



Molecular phylogenetics supports multiple evolutionary transitions from marine to freshwater habitats in ariid catfishes

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ABSTRACT

Transitions between the marine and freshwater environments represent an extraordinary ecological shift that has promoted diversification in many groups of aquatic organisms. Here, molecular phylogenetics is utilized to investigate habitat transitions in a group of catfishes (Ariidae) that includes species inhabiting marine and brackish waters (>110 species) as well as freshwater environments (~40 species). The Ariidae is nested within the Otophysi, the largest clade of primary freshwater fishes with four orders and 67 families. Optimizations of habitat transitions (freshwater vs. marine) onto a previously inferred phylogeny suggest a single invasion of marine waters at the root of the ariid tree followed by 10–15 events of freshwater colonization, implying reversion to the primitive otophysan condition. Thus, ariids provide an extraordinary example of bidirectional habitat transitions in fishes. Freshwater recolonization has occurred in all major provinces where ariids are present, such as the New World (Mesoamerica and South America), Madagascar, Africa, Southeast Asia, and the Sahul continent (Australia and New Guinea). The remarkable diversity of freshwater ariids in Australia–New Guinea and Mesoamerica is presumed to have been facilitated by the originally depauperate freshwater ichthyofaunas in both regions, particularly the low diversity of primary otophysan families in Mesoamerica and their absence in Australia and New Guinea. The lack of phylogenetic resolution among basal Sahul lineages coupled with their extraordinary level of morphological divergence and trophic diversity suggests an ancient rapid radiation promoted by freshwater colonization. For this reason, Sahul ariids represent an excellent system for studying diversification associated with habitat transitions.

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1. Introduction

For aquatic organisms, the boundary between marine and freshwater habitats is a significant physicochemical barrier that imposes physiological and ecological constraints. As a result, 12 out of approximately 30 animal phyla have failed to colonize freshwaters (e.g., Ctenophora, Echinodermata, and Chaetognata; Lee and Bell, 1999; Little, 1990). A wide range of taxa has achieved physiological adaptations to overcome the osmotic barriers (Lee and Bell, 1999; McDowall, 1988). For instance, among invertebrates, transitions from marine to freshwater have occurred in several groups within annelids, mollusks, and crustaceans (Lee and Bell, 1999). Among fishes, distantly related taxa such as lampreys, elasmobranchs, and teleosts have also colonized freshwaters multiple times (Little, 1990; McDowall, 1997). These include species that migrate between marine and freshwater habitats and thus have diadromous life histories (McDowall, 1997), and species that are euryhaline (i.e., tolerating a wide range of salinities; Lee and Bell,

1999). A fraction of such groups have become landlocked (e.g., Bell and Foster, 1994; Lovejoy et al., 2006, 1998; McDowall, 1997). Macroenvironmental factors that have facilitated freshwater colonization and subsequent landlocking of fishes of marine origin are: past incursions of marine waters into freshwater habitats (e.g., during postglacial events; Lovejoy et al., 2006, 1998), rivers with high ionic concentrations that buffer osmotic gradients (Lee and Bell, 1999; Lovejoy and Collette, 2001), habitats with depauperate fish communities (Lee and Bell, 1999), among others.

While marine-to-freshwater transitions are relatively common in fishes and invertebrates (Lee and Bell, 1999; Little, 1990; Lovejoy and Collette, 2001), colonization of marine waters by freshwater organisms is far less frequent (McDowall, 1997). Such is the case of a few otophysan fish groups. The Otophysi is the largest clade of fishes confined to freshwater (primary freshwater sensu Myers, 1938) and includes four orders (Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes) and 67 families (Ferraris, 2007; Nelson, 2006), accounting for about 27% and 64% of the total fish species and freshwater fish species, respectively (Briggs, 2005). Although phylogenetic relationships among otophysan orders are controversial (e.g., Dimmick and Larson, 1996; Fink and Fink, 1996; Peng et al., 2006), all hypotheses coincide in placing the or-

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der Siluriformes (catfishes) in a rather terminal position. Thus, catfishes retain the ancestral otophysan condition of freshwater confinement. However, some siluriform families have adapted to marine environment to varying degrees. For example, the Ariidae and Plotosidae contain mostly marine species. The Auchenipteridae, Loricariidae and Pimelodidae include species that occur in brackish water at river mouths. Some aspredinid species inhabit coastal-marine waters (Ferraris, 2002). Mapping the condition of saltwater tolerance in the catfish tree implies multiple origins [i.e., the aforementioned families form a polyphyletic assemblage, see Sullivan et al. (2006)]. Thus, catfishes appear to have a phylogenetic propensity for invading brackish and marine waters.

Ariids or sea catfishes are the only siluriform family that is widely distributed on the world's tropical and subtropical marine continental shelves. While specific life histories and migratory behaviors for most ariid species are poorly understood, there is

great diversity of habitat preferences within the family, including offshore marine taxa (e.g., *Brustiarius proximus*, and most *Netuma*, *Plicofollis*, *Bagre*, and *Galeichthys* species), inshore coastal and brackish taxa (e.g., *Cathorops dasycephalus*, '*Sciades*' *mastersi*, *S. sator*, and most *Notarius* species), and euryhaline taxa in the biogeographic sense, i.e., with broad habitat distributions (Lee and Bell, 1999; e.g., most *Cathorops*, *Ariopsis*, *Arius*, *Neoarius*, and *Nemapteryx* species). Additionally, as many as 43 ariid species in 19 genera (among over 150 species in ~29 genera) from different regions around the world inhabit predominantly freshwater (Table 1).

Phylogenetic hypotheses provide a framework to investigate the evolution of habitat preferences. Although there is a wide spectrum of habitat states within the Ariidae, which behave more as continuous rather than categorical variables, assuming a binary condition (i.e., freshwater vs. marine, estuarine, or euryhaline) provides a simple method toward approaching questions of habitat

Table 1
Freshwater ariids and their distribution. Compiled from (unpublished data, Ng, pers. comm.; Kottelat, pers. comm.; Allen, pers. comm.; Acero and Betancur-R, 2006; Allen, 1991; Allen and Coates, 1990; Allen et al., 2002; Betancur-R and Willink, 2007; Ferraris, 2007; Jayaram, 1983; Kailola, 2000; Kottelat, 2001; Marceniuk and Betancur-R, 2008; Marceniuk and Menezes, 2007; Ng and Sparks, 2003; Roberts, 1989; Swales et al., 2000; Taylor, 1986). Two letter country codes follow ISO-3166. ICP, Indochina Peninsula; MPN, Malay Peninsula; IMA, Indo-Malayan Archipelago.

