Life in the Fast Lane: A Review of Rheophily in Freshwater Fishes

Nathan K. Lujan and Kevin W. Conway

Abstract Ecological opportunities and physical challenges of fast-water habitats have dramatically shaped the evolution of freshwater fish lineages from a broad diversity of clades globally, often leading to the convergent or parallel evolution of highly similar morphologies. In this chapter, we present a patch dynamics model of how longitudinal shifts in geomorphological and ecological processes from small headwater torrents to large river rapids may differentially affect gene flow among, and evolutionary specialization within, resident rheophilic fish populations. Fast-water habitats offer ecological advantages including predator avoidance and increased foraging efficiency, but require that organisms resist downstream displacement and avoid shifting, crushing substrates. We review the specialized morphological and behavioral characteristics associated with life in fast waters and the taxonomic distribution of these specializations across fishes. We also report results of specific functional studies where available and summarize empirical evolutionary, phylogenetic support for our model and for specific mechanisms or pathways by which rheophilic specializations may arise.

1 Introduction

From cold torrential streams high in the Himalayas to large river rapids in the lower Congo and Amazon basins, mesohabitats defined by concentrated high water velocities and rocky substrates are common features of fluvial ecosystems throughout the world. Variously known as torrents, riffles, rapids, chutes, and shoals,

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N.K. Lujan (✉)
Department of Natural History, Royal Ontario Museum, Toronto, ON, Canada M5S 2C6

Center for Systematic Biology and Evolution, Academy of Natural Sciences of Drexel University, Philadelphia, PA 19103, USA
e-mail: nklujan@gmail.com

K.W. Conway
Biodiversity Research and Teaching Collections and Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA
e-mail: kevin.conway@tamu.edu

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freshwater habitats hosting specialized rheophilic fish assemblages typically have water velocities of at least 40–50 cm/s (Bournaud 1963), but span a wide range of spatial scales, gradients, and maximum water velocities. In high gradient headwaters and montane rivers, particularly those draining young high-elevation mountains like the Andes and Himalayas, torrent zones extend largely uninterrupted for thousands of vertical meters before prevailing channel slopes begin to level out. In medium-sized and mid-elevation rivers where meanders dissipate kinetic energy from the torrent zone, mesohabitats typically coincide with meanders to take on an ordered riffle-run-pool sequence (Keller and Melhorn 1978). In large lowland rivers, average current velocities often exceed those in headwaters (Leopold 1953), but rapids habitats are generally rare, irregularly distributed, and clustered around low-lying, erosion-resistant geological formations.

Organisms that attempt to maintain a fixed position in lotic habitats must avoid or counteract both shear forces (forces created by water flowing in parallel with the channel or substrate) and turbulence (chaotic water movement formed by disruptions to laminar flow). Where streams become constrained by shallow, irregular channel bottoms as in rapids and riffles, both shear forces and turbulence increase (Hoover and Ackerman 2004). A generalized cross section of water velocities over a rounded stone exhibits highest velocities and shear forces within ~5–15 mm of the stone surface along the leading edge and top, with zones of turbulence at the lower upstream and downstream sides of the stone. Despite maximal water velocities near the top of the stone, velocities very close (<5 mm) to the stone surface approach 0 due to frictional drag of the stone on the water in a region known as the boundary layer (Ambühl 1962; Hoover and Ackerman 2004). Larval stages of many insects specialized for life in fast water (e.g., mayflies, stoneflies, psephenid beetles) are small enough or dorsoventrally flattened enough to escape shear stress by living entirely within this boundary layer of very low flow. Many rheophilic fishes also benefit from highly dorsoventrally depressed bodies (see Sect. 4.2), although few if any are small enough to exist entirely within the boundary layer.

Although the thin surface layers of rocks or wood, and spaces within or beneath such objects, can offer refuge from shear forces and the threat of downstream displacement, close association with these substrates also poses a threat to stream organisms when shear stress dislodges the substrates themselves. Indeed, the ever-present threat of both downstream displacement and being injured by shifting substrates makes life in fast-water habitats extremely challenging. Here, we review the distribution of these habitats across the landscape, the gradients in ecological and evolutionary processes that covary with a habitat's longitudinal position, the morphological responses to these processes, and the phylogenetic and functional studies of fast-water fishes and their specializations for life in the extreme. Few species or morphological traits associated with rheophilic habitats have been empirically investigated from a functional, performance, or correlated eco-evolutionary perspective. We therefore consider traits as specialized based largely on theory.

2 Taxonomic Distribution of Rheophilic Fishes

Previous comprehensive overviews of rheophilic fishes have focused on fauna inhabiting particular river drainages (Roberts and Stewart 1976; Zuanon 1999; Casatti and Castro 2006) or a circumscribed geological region encompassing multiple drainages (Hora 1930). Regardless of the scale, such studies frequently attempt to divide rheophilic fishes across a number of general categories, ranging from poorly adapted to highly adapted for life in fast-flowing water, based largely on external morphological features. For example, Hora (1930) recognized four general categories of hill-stream fishes in his overview of the Himalayan torrent fauna, ranging from "ordinary" (Hora's category I) to "flattened… provided with well-developed means of attachment" (Hora's category IV). Along similar lines, Roberts and Stewart (1976) divided the fishes collected in their comprehensive survey of the lower Congo rapids into three categories (poorly, moderately, and highly adapted to rapid habitats) and further divided those taxa that they considered to be highly adapted based on whether they were exposed to strong current (their "rheophilic") or avoided such currents (their "hyporheic").

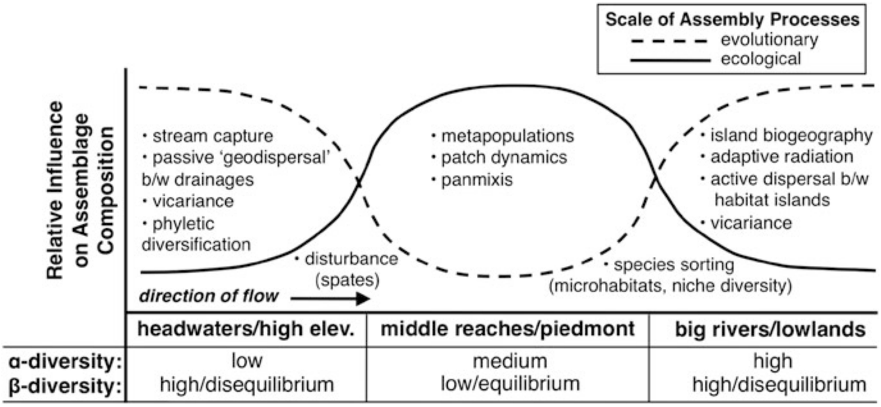
In Appendix Table 1, we have attempted to provide a more global overview of rheophilic fishes than has been attempted previously. Our decision to include a particular taxon is based either on personal observations (for those taxa and regions that we are familiar), on published information contained in larger taxonomic revisions (e.g., Tan 2006; Kottelat 1990), or on faunal overviews for individual river basins (Monsembula Iyaba et al. 2013; Roberts and Stewart 1976; Roberts 1978, 1989a; Kullander et al. 1999; Parenti and Lim 2005; Tan and Kottelat 2009), countries (Chen 1998; Kottelat 2001a, b, 2006; McDowall 1978; Shrestha and Edds 2012; Yue 2000) or larger geographic regions including multiple countries (Talwar and Jhingran 1991; Kottelat et al. 1993; Kottelat and Freyhof 2008; Page and Burr 2011; Skelton 1993). For the sake of simplicity, we focus only on those taxa that would be considered obligate rheophiles, either moderately or highly adapted for life in fast water (sensu Roberts and Stewart 1976). We have included lacustrine or diadromous taxa that may spend only part of their life cycle in fast-flowing water but have excluded marine and estuarine taxa that are reported occasionally from faster water habitats in the lower courses of rivers that exhibit no obvious specializations for life in fast water (e.g., *Dactyloscopus*; Miller and Briggs 1962). Our list, which is likely to be incomplete, contains 419 genera, distributed across 60 families and 16 orders. As one would expect, our list is dominated by teleosts, and otophysans in particular, with 207 genera of Cypriniformes (representing 11 families), 92 genera of Siluriformes (representing 15 families), and 52 genera of Characiformes (representing 11 families). With 37 genera (representing 10 families), the "Perciformes" (sensu Wiley and Johnson 2010) contains the majority of the remaining rheophilic teleosts, most of which belong to one of three families, the Gobiidae (12 genera), the Cichlidae (10 genera), or the Percidae (7 genera). Two genera of lampreys (Petromyzontiformes) represent the only non-teleost taxa that are obligate inhabitants of fast-flowing waters.

3 Ecological Processes

3.1 *Assemblage Composition Model*

River zonation typologies and ecological process models have expanded from static, modular depictions of hydrology and community composition (e.g., Hutchinson 1939; Illies 1961) to contemporary but dynamic linkages between a river's hydrogeomorphology, production sources, and faunal assembly. The recently proposed Riverine Ecosystem Synthesis (RES, Thorp et al. 2006), for example, provides a framework for integrating previous conceptual models (e.g., River Continuum Concept, Flood Pulse Concept, Riverine Productivity Model) into a comprehensive hierarchy of geomorphological processes and metacommunity patch dynamics. Although the original iteration of the RES was explicitly limited to recent ecological timescales (Thorp et al. 2006), a strength of the hierarchical patch dynamics approach is its limitless potential for spatial and temporal expansion. We propose a modified patch dynamics model narrowly focused on the geomorphology of fast-water habitats and community assembly of specialized resident (i.e., non-migratory) fast-water fish assemblages spanning both large, continental drainage basins (e.g., Amazon Basin, Mekong Basin) and timescales long enough to encompass macroevolutionary processes.

Our model (Fig. 1) contrasts high-gradient, high-elevation headwaters, which have low taxonomic and trophic diversity (Lujan et al. 2013) with large lowland rapids hosting species-rich assemblages that are functionally diverse and often narrowly endemic (Roberts and Stewart 1976; Roberts 1978; Zuanon 1999; Camargo et al. 2004). Despite the low α-diversity (i.e., local, site-specific species richness) of headwaters, these habitats often exhibit high β-diversity (i.e., species



	headwaters/high elev.	middle reaches/piedmont	big rivers/lowlands
α-diversity: **β-diversity:**	low high/disequilibrium	medium low/equilibrium	high high/disequilibrium

Fig. 1 A conceptual model describing longitudinal shifts in the evolutionary vs. ecological scale of processes controlling the taxonomic composition of rheophilic fish assemblages from headwaters to large river rapids. See text for further explanation and references supporting specific components of the model

richness summed across sites; Carrara et al. 2012) due to low active dispersal between habitat patches combined with a slow background rate of passive "geodispersal" (i.e., stream capture) and subsequent vicariant speciation (e.g., Waters et al. 2001; Ribeiro 2006). Moreover, headwater populations may be small and have low genetic diversity due to founder effects (Hänfling and Weetman 2006; Barson et al. 2009), increasing rates of genetic drift and vicariant speciation if isolated from larger downstream populations.

