



The shape of biogeography: Endemism, maps, and classification of fish distributions in the western Pacific

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Abstract

Aim: The aim of this study is to describe and illustrate with maps the distribution and shape of biotic areas of endemism of fish clades in the western Pacific, including East Asia and Australasia. This study also depicts the allopatric or sympatric distributions of major subclades and makes general statements about the shared history among the areas using information provided by the shape of the distributions, phylogeny, and geology. This study also tests the hypothesis that Australasia is a locus of survival or differentiation for inferred “basal” subclades of global taxa.

Location: Western Pacific.

Taxa: Teleost fishes.

Methods: Clades are mapped to illustrate the shape of their distribution and to infer the shared relationships among distribution, phylogeny, and geology. Phylogenetic hypotheses for groups of taxa are converted into area cladograms which are used to summarize area relationships. This information is compared with that from other clades, ecology, and geology, to make general statements about the biogeographical history of the fish biota.

Results: The distribution of each clade has an identifiable shape. The “basal” subclades of many widespread teleost fish taxa are endemic to the western Pacific, including East Asia and Australasia; hence, this is the inferred location of a principal vicariant event for each clade. The “basal” subclade and its sister clade may be allopatric and represent remnants of general distributional patterns. The distribution of a clade, including its geography and its relationship with a geographical or geological feature, conveys historical information about the clade and the area in which it evolved: its area of endemism. These features repeat in unrelated or distantly related taxa in the biota indicating a shared history.

Main conclusions: The western Pacific including East Asia and Australasia is a locus of survival or differentiation, the site of the principal breaks in the distribution, for an array of teleost clades. It is not their center of origin. Biology and geology should be integrated in biogeographical analyses. Modern distributions reflect remnants of once more widespread distributions. When biogeography acknowledges the connections and correlations between geology and biology, it implements a guiding principle of the work of Alexander von Humboldt.

KEYWORDS

allopatry, area morphology, biogeographical patterns, dispersal, pantropical, sympatry, terrane fidelity, vicariance

1 | INTRODUCTION

Maps are critical to biogeography: they depict the contours and shapes of biological distributions and contain information about the history of those distributions. To the extent that they coincide with geological or geographical features, past or present, they also illustrate the intimate relationship between biology and geology. Alexander von Humboldt (1850) was among the first scientists to recognize and emphasize the critical role that maps play in biogeography. He understood and used the power of maps, not just to convey his ideas about the relationship between biology and geology, but also to generate them:

Central to Humboldt was the idea that spatial distribution might reveal the complex interdependence in the natural world, and he spent much of his life trying to redefine geography along those lines. To a great extent, he invoked maps and graphical visualizations not only to *illustrate* his ideas about spatial distribution, but to *formulate* them. [Italics in original]. Schulten (2018)

Along with maps, biogeographical classification—the naming and ranking of areas—engaged biogeographers from the start and naturally linked biogeography with evolution. Alfred Russel Wallace (1863) recognized a marked separation between the Asian and Australian biota in the center of the Indo-Australian Archipelago. The division was both biological and geological. Two principles—endemism and

terrane fidelity—came together on maps to illustrate that life and Earth evolved together.

Endemism is the critical concept in biogeography that links the organism with its habitat (Parenti & Ebach, 2009). An area of endemism has a particular shape or morphology that reflects the history of a lineage. An area of endemism has discrete contours and boundaries and may include breaks or broad gaps, as in disjunct or antitropical distributions (e.g., Gill & Mooi, 2017: fig. 6.7). These breaks are not singular, but repeat for many unrelated or distantly related taxa in a biota.

An area may be unique to a clade, but it may also reflect general, congruent distributions, such as Pantropical, Holarctic, Trans-Pacific or Trans-Atlantic, or just remnants of those distributional patterns (Humphries & Parenti, 1999; Parenti, 2008). The broad, general distributional patterns shared across taxa in a biota form the basis of a biogeographical classification (e.g., Ebach & Michaux, 2017; Ebach, Morrone, Parenti, & Vilorio, 2008) (Figure 1).

Biological and geological boundaries that coincide may be hypothesized to share a history, to have been formed at the same time and by the same events. For example, Springer (1982; Figure 1) examined in detail the distribution and endemism of marine shore fishes of the Pacific and their relationship with the Pacific, Philippine, and other lithospheric plates. He inferred that formation and activity of the tectonic plates effected the distribution of the plate's endemic shorefishes and other taxa. Concordance between geology and biology was demonstrated also by Hendrickson (1986) for lungless salamanders distributed on accreted terranes in western North America and, more recently, by Gottscho (2016) for zoogeographical patterns that match

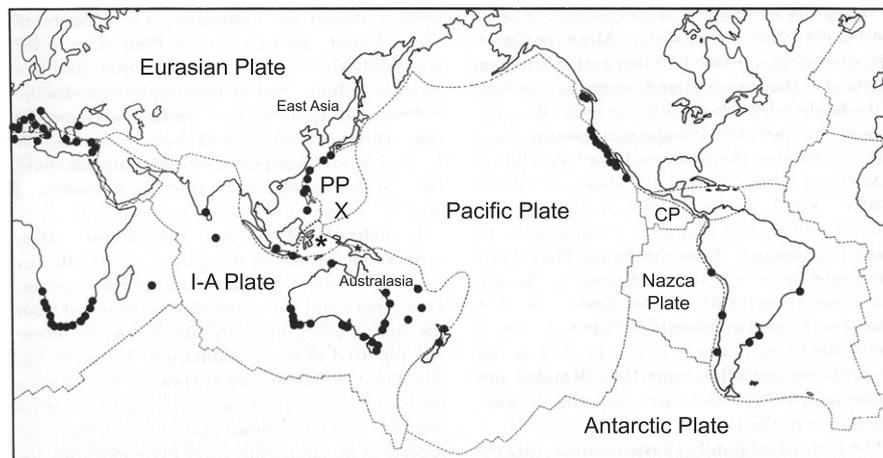


FIGURE 1 One example of the correlation of the distribution of a fish taxon with lithospheric plates; the distribution of fishes of the percomorph family Clinidae (blennies). Each dot represents a collection or report of specimens. The star is an unspecified locality in New Guinea. The X marks the approximate location of Palau on the southeastern margin of the Philippine Plate. The large asterisk (*) marks the island of Sulawesi, which is separated from the other islands to indicate its composite geology that was not shown in the original map. Abbreviations: CP, Cocos Plate; I-A Plate, Indian-Australian Plate; PP, Philippine Plate. Modified from Springer (1982: fig. 15)



fracture zones of the San Andreas Fault system. Terrane fidelity, the persistence of an organism or a lineage on a geological terrane, links an organism with a discrete geological region. Terrane fidelity, coupled with natal philopatry, the regular and routine return to place of birth (Heads, 2012: 383), characterizes the distributions of many migratory taxa, such as birds (e.g., Wolfson, 1948) and fishes (e.g., Parenti, 2008). This method of “spatial correlation” of taxa and tectonics forms the basis of panbiogeography, as expounded by Croizat (1964), Craw, Grehan, and Heads (1999), Michaux (2010), Heads (2005, 2011, 2012, 2014), and Grehan and Mielke (2018), among others.

Australasia, Heads (2014) argued, has a special place in biological evolution: it is home to the “basal” members of many global clades such as the New Zealand tuatara, which is sister to all other lizards and snakes. Heads (2014) defined Australasia—the area south of Asia—as comprising Australia and the large islands of New Guinea, New Caledonia, and New Zealand. It is not a natural biogeographical region and we do not know the relationships among the areas considered to lie within it (see Ebach, 2017). Furthermore, many of the “basal” taxa, as identified by Heads (2014), live more broadly in the western Pacific, including Palau and the Philippines. Therefore, I expand the area of interest for bony fishes to the western Pacific, broadly defined. The western Pacific distribution of fishes occupies an arc from the northern limits of East Asia south to New Zealand and the east coast of Australia (Motomura, Alama, Muto, Babaran, & Ishikawa, 2017:16: Figure 1).

