



FISHES OF THE GUIANA SHIELD

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History

A vast complex of wetlands, lakes, streams, and rivers drains the broad savannas, dense rainforests, extensive uplands, and tepuis of the Guiana Shield. Early European explorers and colonists were impressed not only by the many unusual fish species dwelling in these water systems but also by the diversity of the ichthyofauna. Accounts of fishes from those drainage systems commenced with descriptions by pre-Linnaean naturalists (e.g., Gronovius 1754, 1756) based on specimens returned to Europe, with Linnaeus (1758) formally describing a number of these species.

Much of the early descriptive activity involving fishes of the Guiana Shield centered on the ichthyofauna of British Guiana (= Guyana). Commentaries on fishes from that colony by Bancroft (1769) and Hilhouse (1825) preceded the formal description of catfish species from the Demerara by Hancock (1828). Cuvier and Valenciennes summarized the available information on the ichthyofauna of all of the Guianas in their series entitled *Histoire Naturelle des Poissons* that documented the fish species known worldwide to science to that time; with the catfishes being the first of the groups inhabiting the shield discussed by those authors (Cuvier & Valenciennes 1840a, b). These and the other treatments of that era were, however, largely opportunistic accounts based on scattered samples returned to Europe rather than derivative of focused studies on the fish fauna of any region on the shield. Consequently, the scale of the species-level diversity of that ichthyofauna remained unknown and underappreciated.

Indications of the scale of the richness of the fish fauna inhabiting the rivers of the Guiana Shield commenced with the expeditions of the Schomburgk brothers, Richard and Robert. In a remarkable endeavor for that era, Robert collected fishes from 1835 to 1839 both in the more accessible shorter northerly flowing rivers of the Guianas and through portions of the Río Orinoco and Río Negro and the Rio Branco. Drawings of fishes prepared during Schomburgk's travels across the shield served as the basis for 83 species accounts in Jardine's "Naturalist's Library" (1841, 1843), including the formal descriptions of a series of species. Unfortunately, the specimens that were the basis for the drawings were not preserved, and some illustrations combined details of more than one species. Subsequent expeditions by the Schomburgks traversed portions of what are now Guyana, Venezuela, Suriname, and Brazil and yielded, what was for that time, large numbers of fish specimens. In a series of publications Müller & Troschel (1845,

1848, 1849) recognized 141 species in the Schomburgk collections and provided the first detailed illustrations of fishes from South American freshwaters.

Diverse factors resulted in a lag in the state of knowledge of the fishes inhabiting many portions of the shield, with the comparative difficulty in accessibility to inland regions clearly a paramount issue for many areas. Supplementing that impediment were a series of misadventures that bedeviled collectors who sampled the fish fauna of the western portions of the shield. Alexandre Rodrigues Ferreira headed an expedition that explored a significant portion of the Rio Negro basin, commencing with a major collecting effort through the Rio Branco system in 1786 (Ferreira et al. 2007:12). Confounding Ferreira's attempts to publish his results were a string of unfortunate events that culminated with the 1807 invasion of Portugal by Napoleonic forces and the seizure and shipment of Ferreira's collections to Paris. Ferreira's report on animals from the Rio Branco region remained unpublished until long after his death, and even then, only parts appeared in print (see references in Ferreira 1983). In two expeditions between 1850 and 1852, Alfred Russel Wallace (of Natural Selection fame) collected over 200 species of fishes throughout the Rio Negro basin including rivers draining the shield. Wallace's collections were lost with the sinking of the ship returning him to England. Nonetheless, his field sketches (Wallace 2002) document that the lost collection included a number of species of fishes then unknown to science (Regan 1905a, Toledo-Piza et al. 1999, Vari & Ferraris 2006).

An accelerating pace of ichthyological collecting across many portions of the Guiana Shield during the latter part of the nineteenth century resulted in the discovery and description of numerous species. These collections also documented the presence on the Shield of many species originally described from elsewhere in cis-Andean South America. Notwithstanding those advances, the information was dispersed through revisionary (e.g., Regan 1905b, c) and monographic studies (e.g., Eigenmann & Eigenmann 1890), general ichthyofaunal summaries of regions on the shield (e.g., Pellegrin 1908), and species descriptions in multiple languages.

