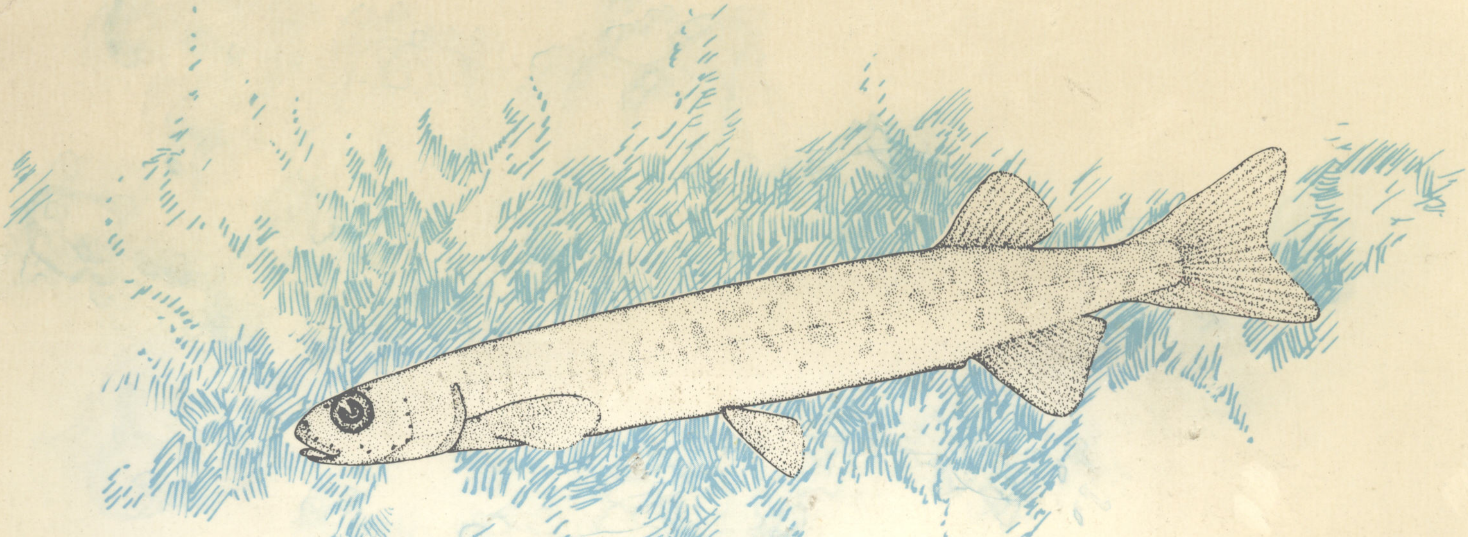
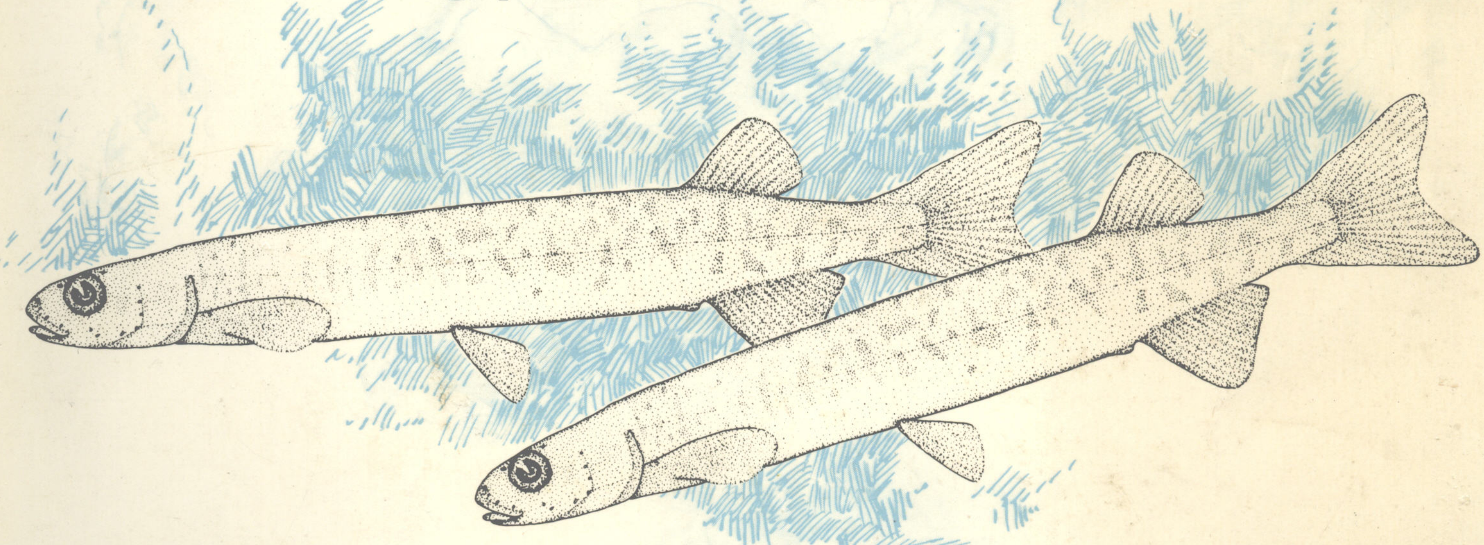


