Ocean Basins and the Biogeography of Freshwater Fishes

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'The natural biogeographic regions for terrestrial and freshwater organisms are not present-day land areas but the world's major ocean basins.' (Craw and Page 1988: 180).

Abstract

Geological evolution of the Indian and Pacific Ocean basins, including the Tethys Sea, is relevant to the evolution and distribution of Indo-Pacific freshwater fishes. Area cladograms derived from phylogenetic analyses of atherinomorph fishes are compared, in part, with those for plant bugs, cicadas and bats. Geologically and biologically composite islands in the Indo-Australian archipelago such as New Guinea, Borneo and Sulawesi, are confirmed. If any lines (such as Wallace's, Weber's and so on) are to be drawn, they should pass through these complex islands, not between them, to mark the closing of the ancient Tethys Sea.

Sicydiines are a group of circumtropical, insular and coastal, amphidromous gobies: adults live and breed in freshwater, whereas larvae are transported to the sea where they undergo transformation. Sicydiine genera are restricted to ocean basins. Hypotheses of relationships among ocean basins, as indicated by phylogenetic relationships among sicydiine genera and by other, distantly related, aquatic vertebrates and plants, share components. Implications of oceanic biogeographic regions for continental biotas are outlined using South America as an example. A continent is part of the biogeographic regions of all the oceans it contacts.

Introduction

This paper addresses two points in historical biogeography: definition of global biogeographic realms or regions, and relationships among those regions. Terrestrial, including freshwater organisms are usually identified by the land mass, often a continent, in which they live. We are accustomed to hearing about 'South American freshwater fishes', 'Australian birds' (Cracraft 1986), 'African mammals' and so on. Similarly, we identify marine organisms by an ocean basin; 'Indo-Pacific fishes' is thought to mean marine fish generally (e.g. Springer 1982) and 'Indo-Pacific molluscs' means marine molluscs (e.g. Kohn 1990).

Botanist and biogeographer Leon Croizat (1964) provided extensive documentation to support his observation that major biotic tracks of both marine and terrestrial organisms cross ocean basins. Panbiogeographers Craw and Page (1988) followed Croizat's lead and proposed a new set of global biogeographic realms or regions that focus on ocean basins rather than continents. Springer (1982) identified the Pacific lithospheric plate as a biogeographic region for marine shorefishes and other organisms. Ocean biogeographic regions have been incorporated into biogeographic discussions of both terrestrial and marine organisms by members of the New Zealand school of biogeography (Page 1989) but rarely by others (e.g. Parenti 1989*a*; Platnick and Nelson 1989).

All biogeographic regions will be altered during geologic history. My purpose is to demonstrate the relevance of ocean basin evolution to the distribution of freshwater fishes and other terrestrial organisms. I modify slightly the biogeographic regions of Craw and Page (1988) to include the Tethys Sea because of its importance in understanding the composite Indo-Australian biota (Fig. 1).

I support the goals and methods of vicariance biogeography as outlined by Nelson and Platnick (1981; see Page 1990). I use the area cladogram, a hierarchical representation of relationships among areas, to interpret relationships among ocean basins.
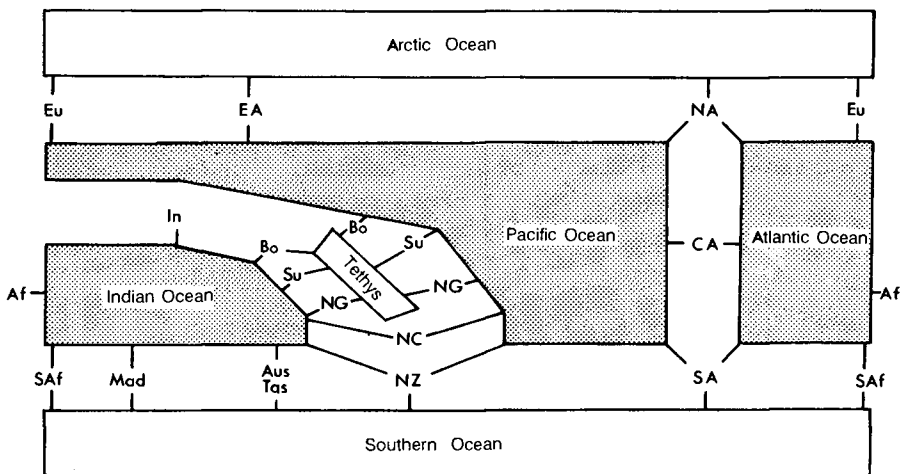

Fig. 1. Biogeographic realms modified from Craw and Page (1988: fig. 12) to show some composite areas of the Tethys Sea. Af, Africa; Aus, Australia; Bo, Borneo; CA, Central America; Eu, Europe; In, India; Mad, Madagascar; NA, North America; NC, New Caledonia; NG, New Guinea; NZ, New Zealand; SA, South America; SAf, South Africa; Su, Sulawesi; Tas, Tasmania.

