

Points of View

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Freshwater Fishes, Dispersal Ability, and Nonevidence: “Gondwana Life Rafts” to the Rescue

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Biogeography, as a topic for discourse or discussion, is in some ways like religion: both topics lend themselves to ever more complicated treatment in the abstract, which is apt to border even on the miraculous, but which is apt to crumble in confrontation with concrete facts of life. Nelson and Platnick (1981:375)

Having failed to dissect these concepts (center of origin, vicariance) to their core, contemporary zoogeographers founder in a self-created morass of chance hops; great capacities for, or mysterious means of, dispersal; rare accidents of over-sea transportation; small probabilities that with time become certainties; and other pseudo-explanations. Croizat et al. (1974:276)

In a recent issue of *Systematic Biology*, Briggs (2003: Fishes and Birds: Gondwana Life Rafts Reconsidered, pp. 548–553) examines the current distributions of four vertebrate clades (cichlid fishes, aplocheiloid killifishes, ratites, and parrots), which have been attributed to the Mesozoic fragmentation of Gondwana (Parenti, 1981; Stiassny, 1991; Murphy and Collier, 1997; Farias et al., 1999). Briggs (2003) contests the vicariance hypotheses offered by these authors for cichlids and aplocheiloid killifishes in favor of scenarios reliant on transoceanic marine dispersal. His conclusions are based on the absence of Cretaceous-age fossils for these clades, as well as strict adherence to Myers' (1938) classification of cichlids and killifishes as secondary freshwater fishes.

For fishes, the arguments Briggs uses to explain their current distributions rely on what he perceives to be a valid and absolute distinction: that between so-called primary and secondary freshwater fishes (Myers, 1938) and what this implies regarding their dispersal ability. According to Briggs (2003:549), the current distribution of aplocheiloid killifishes has a simple explanation (our italics):

If, as the fossil record seems to indicate, the aplocheiloid fishes are too young to have been carried about on tectonic plates, how did they achieve their circumglobal range? *The answer does not appear to be difficult. For many years, these fishes have been allocated to a category called “secondary freshwater fishes”* (Myers, 1938). Some of the species live in brackish water and others can tolerate the higher salinity of seawater ... Their ability to migrate through the sea has been given as the reason for their establishment at oceanic islands such as the Greater Antilles and Madagascar.

Similarly for cichlids (Briggs, 2003:549), Briggs reasons (our italics):

Are we really dealing with an ancient separation by means of tectonic plates, as most of the molecular work suggests, or do we have a more recent separation achieved by dispersal from a center of origin? *The cichlid problem is similar to that posed by the aplocheiloids, and again the answer does not appear to be difficult. The cichlids are also secondary freshwater fishes.* Many species live in brackish water and can tolerate higher salinities. Cichlids have been able to reach the West Indies and Madagascar, places where the primary freshwater species do not occur.

With such statements, Briggs issues a direct challenge to vicariance biogeographers. Cenozoic transoceanic dispersal of both killifish and cichlids would necessitate crossing saltwater gaps spanning thousands of kilometers (e.g., see paleogeographic reconstructions in Smith et al., 1994; Reeves and de Wit, 2000). We consider this far from a “modest saltwater gap” that Briggs (2003:550) maintains “cichlids should have been able to negotiate” (Fig. 1b). Assertions as to whether an organism should (or should not) have been able to negotiate a barrier are meaningless in the realm of hypothesis testing and are nothing more than conjecture in the absence of phylogenetic and paleogeographic evidence. One does not expect every species of bat to exhibit a worldwide distribution simply because bats possess the ability to fly. Either cichlids crossed the Mozambique Channel (between Madagascar and Africa) or they did not, which can be tested using phylogenetic and paleogeographic evidence. It is our goal to set the record straight, at least in the case of the aforementioned freshwater fish clades, as to what can reasonably be inferred from the *evidence at hand*, not the lack thereof.

The purpose of this article is twofold. First, we want to evaluate whether Myers' (1938) division of freshwater fishes into “primary” or “secondary” groups, based on a presumed physiological tolerance to seawater, is meaningful to biogeographers in the absence of robust phylogenies. Taking into consideration phylogenetic evidence and the distributions of the organisms in question, we