An Atlas of Distribution of the Freshwater Fish Families of the World



TIM M. BERRA

Foreword by R. M. McDowall

An Atlas of Distribution of the Freshwater Fish Families of the World

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FOREWORD BY
R. M. McDowall

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Lincoln and London

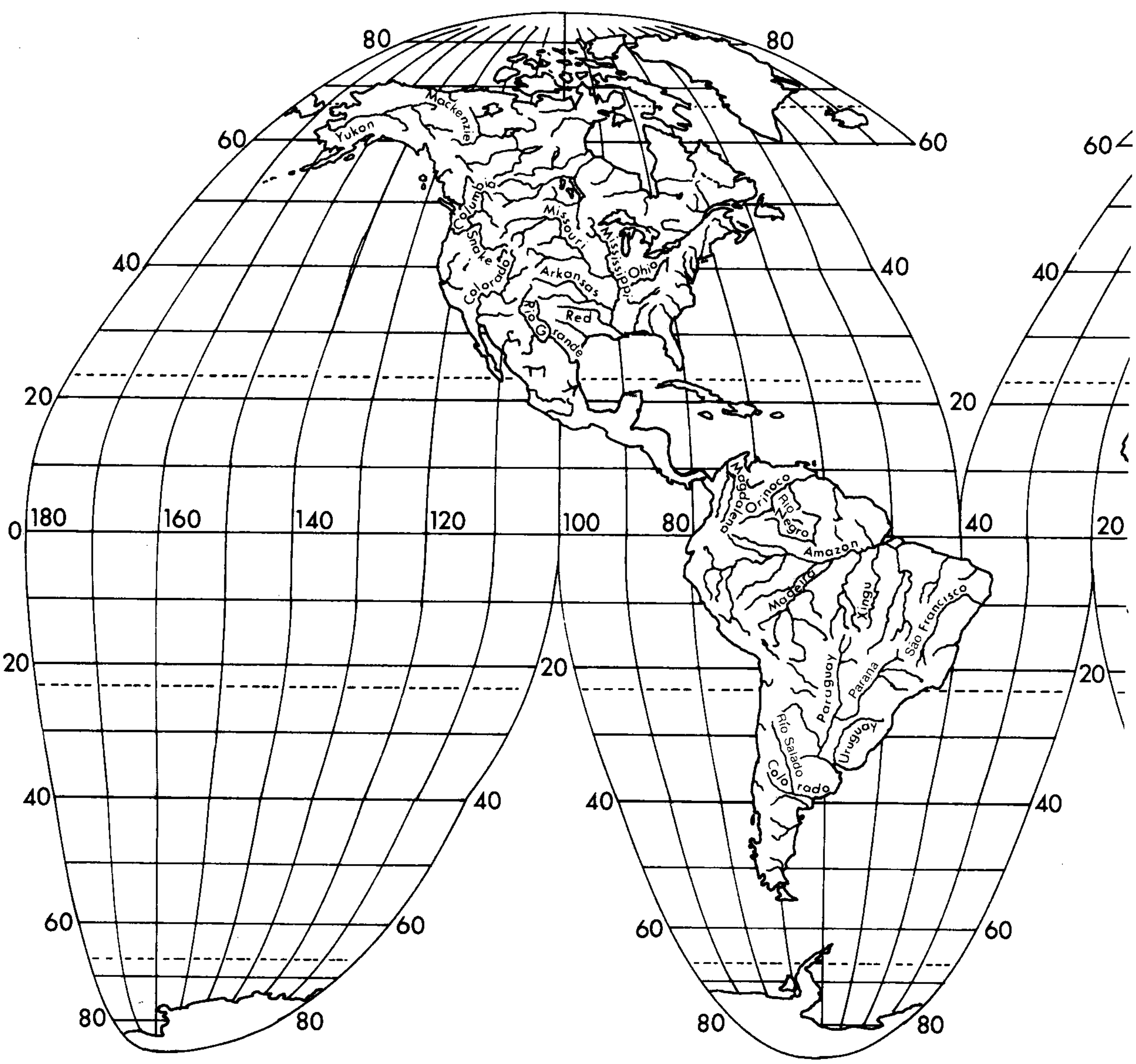
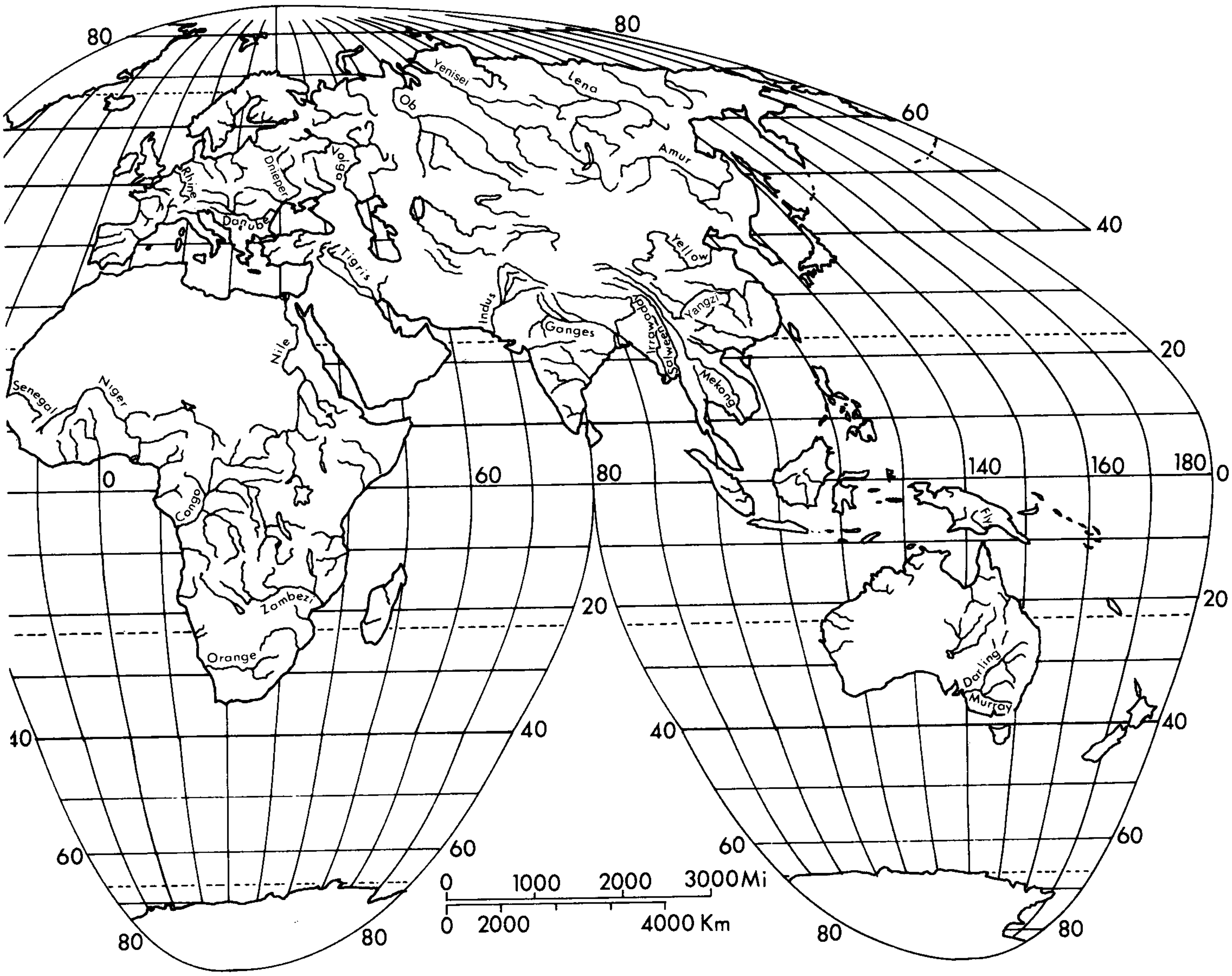


