BIOGEOGRAPHY OF AUSTRALIAN FRESHWATER FISHES

by

Peter John Unmack

A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

ARIZONA STATE UNIVERSITY

August 1999

BIOGEOGRAPHY OF AUSTRALIAN FRESHWATER FISHES

by

Peter John Unmack

has been approved

July 1999

APPROVED:

____, Chair

____

____

____

Supervisory Committee

ACCEPTED:

____
Department Chair

____
Dean, Graduate College

ABSTRACT

Biogeographic patterns of obligate freshwater fishes of Australia were investigated using museum records. Similarity indices, parsimony analysis, and drainage-based plots of species' ranges were used to identify patterns. Relationships among regions were deduced largely by concordance between methodologies, which were then summarized into a series of faunal provinces. The most striking pattern was the incidence of endemism across the continent. Provinces in southern, central, and western Australia have high numbers of endemic fishes, presumably as a result of isolation by aridity and drainage divides. With the exception of one region, northern and eastern Australia provinces have few endemics. In the north, this may be explained by high drainage connectivity during times of lowered sea levels. This explanation does not account for low endemism in the east since drainages appear to have been isolated even during lowered sea levels and faunal patterns suggest an absence of distinct barriers of other kinds. By default, climate again seems the most likely cause of species' distributional limits. Whatever the case, most patterns seem to have been established in the distant past, perhaps as early as Miocene; influences of Plio-Pleistocene events on broader patterns of freshwater fish distributions seem to have been minimal.

ACKNOWLEDGMENTS

I would dearly like to thank my parents, Jean and Stan, for allowing me to pursue my own goals and all their tremendous help and support throughout the years, and my sister Julie for her generous financial assistance. Without them, I would not have been able to accomplish all that I have. I would like to thank my committee members, W. Minckley, T. Dowling, J. Fouquette, and E. Stump for their support and willingness to assist me in whatever way I needed.

During three months in Australia I was assisted by far too many people to mention all of them. However, some deserve special mention, including G. Briggs, C. Brumley, R. Francis, B. Hansen, R. Pulverenti, A. Robbins, J. Wager, and R. Wager. These individuals provided one or more of the following: field assistance, accommodation, and made their vehicles and homes available to me. Several also shared expenses.

Thanks to the following museums and staff for access to collections and for assistance with my many queries: American Museum of Natural History, B. Brown; Australian Museum, M. McGrouther; California Academy of Sciences, D. Catania; Field Museum of Natural History, K. Swagel; Museums and Art Galleries of the Northern Territory, H. Larson; Queensland Museum, J. Johnson; South Australian Museum, T. Sim; United States National Museum, J. Williams; University of Michigan Museum of Zoology, D. Nelson; Museum of Victoria, T. Bardsley and M. Gomon; and the Western Australian Museum, S. Morrison. The following individuals also provided considerable assistance with information regarding fish occurrences and for commenting on fish

distributions: G. Allen, S. Brooks, B. Hansen, B. Herbert, A. Hogan, P. Humphries, P. Kailola, A. Kemp, M. Kennard, C. Marshall, R. McDowall, B. Pusey, T. Raadik, A. Sanger, and R. Wager. Thanks to P. Bishop, B. Joyce, I. McDougall, C. Pain, J. Stephenson, R. Twidale, and P. Wellman for assistance with geological information. Thanks to J. Rohlf for help with NTSYS. M. Douglas, W. Fagan , and R. Minckley also provided valuable assistance and advice regarding the analysis. Thanks to the Australian Geological Survey Office and C. Buchanan for allowing access to bathymetric data and the Australian Bureau of Meteorology and G. de Hoedt for providing GIS coverages. Thanks to H. Hieronimus for providing the comment that rainbowfishes may only be two or three million years old that re-ignited my interest in this subject. Finally, I would like to thank all those people not mentioned above who also provided invaluable support and assistance with achieving my degree.

TABLE OF CONTENTS

Page

APPENDICES

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF ACRONYMS AND ABBREVIATIONS

States

NSW	New South Wales
NT	Northern Territory
QLD	Queensland
SA	South Australia
TAS	Tasmania
VIC	Victoria
WA	Western Australia

Museums

AM	Australian Museum, Sydney
AMNH	American Museum of Natural History, New York
CAS	California Academy of Science, San Francisco
FMNH	Field Museum of Natural History, Chicago
MoV	Museum of Victoria, Melbourne
NTM	Northern Territory Museum, Darwin
QM	Queensland Museum, Brisbane
SAM	South Australian Museum, Adelaide
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum, Washington DC
WAM	Western Australian Museum, Perth

Time

Gy	billion years ago
Ka	thousand years
Ky	thousand years
Ma	million years ago
My	million years

Distance

km	kilometer
m	meter

Region names

ARCH	Archer River
ARNH	Arnhemland
BARK	Barkly Tablelands
BULL	Bulloo-Bancannia Basin
BURD	Burdekin River
CYP	Cape York Peninsula
DALY	Daly River
EGC	Eastern Gulf of Carpentaria
EKIM	Eastern Kimberleys
FITZ	Fitzroy River
LEB	Lake Eyre Basin
MDB	Murray-Darling Basin

Region names cont.

NEN	Northeastern New South Wales
NEQ	Northeastern Queensland
NICH	Nicholson River
NTAS	Northern Tasmania
PILB	Pilbara
SAG	SA Gulf
SECYP	Southeastern Cape York Peninsula
SEN	Southeastern New South Wales
SEQ	Southeastern Queensland
SEV	Southeastern Victoria
SGC	Southern Gulf of Carpentaria
STAS	Southern Tasmania
SWV	Southwestern Victoria
SWWA	Southwestern Western Australia
TORR	Lake Torrens
VOR	Victoria-Ord rivers
WGC	Western Gulf of Carpentaria
WKIM	Western Kimberleys
WP	Western Plateau

INTRODUCTION

Australia,[1] due to its long isolation, lack of major recent geologic activity, and climate, provides an atypical situation in which to investigate freshwater biogeography. It has lacked terrestrial connections with other continents since 95 Ma (Veevers & Eittreim, 1988). Australia also lacks significant relief due to lack of recent major orogenic events. The last one occurred in eastern Australia ca. 90 Ma, and other mountainous areas are substantially older (Veevers, 1984). Present-day drainages were mostly established by Paleocene. Since then, only minor uplift and subsidence has occurred. Pleistocene glaciations were geographically limited, with little probable effect on the aquatic biota.

Having a broad latitudinal spread (ca. 40^{o}), the continent has likely been buffered from complete loss of major climatic types (i.e., temperate, tropical). Furthermore, the direction of continental drift (of ca. 30^{o}) has been largely due north during Tertiary, a time of general global cooling, hence on a broad scale maintaining a diversity of climatic types as it moved from the South Pole. The last 15 My has seen increasing aridity, resulting in decreasing surface water. Considerable attention has focused on Pleistocene events, especially the last glacial maximum. These short-term, regular climatic fluctuations are thought to be controlled by Milankovitch Cycles associated with regular changes in distances of the Earth relative to the sun.

---

[1] Unless otherwise stated, the name is used in the strict sense to refer only to the portion of the continent called Australia, i.e., excluding New Guinea.

How one should approach biogeographic study of such a landmass, and in general can be a contentious issue. The debate between vicariance and dispersalist biogeographers has, however, subsided, with vicariance presently considered more common (Humphries & Parenti, 1986). Today's debates mostly center around algorithms, phylogenetic techniques, and artificial three-taxon datasets. A further confounding issue is the lack of independent tests for hypotheses. My philosophy, given the last, is to examine data using different techniques (allowing for limitations within each technique) and look for concordance between and among results.

In contrast to vagile terrestrial organisms, freshwater organisms (e.g., fishes) suffer unique biogeographic constraints. A freshwater fish is defined as one which cannot survive more than a short time of any life-cycle stage in seawater. Furthermore, their ability to move in response to climate change or geological event is limited to patterns of connectivity of freshwater bodies. Hence, opportunities for range expansion between isolated drainages is limited to rare events such as drainage re-arrangements, changes in continental shelf width and depth which alters connectivity between regular sea-level changes, and perhaps major pulses of freshwater into oceans. Given the difficulty of dispersal, extinction is far more likely than colonization and can occur due to any number of factors, both deterministic (climatic change) and stochastic (disease, volcanism, interspecific factors, etc).

While the great antiquity of some Australian groups, e.g., lungfishes and bony tongues, has been long recognized, many suggest radiation of other groups was relatively recent (Whitley, 1959; Allen, 1982; Merrick & Schmida, 1984; Williams & Allen, 1987;

Allen, 1989). This is partly due to an unsubstantiated belief that because a majority of families are considered secondarily freshwater (Myers, 1938), they entered freshwater only in the last few million years. Others put forth alternative views. Based on limited fossil evidence, Hills (1956) suggested "the chief genera of the extant freshwater fishes of Australia were present in the continent during much if not all of Cainozoic time." Crowley (1990) speculated craterocephalids (and likely melanotaeniids) invaded Australian freshwaters sometime between Mid-Cretaceous and Paleocene. Her belief was based on the conservative nature of modern atherinimorph osteology, and was the first attempt to integrate distributional patterns and phylogenies of Australian fishes specifically to the geological record for a specific family.

This work reports an investigation of biogeographic patterns of the freshwater fish fauna within Australia. Richness and endemism are quantified and patterns identified on a regional scale. The fauna is examined for congruent distributional patterns among species. Shared species between drainages is taken to imply connectivity; hence, biogeographic tracks can be hypothesized and compared with the geologic and climatic record. Furthermore, biogeographic provinces for fishes can be more clearly defined. These results (distributional patterns and geological interpretations) should be viewed as working hypotheses to be tested by phylogenetic analysis. While some may argue biogeographic studies lacking phylogenetic data are unfalsifiable, I provide hypotheses that are directly testable and refutable in the hope of stimulating additional research.

GEOLOGIC AND CLIMATIC SETTING

General background

The western two thirds of Australia have exposed Precambrian blocks (3.5 - 2.5 Gy) with thin Phanerozoic basins, while exposed Phanerozoic fold belts alternate with younger basins in the eastern third. Except for the Arafura and Tasman seas[2], the shoreline has remained in about the same configuration for the last 300 My (Veevers, 1984), with exception of the last continental transgression during Mid-Cretaceous. The most recent major orogeny was 90 Ma along the Eastern Highlands. All major sedimentary basins (hence river basins) of today were established by Paleocene (Veevers, 1991). Since then, Australia has remained relatively quiescent, with only minor, continent-wide uplift and subsidence (Wasson, 1982).

Recent geomorphological work in Australia has seriously challenged long-standing northern-hemisphere-based paradigms of landform evolution (Gale, 1992; Twidale & Campbell, 1995; Nott, 1995; Twidale, 1997). For example, parts of the Kimberleys (WA) have been continuously exposed for the last 700 My, one of the oldest known, continuously exposed landforms in the world (Ollier *et al*., 1988). Some incredibly low erosion rates have been calculated. Nott (1996) detected only 500 m of escarpment retreat on Groote Eylandt (NT) over the last 100 My; and Bierman & Turner (1995) recorded mean weathering/erosion rates of 0.7 ± 1 mm / My on inselbergs (granitic domes). With few exceptions, erosion rates are typically less than 10 m / My for the entire Mesozoic-Cainozoic (Gale, 1992).

Glaciation

The last major glaciation was during Permian. Since then, glaciation was restricted to Mount Kosciusko (NSW) and parts of the Central Plateau (TAS) during Pleistocene (Colhoun & Fitzsimons, 1990).

Volcanism

One of the greatest basaltic provinces in the world in terms of extent (although not by volume), stretches 4400 km from Torres Strait in northeastern Australia southward along the eastern mountain ranges into TAS and westward into southeastern SA with some gaps of up to 500 km (Johnson, 1989). Volcanic activity began in eastern Australia in Late Mesozoic and continued through Quaternary, ending as recently as 13 Ka in northern QLD and 4.6 Ka in southeastern SA. Three broad volcano types are recognized: lava fields, leucitites, and central. Most lava fields are on (within 100 km) or east of the Eastern Highlands, leucitite suites are west of the Eastern Highlands, while central volcanoes appear more spatially random. Lava field activity began ca. 70 Ma with the major pulse between 55 and 30 Ma. Little activity occurred between 30 and 5 Ma, after which activity again increased. The oldest identified central volcanic activity was 34 Ma in the north, continuing southward as new volcanoes were created and northern ones became extinct. By 11 Ma, all volcanic activity had ceased in NSW, with small areas continuing in QLD and SA, as noted above. Causes of volcanic activity are unresolved;

---

[2] Place names are shown in Fig. 1.

however, central volcanoes and leucitites appear related to a hotspot trail; lava fields are thought related to post-rifting uplift that lead to formation of the Eastern Highlands.

