Chapter XX
Life in the fast lane: a review of rheophily in freshwater fishes

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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.

XX.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, 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

47 substrate) and turbulence (chaotic water movement formed by disruptions to laminar flow).
48 Where streams become constrained by shallow, irregular channel bottoms as in rapids and riffles,
49 both shear forces and turbulence increase (Hoover and Ackerman, 2004). A generalized cross-
50 section of water velocities over a rounded stone exhibits highest velocities and shear forces
51 within ~5–15 mm of the stone surface along the leading edge and top, with zones of turbulence
52 at the lower upstream and downstream sides of the stone. Despite maximal water velocities near
53 the top of the stone, velocities very close (<5 mm) to the stone surface approach 0 due to
54 frictional drag of the stone on the water in a region known as the boundary layer (Ambühl, 1962;
55 Hoover and Ackerman, 2004). Larval stages of many insects specialized for life in fast water (e.g.
56 mayflies, stoneflies, psephenid beetles) are small enough and dorsoventally flattened enough to
57 escape shear stress by living entirely within this boundary layer of very low flow. Many
58 rheophilic fishes also benefit from highly dorsoventrally depressed bodies (see *Body Shape*
59 below), although few if any are small enough to exist entirely within the boundary layer.
60   Although the thin surface layers of rocks or wood, and spaces within or beneath such
61 objects, can offer refuge from shear forces and the threat of downstream displacement, close
62 association with these substrates also poses a threat to stream organisms when shear stress
63 dislodges the substrates themselves. Indeed, the ever-present threat of both downstream
64 displacement and being injured by shifting substrates makes life in fast-water habitats extremely
65 challenging. Here we review the distribution of these habitats across the landscape, the gradients
66 in ecological and evolutionary processes that covary with a habitat's longitudinal position, the
67 morphological responses to these processes, and the phylogenetic and functional studies of fast-
68 water fishes and their specializations for life in the extreme. Few species or morphological traits
69 associated with rheophilic habitats have been empirically investigated from a functional,
70 performance, or correlated eco-evolutionary perspective. We therefore consider traits as
71 specialized based largely on theory.
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73 **XX.2 Taxonomic distribution of rheophilic fishes**
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75 Previous comprehensive overviews of rheophilic fishes have focused on fauna inhabiting
76 particular river drainages (Roberts and Stewart, 1976; Zuanon, 1999; Casatti and Castro, 2006)
77 or a circumscribed geological region encompassing multiple drainages (Hora, 1930). Regardless
78 of the scale, such studies frequently attempt to divide rheophilic fishes across a number of
79 general categories, ranging from poorly adapted to highly adapted for life in fast flowing water,
80 based largely on external morphological features. For example, Hora (1930) recognized four
81 general categories of hill-stream fishes in his overview of the Himalayan torrent fauna, ranging
82 from "ordinary" (Hora's category I) to "flattened…provided with well-developed means of
83 attachment" (Hora's category IV). Along similar lines, Roberts and Stewart (1976) divided the
84 fishes collected in their comprehensive survey of the lower Congo rapids into three categories
85 (poorly, moderately and highly adapted to rapid habitats) and further divided those taxa that they
86 considered to be highly adapted based on whether they were exposed to strong current (their
87 "rheophilic") or avoided such currents (their "hyporheic").
88   In Table XX.1, we have attempted to provide a more global overview of rheophilic fishes
89 than has been attempted previously. Our decision to include particular taxa is based either on
90 personal observations (for those taxa and regions that we are familiar) or published information
91 contained in larger taxonomic revisions (e.g., Tan, 2006; Kottelat, 1990) or faunal overviews for
92 individual river basins (Monsembula Iyaba et al., 2013; Roberts and Stewart, 1976; Roberts,

93 1978, 1989a; Kullander et al., 1999; Parenti and Lim, 2005; Tan and Kottelat, 2009), countries
94 (Chen, 1998; Kottelat, 2001a,b, 2006; McDowall, 1978; Shrestha and Edds, 2012; Yue, 2000) or
95 larger geographic regions including multiple countries (Talwar and Jhingran, 1991; Kottelat et al.,
96 1993; Kottelat and Freyhof, 2007; Page and Burr, 2011; Skelton, 1993). For the sake of
97 simplicity, we focus only on those taxa that would be considered obligate rheophiles, either
98 moderately or highly adapted for life in fast water (*sensu* Roberts and Stewart, 1976). We have
99 included lacustrine or diadromous taxa that may spend only part of their lifecycle in fast flowing
100 water but have excluded marine and estuarine taxa that are reported occasionally from faster
101 water habitats in the lower courses of rivers that exhibit no obvious specializations for life in fast
102 water (e.g., *Dactyloscopus*; Miller and Briggs, 1962). Our list, which is likely to be incomplete,
103 contains 419 genera, distributed across 60 families and 16 orders. As one would expect, our list
104 is dominated by teleosts, and otophysans in particular, with 207 genera of Cypriniformes
105 (representing 11 families), 92 genera of Siluriformes (representing 15 families) and 52 genera of
106 Characiformes (representing 11 families). With 37 genera (representing 10 families), the
107 'Perciformes' (sensu Wiley and Johnson, 2010) contains the majority of the remaining rheophilic
108 teleosts, most of which belong to one of three families, the Gobiidae (12 genera), the Cichlidae
109 (10 genera) or Percidae (7 genera). Two genera of lampreys (Petromyzontiformes) represent the
110 only non-teleost taxa that are obligate inhabitants of fast flowing waters.
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112 **XX.3 Ecological processes**
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114 *XX.3.1 Assemblage composition model*
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116 River zonation typologies and ecological process models have expanded from static, modular
117 depictions of hydrology and community composition (e.g., Hutchinson, 1939; Illies, 1961) to
118 contemporary but dynamic linkages between a river's hydrogeomorphology, production sources,
119 and faunal assembly. The recently proposed Riverine Ecosystem Synthesis (RES, Thorp et al.,
120 2006), for example, provides a framework for integrating previous conceptual models (e.g.,
121 River Continuum Concept, Flood Pulse Concept, Riverine Productivity Model) into a
122 comprehensive hierarchy of geomorphological processes and metacommunity patch dynamics.
123 Although the original iteration of the RES was explicitly limited to recent ecological timescales
124 (Thorp et al., 2006), a strength of the hierarchical patch dynamics approach is its limitless
125 potential for spatial and temporal expansion. We propose a modified patch dynamics model
126 narrowly focused on the geomorphology of fast-water habitats and community assembly of
127 specialized resident (i.e., non-migratory) fast-water fish assemblages spanning both large,
128 continental drainage basins (e.g., Amazon Basin, Mekong Basin), and timescales long enough to
129 encompass macroevolutionary processes.
130   Our model (Fig. XX.1) contrasts high gradient, high elevation headwaters, which have
131 low taxonomic and trophic diversity (Lujan et al., 2013), with large lowland rapids hosting
132 species-rich assemblages that are functionally diverse and often narrowly endemic (Roberts and
133 Stewart, 1976; Roberts, 1978; Zuanon, 1999; Camargo et al., 2004). Despite the low α-diversity
134 (i.e., local, site-specific species richness) of headwaters, these habitats often exhibit high β-
135 diversity (i.e., species richness summed across sites; Carrara et al., 2012) due to low active
136 dispersal between habitat patches combined with a slow background rate of passive
137 'geodispersal' (i.e., stream capture) and subsequent vicariant speciation (e.g., Waters et al., 2001,
138 Ribeiro, 2006). Moreover, headwater populations may be small and have low genetic diversity