Figure 1. Drainage map of the world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An Atlas of Distribution of the Freshwater Fish Families of the World

Dedicated to
Gerald E. Gunning
and
Royal D. Suttkus,
Tulane University,
who stimulated and encouraged
my interest in fishes

ERRATA

As this book was going to press, I learned that the joint committee on Names of Fishes of the American Fisheries Society and the American Society of Ichthyologists and Herpetologists had decided on the spelling Petromyzontidae for the family referred to in this book as Petromyzonidae. In addition, Reeve M. Bailey, past chairman of that committee, informed me that the correct spelling of the family name that appears here as Pimelodontidae is Pimelodidae.

On p. 34, second column, lines 12 and 15, the correct date for Bell et al. is 1981.

Foreword

Freshwater fishes are among the most interesting and, for many decades, controversial animal groups in their distribution patterns and the ways these patterns have developed over space and through time. There are "freshwater fishes" almost everywhere. Antarctica lacks them, as do some of the smallest islands, but even deserts may have freshwater fishes, though they be sparse in number, intermittent in occurrence, and low in diversity. Species are found from cold, high alpine torrents, lakes, and tarns to warm coastal lagoons and estuaries. Great river systems in the larger continental masses, like the Nile, the Mississippi, and the Amazon, have large and highly diverse freshwater faunas, with hundreds of species of a wide array of types occupying a range of habitats. Smaller rivers, particularly those of the smaller and more geographically isolated land masses, have much less diverse faunas. Of the larger continents (apart from Antarctica), Australia has the least diverse and spectacular freshwater fish fauna—a product presumably of its geographical isolation, past climatic instability, and present low precipitation—the last of these largely limiting fish to coastal river systems and the moister southeast.

Freshwater fishes have always been a fruitful field for biogeographers. Having assumed that freshwater fish are strictly confined to freshwaters, many early biogeographers affirmed the need for continuity of freshwater (and thus of land) to explain the very obviously disjunct distribution patterns exhibited by some families—like characids in Africa and South America, cyprinids in Africa, Eurasia, and North America (but *not* South America), esocoids in northern, circumpolar cool-temperate waters or galaxiids in southern circumpolar cool-temperate waters.

Early biogeographers beginning with Darwin himself focused on the biogeographic problems that freshwater fishes pose. Explanations offered to cover highly disjunct distributions often involved the "erection" of land bridges in diverse places and across unlikely oceans. Some workers recognized that some of the "freshwater" species were actually diadromous, and turned to transoceanic dispersal as a mechanism for explaining distributions—for example, a brief paper by G. A. Boulenger in 1902 ("The explanation of a remarkable case of geographical distribution in fishes," *Nature* 67 : 84). Some workers who followed noticed, but disagreed with Boulenger that, for instance, galaxiid fishes could disperse through the sea; others seem not to have noticed or to have ignored his hypothesis. And while Boulenger's approach may have been helpful for diadromous species tolerant of sea water, it was of no help for the more strictly freshwater species—families that G. S. Myers was later to categorize as "primary freshwater fishes."

Debates about how freshwater fish distributions have developed continue to the present day. Widespread acceptance, until the 1960s, of a stable conformation of the earth's continents encouraged biogeographers to look for land connections and / or faunal migration routes whereby existing patterns could have developed. These, although often ingenious, were never widely satisfying. With the more general acceptance, initially among geologists and subsequently among biologists, of continental drift and plate tectonics, a whole new approach has developed, such that for some, continental drift has become the explanation for everything—giving seemingly simple answers to what are, in essence, often very complex questions.

The advent of plate tectonics has generated the viewpoint that freshwater fish distributions may be explained by "vicariance"—essentially the movement of biotas resident on shifting land masses. Much controversy relates to these various divergent yet not inconsistent viewpoints, and these simple answers, in my view, ignore some of the very real complexities of the historical development of fish distribution patterns during the last 100 million or so years.

FOREWORD

Essentially, biogeography comprises two activities: (1) identifying the patterns and (2) explaining the processes that produced these patterns.

The first of these is relatively simple, and disagreement occurs largely at the level of alpha taxonomy: are disjunct populations conspecific or not? Such disagreements have little or no real impact on the development of biogeographic hypotheses. It is at the stage of explaining the processes that significant controversy has occurred and continues to occur.

Most freshwater fish groups have left us very meagre fossil records, giving very few hints of their ancestral distributions, diversity, or morphology. Thus we have to deal primarily with existing distributions to explain a long history of past occurrences.

While these freshwater-restricted groups seem certain to have required "land" routes to spread and enlarge distributions, it is not necessarily so for the diadromous groups, some of which may be found hundreds of kilometers out to sea at any stage from newly hatched larvae to large adults. It is the role of these marine stages of supposedly freshwater fish species that is one of the centres of controversy in fish biogeography, a controversy that seems to have no logical solution.

Controversy, or no controversy, the resource materials for such discussions are the fish distributions themselves. With more than 8,000 species of freshwater fish, it is a mammoth task to attain a broad understanding of their distribution patterns. This book is a useful beginning in assisting workers interested in understanding and explaining freshwater fish distributions. By describing family distributions it highlights the distribution patterns that exist. It enables the identification of congruent distribution patterns. It suggests questions that can be asked about these congruent patterns. And it provides some of the resources by means of which investigators can find entry into the voluminous literature pertaining to these fish, thereby obtaining the more detailed distributional data that assist in answering the questions that the more simple "family distributions" provoke.