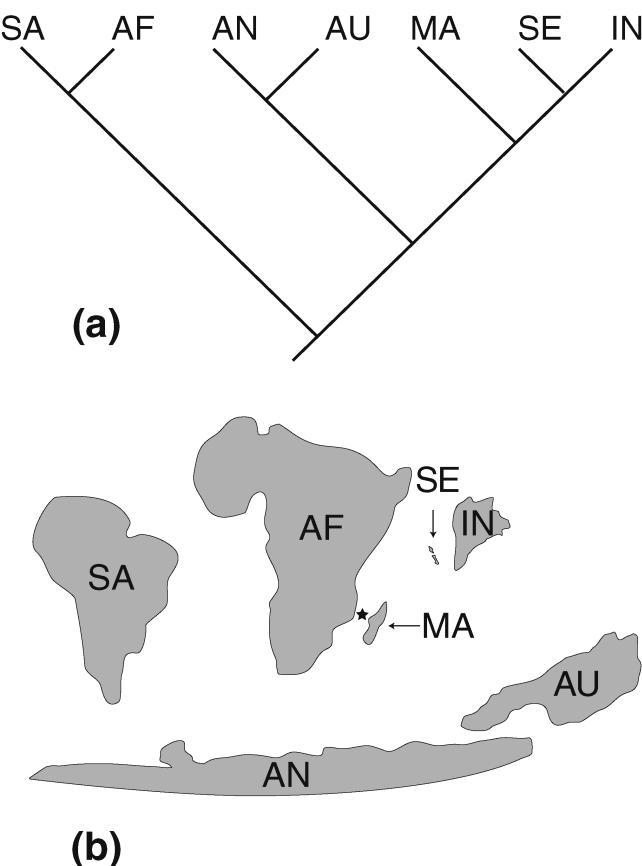


FIGURE 1. (a) Geological area cladogram of Gondwanan break up (after Smith et al., 1994; Storey, 1995; Reeves and de Wit, 2000). (b) Eocene paleogeographic reconstruction (after Smith et al., 1994; Hay et al., 1999; Reeves and de Wit, 2000; Ocean Drilling Stratigraphic Network, 2004) illustrating the relative positions of major Gondwanan landmasses at the earliest time (~50 Mya) for which Briggs suggests that oceanic dispersal for cichlids and aplocheiloid killifishes could have occurred (i.e., assuming that ages of lineages are accurately estimated by existing fossil evidence). The Mozambique Channel is indicated by a star. Abbreviations: AF, Africa; AN, Antarctica; AU, Australia; IN, India; MA, Madagascar; SA, South America; SE, Seychelles.

will demonstrate that the presumption of a direct correlation between Myers' perceived tolerance to seawater and dispersal ability is not reliable for making inferences regarding macroevolutionary processes. Second, we will show that not only are the dispersal arguments advanced by Briggs logically flawed (e.g., the "center-of-origin phenomenon" is incongruent with the concept of common ancestry [ancestor-descendent relationships] and allopatric speciation [vicariance] for both fish groups discussed), but they are not supported by the evidence at hand, whether it is morphological, molecular, paleogeographic, or paleontological in nature. We will demonstrate that Briggs' arguments are narrative, and as such, do not test or attempt to falsify any hypotheses.

PRIMARY AND SECONDARY FRESHWATER FISHES

Myers (1938) classified freshwater fishes into "primary" and "secondary" divisions based on their

presumed historical distributions and their perceived salinity tolerance. Tolerance to seawater was extrapolated via anecdotal observations from a very limited number of species to entire families or suborders (e.g., Myers, 1938:345–346, 1949:317–318). According to Myers, fishes of the "primary division" are those families whose members are very strictly confined to freshwater based on their perceived physiological intolerance to salinity and their present and presumed historical distributions. Myers' fishes of the "secondary division" are those that are generally restricted to freshwater, but in some cases enter the sea voluntarily for short periods. At the time of Myers' (1938) classifications, continental drift scenarios were just gaining popularity (Wegener, 1924). The presence of freshwater fishes on islands, irrespective of whether they were volcanic or continental in origin, was taken as evidence that those fishes were of the "secondary division." For example, the presence of freshwater fish groups on Madagascar and the Greater Antilles, landmasses we now hypothesize to have had former continental connections, necessitated their "secondary" classification. Ironically, Briggs even now exploits similar circular reasoning to justify his dispersal scenarios for aplocheiloid killifishes and cichlids (e.g., Briggs, 2003:549, 552).

In Myers classification scheme, ostariophysans (catfishes, characins, minnows, and relatives) are "primary" freshwater fishes, whereas cichlids, for example, belong in the "secondary division," because some members are known to exhibit a limited tolerance to seawater (and they occur in Madagascar and the Greater Antilles). As Gosline (1944) and Rosen (1974) pointed out, although ostariophysans are members of Myers' "primary division," many species exhibit a tolerance to seawater (including minnows, suckers, catfishes). In addition to the two marine catfish families, Ariidae and Plotosidae, other salt-tolerant lineages, include representatives of various cypriniform families (e.g., Cyprinidae, Catostomidae; Jordan and Fowler, 1903; Berg, 1949; Schwartz, 1964) and some Central American and African characoids (Miller, 1966; Rosen, 1974).