The aim of this paper is to demonstrate that the western Pacific is home to the “basal” clade, or subclade, of many widespread bony fish taxa, including freshwater, coastal, and marine lineages. A “basal” clade is a small sister of a diverse, widespread group. The break between these sister-groups is “basal.” “Basal” does not mean ancestral, and further, the western Pacific should not be misinterpreted as the center of origin for teleost lineages on Earth, but rather recognized as a locus of survival or differentiation where major breaks or interruptions in widespread distributions occurred. These breaks may be explained by geology and ecology. This approach stands in contrast to applications of the prevailing long-distance dispersal from a center of origin model of biological distribution. In those studies, assumptions about the age of taxa and their supposed dispersal ability are treated routinely as evidence of particular biogeographical explanations, rather than as hypotheses (Parenti & Ebach, 2013).

2 | MATERIALS AND METHODS

Clades from across teleost phylogeny with broad distributions throughout the western Pacific, and global sister groups, are mapped to depict their distributional limits and identify where major breaks or disjunctions in distributions occur. The taxa represent a phylogenetic range of teleost fishes, Teleostei *sensu* de Pinna (1996), from the most primitive Osteoglossomorpha to the derived Percomorpha. The teleost clades with the largest number of freshwater (Cypriniformes, about 489 genera and 4,205 species) and marine (Gobioidae or Gobiiformes, about 321 genera and 2,167 species) taxa are included

(Nelson, Grande, & Wilson, 2016). Data on distributions are from systematic analyses and the highly informative maps of Berra (1981, 2001, 2007); these are supplemented by catalog records in FishNet2 (<http://www.fishnet2.net/>). Phylogenetic hypotheses are converted into area cladograms, following the methods outlined by Nelson and Platnick (1981) and elaborated elsewhere (e.g., Parenti & Ebach, 2009): names of taxa are replaced by the areas in which they live. These area cladograms are used to summarize the information on area relationships contained in the phylogenetic hypotheses. This information is compared with geological hypotheses to make general statements about the distributional history of major clades of fishes in the western Pacific.

3 | RESULTS

3.1 | Distribution and phylogenetic relationships of fish clades

3.1.1 | Osteoglossomorpha (bony-tongues), family Osteoglossidae

The osteoglossomorph lineage is one of the most “basal” of all teleost fishes (see recent review by Hilton & Lavoué, 2018). Extant and fossil taxa are distributed broadly throughout the tropics and temperate Laurasia (Hilton & Lavoué, 2018: fig. 18, top).

The family Hiodontidae is the most “basal” of the main osteoglossomorph lineage: its Recent representatives in the genus *Hiodon* live in North American freshwaters; fossils in the genus †*Eohiodon* are known from East Asia and North America. Additional fossil osteoglossomorphs are represented in several assemblages of Late Jurassic–Early Cretaceous fishes of eastern China (Chang & Chow, 1986: fig. 1). Several of the fossil genera are stem-group osteoglossomorphs; others are more closely related to subclades in the main osteoglossomorph lineage. These taxa comprise a boreal or Holarctic group. All other osteoglossomorphs are pantropical (Hilton & Lavoué, 2018: fig. 18, bottom).

Hilton and Lavoué (2018) defined six areas for fossil and living osteoglossomorphs: Afrotropics (A), Neotropics (B), Orient (C), Australia (D), Nearctic (E), and Northeastern Palearctic (Cretaceous) (F). Areas A through D are pantropical; E and F Holarctic or boreal. Information on relationships among the pantropical areas is contained in the osteoglossid clade (Hilton & Lavoué, 2018: fig. 18, bottom): *Arapaima* (B) is sister to *Heterotis* (A) which together are sister to the fossil genus †*Singlossus* (C). This clade is sister to the trans-Pacific sister genera *Osteoglossum* (B) and *Scleropages* (CD). The informative relationships among the four pantropical areas are: ((A, B), (C,D)) (Figure 2). A second clade of genera from areas A (families Mormyridae and Gymnarchidae) and C (family Notopteridae) provide no additional information on area relationships. Holarctic areas E and F repeat on the cladogram, as a widespread area EF or with E as sister to one or more pantropical areas.

The break between the “basal” temperate fossil assemblages of East Asia (area F) and tropical *Scleropages* (in area CD) is marked (Figure 3). These East Asian fossils are part of a Holarctic clade (Figure 2).

Osteoglossomorph Area Relationships

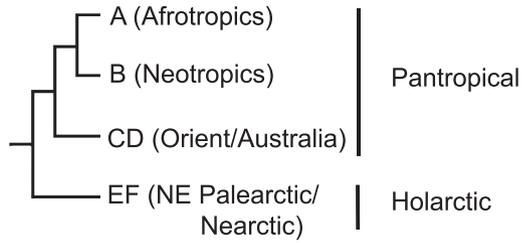


FIGURE 2 Area relationships of osteoglossomorph fishes as inferred from information in the analysis of Hilton and Lavoué (2018). See text for explanation

3.1.2 | Anguilliformes (freshwater and marine eels)

The hypothesized sister group of all other anguilliforms, a broadly distributed taxon, is the deep sea *Protanguilla* (see Johnson et al., 2012). It was described from a 35 m deep cave in Palau, an island chain on the eastern margin of the Philippine tectonic plate (Figures 1 and 4). *Protanguilla* is estimated to have evolved at least

200 Ma, using a molecular clock analysis of sequence divergence (Johnson et al., 2012).

The freshwater eels, the family Anguillidae, comprise some 19 species and subspecies all in the genus *Anguilla* (Teng, Lin, & Tzeng, 2009). The oldest fossils of *Anguilla* are from 50 to 55 Ma (Patterson, 1993). Today anguillids live in pantropical and temperate habitats and exhibit remnants of antitropical distributions (Parenti, 2008: fig. 6). A recent molecular analysis of the species of *Anguilla* concluded that phylogenetic relationships among species were best represented in a polytomy which was congruent with the hypothesis that the genus had undergone several different, potentially rapid, radiations (Teng et al., 2009: fig. 6a). The network was unrooted. One radiation comprises four species: *A. japonica*, *A. reinhardtii*, *A. celebensis*, and *A. megastoma*. In an earlier, rooted molecular analysis by Lin, Poh, and Tzeng (2001), these four species formed a clade comprising two sister group pairs: ((*A. japonica*, *A. reinhardtii*), (*A. celebesensis*, *A. megastoma*)). *Anguilla japonica* (north-western Pacific) and *A. reinhardtii* (south-western Pacific) have an antitropical distribution, whereas *A. celebesensis* (western Pacific) and *A. megastoma* (central-Pacific) are tropical (Teng et al., 2009: fig. 6b).

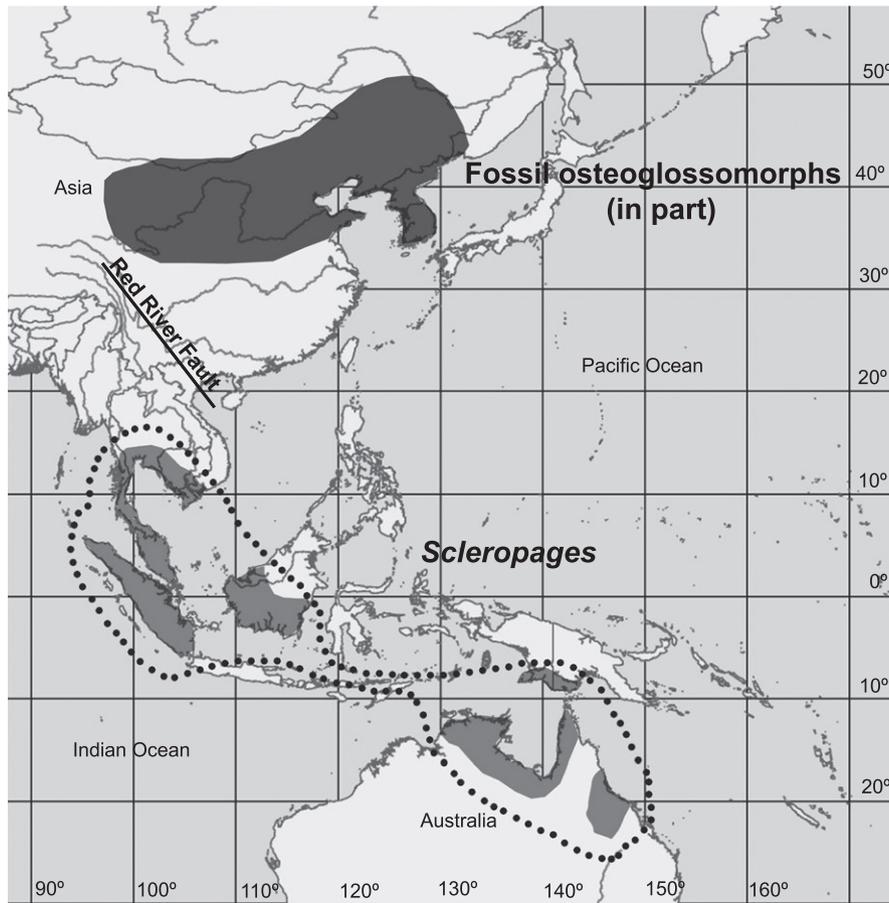


FIGURE 3 Distributional limits of the osteoglossomorph family Osteoglossidae, genus *Scleropages* (following Berra, 2007; Roberts, 2012) and fossil limits of stem-group osteoglossomorphs in East Asia (following Chang & Chow, 1986: fig. 1). A solid line indicates approximate position of the Red River Fault. Two other osteoglossomorph genera, *Notopterus* and *Chitala*, in the family Notopteridae, live in Indo-Malaya, allopatric with the East Asia fossils; their distribution is not illustrated here. All other osteoglossomorphs live in North America, South America, and Africa