Comparative community and habitat diversity data are largely lacking for large, lowland river rapids, but we hypothesize that, as with oceanic islands (Diamond et al. 1976; Losos and Ricklefs 2009), the species richness and functional and habitat diversity of river rapids correlate with their size and their distance from other large rapids. An additional factor unique to rivers is hydraulic energy, which should multiply effects of distance by increasing both the cost of dispersal and the reward of philopatry. Even relatively small distances between rapids with high hydraulic energies may promote isolation, vicariance, and endemic diversification by increasing the universal risk of downstream export should individuals move far from a preferred microhabitat (Markert et al. 2010; Schwarzer et al. 2011). As with both terrestrial islands (Losos and Schluter 2000) and lakes (Wagner et al. 2014), instances and rates of localized diversification (i.e., adaptive radiation) should also scale with rapids size, and vicariant speciation rates among rapids should increase with greater geographic distance and/or hydraulic energy. Also, given spatial variation in localized rates and outcomes of evolutionary specialization and diversification in both headwater and lowland river rapids habitats (i.e., all specialists are not present in all habitats), and the uneven distribution and scale of barriers to dispersal between similar habitat patches, we predict that niche occupancy and assemblage structure across the landscape rarely equilibrate and these disequilibria contribute to greater β-diversity.

At intermediate elevations and reaches, fish populations are typically more genetically diverse (Hänfling and Weetman 2006; Barson et al. 2009) and fish assemblages are more species rich than in headwaters, but they still lack many taxa and functional components of lowland habitats (Lujan et al. 2013). Fast-water habitats at intermediate elevations consist primarily of riffles periodically interrupted by deeper, slower runs and pools. Relative riffle length and pool depth increase as channel slope decreases (Wohl et al. 1993), suggesting that there is a gradient between upstream zones where habitat patches remain close enough and geomorphologically variable enough over long timescales to facilitate the free exchange of genetic diversity (panmixis), and downstream zones where geographic distances between habitat patches may be great enough to impede such gene flow (Langerhans et al. 2003).

Regular dispersal of individuals among habitat patches in intermediate reaches maintains equilibria of species richness and assemblage composition across similar habitat patches (Stewart et al. 2002; Winemiller et al. 2010). These equilibria may be dynamic if differential reproduction and survival across patches create sources and sinks within a metapopulation, evidence of which has been observed in the genetic structure of European sculpin (*Cottus gobio*; Hänfling and Weetman 2006) and in the community structure of a Taiwanese river following disturbance (Chen et al. 2004). At the upstream interface between torrent and riffle zones, where stream hydrologies remain flashy and species richness begins to increase but patch sizes remain small, the heterogeneous and stochastic distribution of disturbance (largely due to spates) should be an important driver of source–sink patch dynamics. At the downstream interface between the riffle and large river rapids zones, where species and habitat diversity begin to approach maxima but where habitat patches remain regularly distributed, species should sort themselves according to microhabitats in a predictable fashion (e.g., Arrington et al. 2005; Fig. 1).

3.2 Drivers of Specialization

Although our model predicts that over long time periods the composition of specialized fish assemblages in upland headwaters and large, lowland river rapids will be under strong evolutionary control (vicariant speciation in both, adaptive radiation in the latter), local species interactions need to be understood to infer the drivers of evolutionary specialization. Studies of fish behavior in torrential headwaters and large river rapids are scarce, but several studies have examined the effects of water velocity on species interactions in the mesohabitats (i.e., riffle, run, or pool reaches) of the North American piedmont streams. For example, Schlosser (1987) observed that in an ecologically diverse, North American assemblage of 15 species of stream fishes, juveniles and small-bodied adults occurred at higher densities in riffles and raceways than in pools, whereas large-bodied adults preferred pools. A choice experiment demonstrated that preference for shallow, fast-water habitat by small individuals was much greater when large fish were present versus absent, suggesting that an important motivation for fish to occupy fast-water habitat is predator avoidance (Schlosser 1987).

Increases in water velocity also reduce predation on macroinvertebrates by other macroinvertebrates (Meissner et al. 2009; Worischka et al. 2012) and contribute to increased rates of primary production, even when effects of habitat depth on light level are removed (Kevern and Ball 1965; Horner et al. 1990). Therefore, both algae and macroinvertebrates tend to be more abundant in mesohabitats that are fast and shallow versus slow and deep (Kevern and Ball 1965; Brown and Brussock 1991; Buffagni and Comin 2000). Together, these trends suggest that specialization on fast-water habitats may also contribute to increased foraging efficiency and reduced competition among herbivores and invertivores. In an elevational survey of an Andean affluent of the Amazon, Lujan et al. (2013) observed that the first native fish species to occur at high elevations were invertivorous, rheophilic catfishes (Astroblepidae, Trichomycteridae). Comparison of macroinvertebrate density in habitats with fish versus without fish showed that these catfishes contributed to a >50 % reduction in macroinvertebrate abundance. The second fish trophic guild to appear along the elevational gradient was herbivores. Considering the physiological challenges that likely limit elevational progression of aquatic organisms (e.g., oxygen limitation; Verberk et al. 2011), the occurrence first of invertivores and then of herbivores suggests that these are the most ecologically and physiologically advantageous trophic niches offered by such extreme habitats. In addition to refuge from predation and increased foraging efficiency, relatively higher dissolved oxygen concentrations and clean substrates also are benefits afforded to fast-water specialists, although the relative importance of these factors is likely much greater in modern, anthropogenically impacted (e.g., sedimented, eutrophied, hydrologically altered) streams than in naturally functioning ecosystems (Agostinho et al. 1994; Orrego et al. 2009). In summary, there is considerable evidence to suggest that fast-water habitats offer a range of ecological opportunities to fish lineages having either preexisting specializations or the evolutionary or behavioral ability to overcome the physical challenges of occupying these zones.

4 Specializations for Rheophily

4.1 Body Shape

Extreme hydrologic forces largely limit the food resources and refuge available in fast-water habitats to species with specializations for resisting downstream displacement while feeding, thus driving the convergent evolution of body shape and mouth orientation (Figs. 2, 3, and 4, Appendix Table 1; Langerhans 2008). Microevolutionary (intraspecific) shifts toward a fusiform body, a higher aspect ratio caudal fin, and respectively upturned or downturned mouths have been associated with occupation of fast-flowing habitats by mid-water and near-bottom dwelling fishes (Langerhans et al. 2003; Langerhans 2008). Macroevolutionary shifts in the body morphology of pelagic rheophiles are harder to generalize, except to say that forked caudal fins and fusiform bodies are common (e.g., *Gila elegans*), but exceptions include compressed and high-bodied rheophilic members of the Cichlidae (e.g., *Retroculus*), Characidae (e.g., *Hemibrycon*), Serrasalmidae (e.g., *Ossubtus*), and Cyprinidae (e.g., *Labeo* or *Schismatorhynchos*).

Among pelagic, rheophilic lineages, repeated trends in mouth orientation are more apparent than trends in body shape. The invertivorous–herbivorous South American characiform family Anostomidae is the most morphologically disparate of these, spanning rheophilic genera with both dorsally directed (e.g., *Sartor*, *Synaptolaemus*) and ventrally directed mouths (e.g., *Hypomasticus*; Sidlauskas and Vari 2008). Most members of the herbivorous, rheophilic family Parodontidae have a ventrally directed mouth (Fig. 2h), and a single herbivorous, rheophilic species in the family Serrasalmidae (*Ossubtus xinguense*) is noteworthy for both its extremely downturned mouth (Fig. 2i) and its narrow endemism to rapids of the lower Xingu (Amazon Basin; Jégu 1992). Other fishes with distinctively downturned mouths include convergent pairs of taxa from South America and Africa: one with curved, tube snouts and the shared ability to generate and sense

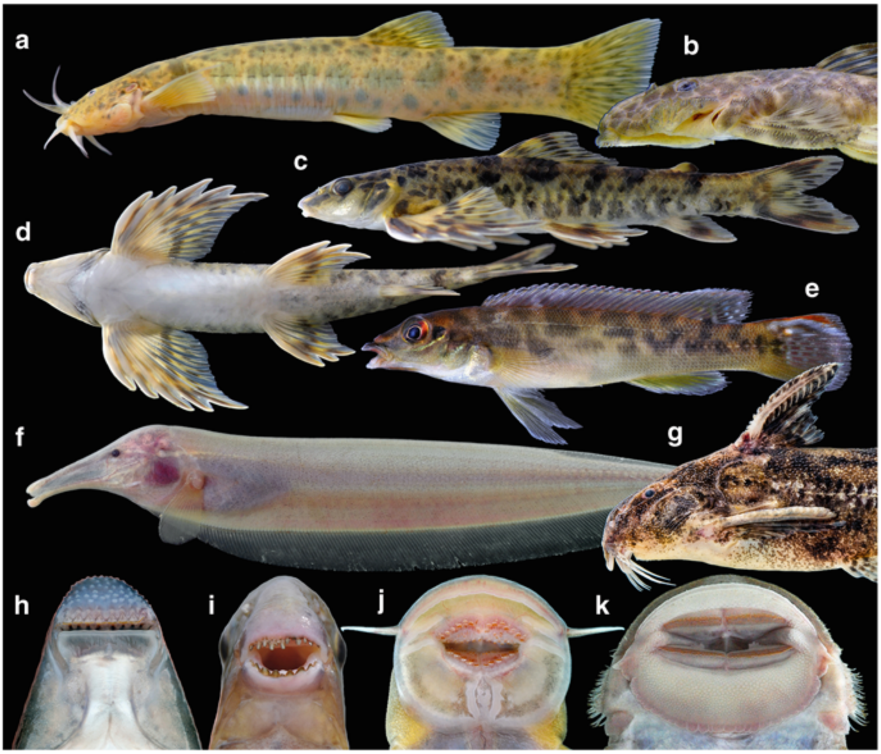


Fig. 2 Examples of specialized rheophilic fishes from neotropical rivers: (**a**) *Trichomycterus guianensis* (Trichomycteridae; Kuribrong River, Guyana), (**b**) *Lithoxus jantjae* (Loricariidae; Ventuari River, Venezuela), (**c**) lateral and (**d**) ventral views of *Characidium declivirostre* (Crenuchidae; Orinoco River, Venezuela), (**e**) *Teleocichla* n.sp. "preta" (Cichlidae; Xingu River, Brazil), (**f**) *Sternarchorhynchus hagedornae* (Apteronotidae; Inambari River, Peru), (**g**) *Rhynchodoras xingui* (Doradidae; Xingu River, Brazil), (**h**) *Parodon buckleyi* (Parodontidae; Inambari River, Peru), (**i**) *Ossubtus xinguense* (Serrasalmidae; Xingu River, Brazil), (**j**) *Astroblepus* sp. (Astroblepidae; Araza River, Peru), (**k**) *Cordylancistrus platycephalus* (Loricariidae; Santiago River, Ecuador). Photo (**g**) by L. M. Sousa, all others by NKL

electrical fields (*Sternarchorhyncus*, Fig. 2f, and *Campylomormyrus curvirostris*, Fig. 3f), and another with short, ventrally directed mouths (*Rhynchodoras*, Fig. 2g, and *Campylomormyrus alces*, Fig. 3g) to presumably extract invertebrate prey from interstitial spaces in substrates (Marrero and Winemiller 1993). A wide range of pelagic rheophilic and mostly herbivorous genera in the order Cypriniformes also contain species with ventrally oriented mouths. Examples include the North American genus *Campostoma*, the European *Chondrostoma*, and the Asian *Scaphiodonichthys*.