For example, a comparison between catfishes (order Siluriformes; 34 families, approximately 412 genera, and 2405 species) and cichlids (1 family, approximately 110 genera, and 1500 species) illustrates the subjectivity of Myers' "primary" and "secondary" divisions. Both clades are species rich, yet within Siluriformes, allegedly a "primary" freshwater lineage, are nested two distantly related marine families, Ariidae and Plotosidae, comprising nearly 200 species (~8% of catfish species) (de Pinna, 1993). By comparison, only a handful of cichlids exhibit even limited tolerance to saline environments, and *there are no marine species!* The perciform family Nandidae (leaffishes) is another group whose classification as a "primary" freshwater lineage seems inappropriate given the criteria outlined by Myers (1938). Of the approximately 10 species, several are quite tolerant of saline environments and live in brackish waters (Nelson, 1994).

Myers (1938) asserts, "...families of the primary division have carried down their physiological inability

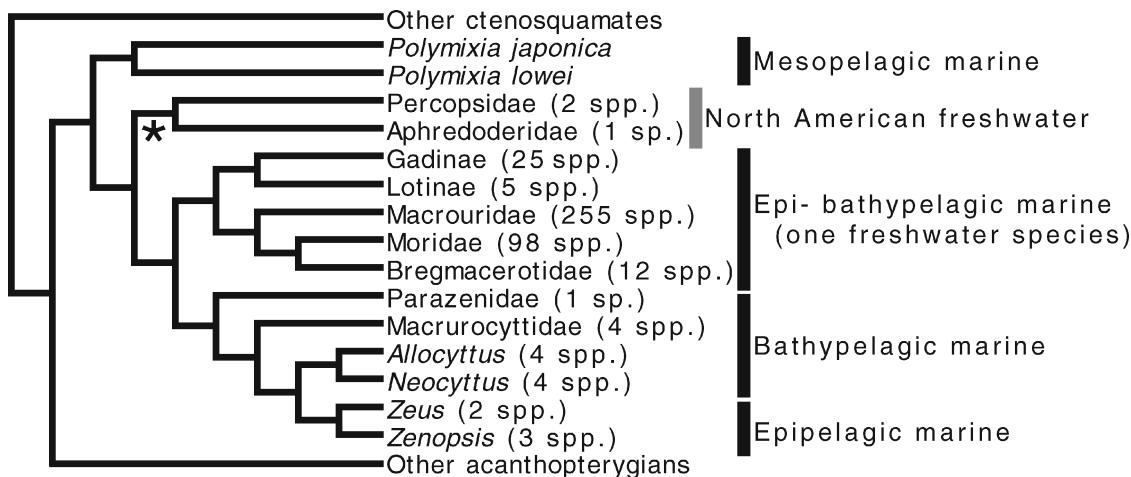


FIGURE 2. Phylogeny indicating placement of percopsiform fishes (marked with * in figure) after Miya et al. (2003). Number of inclusive species, including those found in freshwater, is indicated to the right.

to survive in the sea, as family characters, from early times and probably since the origin of the groups concerned." Phylogenetic evidence for the percopsiform fishes of North America, a "primary" freshwater lineage according to Myers (1938), for example, contradicts this conjecture. Percopsiformes includes three families (Percopsidae [trout perches], Aphredoderidae [pirate perch], Amblyopsidae [cavefishes]), six genera, and nine species (Nelson, 1994; Patterson and Rosen, 1989), which occur exclusively in freshwater. This clade is nested within a much larger assemblage (>500 species) of strictly marine lineages (= Paracanthopterygii) (Miya et al., 2001, 2003) (Fig. 2). Thus, within this large marine radiation only a small percentage of species (<2%) are found in and restricted to freshwater. Based on phylogenetic evidence, the putatively "primary" freshwater percopsiform fishes are clearly descended from marine ancestors.

Not only are Myers' divisions potentially misleading with respect to the dispersal ability of a lineage, but also they have been coopted to formulate uncorroborated generalizations concerning the past connections of landmasses and the diversification of taxa (e.g., Briggs, 1979, 2003; Murray, 2001). Additionally, these divisions continue to be uncritically accepted and presented in both general textbooks (e.g., Nelson, 1994; Helfman et al., 1997) and summary works on freshwater fishes (Berra, 2001). This gives students new to the field the impression that these classifications are necessarily meaningful for inferring dispersal capability and explaining freshwater fish distributions, which they clearly are not. We concur with Lundberg (1993) that the comparison of sister group relationships in conjunction with evidence regarding Earth history and the current distributions of the organisms of interest is the appropriate method for examining whether salinity tolerance in some members of a group implies anything regarding the dispersal capability and diversification of the lineage as a whole.

