



Biogeography of Australian freshwater fishes

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Abstract

Aim To investigate biogeographic patterns of obligate freshwater fishes.

Location Australia.

Methods Similarity indices, parsimony analysis, and drainage-based plots of species' ranges were used to identify patterns.

Results Relationships among regions were deduced largely by concordance between methodologies, then summarized into a proposed series of faunal provinces.

Main conclusions The most striking pattern was in the incidence of endemism across the continent. Provinces in southern, central, and western Australia have high numbers of endemic fishes, presumably resulting from isolation by aridity and drainage divides. With exception of one region, northern and eastern Australia provinces have few endemics, probably explained in the north by high drainage connectivity during times of lowered sea levels. This does not account for low endemism in the east because drainages appear to have remained isolated during lowered sea levels and patterns suggest an absence of distinct barriers of other kinds. By default, climate again seems the most probable cause of species' distributional limits. Whatever the case, most patterns were almost certainly established in the distant past, perhaps as early as Miocene. Influences of Plio–Pleistocene events on broad patterns of freshwater fish distributions seem minimal.

Keywords

Freshwater biogeography, distributional patterns, similarity coefficients, multidimensional scaling, parsimony analysis.

INTRODUCTION

Australia¹, because of its age, stability, and aridity, presents a unique situation for investigating freshwater biogeography. The continent began to break its connections with others 95 Ma (Veevers & Eittrheim, 1988) and was fully severed by 37 Ma (Veevers, 1984). It lacks significant relief because the last major orogenic event in eastern Australia was ~90 Ma and other mountains are even older (Veevers, 1984). Its broad latitudinal spread (~40°) buffered it from loss of any major climatic type (i.e. temperate, tropical) by continental drift of 30° northward from Antarctica over the time of general global cooling in Tertiary. The last 15 Myr

have seen increased drying, resulting in decreased surface water in drainages mostly established by Palaeocene. Although glaciations were geographically limited, considerable attention until now has been focused on Pleistocene events, especially the last glacial maximum.

How one should approach biogeographic study of such a landmass can be contentious. Debate between vicariance and dispersalist biogeographers has, however, subsided, with vicariance presently considered more common (Humphries & Parenti, 1986). Today's arguments mostly centre around algorithms, phylogenetic techniques, and artificial three-taxon data sets. A further 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) and seek concordance between and among results.

In contrast to vagile terrestrial species, freshwater organisms (e.g. fishes) suffer unique biogeographic constraints. A freshwater fish is one which cannot survive any life-cycle stage in seawater for more than a short time. Furthermore, an ability to move in response to climate or geological

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¹Unless 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.

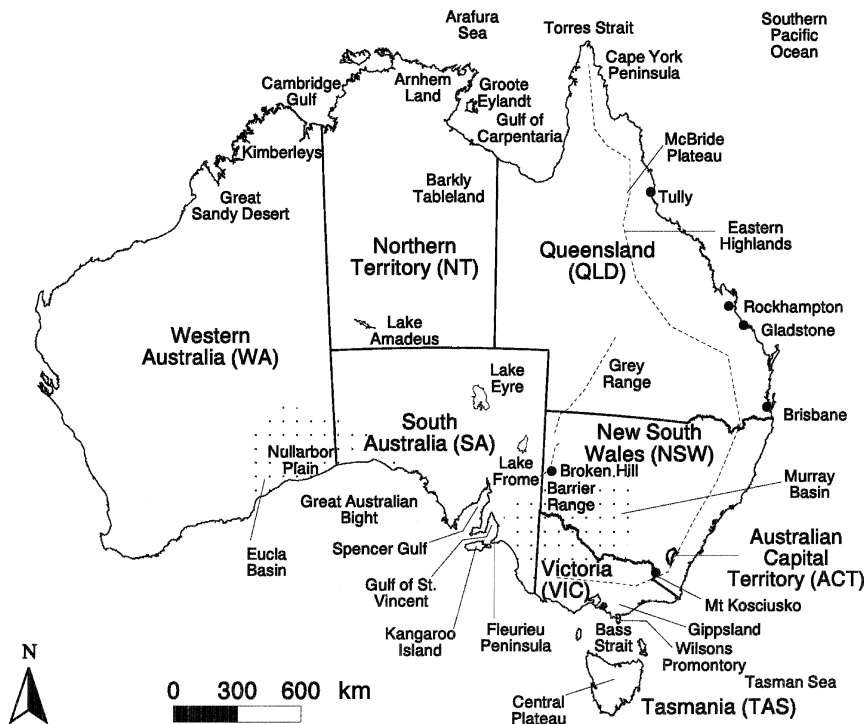


Figure 1 Australian place names used in text.

change is limited to connectivity of fresh waters. Hence, opportunity for range expansion between separate watersheds is limited to rare events such as drainage re-arrangements, temporary hydrologic connectivity over drainage divides, changes in continental shelf width and depth when sea-levels change which influences connectivity, and perhaps pulses of freshwater into oceans. Given the difficulties of dispersal, extinction is far more possible than colonization, and due to any number of factors, both deterministic (climatic change) and stochastic (disease, volcanism, inter-specific factors, etc.).

While the antiquity of some Australian groups (e.g. lungfishes and bony tongues), has long been recognized, many suggest relatively recent radiation of others (Whitley, 1959; Allen, 1982; Merrick & Schmida, 1984; Williams & Allen, 1987; Allen, 1989). This is partly because of unsubstantiated beliefs that because most Australian fish families are secondarily freshwater (Myers, 1938), they moved inland only in the last few million years. Others have 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 Palaeocene based on the conservative nature of modern atherinimorph osteology. Her's was the first attempt to integrate distributional patterns and phylogenies of an Australian fish family to the known geological record.

The present work reports investigations of biogeographic patterns of the freshwater ichthyofauna within Australia. Richness and endemism are quantified and patterns identi-

fied 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 patterns are hypothesized and compared with geological and climatic records, allowing biogeographic provinces for fishes to be more clearly defined. The results should be viewed as working hypotheses to be tested by phylogenetic analysis. While some may argue biogeographic studies lacking *a priori* phylogenetic data are unfalsifiable, I provide testable hypotheses that are directly refutable in hope of stimulating additional research.

Geological and climatic setting

General background

The western two-thirds of Australia have exposed Precambrian blocks (3.5–2.5 Gy) separated by Phanerozoic basins; exposed Phanerozoic fold belts alternate with younger basins in the eastern third. Except for the Arafura and Tasman seas² and with exception of a last continental transgression during mid-Cretaceous, Australian shorelines have remained in about the same configuration for the last 300 Myr (Veevers, 1984). As noted above, the most recent major orogeny was 90 Ma along the Eastern Highlands. All major sedimentary basins (hence river basins) of today were established by Palaeocene (Veevers, 1991). Since then, the land mass has been relatively quiescent with mostly only minor, continent-wide uplift and subsidence (Wasson, 1982).

²Place names are in Fig. 1.

Recent geomorphological work has seriously challenged long-standing, northern-hemisphere-based paradigms of landform evolution (Gale, 1992; Nott, 1995; Twidale & Campbell, 1995; Twidale, 1997). For example, parts of the Kimberleys (WA) are, at 700 Myr, one of the oldest known, continuously exposed landforms in the world (Ollier *et al.*, 1988). Incredibly low erosion rates have been calculated. Nott (1996) detected only ~500 m of escarpment retreat on Grootte Eylandt (NT) over the last 100 Myr Bierman & Turner (1995) recorded mean weathering/erosion rates of $0.7 \pm 1 \text{ mm Myr}^{-1}$ on inselbergs (granitic domes). With few exceptions (e.g. O'Sullivan *et al.*, 1999), erosion rates are usually $< 10 \text{ m Myr}^{-1}$ for the entire Mesozoic and Cainozoic (Gale, 1992).

Glaciation

The last major glaciation was during Permian. Since then, glaciers were restricted to Mount Kosciusko (NSW) and parts of the Central Plateau (TAS) during Pleistocene (Colhoun & Peterson, 1986).

Volcanism

In terms of extent (although not by volume), one of the greatest basaltic provinces in the world stretches 4400 km, with some gaps of up to 500 km, from Torres Strait in north-eastern Australia southward along the eastern mountains into TAS then westward into south-eastern SA (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 south-eastern SA. Three broad types are recognized: lava fields, leucitites, and central volcanos. 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 random. Lava-field activity began ~70 Ma with a major pulse between 55 and 30 Ma. There was little activity 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 activity ceased in NSW, with small areas continuing in QLD, VIC, and SA as noted above. Causes of volcanic activity are unresolved; however, central volcanoes and leucitites appear related to a hotspot trail and lava fields to post-rifting uplift that led to the formation of the Eastern Highlands.

Long-term sea-level changes

Causes of long-term sea-level change include changes in water quantity, uplift and subsidence of continental margins, and volume of ocean basins (Partridge *et al.*, 1995). A significant portion of Australia was inundated by shallow seas in mid-Cretaceous (Aptium-Albian) (Frakes *et al.*, 1987a). Up to four emergent areas remained, south-western WA, northern WA and parts of adjacent NT, and the Eastern Highlands (including TAS), the last separated midway by a seaway in the vicinity of Brisbane (QLD). Withdrawal was probably a combination of broad, contin-

ental uplift and decreasing sea-levels. Global mean sea-level [ignoring Milankovitch-scale (i.e. glacial) fluctuations] decreased on average throughout Tertiary, and was at its lowest (~100 m) several times over the past 10 Myr (Haq *et al.*, 1987).

Throughout Tertiary, submergence was limited largely to coastal margins in three major periods, during each of which several transgressions may have occurred. First was in Eocene, when southern and western coastlines were affected from eastern VIC through mid-northern WA. The most significant inundation included parts of lower Murray Basin (SA, VIC, and NSW), western Gippsland and Bass Strait (VIC), and the Great Australian Bight (SA and WA) (McGowran, 1989). Secondly, Oligocene is generally regarded as a time of lowered seas; however, a second transgression occurred during late Oligocene to early Miocene, flooding the Murray and Eucla basins (SA and WA). Flooding of the Murray Basin lasted for ~20 Myr (from 32 Ma; Brown & Radke, 1989), then the sea retreated in mid-Miocene (~10 Ma). A further, final transgression into the Murray Basin was in late Miocene to early Pliocene (Frakes *et al.*, 1987b; Stephenson & Brown, 1989), however, Eucla Basin had by then been uplifted and was not affected (Jennings, 1967; Benbow, 1990). Connections between the Australian mainland and New Guinea (Doutch, 1972), and probably also 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 south-eastern highlands and the lowest point is Lake Eyre (SA) 16 m below sea-level. The continent consists of a plateau in the western portion and lowlands 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

Global climate is influenced by many factors (Partridge *et al.*, 1995), some with slow gradual impacts, others with dramatic short- and long-term effects. Continental movements may have significant influences on ocean currents, in turn influencing climate. During Tertiary, considerable areas of continents were uplifted, causing both change in atmospheric circulation and decreased temperature. Uplift further promotes weathering and erosion, increasing exposure of silicate rocks whose weathering results in removal of atmospheric carbon dioxide 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 decreases by as much as 200 m and important albedo effects.

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 major ice sheets forming on Antarctica, and the second to establishing ice sheets in the northern hemisphere (Burckle, 1995). Development of polar ice caps had critical influence

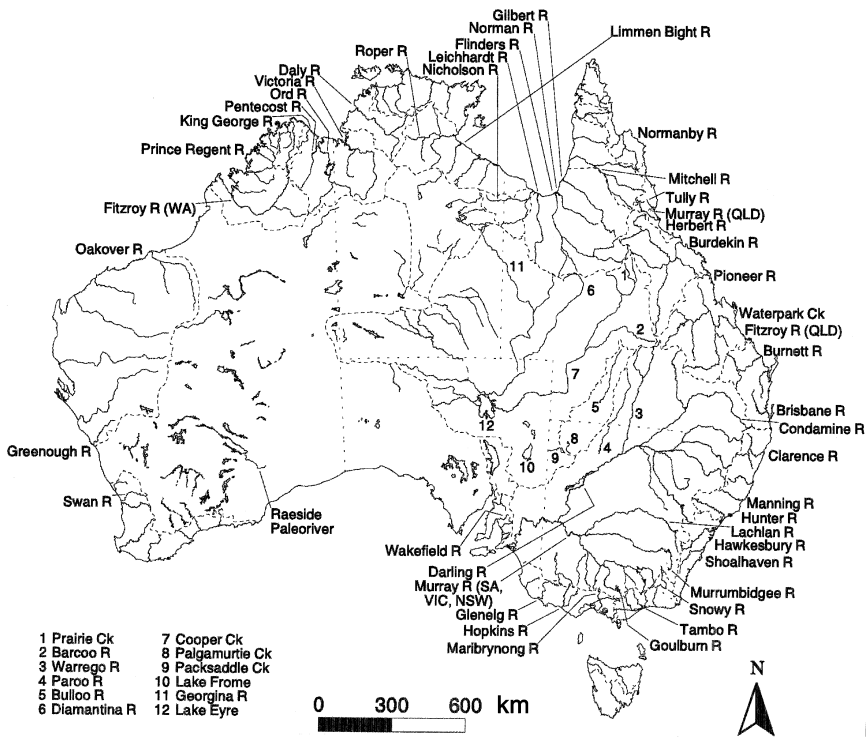


Figure 2 Australian river names used in text.