139 due to founder effects (Hänfling and Weetman, 2006; Barson et al., 2009), increasing rates of
140 genetic drift and vicariant speciation if isolated from larger downstream populations.
141   Comparative community and habitat diversity data are largely lacking for large, lowland
142 river rapids but we hypothesize that, as with oceanic islands (Diamond et al., 1976; Losos and
143 Ricklefs, 2009), the species richness, functional and habitat diversity of river rapids correlate
144 with their size and their distance from other large rapids. An additional factor unique to rivers is
145 hydraulic energy, which should multiply effects of distance by increasing both the cost of
146 dispersal and the reward of philopatry. Even relatively close rapids with high hydraulic energies
147 may promote isolation, vicariance, and endemic diversification by increasing the universal risk
148 of downstream export should individuals move far from a preferred microhabitat (Markert et al.,
149 2010; Schwarzer et al., 2011). As with both terrestrial islands (Losos and Schluter, 2000) and
150 lakes (Wagner et al., 2014), instances and rates of localized diversification (i.e., adaptive
151 radiation) should also scale with rapids size, and vicariant speciation rates among rapids should
152 increase with greater geographic distance and/or hydraulic energy. Also, given spatial variation
153 in localized rates and outcomes of evolutionary specialization and diversification in both
154 headwater and lowland river rapids habitats (i.e., all specialists are not present in all habitats),
155 and the uneven distribution and scale of barriers to dispersal between similar habitat patches, we
156 predict that niche occupancy and assemblage structure across the landscape rarely equilibrate and
157 these disequilibria contribute to greater β-diversity.
158   At intermediate elevations and reaches, fish populations are typically more genetically
159 diverse (Hänfling and Weetman, 2006; Barson et al., 2009) and fish assemblages more species
160 rich than in headwaters, but they still lack many taxa and functional components of lowland
161 habitats (Lujan et al., 2013). Fast-water habitats at intermediate elevations consist primarily of
162 riffles periodically interrupted by deeper, slower runs and pools. Relative riffle length and pool
163 depth increase as channel slope decreases (Wohl et al., 1993), suggesting that there is a gradient
164 between upstream zones where habitat patches remain close enough and geomorphologically
165 variable enough over long timescales to facilitate the free exchange of genetic diversity
166 (panmixis), and downstream zones where geographic distances between habitat patches may be
167 great enough to impede such gene flow (Langerhans et al., 2003).
168   Regular dispersal of individuals among habitat patches in intermediate reaches maintains
169 equilibria of species richness and assemblage composition across similar habitat patches (Stewart
170 et al., 2002; Winemiller et al., 2010). These equilibria may be dynamic if differential
171 reproduction and survival across patches create sources and sinks within a metapopulation,
172 evidence of which has been observed in the genetic structure of European sculpin (*Cottus gobio*;
173 Hänfling and Weetman, 2006) and in community structure of a Taiwanese river following
174 disturbance (Chen et al., 2004). At the upstream interface between torrent and riffle zones, where
175 stream hydrologies remain flashy and species richness begins to increase but patch sizes remain
176 small, the heterogeneous and stochastic distribution of disturbance (largely due to spates) should
177 be an important driver of source-sink patch dynamics. At the downstream interface between
178 riffle and large river rapids zones, where species and habitat diversity begin to approach maxima
179 but where habitat patches remain regularly distributed, species should sort themselves according
180 to microhabitats in a predictable fashion (e.g., Arrington et al., 2005).
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182 *XX.3.2 Drivers of specialization*
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184   Although our model predicts that over long time periods the composition of specialized fish
185   assemblages in upland headwaters and large, lowland river rapids will primarily be under
186   evolutionary control (vicariant speciation in both, adaptive radiation in the latter), local species
187   interactions need to be understood to infer the drivers of evolutionary specialization. Studies of
188   fish behavior in torrential headwaters and large river rapids are scarce, but several studies have
189   examined the effects of water velocity on species interactions in the mesohabitats (i.e., riffle, run,
190   or pool reaches) of North American piedmont streams. For example, Schlosser (1987) observed
191   that in an ecologically diverse, North American assemblage of 15 species of stream fishes,
192   juveniles and small-bodied adults occurred at higher densities in riffles and raceways than in
193   pools, whereas large-bodied adults preferred pools. A choice experiment demonstrated that
194   preference for shallow, fast-water habitat by small individuals was much greater when large fish
195   were present versus absent, suggesting that an important motivation for fish to occupy fast-water
196   habitat is predator avoidance (Schlosser, 1987).
197   Increases in water velocity also reduce predation on macroinvertebrates by other
198   macroinvertebrates (Meissner et al., 2009; Worischka et al., 2012) and contribute to increased
199   rates of primary production, even when effects of habitat depth on light level are removed
200   (Kevern and Ball, 1965; Horner et al., 1990). Therefore, both algae and macroinvertebrates tend
201   to be more abundant in mesohabitats that are fast and shallow versus slow and deep (Kevern and
202   Ball, 1965; Brown and Brussock, 1991; Buffagni and Comin, 2000). Together, these trends
203   suggest that specialization on fast-water habitats may also contribute to increased foraging
204   efficiency and reduced competition among herbivores and invertivores. In an elevational survey
205   of an Andean affluent of the Amazon, Lujan et al. (2013) observed that the first native fish
206   species to occur at high elevations were invertivorous, rheophilic catfishes (Astroblepidae,
207   Trichomycteridae). Comparison of macroinvertebrate density in habitats with fish versus without
208   showed that these catfishes contributed to a >50% reduction in macroinvertebrate abundance.
209   The second fish trophic guild to appear along the elevational gradient were herbivores.
210   Considering the physiological challenges that likely limit elevational progression of aquatic
211   organisms (e.g., oxygen limitation; Verberk et al., 2011), the occurrence first of invertivores and
212   then of herbivores suggests that these are the most ecologically and physiologically
213   advantageous trophic niches offered by such extreme habitats. In addition to refuge from
214   predation and increased foraging efficiency, relatively higher dissolved oxygen concentrations
215   and clean substrates also are benefits afforded to fast-water specialists, although the relative
216   importance of these factors are likely much greater in modern, anthropogenically impacted (e.g.,
217   sedimented, eutrophied, hydrologically altered) streams than in naturally functioning ecosystems
218   (Agostinho et al., 1994; Orrego et al., 2009). In summary, there is considerable evidence to
219   suggest that fast-water habitats offer a range of ecological opportunities to fish lineages having
220   either preexisting specializations or the evolutionary or behavioral lability to overcome the
221   physical challenges of occupying these zones.
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223   **XX.4 Specializations for rheophily**
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225   *XX.4.1 Body shape*
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227   Extreme hydrologic forces largely limit the food resources and refuge available in fast-water
228   habitats to species with specializations for resisting downstream displacement while feeding,
229   thus driving convergent evolution of body shape and mouth orientation (Figs. 2–4, Table XX.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, 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*; Sidlauskus and Vari, 2008). Most members of the herbivorous, rheophilic family Parodontidae have a ventrally directed mouth (Fig. XX.2h), and a single herbivorous, rheophilic species in the family Serrasalmidae (*Ossubtus xinguense*) is noteworthy for both its extremely downturned mouth (Fig. XX.2i) and its narrow endemism to rapids of the lower Xingu (Amazon Basin; Jegu, 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 electrical fields (*Sternarchorhyncus*, Fig. XX.2f, and *Campylomormyrus curvirostris*, Fig. XX.3f), and another with short, ventrally directed mouths (*Rhynchodoras*, Fig. XX.2g, and *Campylomormyrus alces*, Fig. XX.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 paleotropical Cyprinidae. Three cynodontid genera (*Cynodon*, *Hydrolycus*, *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 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 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 perpendicular to the substrate while minimizing lift by disrupting laminar surface flow. Striking examples of extremely dorsoventrally depressed rheophilic fishes include