Long-term sea-level changes

Causes of long-term sea-level change include changes in quantity of water, volume of ocean basins, and uplift and subsidence of continental margins (Partridge *et al.*, 1995).

A significant portion of Australia was inundated by shallow seas during Mid-Cretaceous (Aptium-Albian) times (Frakes *et al.*, 1987a). Up to four principal areas remained emergent, southwestern WA, northern WA and parts of adjacent NT, and the eastern highlands (including TAS), separated in the middle by a narrow seaway in the vicinity of Brisbane (QLD). Withdrawal was likely a combination of broad, gentle, continental uplift and decreasing sea-level. Global mean sea-level (ignoring Milankovitch-scale (i.e., glacial) fluctuations) fell on average throughout Tertiary and was at its lowest several times over the past 10 My at around -100 m (Haq, Hardenbol & Vail, 1987).

Throughout Tertiary, submergence was largely limited to coastal margins in three major periods (during each of which several transgressions may have occurred). The first was Eocene, when most southern and western coastlines were affected from eastern VIC through the mid-northern coast of WA. The most significant areas inundated include parts of the lower Murray Basin (SA, VIC, and NSW), western Gippsland and Bass Strait (VIC), and the Great Australian Bight (SA and WA) (McGowran, 1989). Oligocene is generally regarded as a time of lower seas; however, a second transgression occurred during Late Oligocene - Early Miocene resulting in flooding of the Murray and Eucla basins (SA and WA). Flooding of the Murray Basin lasted for ca. 20 My (from 32 Ma; Brown & Radke, 1989), then the sea retreated in Mid-Miocene (ca. 10 Ma), to end with a further, final transgression into the Murray Basin in Late Miocene - Early Pliocene (Stephenson & Brown, 1989; Frakes, McGowran & Bowler, 1987b). The Eucla Basin had by then been uplifted and was not affected (Jennings, 1967; Benbow, 1990). Connections of the Australian mainland with New Guinea (Doutch, 1972), and likely also with TAS, occurred throughout much of the Tertiary.

Topography

Australia has the lowest relief of any continent. The highest peak is Mt. Kosciusko (NSW) at 2228 m in the southeastern highlands, the lowest is Lake Eyre (SA) at 16 m below sea-level. The continent consists of a plateau in the western portion and a lowland region in the east bordered by the Eastern Highlands, the only major mountain belt in Australia, along the east coast. Relief is shown in Fig. 3.

Long-term global climate change

Long-term global climate is influenced by several factors (Partridge *et al*., 1995), some with slow gradual impacts, others with dramatic, short- and long-term effects. Continental movements may have significant influence on ocean currents, which in turn influence climate. During Tertiary, considerable areas of continents were uplifted, causing both changes in atmospheric circulation and decreased temperature due to higher elevation. Uplift further promotes weathering and erosion, increasing the exposure of silicate rocks, weathering of which results in removal of CO_2 from the atmosphere, decreasing the "greenhouse effect." Throughout Tertiary there was decreased sea-floor spreading, hence less ridge formation, and ocean basins increased in size, leading to sea-level decrease by as much as 200 m and important albedo effects. Shading by dust created by volcanism also causes atmospheric cooling, although its influence is relatively short term.

The overall trend in world climate through Tertiary was of decreasing temperature, with significantly accelerated cooling at 14 and 2.8 Ma. The first is thought to relate to formation of major ice sheets on Antarctica, and the second to establishing ice sheets in the Northern Hemisphere (Burckle, 1995). Development of polar ice caps had a critical influence on climate, with extremes becoming broader and changing more rapidly than before. Glacial maxima were times of low sea-level, minimal temperatures, and drier conditions in the tropics; conditions were warmer at high latitudes and wetter at lower ones during interglacials (Williams, 1984). Glacial maxima and minima typically last around 10 Ky, and each recurs around every 100 Ky. This periodicity appears controlled by Milankovitch Cycles representing variations in revolutions of earth, both on its axis (obliquity and wobble) and around the sun (ellipticity). Three time-scales of Milankovitch Cycles, 23, 41, and 100 Ky are recognized, broadly corresponding to observed climatic cycles. These cycles have likely been responsible for short-term climatic fluctuations throughout Earth's history (Bennett, 1990).

Geological mechanisms for climate change

Australia had minor areas of uplift over the last 90 My which had little influence on local climates. Northward drift of Australia has, however, had significant long-term influence. While drift alone did not drive climate change, it brought the continent toward warmer latitudes. At continental breakup (95 Ma), southern-most Australia was around latitude 76^{o}S. The southern coast was near 70^{o}S at the beginning of Tertiary, while northern Australia was near 40^{o}N (today they are at ca. 40 and 10^{o}S) (Veevers, 1984). With separation from Antarctica, Australia initially drifted northward at 4.4 mm / year from 95 to 49 Ma, increasing to 10 mm / year from 49 to 44 Ma, then to 20 mm / year which continues today (Veevers *et al*., 1990). Around 30 Ma, this displacement allowed the Circum-Antarctic Current to flow unimpeded between Australia and Antarctica. With deep water between South America and Antarctica developing around 23 Ma (Lawver, Gahagan & Coffin, 1992), the current became circumpolar and prevented mixing of warm northern currents around the pole (Burckle, 1995).

Botanical evidence for climate change

Temperate and tropical rainforest dominated Australian landscapes in Early Tertiary. Based on fossil evidence, this flora was never uniform north-south or east-west (Martin, 1994), hence the following summary should be taken only broadly. With gradual decline in wetter conditions, open-canopy forests dominated by a sclerophylous flora of Myrtaceae, Mimosaceae, and others, gradually became common (Kershaw, Martin & McEwen Mason, 1994). The first grasses are recorded in Pliocene, reflecting development of drier conditions. Vegetative communities were broadly similar to those of today by the end of Pliocene, although their boundaries and composition are now changed due to more extreme climatic fluctuations (Kershaw *et al*., 1994).

Through modeling plant growth relative to environmental factors, Nix (1982) suggested similar conditions to today have existed for 150 My in Australia, with additional periods of increasing aridity and expansion of arid zones since Mid-Miocene. Although boundaries have repeatedly shifted, similar conditions have persisted in parts of various regions. Hence, with its northward drift into warmer latitudes combined with global climate cooling, Australia has maintained a broad range of climatic types.

Geologic evidence for developing aridity

Examination of paleodrainages in WA led Van de Graaff *et al*. (1977) to suggest discharge volumes sufficient to modify drainages ceased in Mid-Miocene. This was supported by Clarke (1994), by adding that gypsum precipitation beginning in earliest Pliocene (5 Ma) denoted an evaporative environment. While palynological data are lacking for the western half of Australia, available evidence suggests aridity developed there first and progressed eastward, e.g., the first evidence of aeolian landforms are sand dunes from Lake Amadeus (NT) dated at 0.91 Ma (Chen & Barton, 1991). No aeolian deposits west of Lake Amadeus have been examined; however, further evidence of aridity progressing eastward was provided by dated deposits from Paleo-Lake Bungunnia (SA, VIC, and NSW) at ca. 0.5 Ma (Zhisheng *et al*., 1986).

Present climate

Figures 4 and 5 show today's mean annual rainfall and January maximum temperature. Around 70% of Australia is considered arid. Southern areas, including southwestern WA, VIC, TAS, and southeastern NSW all share similar Mediterranean climates, with cold, wet winters and hot, dry summers. Northern areas have a tropical climate divided into dry winters and wet summers. Cyclones are regular occurrences. Lowest mean annual rainfall is 110 mm in the vicinity of Lake Eyre (SA); highest is 4252 mm at Tully (QLD).

PAST ICHTHYOLOGICAL WORK

The Australian freshwater fish fauna has long been recognized as distinctive relative to the remainder of the world. However, few papers have dealt with biogeography of the entire fauna as it relates to other continents. Most contain short references to specific groups which highlight its distinctiveness. Wallace (1876) recognized relationships between Australia and South America based on galaxiids, aplochitonids, and bovichtids (all of which have marine-tolerant species) and also with Southeast Asia based on living *Scleropages* spp. He also noted many of Australia's genera were endemic and the scarcity of most ostariophysan fishes. McCulloch (1925a) added that most Australian groups had marine relatives and several species were shared with New Guinea. Hills (1934) suggested connections between Australia and North America for Eocene fossils of †*Phareodus* and †*Notogoneus* found in both continents (although the latter also occurred in Asia and Europe (Grande, 1996)). Whitley (1943) discussed similarity of species from Australia and New Guinea. Darlington (1957) gave a summary of the distribution of fish families of the World, including Australian groups. Whitley (1959) pointed out the depauperate nature of the Australian fish fauna and its similarity to New Guinea. Darlington (1965) only briefly mentioned the Australian fauna, adding little except emphasizing dissimilarity to South America. McDowall (1981) was first to compare the number of all genera and species between Australia and other areas of the World. He also categorized Australian families into endemics, pantropicals, southern, Indo-Pacific, and unknown groups, and summarized their occurrences. Little progress has since been made. Allen (1989) updated McDowall's (1981) table of the number of genera and species of each family and Banarescu (1990) provided an account of the families discussed by McDowall based on Myers (1938) categories rather than a distributional one.

The first construction of biogeographic regions based on fishes and mollusks divided Australia into nine regions (Iredale & Whitley, 1938). Lake (1971) divided Australia by river basins based upon a hydrologic system (Bauer, 1955). This system, with trivial modifications (Australian Water Resources Council, 1976), remains in general use today (Merrick & Schmida, 1984; Allen, 1989).

FOSSIL FISHES

Few fossil taxa are recorded in the primary literature, and besides Hills' records (1934, 1943, 1946), they are rarely identified beyond family (and then only tentatively) and sometimes not beyond "fish." Fossil fishes from Australia reported in the primary literature are in Appendix I. Neoceratodontid fossils are relatively well known (Kemp, 1982a, 1982b, 1992, 1993, 1997a, 1997b; Kemp & Molnar, 1981). Around thirteen neoceratodontids were present during Tertiary (and earlier) through until Miocene from LEB, MDB, Gulf of Carpentaria (QLD), and coastal drainages between Brisbane and Rockhampton (QLD). The one living species, *Neoceratodus forsteri*[3], has existed for at least 100 My (Kemp & Molnar, 1981). Several neoceratodontids had geographic ranges similar to extant fishes, suggesting either present-day fish distributions were attained prior to Miocene or barriers between drainages have since been overcome.

Most knowledge of Australian fossil Tertiary freshwater actinopterygians stems from Hills' work (1934, 1943, 1946) on QLD deposits. Taxonomy of the two species to which Hills compared fossil material has, however, changed. *Macquaria* (=*Percalates*) *colonorum* was divided into *M. colonorum* and *M. novemaculeata* (Williams, 1970) and *Maccullochella macquariensis* was separated into *M. p. peelii*, *M. p. mariensis*, *M. ikei*, and *M. macquariensis* (Berra & Weatherley, 1972; Rowland, 1993). As a result, his comparisons can be only broadly interpreted.

Minimum dates for a few taxa are provided by fossils. †*Macquaria antiquus* (Hills), an ancestor to *M. colonorum-M. novemaculeata*, and *Scleropages* cf. *leichardti*, are recorded from Eocene deposits (>45 Ma) (Hills, 1934; Vickers-Rich & Molnar, 1996). A terapontid is also recorded from Eocene deposits (Turner, 1981, 1982; Henstridge & Missen, 1982). *Maccullochella* "*macquariensis*" is recorded from two

---

[3] Unless otherwise noted, nomenclatural authorities are all provided in Appendices II and III.

deposits dating between 13.6-17.1 and 12-21 Ma (Hills, 1946; Johnson, 1989; Tulip, Taylor & Truswell, 1982). Excepting the following examples, all fossil actinopterygians have representatives living today in the same geographic areas. The record of †*Macquaria antiquus* is about 250 km further north than the present distribution of its descendants. Likewise, the record of *Scleropages* cf. *leichardti* at Gladstone (QLD) is in the next drainage south of its descendants present range. Ariid catfish were found during Miocene around Lake Eyre (SA), where they no longer occur (Pledge, 1984; Estes, 1984).