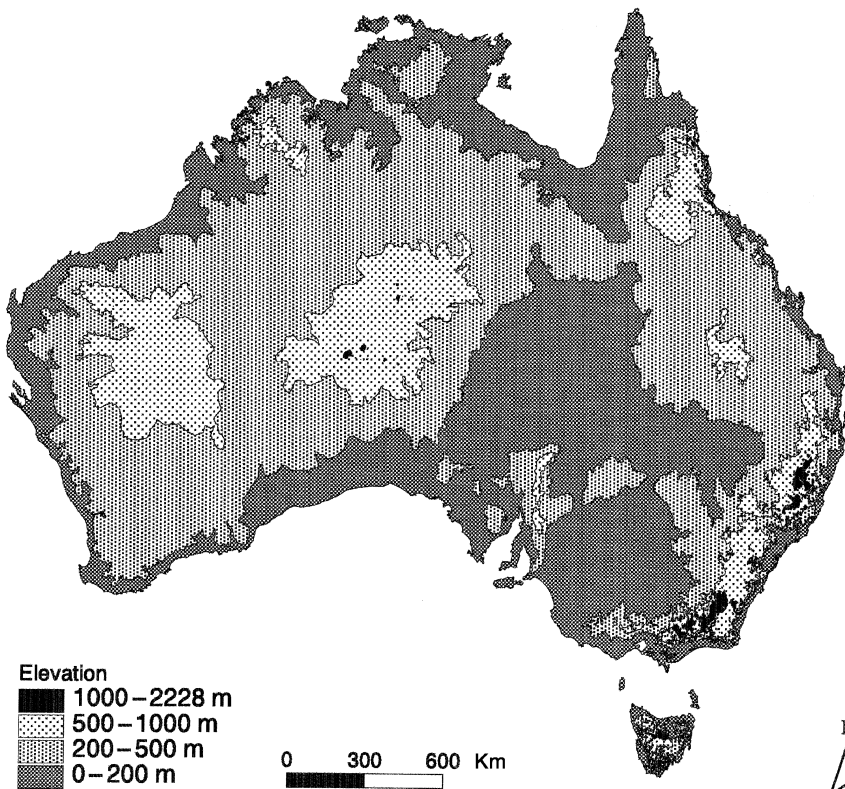


Figure 3 Australian elevations at 30 arc-second (*c.* 1 km) resolution from the US Geological Survey GLOBE project.

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 occur for 100 and 10 Kyr respectively and are controlled by Milankovitch cycles, probably responsible for short-term climatic fluctuations throughout earth's history (Bennett, 1990).

Australia had minor areas of tectonic uplift over the last 90 Myr which had little influence on climate. Northward continental drift, however, had significant influence by moving the continent towards warmer latitudes. At continental breakup (95 Ma), southern-most Australia was near latitude 76° S. The southern and northern coasts were, respectively, near 70° S and 40° N at the beginning of Tertiary. Today they are at ~40 and 10° S (Veevers, 1984). With separation from Antarctica, Australia initially drifted northward at 4.4 mm year⁻¹ from 95 to 49 Ma, increasing to 10 mm from 49 to 44 Ma, then to 20 mm year⁻¹, which continues today (Veevers *et al.*, 1990). About 30 Ma this displacement allowed the Circum-Antarctic Current to flow unimpeded between Australia and Antarctica. With deep water developing between South America and Antarctica around 23 Ma (Lawver *et al.*, 1992), the current became circumpolar and prevented the mixing of warm northern currents around the pole (Burckle, 1995).

Botanical evidence for climate change

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

Through modelling plant growth relative to environmental factors, Nix (1982) suggested conditions similar to today's have existed for 150 Myr, with increasing aridity and expansion of arid zones since mid-Miocene. Furthermore, although boundaries have shifted, similar conditions persist in parts of various regions. Hence, with northward drift into warmer latitudes combined with global climate cooling, Australia maintained a broad range of climatic and vegetative types.

Geological evidence for developing aridity

Examination of palaeodrainages in WA led Van de Graaff *et al.* (1977) to suggest cessation in mid-Miocene of water volumes sufficient to modify drainages. This was supported by Clarke (1994), by adding that gypsum precipitation beginning in early 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 Palaeo-Lake Bungunnia (SA, VIC, and NSW) at ~0.5 Ma (Zhisheng *et al.*, 1986).

Present climate

Figures 4 & 5 show today's mean annual rainfall and January maximum temperature. Around 70% of Australia is considered arid. Southern areas, including south-western WA, VIC, TAS, and south-eastern NSW all share similar Mediterranean climates with cold, wet winters and hot, dry summers. Northern zones have tropical climates with 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 7664 mm at Mt Bellenden Ker (QLD) (Bonell, 1988).

Past ichthyological work

The Australian freshwater ichthyofauna has long been recognized as distinctive relative to the rest of the world. However, few papers have dealt with biogeography of the entire fauna as related to other continents. Most contain short references to specific groups which highlight 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 South-east Asia based on living *Scleropages* spp. He also noted that many of Australia's genera were endemic and a scarcity of 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* in both continents (although the latter also occurred in Asia and Europe, Grande, 1996). Whitley (1943) discussed similarity of species from Australia & New Guinea. Darlington (1957) summarized fish family distributions of the world, including Australian groups and 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 numbers of 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 numbers of genera and species of each family, and Banarescu (1990) provided an account of the families discussed by McDowall based on Myers (1938)

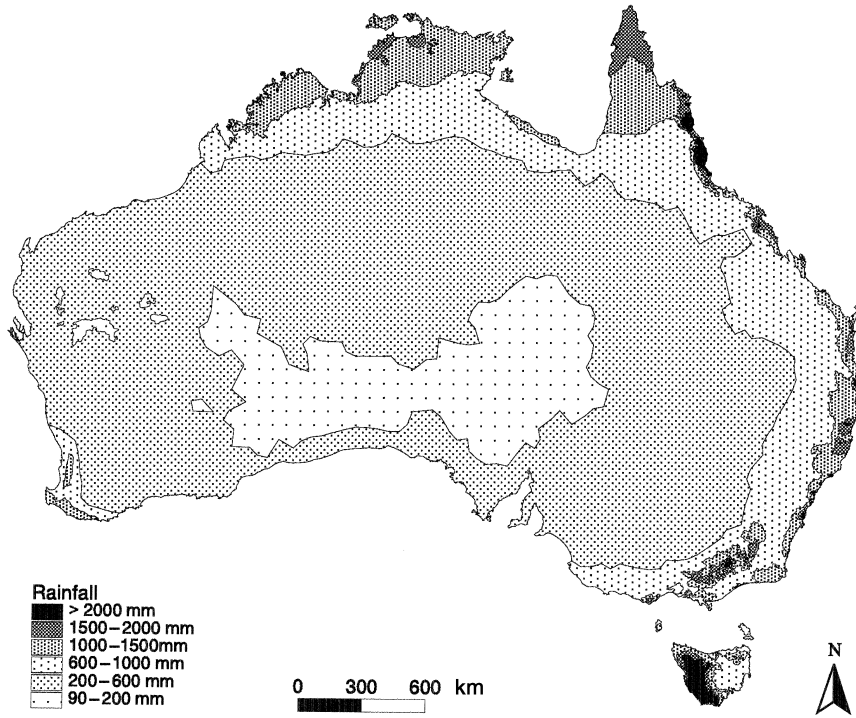


Figure 4 Australian mean annual rainfall based on the period 1961–1990 at $0.025 \times 0.025^\circ$ resolution. Modified from Australian Commonwealth Bureau of Meteorology.

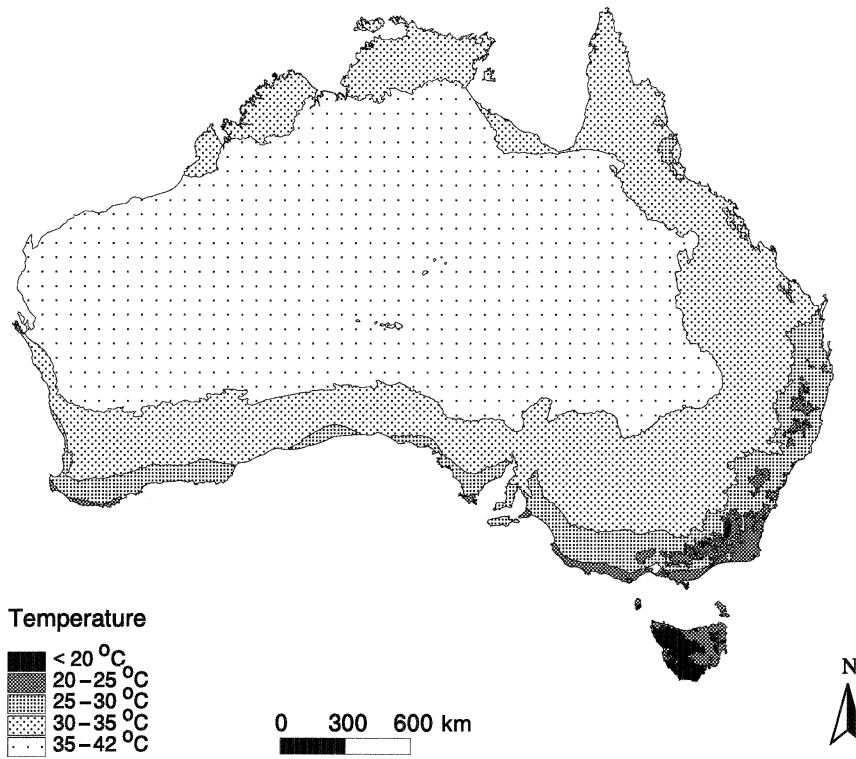


Figure 5 Australian mean January maximum temperature based on the period 1961–1990 at $0.025 \times 0.025^\circ$ resolution. Modified from Australian Commonwealth Bureau of Meteorology.

categories rather than a distributional one. The first construction of biogeographic regions based on fishes and molluscs 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 minor modification [Australian Water Resources Council (AWRC), 1976], remains in use today (Merrick & Schmida, 1984; Allen, 1989).

Fossil fishes

Only some fossil taxa are recorded in the primary literature (Unmack, 1999), and besides the records of Hills (1934, 1943, 1946), they are rarely identified beyond family (and then only tentatively) and sometimes not beyond 'fish.' Neoceratodontid fossils are relatively well known (Kemp & Molnar, 1981; Kemp 1982a, b, 1992, 1993, 1997a, b). Around thirteen neoceratodontids were present during Tertiary (and earlier) through Miocene from LEB, MDB, Gulf of Carpentaria (QLD), and coastal drainages between Brisbane and Rockhampton (QLD). The one living species, *Neoceratodus forsteri*³, has survived for at least 100 Myr (Kemp & Molnar, 1981). Several neoceratodontids had geographical ranges similar to extant fishes, suggesting either present-day fish distributions were attained prior to Miocene or barriers between drainages were since overcome.

Most knowledge of Australian 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* in 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 some taxa are provided by fossils. †*Macquaria antiquus* (Hills), an ancestor to *M. colonorum*–*M. novemaculeata*, and *Scleropages* cf. *leichardti*, are from Eocene deposits (>45 Ma) (Hills, 1934; Vickers-Rich & Molnar, 1996). A terapontid is also recorded from the Eocene (Turner, 1981, 1982; Henstridge & Missen, 1982). *Maccullochella 'macquariensis'* is recorded from two deposits dating between 13.6 and 17.1 and 12–21 Ma (Hills, 1946; Tulip *et al.*, 1982; Johnson, 1989). Excepting the following, fossil actinopterygians have representatives living today in the same geographical areas. The record of †*M. antiquus* is about 250 km further north than the present distributional limits of its descendants. Likewise, the record of *Scleropages* cf. *leichardti* at Gladstone (QLD) is in the next drainage south of its descendant's present range and ariid catfish lived in Miocene around Lake Eyre (SA), where they no longer occur (Pledge, 1984; Estes, 1984).

