# Diversity and distribution of anostomoid fishes (Teleostei: Characiformes) throughout the Guianas**

by

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**ABSTRACT**. - Fifty-six species or approximately 20% of the Neotropical characiform superfamily Anostomoidea (families Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae) occur in the freshwaters of French Guiana, Guyana, and Suriname although these regions span only approximately 6% of the native range of this morphologically and ecologically diverse superfamily. As a result of the high diversity of anostomoids in the Guianas, the taxonomic and/or geographic boundaries of many species are poorly understood, particularly within the family Anostomidae. This contribution unites results of prior taxonomic revisions with surveys of the holdings of the superfamily in seven major natural history collections to provide distribution maps and keys to the identification of all anostomoid species known to occur in the Guianas. These maps reveal six major areas of endemism: the Takutu and Ireng rivers (Rio Branco drainage, Amazon basin), the Barima and Waini rivers (Orinoco drainage), the Essequibo-Rupununi River system (including the Demerara and Berbice rivers), a union of the Corantijn, Nickerie, Coppename, Saramacca and Suriname river drainages, the Marowijne/Maroni River system (including the Litani and Mana rivers), and the Oyapock-Approuague River basins. Of these, the Essequibo-Rupununi system harbours the most exceptionally diverse assemblage of anostomoid species, likely as a result of faunal exchange between the Rio Branco and Essequibo River across the Rupununi portal.

**RÉSUMÉ**. - Diversité et distribution des poissons anostomoides (Teleostei, Characiformes) dans les Guyanes.

Cinquante-six espèces, soit approximativement 20% des Characiformes de la superfamille des Anostomidea (familles des Anostomidae, Chilodontidae, Curimatidae et Prochilodontidae), fréquentent les eaux douces de la Guyane française, du Guyana et du Suriname bien que ces régions ne recouvrent qu'environ 6% de la distribution naturelle de cette superfamille morphologiquement et écologiquement très diverse. Étant donnée cette grande diversité des anostomoides guyanais, les limites taxonomiques et/ou géographiques de nombreuses espèces sont mal définies, particulièrement dans la famille des Anostomidae. Ce travail combine les résultats de révisions taxonomiques antérieures à l'étude de sept collections majeures d'histoire naturelle afin de fournir des cartes de distribution et des clés d'identification de toutes les espèces d'anostomoides connues des Guyanes. Ces cartes révèlent six aires d'endémisme principales : les rivières Takutu et Ireng (bassin du Rio Branco, système de l'Amazone), Barima et Waini (bassin de l'Orénoque), le système Essequibo-Rupununi (incluant le Demerara et le Berbice), les bassins des fleuves Corantijn, Nickerie, Coppename, Saramacca et Suriname, le système Marowijne/Maroni (incluant la Litani et la Mana), et les bassins de l'Oyapock et de l'Approuague. Parmi ces six aires d'endémisme, le système Essequibo-Rupununi héberge un ensemble d'espèces exceptionnellement diversifié, résultant vraisemblablement d'échanges d'ichtyofaune entre le Rio Branco et l'Essequibo via le portail du Rupununi.

Key words. - Biogeography - Dichotomous key - Georeferencing - South America - Synthesis - Taxonomy.

The Neotropical characiform superfamily Anostomoidea contains approximately 275 recognized species (Reis *et al*., 2003, plus species described subsequently). These ecologically and morphologically diverse species range from the often large-sized and economically important detritivores of the families Prochilodontidae and Curimatidae that play critical roles in nutrient cycling in many river systems (Taylor *et al*., 2006), to the omnivorous and herbivorous headstanders of the Anostomidae and Chilodontidae. Though anostomoids clearly form a natural group (Vari, 1983) and are among the best-studied members of the Characiformes, their alpha, beta and gamma diversity remains incompletely understood. Descriptions of new anostomoid species still appear regularly (Britski and Garavello, 2005; Vari and Chang, 2006; Scharcansky and Lucena, 2007; Sidlauskas *et al*., 2007; Britski and Birindelli, 2008; Santos and Zuanon, 2008; Birindelli and Britski, 2009; Vari *et al*., 2012). The taxonomic limits and geographic distributions of some long-recognized species frequently remain hazy, particularly within the family Anostomidae, which has never been the subject of a comprehensive revision.

The north-flowing drainages of the portions of the Guiana Shield in French Guiana, Guyana and Suriname (hereafter the Guianas) along with the Takutu and Ireng rivers which form the northeastern portion of the upper Rio Branco basin in southern Guyana (Fig. 1) comprise a

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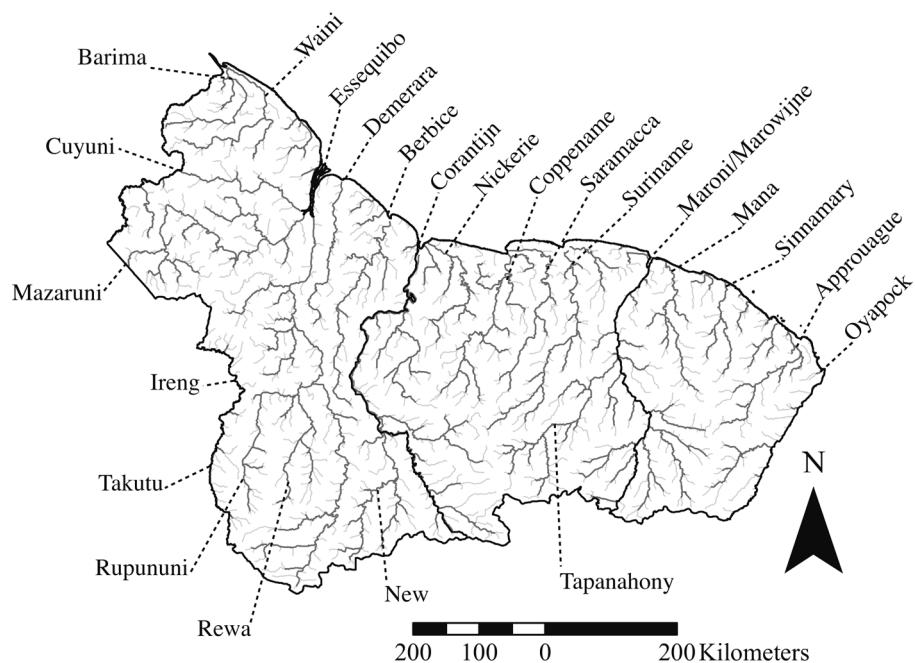
Figure 1. - Major river systems of the Guianas. Stream network prepared by the Nature Conservancy from a digital elevation model.

major area of diversity and endemism for many groups of Neotropical freshwater fishes, including anostomoids. The discovery of the exceptional biodiversity of anostomoids in the Guianas commenced with the earliest surveys of the region in the 18th century. Species now recognized as *Anostomus anostomus* (Linnaeus, 1758)*, Leporinus fasciatus* (Bloch, 1794) and *L. friderici* (Bloch, 1794) were described from localities likely or definitely in Suriname. A continuing stream of descriptions of anostomoid species from the Guianas by Müller and Troschel, Cuvier and Valenciennes, Steindachner, Eigenmann, Fowler and more recent authors ensued. Continuing surveys in the region regularly reveal new species (Sidlauskas *et al*., 2011; Vari *et al*., 2012) although longstanding taxonomic confusion stemming from the imprecise nature of many earlier descriptions hampers formal systematic or faunistic work. Ready identification and understanding of the biodiversity of anostomoids, most notably anostomids, in the Guianas is impeded by myriad factors including brief original species descriptions, complex or lost type series, a proliferation of potential junior synonyms discriminated on less than trenchant differences, and indefinite geographic distributions. Further complications include the historic application of some of the earliest species names to complexes of externally similar forms with distributions spanning huge swaths of South America (e.g., *Leporinus friderici*), the co-occurrence of many superficially similar species, and a confounding tendency of species in the Anostomidae to undergo major ontogenetic shifts in colour pattern and sometimes mouth position (Santos, 1980; Sidlauskas *et al*., 2007; Birindelli and Britski, 2009).

This contribution aims to ameliorate the confusion sur-

rounding the taxonomy and biogeography of anostomoids in the Guianas by synthesizing the extant systematic literature with new surveys, reidentifications and georeferencing of specimens from this region in several natural history collections. Our effort represents an attempt to:

1) sort the anostomoid diversity in the Guianas into distinct morphospecies;

2) illustrate the geographic range of each morphospecies;

3) provide dichotomous keys specific to the anostomoid morphospecies in the Guianas; and

4) determine the extent to which the various river systems of the Guianas harbour endemic faunas.

In the Chilodontidae, Curimatidae, and Prochilodontidae, these efforts derive from comprehensive revisionary studies (Vari, 1982; Isbrücker and Nijssen, 1988; Vari, 1989a; Vari, 1989b; Vari, 1989c; Vari, 1989d; Vari, 1991; Vari, 1992a; Vari, 1992b; Vari *et al*., 1995; Castro and Vari, 2004) and subsequent publications. Neither an encompassing revision nor modern comprehensive keys for the Anostomidae exist. For the purposes of this contribution, individuals within the Anostomidae were sorted into recognizable morphospecies and then identified through reference to the primary taxonomic literature, including original species descriptions and generic and regional taxonomic revisions. This contribution does not constitute a formal revision of all members of the Anostomidae across the Guianas, which for certain species-complexes would require the critical analysis of extensive series of samples originating from vast portions of tropical South America. The results, nonetheless, highlight many range extensions, identify several likely junior synonyms
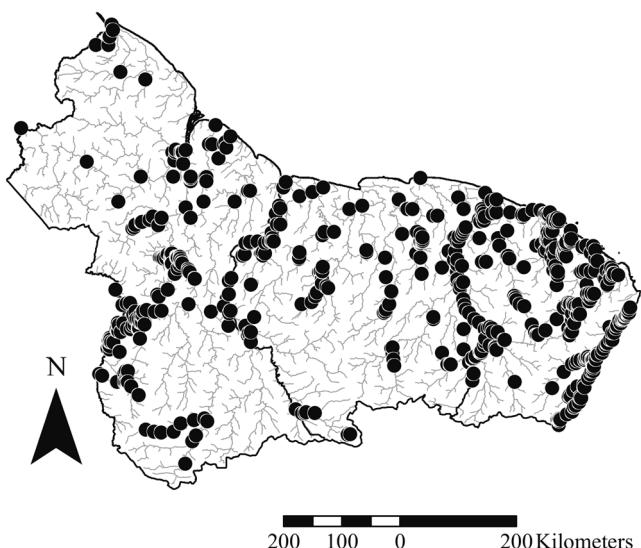
Figure 2. - Total extent of collection localities represented among included specimen lots.

and reveal the existence of morphoclines or multiple recognizable entities within certain nominal species. We discuss these taxonomic issues herein, but leave the formal synonymization of described forms and description of potentially new species to future revisionary efforts.

## MATERIALS AND METHODS

We examined and compiled information on 1,272 lots representing nearly-complete anostomoid holdings of four natural history collections with major holdings from Guyana and Suriname (American Museum of Natural History, AMNH; Academy of Natural Sciences of Philadelphia, ANSP; Auburn University Ichthyology Collection, AUM; and the National Museum of Natural History, USNM) as well as partial holdings from three institutions (Field Museum, FMNH; Muséum d'Histoire Naturelle de la Ville de Genève, MHNG; and Nationaal Natuurhistorisch Museum Naturalis, RMNH). A spreadsheet containing museum catalogue numbers, vouchered identifications and geographic coordinates for these 1,272 lots is available as an online supplement. Individuals of the Chilodontidae, Curimatidae and Prochilodontidae were identified using keys from recent taxonomic revisions, updated where appropriate to reflect subsequent species descriptions and additional data on morphological variation. Material from French Guiana was far less common in the collections of these seven institutions, but time constraints prevented visits to collections housing more extensive holdings of material from that department. Largely offsetting that impediment is the information on the occurrence and distribution of freshwater fish species of French Guiana in the excellent accounts by Planquette *et al.*

(1996), and identifications of additional material from that department at MHNG by Sonia Fisch-Muller and Raphaël Covain based upon the keys presented herein. We included 1,561 records from the Planquette *et al.* (1996) accounts and updated their identifications to reflect subsequent pertinent revisionary efforts (e.g., *Prochilodus* in the Prochilodontidae, Castro & Vari, 2004), resulting in a total of 2,833 lots that underlie this study.

The dichotomous keys for the Chilodontidae, Curimatidae and Prochilodontidae presented herein draw upon previously published keys (Vari, 1989c; Vari, 1991; Vari, 1992a; Vari, 1992b; Vari *et al.*, 1995; Castro and Vari, 2004) updated where appropriate to reflect subsequent publications (e.g., Vari *et al.*, 2012) and revised to clarify certain ambiguities or to more accurately capture and focus on breaks in morphometrics, pigmentation or meristics observed in anostomoids from Guyana, Suriname, and to a more limited extent, French Guiana. A portion of the key to the Anostomidae extracts couplets from earlier efforts (Winterbottom, 1980; Planquette *et al.*, 1996; Sidlauskas and Santos, 2005) supplemented by data from recent species descriptions (Sidlauskas *et al.*, 2011). Much of the key to that family is, however, based on new measurements and observations of specimens from Guyana and Suriname. The keys are intended for use only with samples from the targeted geographic area and will not necessarily diagnose individuals from outside the Guianas to the correct genus, let alone species.

Because members of the Anostomidae exhibit an extreme range in mouth orientation, we follow Winterbottom (1980) and take standard length from the anteriormost point of the head (which in species with upturned mouths is not always the anterior margin of the snout) to the posterior margin of the hypurals. Postorbital length and head length are measured to the posteriormost bony margin of the opercle. Orbital diameter is difficult to measure in some curimatids because of the presence of an adipose eyelid, but is taken from the anterior margin of the orbit at the ventral wing of the lateral ethmoid to the posterior margin of the orbit. Gape width is the distance measured between the opposite limits of the mouth. Vertebral counts include the four vertebrae of the Weberian apparatus and the composite terminal centrum (counted as a single unit).

The distribution maps represent a combination of lots of material that we examined from AMNH, ANSP, AUM, FMNH, MHNG, RMNH and USNM and published lists of examined material that we consider to be reliably identified and georeferenced. Material in that latter category includes type series and specimens cited in recent formal taxonomic revisions, such as the extensive series of specimens of the Guianas deposited in various institutions that was examined in revisions of the genera of the Chilodontidae (Isbrücker and Nijssen, 1988; Vari *et al.*, 1995), Curimatidae (Vari, 1982; Vari, 1989b; Vari, 1989c; Vari, 1991; Vari, 1992a; Vari,

1992b) and Prochilodontidae (Castro and Vari, 2004). Where possible, lots lacking explicit latitude and longitude information were assigned coordinates by reference to gazetteers, maps, publications, and online sources. In total, 2667 lots of material were assigned to point localities spanning much, but not all of Guyana, Suriname and French Guiana (Fig. 2). The 166 examined lots with ambiguous localities (e.g., Suriname or Guiana Highlands) were not plotted. Maps were prepared in ArcMap 9.3 (Environmental Systems Resource Institute, 2008) using an underlying river network based on a digital elevation model that was made available by Paulo Petry of The Nature Conservancy. Every point on these distribution maps is tied to a specific specimen lot, which are listed in the online appendix with the exception of data previously published in Planquette *et al.* (1996) and kindly provided for reproduction in this article by Dr. Philippe Keith (Muséum national d'Histoire naturelle, Paris). Copyright to those data remains with INRA-MNHN. Most photographs were prepared using the phototank immersion method of Sabaj Pérez (2009)

## RESULTS

### Key to families of Anostomoidea in Guyana, Suriname and French Guiana

**1a:** Jaws with well-developed teeth firmly implanted in upper and lower jaws. . . . . . . . . . . . . . . . . . . **Anostomidae**
**1b:** Jaws either lacking dentition in adults or teeth movably attached to fleshy lips . . . . . . . . . . . . . . . . . . . . . . . . . . **(2)**

**2a:** Jaws lacking any teeth other than in larvae; lips thin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Curimatidae**
**2b:** Dentition present on at least upper jaw, although sometimes reduced; lips or at least upper lip variably fleshy. . . **(3)**

**3a:** Jaws evertible into suctorial disk; oral teeth numerous with multiple rows of replacement teeth arranged in linear series extending towards oral cavity; teeth spatulate. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Prochilodontidae**
**3b:** Jaws not evertible; oral teeth sparse and limited to single functional row, sometimes limited to upper jaw; teeth typically conical, rarely bicuspid. . . . . . . . . . . . . **Chilodontidae**

### Key to Anostomidae from Guyana, Suriname and French Guiana

**1a:** Caudal-fin rays largely covered with scales . . . . . . . . . . . . . . . . *Leporellus vittatus* (Valenciennes, 1850) (Fig. 3A)
**1b:** Caudal-fin rays not covered by scales other than immediately proximate to hypurals . . . . . . . . . . . . . . . . . . . . . . **(2)**

**2a:** Mouth inferior. Premaxilla oriented such that long axis of premaxillary teeth points ventrally or slightly posteroventrally . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Hypomasticus* **(3)**

**2b:** Mouth subterminal, terminal, supraterminal or superior, but not inferior. Premaxilla oriented such that long axis of premaxillary teeth points anteriorly or anteroventrally . . . **(4)**

**3a:** Lateral surface of body covered with numerous small spots, with spot below lateral line largest and surrounded by ring of eight discrete and evenly spaced spots (other spots also present on flanks) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Hypomasticus megalepis* (Günther, 1863) (Fig. 4A)
**3b:** Lateral surface of body with multiple longitudinal dark stripes . . . . . *Hypomasticus despaxi* (Puyo, 1943) (Fig. 4H)

**4a:** Premaxillary teeth, including symphyseal tooth, strongly and uniformly bicuspid or multicuspid, with all cusps on each tooth roughly equivalent in size and forming continuous jagged edge. Premaxillary teeth exclusive of tooth furthest from symphysis all of approximately equal size. . . . **(5)**
**4b:** Premaxillary teeth not uniformly bicuspid or multicuspid; each tooth typically with single large central cusp (symphyseal premaxillary tooth bicuspid in *Anostomoides,* and some premaxillary teeth with additional smaller cusps in *Leporinus*). Premaxillary teeth decreasing in size in stepwise fashion posteriorly from symphysis . . . . . . . . . . . . . . . . **(15)**

**5a:** In individuals over 40 mm SL dentary teeth incisiform and forming continuous bladelike cutting edge. Individuals below 40 mm SL with multicuspid dentary teeth. Dark pigmentation pattern of varying intensity present on body in individuals of all sizes, but typically with complete midlateral stripe and four diffuse vertical bars on sides of body. Dorsal surface of body with series of dark transverse bars in individuals smaller than 90 mm SL. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Laemolyta proxima* **(Garman, 1890) (Fig. 3E)**

**5b:** In individuals of all sizes, dentary teeth multicuspid or some teeth with truncate margins, but series never forming continuous bladelike cutting edge. Dark pigmentation pattern variable, but not similar to condition described in 5a except in *Schizodon vittatus* (Valenciennes, 1850), which shares four vertical bars and, but has partial midlateral stripe restricted to caudal peduncle and lacks transverse bars across dorsal surface of body in individuals of all sizes. . . . . . . . **(6)**

**6a:** Body with four vertical dark bars and dark spot or partial lateral stripe at base of median caudal-fin rays. Intensity of vertical bars greatest at lateral-line scale row. All dentary teeth strongly multicuspid resulting in overall jagged distal tooth margins. Exposed portion of dentary teeth wider than high. Mouth terminal in specimens larger than approximately 90 mm SL, slightly supraterminal in individuals between 40 and 90 mm SL and distinctly supraterminal in individuals of less than 40 mm SL. . . . . . . . . . . . . . . . . *Schizodon* **(7)**
**6b:** Dark body pigmentation not as in 6a. Dentary teeth either uniformly with two or more cusps or with symphyseal tooth having truncate margin. Exposed portion of dentary

teeth higher than wide. Mouth superior in individuals of all sizes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(8)**

**7a:** Body with dark lateral stripe connecting posteriormost vertical blotch to dark spot at base of median caudal-fin rays . . . . . . . . *Schizodon vittatus* (Valenciennes, 1850) (Fig. 3D)

**7b:** Body lacking dark lateral stripe connecting posteriormost vertical blotch to dark spot at base of median caudal-fin rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Schizodon fasciatus* Spix & Agassiz, 1829 (Fig. 3C)