CONDITIONS ALLOWING FISH MOVEMENT BETWEEN DRAINAGES

A frequently cited explanation for fish species occurring on opposite sides of a mountain divide is "river capture." Bishop (1995) provided a geomorphological review of such drainage rearrangements in bedrock systems. Three possible types were identified: beheading, capture, and diversion. Diversion can be further divided into channel migration, divide-topping catastrophic events, and tectonic diversion. He concluded that beheading by headward erosion is unlikely and capture would occur only under rather restrictive conditions. Diversion via channel migration and catastrophic event are unlikely in headwaters, while tectonic diversion would occur only under certain conditions depending upon appropriate trunk and tributary gradients and the dip and strike of the tilting. Hence, he concluded drainage rearrangements are likely not as frequent as some biogeographers suggest.

It was long accepted that drainage rearrangements were common across the Eastern Highlands of Australia (Taylor, 1911; Ollier, 1978, 1995; Ollier & Pain, 1994; and others). However, recent re-evaluation (Young, 1978; Bishop, 1982, 1986, 1988; Nott, 1992; Young & McDougall, 1993; and others) has largely overturned previous views and concluded that drainage divides along the Eastern Highlands have remained essentially unchanged since Mesozoic (Van der Beek, Braun & Lambeck, 1999). This has important consequences for past biogeographic work which has emphasized drainage rearrangements as explanations of observed patterns (Musyl & Keenan, 1992, 1996; Rowland, 1993; Waters, Lintermans & White, 1994; Pusey & Kennard, 1996, Pusey, Arthington & Read, 1998; Hurwood & Hughes, 1998). Evidence clearly demonstrates some fishes have crossed the Eastern Highlands (Crowley, 1990; Hurwood & Hughes, 1998; this study), but the mechanism by which this was accomplished remains elusive.

Volcanic activity has also been suggested as a means for drainage rearrangement (Hurwood & Hughes, 1998). Volcanic activity on, or very close to a drainage divide might be likely to cause changes via tectonic diversion through associated uplift, concurrent to and continuing after extrusion of lava (P. Wellman, pers. comm.). Lava outflows would have little effect as they always move downhill, then the only way such could divert a waterway would be to dam it high enough to overtop its divide, a rare situation, except where the drainage divide is very low.

Banarescu (1990) identified several ways by which fish move between drainages, including temporary connections between headwaters through low divides, i.e., swampy regions (i.e., Waldai Plateau, Brazil) or connected headwaters which drain both directions (i.e., Two-Oceans Pass, Wyoming, USA). "River captures" have been dealt with above. Both causes would primarily affect headwater-dwelling species. Lowered sea-level also may connect the lower reaches of rivers, with degree of connection depending upon local topography of the continental shelf. Also, inland salt lakes may become fresh, allowing connections across them. Both changes would allow primarily lowland fishes to move.

Possibilities for random dispersal of fishes include "rains" and accidental movement of eggs by terrestrial organisms (i.e., birds, mammals, etc.), or whole fish being dropped by birds. "Rains of fish" have been reported in Australia (McCulloch, 1925b; Whitley, 1972; Glover, 1990) and elsewhere (Gudger, 1929). Some Australian reports are clearly examples of fish moving short distances by overland flow (i.e., Shipway, 1947) rather than falling from the sky, but some clearly indicate fish have fallen. They are presumably picked up and deposited nearby since tornado-strength winds of sufficient velocity are often of short duration, and if transport is only over short distances, moving fish between drainages is unlikely. Clearly, the implications of this type of dispersal remain poorly understood. Eggs caught on animal feet/feathers/fur are often used to explain fish appearances in formerly uninhabited places. Not all fishes would be susceptible to such transportation; only egg-layers could be transported, eggs would need to be adhesive or in adhesive mud and in shallows where birds or mammals are likely to walk, or deposited near the water surface, and would need to survive at least brief periods of aerial exposure. Subsequently, at least one male and one female must reach adulthood and find each other to mate. Movement via this means has never been documented, although clearly possible over short distances.

METHODS

An overriding assumption of this study is that disjunct distributions of today were formerly connected by intermediate populations (either instantaneously or over time). In other words, it is deemed impossible for species to "jump" drainages. This may conceivably be violated when several drainages connect during lowered sea-levels and for some reason(s) (i.e., a waterfall), a species is unable to colonize drainages intervening between separated ones. It may also be violated if species go over a drainage divide and then at another point cross back into a different drainage not adjacent the original source drainage.

Another assumption is that species as now defined represent monophyletic units. A recognized flaw in this is adjacent populations that may not be the most closely related (Platnick & Nelson, 1978); however, at some hierarchical level (between population and genus), they must be monophyletic if present nomenclature is relatively accurate. Through studying additional species, one can predict where adjacent populations of widespread taxa may not be closely related.

An assumption of many studies is species with similar distributional patterns have similar histories. McDowall (1978, 1990) demonstrated problems with this when the roles of dispersal and ecology are ignored. However, similarity implies connection at some time over an organism's history, which alone is useful to recognize, although determining if changes in distributions occurred simultaneously or otherwise may be extremely difficult. The final assumption of all biogeographic studies is that negative data do not exist except where indicated by the fossil record. This is clearly invalid, but impossible to circumvent without a tardis.

DATA SOURCES

Approximately 200 freshwater fishes are recorded in Australia. Of these, some are marine or estuarine vagrants, while others spend a portion of their life cycle in oceanic conditions and were excluded (Appendix II). My analysis was of 167 species that cannot survive more than brief exposure to seawater during any stage of their life cycle (Appendix III).

Nomenclature of 156 described species followed Eschmeyer (1998), except for *Oxyeleotris selheimi* (see Appendix IV) and *Hephaestus tulliensis* (Allen & Pusey, in prep.), four species described since (Allen & Feinberg, 1998), and family designations follow Allen (1989) for Galaxiodea and Petromyzontiformes, Kemp (1997b) for Dipnoi, and Mooi & Gill (1995) for Latidae. The percichthyid genus *Edelia* is subsumed within *Nannoperca* following Kuiter, Humphries & Arthington (1996). Eleven undescribed species are included, seven of which were listed by Allen (1989); in addition I include *Hypseleotris* sp. C (Unmack, in press); *Mogurnda* sp. 2 (Glover, 1989); a new species and genus of percichthyid being described by B. Pusey and associates; and *Hypseleotris* sp. D being described by H. Larson. Specific designations for several species in Bulloo drainage (BULL; Fig. 6) were problematic. The melanotaeniid was referred to *Melanotaenia splendida*, which it appears to most closely resemble. The *Mogurnda*, *Ambassis,* and *Neosilurus* "false-spined" species could not be assigned to species due to insufficient numbers of specimens and unusual character combinations. All three were excluded from analyses except for richness calculations. A recently discovered population of *Craterocephalus* in the Cooper Creek drainage (LEB) appears nearest *C. stercusmuscarum* (R. Wager, pers. comm.) and was included as such. The status of *Craterocephalus* in TORR was not addressed in a recent revision of the *C. eyresii* complex (Crowley & Ivantsoff, 1990), it is left as *C. eyresii*. Several cryptic species have been alluded to based upon genetic evidence within *Tandanus tandanus* (Musyl & Keenan, 1996; Jerry & Woodland, 1997), *Macquaria ambigua* (Musyl & Keenan, 1992), *M. australasica* (Dufty, 1986), *Mogurnda adspersa*, and *M. mogurnda* (M. Adams, pers. comm.). No formal systematic clarifications have appeared, hence they were treated as single species.

Museum specimens were the primary data sources except for TAS (Frankenberg, 1974; Allen, 1989; Chilcott & Humphries, 1996) and to a lesser extent QLD (Wager, 1993; Herbert *et al*., 1995; Pusey, Kennard & Arthington, pers. comm.) and WA (Hutchins, 1981; Allen 1982, 1989; Allen & Leggett, 1990; Morgan, Gill & Potter, 1998). The following Australian museum collections were examined primarily by browsing their catalogs, AM, MoV, NTM, QM, SAM, and WAM. Several museums in the USA were also visited, AMNH, CAS, FMNH, USNM, and UMMZ. Specimens found therein were examined. In Australian museums, identifications were typically checked only if the record seemed unique or unusual for a given drainage based on primary literature or personal knowledge. Groups and species commonly misidentified, i.e., Plotosidae, *Oxyeleotris lineolatus, O. selheimi, Ambassis* spp., and *Hypseleotris* spp., all were examined. Additional records were obtained from primary and gray literature, or by personal communication with specialists for groups or regions. Several species, as follows, were assumed present based on either widespread occurrences, or by likely artificial gaps due to a lack of sampling. *Scleropages jardinii* is assumed present in SGC; *Pseudomugil tenellus* is assumed present in ARCH; *Ambassis agrammus* is assumed present in NICH; *Ambassis elongatus* is assumed present in EGC; and *Hypseleotris compressa* is assumed present in EKIM, VOR, NICH, EGC, and ARCH. The inclusion of these assumptions were trivial and only resulted in minor changes in the positions of NICH and SGC when analyzing relationships among regions. Richness values are slightly higher as a consequence. Incorrect records and corrections of literature are in Appendix IV.

Presence/absence data were collected at river basin scale (hereafter referred to as a drainage), largely following the drainage designations in Australian Water Resources Council (1976), but with several minor boundary changes. MDB was the only major deviation, divided into three drainages, lower Murray River below Darling River confluence, and Murray and Darling rivers each above their confluence. Drainages were summarized into 31 regions (Fig. 6) for ease of analysis. Boundaries were chosen to maximize differences in presence/absence of fish taxa between adjacent regions. Certain boundaries were somewhat arbitrary; however, this is not expected to have significant effects since some regions with clinal changes between them lack distinct boundaries. Furthermore, poorly sampled areas were problematic to analyze and judicious merging of drainages reduced this difficulty. These include inaccessible portions of the Kimberleys

(WA), drainages between Victoria and Daly rivers (NT), Aboriginal lands in Arnhem Land (NT), drainages between Roper and Nicholson rivers (NT) and to a lesser extent between Nicholson and Mitchell rivers (QLD), between Murray River and Waterpark Creek, except for Burdekin River (QLD), and most of WP (WA, NT, SA). Minor alterations to regional boundaries or scale change some richness and endemism values, but have little effect on overall patterns.

RICHNESS AND ENDEMISM

Presence/absence data were entered into the spreadsheet program Microsoft Excel 97 and richness and endemism computed. Richness is defined as the number of species recorded from a region, determined by summing species occurrences. Endemism is defined as any species restricted to only one region. It was determined by summing the number of records for each species, eliminating all species with values > 1 (i.e., occurring in more than one region), then adding remaining records by region. Both absolute numbers, and percentage endemism were calculated.

SIMILARITY COEFFICIENTS

Data were analyzed via Q-mode which measures the relationship between objects (regions) based on descriptors (taxa) (compared to R-mode which measures the relationship between descriptors based on objects). Similarity coefficients use binary data to measure association between objects. A favorable characteristic of similarity coefficients is their ability to exclude double-zeros, otherwise regions with low species richness would be grouped on the basis of shared absences rather than presences (Legendre & Legendre, 1983). Shi (1993) provided a review and classification of similarity coefficients. On the basis of his review, and availability in NTSYS (Rohlf, 1997), Dice's, Jaccard's, Kulczynski's #2, and Ochiai's coefficients were utilized. Formulae are given in Legendre & Legendre (1983) and Rohlf (1997). The most notable difference between these coefficients is the effect of sample-size is strongest in Kulczynski's #2, moderate in Ochiai's, and low in the remaining two (Shi, 1993). This is an important consideration when choosing a suitable index, as objects with few species will be more closely ranked where sample-size effect is highest. Whether a similarity coefficient is metric or non-metric also is important in deciding which ordination technique(s) is appropriate. Only Jaccard's Coefficient is metric (Shi, 1993). Commands used in batch files for clustering and ordination analyses in NTSYS for Jaccard's Coefficient are provided in Appendix V.

CLUSTERING

All analyses involving similarity coefficients were conducted using the statistical program NTSYS 2.02i (Rohlf, 1997). UPGMA was used to cluster similarities. This technique provides an unweighted arithmetic average between each individual object and other members of the cluster or between members of clusters as they merge (Legendre & Legendre, 1983). To test if data actually contain clusters (as clustering forces objects into clusters whether or not they exist) the cluster matrix is compared to a cophenetic value matrix of the original data to produce a cophenetic correlation value. If the two matrices show the same clustering patterns they will produce high cophenetic correlation, indicating low distortion (Rohlf & Fisher, 1968). Values of r>0.9, 0.8<0.9, 0.7<0.8, and r<0.7 indicate a very good, good, poor, and very poor fit (Rohlf, 1997).