Exceptions to this pattern of scattered publication were limited to a handful of papers focused on subsets of the ichthyofauna from comparatively small regions. Among the more notable of these were the analysis of the catfishes of Suriname (Bleeker 1862), discussions of the fishes present in portions of French Guiana (Vaillant 1899, 1900), and a semi-popular overview of

the fishes of French Guiana (Pellegrin 1908). Compendia of the freshwater fish species known from individual colonies, countries, or regions were not developed, let alone summaries of the fishes inhabiting in the numerous streams, rivers, and lakes across the shield. The dispersed literature prevented an appreciation of the scale of the diversity of the shield ichthyofauna.

The first overview of the freshwater fishes of northeastern South America, including the Guiana Shield, was Eigenmann's (1912) treatise on the freshwater fishes of British Guiana. Although Eigenmann sampled the fish fauna of only a comparatively small section of British Guiana, his collections were extensive for that era. In a series of papers, he and his students described 128 new species from those collections (Eigenmann 1912:133). Eigenmann's monograph included data from his own collections, information from the literature, and records of fishes that originated on the Shield in various museums. Summary tables (Eigenmann 1912:64) detailed the fish species known from ten subunits that fall, at least in part, within the boundaries of the Guiana Shield (Río Orinoco basin, "West Coast" of British Guiana [= Barima River basin], Rio Branco basin, Rupununi River, Lower Essequibo River, Lower Potaro River, Demerara River, Dutch Guiana [= Suriname], and French Guiana [= Guyane Française]).

Eigenmann (1912) reported 493 species from those ten geographic units; a total that was in excess of the species reported to that time from the rivers of the Shield. These additional species were a function of two factors. His total included all of the fish species then known to inhabit the Río Orinoco; however, that vast river system extends far beyond the Shield boundaries with approximately only 40% of that watershed overlying the Shield. Many of the fish species known at the end of the first decade of the twentieth century from the Río Orinoco basin originated in the llanos (savannas) of the north central and western portions of the basin. Aquatic habitats and the fish faunas in these floodplain savanna settings differ dramatically from the ecosystems and fish communities of the more rapidly flowing rivers that drain the forested northern slope of the Guiana Shield. Further inflating Eigenmann's species total was his inclusion of some primarily marine forms. Such species penetrate the lower reaches of the rivers draining the Guianas during periods of low river flow and consequent increased estuarine salinity. Few, if any, of these species are likely to range upriver onto the Shield even during the height of the dry season.

The decades since Eigenmann's monograph have seen numerous ichthyological collecting expeditions in many systems on the Shield. Two wide-ranging and productive collecting endeavors through that region during the first half of the twentieth century remain

relatively poorly known. John Haseman, who collected throughout the Rio Branco basin and the southernmost portion of the Rupununi River system in 1912 and 1913, made the first of these. Haseman deposited these extensive collections in the Naturhistorisches Museum in Vienna where he studied them for a year in collaboration with Franz Steindachner. Nonetheless, only one major publication based on those collections was published (Steindachner 1915), most likely because of the onset of World War I, disruptions during and immediately after the conflict, and the death of Steindachner soon after the cessation of hostilities. Various revisionary studies in recent decades incorporated subsets of Haseman's collection; nonetheless, much of the material is yet-to-be analyzed critically. The second collector, Carl Ternetz, sampled fishes through the Rio Negro, Río Casiquiare, and Río Orinoco basins during 1924 and 1925. Myers (1927:107) remarked that the collection was "a magnificent series of fishes, most of them hitherto unexplored systematically by an ichthyologist." Notwithstanding the description of some new species collected by Ternetz in rivers of the shield by Myers (1927) and other authors and the use of portions of that collection in some studies (e.g., Myers & Weitzman 1960), most of the material remains unstudied, even after its transfer from Indiana University to the California Academy of Sciences.

The 1960s brought a resurgence of major ichthyological collecting efforts in many of the river systems on the shield (e.g., the Brokopondo Project; Boeseman 1968:4), with the pace of these endeavors accelerating during recent decades. A compendium of these collecting efforts lies beyond the purpose and scope of this paper; however, as summarized in the next section many of these expeditions were integral to checklists, regional revisionary studies, and summaries of the ichthyofauna in river basins or regions of the Shield.