**8a:** Pigmentation consisting of many wide dark vertical bands completely ringing body and separated by much thinner light bands. Symphyseal tooth of dentary substantially longer than adjacent tooth. Lips with distinct papillae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Synaptolaemus cingulatus* Myers and Fernández-Yépez, 1950 (Fig. 3J)

**8b:** Pigmentation not as in 8a. Symphyseal tooth of dentary approximately equal in size to adjacent tooth. Lips buckled and ridged, but without distinct papillae . . . . . . . . . . . . . . **(9)**

**9a:** Pigmentation on body consisting of numerous dark longitudinal stripes . . . . . . . . . . . . . . . . . . . . . *Anostomus* **(10)**

**9b:** Pigmentation on body consisting of one or more dark spots centred on lateral-line scale row and dark transverse markings across dorsal surface of body. . . . . . . . . . . . . **(12)**

**10a:** Pale middorsal stripe extending from tip of supraoccipital spine to dorsal-fin origin. Several thin light and dark stripes on anterior half of body dorsal to thick dark stripe along lateral-line scale row. Three branchiostegal rays . . . . . . . . . *Anostomus ternetzi* Fernández-Yépez, 1949 (Fig. 3H)

**10b:** Dark middorsal stripe extending from tip of supraoccipital spine to dorsal-fin origin. Single dark stripe midway between middorsal stripe and midlateral stripe on lateral-line scale row. Four branchiostegal rays . . . . . . . . . . . . . . . **(11)**

**11a:** Greatest body depth 24.0-27.1% of SL (mean 25.6%) among specimens from Suriname. 12 caudal vertebrae, including ural centrum and vertebra of haemal spine which lies just anterior to first anal pterygiophore. Dorsal and caudal fins hyaline in life. Red pigment not present on caudal peduncle, anal or pelvic fins in life . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anostomus brevior* Géry, 1961 (Fig. 3F)

**11b**: Greatest body depth 20.1-24.2% of SL (mean 21.9%) among specimens from Guyana and Suriname, the upper limit reached only in large individuals over 100 mm SL. 11 (rarely 12 or 13) caudal vertebrae. Dorsal and caudal fins with red pigment in life. Red pigment sometimes present on caudal peduncle, anal fin and pelvic fins in life . . . . . . . . . . . . . . . . . . *Anostomus anostomus* (Linnaeus, 1758) (Fig. 3G)

**12a:** Distal margin of symphyseal dentary tooth truncate in individuals greater than 60 mm SL, sometimes multicuspid in smaller individuals. Usually four well-defined dark spots along lateral-line scale row, though anteriormost spot sometimes faded. Dark transverse bars present over entire body

dorsal to lateral line, and usually below lateral line as well. Distance from snout to pelvic-fin origin usually greater than, rarely equal to, distance from dorsal-fin origin to caudal-fin origin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Petulanos* **(13)**

**12b:** Symphyseal dentary tooth bicuspid in individuals of all sizes (occasionally truncate from wear in large individuals > 80 mm SL). Usually two or three well-defined dark spots along lateral-line scale row (four in *Pseudanos gracilis* [Kner, 1858], species not known from the Guianas). Dark transverse bars sometimes present across dorsum, but not present over entire body dorsal to lateral line. Distance from snout to pelvic-fin origin less than, or equal to, distance from dorsal-fin origin to caudal-fin origin . . . . . . *Pseudanos* **(14)**

**13a:** Transverse bars on body broad, typically two scales wide. 40-42 lateral-line scales. Second and third spots on lateral-line scale row typically three scales deep . . . . . . . . . . . . *Petulanos spiloclistron* (Winterbottom, 1974) (Fig. 5B)

**13b:** Transverse bars on body thin, typically one scale wide. 38-39 lateral-line scales. Second and third spots on lateral-line scale row typically less than three scales deep . . . . . . . . . . . . . . . . *Petulanos plicatus* (Eigenmann 1912) (Fig. 3K)

**14a:** Centres of scales dark, forming longitudinal rows of small spots along scale rows . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Pseudanos irinae* Winterbottom, 1980 (Fig. 3I)

**14b:** Centres of scales light. Occurrence in extreme southwestern Guyana based on single specimen from the Rio Puara in Rio Ireng-Takutu-Branco system . . . . . . . . . . . . . . . . . . . . . . . *Pseudanos trimaculatus* (Kner, 1958) (Fig. 5A)

**15a:** Body very deep and diamond shaped. Ten or more branched anal-fin rays. Three branchiostegal rays. Colour pattern with multiple alternating dark and light vertical bars on body and anterior portion of dorsal fin. Margins of pelvic and adipose fins intensely dark. Occurrence in extreme southwestern Guyana based on single specimen from indefinite locality in Ireng-Takutu-Branco system . . . . . . . . . . . . . . . . *Abramites hypselonotus* (Günther, 1868) (not figured)

**15b:** Body fusiform. Eight branched anal-fin rays. Usually four branchiostegal rays (three in *Anostomoides*). Colour pattern variably striped, barred or spotted, but similar to the condition in 15a only in *Leporinus desmotes* . . . . . . . . . **(16)**

**16a:** Mouth supraterminal. Tip of symphyseal premaxillary tooth noticeably notched, forming two cusps. Three branchiostegal rays. Dark pigmentation on body consisting of one to three irregular vertical blotches and occasionally faint stripe along lateral-line scale row; stripe darkest near caudal-fin base . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Anostomoides laticeps* (Eigenmann, 1912) (Fig. 3B)

**16b:** Mouth terminal or subterminal. Symphyseal premaxillary tooth typically with one large central cusp (one or two additional smaller cusps present in some species). Four branchiostegal rays. Dark pigmentation on body variable, but not as in 16a. . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Leporinus* **(17)**

**17a:** Dark pigmentation on body consisting of series of vertical bars with intervening lighter regions . . . . . . . . . . . . **(18)**

**17b:** Dark pigmentation on body not as in 17a (specimens may have dark longitudinal stripes, various patterns of spots, etc.) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(20)**

**18a:** Dark pigmentation on body consisting of alternating wide and narrow vertical bars. Eight (rarely nine) branched pelvic-fin rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .
. . ***Leporinus maculatus*** Müller & Troschel, 1844 (Fig. 4N)

**18b:** Dark pigmentation on body consisting of multiple vertical bars, each of approximately equal width. Nine branched pelvic-fin rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(19)**

**19a:** Dark pigmentation on body in juveniles and adults consisting of seven or eight regularly spaced vertical bars beginning with bar situated on opercle; second bar typically in form of "X". Additional dark bar present dorsal to eye in specimens of all sizes. Anterior portion of dorsal fin darkly pigmented. Mouth slightly subterminal. Symphyseal dentary teeth jaw distinctly elongate, laterally compressed and forming distinct tusks . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .
. . . . . . . . . . . . ***Leporinus desmotes*** Fowler, 1914 (Fig. 4K)

**19b:** Dark pigmentation on body in adults consisting of ten regularly spaced vertical bars beginning with bar situated on opercle. Large adults have bars partially split dorsally and ventrally by lighter regions, giving appearance of very narrow "X"s. Dark bar dorsal to eye present in juveniles, but faded or absent in some adults. Dark pigmentation on body in juveniles with irregularly spaced bars, often arranged in sets of adjacent pairs. Anterior portion of dorsal fin hyaline (sometimes darkly pigmented in small juveniles). Mouth terminal. Symphyseal dentary teeth larger than adjacent teeth but not distinctly elongate and laterally compressed into distinct tusks . . . ***Leporinus fasciatus*** (Bloch, 1794) (Fig. 4C)

**20a:** Multiple dark longitudinal stripes present on body, with stripe along lateral-line scale row widest and most intense. .
. . . . . . . . . . . . ***Leporinus arcus*** Eigenmann, 1912 (Fig. 4B)

**20b:** Dark pigmentation on body not as in 20a . . . . . . . . **(21)**

**21a:** Shallow bodied, with maximum body depth 19-25% of SL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(22)**

**21b:** Deep bodied, with maximum body depth 28-38% of SL . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(24)**

**22a:** Dark partial stripe running along lateral-line scale row from below dorsal-fin base to caudal–fin base in individuals larger than 40 mm SL. Stripe sometimes interrupted with light bars in small juveniles under 40 mm SL. Three or four additional dark spots arranged in oblique row just posterior to opercle and ventral to lateral-line scale row . . . . . . . . . .
. . . ***Leporinus nigrotaeniatus*** (Jardine, 1841) (Figs 4F, 4G)

**22b:** Multiple dark spots present along lateral-line scale row and at least one discrete spot situated ventral to that scale

row in individuals of all sizes. Additional dark spots variably present, but not in pattern described in 22a . . . . . . . . . . . **(23)**

**23a:** Five scales in transverse series above lateral line. Three pairs of spots positioned intermediate to four spots centred along lateral-line scale row. Each pair of spots with one member above lateral-line scale row and one below, with overall form of each pair reminiscent of colon . . . . . . . . . . .
. . . . . . ***Leporinus ortomaculatus*** Garavello, 2000 (Fig. 4E)

**23b:** Six (rarely five) scales in transverse series above lateral line. Four large spots along midlateral surface of body; first centred just below lateral-line scale row and other three centred on lateral-line scale row, but without intervening pairs of dark spots reminiscent of colons. One discrete dark spot present ventral to seventh, eighth or ninth scale of lateral-line scale row, between and below first and second midlateral spot. Series of smaller dark spots variably present dorsal and ventral to lateral-line scale row. . . . . . . . . . . . . . . . . . . .
. . ***Leporinus apollo*** Sidlauskas, Mol & Vari, 2011 (Fig. 6A)

**24a:** Dark vertical bar on body outlining posterior margin of opercle dorsal to pectoral-fin insertion. Four dark spots centred along or just ventral to lateral-line scale row in individuals of all sizes and additional scattered spots in juveniles . . .
. . . . . . ***Leporinus lebaili*** Géry & Planquette, 1983 (Fig. 4D)

**24b:** No discrete dark pigmentation on body outlining posterior margin of opercle dorsal to pectoral-fin insertion. Other dark pigmentation and spotting patterns variably present on body. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(25)**

**25a:** 12 circumpeduncular scales . . . . . . . . . . . . . . . . . . . . .
. . . . . . . . . . . ***Leporinus nijsseni*** Garavello, 1990 (Fig. 6C)

**25b:** 16 circumpeduncular scales . . . . . . . . . . . . . . . . . **(26)**

**26a:** Four scales in transverse series above lateral line . . . . .
. . . . . . . ***Leporinus gossei*** Géry, Planquette & Le Bail, 1991 (Fig. 4L)

**26b:** Five scales in transverse scales above lateral line. . **(27)**

**27a:** Body dorsal to lateral-line scale row with many scattered discrete dark spots in individuals of all sizes. Specimens 65 mm SL or larger usually with spots ventral to lateral line united into diffuse dark stripe. Dark oblique stripe ventral to eye. . . . ***Leporinus granti*** Eigenmann, 1912 (Fig. 6B)

**27b:** Body dorsal to lateral-line scale row unpigmented or with dusky vertical bars, but without many scattered discrete dark spots except in some small juveniles of *L. friderici*. Dark spots ventral to lateral-line scale row variably present but never united into diffuse stripe. No dark stripe ventral to eye . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(28)**

**28a:** Skin covering cleithrum immediately dorsal to pectoral-fin insertion darkly pigmented. Dark pigmentation on remainder of body absent or limited to single spot located on caudal peduncle near base of median caudal-fin rays . . . . . .
. . . . . . . ***Leporinus melanostictus*** Norman, 1926 (Fig. 4M)
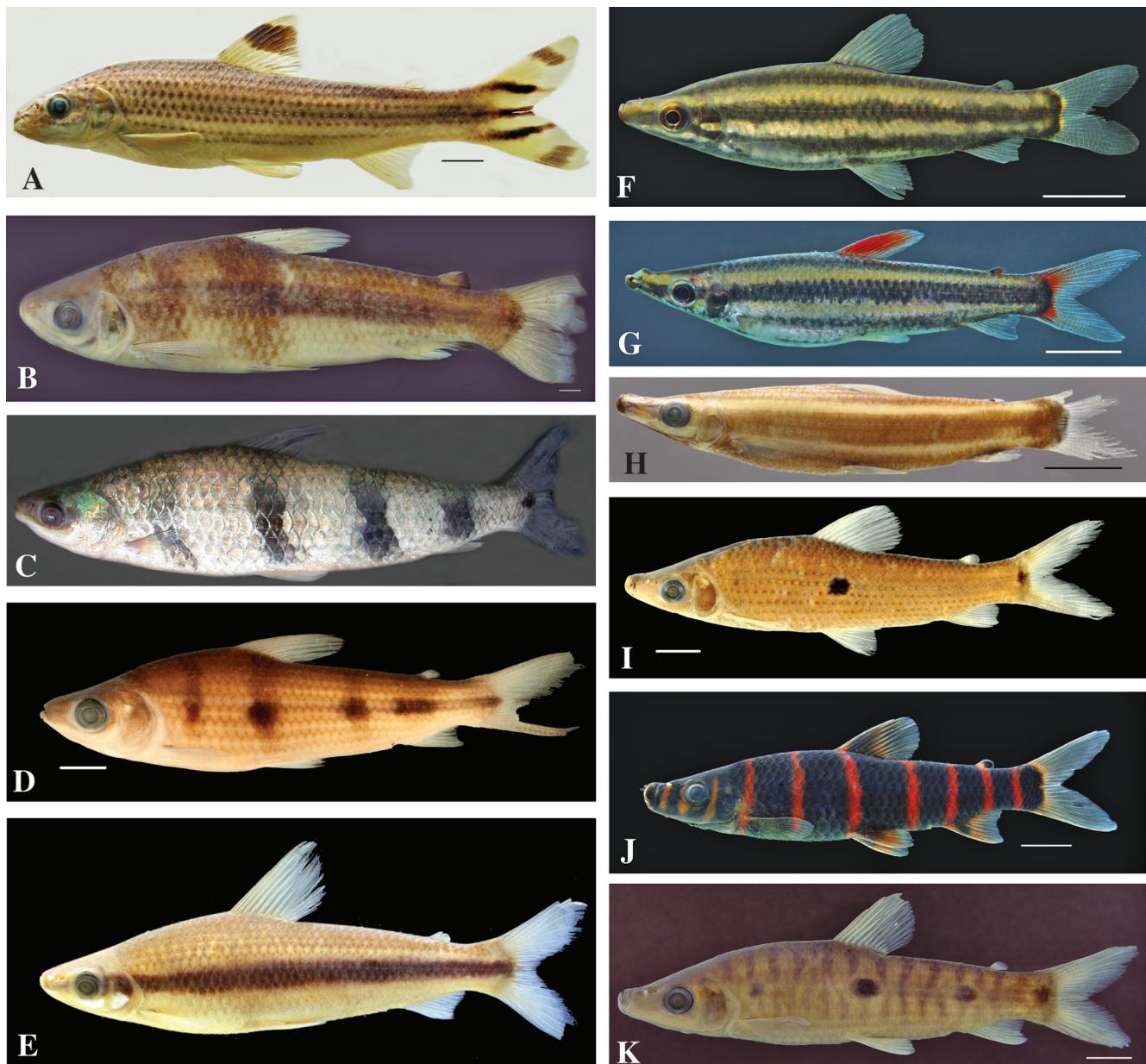
Figure 3. - Anostomidae. **A**: *Leporellus vittatus* (preserved), AUM 20003, 123.6 mm SL, Venezuela, Portuguesa, Río Portuguesa at highway 5 bridge. **B**: *Anostomoides laticeps* (preserved), ANSP 182274, Venezuela, Amazonas, Rio Orinoco, 52.9 km SE of San Antonio. **C**: *Schizodon fasciatus* (live, adult), Guyana, Rupununi River, 5.9 km WSW of village of Sand Creek, 02.967°N, 59.6592°W. **D**: *Schizodon vittatus* (preserved), AUM 35557, 97.1 mm SL, Guyana, Tukutu, Circle W Creek, tributary of Pirara River, 03.654°N, 59.529°W. **E**: *Laemolyta proxima* (preserved), AUM 45035, 134.4 mm SL, Guyana, Tukutu, pond at Yukupari, 3.659°N, 59.360°W. **F**: *Anostomus brevior* (live), FMNH ex ANSP 189141, Suriname, Sipalawini, Lawa River (Marowini drainage), 03.325°N, 54.063°W. **G**: *Anostomus anostomus* (live), USNM 403517, 52.7 mm SL, Guyana, Cuyuni River, 06.97°N 59.993°W. **H**: *Anostomus ternetzi* (preserved), MHNG 2626.021, 56.1 mm SL, French Guiana, Maroni River, Saut Toulalapata. **I**: *Pseudanos irinae* (preserved), AUM 48740, Guyana, Tukutu, Rupununi River, Aruwa Falls, 03.502°N, 59.339°W. **J**: *Synaptolaemus cingulatus* (live), AUM 43269, Venezuela, Amazonas, Río Orinoco, 03.307°N, 66.600°W. **K**: *Petulanos plicatus* (preserved), ANSP 180173, Guyana, Rupununi, Essequibo River, Yukanopito Falls, 01.915°N, 58.521°W. Scale bars indicate one centimetre. Photos by S. Moyers (A), B. Sidlauskas (B, H, K), M. Sabaj Pérez (C, F, J), J. Armbruster (D, E, I), and W. Bronaugh (G),

**28b:** Skin covering cleithrum immediately dorsal to pectoral-fin insertion not darkly pigmented. Dark pigmentation on caudal peduncle present or absent, but with at least one discrete spot or patch of pigmentation present elsewhere on body, particularly along lateral-line scale row below dorsal fin, except in very large individuals of *Leporinus agassizi* (~250 mm SL), which lack dark pigmentation on body and caudal peduncle............................................**(29)**

**29a:** Specimens smaller than approximately 100 mm SL . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(30)**
**29b:** Specimens larger than approximately 100 mm SL . . . .
. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(31)**

**30a:** Primary dark pigmentation on body consisting of inter-mittent longitudinal stripe running along lateral-line scale row from position below dorsal-fin base to caudal pedun-cle. Stripe composed of two to five spots, with at least some spots horizontally elongate. Intensity and completeness of stripe highly variable, with anteriormost region typically darkest. Pigmentation of stripe particularly faint in material from Demerara River, eastern Guyana. Smaller individuals usually with supplementary series of three or four small, vertically elongate spots present ventral to first through ninth scales of lateral-line scale row. Supplementary spots less intense in individuals of approximately 80 mm SL and dis-appear entirely during course of ontogeny . . . . . . . . . . . . . .
. . . . . *Leporinus agassizi* Steindachner, 1876 (Figs 4I, 7A)
**30b:** Primary dark pigmentation on body consisting of three distinct round spots along lateral-line scale row, one situ-ated below dorsal–fin base, one slightly anterior to vertical through adipose-fin origin, and one on caudal peduncle. Juveniles with two or three smaller supplementary spots; first adjacent to opercle and centred on scale row just ventral to lateral-line scale row, second ventral to seventh and eighth lateral-line scales and third (when present) ventral to 20$^{th}$ and 21$^{st}$ lateral-line scales. Supplementary spots less intense in individuals of approximately 70 mm SL and disappear entirely during course of ontogeny . . . . . . . . . . . . . . . . . . . .
. . . . . . . . . . . *Leporinus friderici* (Bloch, 1794) (Fig. 7B)

**31a:** All but largest specimens with single distinct dark spot along lateral-line scale row below dorsal–fin base and with additional dark pigmentation forming diffuse, irregular and interrupted band occasionally present along lateral-line scale row posterior to that point. Intensity of dark pigmentation fades ontogenetically, with largest individuals (~250 mm SL) lacking dark pigmentation entirely, and slightly smaller individuals usually retaining only spot below dorsal-fin base. Midsized specimens occasionally retain patch of darker pig-mentation along lateral-line scale row anterior of vertical through anterior of adipose fin reminiscent of second spot that characterizes adults of *Leporinus friderici* (see below) .
. . . . . . *Leporinus agassizi* Steindachner, 1876 (Figs 4J, 7A)
**31b:** Two or three dark spots present along lateral-line scale row in all but one examined individual; one spot situated below dorsal-fin base, second immediately anterior to ver-tical through adipose-fin origin, and third variably present on caudal peduncle. Larger specimens typically retain dark mid-lateral spots, but intensity of spots sometimes fades in large individuals, with spot beneath dorsal fin darkest and spot over caudal peduncle lightest in those specimens. One large specimen from the Corantijn River weakly pigmented

and displaying only anterior spot below dorsal–fin base. . . .
. . . . . . . . . . . . *Leporinus friderici* (Bloch, 1794) (Fig. 7B)

**Comments on Anostomidae in Guyana, Suriname and French Guiana**

With at least thirty recognizable morphospecies, the Anostomidae represent the most diverse group of anosto-moid fishes in the Guianas. Identification of anostomids to genus is relatively unproblematic when it is possible to examine the dentition critically, but at a finer taxonomic scale the correspondence between many of the morphospecies and the available taxonomic names is unclear. We present below a brief genus-by-genus discussion of the taxonomic conun-drums that abound in this group, and pay particular attention to our reasons for matching certain names to taxa. That said, our effort should not be considered a full taxonomic revision of these genera or their representatives in the Guianas!