We recognize that some cichlids and aplocheiloid killifishes do, in fact, exhibit tolerance to saline environ-

ments; nevertheless, these two clades are dominated by freshwater lineages, and both assemblages represent freshwater radiations (Fig. 3). The ability of one or even a handful of species to temporarily penetrate a few hundred meters into a marine environment does not imply a capability to cross hundreds or thousands of kilometers of open ocean. For example, even limited exposure to seawater is fatal to Malagasy cichlids and killifishes, with 100% mortality recorded for both groups within 12 hours (usually much sooner) (Riseng, 1997). Although counterintuitive, prolonged exposure to seawater presents a

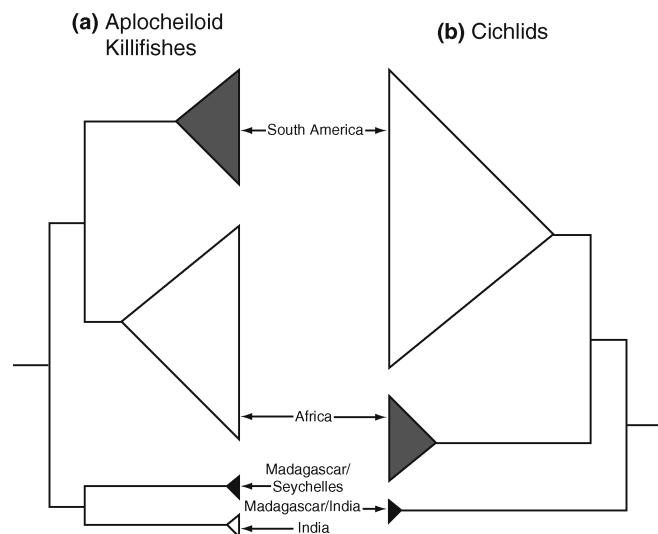


FIGURE 3. Cladograms depicting the relationships of (a) aplocheiloid killifishes (after Murphy and Collier, 1997) and (b) cichlids (after Farias et al., 1999) that were reproduced in Briggs (2003: Fig. 1). The size of the triangle reflects the relative number of taxa from each geographic area that were analyzed in these studies. Gray triangles identify, according to Briggs, the area or center of origin for each group of freshwater fishes, whereas black triangles identify clades that Briggs considers the most "primitive" or "plesiomorphic."

physiologically formidable barrier for freshwater fishes, a constraint not encountered by terrestrial vertebrates capable of dispersing via rafting or swimming.

Phylogenetic pattern and the current distributions of cichlids and aplocheiloid killifishes are consistent with a vicariance hypothesis (Murphy and Collier, 1997; Farias et al., 1999; Sparks, 2004) (Fig. 3). To date, no sister-group relationships have been recovered between Malagasy and African freshwater fish lineages using either morphological or molecular data (Sparks and Smith, 2004), despite the fact that Africa and Madagascar have been separated for 165 Myr via a comparatively narrow marine barrier (i.e., Mozambique Channel) (Rabinowitz et al., 1983; Smith et al., 1994; Storey, 1995) (Fig. 1). On the contrary, the sister groups to the Malagasy cichlids and aplocheiloid killifishes are found in South Asia (= Indian subcontinent) and the Seychelles (Murphy and Collier, 1997; Sparks, 2004) (Fig. 3), both of which are Gondwanan landmasses that have been separated from Madagascar since the early Cenozoic by more than 1000 km of open ocean (Smith et al., 1994; Storey et al., 1995; Reeves and de Wit, 2000) (Fig. 1b). Furthermore, cichlids and aplocheiloid killifishes are effectively restricted to landmasses of continental origin, being absent from intervening, noncontinental (i.e., volcanic) islands throughout their range. The sister group to the strictly freshwater Malagasy rainbowfishes (Bedotiidae) is also found on a distant Gondwanan landmass (Australia), not neighboring Africa (Dyer and Chernoff, 1996; Sparks and Smith, 2004). In other words, the phylogenetic patterns recovered for all three groups of Malagasy "secondary" freshwater fishes, comprising members of three distinct percomorph orders (Perciformes, Cyprinodontiformes, and Atheriniformes), are congruent with the temporal sequence of Gondwanan breakup in the Mesozoic. By comparison, all terrestrial vertebrate lineages, whose presence in Madagascar is attributed to dispersal, are either widely distributed on non-continental landmasses throughout the Mascarene region (e.g., Comoros, Réunion, Mauritius, and the Maldives) and/or exhibit sister group relationships with African taxa (Raxworthy, 2001, and references therein). The presence of cichlids and aplocheiloid killifishes in the Greater Antilles likewise can be explained without recourse to transoceanic dispersal scenarios (e.g., overland dispersal from northern South America via a Cenozoic landbridge [Iturralde-Vinent and MacPhee, 1999], a hypothesis that likewise cannot be casually dismissed due to a lack of Cretaceous-age fossils).