275 members of the Neotropical Loricariidae (e.g. *Lithoxus*, Fig. XX.2b) and the Asian cypriniform
276 family Balitoridae (e.g., *Sinogastromyzon*, Fig. XX.3c).
277   Most benthic species are too large and high-bodied to live entirely within the boundary
278 layer. They are therefore exposed, at least along their dorsum, to some of the fastest flows in the
279 stream. Among benthic, rheophilic fish lineages, hydrodynamic forces have consistently driven
280 selection for a fusiform body with a steep, wedge-shaped head, slender caudal peduncle, and
281 large wing-like paired fins that extend laterally and are steeply canted to deflect flow dorsally
282 (Figs. XX.2b–d, XX.3b,c, XX.4c–e). This body shape and fin arrangement presents a dorsally
283 rounded and ventrally flat shape that maximizes substrate contact and hydrodynamic downforces
284 while minimizing drag. Moreover, the hydrodynamic effects of this morphology may be
285 behaviorally exaggerated by some species as water velocities increase (Carlson and Lauder,
286 2010).
287   An alternative approach taken by some non-scraping benthic rheophilic species is to
288 largely escape the flow by living and foraging mostly within interstitial spaces between or under
289 rocks and retaining or exaggerating an anguiliform body shape. Elongate, anguiliform body types
290 can be observed among rheophilic members of the neotropical catfish families Heptapteridae
291 (e.g., *Myoglanis aspredinoides*) and Trichomycteridae (e.g., *Trichomycterus*, Fig. XX.2a), the
292 African catfish family Clariidae (e.g., *Gymnallabes*), the Eurasian loach families Cobitidae (e.g.,
293 *Pangio*), Nemacheilidae (e.g., *Aborichthys*) and Gastromyzontidae (e.g., *Glaniopsis*), and the
294 spiny eel family Mastacembellidae (e.g., *Macrognathus*, Fig. XX.4a).
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296 *XX.4.2 Attachment organs*
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298 Many benthic rheophiles have specialized 'attachment organs' to prevent displacement by
299 adhering directly to substrates. In neotropical rivers, members of the invertivorous catfish family
300 Astroblepidae and invertivorous/herbivorous family Loricariidae, which are sister groups
301 (Sullivan et al., 2006), have the upper and lower lips fused into a ventrally oriented oral disc,
302 which surrounds jaws specialized for scraping substrates (Fig. XX.2j, k). Analogous oral discs
303 are seen among rheophilic invertivorous-herbivorous members of the African catfish subfamily
304 Chiloglanidinae (Mochokidae, Fig. XX.3j, k; Roberts and Stewart, 1976; Roberts, 1989b;
305 Geerinckx and De Kegel, 2014) and certain genera of the Asian catfish subfamily
306 Glyptosterninae (Fig. XX.4i; Thomson and Page, 2006). Oral adhesive discs of a different sort
307 are found in herbivorous members of the African and Asian tribe Labeonini of the Cyprinidae
308 (e.g., *Garra*, *Discogobio* and *Placocheilus*, Fig. XX.3h, i). In these examples, the lower lip is
309 greatly expanded posteriorly to form a large mental pad that is continuous around the edge of the
310 mouth via a well-developed frenum (Fig. XX.3h, i; Saxena, 1966, Stiassny and Getahun, 2007).
311 The extremities of the mental pad and rostal cap form the outer margin of the oral adhesive disc,
312 the intricacies of which are highly variable both within and between the different labeonin genera
313 in which they are found and the oral disc is thus important for labeonin classification (Zhang,
314 2005; Stiassny and Getahun, 2007) and species identification (e.g., Zhou et al., 2005; Zhang and
315 Zhou, 2012). The well-developed oral discs of lampreys are also used to attach directly to the
316 substrate in fast flowing water, especially during resting periods between bouts of active
317 swimming (Reinhardt et al., 2008).
318   The lips of a number of rheophilic fishes can also be manipulated to form temporary oral
319 adhesive organs. In members of the South East Asian cypriniform family Gyrinocheilidae, the
320 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 *Locomotion* 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 the substrate (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; Geerinkx 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 outwards from the side of the head (de Pinna, 1998; Geerinckx and Adrieaens, 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. XX.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 *Locomotion* below).