Problems with dendrogram clustering methods include loss of information once initial pairs are formed. Hence, it is valuable for describing relationships within pairs of objects and less accurate when determining major clusters of objects (Legendre & Legendre, 1983). To show the most distinct clusters, the consensus of complete- and single-link dendrograms were calculated. Clusters present are called ball clusters which are more similar to each other than any object within the cluster is to any object outside the cluster (Rohlf, 1997).

ORDINATION

The advantage of ordination relative to clustering is all objects are compared together rather than primarily by individual pairs. In other words, the general relationships of objects are more accurately portrayed (Legendre & Legendre, 1983). This compliments clustering methods which find the closest relationships within pairs of objects. Many ordination techniques require data to be distributed in Euclidean space (Shi, 1993). Since both metric and non-metric similarity coefficients were applied, the ordination procedure of non-metric multidimensional scaling was used. It is suitable for showing ordered relationships of objects when either non-metric or metric data are analyzed relative to other ordination methods (i.e., principal coordinate analysis) (Legendre & Legendre, 1983). Stress is the term applied to variance between the two ranked orders, distance and similarity (Shi, 1993), which provides an indication of distortion relative to the original data. Objects are analyzed initially in two dimensions, with the number of dimensions increased until they no longer decrease stress significantly (Kruskal, 1964; Rohlf, 1972). Since stress was decreased to a reasonable value (fair or better) and graphical presentation was restricted to two or three dimensions, data were not analyzed beyond three dimensions. Cophenetic correlations were calculated so distortion between ordination and clustering results could be compared. Outputs are presented in two dimensions for ease of interpretation and because three dimensional plots did not significantly increase information content. A minimum spanning tree connecting regions is shown to indicate whether close pairs of regions in the plot are actually close, or distant if other dimensions are considered. Based on the similarity of several clustering results (see below) only Jaccard's and Kulczynski's #2 coefficients were analyzed through multidimensional scaling.

PARSIMONY ANALYSIS OF ENDEMICITY

Parsimony analysis has a long history of use in systematics for reconstructing phylogenies based on ancestral and derived characteristics. Rosen (1984, 1985) introduced parsimony analysis for examining presence / absence data of taxa by areas to define regions with shared presence of taxa. This differs from the above methods in that clustering is based on individual characters within areas rather than gross similarity between areas. Endemicity here refers to regions with common groupings of species. In order to avoid confusion with endemism (as defined above), I refer to this method as parsimony analysis.

Analysis was conducted using PAUP 4.01b (Swofford, 1998), consisting of heuristic searches with 500 random addition sequences. Characters were coded as Dollo reversed. This specifies it is more difficult to change from absence to presence (zero to one) than presence to absence (one to zero). In other words, extinction is more likely than colonization. All non-informative characters were removed (i.e., taxa only found in one operational taxonomic unit (OTU), e.g., endemic, and OTUs with only one character e.g., WP and TORR). All most parsimonious trees were retained; only the strict consensus of these is presented. Rooting was done artificially for ease of comparison at the separation on the unrooted tree that most closely matched that of the UPGMA trees. Assessment of branch support were made using bootstrapping in PAUP and by decay index (Bremer, 1994).

BATHYMETRY

Drainage patterns during lowered sea-level were modeled using Spatial Analyst 1.1 and ArcView 3.1 based upon a bathymetric 30 arc second grid produced by the Australian Geological Survey Organisation.

RESULTS

RICHNESS AND ENDEMISM

There is a distinct trend in richness from high at low latitudes to low at higher latitudes (Fig. 6). When richness is regressed against latitude, R^2=0.58 (Fig. 7). Seven regions at middle latitudes are somewhat distant relative to the trend line. When those seven (WP, TORR, PILB, BULL, BARK, LEB, and MDB) are removed, the R^2 value for richness versus latitude increases to 0.83 (Fig. 7).

The regions with highest endemism included all western, central and southern regions (Fig. 8). An "endemic line" between areas of "high" and "low" endemism effectively splits Australia into two halves. NEQ was the only region with relatively high endemism east of the line. The number of regions in which each species occurs (Fig. 9) shows seventy-eight species (47% of the fauna) in only one region, sixty-four in two to seven regions, sixteen in eight through fifteen regions, and nine in between sixteen and twenty-two regions.

SIMILARITY COEFFICIENTS

All four similarity coefficients produced similar UPGMA trees (Fig. 10). NTSYS warned of tied tries during calculations; however, the three trees identified as having ties were identical for each similarity coefficient. Cophenetic correlations were all between 0.92 and 0.95. Jaccard's and Dice's coefficients produced identically branched trees, while Ochiai's Coefficient varied only in the position of WP. Kulczynski's #2 Coefficient was different in the positions of PILB, WP, and MDB, and the cluster LEB, BULL, and BARK differed in internal arrangement.

Ball clusters in consensus trees of single- and complete-link trees of Jaccard's and Dice's coefficients were identical (Fig. 11). Ochiai's differed only in the position of W and EKIM (Fig. 11). Kulczynski's #2 differed in positions and composition of the upper cluster, MDB and SAG clustered, and BARK did not cluster with LEB and BULL (Fig. 11).

NON-METRIC MULTIDIMENSIONAL SCALING

Results were similar for both Jaccard's and Kulczynski's #2 coefficients (Fig. 12). Stress values were 0.12 and 0.11 respectively and cophenetic correlations were a high 0.90 and 0.96.

PARSIMONY ANALYSIS

Parsimony analysis found fifteen trees with length 214 (CI=0.411, RI=0.753, RL=0.310, and HI=0.589). Strict consensus produced only two polytomies (Fig. 13). Bootstrap values were mostly low, only 6 branches having values > 50%. This is due to the small number of characters (an average of 2.8) relative to the number of OTUs. Decay index values were also low, maximum values being three.

DISCUSSION

RICHNESS

The differences between the two regressions (Figs. 7) are due to the effects of seven regions. WP and TORR have only single species, while PILB, BARK, and BULL all have low richness (< thirteen spp.) (Fig. 6). These all are within the most arid portions of Australia, hence lack of water is the likely cause. LEB is also in the arid zone but has high richness (thirty). Two factors account for this. Springs, the groundwater source for which originates outside the arid zone, (hence aridity has no effect on water persistence), support eight endemic species. Secondly, LEB is much larger than most regions. When subdivided into individual drainages (which under present-day conditions are largely isolated from one another and areawise would be more similar to other regions), richness would be lowered to one through eleven for nine drainages and sixteen for one drainage when spring endemics are excluded (Unmack, 1995). Hence, if the geographic area was reduced, richness would be similar to other arid regions. The final odd value is for MDB. This region has a high latitudinal extent (ca. 12^{o}), is around twice as large as PILB, the next smallest region (only WP and LEB are larger), and six times larger than all regions on average. While latitude per se does not explain richness, it is notable that mean annual rainfall is higher in the north, lowest in most of central Australia, and high again in southern-most latitudes (Fig. 4). Mean January maximum temperature shows a trend of warm in northern-most areas, hot in middle areas, and coolest in the south (Fig. 5). Hence, the broad north-to-south climate trend is warm and wet, hot and dry, to cool and wet.

COMPARISONS AMONG ANALYSES

Overall results among clustering techniques are similar despite problems with the dataset in differences in the number of particular character states in OTUs, the small number of characters relative to OTUs, and the bias associated with each method. Cophenetic values were high for both clustering and ordination, hence both appeared to represent relationships equally well. Qualitative examination of Figs. 10 and 13 show five regions (CYP, BURD, FITZ, SEQ, and MDB) accounting for much of the variation in clustering results. As shown by ordination (Fig. 12), each of these regions is somewhat of a gradation between extremes rather than forming any discrete groups, or in the case of MDB of composite origin from faunally different regions (SWV, SEQ, and others). The inability of dendrogram clustering to represent regions of composite origin is a methodological limitation, as regions are forced into discrete clusters and hence any continuum of gradual change or multiple origin cannot be clearly represented.

BARRIERS TO FISH MOVEMENT

Before discussing biogeographic divisions it is pertinent to review what barriers exist in Australia, their characteristics and timescales of influence, and provide examples. Four kinds of barriers are considered important: sea-water, drainage divides, climatic, and ecological.

Sea-Water

Changes in sea-water barriers occur on both short- and long-term scales. Short-term changes in sea-level of perhaps up to 100-150 m occur in conjunction with short-term climatic fluctuations, probably on the order of every 100-150 Ky. Causes of these changes appear due to water storage in continental glaciers (Partridge *et al*., 1995). Long-term scales involve primarily three factors, change in the capacity of the oceans, change in continental elevation (Partridge *et al*., 1995), and movement of lowland river channels such that their point of discharge into the ocean changes position (e.g., Nott, Idnurm & Young, 1991; Spry, Gibson & Eggleton, 1999). Another short-term means by which fish have been suggested to move between drainages is via riverine flood plumes (Williams, 1970; Chenoweth & Hughes, 1997; Jerry, 1997). These plumes may extend for sufficient distances to potentially connect adjacent drainages (Wolanski & Jones, 1981; Grimes & Kingsford 1996). However, the salinity and characteristics of these plumes can vary considerably and there are no data regarding fish occurrence within these plumes (Kingsford pers. comm.). Clearly this avenue of dispersal requires investigation.

In order to assess the importance of short-term sea-level fluctuations, drainage patterns were reconstructed to -500 m (Fig. 14). While -500 m is lower than any short-term sea-level known to have been attained, the results are more readily visualized; -100 and -200 m contour intervals are also shown. For some areas, lowered sea-level connects major drainage areas, e.g., between Australia and New Guinea, VIC and TAS, and Cambridge Gulf (WA and NT). Areas presently offshore of FITZ and possibly northern

PILB would experience far higher connectivity than today. However, the remaining drainages are largely unaffected by short-term sea-level change.

Drainage divides

Drainage divides are likely broken only over long time periods, primarily via drainage rearrangement through tectonism (see Introduction). Another possibility includes passage over low divides by fishes without rearrangement, i.e., they swim over. Two types of divides are identified, those between rivers with non-adjacent outlets (i.e., draining opposite directions), and those between rivers with adjacent outlets (i.e., draining the same direction with neighboring river mouths). The principal difference is their direction of flow relative to drainage direction. Those in adjacent drainages have divides parallel to direction of flow and those in non-adjacent drainages have divides perpendicular to direction of flow. Lateral channel migration is more likely to affect parallel divides than perpendicular ones. Parallel divides may allow movement of both upland and lowland species, whereas perpendicular divides only allow movement of upland species. Furthermore, adjacent river outlets have an additional means in their lowermost reaches by which fishes can be exchanged via lowered sea-level. If not adjacent, this is far less possible.

When comparing similarity across divides between non-adjacent inland regions (LEB and MDB) and coastal regions surrounding them, and also between adjacent coastal regions, it is clear the faunas of adjacent drainages are far more similar than in non-adjacent ones (Fig. 15). Hence, given this higher faunal similarity I conclude connectivity occurred more frequently, or at least more recently, between adjacent drainages.

Climate

Climatic barriers occur along similar time frames as sea-water barriers. Regular, short-term fluctuations are on the order of 100-150 Ky, while long-term trends are also known (see Introduction). Climatic barriers differ from sea-water ones in being less sharply delineated and differing more in their effects between species, depending upon ecological tolerances (see below). The principal climatic barriers are minimum and maximum water temperature (which are determined by a combination of solar radiation, atmospheric temperature, and humidity) and rainfall. The first two determine physiological survival, the last permanence of water.

Due to its broad latitudinal and longitudinal area, Australia experiences considerable climatic differences between regions (Figs. 4 and 5). The most obvious climatic barrier is aridity, such as occurs in parts of southern, central, and western Australia where surface runoff is negligible. This has completely isolated SWWA, PILB, WP, TORR, LEB, and BULL from sea-level connections with surrounding regions since the last four are endorheic and the first two are isolated by WP. This limits potential for connectivity between regions and ones surrounding them to passage over divides. In northern, eastern, and southeastern Australia, climate is less extreme. Climatic change tends to be oriented north-south (Figs. 4 and 5). Climatic differences across northern Australia may have been bypassed during lowered sea-level as both adjacent and non-adjacent drainages became continuous at more northerly latitudes (i.e., Gulf of Carpentaria, Cambridge Gulf; Fig. 14). Hence, while climatic differences exist, they likely had less effect on fish movement east to west. Although during glacial maxima, when sea-level was lowest, climate became warmer and drier in tropical areas (Williams, 1984), reducing potential for movement.