Conditions allowing fish movements between drainages

A frequent explanation for a fish species on opposite sides of a divide is 'river capture.' Bishop (1995), however, provided a geomorphological review of such drainage rearrangements in bedrock systems, identifying three possible types: beheading, capture, and diversion, with the last further divided into channel migration, divide-topping catastrophies, and tectonism. 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 such 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, concluding that drainage divides along the Eastern Highlands have remained essentially unchanged during Tertiary (Van der Beek *et al.*, 1999). However, this issue remains controversial, and some evidence for changes to drainage boundaries does exist (Taylor *et al.*, 1985; Erskine & Fityus, 1998; Pain *et al.*, 1999) some of which is yet to be critically examined. Furthermore, conclusive evidence for rearrangements is difficult to obtain. Present debates centre on whether drainage rearrangements occurred during mid-Cretaceous through early Tertiary (e.g. Ollier & Pain, 1994, 1996; Ollier, 1995). This has important consequences for past biogeographic work (Musyl & Keenan, 1992, 1996; Rowland, 1993; Waters *et al.*, 1994; Pusey & Kennard, 1996; Hurwood & Hughes, 1998; Pusey *et al.*, 1998), which emphasized drainage rearrangements as explanations of observed patterns. Given the age of drainage rearrangements (if they occurred), they would have little influence on today's fishes. Some evidence clearly demonstrates, nonetheless, some fishes have crossed the Eastern Highlands (Crowley, 1990; Hurwood & Hughes, 1998, this study). 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 divide might also be likely to cause changes via tectonic diversion through associated uplift, concurrent to and continuing after extrusion of lava (P. Wellman, pers. comm.). Most lava outflows would have little effect as they always move downhill, and the only way which could divert a waterway would be to dam it high enough to overtop the divide which is most likely to occur where the divide is very low (a not uncommon situation in some areas). However, most volcanic activity occurred prior to 30 Ma (Johnson, 1989) and thus probably had little, if any effect, on today's fishes.

³Unless otherwise noted, nomenclatural authorities are provided in Table 1.

Table 1 continued

Taxa	Region																Figure																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	F14	F15	F16								
<i>H. sp. A</i> Midgley's carp gudgeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	1	1	-	-	-	7	32	90								
<i>H. sp. B</i> Lake's carp gudgeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	9	38	-									
<i>H. sp. C</i> Murray carp gudgeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	71	47	-									
<i>H. sp. D</i> Katherine River carp gudgeon	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	62	-	-							
<i>Kimberleyeleotris notata</i> Hoese & Allen	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	44	-	-					
<i>K. hutchinsi</i> Hoese & Allen	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	45	-	-				
<i>Milhyringa veritas</i> Whitley	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	12	-				
<i>Mogurnda adpersa</i> (Castelnau)	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	1	-	-	-	-	-	-	1	-	-	-	-	-	19	25	86	-	-	-					
<i>M. mogurnda</i> (Richardson)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	-	-				
<i>M. oligolepis</i> Allen & Jenkins	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	27	-	-				
<i>M. olivicola</i> Allen & Jenkins	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
<i>Ophieleotris aporos</i> (Bleeker)	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	-				
<i>Oxyeleotris anuensis</i> (Weber)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	81	-	-				
<i>O. fimbriata</i> Weber	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	82	-	-			
<i>O. gyritoides</i> (Bleeker)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79	-	-			
<i>O. lineolatus</i> (Steindachner)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79	-	-			
<i>O. nullipora</i> Roberts	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79	-	-		
<i>O. selheimi</i> (Macleay)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79	-	-		
<i>Philypnodon grandiceps</i> (Kreff)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79	-	-		
<i>P. sp. dwarf</i> flathead gudgeon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79	-	-		
<i>Govidae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Avuauous acritosus</i> Watson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Chlamydogobius eremius</i> (Zietz)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>C. gloveri</i> Larson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>C. japalpa</i> Larson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>C. micropterus</i> Larson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>C. squamigenus</i> Larson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Glossogobius aureus</i> Akihito & Meguro	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>G. celebius</i> (Valenciennes) Cuvier & Valenciennes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>G. concavifrons</i> (Ramsey & Ogilby)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>G. giurus</i> (Hamilton)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>G. sp. A</i> dwarf goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>G. sp. B</i> Mulgrave goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>G. sp. C</i> square-blotch goby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Stiphodon allen</i> Watson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Kurtidae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Kurtus gulliveri</i> Castelnau	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Banareescu (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 draining both directions (i.e. Two-Oceans Pass, Wyoming, USA). Both this and 'river capture' would primarily affect headwater-dwelling species. Lowered sea-level may also connect the lower reaches of rivers, with the degree of connection depending upon local topography of the continental shelf. Also, inland salt lakes may become fresh, allowing connections across them. Both changes primarily allow lowland fishes to move.

Possibilities for random dispersal of fishes include 'rains' and accidental movement 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 reports are clearly examples of fish movement through overland flow (i.e. Shipway, 1947) rather than falling from the sky, but some clearly indicate that fish have fallen. They must be picked up and deposited nearby because tornado-strength winds of sufficient velocity are of short duration, and if transport is only over short distances, moving fish between drainages is impossible. Clearly, the implications of this type of dispersal are poorly understood. Eggs caught on animal feet/feathers/fur are often used to explain fish appearances, however, not all fishes are susceptible to such transport; only egg-layers could be involved, eggs must be adhesive or in adhesive mud and in shallows where birds or mammals likely walk, or deposited near surface, and must survive at least brief periods of aerial exposure. Then, at least one of each sex must reach adulthood and find each other to mate. Movement via this means has never been documented, although is clearly possible over short distances.

METHODS

An over-riding assumption of this study is that disjunct distributions of today were formerly connected (either instantaneously or over time). In other words, it is deemed impossible for species to 'jump' drainages. This might be violated if several drainages connect during low 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 happen if species go over a divide then at another point cross back into a drainage not adjacent to their original source.

Another assumption is that species as now defined represent monophyletic units. A recognized flaw is adjacent populations 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 near accurate. Through studying additional species, one may 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 such problems 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 distributional changes are simultaneous or otherwise may be difficult. The final assumption of all biogeographic study 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 occupy Australia. Of these, some are marine or estuarine vagrants, while others spend a part of their life cycles in oceanic conditions. All these were excluded and analysis was of 167 species (Table 1).

Valid nomenclature of the 159 named species followed Eschmeyer (1998), except for *Hephaestus tulliensis* (Allen & Pusey, 1999), *Oxyeleotris selheimi*, and seven species described since (Allen & Feinberg, 1998; Allen & Jenkins, 1999⁴; Pusey & Kennard, 2001). Family designations follow Allen (1989) for Galaxiodes and Petromyzontiformes and Kemp (1997b) for Dipnoi. The percichthyid genus *Edelia* is subsumed within *Nannoperca* following Kuitert *et al.* (1996). Eight undescribed species are included, six of which were listed by Allen (1989); in addition I include *Hypseleotris* sp. C (Unmack, 2000) 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 most closely resembles. *Mogurnda*, *Ambassis*, and *Neosilurus* 'false-spined' forms could not be assigned to species because of insufficient numbers of specimens and unusual character combinations. All three were excluded from analyses except calculations of richness. A recently discovered population of *Craterocephalus* in 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*. No formal systematic clarifications have appeared for several cryptic species which have been alluded to based upon genetic evidence within *Tandanus tandanus* (Musyl & Keenan, 1996; Jerry & Woodland, 1997), *M. ambigua* (Musyl & Keenan, 1992), *M. australasica* (Dufty, 1986), *Mogurnda adspersa*, and *M. mogurnda* (M. Adams, pers. comm.); hence all were treated as monotypic.

Museum specimens were primary data sources except for TAS (Frankenberg, 1974; Allen, 1989; Chilcott & Humphries, 1996) and to a lesser extent QLD (Wager, 1993;

⁴Allen & Jenkins (1999) added four *Mogurnda* species to the Australian fauna, two of which were not included as they were published post this analysis [*M. larapintae* (Zietz) and *M. thermophila* Allen & Jenkins]. the only bearing they have on results is to add two endemic species to LEB.

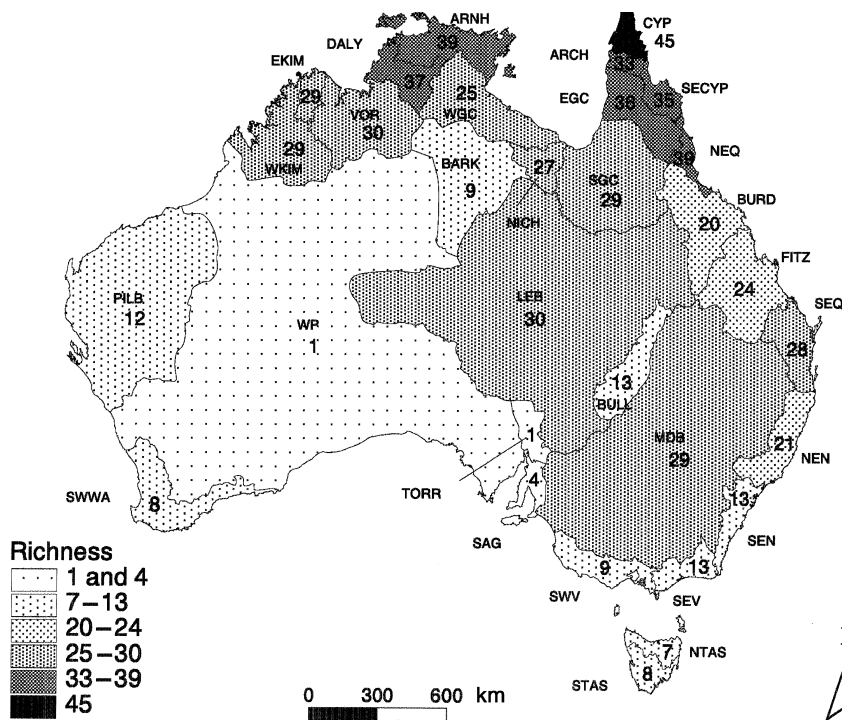


Figure 6 Australian freshwater fish richness (number of species) by region. The number of species with ranges is indicated by differential shading.

Herbert *et al.*, 1995; B. Pusey, M. Kennard & A. Arthington, pers. comm.) and WA (Hutchins, 1981; Allen, 1982, 1989; Allen & Leggett, 1990; Morgan *et al.*, 1998). The following Australian collections were examined primarily by browsing catalogues, AM, NMV, NTM, QM, SAM and WAM. Several museums were also visited in the USA, AMNH, CAS, FMNH, USNM and UMMZ, where all specimens were examined. In Australian museums, identifications were checked only if a record seemed unique or unusual based on primary literature or personal knowledge, however, groups and species commonly misidentified (i.e. Plotosidae, *O. lineolatus*, *O. selheimi*, *Ambassis* spp., and *Hypseleotris* spp.) all were examined. Additional records were obtained from primary and grey literature, or by pers. comm. with specialists for groups or regions. Several, as follows, were assumed present based either on widespread occurrence, or likely artificial gaps because of known lack of sampling. *Scleropages jardinii* is assumed to be present in SGC, *Pseudomugil tenellus* in ARCH, *Ambassis agrammus* in NICH, *A. elongatus* in EGC, and *Hypseleotris compressa* in EKIM, VOR, NICH, EGC, and ARCH. Including these assumptions were trivial, only resulting in minor changes in positions of NICH and SGC when analysing relationships among regions, but richness values are slightly higher as a consequence. Incorrect records and literature citations are available in Unmack (1999).

Presence/absence data were collected at river basin (hereafter drainage) scale, largely following drainage designations in AWRC (1976), with several minor boundary changes. MDB was the only major deviation, which I divided into three drainages; (1) lower Murray River below Darling River

confluence, (2) Murray and (3) Darling rivers each, above their confluence. Drainages were collapsed into thirty-one regions (Fig. 6) for ease of analysis, with boundaries chosen to maximize differences in the presence/absence of fish taxa between adjacent regions. Certain boundaries were somewhat arbitrary; however, this was not expected to have significant effects because some regions with clinal changes lack distinct boundaries. Furthermore, poorly sampled areas were problematic to analyse and judicious merging of drainages reduced this difficulty. These include inaccessible parts of the Kimberleys (WA); drainages between Victoria and Daly rivers (NT); 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 changed some richness and endemism values, but had little effect on overall patterns.

Richness and endemism

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

Similarity coefficients

Data were analysed via Q-mode, which measures the relationship between objects (regions) based on descriptors (taxa) (compared with R-mode which measures the relationship between descriptors based on objects). Similarity coefficients use binary data to measure association between objects. A favourable 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 no. 2, and Ochiai's coefficients were applied. Formulae were given in Legendre & Legendre (1983) and Rohlf (1997). The most notable difference between coefficients is the effect of sample-size which is the strongest in Kulczynski's no. 2, moderate in Ochiai's, and low in the remaining two (Shi, 1993). This is an important consideration when choosing a coefficient, as objects with few species will be more closely ranked where sample-size effect is the highest. Whether a similarity coefficient is metric or non-metric is also 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 available in Unmack (1999).

Clustering

All analyses involving similarity coefficients were conducted using 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 matrix is compared with a cophenetic value matrix of the original data to produce a cophenetic correlation value. If the two 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 very good, good, poor and very poor fits (Rohlf, 1997).