State of Knowledge of the Shield Fish Fauna

The nearly ten decades since the preparation of Eigenmann's 1912 magnum opus saw numerous publications on fishes of the Guiana Shield. Many were revisionary studies of genera or families whose ranges extend far beyond the limits of the Shield, often across major portions of cis-Andean South America and in some instances into trans-Andean regions or occasionally Central America. Other publications were restricted to the members of a genus, subfamily, or family from a country within the Shield region (e.g., Suriname: Boeseman 1968, Nijssen 1970, Kullander & Nijssen 1989) or across a major portion of that area (e.g., Boeseman 1982). Relatively few of these papers involved broad surveys of an entire ichthyofauna in a river system or country on the Shield with those that

did so summarized below arranged by the geographic subdivisions in the checklist. Many include associated ecological and life history information for fish communities and individual species.

Brazil, Pará (PA). The single publication of note from this region is Ferreira (1993) that summarized the results of intensive collecting efforts at sites within the Rio Trombetas, one of the major northern tributaries of the Amazon River east of the Rio Negro.

Brazil, Roraima (RO). Ferreira et al. (1988) summarized the ichthyofauna at several closely situated localities in the Rio Mucajai, a tributary of the Rio Branco. More recently, Ferreira et al. (2007) provided detailed information on the ichthyofauna across the expanse of the Rio Branco basin, supplemented by numerous color photographs, discussions of habitats, and comments on the anthropogenic impact on the aquatic systems within the basin.

French Guiana (FG). French Guiana has the most intensely studied ichthyofauna of any portion of the Guyana Shield. The first attempt to summarize information on the fishes of the entire department was that of Puyo (1949). Géry (1972) followed up with studies of the characiforms (his characoids) from the Guianas with a particular focus on French Guiana. Planquette et al. (1996), Keith et al. (2000), and Le Bail et al. (2000), in a groundbreaking series of publications, brought together information on the spectrum of the freshwater fish fauna in that department. Each species account includes a description, illustration, and comments on its biology. Distributions within and beyond French Guiana are discussed, and the sites of occurrences of the species in the department are plotted.

Guyana (GU). Notwithstanding the title of the publication, Eigenmann's (1912) monographic study was based primarily on collections from the northern portions of Guyana, in particular the Potaro River and lower courses of the Essequibo and Demerara rivers, albeit with that data supplemented with information from the literature. Hardman et al. (2002) reported on the fish fauna captured at Eigenmann's collecting localities nine decades after his expedition and provided a checklist of the 272 species collected in that survey. Lowe (McConnell) (1964) included lists of fishes from the southern most reaches of the Essequibo River system along with observations on their ecology and on the movements of various species during the yearly flood and drought cycles. Watkins et al. (2004) provided a summary of the fishes of the Iwokrama Forest Reserve.

Suriname (SU). The ichthyofauna of Suriname remains relatively poorly documented, with the listing of the freshwater fishes in the country by Eigenmann (1912:64–73) largely derived from literature information. Boeseman (1952, 1953, 1954) supplemented Eigenmann's listing. Ouboter & Mol (1993) presented

the most comprehensive published list of the freshwater fishes of Suriname. Kullander & Nijssen (1989) published a detailed analysis of the cichlids of Suriname.

Venezuela, Amazonas (VA). The state of Amazonas, Venezuela, includes portions of the south-flowing Río Negro of the Amazon basin, the north-draining Río Orinoco and the entirety of the intervening Río Casiquiare. Mago-Leccia (1971) produced the first summary of the fishes of the Río Casiquiare. Lasso (1992), Royero et al. (1992), and Lasso et al. (2004a, 2004b) provided information on the fish faunas of various river systems within the state.

Venezuela, Bolivar (BO). A series of studies treated the fish fauna of several right bank tributaries of the Río Orinoco that drain the northern slopes of the Guyana Shield. These included summaries of species in various basins, with those listings supplemented in some instances by information on fish biology and distribution. Significant publications on the ichthyofauna of the Río Caroni were published by Lasso (1991) and Lasso et al. (1991a, b) and for the Río Caura by Lasso et al. (2003a, b), Rodríguez-Olarte et al. (2003), and Vispo et al. (2003). The Río Cuyuni, a western tributary of the Essequibo River, drains the eastern portions of the Shield in the state of Bolivar. Machado-Allison et al. (2000) summarized the fish fauna of the Venezuelan portions of that river system. Lasso et al. (2004a) and Girardo et al. (2007) provide supplemental information on the ichthyofauna of that drainage basin.