*Abramites*. - There is a single specimen of *Abramites hypselonotus* (MHNG 2195.100) from an ambiguous locality in the Rio Branco drainage of extreme southwestern Guyana, where the Essequibo and Branco ichthyofaunas interchange through the Rupununi savannahs during high water periods (Lowe-McConnell, 1964; Watkins *et al*., 2005; de Souza *et al*., 2012). *Abramites hypselonotus* is primarily distributed through the Amazon and Orinoco basins in northern South America (Vari and Williams, 1987, Fig. 6) and is clearly not a major component of the Guianese ichthyofauna.

*Anostomoides*. - Despite a type locality at Crab Falls in the Essequibo River drainage**,** *Anostomoides laticeps* is apparently a very rare member of the Guianese ichthyofauna. In addition to the type series we encountered only one addi-tional from the Rupununi River (Appendix Fig. 1). Within the Guianas it appears to be endemic to the Essequibo sys-tem, though it also occurs in drainage systems beyond the Guianas, including the Río Orinoco (Garavello and Britski, 2003; Santos and Zuanon, 2006).

*Anostomus*. - Three species of *Anostomus* occur in the Guianas (Appendix Fig. 2), bearing in mind the recent erection of *Petulanos* to contain several species formerly assigned to *Anostomus* (Sidlauskas and Vari, 2008). *Anos-tomus ternetzi* (Fig. 3H) is easily distinguished on the basis of coloration (with a pale middorsal stripe from the tip of the supraoccipital spine to the dorsal-fin origin *versus* a dark median stripe in that region in congeners), but preserved specimens of *A. anostomus* and *A. brevior* are much more difficult to separate. *Anostomus anostomus* is the more slen-der of the two species throughout ontogeny (see morphome-tric diagnosis in key), though it does increase in relative body depth ontogenetically and large individuals of *A. anos-tomus* approach the range of ratios that diagnose *A. brevior*. Identifications are much easier if live coloration is available, as *A. brevior* has hyaline fins (Fig. 3F), while *A. anostomus* has varying degrees of red pigmentation on the dorsal, cau-

dal, anal and pelvic fins and caudal peduncle (Fig. 3G). The relative extent of that red pigment varies considerably across the range of the species (compare Fig. 3G in this publication with plate 5B of Sabaj Pérez [2009]). Whether this difference indicates a morphocline, variable water chemistry or dietary composition, or the presence of multiple species within the present concept of *A. anostomus* is unknown. Within the Guianas, *A. brevior* has a more easterly distribution in the Litani-Marowijne and Oyapock systems of French Guiana and Suriname, while *A. anostomus* occurs in river systems further west. Interestingly, *A. ternetzi* has a disjunct distribution in the Essequibo-Rupununi system and in the Marowijne/Maroni system, without apparent occurrence in the intervening river basins of Guyana and Suriname. Whether these disjunct populations merit formal taxonomic recognition is an open question.

***Hypomasticus***. - *Hypomasticus* was recently elevated from a subgenus of *Leporinus* on the basis of several morphological synapomorphies (Sidlauskas and Vari, 2008). Members of the genus can be recognized externally by their inferior mouths. Two species occur within the Guianas (Appendix Fig. 3), of which *Hypomasticus despaxi* (from the Maroni and Oyapock systems) is the simpler to recognize due to its highly distinctive striped colour pattern (Fig. 4H). *Hypomasticus megalepis* (Fig. 4A) from the Essequibo, Corantijn, Coppename and Maroni river systems is more problematic, as it has a spotted colour pattern very similar to that of *Leporinus nijsseni* (Fig. 6C), *L. ortomaculatus* (Fig. 4E) and *L. granti* (Fig. 6B). Aside from the important difference in mouth position (inferior in *H. megalepis versus* terminal or subterminal in the above species of *Leporinus*), *H. megalepis* also possesses a distinct dark spot anteriorly on the base of the anal fin that is a continuation of a similar spot on the ventrolateral portion of body. Such an anal-fin spot is absent in *Leporinus nijsseni*, *L. ortomaculatus* and *L. granti*.

It is noteworthy that a large percentage of material of *Hypomasticus megalepis* in collections was incorrectly identified as *Leporinus maculatus*, a name that applies correctly to a species of *Leporinus* with alternating thick and thin dark vertical bars (Fig. 4N). The history behind that nomenclatural confusion was discussed extensively by Géry *et al*. (1988).

***Laemolyta***. - Of the five species in *Laemolyta*, only *L. proxima* (Fig. 3E) occurs in the Guianas (Mautari and Menezes, 2006), with its distribution restricted to the Essequibo, Rupununi and Takutu river systems (Appendix Fig. 4). It can be identified easily by the single continuous dark lateral stripe running from the eye to the posterior of the hypural plate and by the continuous incisiform margin formed by its dentary teeth.

***Leporellus***. - The highly distinctive *Leporellus vittatus* (Fig. 3A), with dark stripes on the dorsal and caudal fins and an extensively scaled caudal fin, cannot be easily confused with any other anostomoid fish from the Guianas. It is rare in the ichthyofauna in this study area, being represented by only four examined lots, all from the Takutu or Rupununi rivers of southern Guyana (Appendix Fig. 5). Outside the Guianas this nominal species has an exceedingly broad reputed range, including representation throughout the Amazon and Orinoco systems as well as the trans-Andean drainages of Colombia. Whether all populations from across that vast geographic swath truly belong to a single species is an unanswered question.

***Leporinus*, general comments**. - *Leporinus* is a large group of approximately 90 nominally valid species (Garavello and Britski, 2003). The genus as currently defined is demonstrably paraphyletic (Sidlauskas and Vari, 2008), but in the absence of a comprehensive revision and associated phylogenetic analysis it is uncertain which components of the genus may in fact represent natural groups. Following Géry (1977), we divide our discussion of these fishes into four almost certainly artificial groupings based on colour pattern (barred, striped, spotted or largely unpigmented) to facilitate location of comments pertinent to the identification of fishes in each group.

***Leporinus*, barred forms**. - Within the barred or banded subgroup of *Leporinus*, three distinct morphospecies are present in the Guianas, which we have assigned to *L. fasciatus* (Fig. 4C), *L. desmotes* (Fig. 4K) and *L. maculatus* (Fig. 4N). Of these, *L. maculatus* is easily identified by its very distinctive alternating thick and thin dark bars. *Leporinus fasciatus* and *L. desmotes*, that both possess dark bars of a more regular width are sometimes confused. These two can be separated by the number of dark vertical bars (generally ten in *L. fasciatus versus* seven or eight in *L. desmotes*, including the bar over the posterior of the opercle), the form of the symphyseal dentary teeth (laterally compressed, forward jutting tusks in *L. desmotes versus* well developed but not tusk-like in *L. fasciatus*) and in the coloration of the anterior portion of the dorsal fin (darkly pigmented [Fig. 4K] in *L. desmotes versus* unpigmented [Fig. 4C] in *L. fasciatus*). Within the Guianas *L. desmotes* is limited to the southern portion of the Essequibo River system and the Takutu River (Rio Branco drainage), while *L. fasciatus* and *L. maculatus* are ubiquitous across the Guianas except for the Oyapock basin (Appendix Figs 6, 7).

Though the three morphotypes of banded *Leporinus* are relatively easy to separate, some taxonomic uncertainty is associated with all three names. *Leporinus desmotes* was described from the Rupununi River of Guyana (Fowler, 1914) and is the least problematic, though the nominal species *L. jatuncochi* from Ecuador and Peru (Ovchynnyk, 1971) is extremely similar and may be a junior synonym of *L. desmotes*. *Leporinus fasciatus* (Bloch, 1794) was one of the first three anostomid species to be described and it pos-
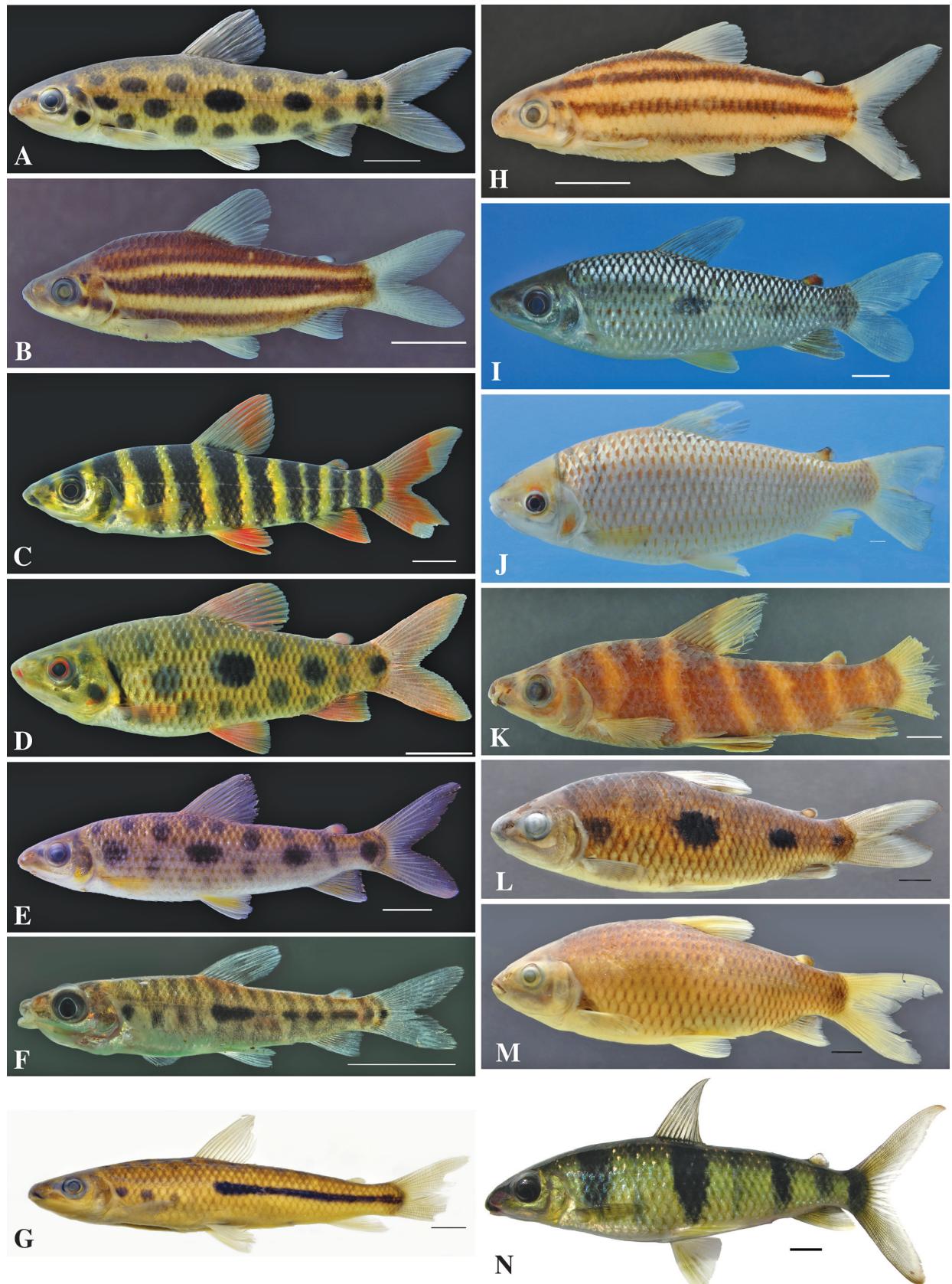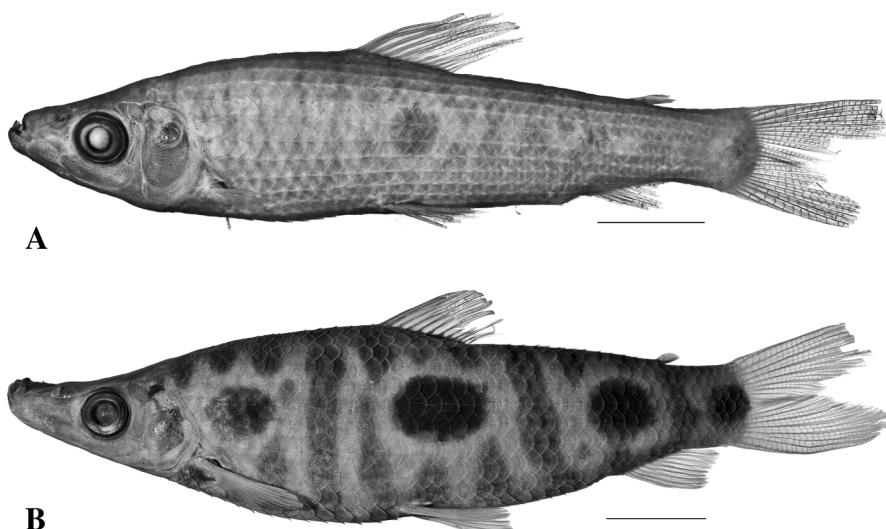
Figure 5. - Anostomidae. **A**: *Pseudanos trimaculatus* (preserved), USNM 224797, 67.7 mm SL, Guyana, Rupununi, Puara River, Amazon drainage. **B**: *Petulanos spiloclistron* (preserved), USNM 209432, 72.3 mm SL, Suriname, Fallawatre River, at rapids five km SSW of Stondansie Falls, 05.150°N, 56.483°W. Photos by T. B. Griswold. Scale bars indicate one centimetre.

sesses a large putative range spanning the major rivers of the Guianas as well the Amazon and possibly the Orinoco systems. Several nominal subspecies (Borodin, 1929) as well as multiple possible junior synonyms have been proposed (Garavello and Britski, 2003). Overall the *L. fasciatus* complex is in need of revision, but is it clear that the species present in the Guianas must be the true *L. fasciatus*, because the species has a type locality within Suriname and no older name is available.

The proper nomenclature of the species assigned herein to *Leporinus maculatus* is much less clear. Within the Guianas, at least four names have been applied to species in this complex: *L. alternus, L. maculatus, L. paralternus* and *L. pellegrinii*, with *L. maculatus* being by far the oldest name. Géry *et al*. (1988) argued convincingly that the other three names are synonyms of *L. maculatus*, with the proliferation of nominal species likely due to the incorrect application by ichthyologists of the name *L. maculatus* to the species recognized herein as *Hypomasticus megalepis*. Géry *et al*. did, however, recognize two subspecies, *L. maculatus maculatus* (including *L. paralternus*) with a supplementary partial bar after the first major bar and a body depth 3.9 to 4.15 in SL,

and *L. maculatus pellegrinii* (including *L. alternus*?) lacking a supplementary partial bar and with a body depth 4.25 to 4.45 in SL. Those cited subspecific differences appear inconsistent among the individuals we examined. One specimen (ANSP 180171), for example, lacks a supplementary bar but has a body depth of 4.18 in SL. The paratype of *L. alternus* (USNM 66219) has a very slight supplementary bar in the form of a dark dot on the dorsum, despite the fact that the presence *versus* absence of the supplementary bar was the primary diagnostic feature used to separate *L. paralternus* from *L. alternus* by Fowler (1914). Perhaps most tellingly, variation within a single lot of specimens sometimes includes individuals demonstrating both colour patterns. A prime example is USNM 225995, which has four specimens with the supplementary bar ranging from dark, long and intense to completely absent. Overall the presence *versus* absence of the supplementary bar does not appear to be ontogenetic, and may represent sexual dimorphism or just natural intraspecific variation among individuals. It does not appear to diagnose reliably any taxon of any rank, and thus we assign all of the specimens of *Leporinus* with alternating thick and thin bars in the Guianas to *L. maculatus*.

Figure 4 (left). - Anostomidae. **A**: *Hypomasticus megalepis* (live), AUM 37999, Guyana, Region 9, Essequibo River, Kassi-Attae rapids, 02.226°N, 58.393°W. **B**: *Leporinus arcus* (preserved), ANSP 179647, Guyana, Cuyuni-Mazaruni, Whitewater Creek, 6.8 km SSW of Bartica, 06.378°N, 58.674°W. **C**: *Leporinus fasciatus* (live), ANSP 189158, Suriname, Sipalawini, Lawa River, eight km SSW of Anapaike-Kawemhakan, 03.325°N, 54.063°W. **D**: *Leporinus lebaili* (live), FMNH ex ANSP 189043, Suriname, Sipalawini, Lawa River, eight km SSW of Anapaike-Kawemhakan, 03.325°N, 54.063°W. **E**: *Leporinus ortomaculatus* (live), AUM 43262, Venezuela, Amazonas, Río Orinoco, 147 km ESE of San Fernando de Atabapo. **F**: *Leporinus nigrotaeniatus* (juvenile, live), USNM 403522, 32.2 mm SL, Guyana, Cuyuni River. **G**: *Leporinus nigrotaeniatus* (adult, preserved), USNM 377393, 106.2 mm SL, Guyana, Rupununi, Coco Creek. **H**: *Hypomasticus despaxi* (preserved), ANSP 189042, Suriname, Sipalawini, Lawa River, Gansoela, rapids eight km SSW of Anapaike, 03.311°N, 54.065°W. **I**: *Leporinus agassizi* (live), USNM 402629, 95.1 mm SL, Guyana, Cuyuni River about 15 km upstream from Waikuri mountains near mouth of Toroparun River, 06.69186°N, 59.57722°W. **J**: *Leporinus agassizi* (live), USNM 403835, Guyana, Cuyuni River about 1 km downstream from Kanaima Falls, 06.88377°N, 60.24786°W. **K**: *Leporinus desmotes* (holotype, preserved), ANSP 39324, Guyana, Rupununi River. **L**: *Leporinus gossei* (preserved), MHNG 2700.051, 110.8 mm SL, French Guiana, Mana River Basin, Crique Aya, 04.603°N, 53.418°W. **M**: *Leporinus melanostictus* (preserved), MHNG 2621.094, 118.0 mm SL, French Guiana, Fleuve Approuague, 04.193°N, 52.319°W. **N**: *Leporinus maculatus* (live), FMNH ex ANSP 189041, Suriname, Sipalawini, Lawa River, eight km SSW of Anapaike-Kawemhakan, 03.325°N, 54.063°W. Scale bars indicate one centimetre. Photos by M. Sabaj Pérez (A, C, D, E, H, K, N), B. Sidlauskas (B, G, L, M) and W. Bronaugh (F, I, J).
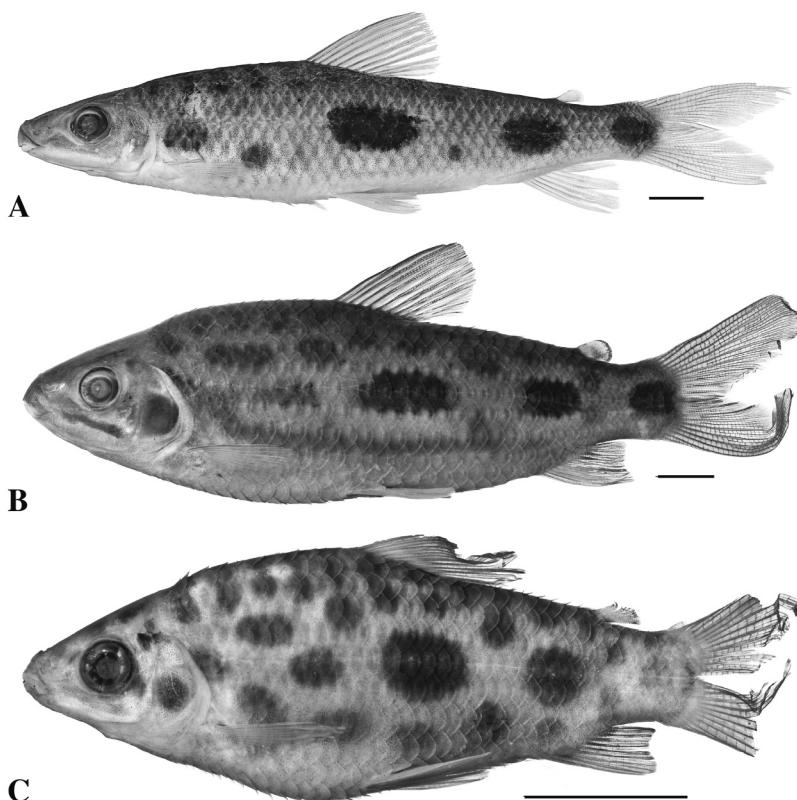
Figure 6. - Anostomidae. **A**: *Leporinus apollo*, holotype, FMNH 116827, 111.1 mm SL Suriname, Saramacca, Coppename River, Sidonkrutu. **B**: *Leporinus granti*, USNM 225402, 110.6 mm SL, Suriname, Nickerie District, stream into Lucie River, 03.600°N, 57.617°W. **C**: *Leporinus nijsseni*, USNM 225377, 40.2 mm SL, Suriname, Nickerie District, stream at Machine Park, 03.833°N, 57.567°W. Scale bars indicate one centimetre. Photos by T. B. Griswold.