Species	Distribution	Major region/province
	New World	
' <i>Arius</i> ' <i>labiatus</i> ^a	Río Peripa, EC	Tropical Eastern Pacific slope
<i>Cathorops aguadulce</i>	Río Usumacinta, GT and MX	Mesoamerica (Atlantic slope)
<i>Cathorops kailolae</i> ^a	Lago Izabal, GT	Mesoamerica (Atlantic slope)
<i>Cathorops melanopus</i> ^a	Río Motagua, GT possibly HN	Mesoamerica (Atlantic slope)
<i>Cathorops festae</i>	Río Guayas basin, EC	Tropical Eastern Pacific slope
<i>Notarius bonillai</i>	Río Magdalena and Río Atrato basins, CO	Southern Caribbean slope
<i>Notarius cookei</i>	Pacific-slope rivers, PA and possibly CO	Tropical Eastern Pacific slope
<i>Potamarius grandoculis</i> ^a	Río Doce and Río Parabaiba do Sul, Southern BR	Southern Brazil
<i>Potamarius izabalensis</i>	Lago Izabal, GT	Mesoamerica (Atlantic slope)
<i>Potamarius nelsoni</i>	Río Usumacinta, GT and MX	Mesoamerica (Atlantic slope)
<i>Potamarius usumacintae</i>	Río Usumacinta, GT and MX	Mesoamerica (Atlantic slope)
	Africa	
<i>Arius brunellii</i> ^a	Juba River, SO	Eastern Africa
<i>Carliarius gigas</i> ^a	Volta and Niger Rivers, GH and NG	Gulf of Guinea, Western Africa
	Madagascar	
<i>Arius festinus</i> ^a	Amboaboa River	Northwestern Madagascar
<i>Arius madagascariensis</i>	Western Madagascar	Western Madagascar
<i>Arius uncinatus</i> ^a	Ankofia River basin	Northwestern Madagascar
	SE Asia	
<i>Arius acutirostris</i> ^a	Salween River, MM	Salween basin, Burma
<i>Arius borneensis</i> ^a	Bandjarmasin, Borneo	Borneo
<i>Arius burmanicus</i> ^a	Irrawaddy River, MM	Salween basin, Burma
<i>Cephalocasis borneensis</i>	IMA, MPN, and ICP (ID, MY, TH, KH, and VN)	Sunda Shelf
<i>Cephalocasis melanochir</i>	Sumatra and Borneo	IMA
<i>Hemiaris stormii</i>	Sumatra and Borneo	IMA
<i>Hemiaris verrucosus</i> ^a	Mekong River	ICP
<i>Plicofollis magatensis</i> ^a	Magat River, PH	Philippines
	Australia–New Guinea	
<i>Brustiarius nox</i>	Sepik River basin, PG	Northern New Guinea
<i>Brustiarius solidus</i>	Sepik River basin, PG	Northern New Guinea
<i>Cinetodus carinatus</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Cochlefelis spatula</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Doiichthys novaeguineae</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Nedystoma dayi</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Neoarius Augustus</i>	Fly River system in PG and Papua, ID	Southern New Guinea
<i>Neoarius berneyi</i>	Fly River system in PG and Papua, ID; northern Australia	Sahul Shelf
<i>Neoarius midgleyi</i>	Victoria, Katherine, Daly and other rivers systems in Northern AU	Northern Australia
<i>Nemapteryx</i> aff. <i>armiger</i>	Fly River system in PG	Southern New Guinea
<i>Pachyula conorhynchus</i> ^a	Lorentz River system, Southern Papua, ID	Southern New Guinea
<i>Pachyula crassilabris</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Potamosilurus coatesi</i>	Sepik River basin, PG	Northern New Guinea
<i>Potamosilurus latirostris</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Potamosilurus macrorhynchus</i>	Southern PG and Papua, ID	Southern New Guinea
<i>Potamosilurus taylori</i> ^a	Fly River system in PG and Papua, ID	Southern New Guinea
<i>Potamosilurus velutinus</i>	Sepik River basin, PG	Northern New Guinea
' <i>Sciades</i> ' <i>paucus</i> ^a	Roper and Flinder river systems in Northern AU	Northern Australia
' <i>Sciades</i> ' <i>utarus</i>	Sepik River basin, PG	Northern New Guinea

^a Not examined.

transitions. In the light of the ancestral otophysan condition, the most parsimonious a priori explanation is that freshwater ariids are basal, implying a single transition from fresh to marine waters (i.e., marine taxa form a monophyletic group). Alternatively, freshwater species may be derived, which would imply secondary invasion of rivers (i.e., reversed to the primitive otophysan state). To address this question, this study optimized habitat transitions onto a comprehensive phylogeny inferred for ariids (123 taxa) using mitochondrial sequences (~3 kb; see Betancur-R, 2009). Additionally, noteworthy instances of freshwater confinement on different regions are discussed and examined as a possible case for an ancient rapid radiation associated with habitat transitions.

2. Materials and methods

Generic nomenclature for New World and Old World ariids follows Betancur-R et al. (2007) and Marceniuk and Menezes (2007), respectively. Datasets include mitochondrial (*cytochrome b* [*cyt b*], *ATP synthase* subunits 8 and 6 [*ATPase 8/6*], and ribosomal 12S and 16S; total 2866 bp and 123 arid taxa) and nuclear (*rag2*; 978 bp and 70 ariid taxa) sequences. Methods of sequence acquisition and phylogenetic reconstructions are detailed in Betancur-R (2009) with additional analyses described below.