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 cup-like structure (Fig. XX.4e), which in combination with greatly enlarged pectoral fins, is considered to function as a suction disc (Gunther, 1874; Wickel, 1971; Tan, 2006; De Meyer and Geerinckx, 2014), presumably generating negative pressure between their bodies and substrates by evacuating water from between their bodies and substrates via respiration and preventing 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 (Guitel, 1888), 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 anteriormost paired-fin rays in many benthic rheophilic ostariophysans (Conway et al., 2012). The narrow paired-fin pads of non-siluriform ostariophysans are externally homogenous (despite being homoplasious) and are formed by a thickening of the epidermis and/or subdermis combined with an unculiferous superficial layer. The largest unculiferous paired-fin pads can be observed among members of the highly rheophilic catfish subfamilies Amphiliinae and Doumeinae in Africa (Amphiliidae, Fig. XX.3c) and the Glyptosterninae in Asia (Sisoridae, Fig. XX.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. XX.4f, e.g., *Glyptothorax*, *Pseudecheneis, Pseudolaguvia, Conta* and *Caelatoglanis*; Bhatia, 1950; Saxena, 1961; Sinha et al., 1990; Singh and Agarwhal, 1991; 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; Ng, 2006). In several highly benthic rheophilic sisorid taxa (e.g., *Exostoma*, *Myersglanis*, *Oreoglanis*, *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., 2012; see *Phylogenetic patterns* below). 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 *Sensation* below, Haspel et al., 2008).

XX.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 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. XX.2j), engage irregularities in the substrate with posteriorly directed odontodes on the ventral surface of their pelvic-fin spines, and propel themselves forward via

413 posterior retraction of the pelvic girdle (Crop et al., 2013). Using this method, astroblepid catfish
414 have also been observed climbing vertical wetted surfaces outside the water column (Johnson,
415 1912). In contrast to longitudinal 'ratcheting,' species in the Neotropical subfamily
416 Trichomycterinae (Trichomycteridae, Fig. XX.2a) can use external teeth (odontodes) on either
417 side of their head to gain lateral traction and 'elbow' their way upstream against fast current (de
418 Pinna, 1998).
419   A third mode of locomotion via surface attachment is the 'power burst' used by goby
420 species that lack an oral disc (e.g., *Lentipes*, *Sicydium*) and by some *Characidium* species
421 (Crenuchidae, Fig. XX.2c, d; Buckup et al., 2000). This involves strong undulations of the body
422 combined with surface detachment and attachment to move forward (Blob et al., 2006; Maie et
423 al., 2012). A fourth form of rheophilic locomotion that also involves substrate interaction is
424 anguiliform movement, in which forward movement is made through serpentine undulations of
425 the body against substrates and/or the water. Anguiliform movement is typically paired with an
426 anguiliform body shape (Fig. XX.4a) and the regular occupation of interstitial spaces under or
427 between substrates.
428
429 ***XX.4.4 Sensation***
430
431 Rheophiles, like other fishes, have at their disposal four different sensory modalities (vision,
432 mechanosensation, chemosensation, and electrosensation) to navigate and detect predators,
433 competitors, mates, and prey. Although many rheophiles have large eyes and likely good visual
434 acuity, the importance of vision can be highly variable depending on a species' activity cycle
435 (diurnal or nocturnal), their preferred water depth, prevailing water clarity (Muntz, 1982), mode
436 of foraging, and the degree to which their non-visual sensory systems are developed. Loss or
437 reduction of eyes was reported for eight rheophilic species endemic to the rapids of the lower
438 Congo River by Roberts and Stewart (1976), all of which are species that live in or under the
439 substrate, including catfishes and spiny eels with well-developed chemosensory systems. Several
440 cave-dwelling rheophilic species from around the world are also blind (e.g., *Astroblepus riberae*,
441 *Cryptotora thamicola*; Cardona and Guerao, 1994, Kottelat, 1988, 1998).
442   Given the importance of flow detection for avoidance and navigation by rheophilic fishes,
443 one might predict that the water velocity of a fish's preferred habitat would correlate with
444 development of the mechanosensory system; however, the only study we are aware of that
445 examined this found no relationship between habitat flow characteristics and the number or
446 distribution of neuromasts across 12 species of European stream fishes (Beckman et al., 2010).
447 Indeed, both the species with the greatest and the least concentrations of neuromasts were
448 considered rheophilic (Beckman et al., 2010). In an apparently exceptional case of coopting
449 dermal teeth (odontodes) for mechanosensation, Haspel et al. (2008) demonstrated that the blind
450 and cave-dwelling naked suckermouth catfish *Astroblepus pholeter* has unusually few
451 neuromasts but is able to obtain flow and substrate information via deflection of modified
452 odontodes distributed around the body (see Chapter XX for further discussion).
453   Otophysan fishes, including all minnows, catfishes, tetras, and South American
454 knifefishes, are abundant and diverse in many freshwater habitats, including rapids (Table XX.1).
455 Otophysans are considered hearing specialists because they have an inner ear–swimbladder (i.e.,
456 otophysic) connection composed of modified peri- and endolymphatic spaces and the Weberian
457 ossicles (the Weberian apparatus). These modifications are known to improve sensitivity to high
458 frequency sound (Ladich, 2000), but some rheophilic otophysans exhibit changes to the