Considerable differences in climate exist along eastern drainages (Figs. 4 and 5). Northern regions (SECYP, NEQ) tend to have moderate rainfall and warm temperatures, with NEQ also having areas with high rainfall and cool temperatures due to higher elevation (Fig. 3). Mid-QLD regions (BURD, FITZ) are warmer and drier. This gradually ameliorates into progressively wetter and cooler conditions in the south.

Three lines of evidence suggest climatic effects have had the greatest impact on fish occurrence along the eastern coast, all the way from CYP south to SEV. There is a complete lack of distinctive faunal breaks, even within regions, as faunal differences between drainages are gradual and indistinct. If distinctive physical barriers existed, one would expect to see disjunction(s) as in other parts of the world where barriers have been identified (e.g., Obregón-Barboza, Contreras-Balderas & Lozano-Vilano, 1994). Also, disjunct populations of several species (detailed below) occur between regions or drainages with intervening areas being distinctively drier. Finally, fossil occurrences (*Scleropages* aff. *leichardti* and †*Macquaria antiquus*) further south and north respectively of their descendant's present-day ranges, lend support to the climatic hypothesis. Areas where climate appears to have had little impact include southern VIC (SEV and SWV) and TAS (STAS and NTAS). Climatic differences between each pair of adjacent regions are negligible, yet several species occur in SEV that are lacking from SWV (see below) while NTAS and STAS have no species in common.

Ecology

Ecological factors can be important when considering biogeographic patterns (Endler 1982). Ecological requirements (tolerances) are unknown for most Australian freshwater fishes, but tend to be broad for most due to uncertain habitat permanence under high within- and between-year (and longer term) variations in climate. Species with narrow tolerances are restricted to more permanent (i.e., more mesic) areas. Extinction probability is higher for a narrow habitat specialist unless it also has high migratory abilities; such abilities seem better developed in habitat generalists. Whatever the case, biology is inextricably interwoven with climatic, topographic, and other non-biological factors. The interplay among them will be sorted out only with accumulation of more ecological data than now exist. I leave that to the future.

BIOGEOGRAPHIC PROVINCES

Distributional relationships among regions (defined largely by the arbitrary hydrological scheme of Australian Water Resources Council (1976)) were compared in a search for broader patterns applicable to a landmass the size of Australia. Major factors influencing fish distributions should be most evident at a larger scale, which I term "biogeographic provinces" as defined by Brown, Reichenbacher & Franson (1998); "… provinces are regional areas having a distinctive recent evolutionary history and hence a more or less characteristic biota at the species and subspecies levels." For Australia, the evolutionary history may not be recent, and the "characteristic biota" may include differentiation to the generic or family level.

Designation of provinces often proves controversial, largely due to arguments about criteria (Horton, 1973), e.g., what percentage of endemism and number or percentage of different species is sufficient to separate one province from another, and how spatially identical should species ranges be? I follow Keast's (1959) view, "… whilst it is legitimate to use the zoogeographic sub-region [=province] concept within the Australian continent it should be used only in broad context. … To think of it to any degree in a static or absolute sense is quite misleading."

Opposing features of distinctiveness vs. similarity were quantified by examining species' occurrences among regions. Inland and surrounding coastal regions are shown from a northern coastal region, through inland Australia and then north to south along eastern coastal regions in Fig. 15, southern ones are shown west to east in Fig. 16, and northern coastal regions are presented sequentially from northwest, to northeast, to southeastern Australia in Fig. 17. Each number in the figures represents the distribution of a species, with continuous lines indicating the presence of a species in adjacent regions. For each region, beginning from one direction, all known species are listed in sequence from those with the broadest range to those which are endemic. Once a region has no more, new species are added sequentially in the next, those with the widest ranges first. In this manner, regions were combined into biogeographic provinces based on highest percentages of endemism supported by the greatest number of species' ranges ending at a given boundary. Provinces resulting from hierarchical analyses (Figs. 10-13) were almost fully congruent with provinces hypothesized *a priori* through qualitative inspection of distributional data.

The following regions may be designated or combined into provinces (Fig. 18). SWWA and STAS (the Southwestern and Southern Tasmanian provinces respectively) each are distinctive since both have 100% endemism (Fig. 8) and as a result they do not group with other regions (Figs. 10 and 12). PILB and LEB each has a high percentage of endemics, 42 and 40% respectively (Fig. 8) and hence are designated Pilbara and Central Australian provinces. PILB does not group near to any other region (Figs. 10 and 13), hence supporting its distinctiveness. LEB has close relationships to BULL and BARK (Figs. 10, 11, 13 and 15), and tentatively TORR; hence they are included with LEB in Central Australian Province. WKIM and EKIM contain seven and six endemic species of twenty-nine total for each, 24 and 21% respectively (Fig. 8). When combined, this increases to sixteen endemics (9.5% of Australia's freshwater fishes) out of thirty-nine species total (41% endemic) (Fig. 17). Their close relationship is also borne out in most results (Figs. 10, 12 and 13), justifying their combination as Kimberley Province. SWV and NTAS have endemism values of 22 and 29% (Fig. 8). NTAS has two endemic species, the remaining five are all in common with SWV and SEV. However, substantial difference occurs between SWV and SEV in what is lacking in SWV. Six species occur in SEV but not in SWV, of the non-endemics in SWV all occur in SEV (Fig. 17). Hence there appears to be a unidirectional or superimposed recent barrier between these regions.

Given this distinctiveness, and their combined endemism of 36%, and their consistent grouping together (Figs. 10 and 12) SWV and NTAS are combined into Bass Province.

MDB has 31% endemicity (Fig. 8) and complicated relationships with several surrounding regions (see below) as is demonstrated by its variable position between analyses relative to other regions (Figs. 10, 12 and 13). Among these, SAG has complete similarity to MDB (Fig. 15), and Kulczynski's #2 Coefficient groups them together (Figs. 10 and 11), hence it is included in the Murray-Darling Province. Other surrounding regions are not included as the contribution of each is relatively small (see below). WP is categorized as the Paleo Province by default since it has only one species with no clear relationship to any one specific province or region.

Coastal areas from VOR east and south to SEV are difficult to categorize into provinces. A gradation of species ranges exists (Fig. 17) with no regional boundary being particularly distinctive and low endemism within-regions (Fig. 8). Clearly, the fauna of northern Australia is very different from that of the southeastern coast (Figs. 12, and 17), hence some degree of sub-division seems appropriate. The greatest difference in species' ranges between adjacent regions anywhere around the coastline occurs at the boundary between NEQ and BURD where thirteen species (disregarding those endemic to NEQ) have their southern-most termini; many are congruent at the boundary. Hence, it seems reasonable to propose a Northern Province from VOR east to NEQ. Within this province, endemism rises to thirty-eight species (50%) (Fig. 17), although twenty-five of these "endemics" and thirty-four species total also occur in southern New Guinea (recalculated from Allen (1991)), emphasizing its close faunal relationship with

Australia. Clustering results support the distinctiveness of Northern Province (Figs. 10 and 11), and parsimony analysis also generally supports it, but with a slight incongruence involving SECYP and NEQ (Fig. 13). Three distinctive sub-provinces exist within the Northern Province. The first is referred to a Speciose Northern Sub-province, comprised of DALY, ARNH, EGC, ARCH, and CYP, with high species richness (Fig. 6) and few differences in faunal composition except four species present in DALY and ARNH not shared with the others (Fig. 17). The second, termed the Depauperate Northern Sub-province, consisting of VOR, WGC, NICH, and SGC, is notable for its lower species richness (Fig. 6). Finally, a Northeastern Sub-province consists of SECYP and NEQ, distinctive relative to the other two sub-provinces in lacking several species (Fig. 17). Further, NEQ has six endemics (Fig. 8).

Finally, an Eastern Province is proposed along the east coast from BURD to SEV. Despite there being no species in common at the extremities, no distinctive breaks are present between regions of this province. This north-south gradation is evident even at the drainage scale. Endemism within this province is 31% (Fig. 17). Ordination demonstrates the gradation between regions within the province most clearly (Fig. 12). Other results are mixed; clustering has an incongruence between BURD and FITZ and the other regions (Fig. 10) while parsimony analysis has three incongruences (Fig. 13).

PATTERNS OF RELATEDNESS AND THEIR CAUSES AMONG PROVINCES

Southwestern Province (SWWA): This province has no species in common with any other, suggesting long-term isolation. One family, Lepidogalaxiidae, and two percichthyid genera, *Bostockia* and *Nannatherina*, are endemic. At the generic level its highest similarity is with eastern regions (Table 1). SWV shares three of seven genera (*Galaxias, Galaxiella*, and *Nannoperca*), while MDB is the nearest region also containing *Tandanus*. There are no families in common with northern regions. Faunal relationships clearly lie with southeastern Australia, although only distantly.

No fishes are recorded north of Southwestern Province until the Greenough drainage in PILB, nor east until TORR/SAG (with one possible exception, see Paleo Province). Mean rainfall decreases northward, while mean January maximum temperature rapidly increases (Figs. 4 and 5), making conditions too dry for survival. Within this province, fishes are largely restricted to areas with mean annual rainfall >700 mm.

Chilcott & Humphries (1996) suggested *Galaxiella* may have migrated east-west across southern Australia as recently as Late Pleistocene. Given the aridity and sedimentary record across the Nullabor Plain this is unlikely. Conditions would have been favorable during Late Eocene when rivers supplied abundant sediments, major dune systems formed along the coast, and climate was temperate (Benbow, 1990). Several transgressions of the sea in this region from Eocene to Mid-Miocene also potentially enhanced dispersal opportunities along coastlines (see Introduction). The Nullabor Plain formed 14-16 Ma with final regression of the sea from Eucla Basin about the time paleodrainage development began across southern Australia (Van de Graaff *et al*., 1977; Benbow, 1990). It lacks any signs of integrated surface drainage due to the fractured nature of its limestone, which allows most surface water to seep underground rather than run off (Jennings, 1967; Benbow, 1990). Hence, Miocene would appear the minimum age when fishes could last migrate east-west across southern Australia.

Pilbara Province (PILB): Five of twelve species are endemic (Figs. 6 and 8), however their relationships to other species are poorly understood. The remainder comprise the most widespread species in Australia, found eastward around the coast to at least BURD, including LEB (Figs. 15 and 17).

Pilbara Province is one of the hottest areas of Australia. Mean January maximum temperatures are ca. 42°C in parts (Fig. 5). Mean annual rainfall is <400 mm (Fig. 4). Perennial surface water is scarce, and mostly persists in gorges. Pilbara Province is separated from Kimberley Province by the Great Sandy Desert (Paleo Province), an area with no surface runoff. No data exist to provide an indication of when this paleodrainage developed and hence isolated the two provinces from each other. The only Tertiary sedimentary records, consisting of minor alluvial and lake deposits (Taylor, 1994), are undated.

Kimberley Province (WKIM and EKIM): Endemism is high in this province. In the family Eleotridae, six of nine species are endemic (one endemic genus); Terapontidae, five of nine (one endemic genus); Atherinidae, two of three; Melanotaeniidae, two of five; and Toxotidae, one of two (Table 1). Several endemics have ranges limited to one or two individual rivers. Only sixteen species are widespread to at least east-coast drainages (Fig. 17). Three have more limited distributions east to

DALY, the remaining four occur across northern Australia between ARNH and CYP. Two species in EKIM have disjunct isolated populations, *Melanotaenia nigrans* (Fig. 17) and *M. exquisita* [which is absent between the King George (EKIM) and Daly (DALY) rivers except one record in Pentecost drainage (VOR) (B. Hansen pers. comm.)]. It is likely other relictual populations of similarly distributed fishes may be found in EKIM, e.g., *Pseudomugil gertrudae*, *P. tenellus*, *Denariusa bandata*, and others. Three species are present in Fitzroy drainage (WKIM), occurring eastward through the Northern Province (Fig. 17), but are absent from the remainder of Kimberley Province. They include *Arius midgleyi*, *Anodontiglanis dahli*, and *Craterocephalus stramineus*. *Glossogobius* sp. C occurs as an isolated population in Prince Regent drainage, the nearest records to it being in the Pentecost drainage.