Despite the wide variety of habitat distributions among ariid taxa, the primary focus of this study is tracing transitions between freshwaters and waters with some degree of salinity. Thus, habitat type was coded as a binary character (0, freshwater; 1, marine, estuarine or euryhaline; compiled from (unpublished data, Ng, pers. comm.; Kottelat, pers. comm.; Allen, pers. comm.; Acero and Betancur-R, 2006; Allen, 1991; Allen and Coates, 1990; Allen et al., 2002; Betancur-R and Willink, 2007; Ferraris, 2007; Jayaram, 1983; Kailola, 2000; Kottelat, 2001; Marceniuk and Betancur-R, 2008; Marceniuk and Menezes, 2007; Ng and Sparks, 2003; Roberts, 1989; Swales et al., 2000; Taylor, 1986). While the binary coding hinders inferences on evolutionary transitions among estuarine, marine, and euryhaline taxa, it allows large-scale interpretations of habitat transitions within the Ariidae in the context of the freshwater otophysan condition. Two taxa with uncertain habitat condition (*Neoarius* aff. *graeffei* sp. 1 and '*Sciades*' aff. *leptaspis*) were coded as missing data ("?"). These discrete character data were optimized onto the mitochondrial phylogeny (inferred under Bayesian Inference [BI], maximum parsimony [MP], and maximum likelihood [ML]; see Betancur-R, 2009) under both likelihood (Pagel, 1999) and parsimony criteria in Mesquite v. 2.5 (Maddison and Maddison, 2008). For likelihood and parsimony reconstructions, the evolution models "mk1" (Pagel, 1999) and Wagner optimization, respectively, were selected, under which any particular change (0 → 1 or 1 → 0) is equally likely.

The parsimony-based nonparametric Templeton test and the likelihood-based Shimodaira–Hasegawa (SH) test (Shimodaira and Hasegawa, 1999) as implemented in PAUP* v.4.0b10 (Swofford, 2002), were performed to evaluate alternative hypotheses on the evolution of the habitat transitions in the Ariidae. To test whether freshwater ariids are basal (i.e., single transition from fresh to marine waters) or derived (i.e., multiple independent recolonization of freshwaters), MP and ML searches (see procedures in Betancur-R, 2009) constraining the monophyly of marine taxa were conducted and the optimal scores with those obtained under unconstrained searches were compared.

Testing for ancient rapid radiations involved additional ML and MP reconstructions on separate (nuclear *rag2*, mitochondrial ribosomal 12S + 16S, mitochondrial protein-coding *cyt b* + *ATPase 8/6*) and combined (mitochondrial, mitochondrial + nuclear) partitions (see also Betancur-R, 2009; Table 1). Additionally, congruence among data partitions was assessed using 100 replicates of the par-

tion homogeneity test in PAUP* [=incongruence length difference test of Farris et al. (1994)]. Genetic distances were calculated under the Kimura two-parameter model.

3. Results and discussion

3.1. Tracing habitat transitions

Mapping of the habitat condition via parsimony and likelihood analyses onto the mitochondrial phylogeny (broadest taxon sampling) suggests multiple marine-to-freshwater transitions in ariid catfishes (Fig. 1). Further MP and ML analyses constraining marine ariids to a monophyletic group yielded scores significantly worse than those obtained under unconstrained searches (SH: *p* value = 0.000; Templeton test: *p* value < 0.0001). These results provide no support for an a priori assumption that freshwater ariids are basal (i.e., retain the ancestral otophysan condition).

The optimizations suggest a single invasion of marine waters at the root of the ariid tree, followed by 10–15 events in the subfamily Ariinae. No habitat transitions occurred in the other ariid subfamily, the Galeichthyinae (Acero and Betancur-R, 2007; see subfamilial divisions in Fig. 1). It is noteworthy that at least 16 freshwater ariid species in 10 genera from different regions were not examined (Table 1); thus, the number of habitat transitions is likely underestimated. Optimizations of marine-to-freshwater transitions in the New World (four transitions), Madagascar (one transition), and India–SE Asia (two transitions) were straightforward; however, the number of (three to eight transitions) and, in some cases, direction of habitat transitions in the Australia–New Guinea clade (node O, Fig. 1) were equivocal. Four major factors account for these ambiguous optimizations: (1) poor phylogenetic resolution (i.e., large basal polytomy; see Section 3.3), (2) many instances of interleaved marine and freshwater taxa, (3) binary coding (combines intermediate states), and (4) missing taxa.

Lee and Bell (1999) suggested that the ability for freshwater invasion by saltwater animals requires an evolutionary innovation, and once the innovation arises the transition may occur repeatedly. Remarkable examples of invertebrate taxa that are frequent colonizers of freshwater include heterodont mollusks (e.g., zebra mussels) and amphipod, decapod, and copepod crustaceans (Lee and Bell, 1999). Among marine fishes, needlefishes, drums, anchovies, toadfishes, and others, also appear to have entered freshwaters multiple times (Lovejoy et al., 2006; Lovejoy and Collette, 2001; Roberts, 1989). The pattern of multiple recolonization of rivers in ariids may be the result of a phylogenetic bias facilitating transitions into freshwater and is probably a primitive signal in the Otophysi. Plotosids, the other catfish group that inhabit chiefly marine waters, also include many species that are freshwater inhabitants (Allen, 1991; Allen et al., 2002). As in the Ariidae, freshwater plotosids are probably derived (Unmack pers. comm.), but this issue remains to be tested in a phylogenetic framework. Among fishes, ariids (and possibly plotosids) provide an extraordinary example of bidirectional habitat transitions (i.e., original invasion of salt waters and subsequent recolonization of rivers).

3.2. Biogeography of the habitat transitions

Marine-to-freshwater transitions occurred in all major regions where ariids are present, including the New World, Madagascar, Africa, SE Asia, and Australia–New Guinea. Not surprising, freshwater ariid diversity is highest in regions that host a rather depauperate ichthyofauna in the primary division, such as Australia–New Guinea and Mesoamerica (Table 1). This section discusses remarkable instances of ariid habitat transitions on major provinces.