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

Ordination

The advantage of ordination relative to clustering in all objects are compared together rather than by individual pairs, thus 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). As 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 analysed 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 analysed initially in two dimensions, with the number of dimensions increased until they no longer decrease stress significantly (Kruskal, 1964; Rohlf, 1972). As stress decreased to a reasonable value (fair or better) and graphical presentation was restricted to two or three dimensions, data were not analysed beyond three dimensions. Cophenetic correlations were calculated so that 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 nearby, or distant if other dimensions are considered. Based on similarities of several clustering results (see below) only Jaccard's and Kulczynski's no. 2 coefficients were analysed through multidimensional scaling.

Parsimony analysis of endemism

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. Endemism 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 that it is more difficult to change from absence to presence (0–1) than presence to absence (1–0). In other words, extinction is more likely than colonization. All non-informative characters were removed (i.e. taxa found only in one operational taxonomic unit

(OTU), e.g. endemic; and OTUs with only one character e.g. WP and TORR). All of the most parsimonious trees were retained; only the strict consensus of these is presented. Rooting was carried out artificially for easy comparison at separation on the unrooted tree that most closely matched that of 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 modelled using Spatial Analyst 1.1 and ArcView 3.1, based upon a bathymetric 30 arc second grid produced by the Australian Geological Survey Organization.

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 arid regions, all at middle latitudes, are distant from the trend line. When they (WP, TORR, PILB, BULL, BARK, LEB and MDB) are removed, the R^2 value for richness vs. latitude increases to 0.83 (Fig. 7) (Both R^2 values are significant, $P < 0.05$). Richness was not correlated with region size. Several larger regions have low richness values (i.e. WP, PILB and BARK, one, twelve and nine species, respectively), while several with high richness (i.e. CYP and NEQ, forty-five and thirty-nine species, respectively) have similar sizes to some with low richness (i.e. TORR and SAG, one and four species, respectively) (Fig. 6).

Highest endemism is in western, central and southern regions (Fig. 8) so that an 'endemic line' between areas of 'high' and 'low' endemism effectively splits Australia in to two. NEQ was the only region with relatively high endemism (15%) east of the line. Seventy-eight species (47% of the fauna) are found only in a single region, sixty-four in two to seven regions, sixteen in eight to fifteen regions, and only nine in 16–22 regions (Table 1).

Similarity coefficients

All four similarity coefficients produced similar UPGMA trees (Fig. 9). NTSYS warned of ties during calculations; however, the three trees identified as having ties were identical for each 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 no. 2 coefficient was different in positions of PILB, WP, and MDB, and the cluster LEB, BULL, and BARK differed in internal arrangement.

Ball clusters in consensus of single- and complete-link trees of Jaccard's and Dice's coefficients were identical (Fig. 10). Ochiai's differed only in position of W and EKIM

(Fig. 10). Kulczynski's no. 2 differed in positions and composition of the upper cluster, MDB and SAG clustered, and BARK did not cluster with LEB and BULL (Fig. 10).

Non-metric multidimensional scaling

Results were similar for both Jaccard's and Kulczynski's no. 2 coefficients (Fig. 11). 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. 12). Bootstrap values were mostly low, only six branches were $> 50\%$. This was 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

Substantial differences between the two regressions (Fig. 7) are effected by seven regions. WP and TORR have only single species, while PILB, BARK, and BULL all have low richness (< 13 spp.) (Fig. 6). 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, whose groundwater

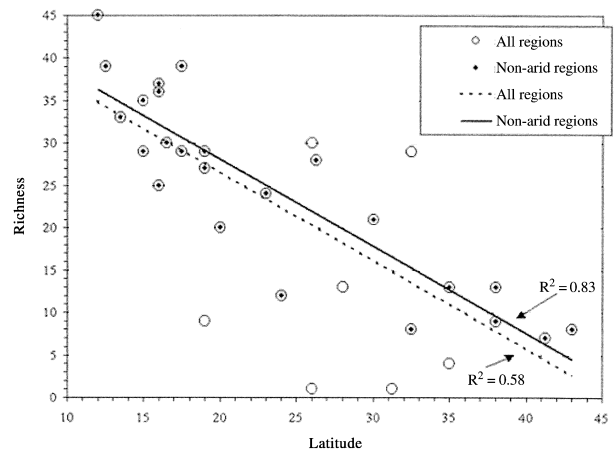


Figure 7 Australian freshwater fish richness (number of species) by region regressed by latitude. The dashed line is a regression of the entire data set, represented by open circles. The solid line is a regression of the data set without the regions WP, TORR, PILB, BARK, BULL, LEB, and MDB, represented by solid circles. Excluded regions all experience considerable aridity (see Fig. 4), except for MDB; WP, LEB, and MDB have particularly broad latitudinal ranges. Both factors likely account for improved fit of the regression when they are excluded.

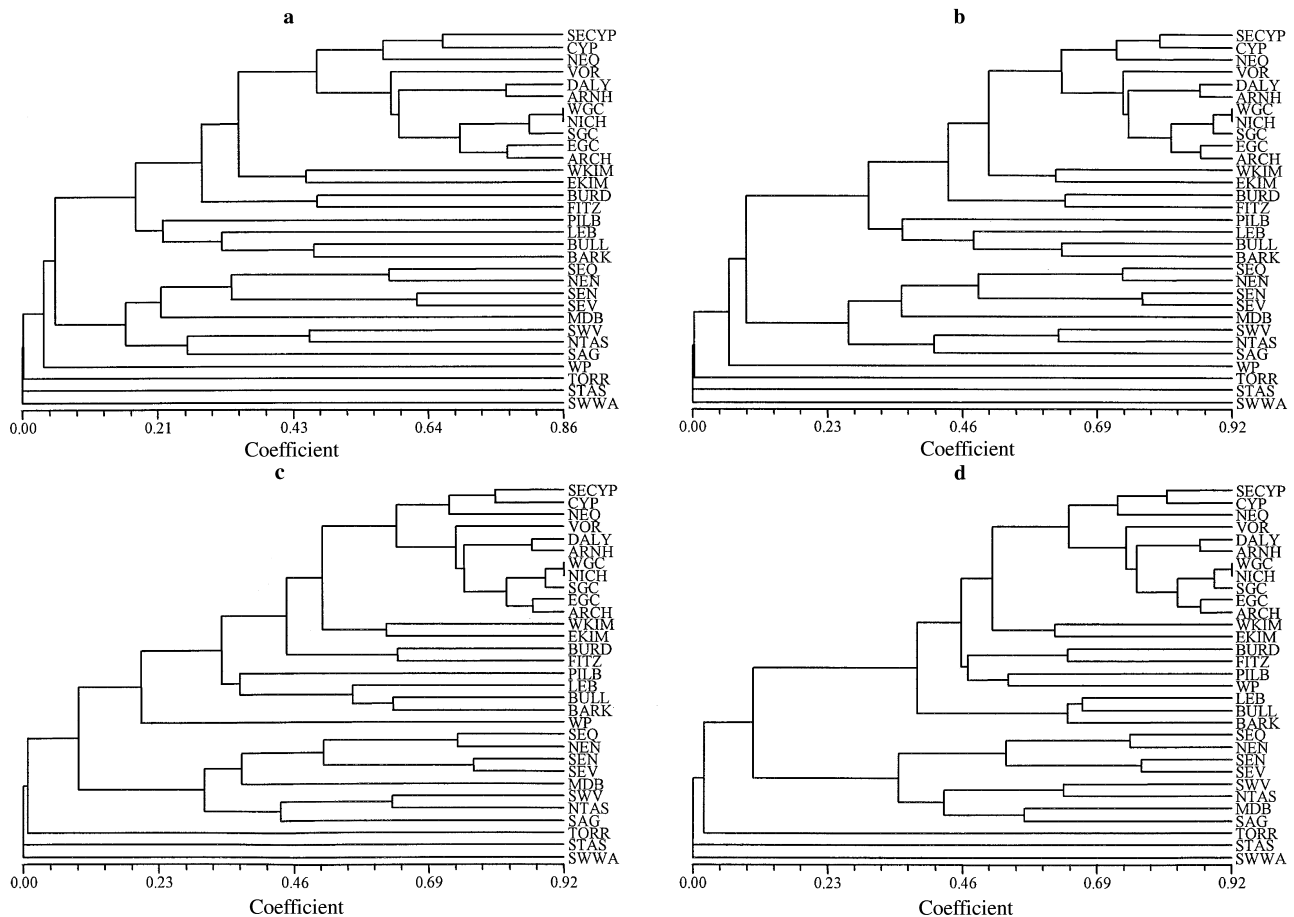


Figure 9 UPGMA trees of 167 species and thirty-one regions based on similarity coefficient matrices are shown for: (a) Jaccard's Coefficient; (b) Dice's Coefficient; (c) Ochiai's Coefficient; (d) Kulczynski's no. 2 Coefficient. Cophenetic correlations were all between 0.92 and 0.95. Jaccard's and Dice's coefficients produced identically branched trees, while Ochiai's Coefficient varied only in the position of WP. Kulczynski's no. 2 Coefficient differs in the positions of PILB, WP, and MDB, and the cluster LEB, BULL, and BARK differed in internal arrangement.

discharge of lowland river channels into the sea (e.g. Nott *et al.*, 1991; Spry *et al.*, 1999). Another short-term means by which fishes may move between drainages is via riverine flood plumes (Williams, 1970; Chenoweth & Hughes, 1997; Jerry, 1997), which may extend for sufficient distances at sea to connect adjacent drainages (Wolanski & Jones, 1981; Grimes & Kingsford, 1996). However, salinity and other characteristics of these plumes vary considerably and there are no data regarding fish occurrence within them (M. Kingsford, pers. comm.). This avenue of dispersal merits investigation.

To assess importance of short-term sea-level fluctuations, drainage patterns were reconstructed to -500 m (Fig. 13). While this is lower than any short-term sea-level known, the results are more readily visualized; the -100 m contour interval is also shown. Lowered sea-level connects major drainages in some areas, e.g. between Australia and New Guinea, VIC and TAS, and Cambridge Gulf (WA and NT). Areas offshore of FITZ and possibly northern PILB would experience far higher

connectivity than today. However, remaining drainages are largely unaffected.

Drainage divides

Drainage divides are likely breached only over long periods of time, 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 with adjacent outlets (i.e. draining the same direction with neighbouring river mouths). The principal difference is direction of flow. Adjacent drainages have divides paralleling direction of flow and non-adjacent drainages have divides perpendicular to direction of flow. Lateral channel migration is more likely to affect parallel divides than perpendicular ones, allowing movement of both upland and/or lowland species, whereas perpendicular divides only allow movement of

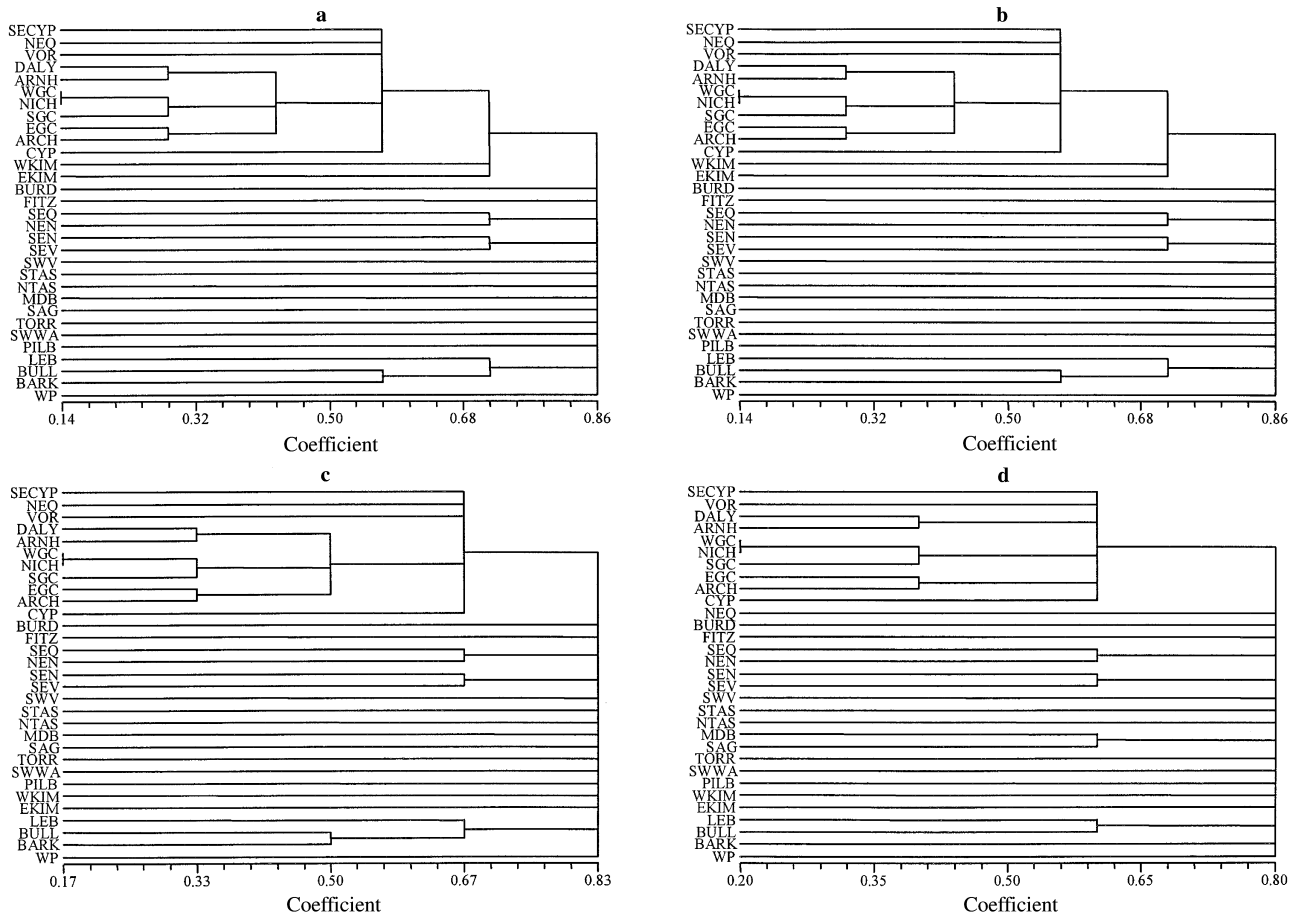


Figure 10 Consensus trees of single- and complete-linkage trees of 167 species and thirty-one regions are shown for the following similarity coefficients: (a) Jaccard's Coefficient; (b) Dice's Coefficient; (c) Ochiai's Coefficient; (d) Kulczynski's no. 2 coefficient. The consensus trees show the most distinctive clusters. Clusters present are more similar to each other than any region within the cluster is to any region outside.