***Leporinus*, striped forms**. - Three striped species of *Leporinus* occur in the Guianas: *L. arcus* (Fig. 4B), *L. nigrotaeniatus* (Fig. 4F,G) and *L. agassizi* (Fig. 7A). *Leporinus arcus* is easy to identify due to its deep body with a wide dark midlateral stripe along the midline and an overall striped colour pattern reminiscent of members of *Anostomus* (Fig. 3F, G, H). *Leporinus nigrotaeniatus* is also very distinctive due to the combination of a very slender body (body depth at dorsal-fin origin approximately 18-21% of SL) with a partial dark midlateral stripe that runs from ventral to the dorsal-fin base to the posterior margin of the hypurals in adults (Fig. 4G). In small juveniles, the midlateral stripe is intermittent (Fig. 4F). At middle stages of ontogeny, *L. agassizi* (Fig. 7A, centre) demonstrates a partial midlateral stripe similar to that present in *L. nigrotaeniatus* (Fig. 4G) but the former species has a distinctly deeper body (body depth at dorsal-fin origin approximately 28-32% of SL). The midlateral stripe in *L. agassizi* is, however, divided into a series of lateral spots at early stages of ontogeny (Fig. 7A, bottom), never completely forms in some individuals (Fig. 4I), and fades later in ontogeny (Fig. 7A, top) to disappear entirely in very large adults (Fig. 4J). *Leporinus agassizi* is discussed more extensively below in a comparison with *L. friderici*. Within the
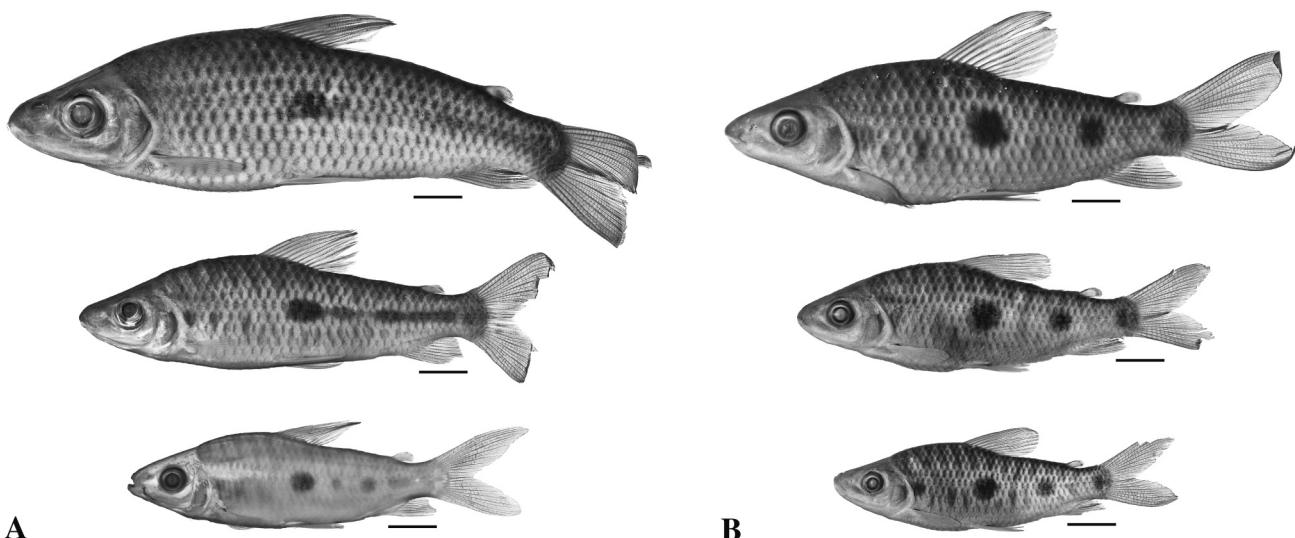


Figure 7. - **A**: Growth series of *Leporinus agassizi*: Top, USNM 377364, 114.7 mm SL, Guyana. Centre, USNM 377410, 87.2 mm SL, Guyana, Burst Mouth Pond. Bottom, USNM 93438, 62.4 mm SL, Guyana, Wismar, 06.00°N, 58.55°W. **B**: Growth series of *Leporinus friderici*. Top, USNM 225383, 95.2 mm SL, Suriname, Nickerie, stream near Camp Anjoemara, 04.833°N, 57.433°W. Centre and bottom, USNM 225409, 68.3 and 55.7 mm SL. Suriname, Nickerie, Kamp Kreek, 04.817°N, 57.467°W. Scale bars indicate one centimetre. Photos by T. B. Griswold.

Guianas, *L. agassizi* and *L. nigrotaeniatus* occur throughout the Essequibo River drainage but are unknown from the Corantijn River and drainages further to the east (Appendix Figs 8, 9). *Leporinus arcus* also occurs in the Essequibo drainage, but appears to be restricted to the northern half of Guyana and is unknown from the rivers of the Rupununi savannah (Appendix Fig. 5).

*Leporinus*, **spotted forms**. - Any discussion of the spotted species of *Leporinus* must confront the taxonomic confusion that has surrounded the concept of *L. friderici*, which along with *L. fasciatus* and *Anostomus anostomus* was among the first three anostomid species to be recognized formally (Linnaeus, 1758; Bloch, 1794). In his description of *Salmo friderici* (now in *Leporinus*), which has an indefinite type locality in Suriname, Bloch illustrated a large, fully adult individual with three distinct dark spots centred along the lateral-line scale row, one situated ventral to the dorsal fin, one just anterior to the vertical through the origins of the adipose and anal fins, and one on the caudal peduncle at the base of the medial caudal-fin rays. Bloch's drawing and description very well match some recently collected *Leporinus* from the river systems of Suriname and French Guiana (Fig. 7B), although specimens smaller than the full adult illustrated by Bloch demonstrate additional faint barring dorsal to the lateral line and a mottled pattern ventral to the lateral line. There is little question that these individuals are the true *L. friderici*.

As is often the case with very early South American species descriptions, the specific epithet of *Leporinus friderici* has also been applied to individuals from across the continent for more than 200 years since Bloch's original work with the resultant species complex very much in need of revision. Though such a revision is beyond the scope of this work, it became clear during our survey that specimens from the Essequibo system of Guyana provisionally assigned to *L. friderici* (e.g., Figs 4I, 7A bottom panel) differ substantially from specimens from the Corantijn River and drainages further east (Fig. 7B). The available material from the Demerara, Essequibo and Rupununi systems exhibits wide colour pattern variation, with most of the variability centred on the degree of completeness of a partial midlateral stripe reminiscent of the colour pattern that typifies the more slender *L. nigrotaeniatus* (Fig. 4F, 4G). Individuals bearing a complete stripe between a point below the dorsal fin and the posterior margin of the hypurals resemble closely *L. agassizi* from the Amazon drainage, while individuals in which the stripe is interrupted are very similar to the type series of *L. punctatus* Garavello, 2000, from the Río Orinoco of Venezuela. Very small individuals (~60 mm SL and smaller, Fig. 6A, bottom panel) have a highly interrupted stripe that often appears as a series of five spots, of which only the spot ventral to the adipose fin is at all horizontally elongate. Such specimens have typically been identified as *L. friderici* in museum col-

lections, but differ from juveniles of *L. friderici* from the Corantijn River and drainages further east which have three distinct round spots centred along the lateral-line scale row in the region from ventral of the dorsal fin to the posterior margin of the hypurals, none of which is horizontally elongate.

Matters are complicated further by ontogenetic variation. At approximately 90 mm SL, the colour pattern of specimens of this complex from Guyana begins to fade and the lateral stripe becomes indistinct and begins to subdivide. Individuals pass through a stage in which they possess horizontally elongate dark markings in positions analogous to the three round spots that characterize *L. friderici* of Suriname and French Guiana (compare Fig. 4I with 7B). The posterior two spots then fade, leaving only a single dark spot ventral to the dorsal fin (Fig. 7A, top panel). Eventually that spot similarly fades with the largest known individuals from the Essequibo drainage completely lacking midlateral dark markings (Fig. 4J). This contrasts sharply with the condition in *L. friderici* from the Corantijn River and drainages further to the east (Appendix Fig. 9), in which adults maintain at least the anterior two dark marks throughout ontogeny. A full series of intermediates can be assembled to link all of the forms in the Essequibo, Rupununi and Demerara systems, and it seems clear that all these represent a single, morphologically variable species. For the most part the variation among individuals of the same size does not appear to be geographically structured, though the available specimens (mostly juveniles) from the Demerara River are particularly weakly pigmented.

Overall, it is very clear that the material from the Demerara, Essequibo and Rupununi rivers is not conspecific with *Leporinus friderici* which occurs in river systems to the east (Appendix Fig. 9). Those western populations are identified herein as *L. agassizi*, which is the oldest available name that appears to match at least a portion of the ontogenetic pigmentation pattern of that nominal species (namely the striped phase). Problematically, *L. agassizi* has a type locality in the Amazon drainage rather than one of the drainages of the northern Guiana Shield. As discussed above, *L. punctatus* from the Río Orinoco basin is another possibly conspecific species, and indeed it is possible that *L. agassizi* and *L. punctatus* are synonymous. A third possibility is that the material from the Demerara, Essequibo and Rupununi rivers represents a species new to science. Only a thorough comparison of samples from these and adjoining drainage basins with the relevant type series can resolve this issue.

Variation within *Leporinus friderici* proper is problematic in that we were unable to examine enough specimens from French Guiana to evaluate the diagnosability of the two putative subspecies *L. friderici friderici* and *L. friderici acutidens*. According to Planquette *et al*. (1996) *L. friderici acutidens* has a concave anal fin margin while *L. friderici friderici* has a straight or convex margin. We would con-

sider the fin margins of the extensive series of material that we examined from Suriname to be straight, or very slightly concave (e.g., Fig. 7B, top panel). That said, there remains substantial colour pattern variation within *L. friderici*. Moderately to large sized specimens from Suriname (e.g., FMNH 116829) have little in the way of supplementary markings above and below the lateral-line scale row and have fairly small, but discrete lateral-line spots. Some material from the Nickerie River of Suriname (e.g., USNM 225772, a lot of specimens at about 97 mm SL) has the pigmentation of the second and third spots in some individuals less intense than that of the spot below the dorsal fin. Material from further east in Suriname and French Guiana (Lawa/Marowijne drainage, e.g., ANSP 189264) tends to have more pigmentation, retains distinct spots below the lateral line until at least 80 mm SL and has overall larger spots. Determination of whether this variation indicates a morphocline, natural variation among individuals or the presence of recognizable eastern and western taxa within the present concept of *L. friderici* will require the examination of more extensive series of specimens, and will unfortunately be complicated by the fact that no types are known for *L. acutidens*, which has a type locality simply of "South America".

Identification of the remaining spotted species of *Leporinus* in the Guianas is much more straightforward. The two species most similar to *L. friderici* and *L. agassizi* are *L. gossei* from the Marowijne and Oyapock drainages of French Guiana (Appendix Fig. 5) and *L. lebaili* from the Marowijne (Appendix Fig. 11). *Leporinus gossei* (Fig. 4L) possesses a colour pattern very similar to that of *L. friderici* but has only four scales in the upper transverse series (*versus* five in *L. friderici*) and usually retains into adulthood a dark spot posterior to the opercular margin centred just ventral to the lateral-line scale row (*versus* the lack of such a dark spot in adulthood). *Leporinus lebaili* (Fig. 4D) is easily recognized by the dark black pigmentation on the body that outlines the posterior margin of the opercular series (*versus* a lack of such pigmentation in *L. friderici*).

*Leporinus nijsseni* (Fig. 6C) can be separated from other spotted species of *Leporinus* in the Guianas by the presence of 12 rather than 16 circumpeduncular scales. This species otherwise looks very similar to *L. granti* at small sizes (under 65 mm SL), as both have a very heavily spotted colour pattern. Interestingly, material fitting the current concept of *L. nijsseni* appears to have a disjoint distribution in the Corantijn, Nickerie, Suriname and Coppename rivers of Suriname and in the Oyapock River of French Guiana, without apparent occurrence in the intervening Litani/Marowijne, Mana, Sinnamary or Approuague river systems (Appendix Fig. 1). *Leporinus nijsseni* also bears a close similarity to the poorly known *L. steyermarki* Inger, 1956, from the Río Abácapa, which drains a tepui in Venezuela at a height of approximately 400 m above sea level (Inger, 1956). *Leporinus steyermarki* also has

a spotted colour pattern and 12 circumpeduncular scales, but can theoretically be separated from *L. nijsseni* by the possession of 32 lateral-line scales (*versus* 33-36 in *L. nijsseni*). A revision is necessary to determine whether the two disjunct populations of *L. nijsseni* merit recognition as distinct species or subspecies, and whether either is in the synonymy of the older *L. steyermarki*.

*Leporinus granti*, another heavily spotted, deep bodied species of *Leporinus* is easily recognized at sizes over 65 mm SL by the presence in most specimens of a diffuse dusky stripe ventral to the lateral-line scale row (Fig. 6B). At small sizes the pigmentation ventral to the lateral-line scale row instead consists of a series of disconnected dark spots and *L. granti* looks very similar to *L. friderici, L. nijsseni* and *Hypomasticus megalepis*. Nevertheless, juveniles of *Leporinus granti* can be recognized by the presence of 16 circumpeduncular scales (*versus* 12 in *L. nijsseni*), a terminal mouth (*versus* inferior in *Hypomasticus megalepis*) and a dark oblique stripe under the eye (*versus* the absence of such a stripe in all three cited species). *Leporinus friderici* is also much less extensively spotted at all stages of ontogeny than is *L. granti*. *Leporinus granti* appears commonly throughout the Branco, Essequibo, Corantijn, and Marowijne up to Approuage basins but is notably absent in the Nickerie, Coppename, Saramacca and Suriname drainages of central Suriname and the Oyapock system of far eastern French Guiana (Appendix Fig. 10). The very similar *L. nijsseni* occurs in drainages where *L. granti* does not (Appendix Fig. 1) except for a possible area of contact in the Corantijn system, suggesting that these two taxa may be allopatrically-generated sister species. Furthermore, both of these species appear to have disjoint distributions, suggesting the possible presence of cryptic species within the present concept of both taxa.

The remaining two species of spotted *Leporinus* from the Guianas are much more slender-bodied than the spotted species discussed above, with body depth at the dorsal-fin origin in the range of 19%-25% of SL, *versus* 28%-38% of SL. *Leporinus ortomaculatus* (Fig. 4E) is widely distributed throughout the Orinoco system (Garavello, 2000) but also occurs in the Takutu and Ireng drainages (Rio Branco basin) of southwestern Guyana (Appendix Fig. 8). It is a heavily spotted species with three pairs of spots positioned intermediate to four spots centred along lateral-line scale row. Each pair of spots is positioned with one member above lateral-line scale row and one below, with the overall form of each pair reminiscent of a colon.

Finally, a new spotted species, *Leporinus apollo* Sidlauskas *et al*. 2011 (Fig. 6A) was discovered recently from the Coppename, Corantijn and Suriname rivers of Suriname (Appendix Fig. 4). It is extremely slender (body depth 18-23% of standard length), has a colour pattern of four large lateral spots and additional dark markings ventral to the lateral line, and has six upper transverse scales *versus* the five

in most other species of *Leporinus* in the Guianas. This new species is most similar to *L. cylindriformis* Borodin, 1929 and *L. niceforoi* Fowler, 1943, from the Amazon drainage, but can be distinguished from those species by details of pigmentation, morphometrics and meristics (Sidlauskas *et al.*, 2011).

***Leporinus*, largely unpigmented species**. - Within the Guianas, *L. melanostictus* from the Approuague and Oyapock river systems of French Guiana is the only species of *Leporinus* that lacks major dark markings on the body at all stages of ontogeny (Fig. 4M). That species usually (but not always) has a dark spot on the caudal peduncle, which is aligned with the bases of the median caudal-fin rays, and has dusky pigmentation in the skin covering the cleithrum just dorsal to the pectoral-fin insertion. Otherwise, the body is unpatterned. Very large (~250 mm SL) individuals of *L. agassizi* from the Essequibo River of Guyana lose the lateral spotting or striping that characterizes that species at earlier stages of ontogeny and potentially can be confused with *L. melanostictus*. Aside from its non-overlapping geographic range, members of *L. agassizi* (Figs 4I, 4J) lack the dusky pigmentation on the cleithrum that is typical of *L. melanostictus*.

***Pseudanos*.** - Though two species of *Pseudanos* appear in the key above, only *P. irinae* (Fig. 3I) is a major component of the ichthyofauna of the Guianas, where it occurs throughout the Essequibo and Rupununi river systems (Appendix Fig. 11). A single specimen of *P. trimaculatus* (USNM 224797, Fig. 5A) is known from the Puara River (Rio Branco drainage) of southern Guyana. This species is a common component of the ichthyofauna of the Rio Negro including the Branco but only occurs peripherally within the Guianas proper.

***Petulanos*.** - Two species within the Guianas were until recently assigned to *Anostomus*, but were assigned to a new genus, *Petulanos*, to reflect the numerous morphological synapomorphies that separate those two genera (Sidlauskas and Vari, 2008). The combination of a superior mouth with a multiply spotted and barred colour pattern readily separates these species from all other anostomids in the Guianas with the possible exception of *Pseudanos*. Members of *Pseudanos* (e.g., Fig. 3I) possess much less extensive transverse barring than do members of *Petulanos* (e.g., Fig. 5B), and have multicuspid rather than truncate symphyseal dentary teeth. Numerous skeletal differences also separate the two genera (Sidlauskas and Vari, 2008). Of the two species of *Petulanos* present in the Guianas, *P. plicatus* (Fig. 3K) has a more westerly distribution in the Essequibo and Corantijn river systems while *P. spiloclistron* (Fig. 5B) is endemic to the Nickerie River (Appendix Fig. 12). Neither species is known to occur outside the Guianas, and with only one other known species in the genus (*P. intermedius* [Winterbottom, 1980] from the Rio Xingu in Brazil), this is one of the most highly endemic fish genera in the region targeted by this study.