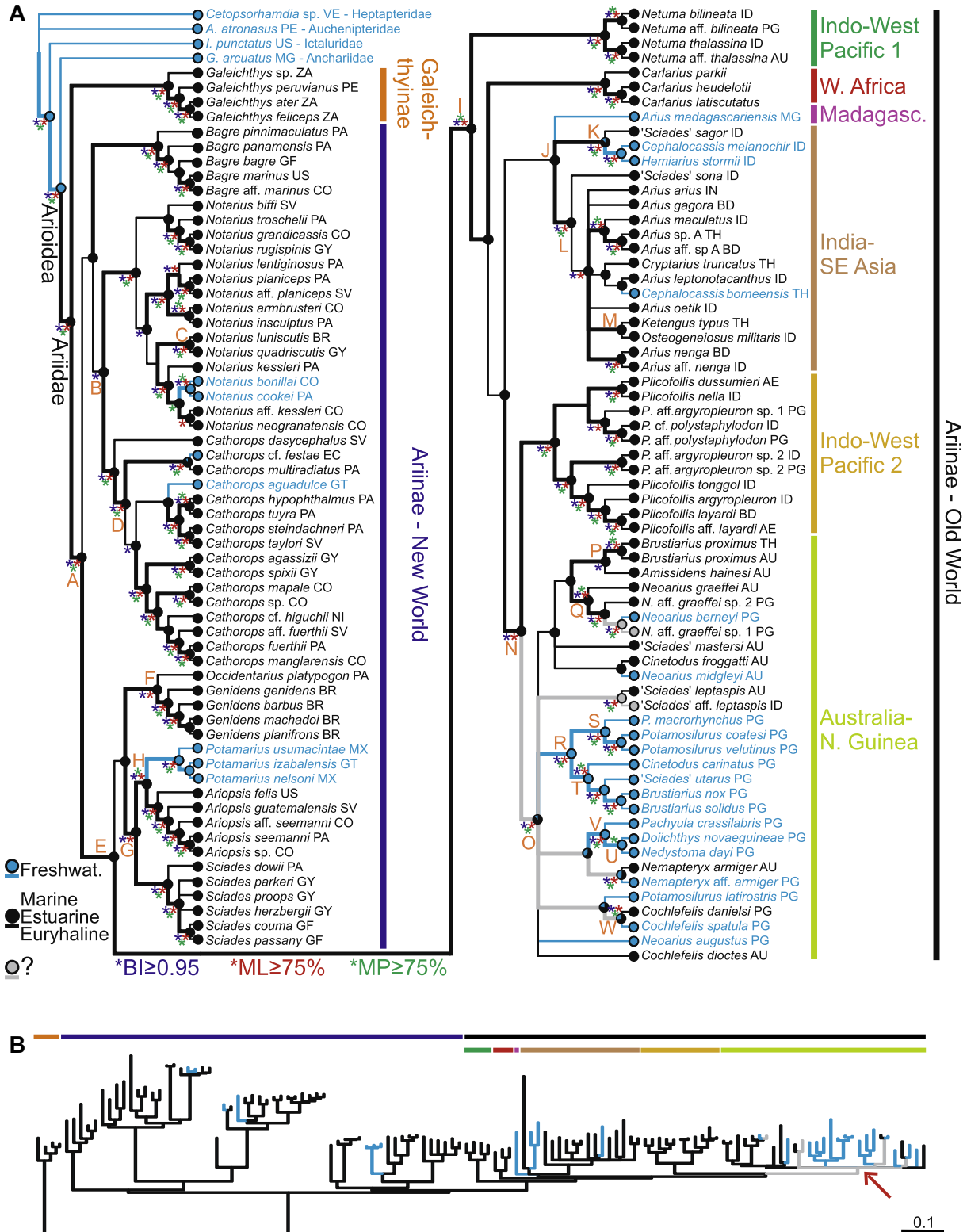


Fig. 1. BI phylogeny of 124 arioid species derived from mitochondrial data (2866 bp; Betancur-R, 2009). (A) cladogram; thicker branches indicate clades that are congruent with MP and ML analyses (see details in Betancur-R, 2009). Asterisks (*) designate clade support; capital letters indicate nodes referred in text (symbols and letters always on left of nodes); vertical bars indicate subfamilial divisions and distribution of major ariine groups. Pie charts and color branches represent ancestral habitat reconstructions based on likelihood (mk1 model) and parsimony (Wagner optimization), respectively; gray question mark “?” indicates uncertain states or ambiguous optimizations. Two letter country codes follow ISO-3166. (B) phylogram (Ariidae only) elucidating rate variation across lineages (taxon arrangement follows the same order in both figures); red arrow indicates basal polytomy in the Australia–New Guinea clade (=node O). Although *Brustarius proximus* occurs in Australia–New Guinea as well as in SE Asia, for the purpose of this study, *B. proximus* is treated as a Sahul taxon (see additional comments in Betancur-R, 2009).



Fig. 2. Approximate distribution of freshwater ariids. Dots indicate regions where purely freshwater ariids occur (some symbols represent more than one locality; see also Table 1). Euryhaline species found in other freshwater locations not plotted (e.g., *Neoarius graeffei*).

Freshwater species and their distribution are summarized in Table 1 and Fig. 2.

3.2.1. New World

The Neotropics host the most diverse freshwater fish fauna in the world, which is estimated to include up to 8000 species (Lundberg et al., 2000). The freshwater ichthyofauna in South America and Mesoamerica is dominated by siluriforms, characiforms, gymnotiforms, cyprinodontiforms, and cichlids (Lundberg et al., 2000), but many families of marine origin have invaded Neotropical rivers as well (Lovejoy et al., 2006, 1998; Lovejoy and Collette, 2001). Within the Ariidae, three species of *Potamarius* (Betancur-R and Willink, 2007) and two species in the *Cathorops aguadulce* species group [*C. kailolae* and *C. aguadulce* (Marceniuk and Betancur-R, 2008)] provide evidence of two independent transitions into the Río Usumacinta and Lago Izabal basins in Mesoamerica. The high percentage of secondary freshwater or peripheral species (sensu Myers, 1938) and micro-endemism in the Río Usumacinta basin have been interpreted as a reflection of an originally depauperate freshwater fish fauna in a region that was subsequently invaded by North American, South American, and marine species (Myers, 1966; Rosen, 1979). Remarkable examples of marine-derived fishes that co-occur with *Potamarius* and *Cathorops* in the Río Usumacinta basin include needlefishes (*Strongylura*), toadfishes (*Batrachoides*), and halfbeaks (*Hyporhamphus*) (Lovejoy and Collette, 2001). Lovejoy and Collette (2001) suggested that the coincidental origin and distribution of such taxa may either be indicative of shared biogeographic histories (i.e., an ancient vicariant event that isolated marine taxa in the region) or particular ecological conditions of the Usumacinta that may facilitate transitions from adjacent marine waters into the system (e.g., high ionic concentrations).