It is becoming increasingly evident and more widely accepted that sound historical biogeography has to be anchored in detailed phylogenetic analyses of fish groups.

No book and no one author can provide the data necessary or the answers to the many questions arising. In most instances, the work just hasn't been done—not even started. For *very few* groups are there detailed phylogenetic analyses.

This atlas, then, is the resource material for beginning biogeographical studies.

There is little doubt that ichthyologists and biogeographers will find this book an extremely useful basic resource for research purposes.

R. M. McDowall
Christchurch, New Zealand

Preface

The purpose of this book is to provide a visual synopsis of the approximate native distributions of the freshwater fish families of the world. The maps are not intended to pinpoint the exact range of each family, as, in many cases, this is not known and ranges are not static, since they are made up of living populations that may be in the process of expansion or contraction. This book is intended as a supplemental text for college level courses in ichthyology, zoogeography, and vertebrate natural history. Fishermen and aquarists will also find it informative.

The idea for the book occurred to me in 1965, when I was a graduate student in zoogeography class at Tulane University. I found that making rough maps of the distribution of each family of vertebrates was an effective way to study. I have since been gathering published maps and descriptions of the distribution of each fish family found in fresh water. I accumulated maps and descriptions in folders. When the time came to write the book in earnest, the information in each folder was spread out on my desk, and a composite distribution based on the references for each family was penciled on a blank map. The result is a sort of "visual Darlington."

The fishes of some areas of the world are better known than others; consequently, more reliability can be placed on the North American distributions than, say, those from South America or Africa, whose faunas and rivers are still relatively poorly known. In areas where data are incomplete a certain generalization is unavoidable.

I have tried to include all the primary and secondary division freshwater fish families and all the zoogeographically important peripheral ones as well as a sampling of marine families having some members that make incursions into coastal rivers. The range of these marine families is shown by shading from the continents into the sea, which implies that the particular family is found along the coast and may enter estuaries or ascend rivers, given their presence, the right temperature, salinity, and other factors. It does not necessarily mean that they are found in all coastal rivers. Likewise, the possible presence of a few families in scattered oases is indicated by shading across the Sahara. Nonnative distributions, such as trout in the Southern Hemisphere, are not included.

One of the biggest problems in studying for my zoogeography class was remembering which family was which. I have attempted to include in this book little tidbits of interesting natural history which, I hope, will make the families easier to remember. The pronunciation guide should help students and professionals alike. I have also included information on size, diet, and habitat for many families. The characteristics given for each group are designed to present an impression of a generalized representative and are not meant to be taxonomically diagnostic. In many cases the reader is referred to revisions of groups or major papers on family members. These references are intended as an entrance into the literature for students who desire further information. The classification and line drawings of most family members basically follow Greenwood et al. (1966) with a few changes. Fossil representatives are dated after Andrews et al. (1967) unless otherwise stated, and sizes mentioned are total lengths. An asterisk (*) after a reference means that a map is given in that publication.

The end matter includes useful handouts, such as geologic time scale, list of rivers and lakes, drainage map, guides to freshwater fishes of the United States and Canada, reading lists, *National Geographic* and *Scientific American* articles on fishes, and a glossary.

How the patterns of distribution indicated on the maps came about is a complicated problem, and I shall not presume to more than touch on it. Many explanations are needed to take into account such diverse information as continental drift, dispersal, vagility, age and area, centers of origin, ancestral versus derived characters, reliable phylogenies, and many other things. It is hoped that the visual impressions created by the maps in this book will be helpful to biogeographers grappling with these and related problems.

Acknowledgments

I owe a great debt of gratitude to the eminent ichthyogeographer, George S. Myers, for his interest and help with this project. He examined each map, wrote voluminous criticisms, then reexamined the corrected maps. He generously provided his pronunciations of family names, pointed out references, and suggested additional families to be included. He saved me from numerous, embarrassing errors. However, I do not want his help or that of anyone listed below to be construed as an imprimatur. The errors that remain, and undoubtedly there are some, are my own. I am confident my colleagues will point them out to me, along with new information, so that the distribution maps can be improved in the future.

Carter R. Gilbert, of the Florida State Museum, devoted a great deal of time to a careful review of the manuscript and provided factual material as well as many suggestions for improvement. P. H. Greenwood, curator of fishes at the British Museum (Natural History), reviewed the maps and made many helpful comments, especially on the African distributions. Donn E. Rosen, of the American Museum of Natural History, reviewed the manuscript and made numerous useful suggestions. Bruce B. Collette, of the National Marine Fisheries Service, provided detailed help on the Hemiramphidae and Belonidae. Tyson Roberts supplied some published and unpublished information that was useful in mapping the distribution of several families. Jack Garrick commented on the shark section, and Robert McDowall examined the Australian and New Zealand families. The following ichthyologists briefly commented upon various maps during the course of the 1977 and 1978 meetings of the American Society of Ichthyologists and Herpetologists: Clyde Barbour, John Briggs, Barry Chernoff, John Fitch, Garrett Glodek, Janet Gomon, Clark Hubbs, Robert Johnson, Robert Lavenberg, Bruce Menzel, Robert R. Miller, Lynne Parenti, K. V. Rama Rao, and Jamie Thomerson. Robert Behnke and George Van Dyke supplied some information via correspondence. Ross Feltes helped with the Polynemidae.

David Dennis drew the base map from the Goode Base Map Series, the drainage map, and Figures 2 and 3. Lisa Gassin plotted the distributions from my rough maps and drew the fish outlines. Ray-Jean Au made numerous Xerox copies of rough drafts. Linda Linn was a cheerful, speedy, and accurate typist. Revisions were retyped by Babette Mullet and Yolanda Allen. My wife, Rita, typed file cards for my growing reprint collection. Lynn Murphy Dominick ceaselessly rounded up odd interlibrary loans. I am very grateful for all of this help.

The College of Biological Sciences of Ohio State University provided a grant-in-aid which covered many of the expenses of this project. The Research Committee of the Mansfield Campus of Ohio State University provided additional funding. I would like to thank the chairman of the Department of Zoology of Ohio State University, Tony J. Peterle, for his overall support of my research efforts. I am also indebted to the former dean of the Mansfield Campus, James B. Heck, the current dean, David Kramer, and the associate dean, Richard Wink, for providing the kind of climate in which research can flourish.