Ichthyofaunal Richness

This checklist of fishes known from the water systems of the Guiana Shield includes 1168 species. Included in that total are representatives of 376 genera, 49 families, and 15 orders. Five orders are dominant in terms of number of species living on the shield and account for 96.7% of the species (Characiformes, 478 species and 41.0%; Siluriformes, 425 species and 36.4%; Perciformes, 126 species and 10.8%; Gymnotiformes, 52 species and 4.5%; Cyprinodontiformes, 47 species and 4.0%). This sum of 1168 species attests to the dramatic improvement of our knowledge of the freshwater fish fauna on the Shield in slightly less than a century since Eigenmann (1912) documented fewer than 500 species from that region. The 1168 species are approximately 4.1% of the 28,400 fish species recently estimated to be present in all marine and freshwater systems worldwide (Nelson 2006), a percentage that amply testifies to the striking diversity of the ichthyofauna within that region. All the more noteworthy is the species-level richness of the ichthyofauna within the context of the overall Neotropical freshwater fish fauna. According to a recent summary, approximately 5000 species of freshwater fishes occur across the

entirety of Central and South America (Reis et al. 2003). Thus, the drainage systems of the Guiana Shield are home to approximately 23% of the freshwater fish species that occur across the vast expanse between southern South America and the southern border of Mexico. Many factors contributed to the Shield region being a repository of freshwater ichthyological diversity, with a few particularly worthy of comment.

Physiography

The Guiana Shield is the ancient Precambrian Guianan formation resulting from the uplift of the underlying craton (Gibbs & Barron 1993) and demonstrates attributes that generally lead to high levels of biodiversity: geological diversity, a topographically variable landscape, and transitions between ecosystems (Killeen et al. 2002). Overall the region has a primarily low to somewhat hilly physiography, albeit with some abrupt changes in topography in the regions proximate to the tepui formations that extend across much of the region in an approximately east to west alignment. Some river valleys have marked shifts in topography with resultant waterfalls, rapids, and riffles that increase the complexity of drainage system structure. These topographic factors result in multiple aquatic habitats with differing levels of physical complexity. At one extreme are the lentic waters of swamps, wetlands, channels, and lowland rivers. With increasing gradient, the drainage systems progress through variably flowing waters interrupted by higher energy settings such as riffles and isolated lower scale rapids. Finally, there are regions of greater gradients with rapidly flowing waters and major repetitive rapids and waterfalls. To the degree that differences in stream structure directly correlate with elevational gradients, there also occur differences in water temperatures.

Water Chemistry

Physical river system attributes are the most obvious manifestation of variation in aquatic systems across the Shield but represent a distinct subset of the spectrum of factors that contribute to shifts in the composition and relative biomass of fish communities across that region. Complementing diversity in river structure are variations in water chemistry that occur not only between but also within drainage basins across the Shield. Three major water types occur in the tropics. The first of these are white waters carrying nutrient-rich sediment loads for at least part of the year and which, despite their name, are actually brown (e.g., Rio Branco; Goulding et al. 2003:42). A second major group are clear water streams and rivers, including those draining many regions of the eastern portion of the Amazonian portion of the Shield (Pará and Amapá; Goulding et al. 2003:43). Finally there are acidic black water rivers

that drain heavily leached soils where decomposing plant matter produces high levels of fluvic and humic acids but with the water poor in dissolved solids and nutrients (e.g., Rio Negro; Goulding et al. 2003:44; Savanna Belt rivers in Suriname, Ouboter & Mol 1993:134). Such water type differences occur both at the level of major river systems and at a much smaller scale within some river basins (Arbeláez et al. 2008). Admixtures of water types resulting from within basin water type differences yield conjoined drainages with variably intermediate chemistries (e.g., downriver of where the black water Rio Negro empties into the white water Rio Solimões at Manaus, Goulding et al. 2003:44; or where the white water Rupununi River empties into the black water upper Essequibo River, Watkins et al. 2005:40).