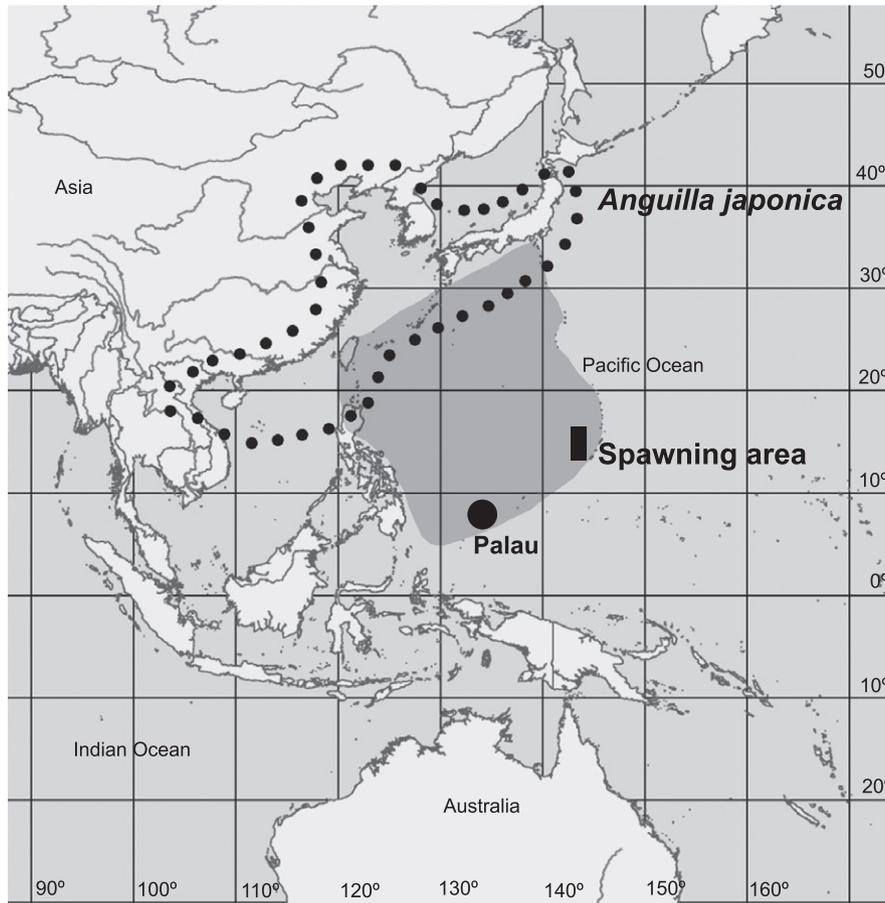


FIGURE 4 Distributional limits of adult *Anguilla japonica* outlined by a dotted line (after Ege, 1939: fig. 32; Tsukamoto, 2009). Anguillid eels are catadromous and migrate to marine spawning grounds. *Anguilla japonica* migrates to a spawning area (rectangle) on the southeastern margin of the Philippine Plate (approximate limits shaded). Palau (large solid circle)

All species of Anguillidae have a catadromous life history with a marine leptocephalus larval phase. *Anguilla japonica*, the Japanese eel, is distributed along the coast of East Asia (Ege, 1939; Tsukamoto, 2009: Figure 4). Adults migrate from their stream habitats to a spawning ground in the southeastern margin of the Philippine Plate.

3.1.3 | Osmeriformes (freshwater smelts)

The smelt suborder Osmeroidei comprises the true smelts and Southern Hemisphere smelts. Three families in the suborder form a clade, following Saruwatari, Oohara, and Kobayashi (2002): Osmeridae (Holarctic in marine and coastal freshwaters), Plecoglossidae (freshwater and marine in East Asia, Japan, and Taiwan), and Salangidae, the icefishes or noodlefishes, a family of small, neotenic, anadromous fishes (East Asia from the Sakhalin Peninsula to Vietnam: Figure 5). The family Plecoglossidae contains just one species, *Plecoglossus altivelis*. In the Saruwatari et al. (2002) analysis, salangids are the “basal” sister group of the smelt families Plecoglossidae and Osmeridae: (Salangidae, (Plecoglossidae, Osmeridae)). The salangids and *Plecoglossus* are sympatric throughout much of their ranges and both are sympatric with osmerids in the northern part of their ranges

(Figure 5). There is an initial break between a western Pacific (East Asia) taxon and the rest of the clade; these are now sympatric. Area relationships for the suborder are: (East Asia, (East Asia, Holarctic)).

3.1.4 | Ostariophysii (tetras, minnows, catfishes, knifefishes); order Cypriniformes (minnows)

Phylogenetic relationships among the Cypriniformes are controversial. A superfamily Cobitoidea was recognized by Conway (2011) and Wang et al. (2016) to comprise seven monophyletic families: the algae eaters, Gyrynocheilidae; the suckers, Catostomidae; and the loaches, Cobitidae, Botiidae, Vaillantellidae, Balitoridae, and Nemacheilidae. In a morphological analysis (Conway, 2011: fig. 43), the Gyrynocheilidae and Catostomidae comprise a sister group that is in turn sister to all remaining cobitoids, the five families of loaches. Betancur-R et al. (2017) rejected cobitoid monophyly following a molecular analysis by Stout, Tan, Lemmon, Lemmon, and Armbruster (2016). In the Stout et al. (2016: fig. 2) tree, the Gyrynocheilidae is “basal” to all other Cypriniformes to which it is related as: (Gyrynocheilidae, (Catostomidae, (all other cypriniformes))).

