moved north in the freshwaters of Australia, or a derivative of a marine dispersing bovichtid ancestor (McDowall, 1981). In either case, *Pseudaphritis* is certainly a relict species.

Nototheniidae—Antarctic notothenis

With 17 genera and 50 species, the nototheniids are the most diverse notothenioid family with respect to size, body form and distribution. They are found throughout the Antarctic and sub-Antarctic regions, as well as in coastal waters of New Zealand and South America. Nototheniids are well represented in the sub-zero waters of McMurdo Sound (Fig. 4). DeVries' (1988 for review) extensive studies of nototheniids at this location have provided much of our knowledge about the role of antifreeze glycopeptides in freezing avoidance.

Most nototheniids are bottom fishes. However, there is evidence of a trend toward diversification, particularly of pelagic species, among this group (Nybelin, 1947; Andriashev, 1970; DeWitt, 1970; Voskoboinikova, 1982; Eastman, 1985a, 1988a; Hubold and Ekau, 1987). Several species are neutrally buoyant, permanent members of the midwater community, and work over the last 10 years has revealed the morphological basis for the diversification in buoyancy (ecological) types (Eastman and DeVries, 1981, 1982, 1985, 1986a, 1989; DeVries and Eastman, 1978, 1981; Clarke *et al.*, 1984). These studies indicate that evolutionary alterations in buoyancy are reflected as specializations in

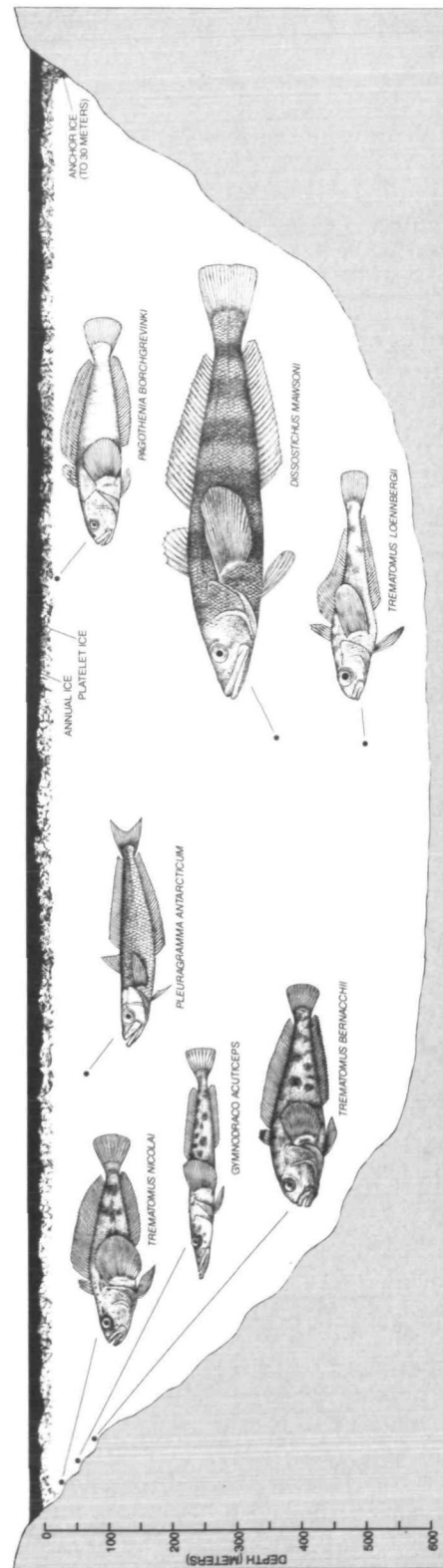


FIG. 4. These seven species from McMurdo Sound demonstrate some of the morphological and ecological divergence mentioned in the text. Pelagic, cryopelagic, benthopelagic and benthic species are illustrated. All are members of the family Nototheniidae except *Gymnodraco acuticeps* which is a bathydraconid. Following the revision of Balushkin (1984, 1989a), the three species of *Trematomus* are now members of the genus *Pseudotrematomus*. Dots indicate typical habitat; however, most species have considerably wider depth ranges. From Eastman and DeVries (1986a), copyright © 1986 by Scientific American, Inc. All rights reserved.

a variety of systems and organs including skeleton, integument, lipid storage, muscles and liver. In addition to displaying the results of evolution, buoyancy studies provide important information about life history and potential interactions with other members of the ecosystem.

The following ecological types are distinguishable within the family Nototheniidae:

1) *Large, pelagic midwater predators.* Averaging 127 cm in total length and 28 kg in weight, *Dissostichus mawsoni* (Fig. 4) is six times longer and 250 times heavier than other nototheniids in McMurdo Sound. With reduced skeletal ossification and nearly 10% of its body weight as lipid deposits, *Dissostichus* are neutrally buoyant, permanent members of the midwater community (Eastman and DeVries, 1981). In McMurdo Sound they live at 300–500 m. Among the nototheniids examined to date, *D. mawsoni* is unique in having eyes with rod-dominated retinae, an adaptation for vision under dim conditions (Eastman, 1988b).