upland species. Furthermore, adjacent river outlets have an additional means by which lowland fishes can be exchanged via lowered sea-level. If not adjacent, this is 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 more similar than in non-adjacent ones (Fig. 14). Hence, I conclude connectivity occurred more frequently, or at least more recently, between more adjacent drainages.

Climate

Climatic barriers occur in similar time frames as sea-water barriers. Regular, short-term fluctuations are on the order of 100–150 Kyr, while long-term trends are also known. Climatic barriers differ from sea-water ones in being less sharply delineated and differing more in their effects among species, depending upon ecological tolerances (below). The principal climatic barriers are minimum and maximum

water temperature (determined by a combination of solar radiation, atmospheric temperature, and humidity) and rainfall. The first two determine physiological survival, the last permanence of water.

Because of its broad latitudinal and longitudinal area, Australia experiences considerable climatic differences between regions (Figs 4 & 5). The most obvious climatic barrier to fishes is aridity, as 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, because the last four are endorheic and the first two are isolated by WP. This limits potential for connectivity between regions to passage over divides. In northern, eastern, and south-eastern Australia, climate is less extreme.

Climatic change tends to be oriented north–south (Figs 4 & 5). Differences across northern Australia may have been bypassed during lowered sea-level, as both adjacent and non-adjacent drainages became continuous (i.e. Gulf of Carpentaria, Cambridge Gulf; Fig. 13). Hence, while climatic differences existed, they probably had less effect on fish

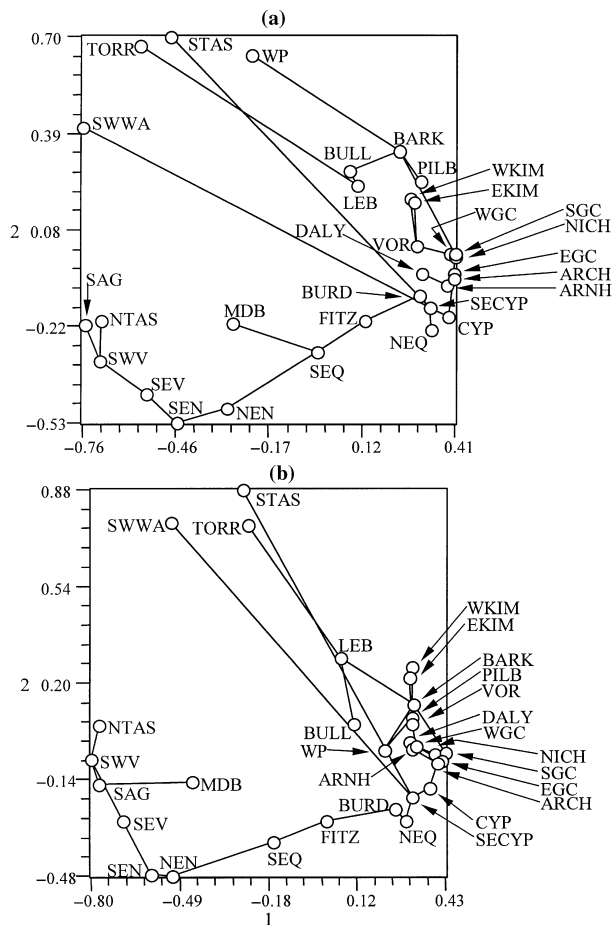


Figure 11 Non-metric multidimensional scaling plots of 167 species and thirty-one regions are shown for the following similarity coefficients: (a) Jaccard's Coefficient; (b) Kulczynski's no. 2 Coefficient. Stress values were 0.12 and 0.11 and cophenetic correlations were 0.90 and 0.96, respectively. A minimum spanning tree connecting regions is shown to indicate whether nearby pairs of regions in the plot are actually close, or distant if other dimensions are considered.

movement east to west. However, during glacial maxima when sea-level was lowest, climate became warmer and drier in tropical areas (Williams, 1984), presumably reducing potential for movement.

Substantial differences in climate exist among eastern drainages (Figs 4 & 5). Northern regions (SECYP, NEQ) have moderate rainfall and warm temperatures, with NEQ also having high rainfall and cool temperatures as a result of higher elevation (Fig. 3). Mid-QLD regions (BURD, FITZ) are warmer and drier, which gradually ameliorate into wetter and cooler conditions in the south.

Three lines of evidence suggest that 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 lack of distinctive faunal breaks, even within regions. Faunal differences between drainages are gradual and

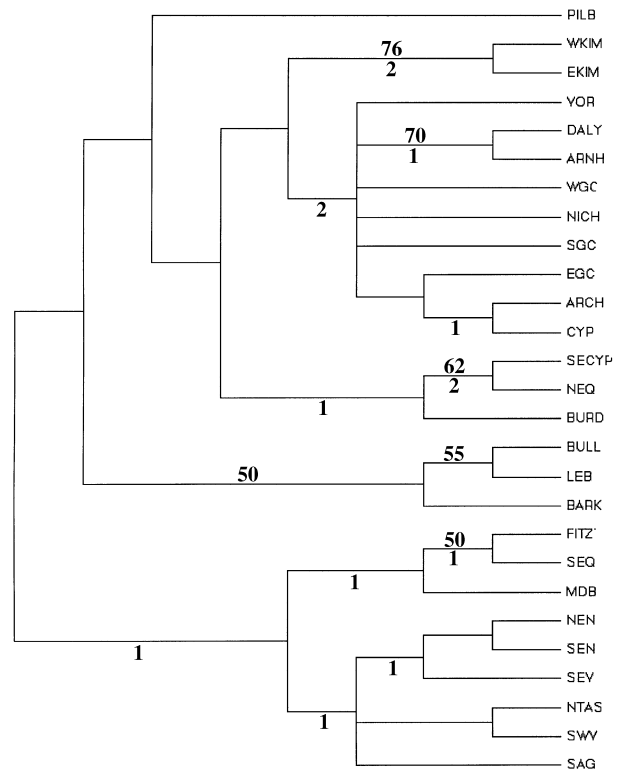


Figure 12 Parsimony analysis consensus tree of eighty-eight species (= characters) and twenty-eight regions (= OTUs) (uninformative characters and OTUs were removed prior to analysis). The fifteen shortest trees were calculated with length 214 (CI = 0.411, RI = 0.753, RL = 0.310, and HI = 0.589). Bootstrap values are shown above the branches with values > 50%, decay index values are shown below the branches with values > 0.

indistinct. If distinctive physical barriers existed, one would expect disjunction(s) as in other parts of the world where barriers have been identified (e.g. Obregón-Barboza *et al.*, 1994). Also, disjunct populations of several species (detailed below) occur between regions or drainages separated by drier intervening areas. Finally, fossil occurrences (*Scleropages* aff. *leichardti* and †*M. antiquus*) further south and north, respectively, of their descendant's present ranges, lend support. 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 these adjacent regions are negligible, yet several species occur in SEV that are lacking from SWV (see below) and 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 because of uncertain

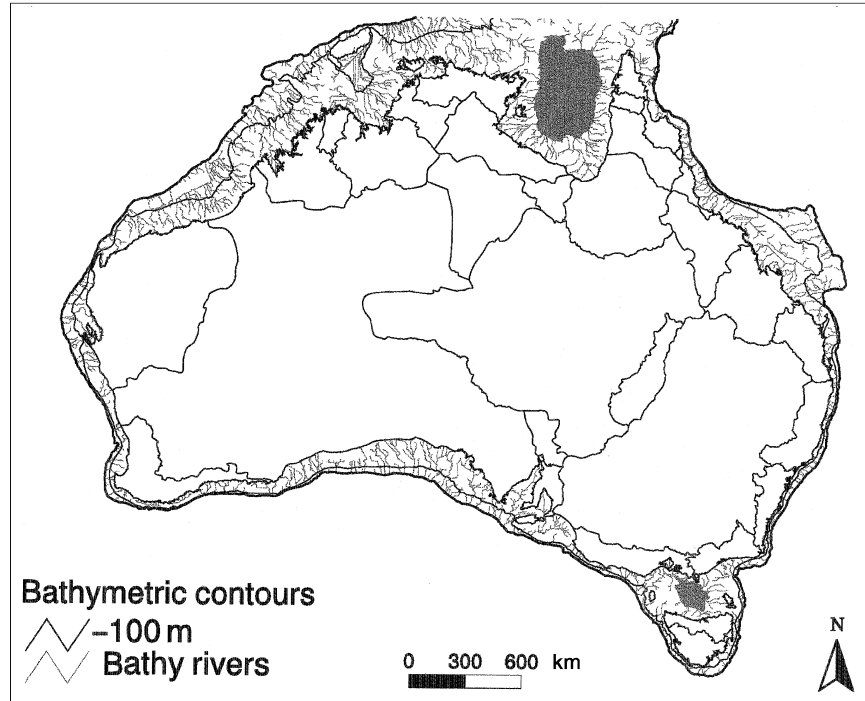


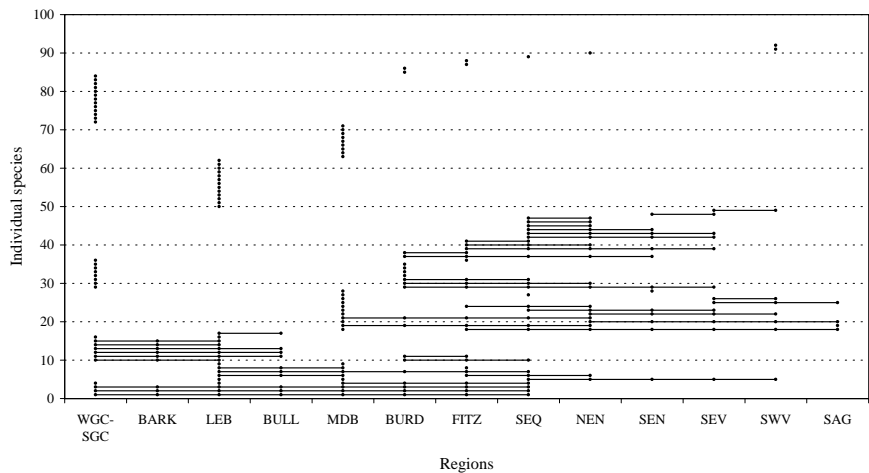
Figure 13 Australian low sea-level drainage patterns to 500 m below sea-level derived in ArcView from a bathymetric 30 arc-second (c. 1 km) data set produced by the Australian Geological Survey Organization. Regional boundaries and the 100 m below sea-level bathymetric contour are given. The margin of the figure represents the 500 m below sea-level contour. See Fig. 6 for regional acronyms.

habitat permanence under high within- and between-year (and longer term) climatic variations. 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, but 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 by accumulating more data than now exist. I leave that to the future.

Biogeographical provinces

Distributional relationships among regions [defined largely by the arbitrary hydrological scheme of AWRC (1976)] were compared in a search for 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 *et al.* (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,

Figure 14 Freshwater fish occurrences by region through central Australia. See Table 1 for species designations. On the y-axis each number represents the distribution of a species, with continuous lines indicating presence of a species in adjacent regions on the x-axis. For each region, beginning from one direction, all known species are listed sequentially from those with the broadest range to those which are endemic. Once all species in a region have been added, new species are added sequentially in the next, those with the widest ranges first.