Introduction

What is a Fish?

This question is not as simple as it sounds at first reading. What makes it a difficult question is that there are many exceptions for each character used to define "fish." For example: Character: fishes swim in water. Exceptions: the mudskipper, *Periophthalmus*, skips about on mangrove flats completely out of water; grunions, *Leuresthes*, spawn on beaches above the low tide mark; the walking catfish, *Clarias*, ambles overland from pond to pond. Character: fishes respire by means of gills. Exceptions: lungfish, *Protopterus*, can breathe atmospheric air via lungs and can even remain encysted in a dry mud cocoon; anabantids have a labyrinth organ in their head that provides a large, highly vascularized surface for oxygen uptake. Character: fishes have scales. Exceptions: catfishes lack scales; some sticklebacks have an armour plating of modified scales; some fishes are only partially scaled, and some (eels) have such tiny, embedded scales that they are easily overlooked. Character: fishes have fins. Exceptions: *Gymnarchus* lacks pelvic, anal, and caudal fins, while *Gymnotus* lacks dorsal and pelvic fins. The swamp eels (Synbranchidae) lack both pectoral and pelvic fins, and the anal and dorsal fins exist only as ridges. Character: fishes are coldblooded. Exceptions: many fast-swimming species such as tunas and their relatives develop muscle temperatures in excess of ambient.

If we allow room for these and other exceptions, we can define a fish as a poikilothermic, aquatic chordate with appendages (when present) developed as fins, whose chief respiratory organs are gills and whose body is usually covered with scales. This broad definition makes no mention of skeletal material and therefore includes the cartilaginous lampreys and elasmobranchs as well as the bony fishes.

Primary, Secondary and Peripheral Division Fish Families

Myers (1938, 1949, 1951) developed a widely used classification of fishes in fresh water based on their tolerance to salt water. This system is, of course, ecological rather than taxonomic. As modified by Darlington (1957) the three divisions are primary, secondary, and peripheral. Primary division freshwater fish families are those whose members have little salt tolerance and are confined to fresh waters. Salt water is a major barrier for them, and their distribution has not depended upon passage through the sea. The salt tolerance of individual species within a family does vary, however.

Secondary division freshwater fish families are those whose members are usually confined to fresh water, but they have some salt tolerance, and their distribution may reflect dispersal through coastal waters or across short distances of salt water. Some peripheral family members may be confined to fresh water, and others may spend a considerable portion of their life cycle in fresh water, but they both are derived from marine ancestors who used the oceans as dispersal routes. Other peripheral division families are basically marine groups, some of whom enter fresh water. The ecological designation followed in this book is taken from Darlington (1957), who wrote, "We may, if we wish, doubt the 'reality' of Myers' divisions, but how can we doubt their usefulness in zoogeography?" On the other hand, Rosen (1974) has challenged the usefulness of such a salt tolerance classification scheme, and he views fishes as being either continental or oceanic. In the family accounts here given, 1st, 2d and Per refer to primary, secondary, and peripheral divisions respectively.

How Many Kinds of Fishes are There?

Cohen (1970) attempted an analysis of this problem by surveying ichthyologists who were experts in the various taxonomic groups. His results indicated about 50 species of Agnatha (lampreys and hagfishes), 535 species of Chondrichthyes (sharks, skates, rays, chimaerids), and about 20,000 species of Osteichthyes (bony fishes), excluding fossil forms. A similar estimate, 18,300, was made by Bailey (1971). Of the 20,000 bony fishes, approximately 33 percent (6,650) are primary division freshwater species, and 93 percent of these are ostariophysan fishes. Secondary division freshwater fishes accounted for about 8 percent (1,625) of the total Osteichthyes, and most of these are cichlids and cyprinodontoids. Thus freshwater fishes make up about 41 percent (8,275) of all bony fishes, and as Cohen (1970) pointed out, this surprisingly high percentage is a reflection of the degree of isolation and diversity of niches possible in the freshwater environment. The large numbers of species in fresh water becomes even more amazing if the volume of fresh water on earth is compared to the volume of the oceans. The oceans account for 97 percent of all the water on earth, whereas the fresh water in lakes and rivers is an almost negligible percentage, 0.0093 percent (Horn 1972). (The rest of the water is tied up as ice, groundwater, atmospheric water, and so forth.) Therefore 41 percent of all fish species live in less than 0.01 percent of the world's water (Horn 1972). Further data on productivity of marine and freshwater environments and calculations—which show that there are about 113,000 km^3 of water for each marine species while only 15 km^3 for each freshwater species—an approximate 7,500-fold difference—can be found in Horn (1972).

The rate at which new species have been named is interesting. The tenth edition of Linnaeus's *Systema naturae* (1758) listed 478 species in 50 teleost genera. By 1870 Gunther put the total number of known teleosts at about 8,700. An analysis of new names proposed for teleosts from 1869 to 1970 (Berra and Berra 1977) yielded an estimate of 15,370 new names for the 100-year period. If this figure is added to Gunther's calculation, we arrive at a total of 24,070 teleost names, which, when synonymies are taken into account, agrees well with Cohen's data derived independently.

Berra and Berra (1977) found that the families receiving the most new names were the cyprinids, gobiids, characins, and cichlids. They also reported that of the newly named freshwater species 35 percent were from South America, 30 percent from Africa, and 23 percent from Asia. This agrees well with the diversity and endemism data shown in tables 1 and 2 and with the figures given by Gilbert (1976).

Wallace's Line

The foundations of biogeography can be traced to the writings of Georges Louis Leclerc, comte de Buffon and Augustin Pyramus de Candolle (Nelson 1978). However, it was Alfred Russel Wallace (1823–1913), a British naturalist and codiscoverer with Charles Darwin of evolution via natural selection, who elaborated the concept of zoogeographic regions with the publication of his classic work, *The Geographical Distribution of Animals*, in 1876. He recognized 6 zoogeographical realms, which he called Nearctic (North America except tropical Mexico), Neotropical (South and Central America with tropical Mexico), Palearctic (nontropical Eurasia and north tip of Africa), Ethiopian (Africa and southern Arabia), Oriental (tropical Asia and nearby islands), and Australian (Australia, New Guinea, New Zealand) (fig. 2). Darlington (1957) gave a detailed discussion of continental patterns of the distribution of vertebrates.