Species of freshwater fishes demonstrate physiological, morphological, and behavioral adaptations that often allow them to specialize for life in particular water types but often simultaneously exclude them from other water types. Some species or genera are, therefore, more common in, or effectively limited to waters with particular chemical characteristics (Lowe-McConnell 1995). Exemplifying this situation are acidic black waters such as those in the Rio Negro that appear to be the primary, if not exclusive, habitat for some fish species (Goulding et al. 1988, table 2). These acidic waters are at the same time apparently inimical to other species and some genera notwithstanding the presence of these taxa in adjoining rivers of different water types (Goulding et al. 1988:98). The different water types also differ in degrees of primary productivity and dependence on detritus-based energy systems (De Jesús & Kohler 2004), factors that further impact fish diversity and community composition.

Allochthonous Influences

Terrestrial habitats further influence freshwater systems via the shift of nutrients and organic matter, with the often-substantial input into water bodies mediated by both water and wind. Terrestrial to freshwater inputs and their impacts on aquatic systems span a broad spectrum of scale. At one extreme, both continuing upland erosion and periodic floods transport dissolved and particulate matter into water bodies (Sioli 1975, Polis et al. 1997). Alternative forms of riparian vegetation also affect the amount and types of allochthonous materials, including detritus, seeds and fruits, and animals (primarily terrestrial insects) input into the aquatic food web via runoff and wind. The input of allochthonous detritus into Neotropical water systems supports particularly large populations of detritivorous fishes (Flecker 1996). Most notably, many species and groups of fishes specialize on exploiting allochthonous seeds, fruits, and insects, with variation in the input of these items impacting the

composition of ichthyofaunal communities (see Goulding et al. 1988, Boujard et al. 1990).

At the other end of the scale spectrum, alternate soil types in conjunction with factors such as rainfall regimes and temperature also support dramatically different plant communities ranging from dense rainforests through open savannas. Physical attributes of differing marginal plant communities directly influence fish community composition and structure in the water bodies that they border. Most obvious of these effects is differential shading by riparian forests, an influence that is particularly significant in terms of the species dwelling in streams and smaller rivers. Marginal vegetation and submerged macrophytes affect the physical complexity of water bodies and thus the composition of the resident ichthyofaunas in various fashions. Most noteworthy among these are differential inputs to the aquatic systems in the amount and type of woody and leafy debris, variation in the submerged portions of overhanging terrestrial plants along water margins, and differing amounts and types of submerged emergent vegetation. Synergy of drainage structure and energy, differences in water types, variation in associated riparian animals and plants, and differences in input of nutrients yield dramatically different fish communities. That variation at the local level is a major contributor to the overall species-level richness of the ichthyofauna across the totality of the Shield.

Drainage System Interconnections

Physiological and physical factors closely tie freshwater fishes to drainage patterns. Historical separations of, and associations between, drainage systems thereby contributed to the present day distributions of many species on the Shield and the richness of that fauna. Notwithstanding the tectonic quiescence of the Guiana Shield for over 550 million years, the highlands resulting from the uplift of the craton underwent progressive erosion of the sedimentary layers overlying that base (Gibbs & Barron 1993). The pronounced degree of endemism in many of the basins across the Shield is indicative of their long isolation, with factors including differences in water types being influential in this regard. Nonetheless, there have been changes in the water flow patterns on and along the margins of the Shield that influenced the present composition of the ichthyofauna in those systems.

At the large scale, tectonic events resulted in the broader details of the present Orinoco and Amazon basins, both of which contribute to the Shield ichthyofauna. A large paleo-drainage encompassing much of the present Orinoco and Amazon basin drained north into the Caribbean Sea approximately at the present location of Lago Maracaibo. Tectonic events at the end of the Miocene resulted in separation

of the Amazon from Orinoco basin (Hoorn 1994). Another consequence of these changes was the shift eastward of the mainstream Orinoco along the northern boundary of the Shield to its present mouth slightly north of the northeastern margin of the Shield. This dramatic realignment led to its capture of drainages flowing from the northern slopes of the Shield. The shift of the mainstream Amazon to its present mouth similarly resulted in the capture of the southern draining rivers of the Shield. Disrupting the continuity between many of those freshwater systems for varying periods were subsequent marine transgressions into the eastern portions of the Amazon valley. Superimposed on these large-scale drainage pattern changes were long-term, often pronounced, climate changes through the region (Baker et al. 2001) with resultant sequential contraction and expansion of suitable aquatic habitats. This combination of hydrographic and climatic changes resulted in disruptions, in some instances repeated disruptions, of previously continuous species ranges, thereby setting the stage for subsequent speciation.