It is noteworthy that proponents of dispersal are more than willing to place a premium on absence of evidence (e.g., lack of Cretaceous-age fossils) to "support" their claims, yet they are not similarly compelled to account for the absence of dispersal in places where it seems likely. The scenarios described by Briggs (2003) and Murray (2001) presume long-distance transoceanic dispersal of both cichlids and aplocheiloid killifishes during the Cenozoic, from Madagascar to India or vice versa, but cannot explain why neither group has ever dispersed across the comparatively narrow Mozambique Channel.

Nor do they address why members of both groups are restricted to landmasses of continental origin throughout the region if these fishes presumably possess the capability to cross major ocean basins (Figs. 1b and 3).

Using cichlids as an example, advocates of a transoceanic dispersal hypothesis (e.g., Lundberg, 1993; Murray, 2001; Vences et al., 2001; Briggs, 2003) fail to consider that (1) There is not a single instance anywhere in the world, not the Greater Antilles, the Middle East, or Madagascar, where one *must* invoke oceanic dispersal to explain their current distribution. (2) The vast majority of cichlids are not salt tolerant, especially for prolonged periods. Salinity tolerance of Malagasy cichlids, in particular, has been frequently cited as contributing to an enhanced dispersal capability (e.g., Murray, 2001), yet the only study to examine their salt tolerance (Riseng, 1997) revealed an inability to withstand exposure to seawater for extended periods. Examples of tilapiine cichlids surviving for prolonged periods in nearshore marine environments are also regularly cited (e.g., Myers, 1938, 1949; Murray, 2001); these are not natural, but human mediated, distributions (e.g., see Trewavas, 1968, 1983; Greenwood, 1994). (3) Regardless of whether one uses morphological features, nucleotide characters, or a combination of both, based on the recovered phylogenetic patterns (Figs. 1, 3, and 4), post-Mesozoic colonization requires long-distance transoceanic dispersal, for example, from Madagascar to India or vice versa. Yet, there is no evidence of dispersal across the Mozambique Channel or anywhere else in the entire Indian Ocean. If, as Briggs (2003) implies, cichlids are unlikely to be much older than the oldest fossils known to date (Eocene of Tanzania [~46 Mya]; Murray, 2000), they must have traversed more than a "modest" saltwater gap to explain the recovered phylogenetic pattern (i.e., India–Madagascar sister group; Fig. 1b). Moreover, Briggs (2003) fails to note that the discovery of these Eocene fossil cichlids not only effectively doubled the age of the family (Murray, 2000), indicating that "as time goes on" the chance of such finds does not necessarily become "less probable," but also that these fossil cichlids represent derived African lineages (Murray, 2001; Sparks, 2004), suggesting a significantly older origin for the family.

Briggs (2003:549) points out that a vicariance scenario for cichlids has also recently been contested by divergence time estimates based on a "molecular clock" (Vences et al., 2001); however, that study is compromised by methodological problems and logical inconsistencies. As Hillis et al. (1996:532–533) stress, even under assumptions of a perfect molecular clock, none of which are ever met, the margin of error inherent in many such studies is generally so great as to render resulting divergence time estimates essentially useless. The study of Vences et al. (2001), using the nuclear Tmo-4c4 locus and mitochondrial 16S fragment to calculate divergence times of major geographic lineages of cichlids, is such an example. Although we commend the authors for attempting to address many of the problems inherent in such studies, nevertheless, the methodological problems are so severe and the margins of error reported (95% confidence