In 1860 Wallace proposed a hypothetical boundary between the Oriental and Australian faunas. This line passes between Bali and Lombok, through the Makasar Strait between Borneo and the Celebes, and south of the Philippines (fig. 3). A few years later T. H. Huxley named the boundary Wallace's line. He also modified it on the basis of bird studies to place the Philippines east of the line within the Australian realm. Mayr (1944) treated this controversy in depth. As the fauna of this region (Wallacea) became better known, many examples of animal groups crossing Wallace's line were noted, and most zoogeographers today do not take Wallace's line literally as an exact boundary between the Oriental and Australian faunas. However, the line does suggest a major faunal break separating the rich Oriental continental fauna from the depauperate Australian island fauna.

Of the vertebrate groups, the freshwater fishes are most inhibited by a saltwater barrier and, therefore, most closely follow Wallace's line. There are 23 families of primary division freshwater fishes on Borneo. Only 1 family, Osteoglossidae, has managed to cross Wallace's line naturally. There are 3 species in 3 genera (*Anabas*, *Ophicephalus*, *Clarias*) that man likely transported across the Makasar Strait to the Celebes. A few salt-tolerant oryziatids have reached the Celebes, Lombok, and Timor, and the endemic secondary division Adrianichthyidae occur in the Celebes. Only 2 cyprinid genera, *Puntius* and *Rasbora*, occur on both Bali and Lombok, with *Rasbora* reaching Sumbawa. These 2 cyprinid genera and a few others also occur in the Philippines along with an endemic silurid and clariid catfish (Darlington 1957). With these few exceptions, the Asian and Australian freshwater fish faunas do not mix but, rather, end abruptly, which is unlike the situation in the New World, where the faunas of North and South America mingle in a Central American transitional zone.

A second line, Weber's line, was proposed by Pelseneer in 1904. Weber's line represents the "line of faunal balance" that separates the islands with a majority of Oriental groups from those with an Australian majority. Mayr (1944) favored this line and provided more details. Weber's line (fig. 3) is closer to Australia and reflects the fact that the Oriental fauna has made more of an intrusion to the east than has the Australian fauna to the west.

Which line, if any, one chooses to defend really depends upon the taxonomic group in question and how many exceptions one is willing to tolerate. Furthermore, these lines are irrelevant to plant geographers, whose subject is much more directly influenced by climate.

Distribution Patterns

Freshwater fishes are one of the most important groups zoogeographically because they are more or less confined to drainage systems which can be thought of as dendritic islands of water surrounded by land, which is in turn bordered by a saltwater barrier. The freshwater fishes provide a relatively conservative system for examining patterns of distribution that may reflect continental changes. The family is the taxon that best reflects the evolution and dispersal of a group, and, in fact, zoogeographic patterns are one of the evidences of evolution cited in introductory zoology texts.

The distribution of 128 primary, secondary, and peripheral division families is given in table 2. The Neotropical realm has the largest number (32) of primary division families (table 1), whereas the Oriental and Ethiopian regions are close behind with 28 and 27 primary division families each. The Nearctic and Palearctic regions have 14 primary division families each. The only primary division freshwater fishes in Australia are the lungfish, *Neoceratodus forsteri*, and 2 species of osteoglossids, *Scleropages*.

The Neotropical realm also has the greatest number of secondary division freshwater families (6), while the Nearctic and Oriental regions have 5 apiece, most of which are cyprinodontoids (table 1). The Ethiopian region has only 2 secondary families, the Cyprinodontidae and the Cichlidae; however, the cichlids are represented by an enormous number of endemic species with a great diversity of forms and habits. In Australia and New Guinea, the Melanotaeniidae occupy many cyprinodont and cyprinid niches. Oryziatids and cyprinodontids make up the secondary freshwater fish fauna of the Palearctic (table 2).

The Neotropical and Oriental realms have the largest number of families, with 46 and 43 respectively (table 1). The Ethiopian, Palearctic, and Nearctic have totals of 32, 29, and 27 families. The Australian freshwater fauna is depauperate, as expected of an island, and is dominated by peripheral groups. If the other marine families with freshwater representatives included in this book were taken into account, the proportion of peripheral representatives in Australian fresh waters would be even more lopsided.

By far the greatest number of endemic primary division families (29) is found in the Neotropical zone (table 1). In fact, all but 3 primary families are endemic. This is a reflection of the extensive radiation of the ostariophysan characoids and siluriforms. The Ethiopian and Oriental regions are a distant second and third place in the endemism race, with 15 and 14 families respectively. The Nearctic region has only 7 endemic primary division families. The only endemic primary division family in Australia is the Ceratodontidae.

The Oriental and Neotropical regions each have 2 endemic secondary division families, the Adrianichthyidae and Horaichthyidae, and the Anablepidae and Jenynsiidae, respectively. The Goodeidae of the Nearctic and the Melanotaenidae of Australia are the only endemic secondary division families of those regions.

The highest percentage of endemism of freshwater fish families is in the Neotropical area, with 70 percent of the families found nowhere else (table 1). About half (44 percent and 47 percent, respectively) of the families found in the freshwaters of the Oriental and Ethiopian realms are endemic to those areas. The fish faunas, at the family level, are about 39 percent endemic in the fresh waters of the Australian realm and 30 percent endemic in the Nearctic realm. The endemic families of the Palearctic region comprise only 10 percent of the freshwater fish families (table 1). Several families share a Nearctic and Palearctic distribution which may be considered a Holarctic pattern. It should be noted that some of the peripheral families excluded from tables 1 and 2 have endemic

Table 1

NUMBER OF FISH FAMILIES AND PERCENT ENDEMISM IN EACH BIOGEOGRAPHICAL REALM, BASED UPON 128 FAMILIES (WIDELY DISTRIBUTED PERIPHERAL FAMILIES EXCLUDED)

	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
No. Primary Families	14	32	14	27	28	2
No. Secondary Families	5	6	2	2	5	1
No. Peripheral Families	8	8	13	3	10	15
Total No. Families	27	46	29	32	43	18*
No. Endemic Primary	7	29	0	15	14	1
No. Endemic Secondary	1	2	0	0	2	1
No. Endemic Peripheral	0	1	3	0	3	4
Total Endemic Families	8	32	3	15	19	7*
Percent Endemic Primary	26	63	0	47	33	6
Percent Endemic Secondary	4	4	0	0	5	6
Percent Endemic Peripheral	0	2	10	0	7	22
Percent Endemic Total	30	70	10	47	44	39*

*The Lepidogalaxiidae is included in the total.