The Indo-Australian Archipelago and the Tethys Sea

Schuh and Stonedahl (1986) presented a comprehensive cladistic summary of area relationships throughout much of the Indo-Pacific, including the Indo-Australian archipelago (Fig. 2). The scheme of area relationships was derived from their phylogenetic systematic studies of plant bugs (Heteroptera, Miridae) and incorporated the results of Duffels (1986) on cicadas and, to a limited degree, observations of Holloway (1984) on Lepidoptera. The sister-area of all those areas in Fig. 2 is Ghana (= West Africa or eastern Atlantic).

Many areas in Schuh and Stonedahl's analysis are islands or island groups (Fig. 2). The cladistic relationship of New Guinea is resolved (Fig. 2), even though Schuh and Stonedahl concluded that the island is a biological, as well as a geological, composite. The Philippines are divided into a northern and southern portion, with the southern portion showing a close relationship to northern Borneo. The relationships of southern India and Sulawesi are unresolved. Some of these area relationships were found by Cracraft (1988) for Indo-Australian birds: the Philippines do not form one area, but Palawan (the southern Philippines) is closely related to Sundaland (Java, Sumatra, Borneo and the Malay Peninsula).

Schuh and Stonedahl (1986) pointed out two limitations of their hypothesis that have been taken as a general criticism of cladistic biogeography (sensu Humphries and Parenti 1986): it does not adequately treat composite areas, and it does not incorporate trans-oceanic relationships (see Craw 1983). Panbiogeographers have long understood that these two perceived limitations really concern the same problem: major composite areas are trans-oceanic (Craw and Page 1988). Of course, some cladistic biogeographers have incorporated composite areas into their studies, and no aspect of the method precludes recognition of composites (Nelson and Platnick 1981; Schuh and Stonedahl 1986).

Smith and Hood (1981) analysed phylogenetic relationships and distribution of Indo-Pacific bats (Fig. 3). When New Guinea was treated as one area, two general patterns were found: (1) New Guinea is the sister-area to islands in the Banda Sea, the Bismark Archipelago and the Solomon Islands (Fig. 3a); (2) islands in the Banda Sea form the sister-area to New Guinea, the Bismark Archipelago and the Solomon Islands (Fig. 3b). A consensus tree between the area cladograms of Fig. 3a and 3b is trivial: the relationship among Banda Sea, New Guinea and the sister-areas Solomon Islands and the Bismark Archipelago is unresolved. Smith and Hood (1981) achieved resolution when they treated New Guinea as a composite, divided into two areas: nuclear New Guinea and tethyan New Guinea (Fig. 3c). What ocean does the composite New Guinea span? 'Tethyan New Guinea' implies some rendition of the ancient Tethys Sea.
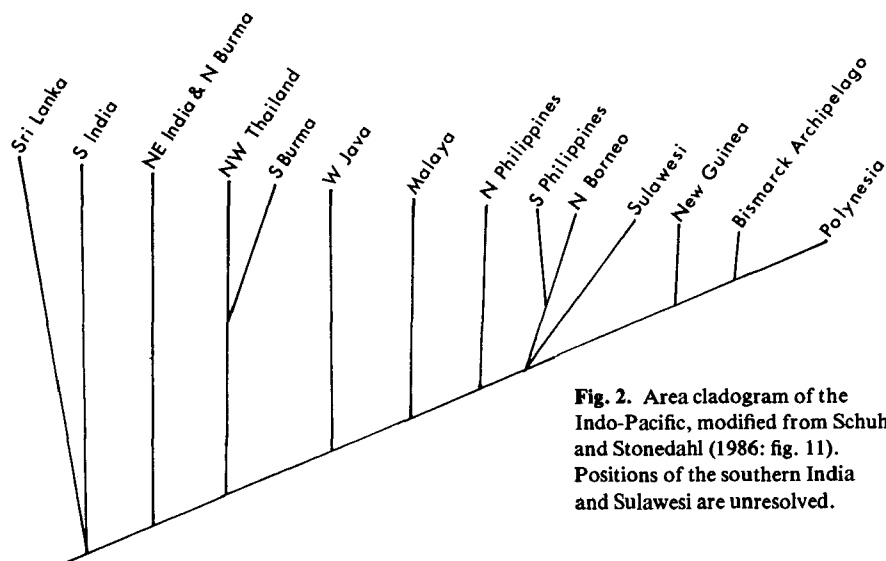

Fig. 2. Area cladogram of the Indo-Pacific, modified from Schuh and Stonedahl (1986: fig. 11). Positions of the southern India and Sulawesi are unresolved.