459 Weberian apparatus that contribute to reduced hearing sensitivity. The actinopterygian
460 swimbladder is typically a single, medial, elongate organ, that occupies much of the dorsal
461 region of the visceral cavity (Longo et al., 2013). In some benthic rheophilic otophysans (e.g.,
462 some catfishes: Amphiliidae, Callichthyidae, Loricariidae, Sisoridae; and loaches:
463 Nemacheilidae, Balitoridae, Gastromyzontidae), the swimbladder is anteroposteriorly shortened,
464 anteriorly shifted to a position immediately posterior to the cranium, and subdivided into two
465 bilaterally symmetrical lobes.
466   Moreover, these groups also show varying degrees of skeletal encapsulation of the
467 bladder (see *Skeleton* below). This encapsulation and reduction in swimbladder size is correlated
468 with a reduction in the Weberian ossicles of some groups (e.g., Callichthyidae, Loricariidae), and
469 a reduction in hearing sensitivity (Lechner and Ladich, 2008). It has been suggested that in
470 benthic fishes with little or no need for buoyancy, the hydrostatic function of the swimbladder is
471 minimized and the organ is shrunk but not entirely lost because of its remaining acoustic utility
472 (Lechner and Ladich, 2008). Many non-otophysan rheophilic fishes have only a vestigial
473 swimbladder (e.g., Cichlidae: *Steatocranus tinanti*; Schulz-Mirbach, 2012) or have lost the
474 swimbladder entirely (e.g., Percidae: *Etheostoma* spp.; Evans and Page, 2003). Although
475 encapsulation of the swimbladder and modification of the external capsule structure have been
476 hypothesized to have an acoustic function in some otophysans (Weitzman, 2003), it seems more
477 likely, given the known decreases in hearing sensitivity associated with swimbladder size
478 reduction (Lechner and Ladich, 2008; Schulz-Mirbach, 2012), that the capsule functions
479 primarily to structurally reinforce a presumably weak region of the body. A second hypothesis
480 focused on the bilateral bifurcation of the bladders and the sometimes megaphone-like shape of
481 the bladder capsules (e.g., Loricariidae: *Otocinclus*; Weitzman, 2003), is that these modification
482 function to increase a fish's directional sensitivity to sound, although this hypothesis requires
483 further testing (Stewart and Smith, 2009).
484   One uninvestigated yet potential mechanosensory specialization that is seen in many
485 neotropical catfish species from fast and turbid whitewater rivers is extreme elongation of
486 caudal-fin filaments. Species in several families (e.g., Cetopsidae, Heptapteridae, Loricariidae,
487 Pimelodidae) produce long caudal filaments either throughout their life or only as juveniles. It
488 has been hypothesized that these caudal filaments may function as a specialized mechanosensory
489 system for the detection of predators approaching from downstream (Lujan and Chamon, 2008).
490 This is supported in part by research on marine (e.g., sea robins, *Prionotus* spp.) and lentic
491 freshwater fishes (e.g., gouramis, *Trichogaster trichogaster*) in which distal portions of
492 elongated fin rays have numerous free nerve endings and elicit a tactile response when touched
493 (Kasumyan, 2011). This example of elongation contrasts with the apparent trend towards
494 reduction of barbels, another typically elongate sensory structure that is shortened in several
495 clades of rheophilic fishes. For example, within the river loaches of the Eurasian family
496 Nemacheilidae members inhabiting lakes or slow flowing rivers (e.g., *Yunnanilus* or *Lefua*)
497 typically exhibit longer barbels than those inhabiting the interstitial spaces between rocks in fast
498 flowing rivers and streams (e.g., *Schistura* or *Turcinoemacheilus*). Likewise, loricariid catfishes
499 from more lentic habitat (e.g., *Pterygoplichthys*) often have much longer barbels than species
500 from fast-water habitats (e.g., *Chaetostoma*).
501   Species that have enhanced chemosensory and/or electrosensory systems are
502 disproportionately represented in specialized rheophilic fish assemblages. Chemosensory
503 specialists include all catfishes and many cypriniforms, whereas electrosensory specialists
504 include neotropical gymnotiforms (e.g., *Sternarchorhynchus*, Fig. XX.2f), African mormyrids

505 (e.g., *Campylomormyrus*, Fig. XX.3f, g) and, to a lesser extent, catfishes in the family
506 Mochokidae. In general, there is little evidence of sensory specializations developing as
507 adaptations specifically for rheophily, but rather a prevailing pattern of preadaptation of chemo-
508 and electrosensory specialists for life in fast water (Roberts and Stewart, 1976).
509
510 *XX.4.5 Feeding*
511
512 As noted under *Body shape*, many rheophilic fishes have strikingly upturned or downturned
513 mouths. The upturned mouths of rheophilic fishes are typically either a specialization for top-
514 water piscivory (e.g., *Belodontichthys*, *Macrochirichthys,* and *Securicula*), or are associated with
515 the removal of invertebrates and sponges from the sides or undersides of rocks and wood (e.g.,
516 *Gnathodolus*, *Sartor*, *Synaptolaemus*; Zuanon, 1999, Sidlauskas and Vari, 2008). Downturned
517 mouths are usually specialized for invertivory when narrow (e.g., *Rhynchodoras*, Fig. XX.2G,
518 *Sternarchorhynchus*, Fig. XX.2f, *Astroblepus*, Fig. XX.2j, *Chiloglanis*, Fig. XX.3j) or epilithic
519 algal scraping when broad (e.g., *Parodon*, Fig. XX.2h, *Cordylancistrus*, Fig. XX.2k,
520 *Euchilichthys*, Fig. XX.3k). Likewise, there is a general trend toward invertivores having
521 relatively few, long, and acute teeth (e.g., *Sartor*, *Leporacanthicus*) and herbivores having
522 smaller, broader, and more numerous teeth (e.g., *Cordylancistrus*, Fig. XX.2k, *Euchilichthys*, Fig.
523 XX.3k; Lujan et al., 2012). As noted under *Attachment organs*, oral discs that surround the
524 downturned mouths of scrapers may facilitate feeding by increasing the surface adhesion and
525 scraping friction of both the oral jaws and the surface of the disc (Ono, 1980; Benjamin, 1986).
526 Oral discs likely also facilitate prey detection when equipped with taste buds (Ono, 1980), and
527 invertivore feeding by helping to occlude the cavities in which mobile prey hide, preventing their
528 escape.
529   The teeth of rheophilic fishes are often highly specialized for particular food items and
530 some of the strangest vertebrate dentitions described to date belong to benthic rheophilic fishes
531 that scrape at substrates. For example, in members of the goby genus *Sicyopterus*, the tiny
532 functional incisor-like teeth of the premaxillae are only the terminal stage in a complicated
533 sequence of tooth development that involves a whorl of 20-40 rows of replacement teeth in
534 various stages of development (Mochizuki and Fukui, 1983). Between the basal pedicel and the
535 dentin shaft of each functional tooth in the upper jaw of *Sicyopterus japonicus* is a complex
536 articulation that provides each tooth with a certain degree of mobility, facilitating the scraping of
537 algae from irregular surfaces (Sahara et al., 2012). The ability of teeth to interact with the
538 substrate is taken to the extreme in certain groups of algivorous loricariid catfishes that possess
539 uniquely flexible teeth with a flattened region along the shaft that is composed of soft dentin and
540 unmineralized tissue, which allow the tooth to flex up to 180 degrees between the tooth's rigid
541 base and its hardened, hypermineralized cusp (Geerinckx et al., 2012). Though the majority of
542 rheophilic substrate scrapers are benthic or demersal species with broad downturned mouths, the
543 ayu (*Plecoglossus*) represents an interesting example of a seemingly unspecialized pelagic
544 rheophile that scrapes algae via rapid lateral strikes of the lower jaw against the surface of rocks.
545 The teeth in the lower jaw of the adult ayu are comb-like and contrast sharply with typical
546 conical teeth present in the upper jaw (Uehara and Miyoshi, 1993). Instead of scraping at the
547 substrate with specialized teeth, substrate scraping members of the Cypriniformes utilize highly
548 keratinized jaw sheaths that are typically formed by low block-like unculi (Roberts, 1982; Pinky
549 et al., 2004).
550

XX.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, little parental care) and only a minority are equilibrium strategists (i.e., late maturation, low fecundity, high parental care, 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, 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).