***Schizodon*.** - Two recognizable morphotypes of *Schizodon* exist within the study area, one with a partial midlateral stripe restricted to the caudal peduncle (Fig. 3D) and the other lacking such pigmentation (Fig. 3C). Both morphotypes occur in the Rupununi (Essequibo basin) and Ireng (Branco basin) rivers of southern Guyana (Appendix Fig. 13) where the genus is a common member of the ichthyofauna, most likely due to the presence of abundant submerged and floating vegetation on which members of the genus feed (Santos, 1981; Sidlauskas *et al.*, 2007). Only the non-striped form is known from Suriname and French Guiana, although admittedly based on a limited sample of six lots from the Corantijn, Maroni and Mana drainages. The occurrence of striped and non-striped morphotypes have been recognized among Amazonian specimens since the mid-nineteenth century (Spix and Agassiz, 1829; Cuvier and Valenciennes, 1850), when they were assigned the nominal species names *Piabuca vittatus* and *Schizodon fasciatus* respectively. Géry (1977) questioned the validity of these two species, and suggested that *Schizodon fasciatus* and its junior synonym *S. vittatus* are colour morphs. Interestingly, in our samples no individuals larger than approximately 130 mm SL exhibited the striped morphotype, while non-striped individuals above and below that size threshold were present. It is possible that the stripe, when present, fades over the course of ontogeny and that only a single species of *Schizodon* inhabits the Guianas. Alternatively, there may in fact be two species of *Schizodon* present in the region, with the striped form (nominally *S. vittatus*) perhaps achieving a lower maximum size. Resolution of this question and the related issue of whether the *Schizodon* populations in the Guianas are conspecific with Amazonian forms requires a full taxonomic revision of the genus; and is beyond the scope of this study. We have tentatively divided the striped *versus* non-striped morphs into the two nominal species and plotted their distributions separately.

***Synaptolaemus*.** - The highly distinctive *Synaptolaemus cingulatus* (Fig. 3J), with its body encircled by numerous thick dark bands separated by lighter bands which are red in life, a strongly superior mouth, and papillose lips, cannot be confused with any other fish in the Guianas. Most of the known range of this species lies within the Río Orinoco drainage of Venezuela (Winterbottom, 1980), but it has also been captured within the Takutu River of southwestern Guyana (Appendix Fig. 1). A population is also known from the upper Rio Xingu of Brazil (Winterbottom, 1980).

## Key to Chilodontidae in Guyana, Suriname and French Guiana

**1a:** Branched anal-fin rays typically ten or eleven, rarely nine. Anal-fin margin convex or straight. Mouth terminal or
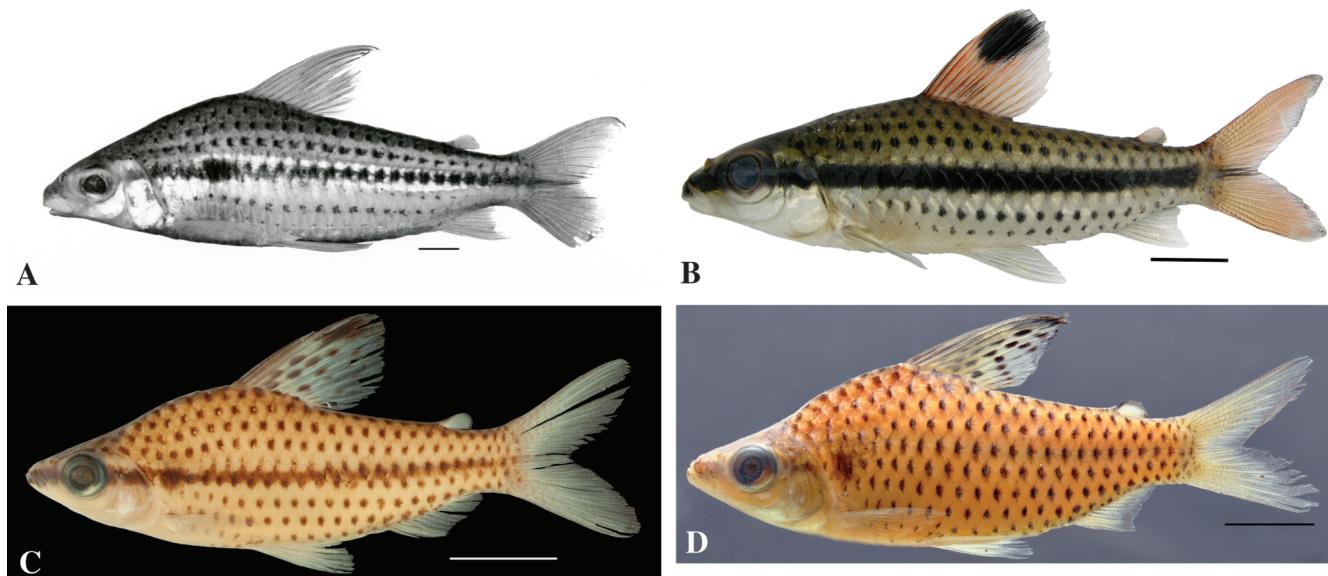
Figure 8. - Chilodontidae. **A**: *Caenotropus labyrinthicus* (preserved). ANSP 135851, Venezuela, Bolivar. Río Nichare, 06.583°N, 64.817°W. **B**: *Caenotropus maculosus* (live), ANSP 189147, Suriname, Sipalawini, Litanie River, 03.290°N, 54.077°W. **C**: *Chilodus punctatus* (preserved), AUM 36902, Guyana, Region 9, Rupununi River, 03.808°N, 59.385°W. **D**: *Chilodus zunevei* (preserved), MHNG 2608.040, 55.6 mm SL, French Guiana, Kaw, Kaw river basin, Wapou Creek at Dégrad Roche, 04.429°N, 52.158°W. Scale bar indicates one centimetre. Photos by T. B. Griswold (A), M. Sabaj Pérez (B), J. Armbruster (C) and B. Sidlauskas (D).

slightly superior. Dorsal fin with series of dark spots on posterior rays. Posterior margin of scales smooth . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*Chilodus* (**2**)

**1b:** Branched anal-fin rays six to eight. Anal-fin margin somewhat concave in nearly all specimens. Mouth subterminal. Dorsal fin with dark pigmentation across distal portions of anterior rays but lacking dark spots on remaining portions of fin. Posterior margin of scales weakly serrate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*Caenotropus* (**3**)

**2a:** Conspicuous dark spots evenly distributed over body; spots about one-half diameter of pupil of eye. Spots prominent on anteroventral portion of body and of approximately same size across entire body. Midlateral stripe absent . . . . . . . . . . . . . . . . . . . .*Chilodus zunevei* Puyo, 1946 (Fig. 8D)

**2b:** Dark spots variably present on body, but largest spots only one-quarter diameter of pupil of eye. Spots more diffuse and nearly absent on anteroventral portion of body and often smaller ventrally. Midlateral portion of body with dark pigmentation ranging from irregular zigzag pattern to distinct stripe . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Chilodus punctatus* Müller & Troschel, 1844 (Fig. 8C)

**3a:** Lateral-line scales, not including terminal elongate scale, typically 27 or 28, most often 27. Most individuals with row of well spaced teeth in lower jaw although with row reduced to one or two teeth in some individuals. Distal portions of anterior dorsal-fin rays with distinct patch of dark pigmentation. Distinct midlateral stripe extending from snout to caudal fin-base without dark spot positioned along stripe in area

slightly anterior of vertical through dorsal-fin origin . . . . . . . . . . . *Caenotropus maculosus* (Eigenmann, 1912) (Fig. 8B)

**3b:** Lateral-line scales, not including terminal elongate scale, 28 to 32, most often 29 or 30 and rarely 28. Teeth absent in lower jaw. Distal portions of anterior dorsal-fin rays sometimes dusky but lacking distinct patch of dark pigmentation. Diffuse midlateral stripe extending from snout to caudal fin-base, most often with rotund dark spot positioned along stripe in area slightly anterior of vertical through dorsal-fin origin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*Caenotropus labyrinthicus* (Kner, 1858) (Fig. 8A)

## Comments on Chilodontidae from Guyana, Suriname and French Guiana

With just four species present in the Guianas, the Chilodontidae represent a relatively minor component of the overall ichthyofauna of that region. It is notable, however, that these four species represent 50% of the total number of species in this small family. Endemicity of the members of this family occurring in the Guianas is also at 50%, with *Chilodus zunevei* (Appendix Fig. 15) and *Caenotropus maculosus* (Appendix Fig. 14) both restricted to the region (Isbrücker and Nijssen, 1988; Vari *et al.*, 1995). The diagnosis of all four species is easily accomplished on the basis of coloration (Fig. 8), meristics and mouth position.

## Key to Curimatidae in Guyana, Suriname and French Guiana

**1a:** Lateral line incomplete in specimens of all sizes. Anterior
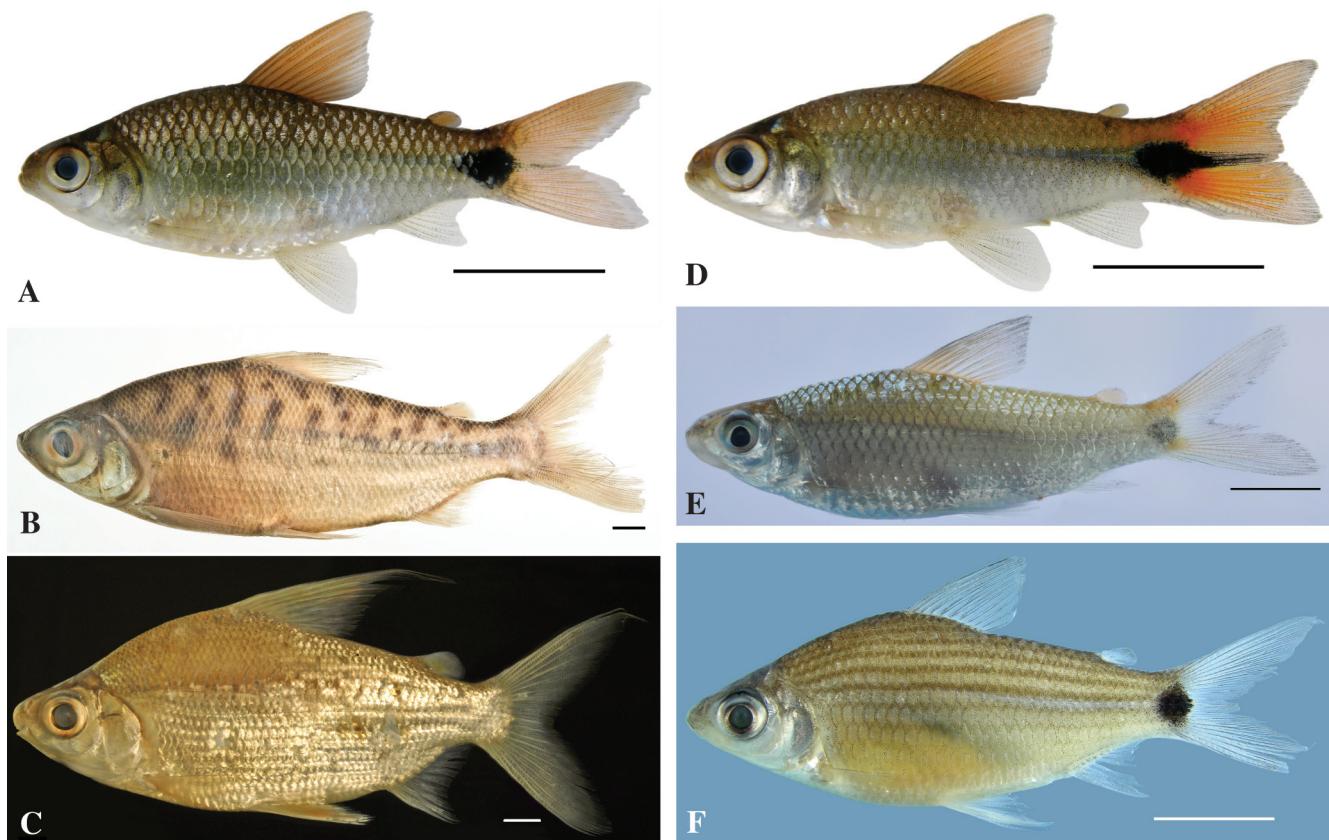
Figure 9. - Curimatidae. **A**: *Curimatopsis crypticus* (female, live), ANSP 189091, Suriname, Para, Suriname River basin, Coropinae Creek, vicinity of Republiek, 05.499°N, 55.214°W. **B**: *Curimata vittata* (male, preserved), USNM 304862, 169.7 mm SL, Venezuela, Amazonas, Río Macava, near Tapirapeco. **C**: *Curimata cyprinoides* (preserved), 137.9 mm SL, USNM 402472, Guyana, Cuyuni River. **D**: *Curimatopsis crypticus* (male, live), FMNH ex ANSP 189091, Suriname, Para, Suriname River basin, Coropinae Creek, vicinity of Republiek, 05.499°N, 55.214°W. **E**: *Cyphocharax spilurus* (live), USNM uncataloged, 34.7 mm SL, Guyana, Cuyuni River, 06.845°N, 60.130°W. **F**: *Cyphocharax helleri* (preserved), ANSP 189154, Suriname, Sipalawini, Lawa River, eight km SSW of Anapaike-Kawemhakan, 03.325°N, 54.063°W. Photos by M. Sabaj Pérez (A, D, F), S. Raredon (B) and W. Bronaugh (C, E).

margin of maxilla distinctly rounded and extending anteriorly to pronounced degree when lower jaw depressed. Mature males with pronounced expansion of penultimate principal ray of lower lobe of caudal fin. Relative depth of caudal peduncle sexually dimorphic, deeper in mature male. . . . . . . . . . . . .
. . . . . . . .**Curimatopsis crypticus** Vari, 1982 (Figs 9A, 9D)
**1b:** Lateral line complete in all but small juveniles. Anterior margin of maxilla slightly convex to slightly concave anteriorly and not extending anteriorly to a pronounced degree when lower jaw depressed. No sexual dimorphism apparent in rays of caudal fin or in relative depth of caudal peduncle . . . . . . .**(2)**

**2a:** Middle rays of caudal-fin lobes covered with patches of scales smaller than those on body, with most of lobes covered by scales in larger specimens. . . . . . . . .**Curimatella (3)**
**2b:** Middle rays of caudal-fin lobes lacking scales smaller than those on body or scales limited to basal portions of lobes even in larger specimens . . . . . . . . . . . . . . . . . . . .**(4)**

**3a:** Interorbital width 45-50% of HL. Gape width 28-33% of HL. Length of postorbital portion of head 39-45% of HL.

Orbital diameter 27-32% of HL . . . . . . . . . . . . . . . . . . . . . .
**Curimatella alburna** (Müller & Troschel, 1844) (Fig. 10A)
**3b:** Interorbital width 38-45% of HL. Gape width 24-29% of HL. Length of postorbital portion of head 36-40% of HL. Orbital diameter 33-39% of HL . . . . . . . . . . . . . . . . . . . . . .
. **Curimatella immaculata** (Fernández-Yépez, 1948) (Fig. 10E)

**4a:** Elaborations of soft tissues on roof of mouth limited to three simple, non-fleshy longitudinal folds (Fig. 11A). Folds not paralleled by series of secondary fleshy folds. No lobulate fleshy bodies extending ventrally into oral cavity . . . **(5)**
**4b:** Roof of mouth with three fleshy longitudinal folds paralleled by series of secondary folds (Fig. 11B), or with series of lobulate fleshy bodies extending ventrally into oral cavity (Fig. 11C) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**(14)**

**5a:** Laterosensory canal segment in sixth infraorbital tripartite (Fig. 12A). Laterosensory canal segments in fourth and fifth infraorbitals forming arch continuous with canal segments in more anterior infraorbitals (Fig. 13A). Fourth infraorbital with distinct posteriorly oriented branch of lat-
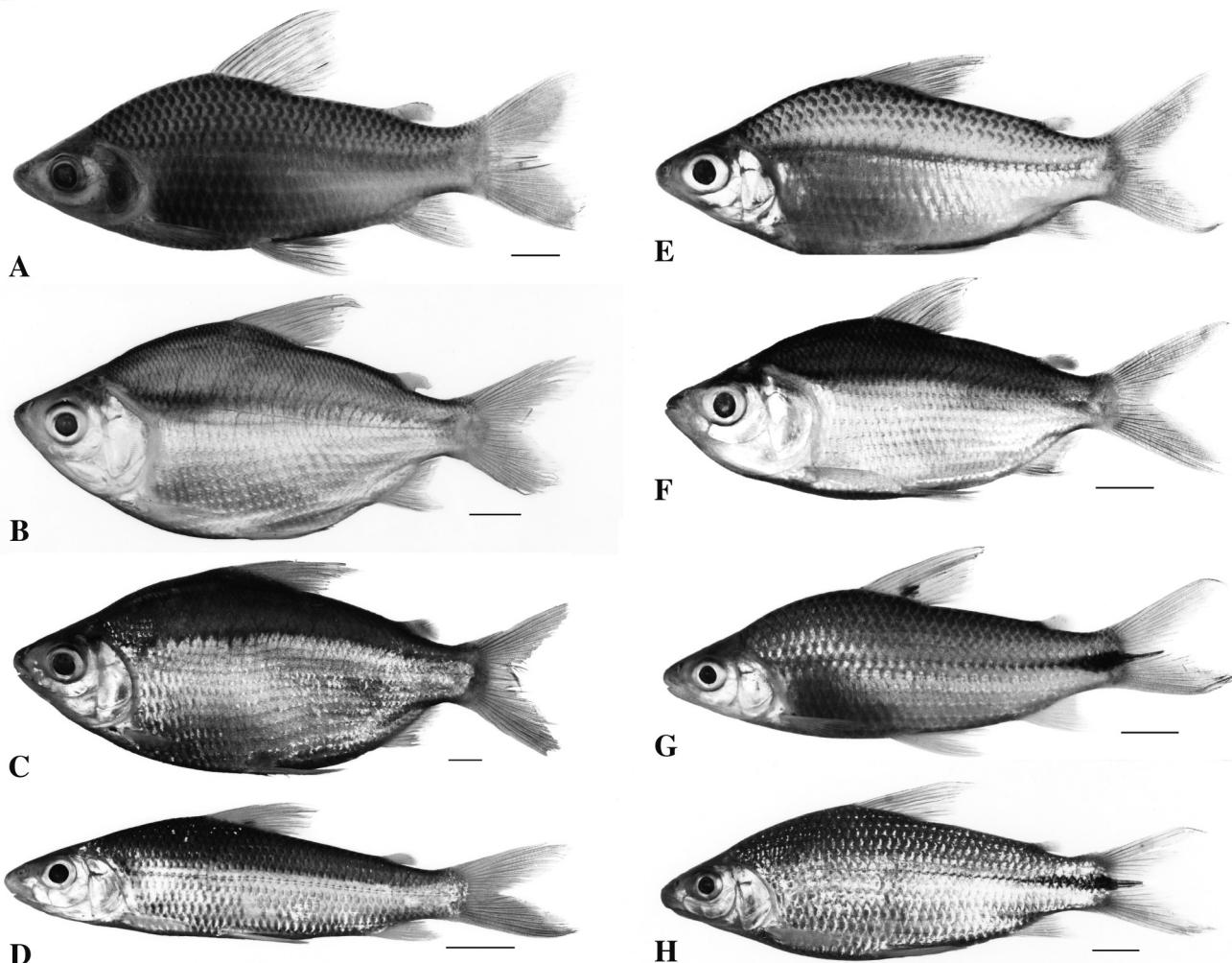
Figure 10. - Curimatidae. **A**: *Curimatella alburna* (preserved), MZUSP 6425, Brazil, Amazonas, Igarapé Chefe, Lago Beruri. **B**: *Psectrogaster ciliata* (preserved), USNM 269990, 84.0 mm SL, Venezuela, Bolivar, caño entering Río Orinoco, S of El Burro. **C**: *Curimata roseni* (preserved, holotype), MZUSP 28651, Brazil, Roraima, Rio Branco, Cachoeira de Bem Querer. **D**: *Steindachnerina planiventris* (preserved), MZUSP 38557, Brazil, Rondônia, Rio Machado, near mouth. **E**: *Curimatella immaculata* (preserved), USNM 269928, 42.3 mm SL, Venezuela, Bolivar, caño entering Río Orinoco S of El Burro. **F**: *Psectrogaster essequibensis* (preserved), USNM 267339, 73.3 mm SL, Peru, Loreto, Río Amazonas, Santa Rosa. **G**: *Steindachnerina guentheri* (preserved), USNM 298034, 77.4 mm SL, Peru, Ucayali, Pucallpa, Río Neshuya, 60 km W of Pucallpa. **H**: *Steindachnerina varii* (preserved), ZMA120.501, Suriname, Brokopondo District, Morawijne or Gran Kreek, 63 km S of Afobaka. Scale bars indicate one centimetre. Photos by T. B. Griswold.

erosensory canal segment in that bone (Fig. 13A) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***Psectrogaster*** **(6)**