Plate tectonics has changed the way we look at the Indo-Australian archipelago. The area is complex. Modern large islands such as Sulawesi, New Guinea and Borneo are composites, as are political entities such as the Philippines. Historical geological details vary and may conflict (Hamilton 1979, 1988; Audley-Charles 1987; Cracraft 1988; Burrett *et al.* 1991). In one summary, by the Middle Mesozoic (Late Jurassic, 160 MYA), New Guinea rifted from Sumatra and was flanked by bits of Borneo and western Sulawesi; Timor rifted from Southern Tibet and Burma; and eastern Sulawesi rifted from Thailand (Audley-Charles 1987: fig. 2.1). The body of water that formed as these land masses separated has been referred to as the Tethys Sea (e.g. Audley-Charles 1987). This should not be confused with the larger, hypothetical Tethys, believed to have once separated the Indian subcontinent from Asia; that ocean is an artefact under theories of an expanding earth (Carey 1983).

Following the rift of widespread, ancestral biotas across an expanding Tethys Sea, sister-taxa on present-day Sumatra and nuclear New Guinea could be called trans-Tethyan. This is simple. What is less clear or less obvious is the distribution throughout present-day large islands such as Borneo, Sulawesi and New Guinea which, in late Jurassic times, were present as separate bits, rifted apart only to come back together again in combinations that give seemingly little indication of their former associations.

Are there trans-Tethyan relationships among freshwater fishes? Firstly, I consider the silversides or hardyheads of the bony fish family Phallostethidae, comprising 19 species (Parenti 1986, 1989b). Phallostethids are primarily coastal (freshwater and marine) fishes, distributed throughout the Malay Peninsula, north-western Borneo and the Philippines, entirely west of Wallace's Line (Parenti 1989b: fig. 1). Their hypothesised sister-group is the monotypic silverside *Dentatherina* (Parenti 1984), a widely distributed marine shorefish described from material collected from the Philippines to north-eastern Australia, and from

the Moluccas to the Trobriand islands (Patten and Ivantsoff 1983). The distributions of phallostethids and *Dentatherina* are complementary, overlapping in Borneo and the southern Philippines.

I classified phallostethids in three tribes (Parenti 1989b), and discuss two here. The tribe Phallostethini contains four species with resolved phylogenetic relationships (Fig. 4). An area cladogram for the tribe is formed by replacing the name of the species with the area in which it occurs (Fig. 5). This cladogram adds little to our broad knowledge of area relationships but does show that Malayan phallostethids are not monophyletic (Fig. 5).
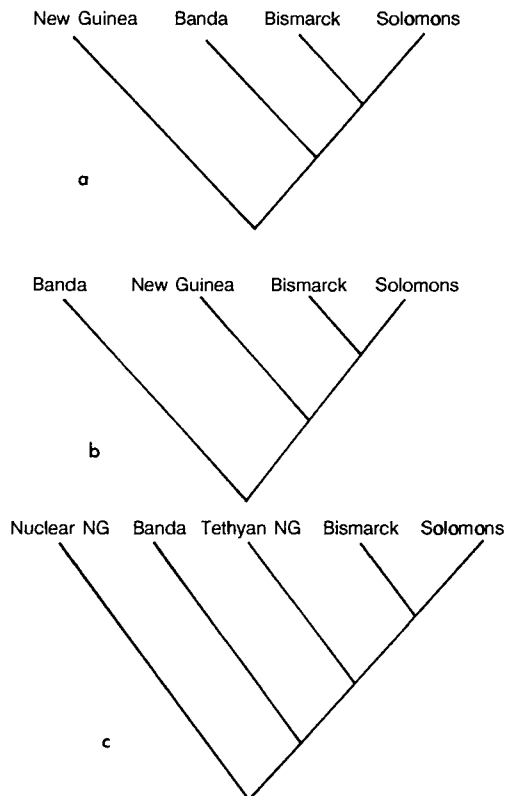

Fig. 3. Area cladogram of bats, from Smith and Hood (1981: fig. 11): (a) and (b) alternate area cladograms for different groups of bats; (c) resolution of alternate patterns in 3a and 3b when New Guinea (NG) is treated as a composite.

The tribe Neostethini comprises 10 species (Fig. 6). An area cladogram reveals that many taxa are widespread and therefore are also uninformative with respect to relationships among areas (Nelson and Platnick 1981; Fig. 7). However, general statements may be made: (1) Philippine species are not monophyletic; (2) Borneo species are not monophyletic; and (3) Malay Peninsula species are not monophyletic. There is no further resolution of Schuh and Stonedahl's hypothesis but, their composites are supported (Northern and Southern Philippines) and additional composites identified (Malaya).