Dissostichus eleginoides, a sister species found largely north of the Antarctic Convergence, reaches a size equivalent to *D. mawsoni*. South of the Convergence it lives near South Georgia and the northern part of the Antarctic Peninsula. Since it does not inhabit subzero waters, *D. eleginoides* lacks antifreezes and has a few glomeruli in its kidneys (Eastman and DeVries, 1986b). It exhibits buoyancy adaptations similar to those of *D. mawsoni* (Oyarzún *et al.*, 1988).

2) *Shoaling midwater zooplanktivores.* *Pleuragramma antarcticum* (Fig. 4) is made neutrally buoyant by a variety of weight saving measures including unconstricted vertebrae, persistent notochord and large lipid sacs (DeVries and Eastman, 1978). *Pleuragramma* have a depth range of 0–900 m (Gerasimchuk, 1986) and are found in both open water and beneath ice. They avoid intraspecific competition by vertical size segregation in the water column (Hubold and Ekau, 1987). A vital component of the food web in the Southern Ocean, *Pleuragramma* are especially numerous and ecologically important nototheniids (Eastman 1985b).

Pleuragramma is a member of the Pleuragramminae, the most phylogenetically derived subfamily of nototheniids (Balushkin, 1989a). Like *Pleuragramma*, the other species in this subfamily also possess buoyancy adaptations for life in the midwaters. *Aethotaxis mitopteryx* (Fig. 3B), originally described from McMurdo Sound (DeWitt, 1962), is almost completely encircled by a subcutaneous layer of adipose tissue. It has a circum-Antarctic distribution (Kotlyar, 1978; Gerasimchuk and Piotrovskiy, 1980), although few specimens have been collected. Although the diet of *Aethotaxis* is unknown, the numerous long, closely set gill rakers indicate that it eats smaller food items than *Pleuragramma* (Eastman, 1985a).

Balushkin (1989b) recently described *Gvozdarus svetovidovi* (Fig. 3C) from a 53 cm TL specimen collected at 550 m in the Ross Sea. A second larger specimen (65 cm TL) has been taken in the Cooperation Sea (A. V. Balushkin, personal communication). The stomach of the holotype contained remains of *Pleuragramma* (A. V. Balushkin, personal communication). If the size, habitat and diet of these two specimens are typical for the species, *Gvozdarus* is a medium to large midwater predator.

3) *Cryopelagic species.* *Pagothenia borchgrevinki* (Fig. 4) is specialized for life and zooplankton feeding near the undersurface of the sea ice (Eastman and DeVries, 1985). Although they may not always feed in the immediate sub-ice habitat, *Pagothenia* are definitely planktivorous (Foster *et al.*, 1987).

4) *Benthopelagic species.* Although they live close to the bottom, their streamlined appearance and absence of contact adaptations indicate that they do not actually reside on the substrate. In McMurdo Sound *Pseudotrematomus loennbergii* (Fig. 4) inhabits depths of at least 450 m.

5) *Benthic species.* Like their ancestors, most nototheniids are benthic, spending their lives on or near the substrate. There is a greater variety of food and micro-habitats available to bottom dwelling fishes than to midwater fishes, consequently bottom dwelling communities are more diverse (Roberts, 1982). In McMurdo Sound, most of the species of *Pseudotrematomus* (Fig. 4) fall into this category.

6) *Species that are difficult to classify ecologically.* *Cryothernia peninsulae* exhibits morphological characteristics of both pelagic and benthic species. It may be an ecological generalist living and feeding in the midwaters or on the bottom. This species belongs to the subfamily Trematominae, and is therefore related to *Trematomus*, *Pseudotrematomus* and *Pagothenia* (Balushkin, 1989a).

7) *Species with an ontogenetic change in life cycle.* Fingerlings of *Notothenia rossii* are pelagic, nearshore juveniles are demersal, and offshore adults are both demersal and pelagic. These changes in habitat are accompanied by changes in color, caudal fin shape and body shape (Burchett, 1983). Other nototheniids probably experience similar ontogenetic habitat shifts.

Harpagiferidae—spiny plunderfishes

With the elevation of the Artedidraconinae to familial status, the Harpagiferidae now contains only the genus *Harpagifer* (Fig. 3D) with seven species. However, some may not be valid species, and additional work may prove that *Harpagifer* includes only a few polymorphic species. Harpagiferids are distinguished from artedidraconids by the presence of subopercular spines and by the absence of a mental barbel. They are found south of the Antarctic Convergence, around sub-Antarctic islands and off southern South America (Andriashev, 1965).