**5b:** Laterosensory canal segment in sixth infraorbital in form of simple tube (Fig. 12D). Laterosensory canal segments in fourth and fifth infraorbitals meeting at acute angle (Fig. 13C). Fourth infraorbital lacking distinct posteriorly oriented branch coming off laterosensory canal segment in that bone (Fig. 13C) . . . . . . . . . . . . . . . . . ***Cyphocharax*** **(7)**

**6a:** Prepelvic region distinctly flattened transversely and bordered laterally by distinct, nearly right, angles in body wall. Longitudinal series of distinctly enlarged median scales along prepelvic region flanked by row of enlarged scales

conforming to lateral angles of body. Nine (rarely eight or ten) branched pelvic-fin rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . .***Psectrogaster essequibensis*** (Günther, 1864) (Fig. 10F)

**6b:** Prepelvic region transversely rounded and not bordered by distinct, nearly right, angles in body wall. Midventral and adjoining scales irregularly arranged and not enlarged. Eight branched pelvic-fin rays . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***Psectrogaster ciliata*** (Müller & Troschel, 1844) (Fig. 10B)

**7a:** Caudal peduncle lacking distinct dark midlateral pigmentation. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**(8)**

**7b:** Caudal peduncle with distinct dark pigmentation in form of rounded, horizontally elongate or triangular spot . . . . **(10)**
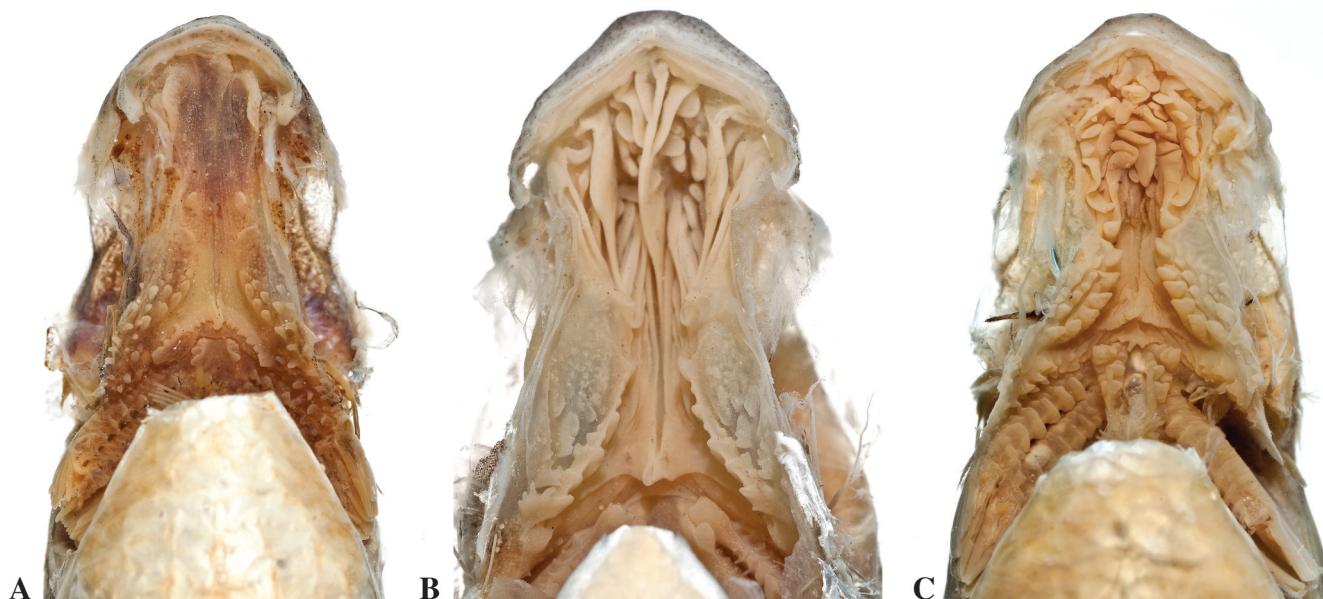
Figure 11. - Ventral views of roof of mouth showing form of projections of soft tissues. **A**: *Cyphocharax gouldingi*, USNM 268006, 82.2 mm SL; **B**: *Curimata cyprinoides*, USNM 267963, 86.1 mm SL; **C**: *Steindachnerina guentheri*, USNM 298031, 90.0 mm SL.

**8a:** Lateral-line scales from supracleithrum to hypural joint 39-45 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .***Cyphocharax leucostictus*** (Eigenmann & Eigenmann, 1889) (Fig. 14C)

**8b:** Lateral-line scales from supracleithrum to hypural joint 29-34 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**(9)**

**9a:** Scales with dark pigmentation more intense along dorsal and ventral margins, forming faint longitudinal stripes in smaller individuals and distinct dark irregular stripes in larger specimens. Greatest body depth equal to distance from tip of snout to posterior margin of fourth scale of lateral line. . . . . *Cyphocharax microcephalus* (Eigenmann & Eigenmann, 1889) (Fig. 14D)

**9b:** Scales lacking concentration of darker pigmentation dorsally and ventrally and longitudinal stripes absent. Greatest body depth equal to distance from tip of snout to posterior margin of second scale of lateral line . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*Cyphocharax festivus* Vari, 1992 (Fig. 14A)

**10a:** Body with dark midlateral spot in region below dorsal-fin base . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**(11)**

**10b:** Body without dark midlateral spot in region below dorsal-fin base. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**(12)**

**11a:** Rounded midlateral dark spot in region below dorsal-fin base in all but specimens under 20 mm SL. Spot ranges from diffuse concentration of dark chromatophores in individuals of 18-45 mm SL to distinct black spot in larger specimens. No dark midlateral spots present in region between spot below dorsal-fin base and spot at rear of caudal peduncle . . . *Cyphocharax biocellatus* Vari, Sidlauskas & Le Bail, 2012

**11b:** One rounded midlateral very dark spot in region below dorsal-fin base in all specimens (18-42 mm SL). Spot under dorsal-fin followed posteriorly by two or three dark spots on midlateral surface of body and dark spot at rear of caudal peduncle . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Cyphocharax punctatus* (Vari & Nijssen, 1986) (Fig. 14E)

**12a:** Dark triangular spot on midlateral surface of caudal peduncle with nearly straight anterior margin. . . . . . . . . . . . . . . . . . . . . . *Cyphocharax gouldingi* Vari, 1992 (Fig. 14B)

**12b:** Dark rounded or horizontally elongate spot on midlateral surface of caudal peduncle with rounded anterior margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**(13)**

**13a:** Body with dark striping along lateral and dorsolateral portions of body; striping located along boundaries between rows of scales but faint in some individuals. Dark spot on midlateral surface of caudal peduncle rounded and reaching to, or nearly to, bases of dorsalmost and ventral principal caudal-fin rays. Dusky pigmentation absent from basal region of exposed portion of scales of lateral and dorsolateral portion of body; body without reticulate pigmentation pattern. In individuals smaller than 70 mm, body depth at dorsal-fin origin 38.3-43.8% of SL, mean 40.9%. Proportional body depth decreasing over ontogeny (Fig. 15), with mean body depth at dorsal-fin origin 37.0% SL (range 35.2%-39.0%) in individuals over 70 mm SL. . . . . . . . . . . . . . . . . . . . . . . . .*Cyphocharax helleri* (Steindachner, 1910) (Fig. 9F)

**13b:** Body without dark striping along lateral and dorsolateral portions of body. Dark spot on midlateral surface of caudal peduncle horizontally elongate and with dorsal and ventral margins of spot falling short of base of dorsalmost
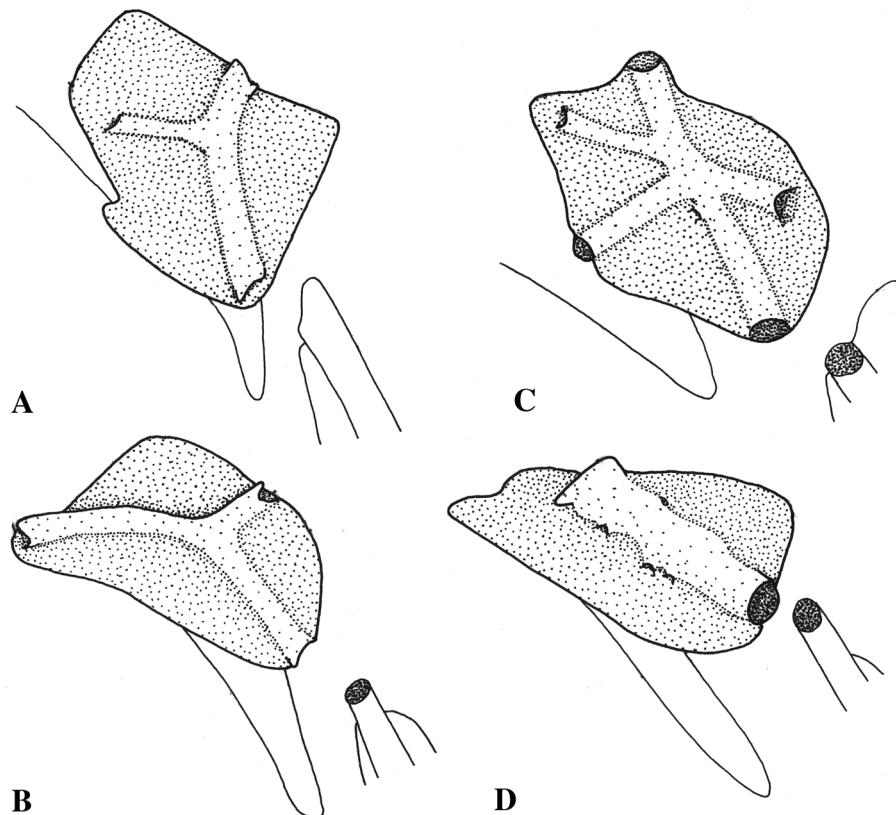
Figure 12. - Sixth infraorbital. **A**: *Psectrogaster amazonica*, USNM 261518, 106.0mm SL. **B**: *Curimata cyprinoides*, USNM 267964, 125.0 mm SL. **C**: *Potamorhina altamazonica*, USNM 257367, 119.8 mm SL. **D**: *Steindachnerina conspersa*, USNM 232224, 83.2 mm SL. Reprinted with permission from Vari 1992a.

and ventral principal caudal-fin rays. Dusky pigmentation on basal portion of exposed scales of lateral and dorsolateral portions of body, sometimes resulting in reticulate pattern. Individuals smaller than 70 mm with body depth at dorsal fin origin 32.3-36.6% of SL, mean 34.1%. Proportional body depth roughly constant (increasing very slightly) over ontogeny (Fig. 15), with mean body depth at dorsal-fin origin 34.4% SL (range 32.1%-38.1%) in individuals over 70 mm SL . . . . . . **Cyphocharax spilurus** (Günther, 1864) (Fig. 9E)

**14a:** Roof of mouth with three fleshy longitudinal folds paralleled by series of secondary folds (Fig. 11B) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .***Curimata*** **(15)**

**14b:** Roof of mouth with series of lobulate fleshy bodies extending ventrally into oral cavity (Fig. 11C) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .***Steindachnerina*** **(17)**

**15a:** Dorsal portion of body with 8-11 dark vertical bars. Bars subdivided into vertically aligned series of spots in some individuals . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Curimata vittata** (Kner, 1858) (Fig. 9B)

**15b:** Dorsal portion of body lacking dark vertical bars or series of vertically aligned spots . . . . . . . . . . . . . . . . . . **(16)**

**16a:** Anteriormost rays of dorsal fin filamentous in all but smaller specimens and reaching beyond posterior limit of adipose fin in largest individuals. Upper lip narrow, distance from tip of snout to midsagittal margin of lip approximately

one-half distance from symphysis to angle along lip margin between premaxilla and maxilla. 32 (rarely 31 or 33) vertebrae . . . . .**Curimata cyprinoides** (Linnaeus, 1766) (Fig. 9C)

**16b.** Anteriormost rays of dorsal fin not filamentous even in larger specimens. Upper lip relatively broad, distance from tip of snout to midsagittal margin of lip approximately equal to distance from symphysis to angle along lip margin between premaxilla and maxilla. 31 vertebrae . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Curimata roseni** Vari, 1989 (Fig. 10C)

**17a:** Prepelvic region of body distinctly flattened transversely. Five scales across flattened area immediately anterior to pelvic-fin origin. Anus distinctly separated from anterior limit of anal fin by five or six scales . . . . . . . . . . . . . . . . . . . . . **Steindachnerina planiventris** Vari & Vari, 1989 (Fig. 10D)

**17b:** Prepelvic region of body transversely rounded or at most obtusely flattened. Three to four scales across obtusely rounded area immediately anterior to pelvic-fin origin. Anus separated from anterior limit of anal fin by one to three scales . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **(18)**

**18a:** Dorsal fin with spot of dark pigmentation on basal portions of middle rays. 30-36 scales present in lateral line to hypural joint (only known within Guianas from extreme northwestern Guyana) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .**Steindachnerina guentheri** (Eigenmann & Eigenmann, 1889) (Fig. 10G)
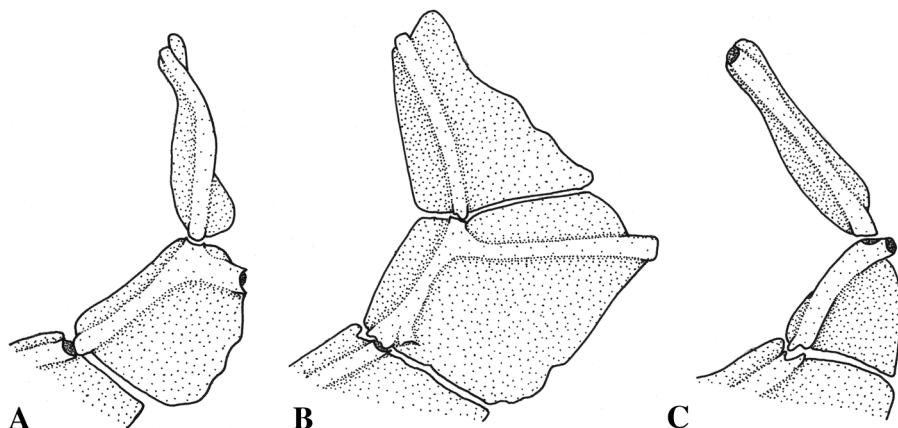
Figure 13. - Fourth and fifth infraorbitals and dorsal portion of third infraorbital. **A**: *Psectrogaster curviventris*, USNM 243221, 72.9 mm SL. **B**: *Potamorhina altamazonica*, USNM257367, 119.8 mm SL. **C**: *Curimatella meyeri*, USNM 26508, 100.1 mm SL. Reprinted with permission from Vari 1992a.

**18b:** Dorsal fin lacking spot of dark pigmentation on basal portions of middle rays. 36-40 scales present in lateral line to hypural joint . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .
. . . ***Steindachnerina varii*** Géry, Planquette & Le Bail, 1991 (Fig. 10H)

## Comments on Curimatidae from Guyana, Suriname and French Guiana

Species of the Curimatidae constitute the second most diverse assemblage of anostomoids in the Guianas (19 morphospecies). Identification of members of the Curimatidae to the generic level is complicated by the fact that the delimiting characters for some genera involve details of the development of the fleshy lining of the roof of the mouth. The pronounced elaboration of the fleshy tissues in this region diagnostic of some genera in the Guianas (*Curimata*, *Steindachnerina*) is not present in smaller specimens of those groups. This renders identifications of small individuals difficult in the absence of ontogenetic series that include adult specimens through progressively smaller individuals lacking the fleshy elaboration of the roof of the mouth present in larger conspecifics. Comments on certain other problematic components of the family follow, and additional discussion of curimatid diversity in the Guianas appears in Vari *et al*. (2012).

*Curimatella*. - Although adults of *Curimatella* have the caudal fin lobes broadly enveloped by scales distinctly smaller than those on the body, the extent of the scale fields is less extensive in smaller specimens making it difficult to unambiguously assign such individuals to the genus in isolation. Ontogenetic series are often the only recourse in such situations. Some species of *Cyphocharax,* including *C. microcephalus* of the Guianas, have fields of scales of about the same size as those on the body extending onto the midbasal portions of each fin lobe in a parabolic pattern (for comparable condition in a congener see Vari *et al*., 2010, Fig. 2). This pattern in these species of *Cyphocharax* differs from that in the species of *Curimatella* in which the scales on the caudal-fin lobes are proportionally much smaller and

extend over a greater portion of the lobes (e.g., *Curimatella alburna*, see Vari, 1992a, Fig. 23).

*Cyphocharax helleri* **and** *C. spilurus*. - Couplet 13 in the above key readily distinguishes these two species when pigmentation patterns are apparent. However, *C. helleri* demonstrates a pronounced range in the intensity of the characteristic series of dark longitudinal stripes along the junctions of the scale rows with this variation perhaps a function of different water types. When the striping pattern is less intense it may be overlooked and such samples might be mistakenly identified as *C. spilurus*. The two species differ in the form of the dark spot on the rear of the caudal peduncle and base of the middle caudal-fin rays (typically more vertically extensive in *C. helleri*) and in the typical presence in *C. spilurus* of a field of dark pigmentation at the base of the exposed portion of the scales on the lateral and dorsal portions of the body contra the lack of such pigmentation in *C. helleri*. The two species also differ in overall body form (compare panels E and F of Fig. 9, or figs 15-17 of *C. helleri versus* figs 76-78 of *C. spilurus* in Vari, 1992b), with *C. helleri* typically the deeper bodied of the two species (Fig. 15). A diagnosis based on body depth is, however, confounded by allometric variation in *C. helleri*, which decreases in proportional body depth over the course of ontogeny and converges on the upper extreme that typifies *C. spilurus*. Thus, body depth only provides a reliable diagnosis for individuals below 70 mm SL (see couplet 13 in the key above).

Interestingly, weakly pigmented members of *C. helleri* and particularly deep-bodied members of *C. spilurus* appear to be common among examined specimens from the river systems of Suriname. Both of these species occur throughout Guyana, Suriname and French Guiana, but *C. spilurus* is more common in western drainages, while *C. helleri* is more common to the east (Appendix Fig. 20). The complementary east-west gradient in the distribution patterns combined with the high frequency of individuals with a somewhat intermediate morphology suggests that hybridization and introgres-

**A**

**B**

**C**

**D**

**E**
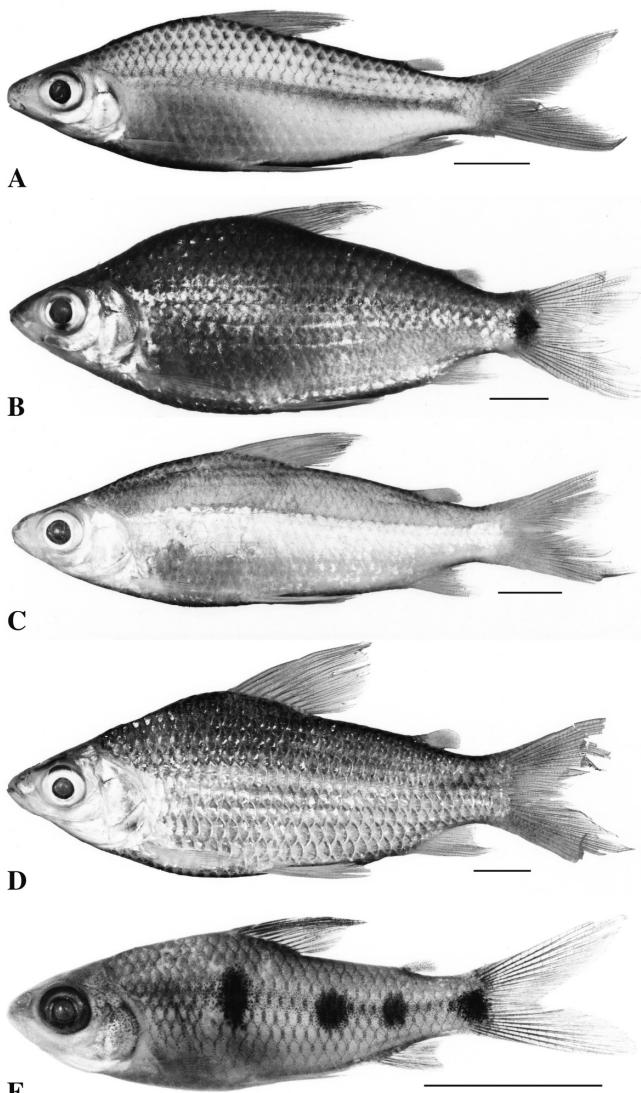
Figure 14. - Curimatidae. **A**: *Cyphocharax festivus* (preserved), USNM 280426, 62.6 mm SL, Peru, Loreto, Río Nanay, NE of Iquitos. **B**: *Cyphocharax gouldingi* (preserved, holotype), MZUSP 41762, Brazil, Amapá, Rio Cupixí, 0°40'N, 51°40'W. **C**: *Cyphocharax leucostictus* (preserved), USNM 268020, 75.1 mm SL, Brazil, Amazonas, Rio Negro, Anavilhanas. **D**: *Cyphocharax microcephalus* (preserved), ZMA 106.815, Suriname, Marowijne Kreek, 63 km S of Afobaka. **E**: *Cyphocharax punctatus* (preserved, holotype), USNM 275000, 25.9 mm SL, Suriname, Marowijne District, Litani River 03.183'N, 54.200'W. Scale bars indicate one centimetre. Photos by T. B. Griswold.

sion may occur between these species. A future genetic study should address this possibility directly.