XX.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. XX.2d, Lujan et al., 2013). A reduction in 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

597 (Kullander, 1988) and percids (Zorach, 1972), and scales covering the body in nemacheiline
598 loaches that inhabit swift currents are typically reported to be small and deeply embedded (e.g.,
599 Kottelat, 1990; Zhou and Kottelat, 2005; Conway et al., 2011). Scales may be completely absent
600 in several groups of benthic rheophiles, either plesiomorphically (e.g., all groups of benthic
601 rheophilic catfishes; Fink and Fink, 1981) or uniquely derived (e.g., middle eastern species of
602 *Turcinoemacheilus*; Bănărescu and Nalbant, 1964; certain species of *Pangio*; Britz et al., 2012).
603 Reasons for scale reduction in benthic rheophilic lineages are likely numerous. In the absence of
604 functional data, we speculate that scales may simply get in the way of maintaining close contact
605 with the substrate (when on the ventral surface) or may interfere with hydrodynamics (when on
606 the head, nape or lateral body surfaces). On the other hand, the development of elongate
607 keratinous ridges (or keels) over the surface of anterior body scales in numerous groups of
608 benthic rheophilic cypriniforms and percids (Wiley and Collette, 1970) that retain them may
609 function to reduce lift by disrupting laminar water flow over the body (A. Summers, pers.
610 comm.).
611
612 *XX.4.8 Skeleton*
613
614 In contrast to the trend towards reduction of scales in benthic rheophiles, other parts of the
615 skeleton may be greatly reinforced, either through suturing, fusion or hyperossification. In
616 addition to being dorsoventrally depressed, the skulls of benthic rheophiles that are exposed to
617 strong currents often exhibit a high degree of suturing between adjacent elements (Sawada, 1982;
618 He, 1999). In members of several groups of rheophilic catfishes (e.g., Amphiliidae, Aspredinidae,
619 Loricarioidea, and Sisoridae) the vertebral column is greatly reinforced through anteroposterior
620 expansion of neural arches and spines and interlocking of pre- and postzygapophyses of adjacent
621 centra (He, 1999) or in some cases through the interlocking of accessory vertebral processes (De
622 Pinna 1996). Similar reinforcement of the vertebral column is exhibited by highly rheophilic
623 members of the Gastromyzontidae and Balitoridae (Sawada, 1982). As described under
624 *Sensation* above, several groups of rheophilic catfishes (e.g., Amphiliidae, Aspredinidae,
625 Loricarioidea, and Sisoridae; de Pinna, 1996) and benthic, rheophilic cypriniforms (e.g., cobitoid
626 loaches, Psilorhynchidae, Gobioninae; Alexander, 1964; Sawada, 1982; Bird and Hernandez,
627 2007; Conway, 2011) have elements of the vertebral column, and in some cases the
628 neurocranium, that are highly modified to form a bony capsule around the swimbladder, and this
629 capsule may serve a primarily structural role.
630 Ventral to the vertebral column, enlargement of the coracoid and basipteygium of the
631 pectoral- and pelvic-fin girdles is also common in benthic rheophilic ostariophysans (e.g.,
632 Loricariidae and Gastromyzontidae; Schaefer, 1984; Sawada, 1982), as is the strengthening of
633 the connection between these elements of the right and left sides of the body (Chang, 1945). Fin
634 rays that frequently encounter the substrate may also be heavily reinforced in benthic rheophiles.
635 Lundberg and Marsh (1976) noted two major trends in the pectoral-fin rays of cypriniform fishes
636 that they associated with degree of substrate contact, including simplification of anterior rays and
637 foreshortening of fin ray segments, with highly benthic species exhibiting higher numbers of
638 simple (unbranched) rays and shorter hemitrichial segments than benthopelagic or pelagic
639 species. They concluded that such modifications acted to increase the flexibility, tensile strength,
640 and resistance to buckling of rays that frequently contact the substrate (Lundberg and Marsh,
641 1976). Along similar lines, Taft (2011) documented a number of structural differences along the

642 length of individual lepidotrichia in the pectoral-fin rays of benthic vs. pelagic percomorphs that
643 likely effect flexibility in the former.
644
645 **XX.5 Phylogenetic patterns**
646
647 With highly divergent scales of habitat, food-web, and ecomorphological diversity, headwaters
648 and large river rapids are predicted to produce dramatically different phylogeographic and
649 morphological patterns. Clades that are widespread across upland habitats should exhibit
650 allopatric lineage diversity, low overall morphological diversity, and specializations for fast
651 water that are synapomorphic for clades encompassing all rheophiles (i.e., plesiomorphic for
652 clade members). Fish communities in large lowland river rapids should be largely paraphyletic
653 while also exhibiting higher rates of localized adaptive radiation and autapomorphic
654 specializations for life in fast water. Distributions of morphological specializations across
655 phylogenies currently available for rheophilic fishes provide support for these predictions.
656   Headwater taxa for which at least partially representative species- or subspecies-level
657 phylogenies are available include the mostly Andean Trichomycterinae (Trichomycteridae) and
658 Astroblepidae, and the predominantly South Asian Sisoridae. In studies of intraspecific genetic
659 diversity in the montane species *Trichomycterus areolatus*, Unmack et al. (2009) and Quezada-
660 Romegialli (2010) found high levels of genetic divergence across river basins draining the
661 Chilean Andes, and this molecular divergence corresponded with subtle variation in body shape
662 that may warrant recognition of additional, undescribed species (Pardo, 2002). Likewise,
663 Schaefer et al. (2011) observed relatively deep, drainage-specific genetic divergence in species
664 of *Astroblepus* from the Andes of southern Peru. Species in this study differed phenotypically
665 only in subtle characteristics of their morphology (e.g., teeth uni- or bicuspid, presence/absence
666 of adipose-fin membrane), but all shared plesiomorphic specializations for life in fast water,
667 including an adhesive oral disc, pelvic-fin friction pads, a highly mobile pelvic girdle, and a
668 distinctive 'ratcheting' form of locomotion (i.e., putative synapomorphies of the Astroblepidae).
669 The highland Andean genus *Chaetostoma* and Guiana Shield genera *Exastilithoxus* and
670 *Neblinichthys* (Loricariidae) reveal a similar pattern of shared specializations for fast water,
671 subtle phenotypic variation, and deep drainage-specific genetic divergence (NKL, unpub. data).
672   The pattern among headwater clades is a bit more complex in members of the Asian
673 catfish family Sisoridae, in which the presence/absence and specific morphology of the thoracic
674 adhesive pad shows considerable homoplasy, with up to four independent origins based on
675 phylogenetic hypotheses derived from both morphological (de Pinna, 1996; Ng, 2006) and
676 molecular data (Jiang et al., 2011). Occurrence of the thoracic adhesive pad is generally
677 correlated with occupation of fast-water habitats, although the pad is entirely absent from one of
678 the most extremely rheophilic clades (Glyptosternoidea *sensu* Peng et al., 2004), being replaced
679 therein by well-developed peripheral friction pads on the underside of the anterior snout margin,
680 barbels, and paired fins. In a molecular phylogenetic study of glyptosternoid biogeography, Guo
681 et al. (2005) attributed much of the lineage diversity within this clade to the breakup of southeast
682 Asian river drainages following uplift of the Himalayan mountains. Based on the presence of
683 well-defined patches of unculi across the body of species in the large-bodied, non-rheophilic
684 genus *Bagarius* (Roberts, 1983) and a close (possibly sister group; Jiang et al., 2011; Ng, 2006)
685 relationship between *Bagarius* and the specialized rheophilic genus *Glyptothorax* (which have a
686 synapomorphic thoracic friction pad; Jiang et al., 2011), de Pinna (1996) hypothesized that the
687 later genus may have been 'preadapted' for development of a friction pad.