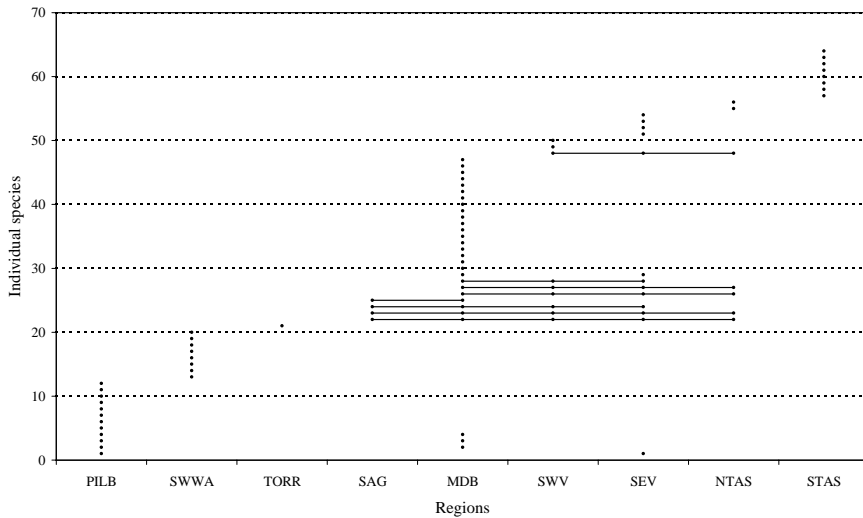


Figure 15 Freshwater fish occurrences by region across southern Australia. See Table 1 for species designations and Fig. 14 for further explanation.

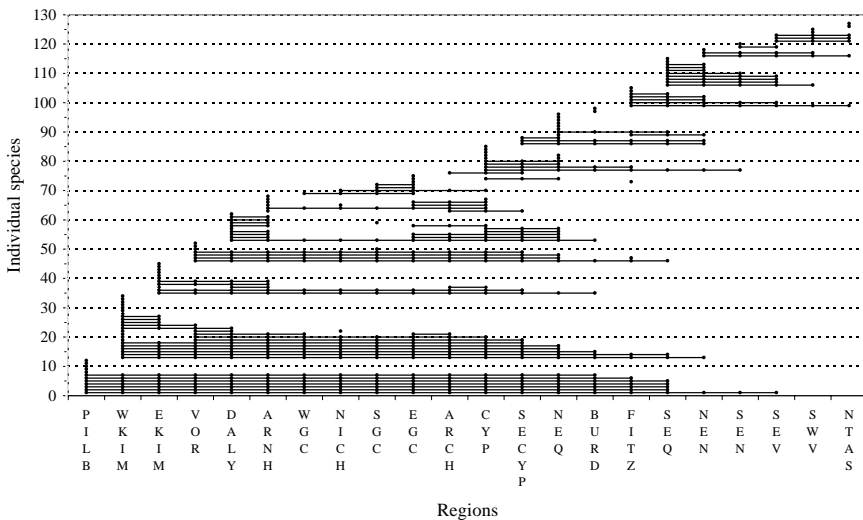


Figure 16 Freshwater fish occurrences by region across western, northern, and eastern Australia. See Table 1 for species designations and Fig. 14 for further explanation.

however, 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 because of 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 subregion (= province) concept within the Australian continent it should be used only in a 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. 14, southern ones are shown west to east in Fig. 15, and northern coastal regions are presented sequentially from north-west, to north-east, to south-eastern Australia in Fig. 16. Each number in the figures represents spatial distribution of a species, with continuous lines indicating its presence 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 9–12) were fundamentally congruent with provinces hypothesized *a priori* through qualitative inspection of distributional data.

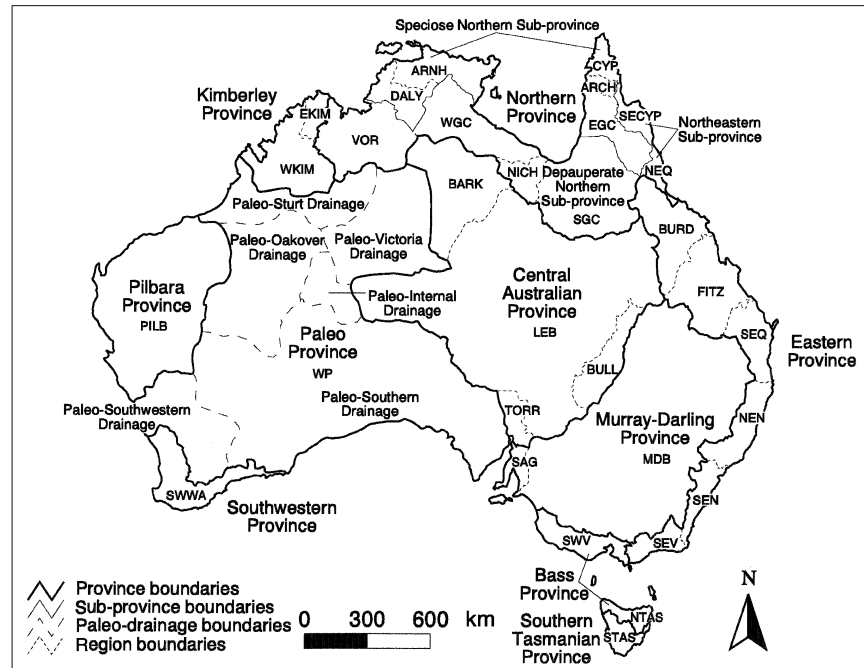


Figure 17 Proposed freshwater fish biogeographic provinces in Australia. See Section Biogeographic Provinces for further explanation.

The following regions may be combined into provinces (Fig. 17). SWWA and STAS (the south-western and southern Tasmanian provinces, respectively) each distinctive because both have 100% endemism (Fig. 8) and as a result do not group with any others (Figs 9 & 11). PILB and LEB each has a high percentage of endemics, 42% and 40%, respectively (Fig. 8), and thus are designated Pilbara and Central Australian provinces. PILB does not group near to any other region (Figs 9 & 12), supporting its distinctiveness. LEB has close relationships to BULL and BARK (Figs 9, 10, 12 & 14), and tentatively TORR; hence they are included with LEB in a Central Australian Province. WKIM and EKIM contain seven and six endemic species (24% and 21%, respectively) of twenty-nine total for each (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. 16). Their close relationship is borne out in most results (Figs 9, 11, 12 & 16), justifying combination as a 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 differences occur between SWV and SEV in what is lacking in SWV. Six species are in SEV but not in SWV, of non-endemics in SWV, all are in SEV (Fig. 16). Hence, there appears a unidirectional or superimposed recent barrier between the regions. Given this distinctiveness, combined endemism of 36%, and consistent grouping together (Figs 9 & 11) SWV and NTAS are combined into a Bass Province.

MDB has 31% endemism (Fig. 8) and complicated relationships with several surrounding regions as demonstrated by its variable position between analyses relative to

other regions (Figs 9, 11 & 12). Among these, SAG has complete similarity to MDB (Fig. 14), and Kulczynski's no. 2 coefficient groups them together (Figs 9 & 10), hence, it is included in a Murray-Darling Province. Other surrounding regions are not included as the contribution of each is relatively small (see below). WP is categorized as a Palaeo Province by default; it has only one species with no clear relationship to any other specific province or region.

Coastal areas from VOR east and south to SEV are difficult to categorize because gradation of species ranges exists (Fig. 16) with no regional boundary being particularly distinctive and low within-region endemism (Fig. 8). Clearly, the fish fauna of northern Australia is very different from that of the south-eastern coast (Figs 11 & 6), hence some degree of subdivision seems appropriate. The greatest difference in species' ranges between adjacent regions anywhere around the coastline is at the boundary between NEQ and BURD, where thirteen species (disregarding endemics in NEQ) have their southern-most termini; many being congruent with that boundary. Hence, it is reasonable to propose a Northern Province from VOR east to NEQ. Within this province, endemism rises to thirty-eight species (50%) (Fig. 16), although twenty-five of the 'endemics' and thirty-four species total also are in southern New Guinea [recalculated from Allen (1991)], emphasizing its close faunal relationship with Australia. Clustering results support distinctiveness of a Northern Province (Figs 9 & 10), and parsimony analysis also generally supports it, with a slight incongruence involving SECYP and NEQ (Fig. 12).

Three distinctive subprovinces exist within the Northern Province. The first, referred to a Speciose Northern subprovince, comprises of DALY, ARNH, EGC, ARCH, and CYP,

with high species richness (Fig. 6) and few differences in faunal composition except four species in DALY and ARNH not shared with the others (Fig. 16). The second, termed as a Depauperate Northern subprovince, consists of VOR, WGC, NICH, and SGC, is notable for its low species richness (Fig. 6). Finally, a north-eastern subprovince consists of SECYP and NEQ, distinctive from the other two subprovinces in lacking several species (Fig. 16) and NEQ has six endemics (Fig. 8).

Finally, an Eastern Province is proposed along the east coast from BURD to SEV. Despite no species in common at the extremities, no distinctive breaks are present between regions, and a north–south gradation is evident even at the drainage scale. Endemism within this province is 31% (Fig. 16). Ordination most clearly demonstrates gradation between regions within the province (Fig. 11). Other results are mixed; clustering has an incongruence between BURD and FITZ and the other regions (Fig. 9) while parsimony analysis has three incongruences (Fig. 12).

Patterns of relatedness among provinces and their causes

South-western 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 the 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, although distant, clearly lie with south-eastern Australia.

No fishes are known north of South-western Province until the Greenough drainage in PILB, nor east until TORR/SAG (with one possible exception, see Palaeo Province). Mean rainfall decreases northward, while mean January maximum temperature increases rapidly (Figs 4 & 5), making conditions too dry for survival. Fishes within this province 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 aridity and the sedimentary record across the Nullabor Plain this is unlikely. Conditions would have been favourable during late Eocene when rivers supplied abundant sediments, major dunes formed along the coast, and climate was temperate (Benbow, 1990). Several transgressions of the sea from Eocene to mid-Miocene also may have enhanced dispersal opportunities along coastlines in this region. The Nullabor Plain formed 14–16 Ma with final regression of the sea from Eucla Basin, about the time palaeodrainage development began across southern Australia (Van de Graaff *et al.*, 1977; Benbow, 1990). It lacks any signs of integrated surface drainage because of the fractured nature of its limestone, which allows surface water to seep underground rather than run off

(Jennings, 1967; Benbow, 1990). Hence, Miocene appears to be the minimum age when fishes could migrate east–west across southern Australia, for the last time.

Pilbara Province (PILB)

Five of twelve species are endemic (Figs 6 & 8); however, their relationships to other species are poorly understood. The remainder comprise of the most widespread species in Australia, found eastward around the coast to at least BURD, including LEB (Figs 14 & 16).

Pilbara Province is one of the hottest areas of Australia. Mean January maxima temperatures are ~42 °C in some parts (Fig. 5). Mean annual rainfall is < 400 mm (Fig. 4). Perennial surface water is scarce, mostly persisting in gorges. Pilbara Province is separated from Kimberley Province by the Great Sandy Desert (Palaeo Province), with no surface runoff. No data exist to provide an indication of when this developed and thus isolated the two from each other. The only Tertiary sedimentary records, consisting of minor alluvial and lake deposits (Taylor, 1994), are not yet dated.

Kimberley Province (WKIM and EKIM)

Endemism is high in this province. Six of nine species in the family Eleotridae are endemic (one endemic genus); Terapontidae, five of nine (one endemic genus); Atherinidae, two of three; Melanotaeniidae, two of five; and in Toxotidae, one of two (Table 1). Several endemics have ranges limited to one or two individual rivers. Only sixteen species are widespread, ranging to at least the east-coast drainages (Fig. 16). 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 populations, *M. nigrans* (Fig. 16) and *M. exquisita* [absent between the King George (EKIM) and Daly (DALY) rivers except one record in Pentecost drainage (VOR) (B. Hansen, pers. comm.)]. It is possible that other relictual populations of similarly distributed fishes may be found in EKIM, e.g. *P. gertrudae*, *P. tenellus*, *Denarius bandata*, and colleagues. Three species are in Fitzroy drainage (WKIM), occurring eastward through the Northern Province (Fig. 16), but absent from the remainder of Kimberley Province. They include *Arius midgleyi*, *Anodontiglanis dabli*, and *Craterocephalus stramineus*. *Glossogobius* sp. C occurs as an isolate in Prince Regent drainage, the nearest other records being in the Pentecost drainage.