The second group is ricefish family Adrianichthyidae (*sensu* Rosen and Parenti 1981). Ricefish are broadly distributed from the eastern U.S.S.R. and India through continental Asia, and along the Indo-Australian archipelago to Sulawesi and Timor (Yamamoto 1975: fig. 2–4; Uwa and Parenti 1988). Ricefish distribution spans Wallace's Line.

Ricefish are absent from Sumatra, Borneo and New Guinea. I agree that absences need not be explained in biogeography (e.g. Schuh and Stonedahl 1986). However, absence from Borneo/Sumatra/New Guinea makes sense if we consider that these land masses were adjacent prior to opening of the Tethys Sea; we may hypothesise that the ancestral distribution of ricefishes did not include these areas. This hypothesis is more parsimonious than creating a separate explanation for each absence on each large island.

Phylogenetic relationships among all ricefish species are under study by myself and others. Preliminary reports indicate that Sulawesi species are polyphyletic (Parenti 1987).

Lake Poso in north-eastern Sulawesi contains large, plesiomorphic ricefishes currently classified in the genera *Adrianichthys* and *Xenopoecilus*; a phylogenetically more derived *Oryzias* species lives in the south-western arm of Sulawesi (Parenti 1987; Kottelat 1990).
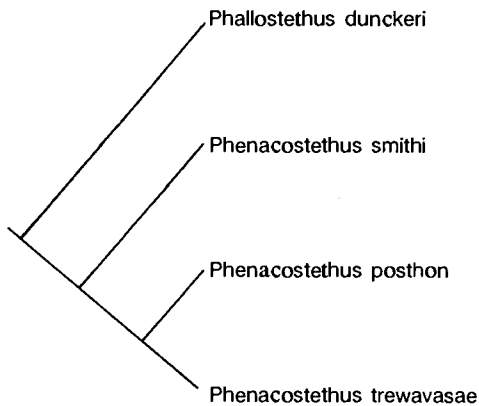
Phallostethus dunckeri

Phenacostethus smithi

Fig. 4. Cladogram of relationships among species in the phallostethid tribe Phallostethini (from Parenti 1986: fig. 5).

Phenacostethus posthon
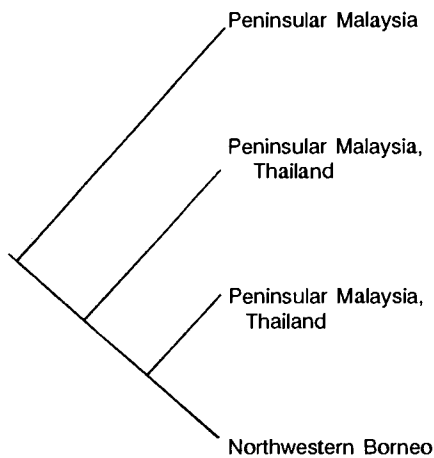
Phenacostethus trewavasae

Peninsular Malaysia

Peninsular Malaysia, Thailand

Fig. 5. Area cladogram for phallostethid species, following relationships in Fig. 4.

Peninsular Malaysia, Thailand

Northwestern Borneo

Distributions like those of ricefishes, phallostethids and their sister-taxon, plant bugs, cicadas and bats have been described in whole or part as Indo-Australian or Indo-Pacific. Relationships indicate that the taxa may also be described as trans-Tethyan; together they confirm the composite biotic relationships of geologically composite Sulawesi, New Guinea and Borneo. Some will argue that these taxa are too young to have been affected by geological events over 150 mya. However, I agree with Heads (1990: 224) that '. . . tectonics and biogeography suggest that the last main phase of modernisation for the world was in the upper Mesozoic . . .'. If modern species were not present their ancestral taxa were. Springer and Williams (1990) proposed Pliocene-Pleistocene extinction owing to lowered sea levels throughout the Indo-Australian archipelago as an explanation for some cases of Pacific plate endemism. Continuously distributed Indo-Pacific taxa went extinct in parts of their ranges with loss of marine habitats. If true, this explanation requires that ancestral populations were widely distributed throughout the Indo-Pacific prior to the Pliocene-Pleistocene.