Several explanations exist for the high percentage of endemics. The province contains rugged topography with more gorges than any other part of Australia. Gorges provide refuges for fish during dry periods as they force hyporeic water to the surface. Bathymetic data provides conflicting evidence. A shallow submerged ridge exists to the north of the boundary between WKIM and EKIM, which could have been an important drainage divide during low sea-levels (Fig. 14), limiting opportunities for dispersal and thus increasing isolation. However, it does not explain, and in fact contradicts the close faunal relationship between WKIM and EKIM and the lower faunal similarity between Kimberley and Northern provinces. Perhaps two patterns exist, an older relationship between EKIM and WKIM (e.g., *Craterocephalus lentigenosus*, *Syncomistes trigonicus*, and *Mogurnda* sp. 1) and a more recent one with Northern Province (e.g., *Neosilurus* *ater*, *Melanotaenia exquisita*, *Melanotaenia nigrans*, *Ambassis macleayi*, and *Syncomistes butleri*) (Table 1, Fig. 17). Further phylogenetic work may help clarify this hypothesis.

Northern Province (VOR, DALY, ARNH, WGC, NICH, SGC, EGC, ARCH, CYP, SECYP, and NEQ): The western boundary of this province is marked by the species it lacks relative to regions to the west as outlined under Kimberley Province. The southern boundary has the largest absolute decline in number of species present, from thirty-nine to twenty (Fig. 6) and is the southern limit for thirteen species, the highest change anywhere along the coast of Australia (Fig. 17). Regions within the Northern Province have fourteen endemic species (Fig. 8), four of which are also shared with New Guinea (Allen, 1991). When the whole province is considered, there are twenty-four additional endemics, raising the total to thirty-eight (twenty-five of which are shared with New Guinea) out of seventy-five species (50% endemic) (Fig. 17). Within this province, three sub-provinces may be recognized: Speciose Northern, Depauperate Northern, and Northeastern Sub-province.

Speciose Northern Sub-Province (DALY, ARNH, EGC, ARCH, and CYP): This sub-province is the richest of the province (Fig. 6), with its own distinctive fauna (Fig. 17). Several taxa occur on each side of the Gulf of Carpentaria in the Speciose Northern Sub-province, but not in the Depauperate Northern Sub-province, e.g., *Anodontiglanis dahli*, *Porochilus obbesi*, *Iriatherina werneri*, *Melanotaenia nigrans*, *M.*

trifasciata, *Pseudomugil gertrudae*, *P. tenellus*, *Denariusa bandata*, and *Oxyeleotris nullipora*. An exception is *Hephaestus carbo* which occurs as an isolated population in NICH (Depauperate Northern Sub-province) as well as in the Speciose Northern Sub-province on each side of the Gulf.

The causes of this trend in richness appear climatic. There is a substantial rise in annual mean rainfall from 600 mm to >1000 mm from southern portions of the Depauperate Northern Sub-province to the Speciose Northern Sub-province (Fig. 4). There also is a corresponding decrease in mean January maximum temperature from the upper 30's to the low 30's (Fig. 5). Mean July minimum temperature also increases from 12-15^{o}C to >15^{o}C.

Depauperate Northern Sub-province (VOR, WGC, NICH, SGC, and EGC): There is a decline in richness from the Speciose Northern to the Depauperate Northern Sub-province (Fig. 6); i.e., thirty-nine (ARNH) to thirty (VOR) and twenty-seven (WGC); and thirty-six (EGC) to twenty-nine (SGC). This sub-province is characterized by lower annual rainfall, higher summer maximum temperatures, and lower winter minimum temperatures, as noted above. With the partial exception of NICH, which is fed by large perennial springs, most regions lack several species. Furthermore, several species are rare and patchy in occurrence, but are otherwise widespread and common in other sub-provinces. *Mogurnda mogurnda* occurs in VOR and NICH, but is only known from a single record in SGC, and from two drainages in WGC. *Craterocephalus stercusmuscarum* is only known from a few small collections. *Hypseleotris compressa* is recorded from only VOR and three other drainages (Limmen Bight (WGC), Leichardt, and Norman (SGC)). There are several drainages from which *Glossamia aprion* is recorded, however, it is far less widespread or common than in northern ones. Few records of *Ambassis agrammus* and *A. mulleri* exist, while *Scleropages jardinii* is only recorded from Roper drainage (WGC) and NICH and *Hephaestus carbo* is only known from NICH.

Within the Depauperate Northern Sub-province, *Pingalla gilberti* is the only endemic, while *Scortum barcoo* and *Porochilus argenteus* are not found in the other sub-provinces (Table 1). The latter two are typical of the Central Australian Province and I speculate they are excluded from northern drainages by competition with tropical-adapted fishes.

Northeastern Sub-province (SECYP and NEQ): A significant drop in richness occurs from CYP to SECYP (forty-five to thirty-five) (Fig. 6) and several species have their eastern range limit here (Fig. 17). These changes may be due to several factors, including lower mean winter minimum temperature, and a lack of major rivers due to closeness of the Eastern Highlands to the coast (with exception of Normanby drainage).

NEQ has both high richness (thirty-nine) (Fig. 6) and number of endemics (six) (Fig. 8). This is an unusually high value for richness compared to surrounding drainages and for endemism compared to drainages east of the "endemic line" (Fig. 8). Several interrelated factors likely account for this. The Eastern Highlands are considerably higher (500 - 1622 m) in NEQ than any regions to the north and southward to FITZ (Fig.

3). Although the area of high elevation stretches beyond NEQ, only ranges near the coast experience high mean annual rainfall (>2400 mm); rainfall decreases to <1200 mm a short distance inland (Fig. 4). Summer maximum temperatures also are lower due to higher elevation (Fig. 5). Hence, it provides a refuge with considerably higher rainfall and cooler summer maximum temperature to species likely more widespread when climate permitted. Further evidence for a refuge can be inferred from other fish distributions. Several species have their southern-most limits here, although some are not continuously present northward. For example, *Oxyeleotris aruensis* and *O. fimbriata* occur as isolated southern populations, while *Melanotaenia maccullochi*, *Pseudomugil gertrudae*, *Denariusa bandata*, and *Oxyeleotris nullipora* occur in patches from CYP south into NEQ.

Northern Province and Southern New Guinea: A strong relationship exists between Fly River, New Guinea (as well as most of southern New Guinea) and the Northern Province of Australia, with thirty-four out of seventy-five freshwater fishes (45%) in common (Roberts, 1978; Allen, 1991). Furthermore, four species, *Nematalosa erebi*, *Amniataba percoides*, *Craterocephalus stercusmuscarum*, and *Hephaestus carbo* (and likely others, yet uninvestigated) have apparent sister species in Fly River (increasing commonality to 51%). Presently, Fly River drains to the Southern Pacific Ocean. However, it is hypothesized to have been diverted from a southern route directly into Arafura Sea (Blake & Ollier, 1969) between 35 and 40 Ka by upwarping (Torgersen *et al*., 1988). The Arafura Sea between Southern New Guinea and the Northern Province is shallow, hence regularly exposed during lowered sea-level, which would potentially connect most drainages in Torres Strait west of Cape York Peninsula (Fig. 14).

When did the fish faunas of Australia and New Guinea last meet? Allen & Hoese (1980) suggested severing of the connection was 6.5-8 Ka during the last sea-level rise. While likely correct for hydrological connectivity, it seems unlikely for most freshwater species as a migration route. During Late Pleistocene, a major lake known as Lake Carpentaria existed east of Groote Eylandt during lowered sea-levels (Fig. 14) (Torgersen *et al*., 1983; Jones & Torgersen, 1988). It is not known when the lake first formed, but, for much of its examined history (up to 40 Ka), it was brackish or fresh-to-brackish (Torgersen *et al*., 1988), which may have prevented migration. Furthermore, during lowered sea-level it is thought this area was more arid than at present (Webster & Streten, 1972), hence possibly decreasing available aquatic habitats. Major faunal exchanges are more likely to have last occurred during low sea-levels during Late Miocene (Haq *et al*., 1987) when global climate was warmer and wetter than today (Partridge *et al*., 1995).

An interesting aside is the absence of five of the six most widespread Australian fishes in New Guinea. *Leiopotherapon unicolor* and *Neosilurus hyrtlii* have no known near relatives in New Guinea, *Nematalosa erebi* and *Amniataba percoides* each have likely sister species (largely restricted to Fly River), while *Melanotaenia splendida* has a widespread allopatric subspecies in New Guinea (Allen, 1991). Given their widespread occurrence and broad environmental tolerances (Merrick & Schmida, 1984), these species are most likely of all to have been able to migrate during the last low sea-level, but they are absent. One could speculate many possible reasons for this, i.e., competitive exclusion or incorrect taxonomy, although insufficient evidence exists to warrant further discussion. There are also species with extensive southern New Guinea distributions that do not occur in Australia. Examples include *Arius carinatus* Weber, *A. latirostris* Macleay, *A. macrorhynchus* (Weber), the catfish genera *Cochlefelis*, *Doiichthys*, and *Nedystoma*, *Zenarchopterus novaegunineae* (Weber), *Melanotaenia goldiei* (Macleay), and *Glossamia sandei* (Weber). Furthermore, there are several species with more limited ranges in central southern New Guinea in the middle and upper Fly River that do not occur in Australia (Allen, 1991). Clearly, this region has a long complex history that is poorly understood.

Eastern Province (BURD, FITZ, SEQ, NEN, SEN, and SEV): The Eastern Province is distinctive for its lack of faunal breaks (Fig. 17), its boundary with the Northern Province being due to a sharp decline in richness (Fig. 6) and disappearance of thirteen species from NEQ to BURD (Fig. 17). No particularly distinct faunal breaks occur even at the drainage level until Wilson's Promontory at the southern boundary of the province (see below). Only five endemics occur at the regional scale (Fig. 8). Even when the entire province is considered, endemism only rises to fifteen out of forty-eight species (31% endemic) (Fig. 17).

The differences in richness and the pattern of species occurrence between regions within this province are likely due to climatic effects (Figs. 4 and 5). BURD and FITZ are both the driest and hottest areas on the east coast. From SEQ south to SEV, rainfall steadily increases; however, mean maximum January temperature also decreases. The continental shelf is particularly narrow in southern regions, being broadest offshore of FITZ (Fig. 14).

Biogeography of Burdekin River (BURD) was recently discussed by Pusey *et al*. (1998), who attributed low richness to several factors including Burdekin Falls, substantial volcanic activity, past climatic stress, and low habitat diversity. The area has experienced considerable volcanic activity, as have several regions in eastern Australia (Johnson, 1989). Also, times between eruptions, while not specifically documented, are likely sufficient to allow recolonization and minimize long-term impacts. Past climatic stress is difficult to infer, however, present-day stress is higher than for any other east-coast drainage (Figs. 4 and 5) and would likely have been more so in the past when climate was drier during glacial maxima (Williams, 1984). Most of the drainage receives <1000 mm of rainfall a short distance inland of the coast while southern parts receive <600 mm. Summer maximum temperatures inland of the coast are higher, and winter minimum temperatures are lower. Low habitat diversity was demonstrated by Pusey *et al*. (1998). I consider harsh climatic factors, combined with low habitat diversity as the most parsimonious explanations for low richness, although clearly the falls have excluded some species.

If Burdekin Falls is a barrier, other species should also be present today in surrounding drainages and below the falls, yet lacking from above them, whereas if climate were the cause, species would also not occur in surrounding drainages with similar climate. Pusey *et al*. (1998) demonstrates the falls are a barrier to species known to require estuarine or marine habitats for reproduction, and for three freshwater species;

Pseudomugil signifer, *Glossamia aprion*, and *Oxyeleotris lineolatus*. However, it is unclear whether *O. lineolatus* is native below the falls and for the purposes here I assume it is introduced due to the lack of records from adjacent drainages (see below). *Tandanus tandanus* and *O. lineolatus* are known to be introduced above the falls and are either not present (Pusey, pers. comm.; Pusey *et al*., 1998), or considered introduced (Hogan, pers. comm.) below them respectively. Given both can survive present conditions in the drainage as demonstrated by their introduction and apparent naturalization, the falls hypothesis would appear to be supported. However, they are absent (except one record of *T. tandanus* from Pioneer drainage (FITZ) which may also be introduced) from north of Fitzroy drainage (FITZ) until one encounters Murray and Herbert drainages respectively (NEQ), areas beyond the influence of Burdekin Falls. Hence, the climatic hypothesis is also supported since *T. tandanus* and *O. lineolatus* are also absent from surrounding drainages. Additional arguments presented by Pusey *et al*. (1998) in support of the Burdekin Falls barrier hypothesis include absence of Gobiidae and the lower richness of Eleotridae and Ambassidae relative to NEQ. Again, all these species lacking from Burdekin drainage are absent from Murray or Herbert drainages southward. Hence, evidence for both climatic and waterfall barrier hypotheses can be demonstrated.