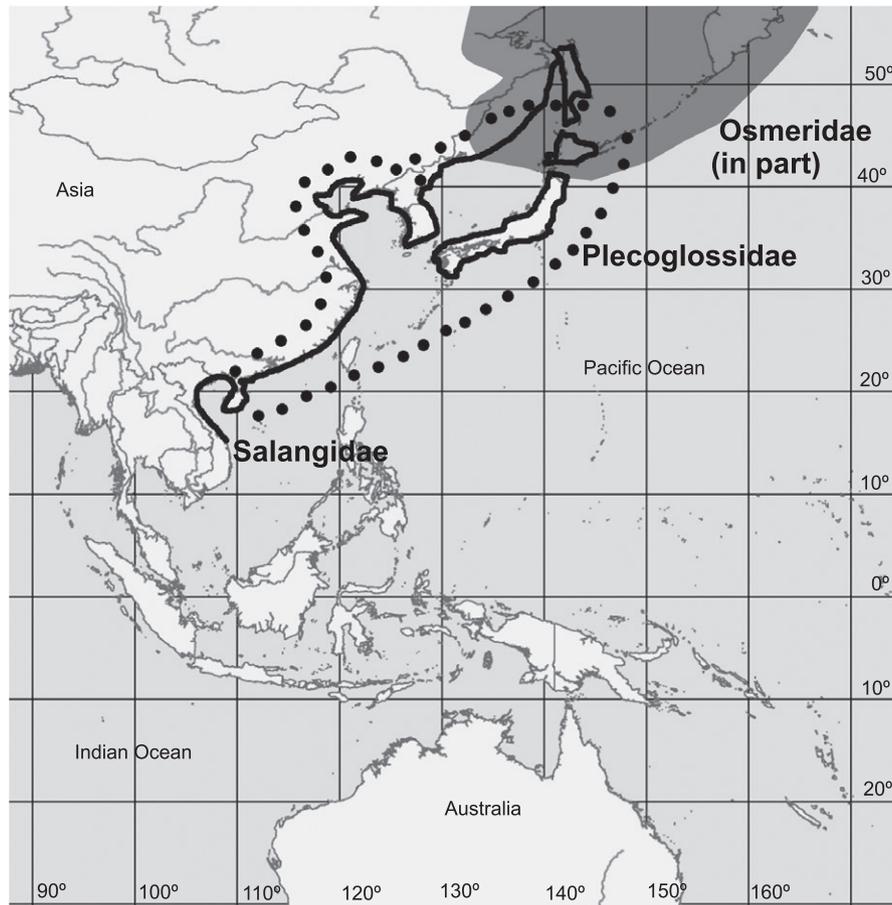


FIGURE 5 Distributional limits of the families of the Osmeroidei, the freshwater smelts (following Berra, 1981: 30–32). The families Salangidae (black line) and Plecoglossidae (enclosed by dotted line) are sympatric throughout much of their ranges in East Asia. They are sympatric with the Osmeridae (shaded), a Holarctic taxon, in the northern part of their ranges. The families are related as: (Salangidae, (Plecoglossidae, Osmeridae)). Their area relationships are: (East Asia, (East Asia, Holarctic))

The Gyrocheilidae has a restricted distribution in Southeast Asia (Figure 6). The Catostomidae is Holarctic with most of its species in North America and Russia and a single living taxon in China (Figure 6). These families are allopatric.

3.1.5 | Synbranchiformes (swamp eels)

The pantropical or subtropical suborder Synbranchioidei is equivalent to the family Synbranchidae, revised by Rosen and Greenwood (1976) to comprise two subfamilies, the Macrotriminae (with one genus, *Macrotrema*) and Synbranchinae (with three genera, *Synbranchus*, *Ophisternon*, and *Monopterus*). (Macrotriminae was corrected to Macrotrimatinae by Bailey & Gans, 1998). These fresh and brackish water fishes are not closely related to the Anguilliformes (above).

The monotypic *Macrotrema* is sister to the three other genera of synbranchids (Rosen & Greenwood, 1976: figs. 66, 67). Its single species, *Macrotrema caligans*, lives in Thailand, Vietnam, and the Malay Peninsula, including Singapore (Kottelat, 1989; Figure 7). *Ophisternon* has a restricted pantropical distribution (Rosen,

1976: fig. 1). *Synbranchus* lives in Central and South America. The natural distribution of *Monopterus* includes South, Southeast, and East Asia, with two species in West Africa (Bailey & Gans, 1998). The cladogram of relationships from Rosen and Greenwood (1976) is: (*Macrotrema*, (*Ophisternon*, (*Synbranchus*, *Monopterus*))). An area cladogram is: (Thailand, Malaysia, Singapore, (Pantropical, (Central and South America, South, Southeast, and East Asia))) (Figure 7).

3.1.6 | Gasterosteiformes (sticklebacks), family Indostomidae (armored sticklebacks)

The Indostomidae comprises a single genus, *Indostomus*, with three species (Britz & Kottelat, 1999). Relationships of the family are controversial. Betancur-R et al. (2017) classified the Indostomidae in the Synbranchiformes. In contrast, Britz and Johnson (2002) concluded that *Indostomus* is a gasterosteoid, sister to the family Gasterosteidae. *Indostomus* is restricted to freshwater habitats in Indo-Burma (Figure 8). Gasterosteids are Holarctic (Figure 8). These two families are allopatric.

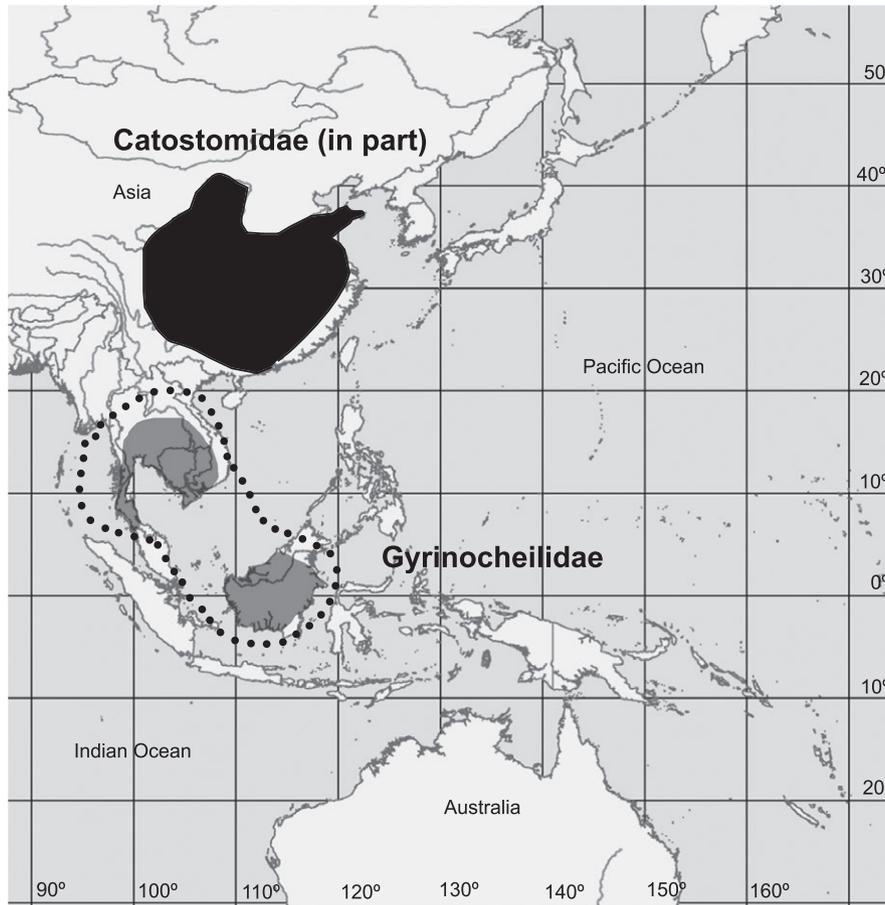


FIGURE 6 Distributional limits of the allopatric cypriniform families Gyrinocheilidae (dotted line; following Berra, 2007: 97) and Catostomidae, in part (shaded; following Berra, 2007: 99). There are two hypotheses of relationships: (a) morphological, Gyrinocheilidae and Catostomidae are sister taxa and, in turn, sister to all other cypriniforms (Conway, 2011); (b) molecular, Gyrinocheilidae is the most "basal" cypriniform, and Catostomidae, a Holarctic taxon, is sister to the remaining cypriniforms (Stout et al., 2016)

3.1.7 | Syngnathiformes (pipefishes and relatives), family Syngnathidae (pipefishes and seahorses)

Seahorses, the subfamily Syngnathinae, are a group of some 40 species of shallow-marine fishes distributed throughout the tropical and temperate zones from approximately 45° N to 45° S (Lourie, 2016:39). Their pelagic larval phase is relatively short, estimated at 2–4 weeks (Lourie, 2016). The species exhibit discrete, endemic distribution patterns and are notable, but not unique among marine fishes, for adherence to geographical boundaries such as Wallace's Line (Figure 9; Lourie & Vincent, 2004: fig. 1; see also Woodland, 1986; Collette, 2005). One species, *H. kuda*, is widespread throughout the Indo-Pacific; it is in need of taxonomic revision as its populations are distinct, with some recognized at the subspecific level (Lourie, 2016: 122, map).

The pygmy Bargibant's Seahorse, *H. bargibanti*, is so deeply genetically distinct from the others that it is hypothesized to represent "...an ancient divergence..." from the main group of seahorses (Teske, Cherry, & Matthee, 2004:281); it was used as an outgroup taxon in the Teske et al. (2004) molecular analysis of seahorse phylogeny. Bargibant's Seahorse is distributed throughout the western Pacific (including the eastern portion of the Indo-Australian Archipelago) from Japan to New Caledonia (Lourie,

2016: 74, map; Figure 10). The "basal" clade of the main seahorse lineage comprises two species: *H. breviceps* and *H. abdominalis* (see Teske et al., 2004) that live in southern Australasia (Heads, 2014:71; Lourie, 2016: 85, 86, maps; Figure 10). These two species overlap in the center of their ranges in south-eastern Australia. Following Teske et al. (2004) and Lourie (2016), relationships of seahorses in the genus *Hippocampus* are: (*H. bargibanti*, ((*H. breviceps*, *H. abdominalis*), (all other species of *Hippocampus*))). The area cladogram is: (Western Pacific, (southern Australasia, (tropical and temperate zones from approximately 45° N to 45° S))).