Relationships among taxa help us identify or confirm composite areas such as nuclear and tethyan New Guinea which can be treated as two areas in further studies. This aspect of
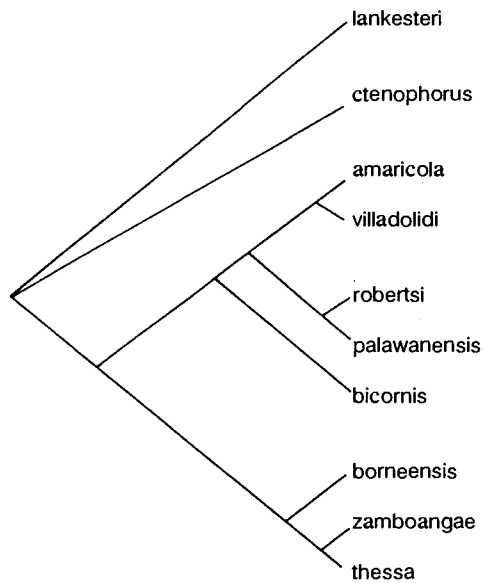
lankesteri

ctenophorus

amaricola

villadolidi

Fig. 6. Cladogram of relationships among species in
the phallostethid tribe Neostethini (= genus
Neostethus) (from Parenti 1989*b*: fig. 8).

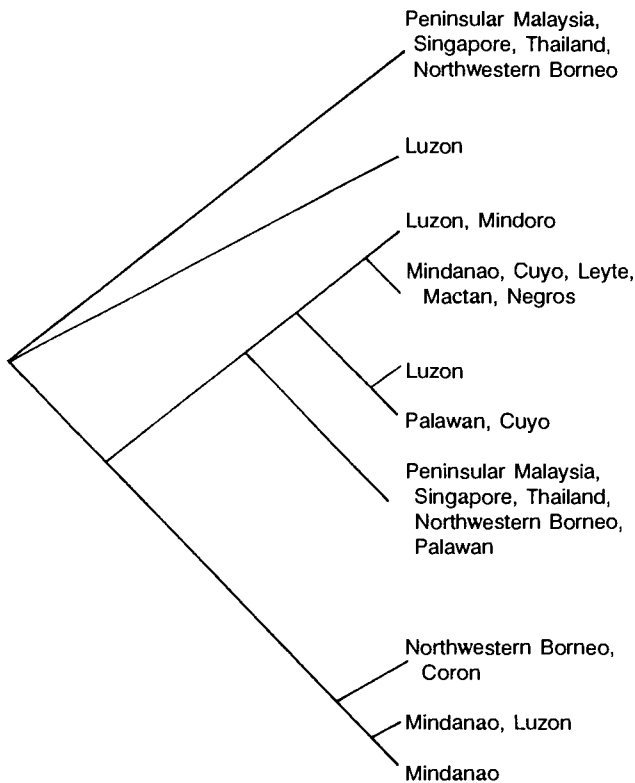robertsi

palawanensis

bicornis

borneensis

zamboangae

thessa

Peninsular Malaysia,
Singapore, Thailand,
Northwestern Borneo

Luzon

Luzon, Mindoro

Mindanao, Cuyo, Leyte,
Mactan, Negros

Luzon

Palawan, Cuyo

Fig. 7. Area cladogram for
Neostethus species, following
relationships in Fig. 6.

Peninsular Malaysia,
Singapore, Thailand,
Northwestern Borneo,
Palawan

Northwestern Borneo,
Coron

Mindanao, Luzon

Mindanao

cladistic biogeography has been criticised as creating an endless regression: incongruent areas
will demand finer and finer subdivision of areas (Patterson 1981). I claim that our experience
tells us the regression will not be endless. We may stop dividing areas after we identify where
phylogenetic relationships span an ocean basin, either past or present.

Recognition of composite areas and oceanic biogeographic realms is not meant to sub-
stitute for recognition of an area of endemism as that area occupied by a monophyletic group

(Nelson and Platnick 1981). Tethyan New Guinea may not be an area of endemism for all members of the tethyan New Guinea biota. However, knowing that it might be an area of endemism for much of the biota will prevent treating New Guinea as one area in biogeographic studies. New Guinea can never be identified as part of the Australian or the Asian realm. Continental realms have little reality when identifying historical relationships of continental biotas; the biota is trans-oceanic. Composite areas treated as one will always occupy unresolved positions on area cladograms, or result in incongruence among area cladograms (see also Cracraft 1989).
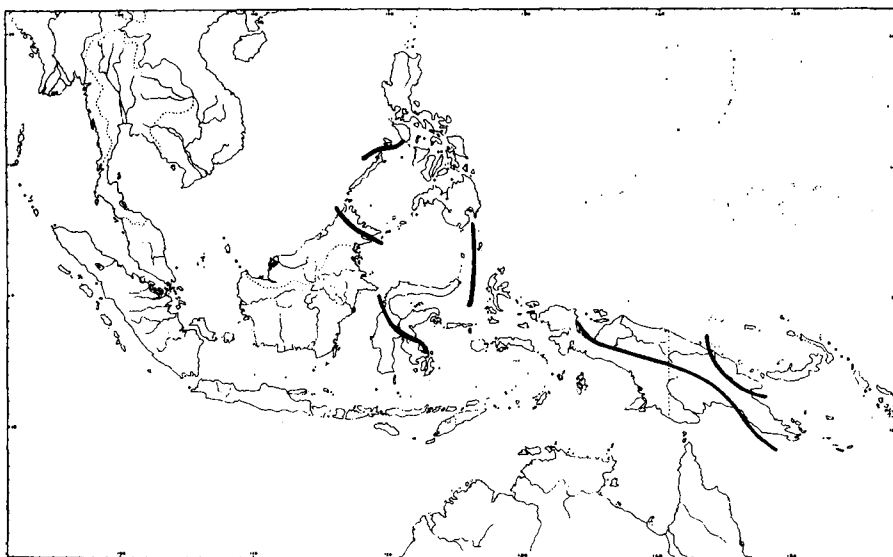