The complex hydrological history of the drainages on the Shield involved not only division of previously continuous drainages but also in new connections between various river systems. Connectivity resulted from landscape tilting during uplift events and via headwater stream capture. Those events permitted, and continue to permit, movements of fishes between what have been isolated basins on the Shield. Subsequent disruptions of connectivity provided an opportunity for the evolution of species. Such past connections may account for unusual present day distribution patterns previously highlighted by some authors (e.g., Armbruster 2005). Prominent among these possible connections was the river hypothesized to have drained directly from the south slope of the Guiana Shield into the Atlantic Ocean through what is now northeastern Guyana (Hammond 2005:137). Faunal similarities and close phylogenetic relationships among included fish species also point to possible past associations between the upper Río Caroni of the Río Orinoco basin and the Río Cuyuni, a western tributary of the Essequibo River (Lasso et al. 1991a, Sabaj Pérez & Birindelli 2008). An interconnection between the Amazon and the upper portions of the Maroni River was proposed by Cardoso & Montoya-Burgos (2009) who also proposed that temporary connections between adjoining river systems during periods of lower sea levels permitted dispersal of freshwater fishes along the coasts of the Guianas.

The paramount example of an extant interconnection between major river systems on the Shield, or indeed across the continent, is the Rio Casiquiare. This over 300 km long natural canal connects the Río Negro of the Amazon River basin with the upper portions of the Río Orinoco. This unusual drainage begins as a

bifurcation of the upper portion of the Río Orinoco and represents an ongoing capture of the upper portion of the latter river system by the Río Negro (Sternberg 1975, Winemiller et al. 2008). Despite its substantial size at the divergence, where it is approximately 100 m wide, and the fact that it carries a significant portion of the total flow of that portion of the Río Orinoco, the Río Casiquiare does not provide unimpeded transit for all species of fishes between those basins. Lack of interbasin species panmixis is, in part, a function of the fact that the Río Casiquiare conjoins headwaters habitats inhabited by a subset of the species resident across the entirety of each basin. Equally, or perhaps more significantly, the gradient in water types along the course of the Río Casiquiare acts as a partial filter that impedes movement of many fish species (Winemiller et al. 2008), thereby maintaining differences in ichthyofaunal composition between the upper Río Negro and upper Río Orinoco.

Although the Río Casiquiare is the most notable connection between major rivers on the Guiana Shield and the only year-round continuity, some degree of seasonal connectivity occurs between the upper reaches of the Río Branco and the southern most portions of the Essequibo River in the Rupununi Savannas of southwestern Guyana. That region is an expansive floodplain where the headwaters of the Rupununi River (Essequibo basin) and the Takutu and Ireng rivers (both components of the Río Branco of the Amazon River basin) come into close proximity. This proximity and varying degree of continuity of the headwaters of these rivers across a vast flooded plan during high water periods [Lowe (McConnell) 1964, Watkins et al. 2005] facilitate movement of at least some fish species between the headwaters of the Río Branco and Essequibo River basins. Although such movements potentially enrich the ichthyofaunas of each of those river systems, they do not add to the overall richness of the fish fauna of the shield.

Future Directions

Notwithstanding the series of papers listed under “State of Knowledge of the Shield Fish Fauna” and many other publications, the continuing discovery and description of freshwater species from water systems on the Shield testifies to the incomplete state of our knowledge of that fish fauna. The primary impediment is the lack of exhaustive ichthyological collecting across that vast region, with many river systems still effectively unsampled (e.g., the upper Mazaruni River in Guyana; Taphorn et al. 2008). Headwater tributary streams, deep mainstream channels, and difficult-to-sample habitats such as swamps and rapids remain unsampled or poorly sampled even in those drainage systems that have been the subject of ichthyological collecting efforts. Those habitats and some largely

ichthyologically unexplored drainage systems hold the greatest promise as sources of undescribed species; however, we must not lose sight of the fact that areas that have been long the foci of ichthyological sampling continue to yield new species and are deserving of continued attention. Recent monographic studies of speciose genera and families of Neotropical freshwater fishes demonstrate that collections in museums, universities, and research institutions of North and South America and Europe house numerous species as of yet unknown to science. Indeed in many groups, the vast majority, if not all, of recently described species were already represented in collections and awaited discovery, often for many decades.