Additional instances of Neotropical freshwater ariids include the transisthmian pair *Notarius cookei*, from rivers in the Pacific Panama and potentially Colombia and Costa Rica (Acero and Betancur-R, 2002), and *N. bonillai*, from the Río Atrato and Río Magdalena basins draining into the Colombian Caribbean (Acero

and Betancur-R, 2006). Other marine-derived fishes, including *Daector quadrizonatus* (Batrachoididae) and *Strongylura fluviatilis* (Belontiidae), have parallel distributions in the Río Atrato (Caribbean) and some Pacific-slope drainages, suggesting an ancient connection between these systems (Lovejoy and Collette, 2001). While there are numerous marine-derived fishes that have extensively colonized the Amazon River, including stingrays, anchovies, needlefishes, drums, flatfishes, and pufferfishes (Lovejoy et al., 2006, 1998), surprisingly no extant freshwater ariids occur in the Amazon or other rivers in northeastern South America; however, this may not always have been the case. La Venta paleontological site (Middle Miocene) in the Magdalena valley in Colombia includes many fossil freshwater fish species presently endemic to the Amazon or the Orinoco basins (but absent from the Magdalena basin; Lundberg, 1997). Thus, fossil records of aff. *Sciades parkeri* from La Venta (Lundberg, 1997, 1998) suggest past ariid transitions into the proto-Amazon/Orinoco basins.

3.2.2. Madagascar

The freshwater ichthyofauna of Madagascar mainly includes marine families that frequently colonize rivers (i.e., peripheral species), such as gobiids, mugilids, and anguillids, as well as three representative groups of the secondary division (aplocheilids, cichlids, and poeciliids; Sparks and Stiassny, 2003). As reported in other faunal and floral groups, many Madagascar freshwater fish taxa are phylogenetically basal (but highly derived) as a result of the long period of isolation of the island from the continental mass (Sparks and Stiassny, 2003). Sparks and Stiassny (2003) pointed out that no primary fishes occur in Madagascar and suggested that the endemic Bedotiidae and Anchariidae are in the secondary division as well. Although from a historical biogeography perspective there are inherent limitations and contradictions of Myer's primary, secondary and peripheral divisions (see Rosen (1974) and Sparks and Smith (2005) for discussion), the concept is still of great value in descriptive zoogeographical and ecological contexts. Optimizations of the habitat transitions suggest that the Anchariidae retains the plesiomorphic otophysan freshwater condition, and

hence it should be included in the primary division. However, the position of the Arioidea (Anchariidae + Ariidae) among other catfish families remains unresolved (Sullivan et al., 2006), which hinders further inferences on the biogeography of Anchariidae as related to continental drift.

Ariids in Madagascar are represented by four species. One (*Plicofollis dussumieri*) is marine and widely distributed along the continental Indian Ocean. The remaining three (*Arius madagascariensis*, *A. uncintatus*, and *A. festinus*) inhabit rivers in eastern Madagascar (Ng and Sparks, 2003). Although the only Malagasy species examined in this study is *A. madagascariensis*, morphological evidence suggests that the three freshwater species may be related (Ng and Sparks, 2003) implying a single habitat transition.

3.2.3. Africa

The ariid diversity endemic to Africa is impoverished, including only three species in *Galeichthys* (southern Africa), two in *Arius* (eastern coast), and four in *Carlarius* (western coast). Of these, *Arius brunellii* (Juba River) and *Carlarius gigas* (Volta and Niger Rivers) are freshwater inhabitants (Marceniuk and Menezes, 2007), likely involving independent habitat transitions.

3.2.4. Southeast Asia

The freshwater biota of SE Asia hosts a high diversity of fish species (Lundberg et al., 2000). While most species in the region are cypriniforms and siluriforms in the primary division, there are several marine-derived groups as well, including clupeids, ariids, and tetraodontids (Kottelat, 2001; Roberts, 1989). Based on the affinities revealed by the freshwater fish assemblages in SE Asia, biogeographic studies show that the region comprises five to nineteen provinces (Kottelat, 1989; Yap, 2002; Zakaria-Ismail, 1994). According to Zakaria-Ismail (1994), five major subregions compose SE Asia: (1) the Salween basin in Burma, (2) the Indochina Peninsula (ICP; Mekong, Chao Phraya, and Mae Khlong drainages), (3) the Malay Peninsula (MPN), (4) the Indo-Malayan Archipelago (IMA; Borneo, Sumatra, and Java), and (5) the Philippines. Freshwater ariids are widely distributed in SE Asia, occupying all these provinces (Table 1 and Fig. 2). Interestingly, the distribution of *Cephalocassis borneensis* extends to different locations on the Sunda shelf (Kottelat, 2001; Kottelat and Widjanarti, 2005; Roberts, 1989), a broad subregion that encompasses the ICP, MPN, and IMA provinces. During the Pleistocene glacial maxima, the sea level reached 120 m below present and the Sunda Shelf was exposed, connecting major river systems of the islands and the mainland (Dodson et al., 1995; McConnell, 2004; Pelejero et al., 1999). Population genetic studies on the bagrid *Hemibagrus nemurus* (Dodson

et al., 1995) and the cyprinid *Barbodes gonionotus* (McConnell, 2004) from disjunct locations on the Sunda Shelf suggests their present distribution reflects faunal exchanges during the Pleistocene. The distribution of *H. nemurus*, *B. gonionotus*, and *C. borneensis* may imply a similar and shared biogeographic history. Alternatively, multiple marine transitions onto different landmasses on the Sunda Shelf might explain the disjunct distribution of *C. borneensis*. Considering the freshwater restriction of *C. borneensis*, a vicariant rather than a dispersalist scenario is favored; however, phylogeographic studies are required for accurate biogeographic inferences to be made. Similarly, the disjunct distribution of *C. melanochir* and *Hemiaris stormii* in Sumatra and Borneo (IMA province) merits further investigation.