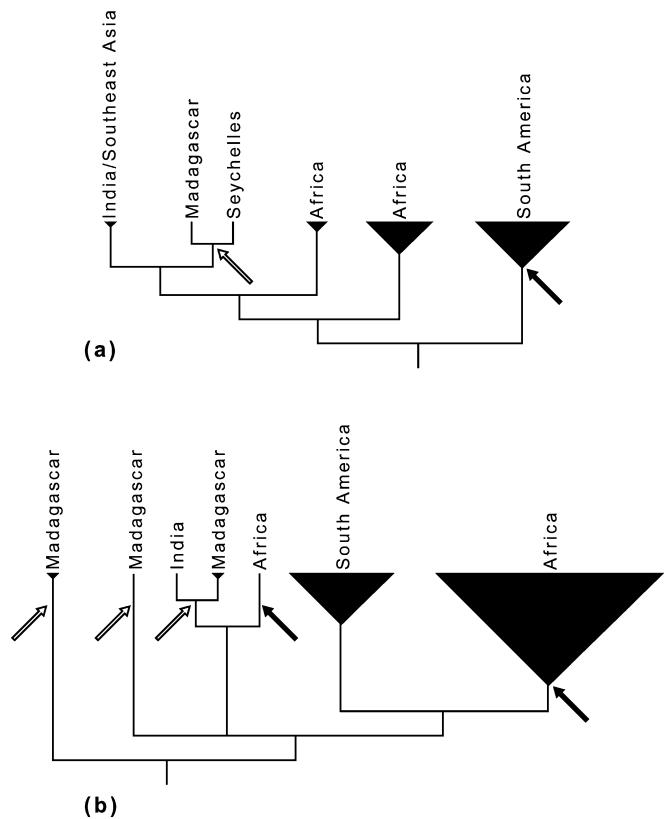


FIGURE 4. Phylogenetic relationships based on morphological evidence of (a) aplocheiloid killifishes (after Parenti, 1981), and (b) cichlid fishes (after Stiassny, 1991). The size of the triangle reflects the relative number of taxa from each geographic area that are currently recognized. Solid arrows identify clades that, according to Briggs, represent the area or center of origin for both groups of freshwater fishes, whereas open arrows identify clades that Briggs considers most "primitive" or "plesiomorphic."

intervals [CI]) so great that the authors' conclusions must be reevaluated in light of these limitations (e.g., see Graur and Martin, 2004). Vences et al. (2001) report that clock-like evolution of both fragments was rejected by the likelihood ratio test and that rate constancy was also rejected for many comparisons upon which the authors base their divergence estimates (e.g., 16S: Africa–South America; Tmo-4c4: Africa–Madagascar/India). Vences et al. (2001) attempted to circumvent the problem of nonindependence of lineages by calibrating their clock using African lake cichlids and estimated basin age, but they were forced to acknowledge a great deal of rate heterogeneity (e.g., about twice as fast for Tmo-4c4 for African taxa) within Cichlidae. If African lineages are evolving at twice the rate of other taxa, divergence times for other familial lineages based on a clock calibrated using this locus may be severely underestimated. Given significant rate heterogeneity between a number of intrafamilial lineages for both fragments, there is simply no reason to assume that the Vences et al. clock can reasonably predict divergence times over the entire assemblage.

Vences et al. (2001) report divergence time estimates (CI based only on maximum likelihood distances of the

faster-evolving 16S fragment) for Malagasy–Indian and African cichlids (56–35 Mya, 95% CI of 84–15 Mya), African and South American cichlids (58–41 Mya, 95% CI of 78–24 Mya), and Malagasy and Indian cichlids (29–5 Mya, 95% CI of 43–5 Mya). Although Vences et al. (2001:1094) maintain that substitution rates were only "slightly lower" for Tmo-4c4 than for 16S, according to their data the substitution rate for 16S is nearly 50% faster (Vences et al., 2001: tables 1 and 2). Consequently, the upper bound for the reported CIs based only on the faster evolving 16S fragment will most likely be severely underestimated. Graur and Martin (2004) stress, "were calibration and derivation uncertainties taken into proper consideration" in such studies, and not treated as errorless numbers, 95% CIs would be considerably larger. Nevertheless, considering only the reported CI estimates, we cannot reject divergence times for African and Malagasy–Indian cichlids, and African and South American cichlids, extending back to the Cretaceous or that are as recent as 15 or 24 Mya or less, respectively. Results are even more ambiguous for the split between Malagasy and Indian cichlids, which may be as early as 43 Mya or more recent than 5 Mya (CI underestimated due to exclusion of data from an "outlier"). Moreover, the average estimated divergence dates reported are inconsistent with the branching pattern the authors present (i.e., the estimated Africa–South America split [58–41 Mya] predates the estimated east–west Gondwanaland split [56–35 Mya]).

The scenario advocated by Vences et al. (2001) also necessitates that cichlids dispersed across thousands of kilometers of open ocean in the Cenozoic, from Madagascar to India (Fig. 1). Vences et al. (2001: 1096–1097) report that similar ("not too different from cichlids") rates were recovered for a number of Malagasy vertebrate lineages exhibiting either India or South America (boas, iguanines [oplidurids-tropidurids/polychrotids], podocnemine [pelomedusoid, side-neck] turtles) connections, "and match better the assumption of Cenozoic than early Cretaceous divergences," suggesting intercontinental oceanic dispersal for these taxa as well. Considering only the Madagascar–South America sister taxa pairs, for this scenario to be credible, one must assume that boas, iguanas, and pelomedusoid turtles not only independently dispersed across thousands of kilometers of ocean (from South America to Madagascar or vice versa), but that all of these lineages somehow also entirely missed Africa in the process! Given that these lineages are not likely transoceanic dispersers and that these sister-group relationships are congruent not only with each other but also with the temporal sequence of Gondwanan breakup advocated by Hay et al. (1999), a more plausible explanation is that molecularly these taxa are simply more slowly evolving than Vences et al. (2001) expect based on their cichlid "molecular clock." This is one of many studies using a "molecular clock" that have found considerable rate heterogeneity of mitochondrial and nuclear DNA between and within numerous animal lineages (see references in Hillis et al., 1996), and it underscores the potential limitations of

using such an approach to generalize across old, diverse assemblages.