A striking exception to these predominantly herbivorous and invertivorous examples is the evolutionary convergence on a pelagic, large-eyed, upturned-mouth morphology by rheophilic, piscivorous members of the neotropical characiform family Cynodontidae, the Eurasian catfish family Siluridae, and the

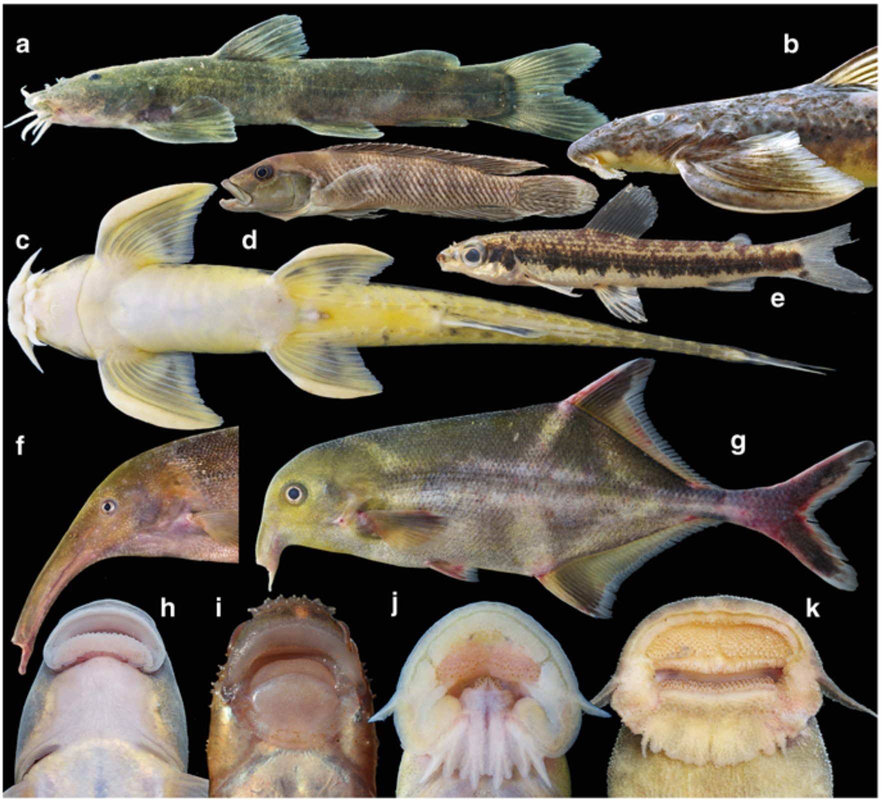


Fig. 3 Examples of specialized rheophilic fishes from tropical African rivers: (**a**) *Amphilius zairensis* [Amphiliidae; Congo River, Democratic Republic of the Congo (DRC)], (**b**) *Doumea gracila* (Amphiliidae; Lobe River, Cameroon), (**c**) *Phractura fasciata* (Amphiliidae; Congo River, DRC), (**d**) *Lamprologus mocquardi* (Cichlidae; Congo River, DRC), (**e**) *Nannocharax gracilis* (Distichodontidae; Congo River, DRC), (**f**) *Campylomormyrus curvirostris* (Mormyridae; Congo River, DRC), (**g**) *Campylomormyrus alces* (Mormyridae; Congo River, DRC), (**h**) *Labeo* sp. (Cyprinidae; Congo River, DRC), (**i**) *Garra* sp. (Cyprinidae; Congo River, DRC), (**j**) *Chiloglanis congicus* (Mochokidae; Congo River, DRC), (**k**) *Euchilichthys* cf. *royauxi* (Mochokidae; Congo River, DRC). Photos by J. P. Sullivan

paleotropical Cyprinidae. Three cynodontid genera (*Cynodon*, *Hydrolycus*, and *Raphiodon*), one silurid genus (*Belodontichthys*), and two cyprinid genera (*Macrochirichthys* and *Securicula*) all share a preference for large river fast-water habitats, a slender elongate body, large eyes, an enormous upturned gape with many sharp teeth (excluding the toothless cyprinids), and large wing-like pectoral fins to facilitate quick dashes to the surface to capture prey.

Many rheophilic fishes resist dislodgement by moving out of the water column and on or into bottom substrates, driving the selection for strongly dorsoventrally depressed (flattened) or anguiliform (eel-like) body shapes. The advantage to a fish of being small-bodied, benthic, and dorsoventally flattened is derived in part from

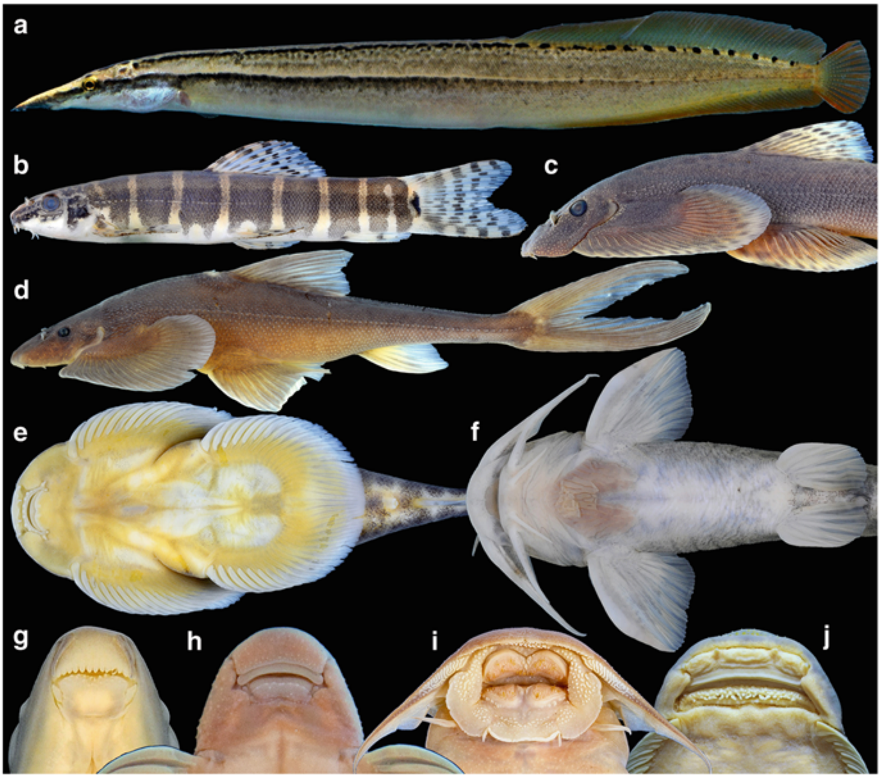


Fig. 4 Examples of specialized rheophilic fishes from tropical Asian rivers: (**a**) *Macrognathus pavo* (Mastacembelidae; Kyeintali Chaung River, Myanmar), (**b**) *Serpenticobitis zonatus* (Serpenticobitidae; Mekong Drainage, Laos), (**c**) *Sinogastromyzon puliensis* (Balitoridae; Wuxi stream, Taiwan), (**d**) *Jinshaia abbreviata* (Balitoridae; Yangtze River, China), (**e**) *Metahomaloptera omeiensis* (Balitoridae; Yangtze River, China), (**f**) *Glyptothorax platypogon* (Sisoridae; Ci'harang River, Indonesia), (**g**) *Crossocheilus elegans* (Cyprinidae, Kinabatangan River basin, Malaysia), (**h**) *Psilorhynchus pseudecheneis* (Psilorhynchidae; Indrawati River, Nepal), (**i**) *Exostoma* sp. (Sisoridae; Chao Phraya River, Thailand), (**j**) *Gastromyzon introrsus* (Balitoridae; Padas and Labuk rivers, Malaysia). Photo (**a**) by R. Britz, (**i**) by H. H. Ng, (**h**) by KWC, all others by H. H. Tan

its maximized occupancy of the thin boundary layer where water velocities approach zero. Dorsoventral depression also maximizes contact with, and therefore frictional adhesion to, solid substrates on which fish can gain access to algal and invertebrate food resources while minimizing energy expenditure. A hydrodynamic dorsal profile along with specialized skin surface features (e.g., unculi, keeled scales, see *Attachment organs* and *Scales* below) may further enhance adhesion by maximizing down pressure created by current flowing parallel with the substrate while minimizing lift by disrupting laminar surface flow across the skin surface. Striking examples of extremely dorsoventrally depressed rheophilic fishes include members of the Neotropical Loricariidae (e.g., *Lithoxus*, Fig. 2b) and the Asian cypriniform family Balitoridae (e.g., *Sinogastromyzon*, Fig. 3c).

Most benthic species are too large and high-bodied to live entirely within the boundary layer. They are therefore exposed, at least along their dorsum, to some of the fastest flows in a stream. Among benthic, rheophilic fish lineages, hydrodynamic forces have consistently driven selection for a fusiform body with a steep, wedge-shaped head, slender caudal peduncle, and large wing-like paired fins that extend laterally and are steeply canted to deflect flow dorsally (Figs. 2b–d, 3b, c, and 4c–e). This body shape and fin arrangement presents a dorsally rounded and ventrally flat shape that maximizes substrate contact and hydrodynamic down forces while minimizing drag. Moreover, the hydrodynamic effects of this morphology may be behaviorally exaggerated by some species as water velocities increase (Carlson and Lauder 2010).

An alternative approach taken by some non algae-scraping benthic rheophilic species is to largely escape the flow by living and foraging mostly within interstitial spaces between or under rocks and retaining or exaggerating an anguiliform body shape. Elongate, anguiliform body types can be observed among rheophilic members of the neotropical catfish families Heptapteridae (e.g., *Myoglanis aspredinoides*) and Trichomycteridae (e.g., *Trichomycterus*, Fig. 2a), the African catfish family Clariidae (e.g., *Gymnallabes*), the Eurasian loach families Cobitidae (e.g., *Pangio*), Nemacheilidae (e.g., *Aborichthys*), and Gastromyzontidae (e.g., *Glaniopsis*), and the spiny eel family Mastacembellidae (e.g., *Macrognathus*, Fig. 4a).

4.2 Attachment Organs

Many benthic rheophiles have specialized "attachment organs" to prevent displacement by adhering directly to substrates. In neotropical rivers, members of the invertivorous catfish family Astroblepidae and invertivorous/herbivorous family Loricariidae, which are sister groups (Sullivan et al. 2006), have the upper and lower lips fused into a ventrally oriented oral disc, which surrounds jaws specialized for scraping substrates (Fig. 2j, k). Analogous oral discs are seen among rheophilic invertivorous–herbivorous members of the African catfish subfamily Chiloglanidinae (Mochokidae, Fig. 3j, k; Roberts and Stewart 1976; Roberts 1989b; Geerinckx and De Kegel 2014) and certain genera of the Asian catfish subfamily Glyptosterninae (Fig. 4i; Thomson and Page 2006). Oral adhesive discs of a different sort are found in herbivorous members of the African and Asian tribe Labeonini of the Cyprinidae (e.g., *Garra*, *Discogobio* and *Placocheilus*, Fig. 3h, i). In these examples, the lower lip is greatly expanded posteriorly to form a large mental pad that is continuous around the edge of the mouth via a well-developed frenum (Fig. 3h, i; Saxena and Chandy 1966; Stiassny and Getahun 2007). The extremities of the mental pad and rostal cap form the outer margin of the oral adhesive disc, the intricacies of which are highly variable both within and between the different labeonin genera in which they are found, making the oral disc important for labeonin classification (Zhang 2005; Stiassny and Getahun 2007) and species identification (e.g., Zhou et al. 2005; Zhang and Zhou 2012). The well-developed oral discs of lampreys also are used to attach directly to the substrate in fast-flowing water, especially during resting periods between bouts of active swimming (Reinhardt et al. 2008).