3.2.5. Australia–New Guinea (=Sahul continent)

Relative to the diverse inland ichthyofauna of tropical regions such as South America, Africa and Asia, the freshwater fish biota in Australia and New Guinea is rather impoverished (Allen, 1991; Allen et al., 2002; Berra, 1998; but see Lundberg et al., 2000). The faunal composition in Australia and New Guinea also differs markedly from other regions as they lack otophysan families from the primary division. Except for the lungfish (Ceratodontidae) and bony tongues (Osteoglossidae), most freshwater fish representatives in the region are of marine origin, including the otophysan ariids and plotosids (Allen, 1991; Allen et al., 2002). Despite the present proximity of the Sunda Shelf and the Sahul, the striking differences in faunal composition of the latter province are a reflection of its long-term isolation after the separation from Antarctica 95–35 mya (Li and Powell, 2001). Sahul hosts the most diverse ariid freshwater fauna, accounting for nearly half of the purely freshwater ariids (Table 1), but also including many euryhaline species that inhabit both inshore coastal waters and lower and middle reaches of rivers (e.g., *Neoarius graeffei*, *Cochlefelis danielsi*, ‘*Sciades*’ *leptaspis*).

The Sahul Shelf proper lies beneath the Torres Strait and the Arafura Sea that separates Northern Australia (NA) and SNG. As with the Sunda Shelf, the Sahul Shelf was exposed during Pleistocene glaciations until 8000–6000 years ago and the inter-connection of major river drainages facilitated faunal exchange (Allen, 1991; Filewood, 1984; Lundberg et al., 2000; Voris, 2000). Although many brackish and marine ariid species are common to both the SNG and NA provinces, surprisingly only one strictly freshwater ariid (*Neoarius berneyi*) occurs in both New Guinea and Australia (Allen, 1991; Allen et al., 2002). The natural history of New Guinea has been both complex and catastrophic. The island includes two major biogeographic provinces separated by the cen-

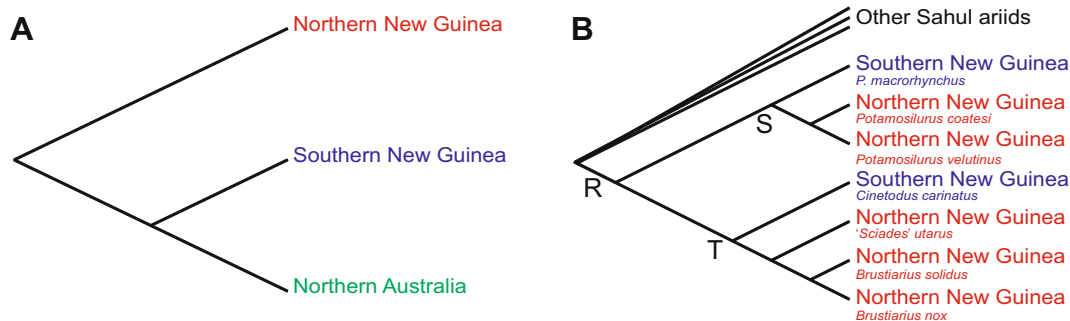


Fig. 3. Area relationships among Australia and New Guinea provinces based on freshwater fish affinities. (A) Allen and Coates' (1990) area cladogram reconstructed from the number of freshwater fish species shared among the two provinces (32 freshwater species common to Southern New Guinea and Northern Australia; three species common to Northern New Guinea and Southern New Guinea). (B) Relationships among Northern and Southern New Guinea freshwater ariids based on mitochondrial data. Nodal letters are as in Fig. 2. All nodes within clade R are well supported (see details in Fig. 1) and the habitat optimizations suggest that their evolutionary history occurred in freshwaters only. Although Northern Australia is missing from node R, another freshwater ariid, *Neoarius berneyi*, is common to both Northern Australia and Southern New Guinea provinces, supporting their sister-area relationship.

tral mountain range (Allen, 1991; van Ufford and Cloos, 2005; Whitley, 1938). The Northern New Guinea (NNG) province, formed ~10 mya as a result of collision between the Pacific and Australian plates, includes a rather impoverished freshwater ichthyofauna [~55 purely freshwater species (Allen, 1991; Allen and Coates, 1990)]. The Southern Province (=SNG), on the other hand, hosts a richer biota of freshwater fishes including over 160 species (Allen and Coates, 1990). The highland drainages of both provinces near the mountain range are largely depleted of fish faunas and no species occur above elevations of 1800 m, reflecting the catastrophic geological history of the region (e.g., volcanism and glaciations; Allen, 1987).

In a zoogeographical analysis of the freshwater ichthyofaunas in the Sahul, Allen and Coates (1990) found 34 species shared be-

tween the NA and SNG, thus reflecting their recent land connection. On the other hand, only three species were common to both northern and southern provinces in New Guinea. This pattern led Allen and Coates to infer the area cladogram shown in Fig. 3A (NNG, (SNG, NA)). As mentioned previously, the presence of the freshwater *N. berneyi* in the NA and SNG match the expected sister-area relationship between these two provinces. Additionally, the topologies place the five ariids from the NNG province into two sister clades (node R: node S + node T; Fig. 1), each of which also includes one species from the SNG province, rendering a duplicate NNG/SNG pattern (Fig. 3B). All nodes within clade R are congruent among different methods and well supported, suggesting robust reconstructions. Furthermore, optimizations of the habitat transition indicate the evolutionary history of node R took place