3.1.8 | Atheriniformes (silversides). Suborder Atherinoidei (Old World silversides and rainbowfishes)

The Atheriniformes is one of three orders in the monophyletic Atherinomorpha, which also comprises the killifishes, ricefishes, flyingfishes, and their relatives (Rosen & Parenti, 1981). In a molecular phylogenetic analysis of atheriniform fishes, Campanella et al. (2015: fig. 3) summarized the hypothesized relationships among representatives of all lineages in a time-calibrated phylogeny. They classified atheriniforms in two suborders: the New World Atherinopsoidae and

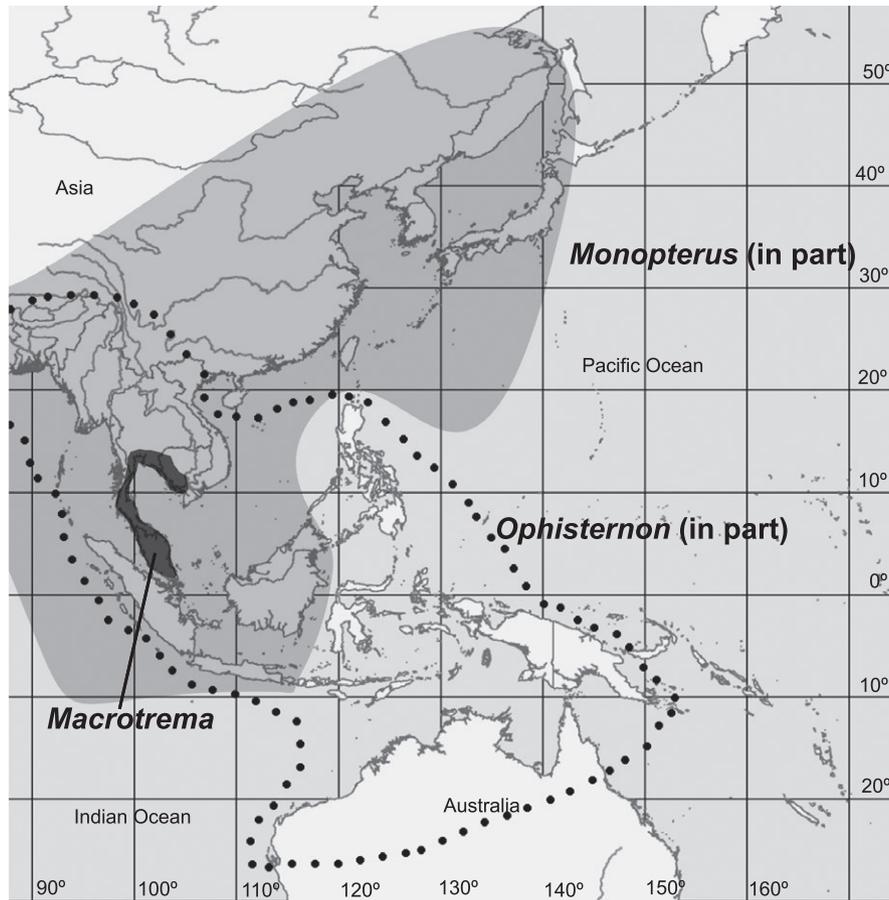


FIGURE 7 Distributional limits of the synbranchid eel genera *Macrotrema* (dark shading), *Ophisternon* (dotted line, in part), and *Monopterus* (light shading, in part). A fourth genus, *Synbranchus*, does not live in the western Pacific. The genera are related as: (*Macrotrema*, (*Ophisternon*, (*Synbranchus*, *Monopterus*))), following Rosen and Greenwood (1976). The area cladogram is: (Thailand, Malaysia, Singapore, (Pantropical, (Central and South America, South, Southeast, and East Asia)))

the Old World Atherinoidei. The family Phallostethidae is the most “basal” lineage in the atherinoid cladogram.

Two subfamilies comprise the family Phallostethidae: the Phallostethinae with 24 species and the Dentatherininae with a single species, *Dentatherina merceri* (see Parenti, 2014). Campanella et al. (2015) included just two species of phallostethids in their analysis: *Neostethus lankesteri* and *N. bicornis*. The phallostethins are coastal freshwater and marine species of Southeast Asia; their sister taxon, the monotypic *Dentatherina*, is a coastal marine species that is sympatric with the phallostethins in the center of the Indo-Australian Archipelago and has a range that extends along the eastern limit of the western margin of the Pacific Plate to Fiji (Figure 11). The phallostethins and *Dentatherina* are sister to the remaining Old World atherinoids. The split between phallostethins/*Dentatherina* and the other atherinoids is estimated at 50–55 Ma (Campanella et al., 2015: fig. 3).

3.1.9 | Gobiiformes, suborder Gobioidi (gobies and sleepers)

Gobioid fishes live broadly in pantropical and temperate freshwater, estuarine, and marine habitats and exhibit a wide range of

life-history patterns. Several subgroups are amphidromous, a specialized type of diadromous life-history pattern in which adults live and breed in freshwater. Larvae are transported passively to the sea where they spend weeks or months transforming before migrating to upstream habitats (e.g., Parenti, 2008). Many gobioids, such as those in the subfamily Sicydiinae, are called freshwater fishes because the adults are always taken in freshwater habitats, yet they have a significant marine life-history phase. This is true also of the anguillid eels discussed above.

Two allopatric families are the most “basal” of the gobioids: Rhyacichthyidae and Odontobutidae. There are two competing hypotheses of their relationships with all other gobioids. In the morphological hypothesis of Hoese and Gill (1993: fig. 9), Rhyacichthyidae is at the base of the gobioid tree, with the Odontobutidae sister to all remaining gobioids, then classified in the family Gobiidae: (Rhyacichthyidae, (Odontobutidae, Gobiidae)). In a recent molecular hypothesis of Li, He, Jiang, Liu, and Li (2018), these two families are sister taxa, and in turn sister to all remaining gobioids: ((Rhyacichthyidae, Odontobutidae), all other gobioids).

The Rhyacichthyidae, with two species classified in the genus *Rhyacichthys* and one species in the genus *Protogobius*, lives broadly

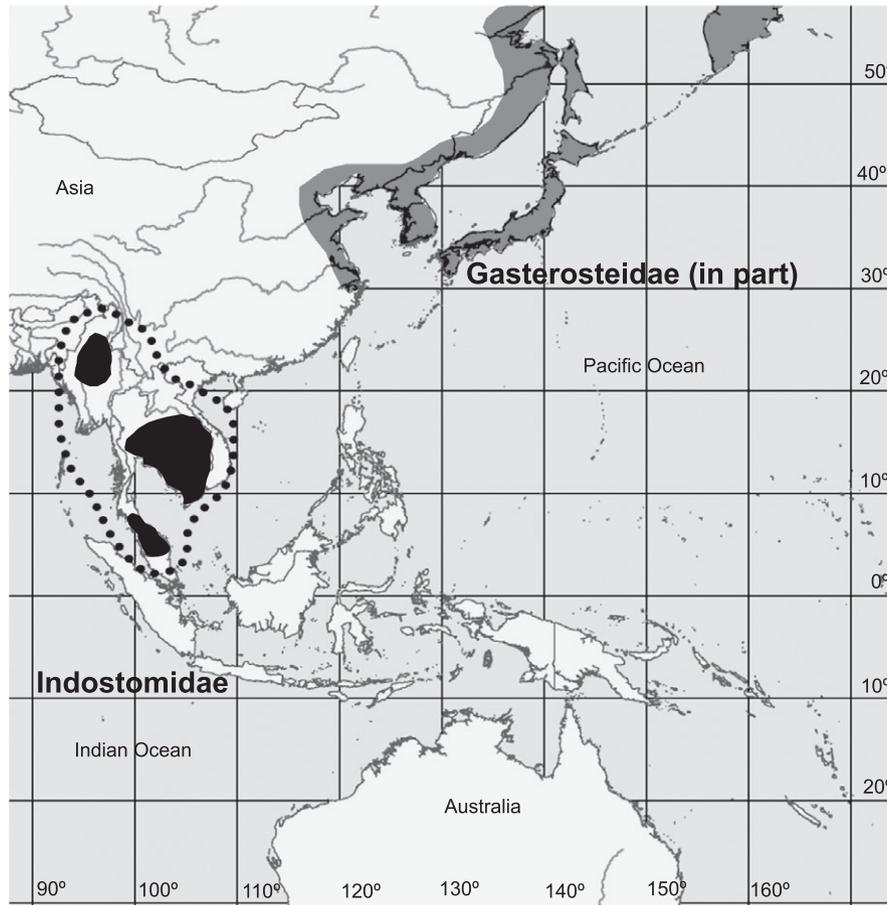


FIGURE 8 Distributional limits of the family Indostomidae (black shading; following Berra, 2007: 357) and its inferred sister taxon, the Gasterosteidae, in part (gray shading; following Berra, 2007: 351). Gasterosteidae is a Holarctic taxon