In light of many recent higher-level phylogenetic studies, including those discussed in detail above, many of Myers' (1938) classifications now seem not only arbitrary but also misleading with respect to dispersal capability. Based on phylogenetic pattern and paleogeographic data, we have shown that vicariance, not random transoceanic dispersal, is the most parsimonious explanation for the current (coincident) distributions of cichlids and aplocheiloid killifishes (Figs. 1, 3, and 4). The specific examples we discuss underscore the essential role phylogeny and Earth history play in formulating hypotheses regarding the diversification of lineages.

Despite criticism regarding the utility of the two categories for biogeographic studies, extending back 60 years, classification of a group within either Myers' "primary" or "secondary" division continues to be used by many as the principal source of evidence (i.e., to argue for or against dispersal) to account for the current distribution of freshwater fishes. Shortly after Myers (1938) proposed his freshwater divisions, Gosline (1944:214–215) questioned whether they were in fact distinct, and stressed that salt tolerant ("semimarine") forms could also be informative in "continental distributional work." Similarly, Rosen (1974:323) considered Myers' classifications to be arbitrary in many cases, and advocated instead the terms "continental" and "oceanic":

Instead of primary and secondary fishes, there seem to me to be only continental and oceanic groups of fishes, as long ago suggested by Boulenger, Pellegrin, and Regan (see Myers, 1949), the assignment to which is determined not by what we imagine to be the habits of the fishes and their possible dispersal mechanisms but by their distribution in relation to phylogeny and in relation to the distributions of other organisms.

We concur with Rosen (1974) and consider his terminology to be a significant improvement that gets closer to the core of the issue. We agree also that many continental, yet marine, groups are extremely useful for inferring past geologic connections (e.g., Springer, 1982; Stiassny, 2002; Ng and Sparks, 2003) and disagree with Myers (1938, 1949) and Briggs (2003) that only freshwater fishes of the "primary division" are useful for making such inferences. However, we question the value of classifying organisms for biogeographic studies based exclusively on presumed physiological tolerance and their perceived present and historical distributions. Instead, we suggest that inferences regarding the dispersal ability of various fish groups, historical connections of landmasses based on shared biotas, and macroevolutionary process in general should only be considered in conjunction with sound phylogenetic evidence. Myers (1938:344) states, "...fishes of the primary and secondary divisions tend to group themselves along natural family lines," and that these physiological abilities have been carried down since the origin of the lineages. Nevertheless, as we have shown for percopsiform fishes, reasonable inferences regarding their origin (marine not freshwater) and diversification can only be formulated provided we

have information regarding their relationships to other taxa.

The goal of this article is not to condemn the works of Myers (1938, 1949), whose studies were illuminating for their time, but to challenge those who continue to apply these potentially arbitrary divisions (e.g., to muster support for dispersal scenarios) indiscriminately, despite multiple lines of evidence to the contrary. Nor do we intend to imply that Myers was necessarily wrong in most cases, but that in the absence of corroborative phylogenetic evidence we cannot evaluate his freshwater fish divisions and, in turn, their implications regarding lineage diversification.

CENTERS OF ORIGIN

An important biogeographic question is, where did the aplocheiloid fishes originate? *Instead of assuming the existence of a widespread ancestor on Gondwana, one can look for the area in which most of the evolution has taken place.* Briggs (2003:549, our italics)

From the discussion (Briggs, 2003:549–550), we can infer that Briggs equates "area of origin" with organismal diversity (e.g., generic diversity). According to Briggs this "phenomenon," which he attributes to Matthew (1915), but which can be traced to Darwin (see Darlington, 1957, 1965), further posits that "primitive" or "plesiomorphic" taxa will necessarily accumulate on the periphery of an "evolutionary group." Thus for cichlids, Briggs concludes that most of the evolution has taken place in Africa; likewise for aplocheiloid killifishes, most of the evolution supposedly occurred in South America (Figs. 3 and 4), which he presumes represent the centers of origin for these lineages, respectively. We will demonstrate, however, that the phylogenetic evidence Briggs draws on does not support these claims. Despite the patterns of relationships recovered in the phylogenies presented, Briggs (2003:549) erroneously states, "the presence of the most plesiomorphic aplocheiloids on Madagascar and the Seychelles is consistent with the concept that relatively primitive taxa should accumulate on the periphery of an evolutionary group." If we assume that by "primitive" or "most plesiomorphic" Briggs is referring to the oldest (= basal) lineage, where, we wonder, is this pattern of relationships for Aplocheiloidei recovered? The Malagasy and Seychellian killifishes have never been recovered as the sister group to the remainder of Aplocheiloidei (= "most plesiomorphic aplocheiloids" according to Briggs) in any molecular or morphological study that we know of, and certainly not in any study that Briggs references (i.e., Parenti, 1981; Murphy and Collier, 1997). In the molecular phylogeny cited by Briggs (2003) (Fig. 3a), the Malagasy–Seychellian aplocheiloid killifishes are recovered as the sister taxon to the Indian aplocheiloids. Contrary to Briggs' assertion, they are not the sister taxon to the remaining aplocheiloids, a criterion of Briggs' center-of-origin "phenomenon" (Fig. 3a).