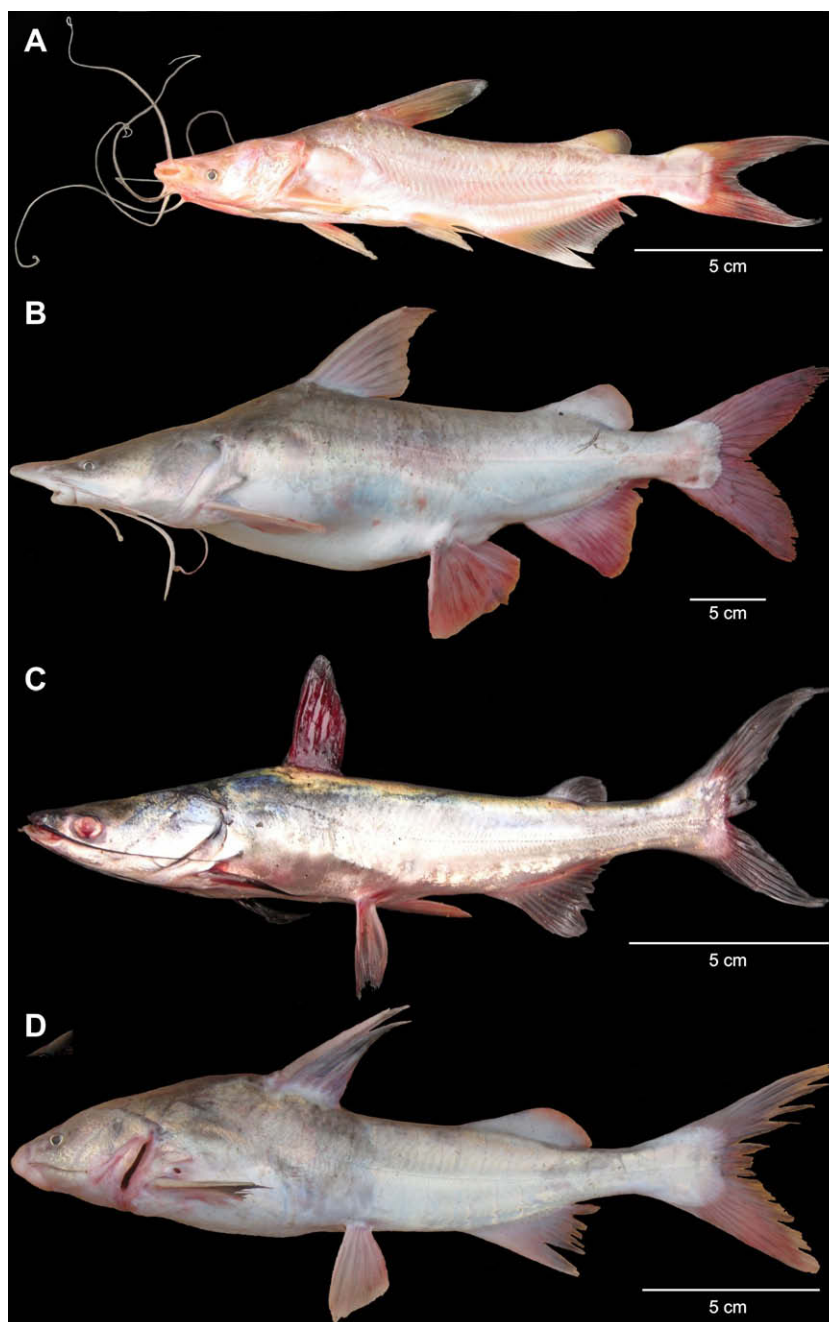


Fig. 4. Remarkable examples of morphological divergence among New Guinean freshwater ariids. (A) *Doiichthys novaeguineae*; (B) *Cochlefelis spatula*; (C) *Brustiarus nox*; (D) *Pachyuula crassilabris*.

entirely in freshwaters (Fig. 1), and thus marine dispersal is an unlikely scenario. The biogeographic pattern of node R differs from Allen and Coates' area cladogram in that the NA province is absent from both node S and node T. Nonetheless, the duplicate NNG/SNG pattern is compatible with the idea that New Guinean ichthyofauna from the north evolved from ancestral southern species due to cladogenesis induced by orogenesis of the central range (Allen, 1991; van Ufford and Cloos, 2005).

3.3. The Australia–New Guinea clade: an ancient rapid radiation associated with freshwater colonization?

Species penetrating into new habitats or geographical areas may diversify to occupy a wide range of niches via ecological speciation (Hendry et al., 2000; Schluter, 2001). Specialization for different niches may promote rapid radiations (Hendry et al., 2000) and enormous phenotypic diversification (Bell and Foster, 1994; Schluter, 1996). While some classical examples of rapid radiations associated with habitat specialization involve terrestrial animals (e.g., Darwin's Galapagos finches; Schluter, 1988), freshwater colonization by marine organisms provides a major case study including well-studied fish systems such as North American sticklebacks (Bell and Foster, 1994; Schluter, 1996) and New Zealand galaxiids (Waters and Wallis, 2001).

Australia–New Guinea is among the most diverse provinces for ariids in terms of both species richness and morphological diver-

gence. New Guinea, the world's second largest island ($7.86 \times 10^5 \text{ km}^2$), hosts the greatest diversity per area of ariids in the world, including over 38 species in 11 genera (including potential new taxa), of which 21 species and five genera are endemic. New Guinean ariids exhibit extraordinary levels of morphological divergence, which is most pronounced among freshwater taxa (e.g., *Doiichthys novaeguineae*, *Cochlefelis spatula*, *Brustiarius nox*, *Pachyula crassilabris*; Fig. 4). There also is a wide range of trophic specialization, including filter feeding (e.g., *Brustiarius nox*), fruit and plant feeding (e.g., *Potamosilurus taylori*, *P. macrorhynchus*), carnivory (e.g., *Cochlefelis* spp.), omnivory ('*Sciades*' *leptaspis*), and insectivory (e.g., *Pachyula crassilabris*) (Allen, 1991; Allen and Coates, 1990; Kailola, 1999).

Excluding the genera *Netuma* and *Plicofollis* (Indo-West Pacific clades 1 and 2, Fig. 1), which encompass wide Indo-West Pacific distributions, ariids from Australia and New Guinea form a well supported and mostly endemic clade [see comments on Fig. 1 caption and Betancur-R (2009) regarding the distribution of *Brustiarius proximus*, node O, Fig. 1]. Genetic differentiation among lineages is high, with intergeneric divergence values calculated from mitochondrial and nuclear (*rag 2*) protein-coding genes varying between 6.1%–13.8% and 0.33%–3.0%, respectively. Despite the large genetic distances, reconstructions on the mitochondrial dataset (2866 bp) provide little phylogenetic resolution among basal lineages, as evidenced by a large polytomy containing six major branches showing interleaved habitat patterns (Fig. 1, node O).