688   Despite a lack of phylogenetic diversity estimates for whole fish communities in large
689 river rapids, it is clear from species lists for various rapids (e.g., lower Congo River rapids,
690 Africa; Roberts and Stewart, 1976; lower Xingu River rapids, South America; Camargo et al.,
691 2004) that these fish communities are assembled from a wide range of clades with broad
692 geographic distributions. Limited phylogenetic hypotheses available for clades inclusive of large
693 river rheophiles support the repeated occurrence of both endemic specialists (e.g., *Ossubtus
694 xinguense*, Orti et al., 2008) and localized diversification of these specialists within rapids (e.g.,
695 *Lamprologus* spp., Schelly and Stiassny, 2004; *Steatocranus* spp., Schwarzer et al., 2011;
696 *Teleocichla* spp., Kullander, 1988; *Teleogramma depressum*, Markert et al., 2010).
697
698 **XX.6 Conclusions**
699
700 Fast-water habitats in the headwaters and lowland channels of river drainages host diverse and
701 often highly specialized fish assemblages. In addition to promoting endemism and specialization
702 within their boundaries, rapids can play an import role in limiting the distributions of, and gene
703 flow among, large-bodied and/or more lentic species (Lovejoy and Araujo, 2000; Willis et al.,
704 2007; Torrente-Vilara et al., 2011). Unfortunately, humans have historically viewed large river
705 rapids less as evolutionary incubation chambers than as impediments to navigation and
706 opportunities to generate hydroelectric power. In order to both facilitate navigation and produce
707 hydroelectricity, a large shoal on the Tennessee River (Mississippi River drainage) that was long
708 famous for its diversity and abundance of unionid mussels ('Muscle Shoals') was inundated by
709 Wilson Dam in 1922 (Williams et al., 2008). Currently, the large Belo Monte dam complex is
710 under construction on the rapids of the lower Xingu River in Brazil, and the Grand Inga dam
711 complex has been proposed for rapids of the lower Congo River. Moreover, hundreds of smaller
712 dams are already under construction or are being proposed for high elevation rivers draining the
713 Andes (Finer and Jenkins, 2012) and Himalayas (Grumbine and Pandit, 2013).
714   As the shortcomings and gaps in this review illustrate, there is much yet to be discovered
715 about the ecology, diversity and evolutionary specialization of rheophilic fishes. Such studies are
716 needed now more than ever in order to fully understand the threat to biodiversity posed by major
717 human impacts. Some of these studies will require innovative techniques or new technologies.
718 For example, obtaining precise information on microhabitats and associated fish assemblages
719 within the deep and fast-flowing rapids of large river might only be possible with the use of
720 submersible video, 3D laser-mapping (e.g., Pizarro et al., 2004), and Doppler velocimetry (e.g.,
721 Jackson et al., 2009) technologies. Other studies can be conducted using currently available
722 whole specimens, tissues, and technologies. These include comparative functional studies of
723 morphological features considered to be adaptations for life in fast-flowing water, including
724 many poorly understood specializations mentioned herein (e.g., hydrodynamic function of
725 keratinous ridges on scales and sensory function of elongate caudal-fin filaments). Many aspects
726 of the patch dynamics model presented herein would benefit from more detailed phylogenetic
727 and phylogeographic studies from which interspecific relationships and gene flow between
728 populations may be inferred. To the extent possible using fossil and independent geologic
729 calibrations, it will be important to time calibrate phylogenies so that correlations between rapids
730 formation and lineage diversification may be examined. Some of these studies are currently
731 underway by ourselves and others, but many await future inquiring minds.
732
733 **XX.7 Acknowledgments**