throughout the tropical western Pacific, along the eastern portion of the Indo-Australian Archipelago, and extends along the eastern limit of the western margin of the Pacific Plate to New Caledonia (Figure 12). The family Odontobutidae lives in temperate and subtropical waters of East Asia including Japan, Hainan Island, and northern Viet Nam and Laos (Figure 12). They are allopatric. Estimates of molecular divergence times between Rhyacichthyidae and Odontobutidae range from 47.3 Ma (Li et al., 2018) to 98 Ma (Chakrabarty, Davis, & Sparks, 2012).

4 | DISCUSSION

The western Pacific, including East Asia and Australasia, is home to the “basal” clade for an array of widespread teleost fish clades. It is not considered the center of origin of these clades, but as a locus of differentiation—a place where many global clades were disrupted. Endemism and allopatry characterize the distributional patterns, but there is also sympatry or overlap of sister clades or other closely related taxa. This is not the sole major area of differentiation of teleost taxa on Earth; many teleost clades, such as the Characiformes and the Cichlidae, for example, have no

representatives—living or fossil—in the western Pacific. But the generality of this pattern will be tested as our understanding of phylogenetic relationships increases. The cichlids are a pantropical and subtropical freshwater family with no natural representatives in Indo-Australia outside of India and Sri Lanka (Berra, 2001: 440). Yet, in recent molecular phylogenetic studies (Betancur-R et al., 2017), the sister group of the cichlids is hypothesized to be the marine Pholidichthyidae, broadly distributed throughout the western Pacific (Springer, 1982).

One general global biogeographical pattern, ((Austral, Boreal), Pantropical) (see Humphries & Parenti, 1999), is not duplicated wholly in any of the teleost taxa examined here, but there are remnants of the pattern in nearly all the distributions (Figure 2). Holarctic (or boreal) clades are sister to, or the next breaks in the cladogram, in osteoglossomorphs (Figure 3), osmeroids (Figure 5), cypriniforms (Figure 6), gasterosteiforms (Figure 8), and gobioids (Figure 12). Austral clades are sister to, or the next breaks in the cladogram, in the seahorses, *Hippocampus* (Figure 10). In all of these clades except for the osmeroids, the “basal” lineage and its relative are allopatric.

Terrane fidelity marks the distribution of the anguilliforms, including the anguillids (Figure 4), the seahorses (Figures 9 and 10), and the atheriniforms and gobioids (Figures 11 and 12). In these last

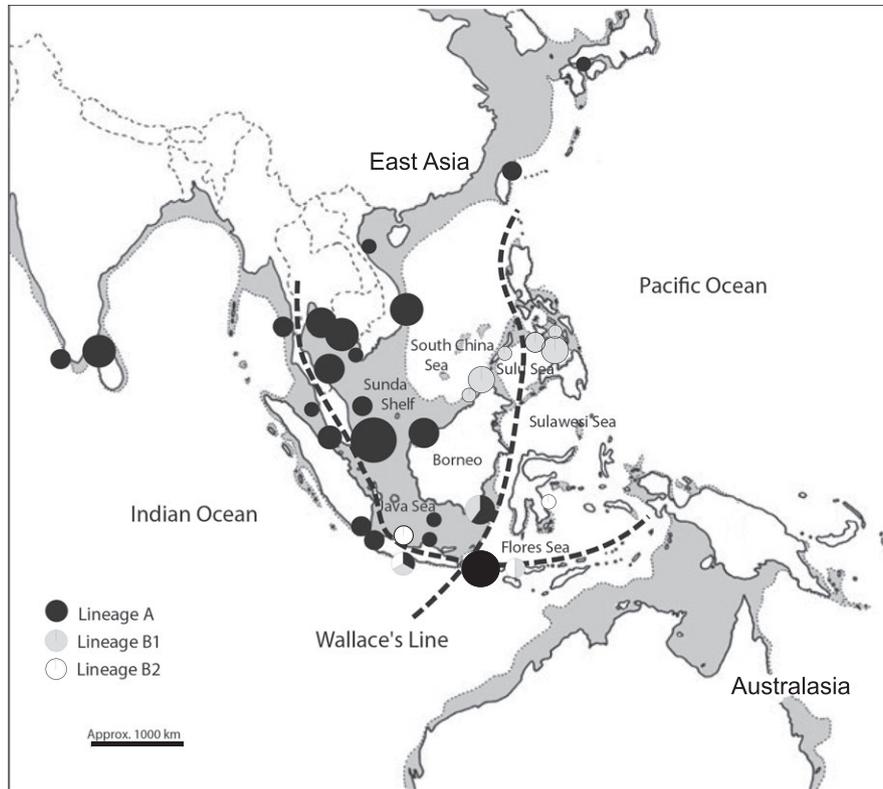


FIGURE 9 Geographical distribution of lineages of the seahorse *Hippocampus trimaculatus* (modified from Lourie & Vincent, 2004: fig. 1) to demonstrate the close relationship between population distribution and Wallace's Line. Symbol size is in proportion to the number of individuals sampled from each location. Continental shelves that would have been subaerial during periods of low sea-level are shaded

two clades, the distributional limit of the easternmost taxon is at the eastern margin of the Indian-Australian lithospheric plate where it meets the western margin of the Pacific lithospheric plate (Figure 1). The “basal” anguilliform, *Protanguilla*, is marginal on the Philippine lithospheric plate. The age estimate of *Protanguilla*, at 200 Myr, is “...much older than the Palau-Kyushu Ridge itself, which formed as an island arc at ~60–70 Ma. The clade is older than the geomorphic structure to which it is endemic, a pattern shown in many groups” (Heads, 2014:388).

Sympatry of sister taxa results from the inferred range expansion of either taxon (Croizat, Nelson, & Rosen, 1974). The osmeroid families, related as (Salangidae, (Plecoglossidae, Osmeridae)), are sympatric throughout much of their ranges in East Asia (Figure 5). The initial break between the Salangidae and the rest of the osmeroids is inferred to have been followed by the expansion of the range of one taxon into the other. The mechanism for these breaks and overlap could have been subsequent changes in sea level and other macroenvironmental fluctuations (see Li et al., 2018, for odontobutids in East Asia). The phylogenetic relationships and distribution of synbranchiform eels (Figure 7), with *Macrotrema* sister to the remaining taxa, led Rosen (1976:434) to hypothesize that “...the primary event in the history of the Synbranchidae may have occurred in the Old World Tropics.” The overlapping (sympatric) distribution of the sister taxa Phallostethinae and Dentatherininae (Figure 11) was hypothesized to have been formed as the widespread ancestral population ‘...was disrupted by reconstruction and rearrangement of land and

changes in sea level that may have facilitated expansion of one taxon into the range of the other” (Parenti & Ebach, 2013:815). The clades overlap in regions of accreted terranes, such as the southwestern arm of Sulawesi, a phenomenon seen in the distributions of other taxa (Heads, 2012: 286).