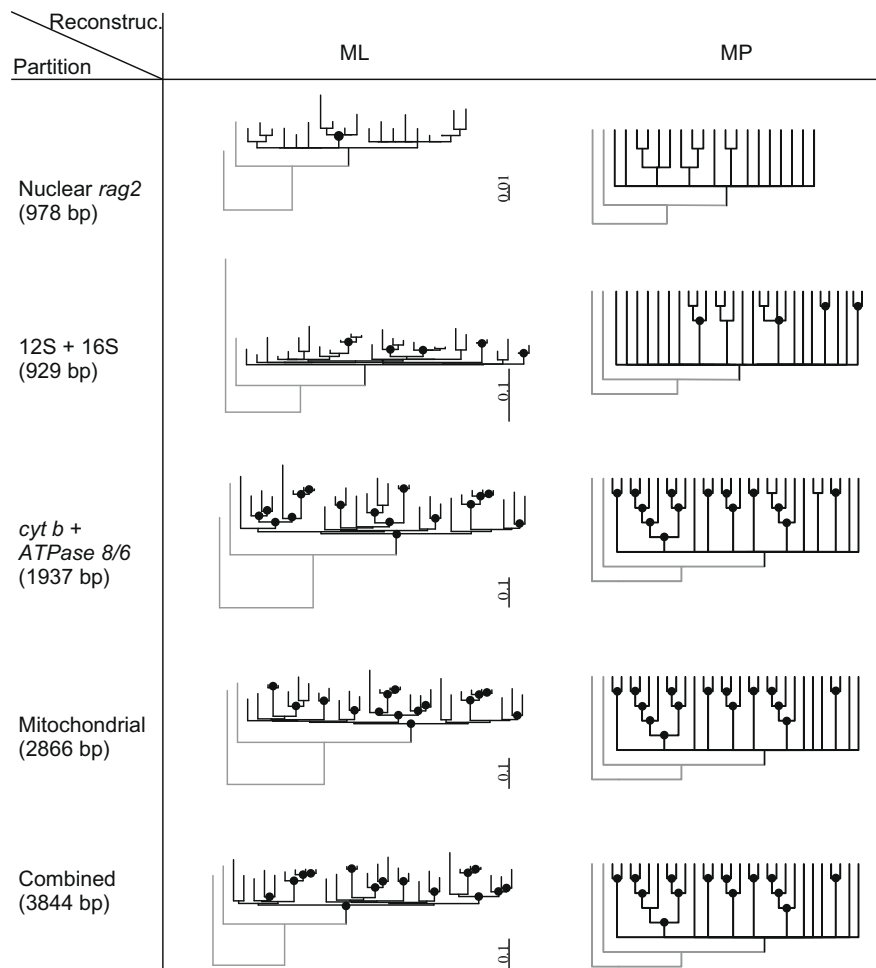


Fig. 5. MP and ML analyses using a reduced taxon sampling on different partitions, showing poor phylogenetic resolution among basal Australia–New Guinea ariid lineages (black branches; see also node O, Fig. 1). Nodal dots indicate ML and MP bootstrap values $\geq 75\%$ (MP clades with $< 50\%$ bootstrap support were collapsed). Gray branches are outgroups (*Galeichthys ater* [most basal] and *Cathorops dasycephalus*).

Further analyses conducted under MP and ML on different partitions (including nuclear *rag2*) using a reduced taxon sampling all resolved the relationships among basal Sahul lineages with short internodes and/or low support values (Fig. 5).

Clades lacking phylogenetic resolution in trees may result from inadequate sampling (soft polytomies) or may signal ancient radiations that cannot be resolved with increased sampling effort (hard or near-hard polytomies) (Fishbein et al., 2001; Whitfield and Lockhart, 2007). Deciphering whether unresolved clades are the result of inadequate character sampling or a reflection of the true evolutionary history of the group requires analytical examination of the dataset and the reconstruction methods. Whitfield and Lockhart (2007) outlined four situations where poorly supported or short internodes reflect problems inherent to the data or the method rather than rapid radiations: (1) inappropriate marker choice (e.g., low variability), (2) conflicting signal among data partitions, (3) use of incorrect reconstruction method or substitution model, (4) insufficient data. Here, the first and third factors are likely not the case considering the high genetic distances and the similar patterns obtained under different reconstruction criteria. Furthermore, at least three circumstances make the second scenario unlikely: (a) partition homogeneity tests performed among separate partitions (i.e., mitochondrial protein-coding genes, mitochondrial ribosomal genes, nuclear *rag2*) reveal no conflicting phylogenetic signal (p value = 0.85); (b) clades strongly supported at either shallower (e.g., nodes Q, R, W) or deeper levels (e.g., Ariinae, node I) in the ariid tree, suggest that the large polytomy is not the result of phylogenetic signal loss due to substitutional saturation; (c) plots of third codon position transitions vs. Kimura two-parameter distances for mitochondrial protein-coding genes (fastest evolving markers, Betancur-R et al., 2007) reveal no asymptotic accumulation of third codon transitions among Australia–New Guinea ariids (results not shown).

Unfortunately, ruling out the fourth factor is more difficult as it would involve obtaining additional DNA data (e.g., Rokas et al., 2003); however, the different markers utilized in this study contain differing levels of phylogenetic signal (Betancur-R et al., 2007) and combined vs. partitioned analyses show no improvement in resolution among basal Sahul lineages (although more terminal nodes do reveal better resolution and/or support in combined analyses; Fig. 5). Thus, the basal polytomy observed here likely reflects a true hard or near-hard polytomy resulting from an ancient rapid radiation. Divergence time estimations derived from molecular clock analyses indicate that the timing of the putative radiation is 59–19 my [see Betancur-R (2009) for discussion on variable molecular clock estimations].

As mentioned previously, nearly half of the freshwater ariid species occur in the rivers of Australia and New Guinea, which are otherwise impoverished of fish species and lack otophysan groups in the primary division (Allen, 1991; Allen et al., 2002; Berra, 1998). The high degree of morphological divergence and trophic specialization among freshwater ariid forms in this geographic region raises the possibility that, upon colonization of rivers, availability of new and variable habitats promoted an ancient radiation. While further research is required to test correspondence between the varying phenotypes and the divergent environments as well as functionality of traits (Schluter, 2000), Sahul ariids might provide a valuable opportunity for studying the underlying mechanisms driving diversification in relation to habitat transitions.

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