Superficially resembling sculpins, harpagiferids are small bottom fishes living in relatively shallow water or in tidepools. *Harpagifer bispinis*, the only species ranging outside the Antarctic Region, is particularly accessible and well studied. This relatively long-lived, slow-growing species (Daniels, 1983) exhibits nesting and possibly altruistic behavior in guarding its eggs (Daniels, 1978, 1979). It is a sit-and-wait feeder that consumes primarily amphipods (Wyanski and Targett, 1981; Duarte and Moreno, 1981).

Artedidraconidae—barbeled plunderfishes

Artedidraconids (Fig. 2B) are easily distinguished from harpagiferids by the presence of a mental barbel, which is usually specifically distinct, and by the blade-like

and hooked opercular spines. With four genera and 24 species, artedidraconids are considerably more diverse than harpagiferids, and many new species have recently been described (Eakin, 1977, 1981b, c, 1987, 1988a, b; Eakin and Kock, 1984; Balushkin, 1988b). Artedidraconids have a wider depth distribution than harpagiferids, and one species (*Pogonophryne immaculata*) lives at depths of 2,500 m (Eakin, 1981c). They are largely confined to the Antarctic continental shelf and slope, although one species is found at South Georgia (Andriashev, 1965).

Bathydraconidae—dragonfishes

Bathydraconids (Figs. 2C, 4) are elongated, slender fishes that are easily separated from all other notothenioids by the absence of the spiny (first) dorsal fin. *Gymnodraco* (Jakubowski, 1975) and *Psilodraco* (H. H. DeWitt, personal communication) have internal nares. There are ten genera and 15 species of bathydraconids. With the exception of species at South Georgia, the South Orkneys and the Kerguelen-Heard area, they are confined to the cold waters near the Antarctic continent (Andriashev, 1965). Most inhabit depths of 500–700 m, but some species of *Bathydracono* have been collected at 2,000–3,000 m, deeper than any other notothenioid (DeWitt, 1985). In McMurdo Sound *Gymnodraco acuticeps* (Fig. 4) lives in relatively shallow water under cover of heavy sea ice, and may even live beneath the Ross Ice Shelf at 82°S (Bruchhausen *et al.*, 1979).

Channichthyidae—icefishes

Channichthyids (Fig. 2D) are the most phylogenetically derived family of notothenioids (Iwami, 1985), and one of the most unusual groups of teleosts in the world. They are commonly called “white-blooded” fishes as all 18 species (11 genera) lack hemoglobin, although a few nonpigmented erythrocytes may be present. In addition, the muscles of these fishes do not contain myoglobin. This highly specialized condition, involving evolutionary loss of hemoglobin and myoglobin, is compatible with life only under the unique conditions of the Antarctic environment where waters are always close to saturation with oxygen.

As the only vertebrates without respiratory pigments, channichthyids have received considerable attention from physiologists. The reviews of Everson (1984) and Macdonald *et al.* (1987) contain details of the physiological ecology of these fishes.

Channichthyids are large fusiform fishes with big heads, elongated snouts and long pelvic fins. With the exception of one species (*Champscephalus esox*) in the Patagonian-Falkland area, they have an Antarctic and sub-Antarctic distribution (Andriashev, 1965). Most live at depths of 200–700 m (Andriashev, 1965); however, *Chionobathyscus dewitti* inhabits water 1,000–2,000 m deep (Andriashev, 1987). While most channichthyids are bottom fishes, some are pelagic and a few alternate between these two modes of life. This probably facilitates feeding in the water column on krill when these crustaceans are abundant.

FINAL REMARKS

Like the continent itself, the Antarctic ichthyofaunas have undergone remarkable changes through geological time. The various fossil faunas are not ancestral to each other and are different than the modern fauna. Furthermore, the modern fauna is not represented in the fossil record of Antarctica. Unlike the situation in the shelf waters of other continents, the modern Antarctic fish fauna is dominated by a single endemic group—the notothenioids. Continuing work in paleoichthyology, paleoceanography and tectonic geology will enhance our understanding of the evolutionary history of both fossil and modern faunas.

Although they are the key component of the Antarctic fish fauna, much remains to be learned about all aspects of the biology of notothenioids. The evolutionary diversification of notothenioids probably indicates that the Southern Ocean is, in an ecological sense, underutilized by fishes and theoretically capable of supporting more species. Recent descriptions of new species indicate that our knowledge of notothenioid diversity, especially in the midwaters, is incomplete. Consequently we cannot formulate accurate hypotheses concerning the role of notothenioids in the marine eco-

system. It is essential that collecting and systematic work continue, and that studies of notothenioids persist at levels of biological organization from the molecular to the organismal. The acquisition and analysis of molecular data should provide additional information useful in elucidating the phylogenetic relationships of notothenioids.

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