The lips of a number of rheophilic fishes can also be manipulated to form temporary oral adhesive organs. In members of the South East Asian cypriniform family Gyrinocheilidae, the greatly enlarged and fleshy lips are supported internally by highly flexible chondroid bodies, which enable the lips to evert and form an oral sucker (Benjamin 1986). The waterfall-climbing amphidromous gobies of the genus *Sicyopterus*, which inhabit fast-flowing streams along continental margins and on remote oceanic islands as juveniles and adults, possess a greatly enlarged, fleshy upper lip, which when pushed down onto the substrate also forms a type of oral sucker (Schoenfuss and Blob 2003; Maie et al. 2012; Cullen et al. 2013; see Sect. 4.3 below). Recent functional morphological studies focused on the oral disc of the Neotropical loricarioid genera *Astroblepus* (Geerinckx et al. 2011) and *Pterygoplichthys* (Crop et al. 2013) and the oral sucker of the goby *Sicyopterus* (Cullen et al. 2013) have demonstrated the adhesive capability of these oral structures and, at least among the catfishes, the capacity to feed and respire while also adhering to substrates (Geerinckx et al. 2011; Crop et al. 2013). Scanning electron microscopy studies of the surface of loricariid and cypriniform oral discs have revealed a bewildering diversity of unicellular, keratinized projections or unculi (sensu Roberts 1982) that vary from short rounded knobs in some species to long, digitate or hooked projections in others (Roberts 1982; Benjamin 1986; Pinky et al. 2004; Geerinckx et al. 2011). Roberts (1982) and Pinky et al. (2004) have hypothesized that unculi likely function to both protect the epidermis from abrasion and to increase friction against substrates, thereby enhancing the ability of oral discs to both adhere to substrates and rasp them of epilithic algae.

The South American catfish families Loricariidae and Trichomycteridae both have specialized opercular apparati that allow for clusters of elongate, external teeth (odontodes) to be forcefully everted or shifted from a position flush with the body, to jutting outward from the side of the head (de Pinna 1998; Geerinckx and Adriaens 2006). This mechanism has been coopted for different purposes among the Loricariidae and derived subfamilies of the Trichomycteridae (e.g., territorial defense, parasitic station holding; de Pinna 1998), but basal lineages comprising the subfamily Trichomycterinae (Fig. 2a) are hypothesized to use this mechanism primarily as an attachment organ to assist with benthic station holding and locomotion in fast-water habitats (de Pinna 1998; see Sect. 4.3).

Post-cranial attachment organs also are diverse in benthic rheophilic fishes and include adhesive discs formed through various configurations or modification of the paired fins and a wide variety of unculiferous pads in ostariophysans. The pelvic fins, when well developed, are usually united to form a ventral adhesive disc in members of the Gobiidae, which have been shown to exhibit strong adhesion in the amphidromous sicydiine gobies that have been investigated to date (Blob et al. 2006; Maie et al. 2012). In several genera of the Gastromyzontidae (e.g., *Gastromyzon*, *Hypergastromyzon*, *Neogastromyzon*, and *Sinogastromyzon*), the pelvic fins are united across the midline to form a single cuplike structure (Fig. 4e), which in combination with greatly enlarged pectoral fins is considered to function as a suction disc (Wickler 1971; Tan 2006; De Meyer and Geerinckx 2014), presumably generating negative pressure between the body and substrate by evacuating interstitial water via respiration and preventing the inflow of water via broad and closely adpressed paired fins. A more sophisticated ventral suction disc, formed by elements of the pectoral- and pelvic-fin girdles is found in members of the predominantly marine family Gobiesocidae, which also includes a small number of freshwater members in the genus *Gobiesox* that inhabit short coastal rivers and streams throughout Central America and northern South America (Briggs 1955; Briggs and Miller 1960). Though the adhesive capabilities of freshwater clingfishes have yet to be investigated, a recent investigation of the adhesive capabilities of a large intertidal species of *Gobiesox* revealed an astonishing ability to adhere to irregular surfaces (Wainwright et al. 2013).

Putative friction devices, formed by aggregations of acute, posteriorly directed unculi, are present on the anteroventral surface of the body in several unrelated groups of benthic rheophilic ostariophysans (Roberts 1982). To date, these structures have been investigated only from gross morphological perspectives, with much remaining to be learned about their specific function in different groups. Perhaps the simplest of these putative friction devices are paired-fin pads, located along the ventral surface of the anterior-most paired-fin rays in many benthic rheophilic ostariophysans (Conway et al. 2012a). The narrow paired-fin pads of non-siluriform ostariophysans are externally homogeneous (despite being homoplasious) and are formed by a thickening of the epidermis and/or subdermis combined with an unculiferous superficial layer (Conway et al. 2012a). The largest unculiferous paired-fin pads can be observed among members of the highly rheophilic catfish subfamilies Amphiliinae and Doumeinae in Africa (Amphiliidae, Fig. 3c) and the Glyptosterninae in Asia (Sisoridae, Fig. 4f), associated with the ventral surface of a highly modified pectoral-fin spine (Hora 1922, 1930).

A more extensive friction pad, referred to as the thoracic adhesive organ, is located between the pectoral fins in members of certain sisorid genera (Fig. 4f; e.g., *Glyptothorax*, *Pseudecheneis, Pseudolaguvia, Conta*, and *Caelatoglanis*; Bhatia 1950; Saxena 1961; Sinha et al. 1990; Singh and Agarwal 1993; Das and Nag 2005; Ng and Kottelat 2005; Ng 2006) and formed by a series of longitudinal or oblique folds of skin. The unculi distributed across the surface of the thoracic adhesive organ are typically arranged in regular rows and often exhibit a hooked tip (Das and Nag 2005, 2009; Ng 2006). In several highly benthic rheophilic sisorid taxa (e.g., *Exostoma*, *Myersglanis*, *Oreoglanis*, and *Parachiloglanis*), a thoracic adhesive organ is absent (Ng 2006), yet similar folds of unculiferous skin are present instead along the leading edge of the snout, ventral surface of the highly flattened barbels and the surface of the paired-fin pads (Ng 2006; Conway et al. 2012a; see Sect. 5). Instead of unculi, the entire bodies of loricariid catfishes and the pelvic-fin spines of astroblepid catfishes are covered with small, posteriorly oriented odontodes, which likely serve similar functions to unculi, i.e., abrasion resistance and substrate friction (Alexander 1965; Blake 2006), although a single cave-dwelling astroblepid species is known to have coopted odontodes for a mechanosensory function (see Sect. 4.4, Haspel et al. 2012).

4.3 Locomotion

Fishes adapted for life in high-flow environments tend to share a number of specialized physiological and biomechanical traits related to swimming, including relatively more red muscle, stiffer bodies, higher steady swimming performance, and lower unsteady swimming performance (Langerhans 2008). Several rheophilic species specialized for life in particularly high flow environments have even evolved distinctive modes of locomotion that exploit the traction provided by adhesive organs. The most extreme of these is the “ratcheting” mode that has been observed in the goby *Sicyopterus* and in astroblepid catfishes. *Sicyopterus* are capable of climbing vertical surfaces that are wetted but out of the water column by attachment with the oral and pelvic-fin discs, and by use of repeated extension and retraction of the upper lip to inch forward (Blob et al. 2006; Maie et al. 2012; Cullen et al. 2013). Astroblepid catfishes, on the other hand, have a highly mobile pelvic girdle with long, strap-like *protractor* and *retractor ischii* muscles that can slide the girdle anteroposteriorly along the trunk. In this way, they can maintain station with their oral disc (Fig. 2j), engage irregularities in the substrate with posteriorly directed odontodes on the ventral surface of their pelvic-fin spines, and propel themselves forward via posterior retraction of the pelvic girdle (Crop et al. 2013). Using this method, astroblepid catfish have also been observed climbing vertical wetted surfaces outside the water column (Johnson 1912). In contrast to longitudinal “ratcheting,” species in the Neotropical subfamily Trichomycterinae (Trichomycteridae, Fig. 2a) can use external teeth (odontodes) on either side of their head to gain lateral traction and “elbow” their way upstream against fast current (de Pinna 1998).

A third mode of locomotion via surface attachment is the “power burst” used by goby species that lack an oral disc (e.g., *Lentipes*, *Sicydium*) and by some *Characidium* species (Crenuchidae, Fig. 2c, d; Buckup et al. 2000). This involves strong undulations of the body combined with surface detachment and attachment to move forward (Blob et al. 2006; Maie et al. 2012). A fourth form of rheophilic locomotion that also involves substrate interaction is anguiliform movement, in which forward movement is made through serpentine undulations of the body against substrates and/or the water. Anguiliform movement is typically paired with an anguiliform body shape (Fig. 4a) and the regular occupation of interstitial spaces under or between substrates.

4.4 Sensation

Rheophiles, like other fishes, have at their disposal four different sensory modalities (vision, mechanosensation, chemosensation, and electrosensation) to navigate and detect predators, competitors, mates, and prey. Although many rheophiles have large eyes and likely good visual acuity, the importance of vision can be highly variable depending on a species' activity cycle (diurnal or nocturnal), their preferred water depth, prevailing water clarity (Muntz 1982), mode of foraging, and the degree to which their nonvisual sensory systems are developed. Loss or reduction of eyes was reported for eight rheophilic species endemic to the rapids of the lower Congo River by Roberts and Stewart (1976), all of which are species that live in or under the substrate, including catfishes and spiny eels with well-developed chemosensory systems. Several cave-dwelling rheophilic species from around the world are also blind (e.g., *Astroblepus riberae*, *Cryptotora thamicola*; Cardona and Guerao 1994; Kottelat 1988, 1998).

Given the importance of flow detection for avoidance and navigation by rheophilic fishes, one might predict that the water velocity of a fish's preferred habitat would correlate with development of the mechanosensory system; however, the only study we are aware of that examined this found no relationship between habitat flow characteristics and the number or distribution of neuromasts across 12 species of European stream fishes (Beckman et al. 2010). Indeed, both the species with the greatest and the least concentrations of neuromasts were considered rheophilic (Beckman et al. 2010). In an apparently exceptional case of coopting dermal teeth (odontodes) for mechanosensation, Haspel et al. (2012) demonstrated that the blind and cave-dwelling naked suckermouth catfish *Astroblepus pholeter* has unusually few neuromasts but is able to obtain flow and substrate information via deflection of modified odontodes distributed around the body (see chapter "Cave Environments").

Otophysan fishes, including all minnows, catfishes, tetras, and South American knifefishes, are abundant and diverse in many freshwater habitats, including rapids (Appendix Table 1). Otophysans are considered hearing specialists because they have an inner ear–swimbladder (i.e., otophysic) connection composed of modified peri- and endolymphatic spaces and the Weberian ossicles (the Weberian apparatus). These modifications are known to improve sensitivity to high frequency sound (Ladich 2000), but some rheophilic otophysans exhibit changes to the Weberian apparatus that contribute to reduced hearing sensitivity. The actinopterygian swimbladder is typically a single, medial, elongate organ that occupies much of the dorsal visceral cavity (Longo et al. 2013). In some benthic rheophilic otophysans (e.g., some catfishes: Amphiliidae, Callichthyidae, Loricariidae, Sisoridae; and loaches: Nemacheilidae, Balitoridae, and Gastromyzontidae), the swimbladder is anteroposteriorly shortened, anteriorly shifted to a position immediately posterior to the cranium, and subdivided into two bilaterally symmetrical lobes.