Fig. 8. Some major suture and fault lines through the Indo-Australian region (Hamilton 1988: fig. 2).

Wallace's and Other Lines

Simpson (1977) wrote that 'too many lines' had been proposed to separate the Asian from the Australian zoogeographic realm. He identified seven such lines: Müller's, Wallace's, Murray's, Huxley's, Sclater's, Lydekker's and Weber's. Wallace's Line has been given special status in biogeography of both terrestrial and marine organisms (e.g. Whitmore 1981; Woodland 1986). However, Humphries (1989) criticised Wallace's Line as an over-emphasised boundary that is no different from other major zones of biotic contact. I agree that too many vertical lines have been drawn to separate islands or island groups from one another. If we cannot decide whether to draw a line to the east or the west of modern Sulawesi, for example, then perhaps we should draw a line through it.

Were we to draw new lines to describe Indo-Australian distribution patterns, the lines would pass through and bisect the traditional lines, through New Guinea, through Sulawesi and through Borneo. Huxley's line separates the southern and northern Philippines (Simpson 1977). Suture and fault lines mark the closing of the Tethys Sea (Hamilton 1988; Fig. 8). These lines may be connected to create a new line, perhaps to be called Hamilton's Line. Like Wallace's and other lines, it too would separate areas but would remind us that there is an ancient ocean basin hidden inside the Indo-Australian archipelago, and that distribution of organisms throughout the archipelago may be better understood if we consider the Tethys Sea when trying to resolve relationships among areas.

The Indo-Australian Archipelago and Modern Oceans

How is the Indo-Pacific region related to the rest of the world? To address this question for freshwater fishes, I add a more widespread group to the study. The sicydiine gobies comprise a diverse, circumtropical group of about 60 species. They are amphidromous: adults live and breed in freshwater, whereas larvae are transported to the sea where they undergo transformation, returning to rocky bottom, fast-flowing streams where they live

as adults (Erdman 1986, personal observation, New Guinea and Maui). Life history requirements of sicydiines may affect distribution patterns on a small scale (e.g. Leis 1986); however, sicydiine distribution is interpreted below as part of a larger, global pattern.

Sicydiines may be classified in five genera: *Sicyopus, Lentipes, Sicydium, Stiphodon* and *Sicyopterus* (see Hoese 1984). A preliminary hypothesis of phylogenetic relationships among genera is principally on a transition series of outer jaw teeth morphology (Fig. 9; see Sakai and Nakamura 1979: fig. 8). Characters are polarised using the pantropical gobiid *Awaous* as an outgroup (Harrison 1989). Phylogenetic relationships among the genera are under study and new species remain to be described; however, this preliminary cladogram is well founded.
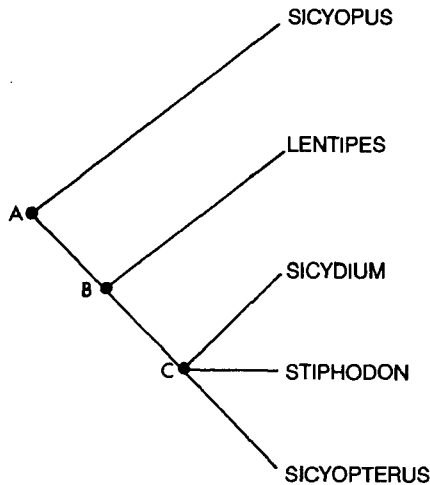