Several explanations exist for the high percentage of endemics. The province contains rugged topography with more gorges than other parts of Australia. Gorges provide refuges for fish during dry periods as they force hyporeic water to the surface. Coastal bathymetric data provide conflicting evidence. A shallow, submerged ridge exists north of the boundary between WKIM and EKIM, which could have been a drainage divide during low sea-levels (Fig. 13) 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. *C. lentigenosus*, *Syncomistes trigonicus*, and *M. oligolepis*) and a more recent one with Northern Province (e.g. *Neosilurus ater*, *M. exquisita*, *M. nigrans*, *A. macleayi*, and *S. butleri*) (Table 1, Fig. 16). 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 species it lacks relative to regions to the west, as outlined under Kimberley Province. The south-eastern boundary has the largest absolute decline in the number of species between adjacent coastal regions (NEQ–BURD), from thirty-nine to twenty (Fig. 6), and is the southern limit for thirteen species, the highest changes of these kinds anywhere along the coast (Fig. 16). Regions within the Northern Province have fourteen endemic species (Fig. 8), four 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 shared with New Guinea) out of seventy-five species (50% endemic) (Fig. 16). Within the province, three subprovinces are recognized: Speciose Northern, Depauperate Northern, and North-eastern.

Speciose Northern sub-Province (DALY, ARNH, EGC, ARCH, and CYP)

This subprovince is the richest of these (Fig. 6), with its own distinctive fauna (Fig. 16). Several taxa are on each side of the Gulf of Carpentaria in the Speciose Northern sub-Province, but not in the Depauperate Northern sub-Province, e.g. *A. dahli*, *Porochilus obbesi*, *Iriatherina wernerii*, *M. nigrans*, *M. trifasciata*, *P. gertrudae*, *P. tenellus*, *D. bandata*, and *O. nullipora*. An exception is *H. carbo* which occurs as an isolate 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 correlated with climate. There is a rise in annual mean rainfall from 600 to > 1000 mm from southern parts of the Depauperate Northern sub-Province into the Speciose Northern sub-Province (Fig. 4). There also is a corresponding decrease in mean January temperature maxima from upper 30s to low 30s (Fig. 5). Mean July minimum temperature also increases from 12–15 °C to > 15 °C.

Depauperate Northern sub-Province (VOR, WGC, NICH, SGC, and EGC)

There is an abrupt 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 subprovince is characterized by lower annual rainfall, higher summer temperature maxima, and lower winter minima, as just noted. With partial exception of NICH, fed by large perennial springs, most regions lack several species. Furthermore, several species otherwise

widespread and common in other subprovinces are rare and patchy in occurrence. *M. mogurnda* is in VOR and NICH, but only a single record in SGC exists, and from two drainages in WGC. *C. stercusmuscarum* is only known from some 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 the north. Few records of *A. agrammus* and *A. mulleri* exist, while *S. jardiinii* is only known from Roper drainage (WGC) and NICH, and *H. carbo* is only known from NICH.

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

North-eastern sub-Province (SECYP and NEQ)

Another significant drop in richness (forty-five to thirty-five) occurs from CYP to SECYP (Fig. 6) and several species have their eastern range limit here (Fig. 16). These changes may be because of several factors, including lower mean winter temperature minima, and a lack of major rivers due to nearness of the Eastern Highlands (with exception of Normanby drainage) to the coast.

NEQ has both high richness (thirty-nine) (Fig. 6) and number of endemics (six) (Fig. 8). This is unusually high for richness compared with surrounding drainages and for endemism compared with drainages east of the 'endemic line' (Fig. 8), which may be explained by several inter-related factors. The Eastern Highlands are considerably higher (500–1622 m) in NEQ than regions to the north and southward to FITZ (Fig. 3). Although high elevations stretch beyond NEQ, only near-coast ranges have high mean annual rainfall (> 2400 mm), which decreases to < 1200 mm a short distance inland (Fig. 4). Summer maximum temperatures also are lower at higher elevation (Fig. 5). Hence, it provides a refuge to species probably more widespread when climate permitted. Further evidence for 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, *O. aruensis* and *O. fimbriata* occur as isolated southern populations, while *M. maccullochi*, *P. gertrudae*, *D. bandata*, and *O. nullipora* live 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 of seventy-five freshwater fishes (45%) in common (Roberts, 1978; Allen, 1991). Furthermore, four species, *Nematalosa erebi*, *Amniataba percoides*, *C. stercusmuscarum*, and *H. carbo* (and probably others, yet uninvestigated) have apparent sister species in Fly River (increasing commonality to 51%). Presently, Fly River drains into the southern Pacific Ocean. However, it is

hypothesized to have been diverted by upwarping from a southern route directly into Arafura Sea (Blake & Ollier, 1969) between 35 and 40 Ka (Torgersen *et al.*, 1988). The Arafura Sea between southern New Guinea and the Northern Province is shallow, and regularly exposed during lowered sea-level, which potentially connected most drainages in Torres Strait west of Cape York Peninsula (Fig. 13).

When did the fish faunas of Australia and New Guinea last meet? Allen & Hoese (1980) suggested severing of the connection 6.5–8 Ka during the last sea-level rise. While probably correct for hydrological connectivity, it seems improbable for freshwater species as a migration route. During late Pleistocene, a major waterbody known as Lake Carpentaria existed east of Groote Eylandt during lowered sea-levels (Fig. 13) (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, the area is thought to have been more arid than present (Webster & Stretten, 1972), possibly decreasing available aquatic habitats. Major faunal exchanges are more likely 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 *N. byrtlii* have no known, near relatives in New Guinea, *N. erebi* and *A. percoides* each have likely sister species (largely restricted to Fly River), while *M. splendida* has a widespread, allopatric subspecies in New Guinea (Allen, 1991). Given their ubiquitous occurrence and broad environmental tolerances (Merrick & Schmida, 1984), these are most likely of all to have migrated during low sea-level, but they are absent. Many possible reasons may exist, 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 are not in Australia. Examples include *A. carinatus* Weber, *A. latirostris* Macleay, *A. macrorhynchus* (Weber), the catfish genera *Cochlefelis*, *Doiichthys*, and *Nedystoma*, *Zenarchopterus novaeguineae* (Weber), *M. goldiei* (Macleay), and *G. sandei* (Weber) and several other species with more limited ranges are also in south-central New Guinea in the middle and upper Fly River that do not occur in Australia (Allen, 1991). Clearly, the 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. 16), 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. 16). No particularly distinct faunal breaks occur even at the drainage level, until Wilson's Promontory at the southern boundary of the province. Only five endemics are present at a regional scale (Fig. 8). Even when the entire

province is considered, endemism only rises to fifteen out of forty-eight species (31%) (Fig. 16).

The differences in richness and the pattern of species occurrence between regions within this province are possible because of climatic effects (Figs 4 & 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. 13).

Biogeography of Burdekin River (BURD) was recently discussed by Pusey *et al.* (1998), who attributed low richness to several factors including Burdekin Falls, 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), but times between eruptions, while not specifically documented, were probably sufficient to allow recolonization and minimize long-term impacts. Past climatic stress is difficult to infer, but now is higher than for any other east-coast drainage (Figs 4 & 5) and would probably have been more so 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 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 the falls have clearly excluded some species.

If Burdekin Falls is a barrier, other species should also be present today in surrounding drainages and below, yet absent above, whereas if climate were the cause, species also would not occur in surrounding drainages with similar climate. Pusey *et al.* (1998) demonstrated that the falls are a barrier to species requiring estuarine or marine habitats for reproduction, and for three freshwater species; *P. signifer*, *G. aprion*, and *O. lineolatus*. However, it is unclear whether *O. lineolatus* is native below the falls and for the purposes here I assume it is introduced because of the lack of records from adjacent drainages. *T. tandanus* and *O. lineolatus* are known to be introduced above the falls and are either not present (Pusey *et al.*, 1998; B. Pusey, pers. comm.), or considered introduced (A. Hogan, pers. comm.) below them, respectively. Given both can survive present conditions in the drainage as demonstrated by 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 any influence of Burdekin Falls. Hence, the climatic hypothesis is also supported because *T. tandanus* and *O. lineolatus* are also absent from surrounding drainages. Additional arguments presented by Pusey *et al.* (1998) include absence of Gobiidae and the lower richness of Eleotridae and Ambassidae relative to NEQ. Again, all these species, lacking from Burdekin drainage are also 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 ~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 *N. mollespiculum* (as sp. C), *P. rendahli*, and *Scortum*, as they all are 'common' in the Gulf of Carpentaria drainages (CYP west to ARNH) and uncommon in north-eastern 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 not known from the Gulf of Carpentaria regions. *Porochilus rendahli* is widespread, 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 *S. parviceps*, when defined, may help clarify relationships, hence history. Thus, definitive data supporting a western colonization route are lacking. Additional species listed as possible invaders include *A. percooides*, *H. fuliginosus*, and *L. unicolor*, although all are widespread (Table 1) and could have migrated along the coast. Furthermore, several species in the southern Gulf of Carpentaria regions are absent from east coast regions (Fig. 16, Table 1). If colonization did occur via this route, its 'signature' may be been overwritten or confounded by later events; present evidence is equivocal.

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

SEQ has a mix of northern and southern species, hence giving it the highest richness in Eastern Province (Figs 6 & 16). Eight species have their southern coastal limit at SEQ, a further five continue south via MDB (Fig. 14). Eight also have their northern-most occurrence in this region (Fig. 14).

SEN is distinctive because of the occurrence of *M. 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 along much of the Eastern Province would seem neither easy nor frequent. While sea-level and climatic

changes are relatively frequent, few drainages must have actually connected during low sea-levels (Fig. 13), unless present offshore topography has changed significantly. Hence, to move, fishes must rely on longer-term processes such as drainage rearrangement or they swam over low divides. Several species had historically broader ranges along the coast, now fragmented most probably by climatic change. Most species, at both their northern and/or southern range extremities, tend to have termini independent of coexisting species, suggesting a differential 'filter' again probably caused by climate. Evidence supporting a significant absence of mixing between adjacent (or relatively nearby) drainages comes from studies on *T. tandanus* (Musyl & Keenan, 1996; Jerry & Woodland, 1997), *M. duboulayi* (Crowley *et al.*, 1986), *Maccullochella* (Rowland, 1993) and *M. australasica* (Dufty, 1986). Other examples demonstrate higher levels of gene flow; *P. signifer* exhibits clinal variation along its range (Hadfield *et al.*, 1979) and *M. novemaculeata* follows an isolation-by-distance model, with limited gene flow between adjacent populations (Chenoweth & Hughes, 1997; Jerry, 1997; Jerry & Baverstock, 1998; Jerry & Cairns, 1998). Both spawn and/or occur in upper estuarine areas, and may have a higher proclivity for dispersal between river mouths via riverine flood plumes because of higher salinity tolerance. It is probable *Retropinna semoni*, *M. colonorum*, *G. australis*, *G. coxii*, *H. compressa*, *Philypnodon grandiceps*, and *Philypnodon* sp. all will show similar patterns of minor variation between drainages, as they all are also in upper estuarine areas. It is also notable that this group of species is dominant and widespread in the southern half of the province where the continental shelf is the narrowest. Hence, for some species, limited evidence suggests distribution patterns along the Eastern Province which have been achieved over a long 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 in SEV are absent here (Fig. 16). Each region has two endemic species, *Nannoperca obscura* and *N. variegata* (SWV) and *G. tanycephalus* and *Paragalaxias mesotes* (TAS) (Table 1). Of the latter pair, the first is land-locked, derived from diadromous *G. truttaceus* Valenciennes, 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. 15). While the two regions are presently isolated by Bass Strait, it is shallow and was fully exposed during lowered sea-levels (Fig. 13). Of note is the former drainage pattern during low sea-level near Wilson's Promontory (Fig. 13). The faunal disjunction between Bass and Eastern provinces occurs here, but the former drainage divide appears eastward. The bathymetric reconstruction may be misleading, as the sea-floor is relatively flat making it difficult to predict drainage direction. Shifts in direction would only require minor changes in topography. Of the four species whose ranges end at

Wilson's Promontory, two (*M. novemaculeata* and *Philyponodon* sp.) are common and it is likely they would survive in Bass Province had they dispersed there. The other two (*G. australis* and *G. coxii*) are rare in this portion of their range and may be limited by some ecological factor(s). Despite this incongruence, present-day data demonstrate faunal divide near Wilson's Promontory.

Southern Tasmanian Province (STAS)

This province has no shared species, all eight are endemic (Fig. 8). Three galaxiids, *G. auratus*, *G. fontanus*, and *G. johnstoni* appear derived from the diadromous species *G. brevipinnis* Günther and *G. truttaceus* (Merrick & Schmida, 1984). Three *Paragalaxias* spp. occur in Central Plateau lakes. With the exception of *P. 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 probably evolved *in situ*. All have restricted ranges, often one or a few lakes and/or streams (Allen, 1989). Lack of dispersal is likely a combination of being at the extreme southern end of Australia and experiencing the coldest extremes during climatic fluctuations, and effective ocean barriers because the continental shelf is narrow.