Moreover, these groups also show varying degrees of skeletal encapsulation of the bladder (see Sect. 4.8). This encapsulation and reduction in swimbladder size is correlated with a reduction in the Weberian ossicles of some groups (e.g., Callichthyidae, Loricariidae), and a reduction in hearing sensitivity (Lechner and Ladich 2008). It has been suggested that in benthic fishes with little or no need for buoyancy, the hydrostatic function of the swimbladder is minimized and the organ is shrunk but not entirely lost because of its remaining acoustic utility (Lechner and Ladich 2008). Many non-otophysan rheophilic fishes have only a vestigial swimbladder (e.g., Cichlidae: *Steatocranus tinanti*; Schulz-Mirbach et al. 2012) or have lost the swimbladder entirely (e.g., Percidae: *Etheostoma* spp.; Evans and Page 2003). Although encapsulation of the swimbladder and modification of the external capsule structure have been hypothesized to have an acoustic function in some otophysans (Weitzman 2003), it seems more likely, given the known decreases in hearing sensitivity associated with swimbladder size reduction (Lechner and Ladich 2008; Schulz-Mirbach et al. 2012), that the capsule functions primarily to structurally reinforce a presumably structurally weak region of the body. A second hypothesis focused on the bilateral bifurcation of the bladders and the sometimes megaphone-like shape of the bladder capsules (e.g., Loricariidae: *Otocinclus*; Weitzman 2003) is that these modifications function to increase a fish's directional sensitivity to sound, although this hypothesis requires further testing (Stewart and Smith 2009).

One uninvestigated yet potential mechanosensory specialization that is seen in many neotropical catfish species from fast and turbid whitewater rivers is the extreme elongation of caudal-fin filaments. Species in several families (e.g., Cetopsidae, Heptapteridae, Loricariidae, and Pimelodidae) produce long caudal filaments either throughout their life or only as juveniles. It has been hypothesized that these caudal filaments may function as a specialized mechanosensory system for the detection of predators approaching from downstream (Lujan and Chamon 2008; K. Winemiller, pers. comm.). This is supported in part by research on marine (e.g., sea robins, *Prionotus* spp.) and lentic freshwater fishes (e.g., gouramis, *Trichogaster trichogaster*) in which distal portions of elongated fin rays have numerous free nerve endings and elicit a tactile response when touched (Kasumyan 2011). This example of elongation contrasts with the apparent trend toward reduction of barbels, another typically elongate sensory structure that is shortened in several clades of rheophilic fishes. For example, within the river loaches of the Eurasian family Nemacheilidae members inhabiting lakes or slow-flowing rivers (e.g., *Yunnanilus* or *Lefua*) typically exhibit longer barbels than those inhabiting the interstitial spaces between rocks in fast-flowing rivers and streams (e.g., *Schistura* or *Turcinoemacheilus*). Likewise, loricariid catfishes from more lentic habitat (e.g., *Pterygoplichthys*) often have much longer barbels than species from fast-water habitats (e.g., *Chaetostoma*).

Species that have enhanced chemosensory and/or electrosensory systems are disproportionately represented in specialized rheophilic fish assemblages. Chemosensory specialists include all catfishes and many cypriniforms, whereas electrosensory specialists include neotropical gymnotiforms (e.g., *Sternarchorhynchus*, Fig. 2f), African mormyrids (e.g., *Campylomormyrus*, Fig. 3f, g), and, to a lesser extent, catfishes in the family Mochokidae (Boyle et al. 2014). In general, there is little evidence of sensory specializations developing as adaptations specifically for rheophily, but rather a prevailing pattern of preadaptation of chemo- and electrosensory specialists for life in fast water (Roberts and Stewart 1976).

4.5 Feeding

As noted in Sect. 4.1, many rheophilic fishes have strikingly upturned or downturned mouths. The upturned mouths of rheophilic fishes are typically either a specialization for top-water piscivory (e.g., *Belodontichthys*, *Macrochirichthys,* and *Securicula*) or are associated with the removal of invertebrates and sponges from the sides or undersides of rocks and wood (e.g., *Gnathodolus*, *Sartor*, and *Synaptolaemus*; Zuanon 1999; Sidlauskas and Vari 2008). Downturned mouths are usually specialized for invertivory when narrow (e.g., *Rhynchodoras*, Fig. 2g; *Sternarchorhynchus*, Fig. 2f; *Astroblepus*, Fig. 2j; *Chiloglanis*, Fig. 3j) or epilithic algal scraping when broad (e.g., *Parodon*, Fig. 2h; *Cordylancistrus*, Fig. 2k; *Euchilichthys*, Fig. 3k). Likewise, there is a general trend toward invertivores having relatively few, long, and acute teeth (e.g., *Sartor*, *Leporacanthicus*) and herbivores having smaller, broader, and more numerous teeth (e.g., *Cordylancistrus*, Fig. 2k; *Euchilichthys*, Fig. 3k; Lujan et al. 2012). As noted in Sect. 4.2, oral discs that surround the downturned mouths of algae-scrapers may facilitate feeding by increasing the surface adhesion and scraping friction of both the oral jaws and the surface of the disc (Ono 1980; Benjamin 1986). Oral discs likely also facilitate prey detection when equipped with taste buds (Ono 1980), and invertivore feeding by helping to occlude the cavities in which mobile prey hide, preventing their escape.

The teeth of rheophilic fishes are often highly specialized for particular food items and some of the strangest vertebrate dentitions described to date belong to benthic rheophilic fishes that scrape at substrates. For example, in members of the goby genus *Sicyopterus*, the tiny functional incisor-like teeth of the premaxillae are only the terminal stage in a complicated sequence of tooth development that involves a whorl of 20–40 rows of replacement teeth in various stages of development (Mochizuki and Fukui 1983). Between the basal pedicel and the dentin shaft of each functional tooth in the upper jaw of *Sicyopterus japonicus* is a complex articulation that provides each tooth with a certain degree of mobility, facilitating the scraping of algae from irregular surfaces (Sahara et al. 2013). The ability of teeth to interact with the substrate is taken to the extreme in certain groups of algivorous loricariid catfishes that possess uniquely flexible teeth with a flattened region along the shaft that is composed of soft dentin and unmineralized tissue, which allow the tooth to flex up to 180° between the tooth's rigid base and its hardened, hypermineralized cusp (Geerinckx et al. 2012). Though the majority of rheophilic substrate scrapers are benthic or demersal species with broad downturned mouths, the ayu (*Plecoglossus*) represents an interesting example of a seemingly unspecialized pelagic rheophile that scrapes algae via rapid lateral strikes of the lower jaw against the surface of rocks. The teeth in the lower jaw of the adult ayu are comblike and contrast sharply with the typical conical teeth present in the upper jaw (Uehara and Miyoshi 1993). Instead of scraping at the substrate with specialized teeth, substrate-scraping members of the Cypriniformes utilize highly keratinized jaw sheaths that are typically formed by low block-like unculi (Roberts 1982; Pinky et al. 2004).

4.6 Reproduction

Few if any rheophilic fishes are opportunistic life history strategists (i.e., early maturation, continuous reproduction, small body size, small clutch size, and little parental care), and only a minority are equilibrium strategists (i.e., late maturation, low fecundity, high parental care, and high juvenile survivorship, e.g., cave spawners listed below; Winemiller and Rose 1992). Most fishes, including most rheophiles, are periodic strategists (i.e., late maturation, high fecundity, little parental care, and low juvenile survivorship) and spawn by males and females aligning themselves and synchronously broadcasting gametes for external fertilization. Viviparity (internally fertilizing with live birth) and oviparity (internal fertilizing with egg laying) are rare, if not entirely absent from specialized rheophilic fishes, although viviparous poeciliids (e.g., *Priapella*, *Alfaro*, *Pseudoxiphophorus*; M. Tobler, pers. comm.) are common occupants of lotic habitats throughout Central America, and some oviparous members of the South American catfish family Auchenipteridae (e.g., *Auchenipterus*; Mazzoldi et al. 2007) can also be found in marginal areas near rapids.

One would nonetheless predict that in a fast-flowing stream environment there would be selection for specializations that minimize the risk of gametes being washed downstream before fertilization. Indeed, there are examples among rheophiles of both behavioral and morphological responses to this challenge. Behavioral responses include the synchronous deposition of eggs into cracks in rocks or wood (e.g., *Cyprinella*: Mayden and Simons 2002), the synchronous burrowing of males and females into sand or gravel substrates while spawning (e.g., North American darters of the genera *Etheostoma* and *Nothonotus*: Page and Swofford 1984; Warren et al. 1986; members of the south Asian genus *Opsarichthys*: R. Britz, pers. comm.), and the establishment and defense of sheltered nest cavities in or under rocks or wood (e.g., *Etheostoma*, subgenus *Catanotus*: Page 1980; Loricariidae, tribe Ancistrini: Sabaj et al. 1999). Morphological responses appear to be largely limited to elongation of the male genital papilla, which is seen in rheophilic catfishes of the African families Amphiliidae and Mochokidae (Roberts and Stewart 1976) and is taken to an extreme in the neotropical family Astroblepidae (Buitrago-Suárez and Galvis 1997). Male *Astroblepus* can have a robust genital appendage that extends to over a centimeter in length, and they are exceptional among fishes in having seminal vesicles near their testes, suggesting that the elongate papilla may have an intromittent function and that fertilization may be internal (Buitrago-Suárez and Galvis 1997).

4.7 Scales

Many benthic rheophiles exhibit reduced squamation compared to pelagic close relatives. Within monophyletic groups of benthic rheophiles, there is a general correlation between the extent of ventral squamation, particularly between the paired fins (the region of the body in closest contact with the substrate), and exposure to strong currents. For example, in the cypriniform genus *Psilorhynchus*, ventral squamation ranges from relatively complete in those taxa found in riffle habitats at lower elevations to a few poorly ossified, flap-like scales or complete absence of scales in members inhabiting higher elevation mountain torrents (Conway et al. 2012b). Similar trends in ventral squamation are present in the African/Asian cyprinid genus *Garra* (Stiassny and Getahun 2007) and the South American characid genus *Characidium* (Fig. 2d, Lujan et al. 2013). A reduction in the overall size combined with an increase in depth of embedment has been noted in scales covering the head, nape, and ventral surface in benthic rheophilic cichlids (Kullander 1988) and percids (Zorach 1972), and scales covering the body in nemacheiline loaches that inhabit swift currents are typically reported to be small and deeply embedded (e.g., Kottelat 1990; Zhou and Kottelat 2005; Conway 2011). Scales may be completely absent in several groups of benthic rheophiles, either plesiomorphically (e.g., all groups of benthic rheophilic catfishes; Fink and Fink 1981) or uniquely derived (e.g., middle eastern species of *Turcinoemacheilus*, Bănărescu and Nalbant 1964; certain species of *Pangio*, Britz et al. 2012). Reasons for scale reduction in benthic rheophilic lineages are likely numerous. In the absence of functional data, we speculate that scales may simply get in the way of maintaining close contact with the substrate (when on the ventral surface) or may interfere with hydrodynamics (when on the head, nape, or lateral body surfaces). On the other hand, the development of elongate keratinous ridges (or keels) over the surface of anterior body scales in numerous groups of benthic rheophilic cypriniforms and percids (Wiley and Collette 1970) that retain them may function to reduce lift by disrupting laminar water flow over the body (A. Summers, pers. comm.).

4.8 Skeleton

In contrast to the trend toward reduction of scales in benthic rheophiles, other parts of the skeleton may be greatly reinforced, either through suturing, fusion, or hyperossification. In addition to being dorsoventrally depressed, the skulls of benthic rheophiles that are exposed to strong currents often exhibit a high degree of suturing between adjacent elements (Sawada 1982; He et al. 1999). In members of several groups of rheophilic catfishes (e.g., Amphiliidae, Aspredinidae, Loricarioidea, and Sisoridae), the vertebral column is greatly reinforced through the anteroposterior expansion of neural arches and spines and interlocking of pre- and postzygapophyses of adjacent centra (He et al. 1999), or in some cases through the interlocking of accessory vertebral processes (De Pinna 1996). Similar reinforcement of the vertebral column is exhibited by highly rheophilic members of the Gastromyzontidae and Balitoridae (Sawada 1982). As described in Sect. 4.4, several groups of rheophilic catfishes (e.g., Amphiliidae, Aspredinidae, Loricarioidea, and Sisoridae; de Pinna 1996) and benthic, rheophilic cypriniforms (e.g., cobitoid loaches, Psilorhynchidae, Gobioninae; Alexander 1964; Sawada 1982; Bird and Hernandez 2007; Conway 2011) have elements of the vertebral column, and in some cases the neurocranium, that are highly modified to form a bony capsule around the swimbladder, and this capsule may serve a primarily structural role.