Fig. 9. Cladogram of relationships among sicydiine genera. Derived characters to support each node: (A) adnate tongue (skin covering basihyal and floor of mouth), fused, thickened and highly branched pelvic fin-rays, and fleshy pads at posterior tips of pelvic spines (Hoese 1984), (B) medial and anterolateral portion of upper and lower oral jaw with external row of thin, closely set teeth (Sakai and Nakamura 1979); (C) upper and lower oral jaw with external row of thin, closely set teeth (Akihito and Meguro 1979).
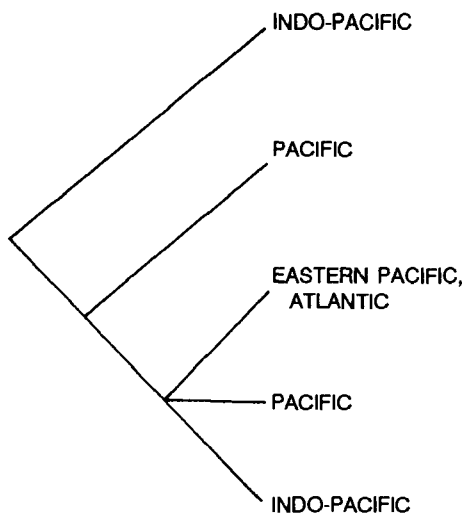

Fig. 10. Area (ocean) cladogram for sicydiine genera, with the name of a genus in Fig. 9 replaced by the name of the ocean basin(s) in which it occurs. See text for further discussion.

To construct an area cladogram for sicydiines, I could replace the name of each genus with a list of the areas in which it lives. However, the distribution of each genus can best and most easily be described in terms of an ocean basin (Fig. 10). *Sicyopus* lives in the Indo-Pacific (Klausewitz and Henrich 1986). *Lentipes* is known from Hawaii and the Ryukyus (Sakai and Nakamura 1979; although Springer (1982) questioned classification of the Japanese species). *Sicydium* is found in the eastern Pacific and the Atlantic; eastern Pacific includes freshwater coastal streams of Ecuador and western Central America, as well as insular streams of, for example, Cocos Island (Hertlein 1963). *Sicydium stimpsoni* Gill, common in Hawaii as well as throughout the central Pacific (Tinker 1978), has been reclassified in *Sicyopterus* (Akihito and Meguro 1979). *Sicyopterus* is Indo-Pacific, found

from Madagascar, through the Indo-Australian archipelago to Rapa and Pitcairn Islands in the south-eastern Pacific (Koumans 1953; Randall *et al.* 1990).

The set of area (ocean) relationships (Fig. 10) is hierarchical. Were this a character state tree in phylogenetic systematic analysis, we could say that the Pacific, or the Indo-Pacific, is plesiomorphic. In cladistic biogeography, this means that vicariance between the Western (or Indo-) and eastern Pacific preceded vicariance between the Atlantic and the eastern Pacific. One contribution of cladistic biogeography that sets it apart from other biogeographic methods is that it allows the ordering of evolutionary events without relying on arbitrary measure of age, such as oldest known fossil, relative taxonomic rank, or conformation to a geologic hypothesis (Nelson and Platnick 1981; Humphries and Parenti 1986).
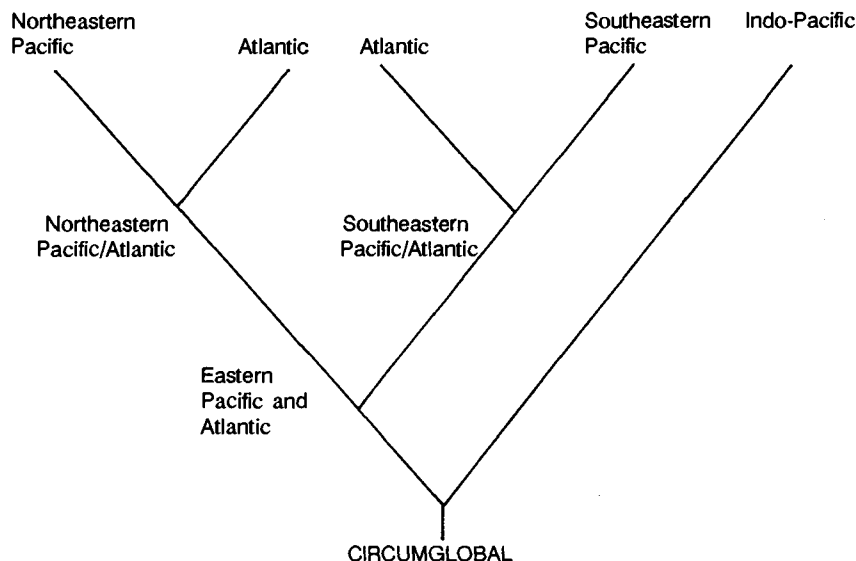

Fig. 11. Model of some relationships among modern ocean basins, modified in part from Brooks *et al.* (1981: fig. 16). Differentiation across the Indo-Pacific and the Atlantic is not considered here.