What information a phylogeny may contribute to a biogeographical analysis has been the focus of intense methodological debate for decades (Mooi, 2017; Parenti, 2017). The significance of fish distributions in the debate is exemplified by the distribution of the osteoglossid fishes, which was compared to “... the ratites and *Nothofagus* [southern beeches] combined, with a trans-Pacific distribution extending beyond the shoulder into India and Africa, the heart of Gondwana” (Nelson & Ladiges, 2001:394). Despite the arguments in favor of the discovery of general patterns and repeated components of relationships in a biota, many modern biogeographical studies follow another paradigm. The CODA (Centre of Origin, Dispersal, and Adaptation) model of evolution, as defined by Lomolino and Brown (2009), is prominent (Heads, 2014). In this model, the history of each lineage is interpreted separately, starting with the inference of a center of origin followed by an inferred dispersal path, as specified by the phylogeny, to form the modern distribution (viz. Campanella, et al., 2015 for atheriniforms; Teng et al., 2009, for anguillid eels; Thacker, 2015, for gobioids). Teng et al. (2009: 6b) provide small maps of the distributional limits of each species of *Anguilla*. Thacker (2015) has no maps of taxon distributions, but includes two maps of inferred dispersal routes from a center of origin in the Indo-West

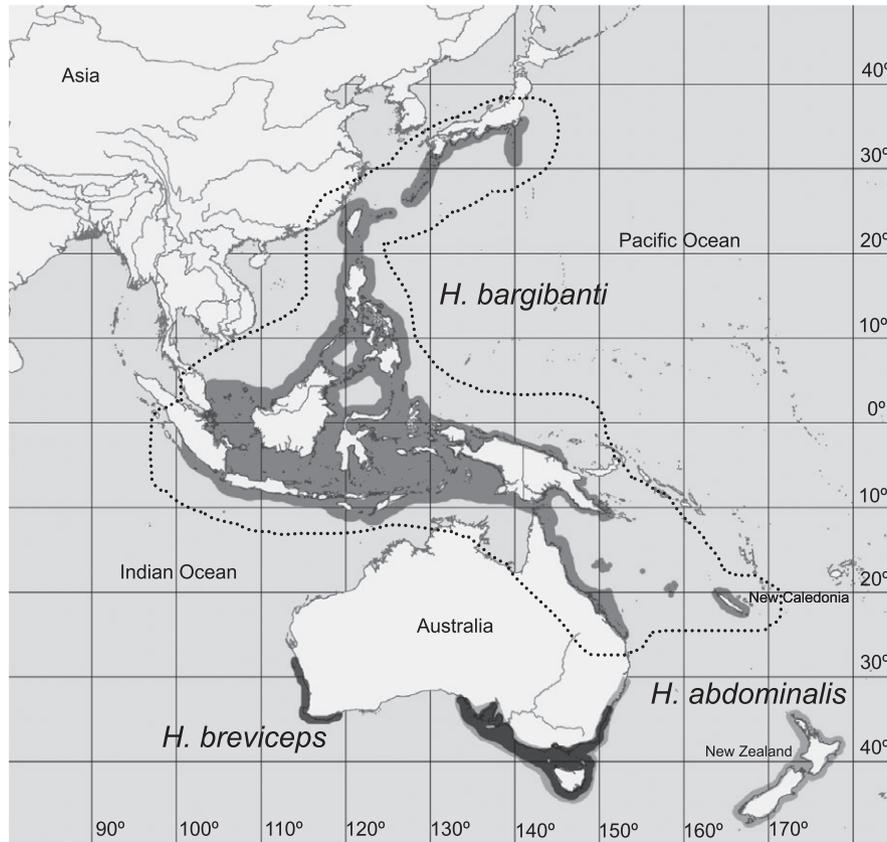


FIGURE 10 Distributional limits of the seahorses *Hippocampus bargibanti* (surrounded by a dotted line), *H. breviceps* (dark shading), and *H. abdominalis* (light shading), following Lourie (2016). *Hippocampus breviceps* and *H. abdominalis* are sympatric in the center of their ranges in south-eastern Australia. Relationships of seahorses in the genus *Hippocampus* are: (*H. bargibanti*, ((*H. breviceps*, *H. abdominalis*) (all other species of *Hippocampus*))), following Teske et al. (2004) and Lourie (2016)

Pacific of the families Gobionellidae (Thacker, 2015; fig. 2a) and Gobiidae (Thacker, 2015; fig. 2b). Campanella et al. (2015) include no maps.

Using a center of origin method (ancestral area analysis; Matzke, 2013; Ree & Smith, 2008), Hilton and Lavoué (2018) concluded that osteoglossomorphs originated in East Asia and dispersed to their present locations. East Asia was "...the main place where the early diversification of the Osteoglossomorpha took place (including the most recent common ancestor, mrca) of the crown group Osteoglossomorpha, which lived during the Jurassic (about 190–150 Ma)..." (Hilton & Lavoué, 2018:26).

The break between the Holarctic and Palearctic regions of osteoglossomorphs is illustrated as the break between the East Asian fossils and *Scleropages*, a representative of the Palearctic areas defined by Hilton and Lavoué (2018) as Orient and Australia (Figures 2 and 3). Disruption of a widespread ancestor is inferred here to have formed the pattern of Figures 2 and 3 as an alternative to the CODA hypothesis.

Assumptions about dispersal ability also affect biogeographical analyses (Parenti & Ebach, 2013). Some assume the absence of dispersal ability and a global distributional pattern to be at odds. According to Bailey and Gans (1998: 3): "Synbranchids presumably have a limited capacity for active dispersal. Nonetheless the family

as a whole and the genus *Ophisternon* in particular (Rosen, 1976) have a broad pantropical distribution." On seahorses, the genus *Hippocampus*, Teske et al. (2004: 274) assumed that "...the circum-global distribution of seahorses reflects major dispersal events." In contrast, the vicariance assumption about cosmopolitan distributions is that they were formed prior to major continental rearrangement (viz. Croizat et al., 1974).

These modern biogeographical distributions of fishes reflect just remnants of once more complex and widespread distributions; they are incomplete spatial records, just as the fossil record is an incomplete temporal record. The ages of lineages known from fossils are underestimated, and can only get older with new fossil discoveries. The Holostei, sister group of the Teleostei, includes the gars (Lepisosteiformes) and the bowfins (Amiiformes). Brito, Alvarado-Ortega, and Meunier (2017) recently described a new gar from the Upper Jurassic (about 157 Ma) of Mexico. The new fossil taxon "... extends the chronological range of lepisosteoids by about 46 Myr and of the lepisosteids by about 57 Myr, and fills a major morphological gap in current understanding [of] the early diversification of this group" (Brito et al., 2017). Calibrations of molecular clocks using the oldest known fossils of a clade will always result in underestimated ages. Despite this, fossils continue to be used to "anchor" the ages of phylogenies and dictate hypothetical dispersal routes. Teng et al.

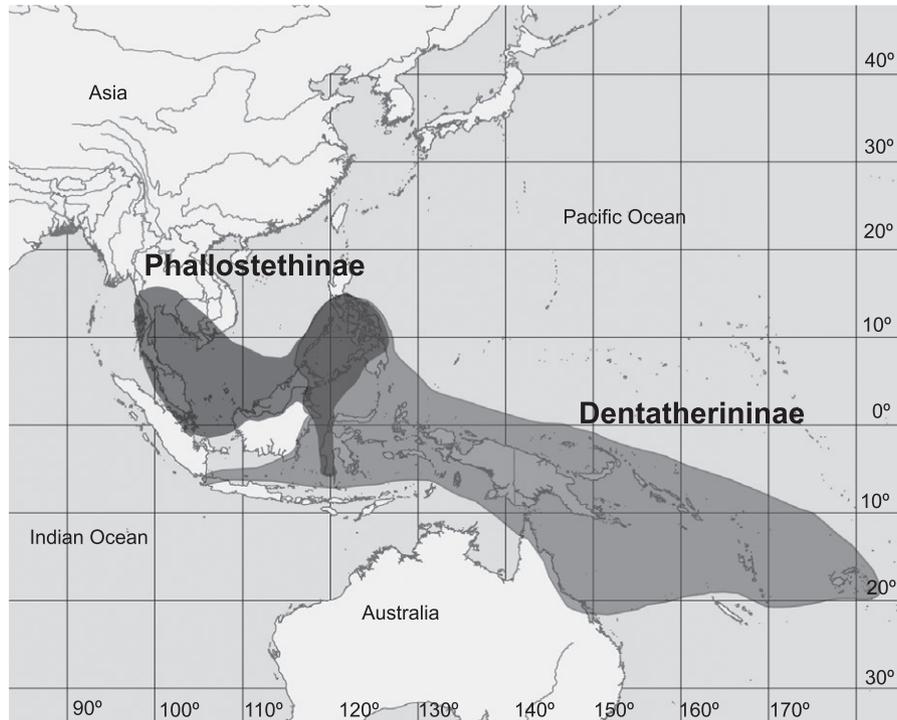


FIGURE 11 Distributional limits of the atherinoid sister taxa Phallostethinae and Dentatherininae (= *Dentatherina*); following Parenti & Ebach, 2013). They are related to the rest of the Old World atherinoid fishes as: ((Phallostethinae, *Dentatherina*), all other Old World atherinoids) (Campanella et al., 2015)

(2009: 819) hypothesized that "...The area near the equator of the Indo-West Pacific Ocean accommodates most *Anguilla* species and is therefore considered to be the center of origin of freshwater eels...". On the evolution of the antitropical *Anguilla japonica* (north-western Pacific) and *A. reinhardtii* (south-western Pacific), Teng et al. (2009: 818) further hypothesized that "One moved northward (*A. japonica*), one moved southward (*A. reinhardtii*)..." They further argued that the global distribution of anguillids took place during the past 20 Myr, despite the occurrence of much older (50–55 Ma) fossils (Patterson, 1993).