Ventral to the vertebral column, enlargement of the coracoid and basipterygium of the pectoral- and pelvic-fin girdles is also common in benthic rheophilic ostariophysans (e.g., Loricariidae and Gastromyzontidae; Schaefer 1984; Sawada 1982), as is the strengthening of the connection between these elements of the right and left sides of the body (Chang 1945). Fin rays that frequently encounter the substrate may also be heavily reinforced in benthic rheophiles. Lundberg and Marsh (1976) noted two major trends in the pectoral-fin rays of cypriniform fishes that they associated with the degree of substrate contact, including the simplification of anterior rays and foreshortening of fin ray segments, with highly benthic species exhibiting higher numbers of simple (unbranched) rays and shorter hemitrichial segments than benthopelagic or pelagic species. They concluded that such modifications acted to increase the flexibility, tensile strength, and resistance to buckling of rays that frequently contact the substrate (Lundberg and Marsh 1976). Along similar lines, Taft (2011) documented a number of structural differences along the length of individual lepidotrichia in the pectoral-fin rays of benthic vs. pelagic percomorphs that likely affect flexibility in the former.

5 Phylogenetic Patterns

With highly divergent scales of habitat, food-web, and ecomorphological diversity, headwaters and large river rapids are predicted to produce dramatically different phylogeographic and morphological patterns. Clades that are widespread across upland habitats should exhibit allopatric lineage diversity, low overall morphological diversity, and specializations for fast water that are synapomorphic for clades encompassing all rheophiles (i.e., plesiomorphic for clade members). Fish communities in large lowland river rapids should be largely paraphyletic while also exhibiting higher rates of localized adaptive radiation and autapomorphic specializations for life in fast water. Distributions of morphological specializations across phylogenies currently available for rheophilic fishes provide support for these predictions.

Headwater taxa for which at least partially representative species- or subspecies-level phylogenies are available include the Andean Trichomycterinae (Trichomycteridae) and Astroblepidae, and the predominantly South Asian Sisoridae. In studies of intraspecific genetic diversity in the montane species *Trichomycterus areolatus*, Unmack et al. (2009) and Quezada-Romegiall et al. (2010) found high levels of genetic divergence across river basins draining the Chilean Andes, and this molecular divergence corresponded with subtle variation in body shape that may warrant recognition of additional, undescribed species (Pardo 2002). Likewise, Schaefer et al. (2011) observed relatively deep, drainage-specific genetic divergence in species of *Astroblepus* from the Andes of southern Peru. Species in this study differed phenotypically only in subtle characteristics of their morphology (e.g., teeth uni- or bicuspid, presence/absence of adipose-fin membrane), but all shared plesiomorphic specializations for life in fast water, including an adhesive oral disc, pelvic-fin friction pads, a highly mobile pelvic girdle, and a distinctive "ratcheting" form of locomotion (i.e., putative synapomorphies of the Astroblepidae). The highland Andean genus *Chaetostoma* and Guiana Shield genera *Exastilithoxus* and *Neblinichthys* (Loricariidae) reveal a similar pattern of shared specializations for fast water, subtle phenotypic variation, and deep drainage-specific genetic divergence (Lujan et al. 2015).

The pattern among headwater clades is a bit more complex in members of the Asian catfish family Sisoridae, in which the presence/absence and specific morphology of the thoracic adhesive pad show considerable homoplasy, with up to four independent origins based on phylogenetic hypotheses derived from both morphological (de Pinna 1996; Ng 2006) and molecular data (Jiang et al. 2011). Occurrence of the thoracic adhesive pad is generally correlated with occupation of fast-water habitats, although the pad is entirely absent from one of the most extremely rheophilic clades (Glyptosternoidea sensu Peng et al. 2004), being replaced therein by well-developed peripheral friction pads on the underside of the anterior snout margin, barbels, and paired fins. In a molecular phylogenetic study of glyptosternoid biogeography, Guo et al. (2005) attributed much of the lineage diversity within this clade to the breakup of Southeast Asian river drainages following uplift of the Himalayan Mountains. Based on the presence of well-defined patches of unculi across the body of species in the large-bodied, non-rheophilic genus *Bagarius* (Roberts 1983) and a close (possibly sister group; Jiang et al. 2011; Ng 2006) relationship between *Bagarius* and the specialized rheophilic genus *Glyptothorax* (which have a synapomorphic thoracic friction pad; Jiang et al. 2011), de Pinna (1996) hypothesized that the latter genus may have been "preadapted" for the development of a friction pad.

Despite a lack of phylogenetic diversity estimates for whole fish communities in large river rapids, it is clear from species lists for various rapids (e.g., lower Congo River rapids, Africa: Roberts and Stewart 1976; lower Xingu River rapids, South America: Camargo et al. 2004) that these fish communities are assembled from a wide range of clades with broad geographic distributions. Limited phylogenetic hypotheses available for clades inclusive of large river rheophiles support the repeated occurrence of both endemic specialists (e.g., *Ossubtus xinguense*, Ortí et al. 2008) and localized diversification of these specialists within rapids (e.g., *Lamprologus* spp., Schelly and Stiassny 2004; *Steatocranus* spp., Schwarzer et al. 2011; *Teleocichla* spp., Kullander 1988; *Teleogramma depressum*, Markert et al. 2010).

6 Conclusions and Outlook

Fast-water habitats in the headwaters and lowland channels of river drainages host diverse and often highly specialized fish assemblages. In addition to promoting endemism and specialization within their boundaries, rapids can play an import role in limiting the distributions of, and gene flow among, large-bodied and/or more lentic species (Lovejoy and De Araújo 2000; Willis et al. 2007; Torrente-Vilara et al. 2011). Unfortunately, humans have historically viewed large river rapids less as evolutionary incubation chambers than as impediments to navigation and opportunities to generate hydroelectric power. In order to both facilitate navigation and produce hydroelectricity, a large shoal on the Tennessee River (Mississippi River drainage) that was long famous for its diversity and abundance of unionid mussels ("Muscle Shoals") was inundated by Wilson Dam in 1922 (Williams et al. 2008). Currently, the large Belo Monte dam complex is under construction on the rapids of the lower Xingu River in Brazil, and the Grand Inga dam complex has been proposed for rapids of the lower Congo River. Moreover, hundreds of smaller dams are already under construction or are being proposed for high elevation rivers draining the Andes (Finer and Jenkins 2012) and Himalayas (Grumbine and Pandit 2013).

As the shortcomings and gaps in this review illustrate, there is much yet to be discovered about the ecology, diversity, and evolutionary specialization of rheophilic fishes. Such studies are needed now more than ever in order to fully understand the threat to biodiversity posed by major human impacts. Some of these studies will require innovative techniques or new technologies. For example, obtaining precise information on microhabitats and associated fish assemblages within the deep and fast-flowing rapids of large rivers might only be possible with the use of submersible video, 3D laser-mapping (e.g., Pizarro et al. 2004), and Doppler velocimetry (e.g., Jackson et al. 2009) technologies. Other studies can be conducted using currently available whole specimens, tissues, and technologies. These include comparative functional studies of morphological features considered to be adaptations for life in fast-flowing water, including many poorly understood specializations mentioned herein (e.g., hydrodynamic function of keratinous ridges on scales and sensory function of elongate caudal-fin filaments). Many aspects of the patch dynamics model presented herein would benefit from more detailed phylogenetic and phylogeographic studies from which interspecific relationships and gene flow between populations may be inferred. To the extent possible using fossil and independent geologic calibrations, it will be important to time-calibrate phylogenies so that correlations between rapids formation and lineage diversification may be examined. Some of these studies are currently under way by ourselves and others, but many await future inquiring minds.

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Appendix

Table 1 Summary of genera containing rheophilic taxa and morphological specializations associated with each

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
Petromyzontiformes																					
	Petromyzontidae																				
			Ichthyomyzon	North America	X	X	-	-	-	X	-	-	-	?	-	-	-	X	-	-	-
			*Entosphenus**†	Pacific coasts	X	X	-	-	-	X	-	-	-	?	-	-	-	X	-	-	-
Anguilliformes																					
	Anguillidae																				
			Anguilla†	Circumglobal	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-	-	-
Osteoglossiformes																					
	Mormyridae																				
			Campylomormyrus	West/Central Africa	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-
			Mormyrops	West/Central Africa	-	-	-	X	-	X	-	-	X	-	X	X	-	-	-	-	-
			*Mormyrus**	West/Central Africa	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-
			*Paramormyrops**	West/Central Africa	-	-	-	X	-	X	-	-	X	-	X	-	-	-	-	-	-
			*Petrocephalus**	West/Central Africa	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-
			*Pollimyrus**	West/Central Africa	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-
			Stomatorhinus	West/Central Africa	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-
Clupeiformes																					
	Clupeidae																				
			*Clupeoides**	South East Asia	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
Gonorynchiformes																					
	Kneriidae																				
		Kneriinae																			
			Kneria	Africa	-	X	-	-	-	X	-	-	X	-	X	-	-	-	Xa	-	-
			Parakneria	Africa	-	X	-	-	-	X	-	-	X	X	-	-	-	-	Xa	-	-

(continued)

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Table 1 (continued)