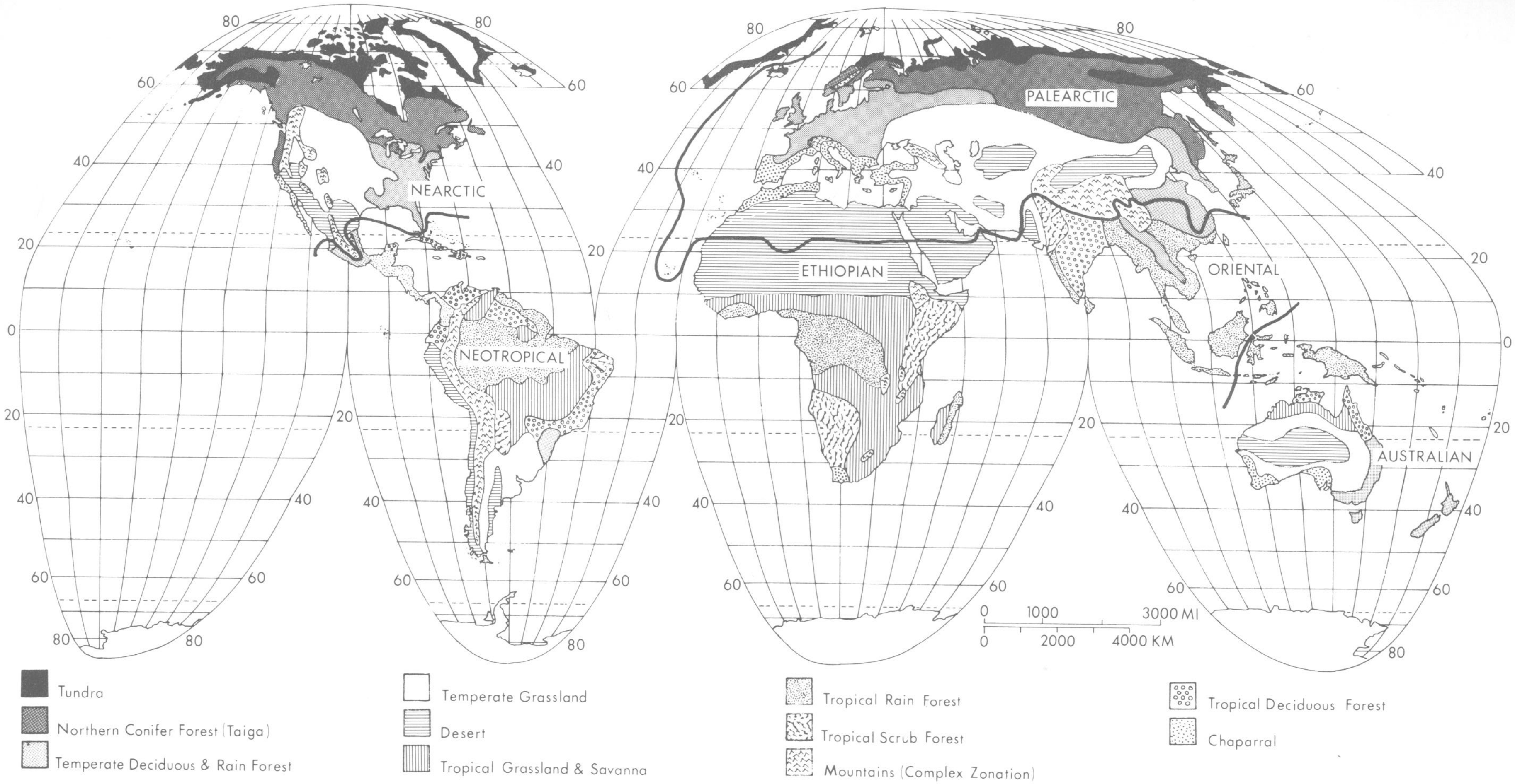

Figure 2. Wallace's six zoogeographic realms and the major biomes of the world

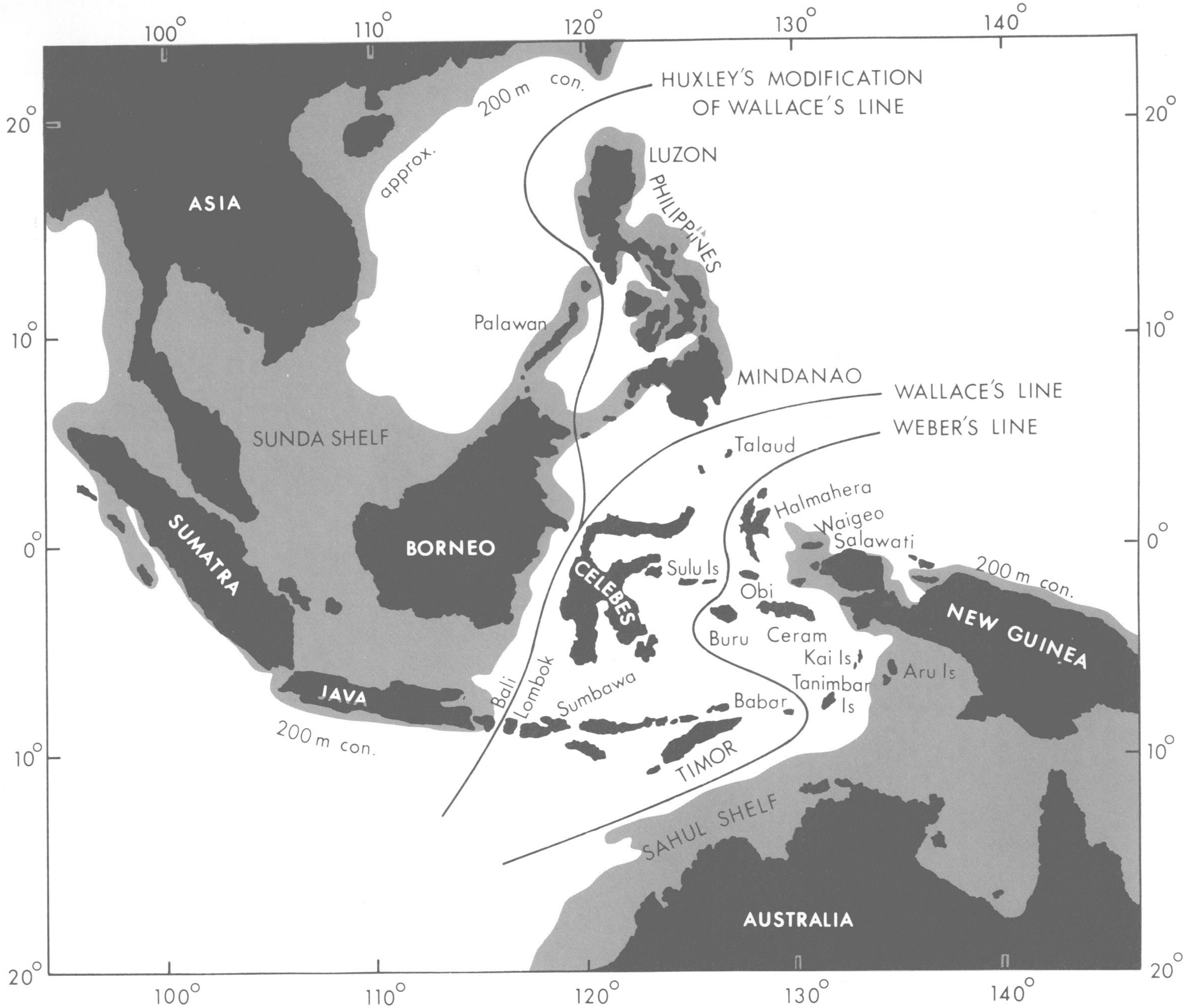

Figure 3. Lines of zoogeographic importance in the Malay Archipelago. *Redrawn from Mayr (1944)*

freshwater species in the various biogeographical realms. This is not reflected in an analysis based on families.

Continental Drift

One of the most exciting areas of zoogeography today is the idea that the distribution of certain fish groups can be explained by the past movement of the continents. In 1915 Alfred Wegener published the first edition of *Die Entstehung der Kontinente und Ozeane* (*The Origin of Continents and Oceans*), in which he called attention to the similarity of the east coast of South America and the west coast of Africa and suggested that they fit together like the pieces of a giant jigsaw puzzle. This concept was slow to be accepted, but in light of the modern geophysical evidences of plate tectonics and paleomagnetics, this hypothesis has become elevated to one of the basic theories in nature.

Continental drift theory states that all the continents were once part of a large land mass, Pangaea. This supercontinent became divided about 180 million years ago (Jurassic) into a northern portion, Laurasia (North America and Eurasia), and a southern portion, Gondwanaland (South America, Africa, India, Antarctica, Australia and New Zealand). About 90 million years ago (Cretaceous), Gondwanaland broke apart into the separate southern continents (see references cited by Novacek and Marshall [1976] for the geologic timing of these events). The propulsive forces for these movements, which are still going on today, are convection currents in the earth's mantle generated by the heat of radioactivity within the interior. These currents move the 6 major plates which make up the earth's surface and which float on the mantle. (Further reading on this subject should include: Mayr [1952], Wegener [1966], Runcorn [1962], Dietz and Holden [1970], Colbert [1973], Berggren and Hollister [1974], Cox [1974], Cracraft [1974, 1975], Howden [1974], Glen [1975], Brundin [1975], Tarling [1975], the Scientific American book *Continents Adrift* [1973], and Smith and Briden [1977].)

Dispersal