J. Stephenson (pers. comm.) (also quoted in Pusey *et al*., 1998) suggested part of the upper Burdekin River formerly flowed into Gilbert drainage (SGC) prior to uplift of McBride Plateau ca. 8-10 Ma, prior to widespread volcanism. This diversion is largely inferred; direct physical evidence is lacking. Pusey *et al*. (1998) suggested this as a possible colonization route for *Neosilurus mollespiculum* (as sp. C), *Porochilus rendahli*, and *Scortum* as they are all "common" in Gulf of Carpentaria drainages (CYP west to ARNH) and uncommon in northeastern drainages. However, the nearest populations appearing closely related to *N. mollespiculum* are in BULL (the species remains unidentified there and may be distinct) and DALY, west to WKIM (*N. pseudospinosus*) (Table 1). It is unrecorded from Gulf of Carpentaria regions. *Porochilus rendahli* is widespread, occurring, albeit patchily and in low abundance, from Brisbane drainage (SEQ) northwards up the entire east coast and across northern Australia (Table 1). *Scortum* also occurs south in Fitzroy drainage (FITZ) and west in the Central Australian Province (Table 1). The phylogenetic position of *Scortum parviceps,* when defined, may help clarify relationships and hence history. Hence, definitive data supporting a western colonization route are lacking. Additional species listed as possible invaders include *Amniataba percoides*, *Hephaestus fuliginosus,* and *Leiopotherapon unicolor*, although all are widespread (Table 1) and could have migrated around the coast. Furthermore, several species present in southern Gulf of Carpentaria regions are absent from east coast regions (Fig. 17, Table 1). If colonization did occur via this route, its "signature" may be been overwritten or confounded by events since; present evidence is equivocal.

FITZ is notable for its isolated southern population of *Oxyeleotris lineolatus,* coastal occurrences of *Macquaria ambigua* and *Scortum hillii* (Table 1), and disjunct northern populations of *Rhadinocentrus ornatus*, *Pseudomugil mellis,* and *Gobiomorphus australis*. A similar species tentatively identified as *S. hillii* is also found in EGC and possibly LEB (Vari, 1978). Other possible relationships could be either to *S. parviceps* in BURD or *S. barcoo* in Central the Australian Province and Depauperate Northern Sub-province. Electrophoretic evidence suggests coastal *M. ambigua* are most closely related to those from MDB rather than LEB (Musyl & Keenan, 1992).

SEQ has a mix of northern and southern species, hence giving it the highest richness (Figs. 6 and 17). Eight species have their southern coastal limit at SEQ, a further five continue south via MDB (Fig. 15). Eight also have their northern-most occurrence in this region (Fig. 15).

SEN is distinctive due to the occurrence of *Macquaria australasica* in Shoalhaven and Hawkesbury drainages; it is otherwise only known from MDB. Dufty (1986) suggested Shoalhaven and Hawkesbury populations may be separate species from each other as well as from MDB based on electrophoretic and morphological data.

Clearly, fish movement between adjacent coastal drainages is neither easy nor frequent along much of the Eastern Province. While sea-level and climatic changes are relatively frequent, few drainages actually connect during low sea-levels (Fig. 14). Hence, to move, fish must rely on long-term processes such as drainage rearrangement. Several species had historically broader ranges along the coast, now fragmented likely by climatic changes. Most species, in both their northern and/or southern range extremities, tend to have their termini independent of co-existing species, suggesting a differential "filter" again likely caused by climate. Evidence supporting a significant long-term (perhaps greater than a few million years) lack of mixing between adjacent (or relatively close) drainages comes from studies on *Tandanus tandanus* (Musyl & Keenan, 1996; Jerry & Woodland, 1997), *Melanotaenia duboulayi* (Crowley, Ivantsoff & Allen, 1986), *Maccullochella* (Rowland, 1993) and *Macquaria australasica* (Dufty, 1986). Other examples demonstrate a higher level of gene flow; *Pseudomugil signifer* exhibits clinal variation along its range (Hadfield, Ivantsoff & Johnston, 1979) and *Macquaria novemaculeata* follows an isolation by distance model with limited gene flow between adjacent populations (Jerry, 1997; Chenoweth & Hughes, 1997; Jerry & Baverstock, 1998; Jerry & Cairns, 1998). Both species spawn and/or occur in upper estuarine areas, and may have a higher proclivity for dispersal between river mouths via riverine flood plumes due to higher salinity tolerance. It is likely *Retropinna semoni*, *Macquaria colonorum*, *Gobiomorphus australis*, *G. coxii*, *Hypseleotris compressa*, *Philypnodon grandiceps*, and *Philypnodon* sp. will all show a similar pattern of minor variation between drainages as they all may also be found in upper estuarine areas. It is also notable that this group of species is dominant and widespread in the southern half of this province where the continental shelf is narrowest. Hence, for some species, the limited evidence suggests distribution patterns along the Eastern Province have been achieved over a vast period of time, while others may be continuing to occasionally exchange individuals today.

Bass Province (SWV and NTAS): Bass Province is distinctive in what it lacks relative to SEV (Eastern Province). Both SWV and NTAS share five species with SEV, however six species present in SEV are absent here (Fig. 17). Each region has two endemic species, *Nannoperca obscura* and *N. variegata* (SWV) and *Galaxias tanycephalus* and *Paragalaxias mesotes* (TAS) (Table 1). Of the latter, the first is a land-locked species derived from the diadromous *G. truttaceus*, while *P. mesotes* is related to other *Paragalaxias* spp. in STAS. One species has its western limit in SWV, five have their southern limit in NTAS (Fig. 16). While the two regions are presently isolated by Bass Strait, it is shallow and was fully exposed during low sea-levels (Fig. 14). Of note is the former drainage patterns during low sea-level in the vicinity of Wilson's Promontory (Fig. 14). The faunal disjunction between Bass and Eastern provinces occurs here, but the former drainage divide appears to the east of it. The bathymetric reconstruction may be misleading, as that portion of the sea-floor is relatively flat making it difficult to predict drainage direction. Shifts in drainage direction would only require minor changes in topography. Of the four species whose ranges end at Wilson's Promontory, two (*Macquaria novemaculeata* and *Philypnodon* sp.) are common, and it is most likely they would survive in Bass Province. The other two (*Gobiomorphus australis* and *G. coxii*) are relatively rare in this portion of their range, hence may be limited by some ecological factor(s). Despite this incongruence, present day data demonstrate the faunal divide is near Wilson's Promontory.

Southern Tasmanian Province (STAS): This province has no shared species, all eight are endemic (Fig. 8). Three galaxiids, *Galaxias auratus*, *G. fontanus*, and *G. johnstoni* appear derived from the diadromous species *G. brevipinnis* and *G. truttaceus* (Merrick & Schmida, 1984). Three *Paragalaxias* spp. occur in Central Plateau lakes. With the exception of *Paragalaxias mesotes* (NTAS), which almost definitely crossed the drainage divide, and possibly *G. parvus* and *G. pedderensis* (STAS), no other fishes have dispersed to or from the Southern Tasmanian Province. The remainder have all likely evolved *in situ*. All have quite restricted ranges, often to one or a few lakes and/or streams (Allen, 1989). This lack of dispersal is likely a combination of being at the extreme southern end of Australia, hence experiencing the coldest extremes during climatic fluctuations, and effective ocean barriers since the continental shelf is quite narrow.

Murray-Darling Province (MDB and SAG): SAG is combined with MDB to form this province as it shares all four species with it (Fig. 15). During low sea-level, all drainages south of Wakefield (SAG) exit southward via the Gulf of St. Vincent (SA) (northern drainages flowing into Spencer Gulf lack freshwater fishes). Present subsurface topography in the Gulf of St. Vincent would divert drainage to between Kangaroo Island and Fleurieu Peninsula, eventually joining the lower Murray (Fig. 14), hence explaining similarities of their fauna. This gulf is relatively shallow, however, minor changes in topography could easily divert drainage to either side of Kangaroo Island and hence away from Murray drainage.

Murray-Darling Province has complex relationships to surrounding regions. It has high similarity to SEQ (thirteen of twenty-eight species), SWV (six of nine species), and LEB (nine of thirty species) (Fig. 15). It is worth noting LEB and SWV have one species in common (it occurs in all southeastern regions), LEB and SEQ have nine (six of which are widespread northern species), and SWV and SEQ have two in common (Fig. 15). Additionally, Murray-Darling Province has nine endemic species (Fig. 8). Overall, it appears to have experienced mixing of faunas from different surrounding regions with distinctive faunas relative to each other, while also maintaining a high degree of endemism. With the possible exception of SWV (which is adjacent), all faunal connections must have occurred across drainage divide barriers.

It is not possible to assume fish distribution patterns of today are directly reflective of historical ones in as far as species ranges in Eastern Province. Some species may have occurred further south in Eastern Province than at present. The following discussion should thus be regarded as tentative; several alternatives may exist.

A peculiar pattern in southeastern Australia is the occurrence of several species southward along the east coast of Australia to around Brisbane drainage (with some occurring southwards until Manning and Hunter drainages), then continuing further south via Murray-Darling Province although absent from other intervening southeastern coastal regions. A number of recent ichthyological papers (Crowley, 1990; Musyl & Keenan, 1992, 1996; Rowland, 1993; Waters *et al*., 1994; Pusey & Kennard, 1996; Pusey *et al*., 1998; and others) have considered river captures across the Eastern Highlands common, based upon geological evidence, and hence used that explanation for this pattern. However, the dominant geomorphic paradigm has shifted to where river captures are thought rare, or non existent there (see Introduction). The Eastern Highlands (ca. 90 Ma) predates most of the fishes, hence they must have crossed it. The alternate possibility of once being widespread throughout southeastern Australian and dispersing via coastal drainages to subsequently become extinct, seems unlikely, especially since there are no gaps in species' ranges along the southeastern coast (Fig. 17). Other confounding difficulties in interpreting this history include the possibility that fish may have crossed the Eastern Highlands at one site or several, on single or multiple occasions, and from alternating directions. Limited evidence suggests options for crossing are limited to only a few sites, however, the number and direction of exchange is going to be difficult to determine.

Several areas of lesser elevation occur in the Eastern Highlands along the boundaries between Eastern and Murray-Darling provinces. These include headwaters of the Clarence, Hunter, Hawkesbury (NSW), Snowy, Tambo, and Maribyrnong (VIC) drainages (Taylor, 1911; Haworth & Ollier, 1992). Broad, low divides also are found between Fitzroy and Burnett drainages (QLD) and MDB and in eastern VIC between Hopkins and Glenelg drainages and MDB (Fig. 3). Upper parts of some of these have experienced volcanism. Activity in Brisbane and Clarence drainages was from 22.6-27.2 Ma, Hunter from 31.8-42.7 Ma, Hawkesbury from 14.4-26.0 Ma, Snowy from 36.9-54.9 Ma, Tambo from 25.8-37.2 Ma, and Maribyrnong from 4.6-7.0 Ma (Johnson, 1989). Many of these dates are likely too old to have contributed to faunal exchange, but it could be modification due to volcanism subsequently made it easier for certain species to cross.

Faunal similarity clearly exists between drainages either side of several low places. Fitzroy drainage has *Macquaria ambigua* among eleven species in common with MDB, which is absent from other coastal drainages (Fig. 15). Clarence drainage has nine species in common with MDB (Fig. 15). Hunter drainage has six species in common, however, a record for *Craterocephalus amniculus* is more notable if it reflects natural occurrence in this drainage. I have considered it introduced due to its recency of collection (1976 and 1980, one and five specimens respectively) and lack of further records despite efforts to find it (Crowley & Ivantsoff, 1990). The Hawkesbury and Shoalhaven drainages are notable for their coastal populations of *Macquaria australasica*; otherwise only found in MDB. They have five species total in common with MDB (Fig. 15). There is nothing unique on the coastal side of the low region in the Snowy, Tambo, or Maribyrnong drainages; however, five species are in common. The same situation holds in other drainages in western VIC, where the divide is particularly low (Fig. 15).

Absence from coastal regions relative to MDB is demonstrated by *Gadopsis bispinosus* in upland streams in the Murray drainage (from the Goulburn River east to the Murrumbidgee River). Seemingly suitable habitat is unoccupied in coastal drainages. *Gadopsis marmoratus* also is absent from coastal NSW drainages, yet occurs over the drainage divide in MDB from Lachlan River north to Condamine River. Given their upland habitat both would be expected to have crossed the Eastern Highlands, one way or another. One species that may hold the key to identifying migration over the Eastern Highlands is *Galaxias olidus*. It occurs at all elevations in virtually all drainages along it on both sides, but is more frequently at higher elevations and in smaller headwaters than any other fish in southeastern Australia.