					Microhabitat					Body Shape				Mouth Position				Attachment Organ			
Ord.	**Fam.**	**Subf.**	**Genus**	**Distribution**	**Hyp.**	**Ben.**	**B.P.**	**M.P.**	**T.P.**	**Ang.**	**Dep.**	**Fus.**	**Com.**	**Inf.**	**Sub.**	**Ter.**	**Sup.**	**O.D.**	**P.-F.P.**	**T.P.**	**P.-F.D.**
Cypriniformes																					
	Cyprinidae																				
		Cyprininae																			
			Akrokolioplax	South East Asia	-	-	X	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Bangana	South Asia	-	-	X	-	-	-	-	-	X	X	-	-	-	-	Xa	-	-
			Barbichthys	South East Asia	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Barbus	Eurasia	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			"*Barbus*"*	Africa	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Chuanchia	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Cirrhinus	South Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Cophecheilus	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Crossocheilus	South Asia	-	X	X	-	-	-	-	X	-	-	X	-	-	-	Xa	-	-
			Cyprinion	South Asia	-	-	X	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Discherodontus	South East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Discocheilus	China	-	X	-	-	-	-	-	X	-	X	-	-	-	X	Xa	-	-
			Discogobio	South East Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	X	Xa	-	-
			Diplocheilichthys	South East Asia	-	-	X	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Diptychus	South Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Folifer	South East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Garra	Africa and Asia	-	X	-	-	-	-	X	X	-	X	-	-	-	X	Xa	-	-
			Gymnocypris	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Gymnodiptychus	South Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Gymnostomus	South East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Hongshuia	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Incisilabeo	South East Asia	-	-	X	-	-	-	-	-	X	-	X	-	-	-	Xa	-	-
			*Labeo**	Africa and Asia	-	X	X	-	-	-	-	X	X	X	X	-	-	-	Xa	-	-
			Labeobarbus	Africa	-	-	X	X	-	-	-	X	-	-	X	-	-	-	-	-	-
			Laocypris	Laos	-	-	-	X	-	-	-	X	-	-	X	-	-	-	-	-	-
			Lobocheilos	South East Asia	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Mekongina	South East Asia	-	X	X	-	-	-	-	-	X	X	-	-	-	-	Xa	-	-
			Neolissochilus	South Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Onychostoma	South East Asia	-	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-
			Paracrossocheilus	South East Asia	-	-	X	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Parapsilorhynchus	India	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Parasinilabeo	China	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Placocheilus	East Asia	-	X	-	-	-	-	X	X	-	X	-	-	-	X	Xa	-	-
			Platypharodon	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Probarbus†	South East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Pseudocrossocheilus	China	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Pseudogyrinocheilus	China	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Ptychidio	East Asia	-	-	X	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Ptychobarbus	South Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Scaphiodonichthys	South East Asia	-	-	X	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Schismatorhynchos	South Asia	-	X	X	-	-	-	-	X	X	X	X	-	-	-	-	-	-
			Schizopygopsis	South Central Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Schizothorax	South Central Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Semilabeo	South East Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Semiplotus	South Asia	-	-	X	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Sinocrossocheilus	China	-	X	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			*Varicorhinus**	Africa	-	-	X	-	-	-	-	X	-	X	X	-	-	-	-	-	-
			Tor†	South Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
		Danioninae																			
			Barilius	South Asia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Devario	South Asia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Opsaridium	Africa	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Opsarius	South Asia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Raiamas	Africa/South Asia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			*Rasbora**	South Asia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
			Salmostoma	South Asia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Securicula	South Asia	-	-	-	-	X	-	-	X	-	-	-	-	X	-	-	-	-
		Opsarichthyinae																			
			Opsariichthys	East Asia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Zacco	East Asia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Candidia	East Asia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Nipponocypris	East Asia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Macrochirichthys	South East Asia	-	-	-	-	X	-	-	X	-	-	-	-	X	-	-	-	-
		Leuciscinae																			
			Alburnoides	Eurasia	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			*Alburnus**†	Eurasia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Anaecypris	Europe	-	-	-	X	-	-	-	X	-	-	-	-	X	-	-	-	-
			Aspius†	Eurasia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Ballerus†	Eurasia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Campostoma	North America	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			*Chondrostoma**	Europe	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Cyprinella	North America	-	-	X	X	-	-	-	X	-	X	X	-	-	-	-	-	-
			Erimystax	North America	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Exoglossum	North America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Gila	North America	-	-	X	X	-	-	-	X	-	-	X	X	-	-	-	-	-
			Hybognathus	North America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Hybopsis	North America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			*Leuciscus**†	Eurasia	-	-	X	X	-	-	-	X	-	-	X	X	-	-	-	-	-
			Luxilus	North America	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Macrhybopsis	North America	-	X	X	-	-	-	-	X	-	X	X	-	-	-	-	-	-
			Margariscus	North America	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			Nocomis	North America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			*Notropis**	North America	-	-	X	X	-	-	-	X	-	-	X	X	-	-	-	-	-
			Parachondrostoma	Europe	-	-	X	X	-	-	-	X	-	-	X	X	-	-	-	-	-
			Phenacobius	North America	-	X	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Phoxinus	Eurasia	-	-	X	X	-	-	-	X	-	-	X	-	-	-	-	-	-
			*Pimephales**	North America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Platygobio	North America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Protochondrostoma	Europe	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Pseudochondrostoma	Europe	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Ptychocheilus	North America	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Rhinichthys	North America	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Richardsonius	North America	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			*Rutilus**†	Eurasia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			*Squalius**†	Eurasia	-	-	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Telestes	Europe	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			Tiaroga	North America	-	X	-	-	-	-	-	X	-	-	X	-	-	-	Xa	-	-
			*Tropidophoxinellus**	Europe	-	-	-	X	-	-	-	X	-	-	-	X	X	-	-	-	-
			Vimba†	Eurasia	-	-	-	X	-	-	-	X	-	-	X	-	-	-	-	-	-
		Gobioninae																			
			Abbottina	East Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Belligobio	China	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Biwia	Japan	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Coreius†	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Coreoleuciscus	Korean Peninsular	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Gobio	Eurasia	-	X	-	-	-	-	-	X	-	X	X	-	-	-	-	-	-
			Gobiobotia	Eurasia	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Hemibarbus	East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Huigobio	China	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Ladislavia	East Asia	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Mesogobio	East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Microphysogobio	East Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Platysmacheilus	China	-	X	-	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Pseudogobio	East Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Pseudopungtungia	East Asia	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
			Rhinogobio	China	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Romanogobio	Eurasia	-	X	-	-	-	-	-	X	-	X	X	-	-	-	-	-	-
			Sarcocheilichthys	East Asia	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Saurogobio	East Asia	-	X	X	-	-	-	-	X	-	X	X	-	-	-	-	-	-
			Xenophysogobio	China	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
	Psilorhynchidae																				
			Psilorhynchus	South Asia	-	X	-	-	-	-	X	X	-	X	-	-	-	-	Xa	-	-
	Gyrinocheilidae																				
			Gyrinocheilus	South East Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	X	Xa	-	-
	Catostomidae																				
		Catostominae																			
			Xyrauchen	North America	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
		Cycleptinae																			
			Cycleptus	North America	-	X	X	-	-	-	-	X	-	X	-	-	-	-	Xc	-	-
		Moxostominae																			
			*Moxostoma**	North America	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Hypentelium	North America	-	X	-	-	-	-	-	X	-	X	-	-	-	-	Xc	-	-
	Cobitidae																				
			Acantopsis	South East Asia	X	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Bibarba	China	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Canthophrys	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			*Cobitis**	Eurasia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Iksookimia	South Korea	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Kichulchoia	South Korea	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Lepidocephalichthys	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Neoeucirrhichthys	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Niwaella	East Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			*Pangio**	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Paralepidocephalus	China	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Sabanejewia	Europe	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
	Botiidae																				
			*Botia**	South Asia	-	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Chromobotia	South East Asia	-	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Leptobotia	China	-	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Sinibotia	China	-	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Syncrossus	South East Asia	-	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Yasuhikotakia	South East Asia	-	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
	Nemacheilidae																				
			Aborichthys	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Acanthocobitis	South Asia	X	-	-	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Afronemacheilus	East Africa	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Barbatula	Eurasia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Claea	China	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Dzihunia	Central Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Homatula	China	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Ilamnemacheilus	Iran	-	X	-	-	-	-	-	-	X	X	-	-	-	-	Xa	-	-
			Indoreonectes	India	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Indotriplophysa	South Asia	-	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Iskandaria	Central Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Labiatophysa	Central Asia	-	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Mesonoemacheilus	India	X	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Metaschistura	Central Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			*Nemacheilus**	South East Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Nemachilichthys	India	X	-	-	-	-	-	-	-	X	X	-	-	-	-	Xa	-	-
			Neonoemacheilus	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Oreonectes	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Oxynoemacheilus	Eurasia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Paracobitis	West Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Paraschistura	West Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Physoschistura	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
			Protonemacheilus	China	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Pteronemacheilus	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Schistura	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Sectoria	South East Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Seminemacheilus	Turkey	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Sundoreonectes	Borneo	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Tarimichthys	China	-	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Traccatichthys	South East Asia	X	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Triplophysa	Asia	-	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Tuberoschistura	South East Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
			Turcinoemacheilus	Middle East/Nepal	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
	Balitoridae																				
			Balitora	South Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Balitoropsis	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Bhavania	India	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Cryptotora	Thailand	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Hemimyzon	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Homaloptera	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Homalopteroides	South East Asia	X	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Homalopterula	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Jinshaia	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Lepturichthys	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Metahomaloptera	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	Xa
			Neohomaloptera	South East Asia	X	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Sinogastromyzon	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	Xa
			Travancoria	India	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
	Gastromyzontidae																				
			Annamia	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Beaufortia	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	Xa
			Erromyzon	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Formosania	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Gastromyzon	Borneo	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	Xa
			Glaniopsis	Borneo	X	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Hypergastromyzon	Borneo	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	Xa
			Katibasia	Borneo	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Liniparhomaloptera	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Neogastromyzon	Borneo	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	Xa
			Paraprotomyzon	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Parhomaloptera	Borneo	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Plesiomyzon	China	-	X	-	-	-	-	-	X	-	X	-	-	-	-	Xa	-	-
			Protomyzon	Borneo	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Pseudogastromyzon	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Sewellia	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Vanmanenia	South East Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Yaoshania	China	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
	Barbuccidae																				
			Barbucca	South East Asia	X	-	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
	Serpenticobitidae																				
			Serpenticobitis	South East Asia	-	X	-	-	-	-	-	-	X	X	-	-	-	-	Xa	-	-
Characiformes																					
	Alestidae																				
			Bryconaethiops	West/Central Africa	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
	Bryconidae																				
		Bryconinae																			
			Brycon	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
		Salmininae																			
			Salminus	Tropical S America	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
	Characidae																				
		incertae sedis																			
			Astyanacinus	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Astyanax	Central/South America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Attonitus	Andes Mountains	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Bryconamericus	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Bryconexodon	Lower Amazon	-	-	-	-	X	-	-	-	X	-	-	X	-	-	-	-	-
			Bryconops	Tropical S America	-	-	-	-	X	-	-	X	-	-	-	X	-	-	-	-	-
			Deuterodon	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Engraulisoma	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Exodon	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Genycharax	Upper Cauca River	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Jupiaba	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Knodus	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Piabina	Southeastern Brazil	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
		Agoniatinae																			
			Agoniates	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-
		Clupeacharacinae																			
			Clupeacharax	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
		Aphyocharacinae																			
			Aphyocharax	Tropical S America	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
		Characinae																			
			Galeocharax	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Roeboexodon	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
		Stevardiinae																			
			Bryconacidnus	SW Amazon Basin	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			Ceratobranchia	Andes Mountains	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			Creagrutus	Tropical S America	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Hemibrycon	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
	Cynodontidae																				
			Cynodon	Tropical S America	-	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-
			Hydrolycus	Tropical S America	-	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-
			Rhaphiodon	Tropical S America	-	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-
			Roestes	Tropical S America	-	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-
	Distichodontidae																				
			*Distichodus**	West/Central Africa	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			*Nannocharax**	West/Central Africa	-	-	X	-	-	-	-	-	X	-	X	-	-	-	Xa	-	-
	Lebiasinidae																				
			Lebiasina	Tropical S America	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
			Piabucina	Tropical S America	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
	Parodontidae																				
			Parodon	Tropical S America	-	-	X	-	-	-	-	X	-	X	-	-	-	-	Xb	-	-
			Apareiodon	Tropical S America	-	-	X	-	-	-	-	X	-	X	-	-	-	-	Xb	-	-

(continued)

Table 1 (continued)