Likewise, in the phylogeny for Cichlidae Briggs presents (Fig. 3b), the Malagasy–Indian lineage is the sister taxon to the African–Neotropical lineage,

and as such cannot be considered "basal" cichlids. Nothing can be inferred from the cladograms presented with respect to the relative "plesiomorphic" or "primitive" nature of any nested clade (e.g., Malagasy–Seychellian aplocheiloids) within one lineage (Malagasy–Seychellian + Indian) with respect to a clade (e.g., South American aplocheiloids) nested within its sister lineage (Africa + South America). Similarly, in the morphological hypothesis of Parenti (1981) that Briggs cites, the Malagasy–Seychellian aplocheiloid killifishes are nested well within Aplocheiloidei (Fig. 4a). Was Briggs deceived because the Malagasy–Seychellian + Indian aplocheiloid fauna (or Malagasy–Indian lineage for Cichlidae) was poorly sampled and/or less species rich than the African + Neotropical clades, or possibly due to their placement at the bottom of the cladograms he presents (Fig. 3)? Moreover, as Nelson and Ladiges (2001) point out, even considering an area cladogram in which there is duplicated geography a paralogous basal node (e.g., Madagascar, Fig. 4b), paraphyly is only evidence of paraphyly, not a center of origin.

It is impossible for Briggs to justify or reconcile his "center-of-origin phenomenon" in light of the phylogenies available for both clades of fishes, regardless of the data set analyzed (Figs. 3 and 4). In order for one to accept Briggs' area of origin hypothesis for both freshwater fish clades, one would either have to be willing to acknowledge that younger (derived) lineages can give rise to "plesiomorphic" (= older/basal) lineages, or that higher taxa can give rise to other higher taxa (Figs. 3 and 4). Obviously, this is impossible. In rejecting the concept of center of origin as a model of general applicability in historical biogeography in favor of a model based on generalized patterns of biotic distribution (i.e., generalized tracks), Croizat et al. (1974) warned that the concept may conflict with the principles of common ancestry and allopatric speciation. The arguments advanced by Briggs clearly illustrate and verify these criticisms. As Platnick (1981:149) stressed, determining the area of origin for a particular group of organisms "may well be an important question. But with regard to the problems that vicariance biogeography attempts to solve," the question turns out to be unnecessary and (possibly) irrelevant.

As we have demonstrated, Briggs' dispersal scenarios rely entirely on negative evidence (lack of Cretaceous-age fossils) and the presumed dispersal ability of lineages based on perceived tolerance to saline environments. Although Briggs implies that his arguments take phylogenetic relationships into account, phylogeny (i.e., common ancestry) has no bearing on the scenarios he presents. We are not opposed to dispersalist arguments, provided they are corroborated by evidence. Likewise, we are well aware that dispersal has played a major role in the diversification of numerous plant and animal groups and can account for their current distributions. Briggs attacks the hypotheses of others, whose conclusions receive evidential support, yet is only able to "bolster" his dispersal arguments with unsubstantiated conjectures. The one idea that Briggs conveys clearly is that when you are unconstrained by evidence, anything is possible. It is ironic that

Briggs, who begins and ends his criticism of vicariance biogeography by emphatically stating that we should use all available evidence to make historical inferences regarding macroevolutionary process, falls back on negative evidence and an outdated, nonphylogenetic classification scheme.

The cladograms for cichlids and aplocheiloid killifishes Briggs references are incongruent with the dispersal scenarios from a center of origin that he advocates, yet they are congruent with Gondwanan vicariance (Figs. 1a, 3, and 4). The absence of any sister group relationship between Malagasy and neighboring African freshwater fish faunas, and instead the presence of sister groups on remote Gondwanan landmasses that were more recently in contact with Madagascar than Madagascar to Africa, provides compelling evidence for vicariance. We have demonstrated that Myers' (1938) physiological classification of freshwater fishes is not reliable for formulating historical biogeographic hypotheses, certainly not in the absence of corroborative phylogenetic data, and that to do so can lead to erroneous conclusions regarding the diversification of lineages. Briggs concludes his critique with the most insightful comment of the article: "although molecular research has generally been a boon to biogeography, some of it could be made more meaningful if it were better integrated with the body of knowledge that already exists." We couldn't agree more.

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