*Curimata*. - Two of the species of *Curimata* (*C. roseni*, *C. vittata*) in the area of interest are broadly distributed through the Amazon River system (see Vari, 1989b: figs. 20, 25) with their occurrence in the Guianas limited to the upper portion of the Rio Branco system, the adjacent Rupununi River, the central Essequibo, and in the case of *C. roseni*, the Demerara
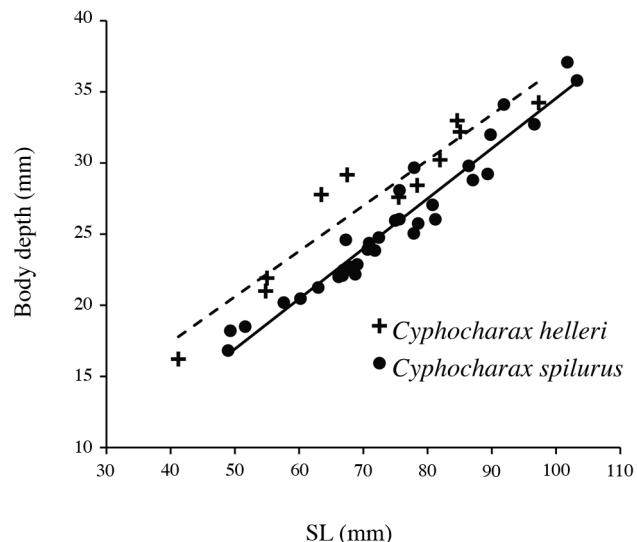


Figure 15. - Relationship of body depth at dorsal fin origin to standard length (SL) over ontogeny in *Cyphocharax helleri* (crosses, N = 11) and *C. spilurus* (circles, N = 34). Trendlines indicate least-squares linear regressions.



**A**

**B**
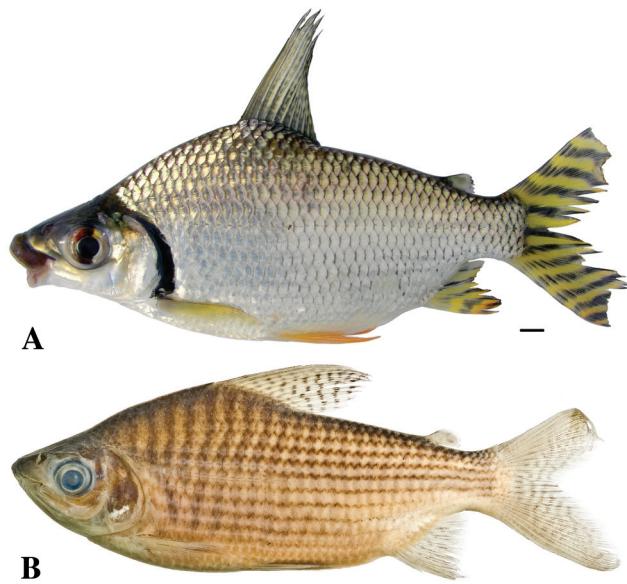
Figure 16. - Prochilodontidae. **A**: *Semaprochilodus varii* (live). ANSP 187435. Suriname, Sipalawini, Lawa River, Marowini drainage, 03.325°N, 54.063°W. **B**: *Prochilodus rubrotaeniatus* (preserved), USNM 3768707, 123.7 mm SL, Guyana, Morai Creek. Scale bars indicate one centimetre. Photos by M. Sabaj Pérez (A) and S. Raredon (B).

River (Appendix Fig. 16). Similarly, this study revealed that the common Amazonian species *Cyphocharax leucostictus* and *Steindachnerina planiventris* also occur in the Branco and Rupununi rivers of Guyana (Appendix Figs 19, 23). It is likely that the occurrence of these four species in the Essequibo basin is a result of their past movement from the

upper Rio Branco system into the adjacent portions of the Rupununi River basin during flood conditions which result in continuity of those two river systems across the Rupununi savannahs (Lowe-McConnell, 1964; Lujan and Armbruster, 2011; de Souza *et al.*, 2012). Interestingly, no samples of *Curimata roseni, Curimata vittata, Cyphocharax leucostictus* or *Steindachnerina planiventris* from the Rupununi or Essequibo system were known to have been collected until recent decades. This admittedly may be a function of earlier incomplete sampling of that ichthyofauna or failure of such specimens to come to our notice, but may also indicate that these species are relatively recent additions to the fish fauna of the upper Rupununi and Essequibo rivers.

*Steindachnerina*. - One of the species of the Curimatidae in our listing, *Steindachnerina guentheri*, is limited in the Guianas to the extreme northwestern portion of Guyana in the Arau, Barama and Waini river systems (Appendix Fig. 23). These rivers all drain northwest into the delta of the Río Orinoco, a basin through which *S. guentheri* is broadly distributed (Vari, 1991, Fig. 30).

**Key to Prochilodontidae from Guyana, Suriname and French Guiana**

**1a:** Caudal fin with series of irregular vertical bars or wavy lines formed by small dark spots, but without distinct stripes across lobes. Scales between posterior terminus of dorsal-fin base and adipose-fin origin comparable in form to adjacent scales and lacking membranous spatulate process along posterior margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Prochilodus rubrotaeniatus** Jardine & Schomburgk, 1841 (Fig. 16B)

**1b:** Caudal fin with total of seven to 14 distinct dark stripes, one stripe along middle caudal-fin rays, three to six oblique stripes on upper lobe and three to seven oblique stripes on lower lobe. Scales between posterior terminus of dorsal-fin base and adipose-fin origin with membranous spatulate process along posterior margin of scale . . . *Semaprochilodus* **(2)**

**2a:** Membranous opercular border and exposed surface of pectoral girdle intensely pigmented with black. Lateral-line scales 47-53, circumpeduncular scales 18-22 . . . . . . . . . . . . . . . . . . . . . . *Semaprochilodus varii* Castro, 1988 (Fig. 16A)

**2b:** Membranous opercular border and exposed surface of pectoral girdle weakly pigmented with black. Lateral-line scales 39-41; circumpeduncular scales 16. Known in the Guianas from a single specimen from extreme southwestern Guyana (Rio Branco drainage) . . . . . . . . . . . . . . . . . . . . . . *Semaprochilodus insignis* (Jardine & Schomburgk, 1841) (not figured)

**Comments on Prochilodontidae from Guyana, Suriname and French Guiana**

Only two species of the Prochilodontidae (*Prochilodus rubrotaeniatus, Semaprochilodus varii*) are major components of the ichthyofauna in the Guianas. Both are easily identified by differences in pigmentation (Fig. 16). *Prochilodus rubrotaeniatus* is nearly ubiquitous throughout the region and found in the Essequibo, Corantijn, Marowijne, Oyapock rivers and intervening systems while *Semaprochilodus varii* is endemic to the Marowijne/Maroni drainage (Appendix Fig. 24). A single specimen (AUM 36944) of *Semaprochilodus insignis* is known from the Rio Branco drainage in extreme southwestern Guyana. That species is widespread through the major portions of the Amazon basin including the Rio Branco (Castro and Vari, 2004, Fig. 61).

**DISCUSSION**

**Distributions and endemicity**

Fifty-six anostomoid species are currently known to inhabit the river systems of the Guianas. This is a remarkably high number representing about 20% of the total diversity of that superfamily, despite the fact that the Guianas span only 6% of the total geographic area inhabited by the clade. Factors potentially contributing to this diversity include: the isolation of the north-flowing drainage systems from each other and to a considerable although not absolute degree from the neighbouring Amazon and Orinoco systems, historical factors such as the very long term stability of the underlying Guiana Shield, an exceptional diversity of habitats, and perhaps chance (Vari and Ferraris, 2009; Lujan and Armbruster, 2011).

Of the four anostomoid families, the Anostomidae with 30 species is most diverse in this region, followed by the Curimatidae (19 species), Chilodontidae (4 species) and Prochilodontidae (3 species). Distribution maps for 54 of these species appear in the Appendix, with *Abramites hypselonotus* and *Pseudanos trimaculatus* not plotted because their occurrence in the Guianas is known only from single specimens with indefinite collection localities in the Rio Branco system in southwestern Guyana. While some species are nearly ubiquitous throughout the region (e.g. *Prochilodus rubrotaeniatus, Leporinus fasciatus, L. granti, Cyphocharax helleri, C. spilurus*), most have more restricted distributions. Inspection of species distribution limits reveals six regions harbouring distinct faunas: 1) the Takutu and Ireng rivers of southwestern Guyana, which form part of the upper Rio Branco drainage, which is in turn part of the Negro-Amazonas system 2) the Barima and Waini rivers of northwestern Guyana, which are tributaries to the Río Orinoco delta, 3) the Essequibo-Rupununi River system (including the separately draining Demerara and Berbice rivers) of

Guyana, 4) a union of the Corantijn, Nickerie, Coppename, Saramacca and Suriname river drainages in Guyana and Suriname, 5) the Marowijne/Maroni River system of Suriname and French Guiana (including the Litani, Tapanahony and Mana rivers), and 6) the Oyapock and Approuague river basins of French Guiana. Of these, the first two are peripheral to the core Guianas and form part of much larger river drainages in neighbouring Venezuela (Río Orinoco) and Brazil (Rio Amazonas), while the remaining four drainage systems lie entirely or largely within the three targeted countries (Fig. 1).

Of the four core faunistic regions in the Guianas, the greater Essequibo River system contains the highest number of anostomoid species (35), followed by the Maroni and associated rivers (22 species), the Corantijn and associated rivers (19 species) and the Oyapock-Approuague region (14 species). However, the vast majority (27 of 35) of the anostomoid species inhabiting the Essequibo system also occur in the neighbouring Rio Branco (part of the Amazon basin), with many of these restricted to the river systems of the Rupununi savannahs, to which they likely dispersed during seasonal inundations (Lowe-McConnell, 1964; Lujan and Armbruster, 2011; de Souza *et al.*, 2012). If one excludes these species of probable Amazonian origin, the resulting pattern of anostomoid species richness is much more constant across the Guianas. Eight remaining species inhabit the Essequibo system, ten in the Corantijn and associated rivers, 14 in the Maroni drainage, and ten in the Oyapock.

Many of these truly Guianese species occur in more than one of the major faunal regions, but several are endemic to only one. Only the Corantijn, Suriname and intervening rivers harbour *Leporinus apollo* and *Petulanos spiloclistron*. *Cyphocharax biocellatus*, *C. punctatus*, *Leporinus lebaili* and *Semaprochilodus varii* are unique to the greater Maroni system, and *Leporinus melanostictus* is limited to the Oyapock and Approuague systems. Interestingly, there are no species in our sample endemic to the Essequibo (*Anostomoides laticeps* and *Leporinus arcus* appear to be so on the distribution maps but are also known from the Río Orinoco of Venezuela, and in the former case, from the Rio Solimões of Brazil). The numbers of species endemic to a single region may increase once revisionary studies are undertaken on the several nominal species revealed to have disjunct distributions (*Anostomus ternetzi*, *Leporinus nijsseni*, *Leporinus granti* and possibly *Schizodon fasciatus* and *Curimatopsis crypticus*) or substantial morphological variation across a broad putative range (*Anostomus anostomus*, *Cyphocharax helleri*).

### New records

This survey revealed four newly recorded species in the Guianas, yielding a 8% increase in known species richness for this group in the three countries combined. Two of these represent species new to science, one of which is described in this volume as *Cyphocharax biocellatus*, and the other of which (*Leporinus apollo*) was described very recently (Sidlauskas *et al.*, 2011). The other two new records, *Cyphocharax leucostictus* and *Steindachnerina planiventris* of the Curimatidae, represent species that are common in the Rio Branco of Brazil and are now recorded within the Ireng and Takutu river systems of southern Guyana and/or the waterways of the Rupununi savannah. Five other species (*Abramites hypselonotus* and *Pseudanos trimaculatus* of the Anostomidae, *Curimata vittata* and *C. roseni* of the Curimatidae and *Semaprochilodus insignis* of the Prochilodontidae) had previously been recorded from Guyana in general terms in a recent checklist (Vari *et al.*, 2009), but are now tied to specific localities. The known specimens of *Abramites hypselonotus*, *Pseudanos trimaculatus* and *Semaprochilodus insignis* from Guyana occur only in the Rio Branco drainage and represent perhaps the most northeasterly records of these species in the Rio Branco basin. The other four species discussed above occur within the Essequibo-Rupununi system proper, with the two species of *Curimata* found further afield in the Essequibo system than *Cyphocharax leucostictus* and *Steindachnerina planiventris* (Appendix Figs 16, 19, 23). Whether this greater range indicates an earlier transition through the Rupununi portal, higher vagility, different habitat tolerances or pure chance is not known. Sabaj *et al.* (2008), citing McConnell (1959), discussed the possibility of a Paleogene (23 mya) stream capture of the Rio Takutu by the Rio Branco as another possible explanation for the co-occurrence of channel-dwelling species such as *Rhinodoras armbrusteri* in both systems. Adults of *Curimata* species also dwell in main channel habitats, but if such an ancient dispersal scenario were responsible for their presence in both systems we would expect those species to be more broadly distributed throughout the Essequibo basin, and to have been long ago collected there. Instead, the specimens of the four new records within the Essequibo were all collected in recent decades. The recency of these collections implies that these species are new immigrants to Guyana, but it is still possible that the range extensions simply result from increased sampling effort.

### Unsampled regions

The synthesis of nearly 3000 lots of georeferenced museum anostomoid specimens provides a very detailed summary of historic ichthyological collecting efforts within the lowlands of the Guianas (Fig. 2). While some river systems, such as the Essequibo, Rupununi and Lower Corantijn, have been sampled very extensively, as have all major drainages of French Guiana (the latter thanks to the exhaustive efforts reported by Planquette *et al.* [1996]), other regions have never been sampled or have been sampled very sparsely. Of the apparent lacunae in Fig. 2, the Berbice, Cuyuni and

Mazaruni rivers in Guyana have all been sampled too recently to have been included in this publication (with specimens deposited at the University of Guyana, the Royal Ontario Museum, National Museum of Natural History and Oregon State University). The remaining regions most in need of ichthyological exploration include the Rewa and New rivers of southeastern Guyana, the upper Corantijn and Tapanahony rivers of southern Suriname which are yet to be sampled, and possibly the rivers of northwestern Guyana (Río Orinoco drainage) which do not appear to have been surveyed ichthyologically since the 1930s.

**Concluding remarks**

Despite more than 250 years of ichthyological exploration, the many rivers of the Guianas continue to yield new discoveries, and we surely have not yet catalogued fully the extraordinary diversity of the fishes in that region. Nevertheless, thanks to the long and sustained interest in the Guianas, the world's ichthyological collections hold a formidable sum of accumulated knowledge about the biogeography and diversity of the fishes in that region. This contribution set out to aggregate the large amount of available data on one important clade in the Characiformes in order to clarify taxonomic and geographic boundaries and provide identification keys and distribution maps as a service to other ichthyologists. This process revealed new species, new records, major gaps in historic collecting effort, disjunct distributions that may indicate the presence of cryptic species, possible evidence of hybridization between two congeneric species, and evidence for six distinct regions of endemicity within the fishes of the Guianas. These unexpected results provide another good example of the power of aggregate data to yield insights unattainable from the data in isolation (for an extended discussion, see Sidlauskas *et al*., 2010). We hope that specialists on the other components of the rich biodiversity of the Guianas that are yet to be examined in comparable detail will follow our lead and synthesize the available information in their realm of expertise. If enough such studies can be completed, the depth and detail of the resulting picture of diversity and distribution could revolutionize our ability to study, conserve and understand one of the world's richest biotas.

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**APPENDIX**
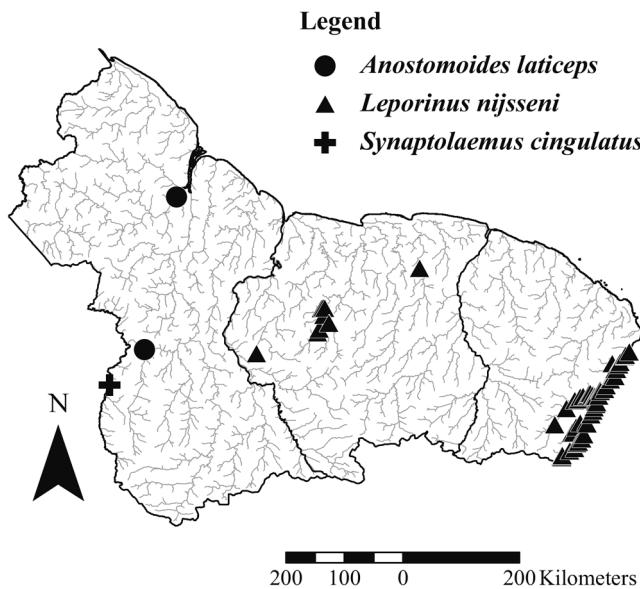


Appendix Figure 1. - Distribution map of *Anostomoides laticeps* (circles), *Leporinus nijsseni* (triangles) and *Synaptolaemus cingulatus* (cross).
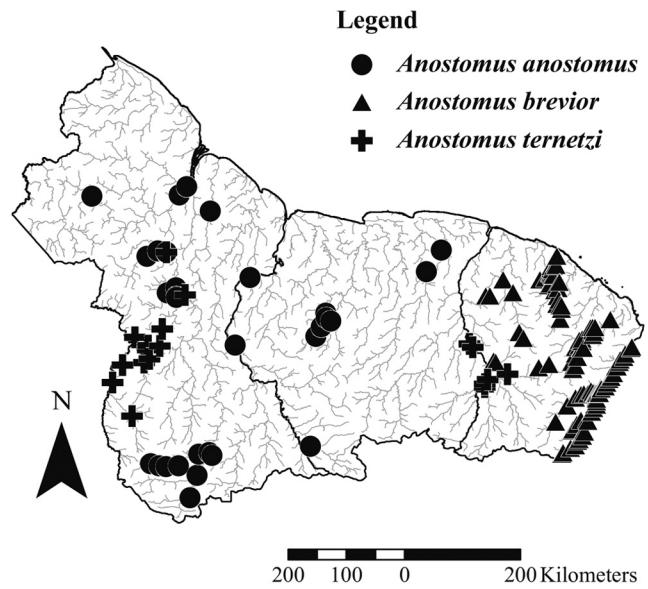


Appendix Figure 2. - Distribution map of *Anostomus anostomus* (circles), *A. brevior* (triangles) and *A. ternetzi* (crosses).
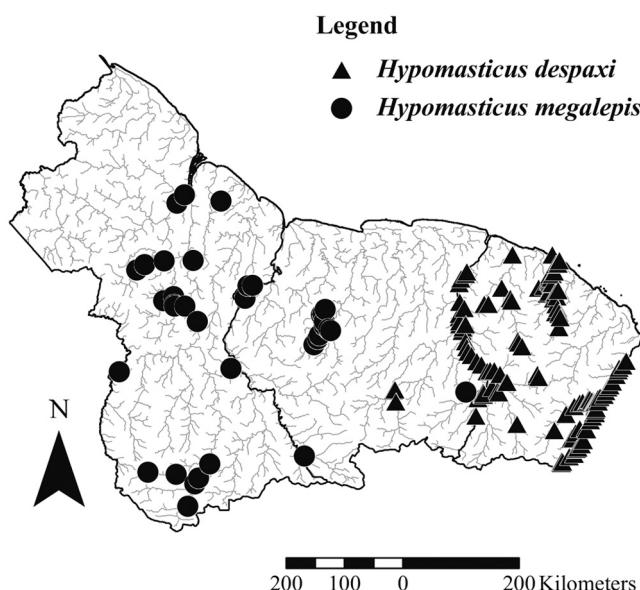


Appendix Figure 3. - Distribution map of *Hypomasticus despaxi* (triangles) and *H. megalepis* (circles).
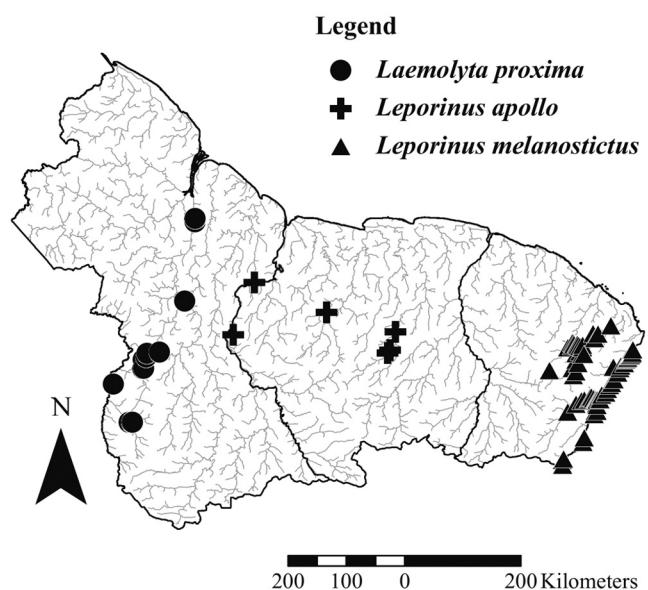


Appendix Figure 4. - Distribution map of *Laemolyta proxima* (circles), *Leporinus apollo* (crosses) and *Leporinus melanostictus* (triangles).