XX.8 References

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1140
1141

1142   **Table Caption**
1143

1144 **Table XX.1** Summary of genera containing rheophilic taxa and morphological specializations
1145 associated with each. See text for further explanation. Taxonomic classification generally
1146 follows that of Nelson (2006). 'Perciformes' follows Wiley and Johnson (2011). Abbreviations
1147 (listed from left to right across table): Hyp., hyporeic; Ben., benthic; B.P., bentho-pelagic; M.P.,
1148 midwater-pelagic; T.P., topwater-pelagic; Ang., anguilliform; Dep., depressed; Fus., fusiform;
1149 Com., compressed; Inf., inferior; Sub., subterminal; Ter., terminal; Sup., superior; O.D., oral
1150 disc; P.-F.P., paired-fin pads; T.P., thoracic pad; P.-F.D., paired-fin disc. Paired-fin pads are
1151 divided between the following types: Xa, pads that are restricted to the ventral surface of rays,
1152 equipped with a superficial unculiferous layer; Xb, as in Xa but without an unculiferous layer;
1153 Xc, as in Xb but with odontodes; Xd, thickened skin continuous around ray, without forming an
1154 obvious pad and without an unculiferous layer (for detailed discussion of paired-fin pads see
1155 Conway et al., 2012a). Paired-fin discs are divided into the following types: Xa, balitorid type;
1156 Xb, gobiesocid type; Xc, gobiid type. An asterisk (*) after a generic name indicates that only
1157 some members of genus are rheophilic and a cross (†) indicates that members of this genus are
1158 migratory (either within freshwater or diadromous).
1159
1160 **Figure Captions**
1161
1162 **Fig. XX.1** A conceptual model describing longitudinal shifts in the evolutionary vs. ecological
1163 scale of processes controlling the taxonomic composition of rheophilic fish assemblages from
1164 headwaters to large river rapids. See text for further explanation and references supporting
1165 specific components of the model.
1166
1167 **Fig. XX.2** Examples of specialized rheophilic fishes from neotropical rivers: **a** *Trichomycterus*
1168 *guianensis* (Trichomycteridae; Kuribrong River, Guyana), **b** *Lithoxus jantjae* (Loricariidae;
1169 Ventuari River, Venezuela), **c** lateral and **d** ventral views of *Characidium declivirostre*
1170 (Crenuchidae; Orinoco River, Venezuela), **e** *Teleocichla* n.sp. 'preta' (Cichlidae; Xingu River,
1171 Brazil), **f** *Sternarchorhynchus hagedornae* (Apteronotidae; Inambari River, Peru), **g**
1172 *Rhynchodoras xingui* (Doradidae; Xingu River, Brazil), **h** *Parodon buckleyi* (Parodontidae;
1173 Inambari River, Peru), **i** *Ossubtus xinguense* (Serrasalmidae; Xingu River, Brazil), **j** *Astroblepus*
1174 sp. (Astroblepidae; Araza River, Peru), **k** *Cordylancistrus platycephalus* (Loricariidae; Santiago
1175 River, Ecuador). Photo **g** by L. M. Sousa, all others by NKL.
1176
1177 **Fig. XX.3** Examples of specialized rheophilic fishes from tropical African rivers: **a** *Amphilius*
1178 *zairensis* (Amphiliidae; Congo River, Democratic Republic of the Congo [DRC]), **b** *Doumea*
1179 *gracila* (Amphiliidae; Lobe River, Cameroon), **c** *Phractura fasciata* (Amphiliidae; Congo River,
1180 DRC), **d** *Lamprologus mocquardi* (Cichlidae; Congo River, DRC), **e** *Nannocharax gracilis*
1181 (Distichodontidae; Congo River, DRC), **f** *Campylomormyrus curvirostris* (Mormyridae; Congo
1182 River, DRC), **g** *Campylomormyrus alces* (Mormyridae; Congo River, DRC), **h** *Labeo* sp.
1183 (Cyprinidae; Congo River, DRC), **i** *Garra* sp. (Cyprinidae; Congo River, DRC), **j** *Chiloglanis*
1184 *congicus* (Mochokidae; Congo River, DRC), **k** *Euchilichthys* cf. *royauxi* (Mochokidae; Congo
1185 River, DRC). Photos by J. P. Sullivan.
1186
1187 **Fig. XX.4** Examples of specialized rheophilic fishes from tropical Asian rivers: **a** *Macrognathus*
1188 *pavo* (Mastacembelidae; Kyeintali Chaung River, Myanmar), **b** *Serpenticobitis zonatus*
1189 (Serpenticobitidae; Mekong Drainage, Laos), **c** *Sinogastromyzon puliensis* (Balitoridae; Wuxi

1190   stream, Taiwan), **d** *Jinshaia abbreviata* (Balitoridae; Yangtze River, China), **e** *Metahomaloptera*
1191   *omeiensis* (Balitoridae; Yangtze River, China), **f** *Glyptothorax platypogon* (Sisoridae; Ci'harang
1192   River, Indonesia), **g** *Crossocheilus elegans* (Cyprinidae, Kinabatangan River basin, Malaysia), **h**
1193   *Psilorhynchus pseudecheneis* (Psilorhynchidae; Indrawati River, Nepal), **i** *Exostoma* sp.
1194   (Sisoridae; Chao Phraya River, Thailand), **j** *Gastromyzon introrsus* (Balitoridae; Padas and
1195   Labuk rivers, Malaysia). Photo **a** by R. Britz, **i** by H. H. Ng, **h** by KWC, all others by H. H. Tan.

1196 **Table XX.1** Summary of genera containing rheophilic taxa and morphological specializations associated with each. See text for
1197 further explanation. Taxonomic classification generally follows that of Nelson (2006). 'Perciformes' follows Wiley and Johnson
1198 (2011). Abbreviations (listed from left to right across table): Hyp., hyporeic; Ben., benthic; B.P., bentho-pelagic; M.P., midwater-
1199 pelagic; T.P., topwater-pelagic; Ang., anguilliform; Dep., depressed; Fus., fusiform; Com., compressed; Inf., inferior; Sub.,
1200 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-
1201 fin pads are divided between the following types: Xa, pads that are restricted to the ventral surface of rays, equipped with a superficial
1202 unculiferous layer; Xb, as in Xa but without an unculiferous layer; Xc, as in Xb but with odontodes; Xd, thickened skin continuous
1203 around ray, without forming an obvious pad and without an unculiferous layer (for detailed discussion of paired-fin pads see Conway
1204 et al., 2012a). Paired-fin discs are divided into the following types: Xa, balitorid type; Xb, gobiesocid type; Xc, gobiid type. An
1205 asterisk (*) after a generic name indicates that only some members of genus are rheophilic and a cross (†) indicates that members of
1206 this genus are migratory either within freshwater or diadromous.

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	-	-
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	-	-

Genus	Distribution	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
*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	-	-	-	-	-

Genus	Region																	
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	-	-	-	-	-	-

Genus	Region																	
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	-	-	-	-	-	-
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	-	-

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Taxon	Region																		
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	-	-
Mesonemacheilus	India	X	X	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
Metaschistura	Central Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
Nemacheilus*	South East Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
Nemacheilichthys	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	-	-
Protonemacheilus	China	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
Pteronemacheilus	South Asia	X	-	-	-	-	X	-	-	-	X	-	-	-	-	Xa	-	-
Rakhinia	Myanmar	-	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	-	-
Tuberoshistura	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	-	-	-	-	-
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																		

Taxon	Region																		
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	-	-
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	-	-	-	Xb	-
Myloplus	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-
Ossubtus	Xingu River	-	-	X	-	-	-	-	-	X	X	-	-	-	-	-	-	-
Tometes	Tropical S America	-	-	-	X	-	-	-	-	X	-	-	X	-	-	-	-	-

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Taxon	Distribution																
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	-	-
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	-	-

Genus	Distribution																
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																	

Genus	Distribution																	
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	-	-	-	-	-	-	-
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	-	-	-	-	-	-	-
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	-	-	-	-	-

Taxon	Region																	
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	-	-	-	-	-
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

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1208   **Figure 1**

Scale of Assembly Processes
- - - - - evolutionary
————— ecological

Relative Influence on Assemblage Composition

- stream capture
- passive 'geodispersal' b/w drainages
- vicariance
- phyletic diversification

- disturbance (spates)

direction of flow →

- metapopulations
- patch dynamics
- panmixis

- island biogeography
- adaptive radiation
- active dispersal b/w habitat islands
- vicariance

- species sorting (microhabitats, niche diversity)

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

1209
1210

47

Figure 2

Figure 3

Figure 4