Murray-Darling Province (MDB and SAG)

SAG is combined into this province as it shares all four species with MDB (Fig. 14). During low sea-level, all drainages south of Wakefield (SAG) exited 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 between Kangaroo Island and Fleurieu Peninsula, eventually joining the lower Murray (Fig. 13) and explaining similarities of their faunas. The gulf is relatively shallow, and minor changes in topography could divert drainage to either side of Kangaroo Island and 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. 14). It is notable LEB and SWV have one species in common (it occurs in all south-eastern regions), LEB and SEQ have nine (six widespread northern species) and SWV and SEQ have two in common (Fig. 14). Additionally, Murray-Darling Province has nine endemics (Fig. 8). Overall, it appears to have experienced mixing of faunas from surrounding regions with distinctive faunas, while maintaining a high degree of endemism. With possible exception of SWV (adjacent), all faunal connections must have occurred across drainage divides.

It is not possible to assume today's fish distributional patterns directly reflect historical ones with reference to species in Eastern Province. Some species may have occurred further south or north in Eastern Province in the past. The following discussion should, therefore, be regarded as tentative; several alternatives may exist.

A peculiar pattern in south-eastern Australia is the occurrence of several species southward along the east coast to Brisbane drainage (with some occurring southwards to Manning and Hunter drainages), then continuing south via Murray-Darling Province although absent from intervening south-eastern 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 accepted drainage rearrangements across Eastern Highlands as common, based on geological evidence, and hence explained this pattern. However, the dominant geomorphological paradigm has shifted to where these are thought to have been rare, or non-existent in this region at least throughout most of the Tertiary (see Introduction). The Eastern Highlands (~90 Ma) pre-date most fishes, hence they must have crossed it. The alternative possibility of once being widespread throughout south-eastern Australia and dispersing via coastal drainages where subsequently becoming extinct, seems unlikely, especially because no gaps in species' ranges occur along that coast (Fig. 16). Other confounding difficulties include the possibility that fishes may have crossed the Eastern Highlands at one site or several, on single or multiple occasions, and from alternating directions. Limited evidence suggests the easiest options for crossing are limited to only some sites, however, numbers and directions of exchange will be difficult to determine.

Several areas of lesser elevation occur in the Eastern Highlands 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 exist 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 have experienced volcanism, in Brisbane and Clarence drainages from 22.6 to 27.2 Ma, Hunter from 31.8 to 42.7, Hawkesbury from 14.4 to 26.0, Snowy from 36.9 to 54.9, Tambo from 25.8 to 37.2 and Maribyrnong from 4.6 to 7.0 Ma (Johnson, 1989). Many of these are probably too old to have influenced faunal exchange, but volcanism could have subsequently made it easier for certain species to swim across.

Faunal similarity clearly exists between drainages on either side of several low places. Fitzroy drainage has *M. ambigua*, absent from other coastal drainages, among eleven species in common with MDB (Fig. 14). Clarence drainage has nine species in common with MDB (Fig. 14). Hunter drainage has six in common, however, a record for *C. amniculus* is more notable if it reflects a natural occurrence. I consider it introduced because of recency of collections (1976 and 1980, one and five specimens, respectively) and lack of further records despite specific efforts (Crowley & Ivantsoff, 1990). The Hawkesbury and Shoalhaven drainages are notable for coastal populations of *M. australasica*; otherwise only in MDB. They have a total of five species in common with MDB (Fig. 14). 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, and the same situation holds in other drainages in western VIC where the divide is particularly low (Fig. 14).

Absence from coastal regions relative to MDB is demonstrated by *Gadopsis bispinosus* in upland streams in the Murray drainage (from Goulburn River east to Murrumbidgee River). Seemingly suitable habitat is unoccupied in coastal drainages. *Gadopsis marmoratus* also is absent from coastal NSW drainages, yet occurs over the 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 species that when studied may hold a key to migration over the Eastern Highlands is *G. olidus*, occupying all elevations in virtually all drainages on both sides and more frequently at high elevation and in smaller headwaters than any other fish in south-eastern Australia.

The relationships between LEB to the north and MDB also are obscure. Musyl & Keenan (1992) suggested MDB and LEB 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 a southern outlet for LEB has never been identified, although one is hypothesized to have existed in Miocene, because of 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 Palaeocene (Stephenson & Brown, 1989). Others suggested with no supporting evidence that LEB formerly had an outlet into MDB near Broken Hill (NSW) (Tedford *et al.*, 1977). Alternative connections may have existed via headwaters of Barcoo River and north-western parts of MDB, or via Bulloo drainage (BULL).

Clearly the fauna of BULL is most closely related to LEB (Fig. 14), and several of its species have been tentatively classed as intermediate between those of LEB and MDB. Musyl & Keenan (1992) suggested *M. ambigua* from BULL may demonstrate hybrid influences between MDB and LEB stocks. Based on two specimens, G. Allen (pers. comm.) could not identify the *Ambassis* sp. from BULL, as they were intermediate between *A. mulleri* and *A. agassizii* in LEB and MDB, respectively. Hence, although tentative, a connection via BULL between MDB and LEB appears possible. How or when this occurred is unknown.

Central Australian Province (BARK, LEB, BULL, and TORR)

Four regions are amalgamated on the basis of high faunal similarity (Figs 9–14), and most likely connections to other regions.

Because of its large size LEB borders many regions which may account for its complex fauna. Its relationships with MDB have been discussed. Nine species are shared between LEB and Fitzroy drainage of the Eastern Province, although one of these, *M. ambigua*, is more closely related to MDB

populations and another, *M. splendida tatei* (of LEB), is considered more closely related to *M. s. inornata* from northern regions rather than *M. s. splendida* on the east (Allen & Cross, 1982). 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. Thus evidence is weak for direct eastern coastal relationships.

LEB has ten species in common with Flinders drainage (SGC), which, aside from seven widespread species, also has *P. argenteus* and *S. barcoo* in common. These two species only have limited distributions in the Depauperate Northern sub-Province and Central Australian Province (Table 1). Connections between provinces have been documented for headwaters of Cooper (LEB) and Flinders drainages 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 *et al.*, 1985). Also, present headwaters of Diamantina drainage formerly flowed into Flinders drainage based on geomorphological changes to the latter's lessened stream profile (Twidale, 1966). Unfortunately, no firm evidence exists as to when this occurred, but it was probably between 5 Ma to possibly late Pleistocene (R. Twidale, pers. comm.). Hence, two connections are identified, each in a different direction. Overall, strong biological and geological evidence exist for connections of LEB with northern Australia.

Presently, drainage in BARK is internal, all ending in ephemeral lakes in the region's centre. Relationships of fishes appear nearest to LEB, based on *M. splendida tatei* in both. However, aside from that subspecies, all other taxa are in common to both LEB and WGC (Fig. 14). The eastern edge of BARK is barely separated from LEB in terms of elevation, heavy runoff might allow fishes to swim today between regions. Further, the low divide is downstream of headwaters in the area (Fig. 2), enhancing potentials 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 elevation. It would only take slight tectonic shift to change drainage direction. Overall evidence suggests that the most recent connections were with LEB, hence its placement in that province.

Hydrologic association 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. 14); (although see discussion under MDB concerning possible hybrids). Furthermore, BULL appears to have formerly flowed south of its present terminus, likely into Lake Frome (SA). My only evidence for this is valley slope confluence except for a low divide between Palgamurtie Creek (BULL) and Packsaddle Creek (LEB) between Grey and Barrier ranges (NSW) (Fig. 2). When such drainage last occurred is unknown, but is likely to have been before aridity enveloped this area (perhaps since at least 1 Ma). Only one species in BULL, an

unidentified plotosid related to *N. mollespiculum* and *N. pseudospinosus* from BURD and north-western regions, respectively, is not found in surrounding drainages. Presumably, it 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), tentatively identified as *C. eyresii* although this may be incorrect. *C. eyresii* was reviewed by Crowley & Ivantsoff (1990), who separated it into four species. Unfortunately, no material from TORR was examined. Its closest affinities are probably to LEB, given their geographical proximity, and thus TORR is tentatively included in Central Australian Province.

Palaeo Province (WP)

Palaeo Province contains former connections to surrounding drainages severed as aridity began in mid-Miocene (Van de Graaff *et al.*, 1977). Six palaeodrainage catchments exist based on former connections to surrounding drainages: Palaeo-Victoria, Palaeo-Sturt, Palaeo-Internal, Palaeo-Oakover, Palaeo-south-western, and Palaeo-southern (Fig. 17). Most of this province in NT formerly drained into Victoria drainage, northern and middle WA into Oakover drainage and through the Great Sandy Desert, south-western WA into Swan drainage, and those north of it into South-western Province, and southern portions of WA and all of SA drained into the Great Australian Bight. Only some records of *L. 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 south-draining Raeside Palaeoriver (WA), draining into the Great Australian Bight. It is yet to be confirmed if this record is valid, as only one collection exists. Former 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 Palaeo-Victoria drainage are adjacent to those of Palaeo-Oakover drainage, BARK and LEB, which clearly would potentially enhance faunal exchange across a major area. However, when this may have last been possible is unknown because no deposits are dated from a majority of the province.

CONCLUSIONS

The most striking pattern in distribution of freshwater fishes across Australia is endemism. Most provinces in southern, central, and western parts of the continent have large proportions of endemics, whereas Northern and Eastern provinces, with exception of NEQ in the latter, have few. The pattern results from isolation because of aridity and drainage divides. Low endemism in Northern Province must result from high drainage connectivity during lowered sea level (Fig. 14), preventing isolation sufficient for local speciation. Low endemism in Eastern Province is more difficult to explain. Drainages appear long isolated, even during lowered sea levels, yet faunal patterns suggest no distinct barriers and short-term isolation. Hence,

climate seems the most likely cause of species' distributional limits.

Fossil evidence demonstrates persistence of certain families and genera over at least the last 30–45 Myr. The record is strongly biased towards larger taxa, most families containing fossils have species > 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 Plio-Pleistocene and 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. 14). The remainder 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 lowered 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 a presumptive drainage divide). Where widespread species cross faunal breaks, if barriers are geomorphological rather than climatic or ecological, they should show discontinuities similar in degree of relatedness to populations in surrounding drainages.

Movements between drainages in regions not influenced by sea-level changes appear probably only over very long time-scales given the geological stability of Australia. Interacting with this process are 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 Kyr is considerable, and, if extinction occurs, may operate over too short a time period 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. 15). 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 colleagues not (assuming the cause of

exchange did not discriminate between species)? It seems possible that the relationships between populations of widespread species will be complex and difficult to unravel, as a result of possible faunal exchange from several regions and different and possibly multiple times and/or directions. Additional difficulties in interpreting patterns of species occurrence among regions are questions of how and when fishes crossed a drainage divide. Among situations where crossings are indicated, the drainage rearrangement between Flinders River and Praire Creek (SGC and LEB) is well defined and dated (Coventry *et al.*, 1985). 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 connections might have occurred are obvious. Based on differences between likelihood of movement between adjacent vs. non-adjacent drainages, I predict when a species is on both sides of non-adjacent divides, 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 in 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 and/or merging through hybridization.

Today, biogeographic studies without phylogenetic data are uncommon. Furthermore, the techniques applied here are not commonly used, and few studies of this nature have combined analytical techniques (see, however, Huguency & Lévêque, 1994). Most examine data using only one technique; either clustering (Warren *et al.*, 1991), or ordination (Reshetnikov & Shakirova, 1993) or parsimony analysis (Watanabe, 1998). Clearly, a minimum combination of clustering and ordination should be used as they complement each other's weaknesses to some extent. Phylogenetic data are lacking for fishes over most of the world, and this condition will probably continue for some time. I suggest the present kind of study based on distributional and geological data is a useful precursor to phylogenetic studies, as it provides testable hypotheses otherwise unavailable until far into the future.

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BIOSKETCH

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Appendix I List of acronyms and abbreviations

<i>States</i>	
NSW	New South Wales
NT	Northern Territory
QLD	Queensland
SA	South Australia
TAS	Tasmania
VIC	Victoria
WA	Western Australia
<i>Museums</i>	
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
NMV	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
<i>Time</i>	
Gy	Billion years ago
Ka	Thousand years ago
Kyr	Thousand years
Ma	Million years ago
Myr	Million years
<i>Distance</i>	
km	Kilometer
m	Meter

<i>Region names</i>	
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
NEN	North-eastern New South Wales
NEQ	North-eastern Queensland
NICH	Nicholson River
NTAS	Northern Tasmania
PILB	Pilbara
SAG	South Australian Gulf
SECYP	South-eastern Cape York Peninsula
SEN	South-eastern New South Wales
SEQ	South-eastern Queensland
SEV	South-eastern Victoria
SGC	Southern Gulf of Carpentaria
STAS	Southern Tasmania
SWV	South-western Victoria
SWWA	South-western Western Australia
TORR	Lake Torrens
VOR	Victoria-Ord rivers
WGC	Western Gulf of Carpentaria
WKIM	Western Kimberleys
WP	Western Plateau