The relationships between LEB to the north and MDB also are obscure. Musyl & Keenan (1992) suggested MDB and LEB were connected during lower sea-levels via their southern exits to the sea when MDB "previously" flowed further westward into Spencer Gulf (SA) (Williams & Goode, 1978). However, the position of the southern outlet for LEB has never been identified, although one is hypothesized to have existed in

Miocene due to the presence of freshwater dolphins (Tedford *et al*., 1977). Furthermore, earlier suggestions of a more westerly outflow for MDB (Williams & Goode, 1978) have been rejected and its position considered unchanged since Paleocene (Stephenson & Brown, 1989). Others suggested LEB formerly had an outlet into MDB near Broken Hill (NSW) (Tedford *et al*., 1977), although no supporting evidence was presented. Alternative connections may have existed via headwaters of Barcoo River and northwestern portions of MDB, or via Bulloo drainage (BULL).

Clearly the fauna of BULL is most closely related to LEB (Fig. 15), and several of its species have been tentatively classed as intermediate between those of LEB and MDB. Musyl & Keenan (1992) suggested *Macquaria ambigua* from BULL may demonstrate hybrid influences between MDB and LEB stocks. *Melanotaenia "splendida"* appears related to populations of an undescribed *Melanotaenia* from the adjacent Paroo and Warrego rivers in MDB as well as *M. s. tatei* from LEB. Based on two specimens, G. Allen (pers. comm.) could not identify the *Ambassis* sp. from BULL, as they had intermediate counts between *A. mulleri* and *A. agassizii*, in LEB and MDB, respectively. Hence, although tentative, a connection via BULL between MDB and LEB appears likely. How or when this occurred is unknown.

Central Australian Province (BARK, LEB, BULL, and TORR): Four regions are amalgamated on the basis of their high faunal similarity (Figs. 10-15), and their most likely connections to other regions.

LEB has a complex relationship to surrounding regions. Due to its large size it borders many regions, which may account for its complex fauna. Its relationships with MDB have already been discussed. Nine species are shared between LEB and Fitzroy drainage of the Eastern Province, although one of these, *Macquaria ambigua*, is more closely related to MDB populations (see above), and another, *Melanotaenia splendida tatei* (of LEB) is considered more closely related to *M. s. inornata* from northern regions rather than *M. s. splendida* from the east (Allen & Cross, 1978). LEB and Burdekin drainage of the Eastern Province have eight species in common. In both cases, most species in common are widespread across northern and/or eastern Australia. Also, there is only a small segment of shared drainage divide between LEB and Fitzroy drainage. Overall, evidence thus is weak for eastern coastal relationships.

LEB has ten species in common with Flinders drainage (SGC), which, aside from seven widespread species also has *Porochilus argenteus* and *Scortum barcoo* in common. The latter two species only have a limited distribution in the Depauperate Northern Sub-province and Central Australian Province (Table 1). Connections between these provinces have been reported for the headwaters of Cooper drainage (LEB) and Flinders drainage via drainage rearrangement. Based on data and ages from volcanic outflows upper Prairie Creek was rearranged into Flinders River between 5.5 and 3.3 Ma (Coventry, Stephenson & Webb, 1985). Also, the present headwaters of Diamantina drainage are thought to formerly have flowed into Flinders drainage based on geomorphologic changes to the latter in the form of a lessened stream profile (Twidale, 1966). Unfortunately, no firm evidence exists as to when this occurred, but it was likely between 5 Ma to possibly Late Pleistocene (R. Twidale, pers. comm.). Hence, two connections, each in a different direction are identified. Overall, strong evidence, both biological and geological, exists for connections of LEB with northern Australia.

Presently, all drainage in BARK is internal, ending in intermittent lakes in the region's center. Relationships of fishes appear closest to LEB, based on presence of *Melanotaenia splendida tatei* in both. However, aside from this subspecies, all other taxa are common to both LEB and WGC (Fig. 15). The eastern edge of BARK is barely separated from LEB in terms of elevation and heavy runoff might allow fishes to swim today between regions. Further, this low divide is downstream of the headwaters of streams in the area (Fig. 2), hence enhancing the potential for faunal exchange. Alternatively, headwaters of many drainages in WGC are on the northern edge of the Barkley Tableland, also barely separated in terms of elevational difference. It would only take slight tectonic shifts to change drainage directions. Overall evidence suggests the most recent connections were with LEB, hence its placement in that province.

Hydrologic associations of BULL with MDB have been suggested (Lake, 1971). While BULL contains a number of species in common with both MDB and LEB, it also has several species in common with LEB that are not in MDB; the reverse does not occur (Fig. 15) (although see discussion under MDB concerning hybrids). Furthermore, topographically BULL appears to have formerly flowed south of its present terminus, likely into Lake Frome (SA). My only evidence for this is slope of the valley, except for a slight rise over a low divide between Palgamurtie Creek (BULL) and Packsaddle Creek (LEB) between the southern end of Grey Range and northern end of Barrier Range

(NSW) (Fig. 2). When such drainage last occurred is unknown, but is unlikely to have been since aridity enveloped this area (perhaps since at least 1 Ma). Only one species in BULL is not found in surrounding drainages, an unidentified plotosid related to *Neosilurus mollespiculum* and *N. pseudospinosus* from BURD and northwestern regions, respectively. Presumably, this species was once more widespread and is a relict. Its true relationships are unlikely to be clarified unless further material becomes available.

Only one species is recorded from TORR (Fig. 6), and is tentatively identified as *Craterocephalus eyresii*, although this is likely incorrect. *Craterocephalus eyresii* was reviewed by Crowley & Ivantsoff (1990), resulting in separation into four species. Unfortunately, no material from TORR was examined. Its closest affinities are probably to LEB, given their close geographic proximity, and it is thus tentatively included in Central Australian Province.

Paleo Province (WP): Paleo Province contains former connections to surrounding drainages that were severed as aridity began in Mid Miocene (Van de Graaff *et al*., 1977). Six paleodrainage catchments exist relative to their former connections to surrounding drainages: Paleo-Victoria, Paleo-Sturt, Paleo-Internal, Paleo-Oakover, Paleo-Southwestern, and Paleo-Southern (Fig. 18). Most of this province in NT formerly drained into Victoria drainage, northern and middle WA drained into Oakover drainage and through the Great Sandy Desert, southwestern WA drained into Swan drainage, and those north of it in Southwestern Province, southern portions of WA and all of SA drained into the Great Australian Bight. Only a few records of *Leiopotherapon unicolor* are known from this vast region, which remains relatively unexplored in WA and SA. The only unusual record of this species (WAM) is from the southern draining Raeside Paleoriver (WA), which drains into the Great Australian Bight. It is yet to be confirmed if this record is valid, as only one collection exists. Former drainage connections within WP could have easily allowed northern fishes to migrate across Australia via an inland route, rather than around the coastal fringe. The former headwaters of Paleo-Victoria drainage are adjacent to those of Paleo-Oakover drainage, BARK, and LEB which clearly potentially enhances faunal exchange across a major area of Australia. However, when this may have last been possible is unknown since no deposits have been dated from the majority of this province.

CONCLUSIONS

The most striking pattern shown in the distribution of freshwater fishes across Australia is endemism. Most provinces in southern, central, and western parts of the continent have a large proportion of endemics, whereas Northern and Eastern provinces, with exception of NEQ in the latter, have few. The pattern results from isolation due to aridity and drainage divides. Low endemism in Northern Province must be a result of high drainage connectivity during lowered sea level (Fig. 15), preventing isolation sufficient to promote local speciation. Low endemism in Eastern Province is more difficult to explain. Drainages appear to have been long isolated, even during lowered sea levels, yet faunal patterns suggest no distinct barriers and only short-term isolation. Hence, climate seems the most likely cause of species' distributional limits.

Fossil evidence (Appendix I) demonstrates persistence of certain families and genera in freshwaters of Australia over at least the last 30-45 My. The record is strongly biased toward larger taxa, with most fossils of families containing species longer than 20 cm; smaller taxa are rarely found. Given the small size of many Australian species, their fluvial habitats where fossilization may be a rare event, and a general lack of small, whole fossils of any kind, this is not surprising. Crowley (1990) nonetheless suggested craterocephalids and possibly melanotaeniids have existed for a long time. Earlier hypotheses (Whitley, 1959; Allen, 1982; Merrick & Schmida, 1984; Williams & Allen, 1987; Allen, 1989) of the recent radiation of Australian groups in general seem unlikely.

Further, Plio-Pleistocene phenomena seem to have had little influence on expansions of ranges for most of the Australian Continent. Lowered sea-levels potentially connected SWV and NTAS, Gulf of Carpentaria regions and New Guinea, Cambridge Gulf regions, SAG and MDB, and drainages within FITZ (Fig. 15), however, the rest of Australia's coastline remained essentially uninfluenced by sea-level changes. Examination of drainage patterns during lowered sea-levels clearly establishes many hypotheses for testing. Some low sea-level divides occurred at boundaries between regions (i.e., BURD and FITZ, and FITZ and SEQ), while others do not match at all (i.e., bathymetry would predict EKIM to be similar to VOR and DALY rather to WKIM, and the boundary between SEV and SWV also does not match the presumptive drainage divide). Where widespread species cross faunal breaks, they should show discontinuities similar in degree of relatedness to populations in surrounding drainages if barriers are geomorphic rather than climatic or ecologic.

Movements between drainages in regions not influenced by sea-level changes appear likely only over very long time-scales, especially given the geologic stability of Australia. Interacting with this process are both long- and short-term climatic changes. However, I doubt short-term changes have played a major role in allowing species ranges to expand in areas not influenced by sea-level change. The amount of climate change every 100 Ky is considerable, and, if extinction occurs, may operate over too short a period of time for recolonization given the difficulty of moving between drainages. Further, when sea levels are lowest, climate is typically driest in the tropics (Williams, 1984), possibly countering opportunities for dispersal there.

Interpretation of relationships between inland drainages (LEB, BULL, and MDB) and surrounding regions is difficult. However, the following seems clear, fishes have been exchanged between the Northern Province and LEB, LEB and BULL, MDB and BULL and/or LEB, MDB and SWV, MDB and one or more of FITZ, SEQ, and NEN, and possibly also between SEN and SEV (Fig. 16). Some species are common to many regions, some are shared by only a few, and some by only two. Few species have common range boundaries. Why might some species have been exchanged and others not (assuming the cause of exchange did not discriminate between species)? It seems likely the relationship between populations of widespread species will be complex and difficult to unravel, due to possible faunal exchange from several regions and different and possibly multiple times and/or directions. An additional difficulty in interpreting patterns of species occurrence among these regions is the question of how and when fish crossed a drainage divide. Among situations where such crossings are indicated, the drainage rearrangement between Flinders River and Praire Creek (SGC and LEB) is well defined and dated (Coventry *et al*., 1985). One other, the location of connection between LEB and BULL (see Discussion) appears intuitively obvious, although undated. To my knowledge, no other locations or mechanisms by which other connections might have occurred are obvious. Based on differences between likelihood of movement between adjacent *versus* non-adjacent drainages, I predict when a species occurs on both sides of non-adjacent divides that populations on each side will be more similar to those in adjacent drainages than to each other.

Excepting parts of northern Australia, coexisting congeners are unusual, except for Galaxiidae, Pseudomugilidae, Percichthyidae, *Philypnodon*, and *Hypseleotris*. *Craterocephalus* spp. often are sympatric, but the congeners are of distinct lineages

(Crowley, 1990), with species within a lineage never sympatric except perhaps in one habitat at Dalhousie Springs (LEB; Unmack 1995). This suggests when congeners come into contact, sympatry is temporary, ending in extinction of one taxon and/or hybridization after mixing, another potential hypothesis for testing.

Today, biogeographic studies lacking phylogenetic data are uncommon. Furthermore, the techniques applied here are not commonly used. Few studies of this nature have combined analytical techniques (see, however, Hugueny & Lévêque, 1994). Most examine data using only one technique; either clustering (Warren, et al., 1991), ordination, (Reshetnikov & Shakirova, 1993) or parsimony analysis (Watanabe, 1998). Clearly, a minimum combination of clustering and ordination should be used as they to some extent complement each other’s weaknesses. Phylogenetic data are lacking for fishes over most of the world, and this situation likely will continue for some time. I suggest the present type of study based on distributional and geologic data is a useful precursor to phylogenetic studies, as it provides testable hypotheses that would otherwise be unavailable until far into the future.