How the present patterns of fish distribution evolved is beyond the scope of this atlas and requires a knowledge of the factors mentioned in the preface. (A few attempts at explaining various aspects of ichthyogeography include Darlington [1957], Miller [1958], Myers [1966, 1967], Rosen and Bailey [1963], Chardon [1967], Nelson [1969], Croizat, Nelson, and Rosen [1974], Briggs [1974, 1979], Rosen [1974, 1975, 1978], Novacek and Marshall [1976], Gilbert [1976], Platnick and Nelson [1978], McDowall [1978], and Vari [1978]. A lively discussion of the relationship between vicariance and dispersal as related to the distribution patterns of freshwater fishes can be found in 1974–79 issues of *Systematic Zoology* and *Copeia*. The bibliographies of the papers cited above extend the discussion.)

Naturally, major vicariant events such as the movement of land masses will affect worldwide fish distribution. In addition to these rather dramatic movements, freshwater fishes may also disperse over a continent in a variety of ways. During times of flooding, drainage systems may overlap on a flood plain, allowing fishes access to other drainages. Stream capture, whether by headwater piracy or lowland meanders, may allow fishes to move from one river system to another and thereby spread across large continental areas. Freshwater fishes with some salt tolerance may swim from one river mouth through brackish or marine waters into another river mouth and then move upstream. During periods of glacial melt, drainage systems may be connected by overflow streams. Conversely, streams may be isolated in times of glacial advance because of lowered sea levels. Some fishes such as eels can actually wiggle across grassy areas from one stream to another. Other fishes may survive dispersal in the egg or other stages on mud attached to aquatic birds' feet, or by waterspouts. The uplifting of mountain ranges may separate river systems, which can result in a similar fauna on both sides of a divide, which may then diverge. These are just a few of the considerations necessary for the understanding of the patterns of freshwater fish distribution.

Table 2

Primary, Secondary, and Selected Peripheral Freshwater Fish Families and the Geographical Areas Where They Occur

Family	Division	Nearctic	Neotropical	Palearctic	Ethiopian	Oriental	Australian
Petromyzonidae	per	X		X			
Geotriidae	per		X				X
Mordaciidae	per		X				X
Potamotrygonidae	per		X				
Ceratodontidae	1st						X
Lepidosirenidae	1st		X				
Protopteridae	1st				X		
Polypteridae	1st				X		
Acipenseridae	per	X		X		X	
Polyodontidae	1st	X		X			
Lepisosteidae	2nd	X	X				
Amiidae	1st	X					
Denticipitidae	1st				X		
Osteoglossidae	1st		X		X	X	X