Thorough sampling of the freshwater fish fauna is vital as is the thorough examination of materials in collections, but equally or perhaps more important for furthering our knowledge of the fishes on the Shield are comprehensive revisionary studies of all groups of fishes represented in that ichthyofauna. Such in-depth studies are critical given our inadequate understanding of the species-level diversity of many Neotropical freshwater groups (Vari & Malabarba 1998). Inclusive revisions of complex groups of Neotropical freshwater fishes have repeatedly demonstrated that the sum of long recognized species within a genus typically underestimates the actual number of species in a taxon, sometimes to a pronounced degree. An example is the 67 species now recognized in *Creagrutus*; a total three and one-half times the number of species (19) recognized in the genus prior to 1994 (Harold & Vari 1994, Vari & Harold 2001, Vari & Lima 2003, Ribeiro et al. 2004, Torres-Mejia & Vari 2005). Comprehensive revisions similarly further the subsequent identification of additional previously unrecognized species by other researchers (Reis 2004).

It is impossible to estimate the degree to which the total number of freshwater fish species summarized in this checklist falls short of the actual count of species dwelling on the Shield. Nonetheless, it is clear that the rate of continued additions to this speciose fish fauna, the many regions and habitats that have not yet been thoroughly explored ichthyologically, and the large numbers of groups of fishes in the region that have not yet been exhaustively studied portend a significant increase in the species total.

Conservation Challenges

Deleterious anthropogenic activities impact freshwater ichthyofaunas across the Neotropics (Killeen 2007), with many affecting various portions of the Guiana Shield and adversely influencing fish communities in the region. Adverse impacts are pervasive across freshwater ichthyofaunas worldwide (Millennium Ecosystem Assessment 2005, Revenga et al. 2005), with freshwater fishes consequently the most threatened

groups of vertebrates across the world in terms of affected species (Dudgeon et al. 2006, Chapman et al. 2008). Major impacts on freshwater ichthyofaunas of the Guiana Shield cover the spectrum of human activities. These include overfishing for human consumption and the aquarium trade, pollution from agricultural, domestic, industrial and mining sources, diversion of water for agricultural, domestic, and industrial purposes, mining within river channels, introductions of exotic species, transplanting of native species between separate drainage systems, deforestation within drainage basins with consequent changes in water flow patterns and quality, increased erosion and siltation as a consequence of development, agriculture, and mining operations, and impoundments for hydroelectric and irrigation systems with disruption of migration routes for fishes.

Major advances are necessary before we approach a definitive understanding of the species-level diversity for the fishes inhabiting the rivers, streams, lakes, and other water bodies on the Guiana Shield. Nonetheless, the following Checklist can serve as a foundation for future studies, leading to a better appreciation of the diversity of that ichthyofauna. Such information is vital to inform decisions by resource managers, government agencies, and members of the public interested in protecting both the fish fauna and the broader aquatic communities, both of which provide essential and important ecosystem services across the Shield.

Species of the Guiana Shield

The Checklist includes species recognized at the time that contributors completed their accounts (mid-2008) with these supplemented whenever possible by information on new species described from the Shield through early 2009. Readers interested in further information on the families and species included in the listing can refer to CLOFFSCA (Reis et al. 2003). That listing includes bibliographic information for all fish species in Central and South America, including those known to occur on the Guiana Shield, through the end of 2002. References to the original descriptions of species published post that date are listed under the following Guide to the Checklist. The regions utilized in the checklist correspond to those used for terrestrial vertebrates in Hollowell & Reynolds (2005). Abell et al. (2008) recently proposed a hydrographically delimited series of zones for South America. The more fine-scaled resolution of that system is potentially more informative in terms of areas of regional endemism for aquatic organisms. We defer, however, from applying it to the freshwater fishes of the Guiana Shield given the large degree of uncertainty as to distributional limits for most species in that fish fauna.

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