Because the divergence dates among the families of atheriniforms, as estimated using fossil calibrations of molecular sequence data, are all younger than Gondwanan break-up, Campanella et al. (2015) rejected vicariance explanations in favor of long-distance dispersal. They concluded (p. 21): "Ultimately, we do not have conclusive evidence for a vicariance hypothesis in New World silversides, but do find that oceanic dispersal was a primary driver in shaping the modern distribution of Atheriniformes." But, as noted by Heads (2014) and others, rejection of a Gondwanan break-up model does not mean rejection of all vicariance. The overlap of the phallostethid clades (Figure 11) may be explained by the juxtaposition of these areas during assembly of the modern Indo-Australian archipelago over the past 50 My (Hall, 2002; Parenti & Ebach, 2010, 2013). Furthermore, estimates of divergence time using molecular data may differ markedly depending on the method of calibration and the loci. For example, the divergence time between the gobioid families Rhyacichthyidae and Odontobutidae was estimated at

98 Ma (Late Cretaceous) by Chakrabarty et al. (2012) and at 47.3 Ma (mid-Eocene) by Li et al. (2018). The geology of the broad western Pacific region treated here is complex. Throughout the Phanerozoic, continental terranes/blocks rifted from the Indian-west Australian margin of eastern Gondwana to form, in successive stages, the Paleotethys, Mesotethys, and Cenotethys oceans (Metcalf, 2011, 2013). In turn, each of these ocean basins closed and are represented on present-day Asia by complex suture zones of accreted terranes.

A general break between the Southeast Asian/Australasian and East Asian biota is recognized by endemism and allopatry (e.g., Figures 3, 6, 8, 12). The break is coincident with the Red River Fault, a major strike-slip fault between the South China and Indochina blocks (Zhu, Graham, & McHargue, 2009; Figure 3). This break or disruption between "basal" clades and their sister taxa is hypothesized to date at least to the Mesozoic, based on the maximum estimated divergence times between the basal gobioid families. It could be older based on the age of osteoglossomorph fossils, which date to the Late Jurassic-Early Cretaceous. The divergence time between the Southeast Asian and Australian species of the osteoglossid genus *Scleropages* (Figure 3) was estimated, using molecular data, at 138 ± 18 Ma by Kumazawa and Nishida (2000). They offered this as support for the hypothesis that part of the fauna was carried on Gondwanan terranes and accreted to the Asian continent in the Early Cretaceous. Biotic distributional patterns are a record of the geological history of the region.

The celebrated high biological diversity of the western Pacific has been documented by tallying the high number of marine

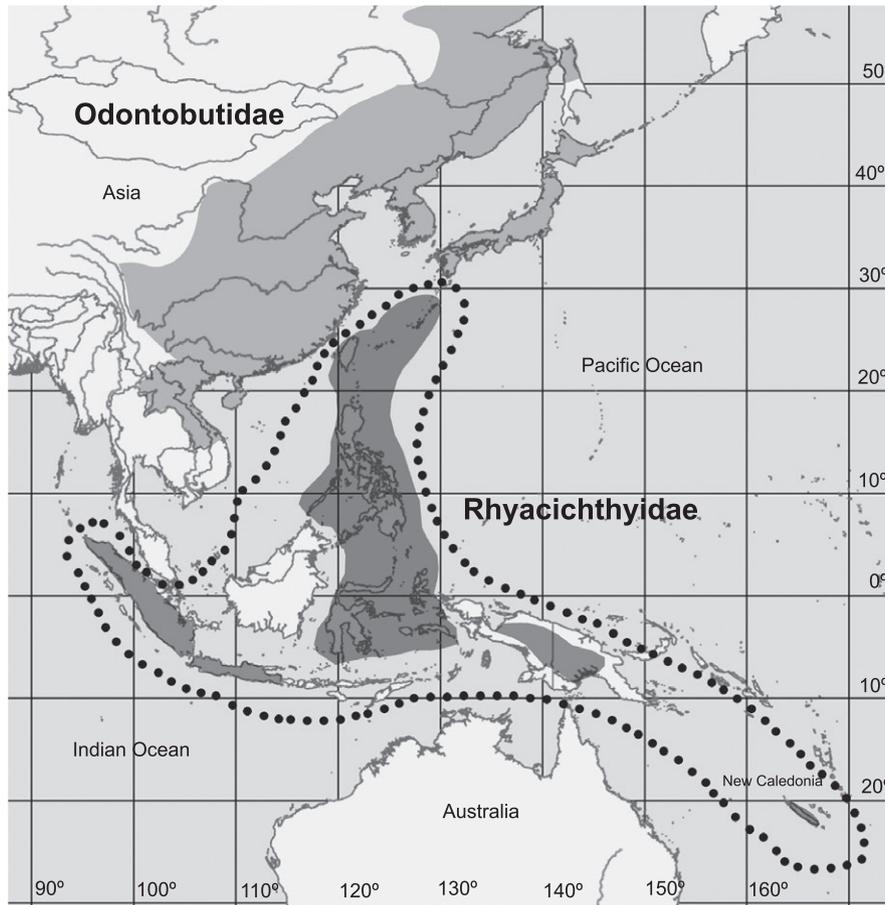


FIGURE 12 Distributional limits of the allopatric gobioid families *Odontobutidae* (light shading; following information in Berra, 2007:460 and Li et al., 2018: fig. 5) and *Rhyacichthyidae* (dark shading and encircled by dotted line; following Berra, 2007: 458). There are two competing hypotheses of their relationships to all other gobioids: (*Rhyacichthyidae*, (*Odontobutidae*, all other gobioids)) and ((*Rhyacichthyidae*, *Odontobutidae*), all other gobioids). All other gobioids are pantropical and temperate, and many sympatric with these two families

species that live there, especially in the central area bounded by New Guinea, the Philippines, and the Malay Peninsula, known as the East Indies Triangle (Briggs, 1966, 2005), the “fertile triangle” (Briggs, 1974), the Indo-Malayan Triangle (Donaldson, 1986) or the Coral Triangle (Barber, 2009; Hoeksema, 2007), among other names. The Philippines have been further characterized as the “center of the center” of marine shore fish biodiversity (Carpenter & Springer, 2005). This high species diversity (or the presence of a “basal” taxon) does not mean that this is the center of origin of teleost fishes or even that it is a fixed center of diversity. As noted by Dornburg, Moore, Beaulieu, Eytan, and Near (2014), Thacker (2015), and others, the center of diversity of teleosts, as measured in numbers of species, has shifted through time with openings and closures of the succession of Tethyan oceans (Metcalf, 2011, 2013). Patterns described here are for clades regardless of the numbers of species in each.

Distributional patterns retain the historical component of clades: where and how they evolved, where and how they were disrupted. The distributions for teleost fishes, when combined with information from phylogenetic analyses, reveal general, repeated patterns.

They demonstrate terrane fidelity, allopatry, sympatry on accreted terranes, and other characteristics conveyed readily in maps. These distributional patterns are the shape of biogeography, the shape of distributions and phylogenies that allows us to infer shared histories. To find congruence between biological and geological phenomena as illustrated with maps was at the core of the science of Alexander von Humboldt. Biogeography will move forward when we acknowledge the connections and correlations between geology and biology, especially when we look for them in distributional maps.

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BIOSKETCH

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