					Microhabitat					Body Shape				Mouth Position				Attachment Organ			
Ord.	Fam.	Subf.	Genus	Distribution	Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
	Prochilodontidae																				
			Prochilodus	Tropical S America	-	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-
	Crenuchidae																				
			*Characidium**	Tropical S America	-	X	-	-	-	-	-	X	-	-	X	-	-	-	Xa	-	-
	Anostomidae																				
			Abramites	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			*Anostomoides**	Tropical S America	-	-	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-
			Anostomus	Tropical S America	-	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-
			Hypomasticus	Tropical S America	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Leporellus	Tropical S America	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-
			*Leporinus**	Tropical S America	-	-	X	-	-	-	-	X	-	-	X	X	-	-	-	-	-
			Petulanos	Tropical S America	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			Pseudanos	Tropical S America	-	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-
			Sartor	Lower Amazon	-	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-
			Synaptolaemus	Guiana/Brazilian Shield	-	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-
			Gnathodolus	Orinoco/Casiquiare	-	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-
	Serrasalmidae																				
			Acnodon	Tropical S America	-	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-
			Myleus	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Myloplus	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Ossubtus	Xingu River	-	-	X	-	-	-	-	-	X	X	-	-	-	-	-	-	-
			Tometes	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
Siluriformes																					
	Diplomystidae																				
			Diplomystes	Southern Andes	-	-	X	-	-	-	X	-	-	X	-	-	-	-	-	-	-
	Astroblepidae																				
			Astroblepus	Andes Mountains	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
	Trichomycteridae																				
			*Trichomycterus**	South America	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xc	-	-
			Ituglanis	Tropical S America	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xc	-	-
	Loricariidae																				
		Ancistrini																			
			Acanthicus	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			*Ancistrus**	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Baryancistrus	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Chaetostoma	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Cordylancistrus	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Corymbophanes	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Dolichancistrus	Northern Andes	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Exastilithoxus	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Guyanancistrus	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			*Hemiancistrus**	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Hopliancistrus	Brazilian Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			*Lasiancistrus**	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
			Leporacanthicus	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Leptoancistrus	Northern Andes	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Lithoxancistrus	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Lithoxus	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Megalancistrus	Paraná/São Francisco	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Neblinichthys	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Oligancistrus	Brazilian Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Panaqolus	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Panaque	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Parancistrus	Brazilian Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Paulasquama	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Peckoltia	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Pseudacanthicus	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Pseudancistrus	Guiana/Brazilian Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Pseudolithoxus	Orinoco Basin	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Scobinancistrus	Brazilian Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Spectracanthicus	Brazilian Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Zonancistrus	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
		Neoplecostominae																			
			Isbrueckerichthys	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Kronichthys	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Neoplecostomus	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Pareiorhaphis	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Pareiorhina	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Pseudotocinclus	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
		Lithogeninae																			
			Lithogenes	Guiana Shield	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
		Delturinae																			
			Delturus	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Hemipsylichthys	Southeastern Brazil	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
		Loricariinae																			
			Lamontichthys	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Harttia	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
			Spatuloricaria	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xc	-	-
	Bagridae																				
			Bagrus	Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
	Claroteidae																				
			Chrysichthys	Africa	-	X	X	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Notoglanidium	Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
	Amblycipitidae																				
			Amblyceps	South Asia	X	X	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
			Liobagrus	East Asia	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
	Amphiliidae																				
		Amphiliinae																			
			Amphilius	Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Paramphilius	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
		Doumeinae																			
			Andersonia	Northeastern Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Belonoglanis	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Congoglanis	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Doumea	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Phractura	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xa	-	-
			Trachyglanis	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
		Leptoglanidinae																			
			Dolichamphilius	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xa	-	-
			Leptoglanis	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Psammphiletria	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Tetracamphilius	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Zaireichthys	Africa	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
	Clariidae																				
			*Clarius**	Paleotropical	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Gymnallabes	West/Central Africa	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-	-	-
	Mochokidae																				
			*Synodontis**	Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	-	-	-
		Chiloglaninae																			
			Atopochilus	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	-	-	-
			Atopodontus	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	-	-	-
			Chiloglanis	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	-	-	-
			Euchilichthys	West/Central Africa	-	X	-	-	-	-	X	-	-	X	-	-	-	X	-	-	-
	Sisoridae																				
		Sisorinae																			
			Bagarius	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Caelatoglanis	SE Asia	-	X	-	-	-	-	X	X	-	X	-	-	-	-	-	X	-
			Conta	India/SE Asia	-	X	-	-	-	-	X	X	-	X	-	-	-	-	-	X	-
			Nangra	South Asia	-	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-
			Pseudolaguvia	India/SE Asia	X	X	-	-	-	-	X	X	-	X	-	-	-	-	-	X	-
			Glyptothorax	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	X	-
		Glyptosterninae																			
			Creteuchiloglanis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xa	-	-
			Euchiloglanis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Exostoma	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xa	-	-
			Glaridoglanis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Glyptosternon	South Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	X	-
			Myersglanis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Oreoglanis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xa	-	-
			Pareuchiloglanis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	-	-
			Pseudecheneis	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	-	Xa	X	-
			Pseudexostoma	India/SE Asia	-	X	-	-	-	-	X	-	-	X	-	-	-	X	Xa	-	-
	Heptapteridae																				
			Chasmocranus	Tropical S America	X	-	-	-	-	X	X	-	-	X	-	-	-	-	-	-	-
			Leptorhamdia	Tropical S America	X	-	-	-	-	X	X	-	-	X	-	-	-	-	-	-	-
	Pimelodidae																				
			Brachyplatystoma	Tropical S America	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
	Ictaluridae																				
			*Noturus**	North America	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
	Aspredinidae																				
			Hoplomyzon	Northern Andes	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
			Ernstichthys	Andes	X	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-
Gymnotiformes																					
	Gymnotidae																				
			*Gymnotus**	Tropical S America	-	-	-	X	-	X	-	-	-	-	-	-	X	-	-	-	-
			Sternarchogiton	Tropical S America	-	-	-	X	-	-	-	-	X	-	X	-	-	-	-	-	-
			Sternarchorhynchus	Tropical S America	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-
Osmeriformes																					
	Plecoglossidae																				
			*Plecoglossus**†	East Asia	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
	Galaxiidae																				
			*Galaxias**†	Southern Hemisphere	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
Salmoniformes																					
	Salmonidae																				
		Salmoninae																			
			Brachymystax	North East Asia	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			*Hucho**	Eurasia	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			*Oncorhynchus**†	North America	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
			Salmo†	Europe	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
		Thymallinae																			
			Thymallus	Northern Hemisphere	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-
Mugiliformes																					
	Mugilidae																				
			Agonostomus†	W Central Atlantic/E Central Pacific/Madagascar	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
Atheriniformes																					
	Melanotaenidae																				
			*Chilatherina**	Australia and New Guinea	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-	-
Synbranchiformes																					
	Mastacembelidae																				
			*Mastacembelus**	Africa/Asia	X	-	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-
			Sinobdella	Southeast Asia	X	-	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-
Scorpaeniformes																					
	Cottidae																				
			*Cottus**	Northern Hemisphere	X	X	-	-	-	-	X	-	X	-	-	X	-	-	Xd	-	-
"Perciformes"																					
	Badidae																				
			*Badis**	South Asia	-	X	-	-	-	-	-	X	X	-	-	X	-	-	Xd	-	-
	Percidae																				
		Etheostomatinae																			
			Ammocrypta	North America	-	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
			Crystallaria	North America	X	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
			*Etheostoma**	North America	X	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
			Nothonotus	North America	X	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
			Percina	North America	-	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
		Luciopercinae																			
			Romanichthys	Danube River	X	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
			Zingel	Southern Europe	-	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
	Cheimarrichthyidae																				
			Cheimarrichthys†	New Zealand	-	X	-	-	-	-	X	-	X	-	X	-	-	-	Xd	-	-
	Cichlidae																				
			Gobiocichla	West Africa	-	-	X	-	-	X	-	-	-	-	X	-	-	-	-	-	-
			*Hemichromis**	West Africa	-	-	X	-	-	-	-	X	X	-	-	X	-	-	-	-	-
			*Lamprologus**	Central Africa	X	-	X	-	-	X	-	X	-	-	X	X	-	-	-	-	-
			Nanochromis	Central Africa	-	-	X	-	-	-	-	X	-	-	-	X	-	-	-	-	-

(continued)

Table 1 (continued)

Ord.	Fam.	Subf.	Genus	Distribution	Microhabitat					Body Shape				Mouth Position				Attachment Organ			
					Hyp.	Ben.	B.P.	M.P.	T.P.	Ang.	Dep.	Fus.	Com.	Inf.	Sub.	Ter.	Sup.	O.D.	P.-F.P.	T.P.	P.-F.D.
			_Paraneetroplus_*	Central America	-	-	X	X	-	-	-	-	X	-	-	X	-	-	-	-	-
			Retroculus	South America	-	-	X	-	-	-	-	-	X	-	X	X	-	-	-	-	-
			Steatocranus	Central Africa	-	X	X	-	-	X	-	X	-	-	-	X	-	-	-	-	-
			Teleocichla	South America	-	X	X	-	-	X	-	X	-	-	-	X	-	-	Xd	-	-
			Teleogramma	Central Africa	-	X	X	-	-	X	-	X	-	-	-	X	X	-	-	-	-
			_Theraps_*	North/Central America	-	-	X	X	-	-	-	X	X	-	-	X	-	-	-	-	-
	Blenniidae																				
			_Salaria_*†	Mediterranean	-	X	-	-	-	-	-	X	-	-	-	X	-	-	Xd	-	-
	Gobiesocidae																				
			_Gobiesox_*†	Central/Northern S America	-	X	-	-	-	-	X	-	-	-	-	X	-	-	-	-	Xb
	Rhyacichthyidae																				
			Protogobius†	New Caladonia	-	X	-	-	-	-	X	X	-	-	X	-	-	-	Xd	-	-
			Rhyacichthys†	Southeast Asia/Oceania	-	X	-	-	-	-	X	-	-	-	X	-	-	-	Xd	-	-
	Eleotridae																				
			_Eleotris_*†	Pantropical	-	X	-	-	-	-	-	X	-	-	-	X	X	-	-	-	-
			_Gobiomorphus_*†	Australasia	-	X	-	-	-	-	-	X	-	-	-	X	X	-	-	-	-
	Odontobutidae																				
			_Odontobutis_*	East Asia	-	X	-	-	-	-	-	X	-	-	-	X	-	-	-	-	-
	Gobiidae																				
		Gobionellinae																			
			Awaous†	Pantropical	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Parawaous†	Borneo	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Rhinogobius	East Asia	-	X	-	-	-	-	-	X	X	-	X	X	-	-	-	-	Xc
			_Schismatogobius_*†	Asia/Oceania	X	X	-	-	-	X	-	-	-	-	-	X	-	-	-	-	Xc
		Sicydiinae																			
			Akihito†	South Pacific	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Cotylopus†	Indian Ocean	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Lentipes†	Southeast Asia/Oceania	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Parasicydium†	West Africa	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Sicyopterus†	Indo_Pacific	-	X	-	-	-	-	-	X	X	-	X	-	-	X	-	-	Xc
			Sicyopus†	Southeast Asia/Oceania	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Stiphodon†	Southeast Asia/Oceania	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc
			Sycidium†	Tropical Atlantic/E Pacific	-	X	-	-	-	-	-	X	X	-	X	-	-	-	-	-	Xc

See text for further explanation. Taxonomic classification generally follows that of Nelson (2006). ‘Perciformes’ follows Wiley and Johnson (2011). Abbreviations (listed from left to right across table): Hyp., hyporeic; Ben., benthic; B.P., bentho-pelagic; M.P., midwater-pelagic; T.P., topwater-pelagic; Ang., anguilliform; Dep., depressed; Fus., fusiform; Com., compressed; Inf., inferior; Sub., subterminal; Ter., terminal; Sup., superior; O.D., oral disc; P.-F.P., paired-fin pads; T.P., thoracic pad; P.-F.D., paired-fin disc. Paired-fin pads are divided between the following types: Xa, pads that are restricted to the ventral surface of rays, equipped with a superficial unculiferous layer; Xb, as in Xa but without an unculiferous layer; Xc, as in Xb but with odontodes; Xd, thickened skin continuous around ray, without forming an obvious pad and without an unculiferous layer (for detailed discussion of paired-fin pads see Conway et al. 2012a). Paired-fin discs are divided into the following types: Xa, balitorid type; Xb, gobiesocid type; Xc, gobiid type. An asterisk (*) after a generic name indicates that only some members of genus are rheophilic and a cross (†) indicates that members of this genus are migratory (either within freshwater or diadromous)