A model that incorporates some of the same ocean basin relationships was proposed by Brooks *et al.* (1981) for stingrays of the genus *Urolophus* and their helminth parasites. Their model may be rejected, in part, because monophyly of *Urolophus* may not be confirmed; South American species studied by Brooks *et al.* should be referred to *Urobatis* (John McEachran, personal communication). However, I treat the model like any hypothesis of area relationships, and ask if it has any general significance. The model was confirmed, in part, for cladistic area relationships of *Cetengraulis* anchovies by Nelson (1984: fig. 3): a South American freshwater species is plesiomorphic to a Eastern Pacific and an Atlantic sister-group pair. Valdebenito *et al.* (1990) documented the close relationship between species in the plant genus *Peperomia* from the Juan Fernandez Islands (Eastern Pacific) and the Tristan de Cunha archipelago (Southern Atlantic). Valdebenito *et al.*, (1990) proposed dispersal of plesiomorphic Juan Fernandez species to Tristan de Cunha. It is more parsimonious to suggest that stingrays and their parasites, anchovies, gobies and *Peperomia* are all part of the same general biogeographic pattern.

Brooks *et al.* (1981) considered a circumpacific distribution ancestral; the model works also with a circumglobal ancestral distribution (Fig. 11). They hypothesised vicariance first across the Pacific basin to create a western Pacific and an eastern Pacific biota, followed by a differentiation of the south-eastern Pacific into a South American freshwater and a Caribbean/Western Atlantic biota.

Brooks *et al.* (1981) proposed dispersal from the eastern Pacific to the Caribbean/ Western Atlantic to account for closely related taxa in both the eastern Pacific and the Atlantic. One could alternatively consider a circumglobal ancestral distribution disrupted by formation of the ocean basins with vicariance between the eastern Pacific and the Atlantic when the Panamanian isthmus was formed (Nelson 1984). Formation of antitropical

distributions in conjunction with disruption of the Pacific basin is also implied by this model and has been discussed elsewhere (Nelson 1984; Humphries and Parenti 1986).

Implications for Continental Biotas: South America, an Example

If global biogeographic regions are ocean basins, then the regions cannot at the same time be continents. A continent is part of the biogeographic regions of all the oceans that it contacts. We can predict realistically that the South American biota will have relationships across three oceans: Atlantic, Pacific and the southern ocean (Fig. 1). Trans-Atlantic relationships are well known for many portions of the tropical, lowland South American biota. However, oceanic regions will be of little interest to those studying biogeographic patterns of taxonomic groups distributed solely within tropical lowland South America (e.g. Weitzman et al. 1988).

Brundin (1966) and Crisci et al. (1990) provide reasons for treating southern South America and the Andes as part of a southern oceans biota, rather than part of a continental biota. Southern South America and the Andes were not included in a discussion of areas of endemism of the widespread freshwater fish family Curimatidae, which has no representatives in those portions of South America (Vari 1988).

Trans-Pacific relationships for South America taxa are less obvious, principally because differentiation across the Pacific is proposed to have occurred before differentiation between the eastern Pacific and the Atlantic (Fig. 11). Sicyciine gobies of the genus Sicydium are found throughout the tropical eastern Pacific and the Atlantic. I consider the eastern Pacific distribution to include Sicydium hildebrandi from coastal streams of Ecuador (Barriga 1989) and the Atlantic distribution to include Sicydium montanum from coastal streams near Caracas, Venezuela (Hubbs 1920). Distributions of closely related taxa in, for example, coastal eastern Venezuela and coastal western Ecuador are often called trans-Andean. Andean orogeny is usually proposed as the vicariant event that disrupted a more widespread, hypothetical, ancestral biota to form trans-Andean sister-group pairs (e.g. Cracraft and Prum 1988). The model of Fig. 11 implies that such a distribution could also be called trans-eastern Pacific/Atlantic, and that formation of the Panamanian isthmus, along with expansion of ocean basins, were the vicariance events that disrupted the ancestral biota, separating eastern Pacific from western Atlantic taxa. Additional reinterpretations of distributions of South American freshwater (terrestrial) taxa as part of an oceanic biogeographic region, rather than a continental biogeographic region, are possible.

The history of continental biotas is undoubtedly complex (Cracraft 1989). Despite recent vigorous debate on the methods of cladistic biogeography (e.g. Brooks 1985; Humphries et al. 1988; Wiley 1988; Platnick and Nelson 1989; Page 1990), no consensus has been reached on how to choose among competing general area cladograms for continental taxa (e.g. Cracraft 1989). Recognition of composite areas and oceanic regions will help to eliminate incongruence (e.g. Fig. 3) from historical biogeographic studies.

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