**Legend**

+ *Leporellus vittatus*
▲ *Leporinus arcus*
● *Leporinus gossei*

**Legend**

● *Leporinus fasciatus*

N

200 100 0 200 Kilometers
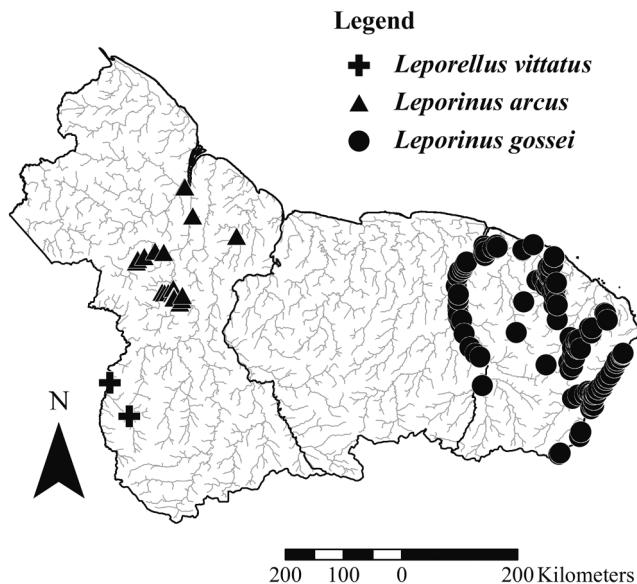
Appendix Figure 5. - Distribution map of *Leporellus vittatus* (crosses), *Leporinus arcus* (triangles) and *Leporinus gossei* (circles).

N

200 100 0 200 Kilometers
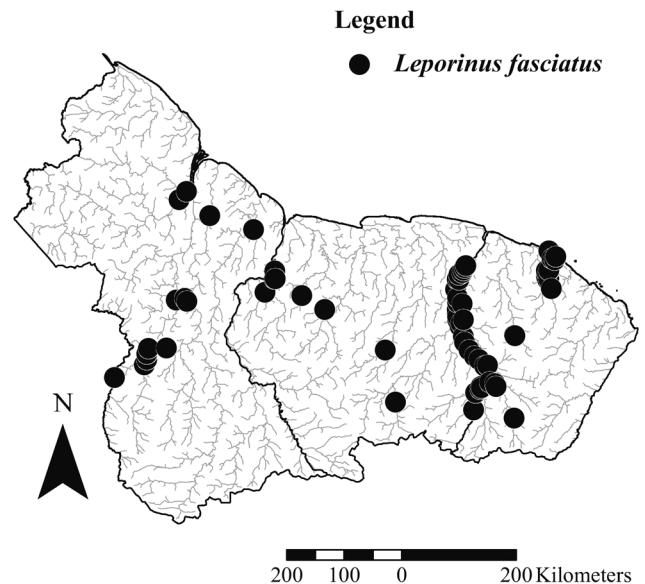
Appendix Figure 6. - Distribution map of *Leporinus fasciatus* (circles).

**Legend**

● *Leporinus maculatus*
+ *Leporinus desmotes*

**Legend**

▲ *Leporinus nigrotaeniatus*
● *Leporinus ortomaculatus*

N

200 100 0 200 Kilometers
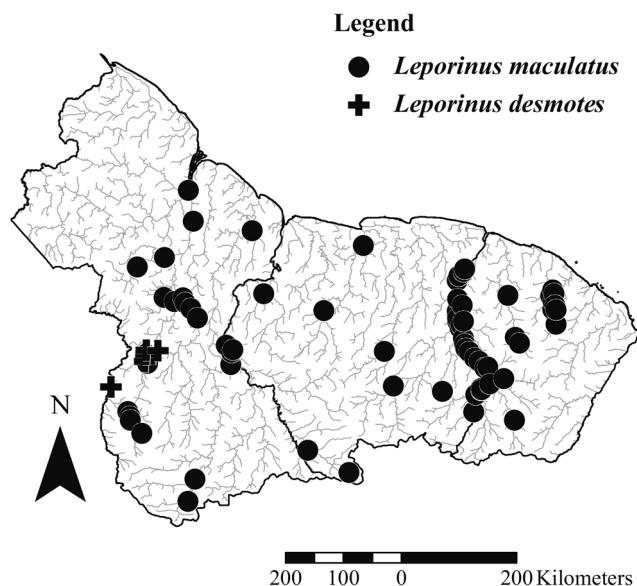
Appendix Figure 7. - Distribution map of *Leporinus maculatus* (circles) and *L. desmotes* (crosses).

N

200 100 0 200 Kilometers
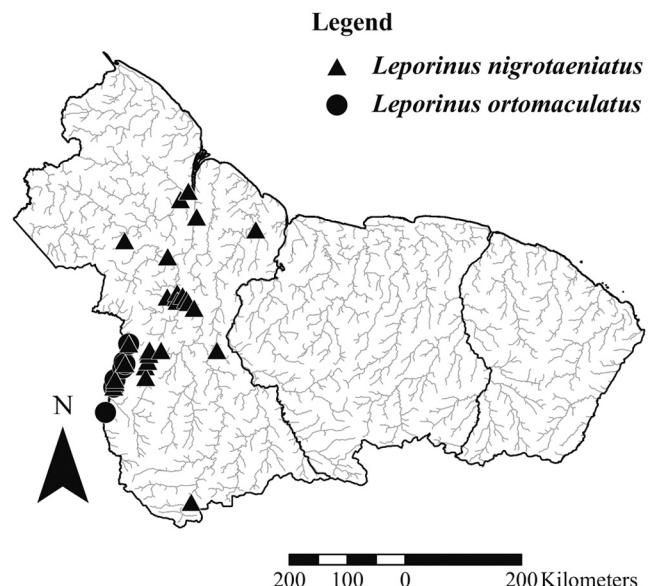
Appendix Figure 8. - Distribution map of *Leporinus nigrotaeniatus* (triangles) and *L. ortomaculatus* (circles).

**Legend**
● *Leporinus agassizi*
▲ *Leporinus friderici*
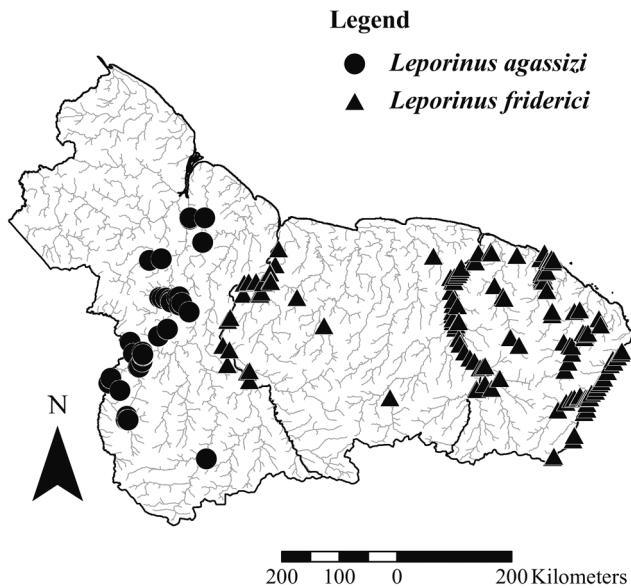
Appendix Figure 9. - Distribution map of *Leporinus agassizi* (circles) and *L. friderici* (triangles).

**Legend**
● *Leporinus granti*
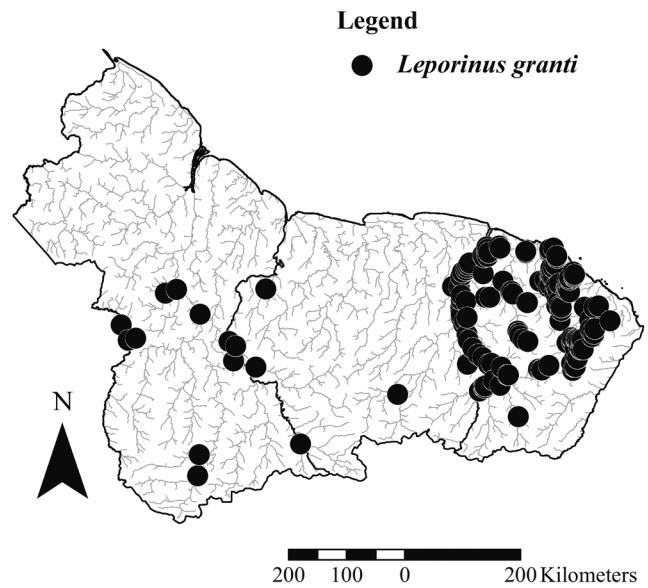
Appendix Figure 10. - Distribution map of *Leporinus granti* (circles).

**Legend**
▲ *Leporinus lebaili*
● *Pseudanos irinae*
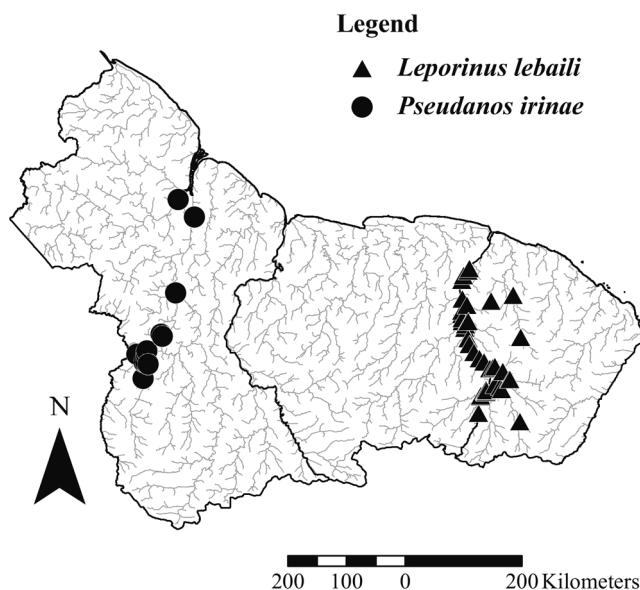
Appendix Figure 11. - Distribution map of *Leporinus lebaili* (triangles) and *Pseudanos irinae* (circles).

**Legend**
▲ *Petulanos plicatus*
● *Petulanos spiloclistron*
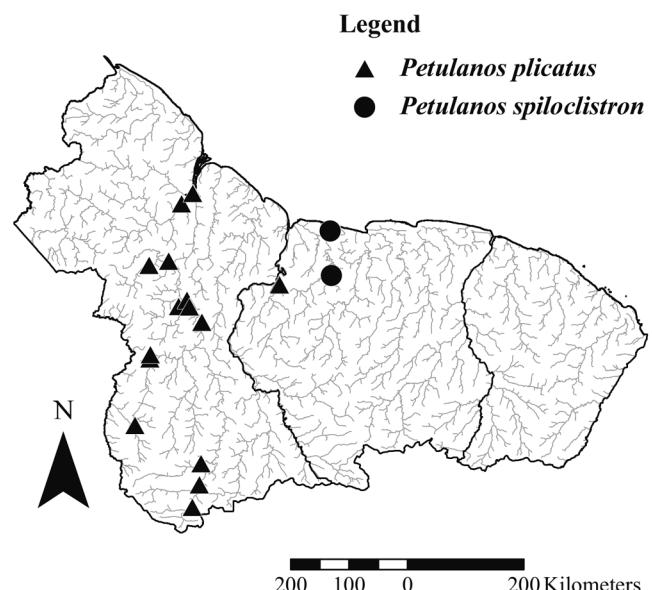
Appendix Figure 12. - Distribution map of *Petulanos plicatus* (triangles) and *P. spiloclistron* (circles).
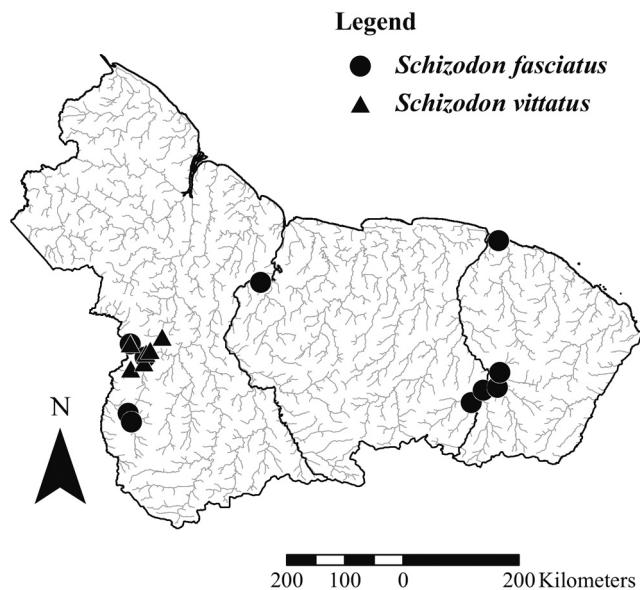
Appendix Figure 13. - Distribution map of *Schizodon fasciatus* (circles) and *S. vittatus* (triangles).
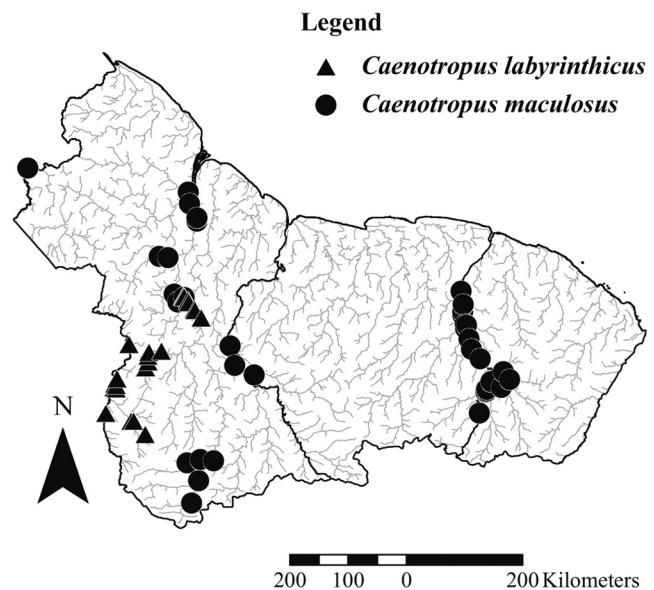


Appendix Figure 14. - Distribution map of *Caenotropus labyrinthicus* (triangles) and *C. maculosus* (circles).
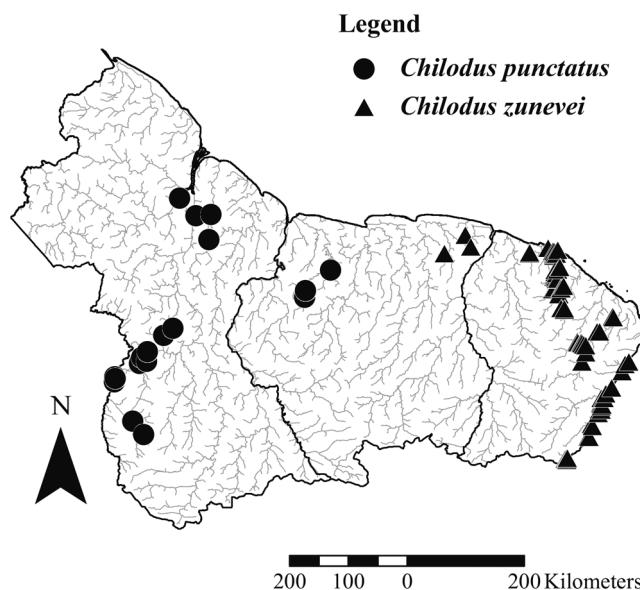


Appendix Figure 15. - Distribution map of *Chilodus punctatus* (circles) and *C. zunevei* (triangles).
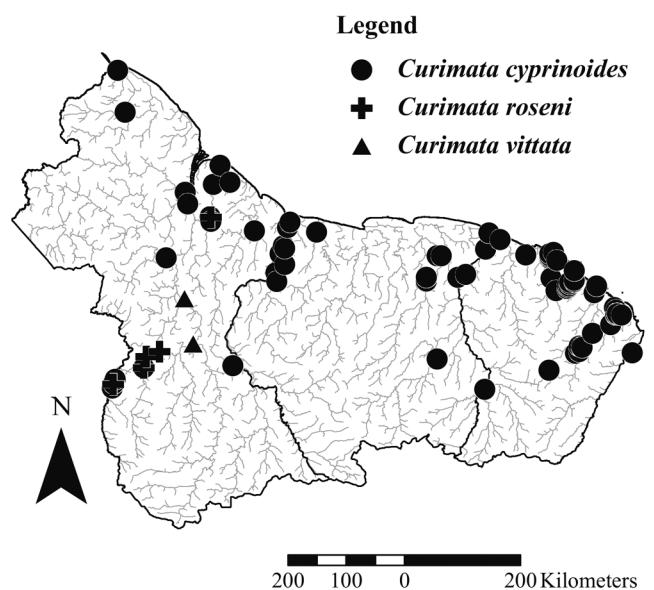


Appendix Figure 16. - Distribution map of *Curimata cyprinoides* (circles), *C. roseni* (crosses) and *C. vittata* (triangles).
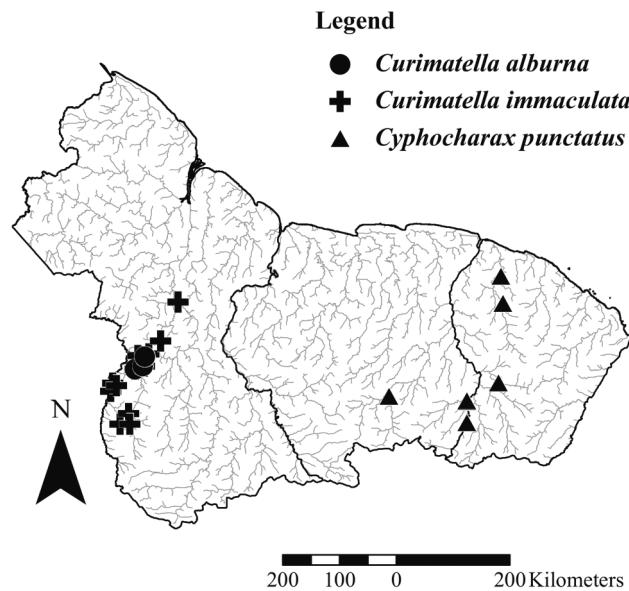
Appendix Figure 17. - Distribution map of *Curimatella alburna* (circles), *Curimatella immaculata* (crosses) and *Cyphocharax punctatus* (triangles).
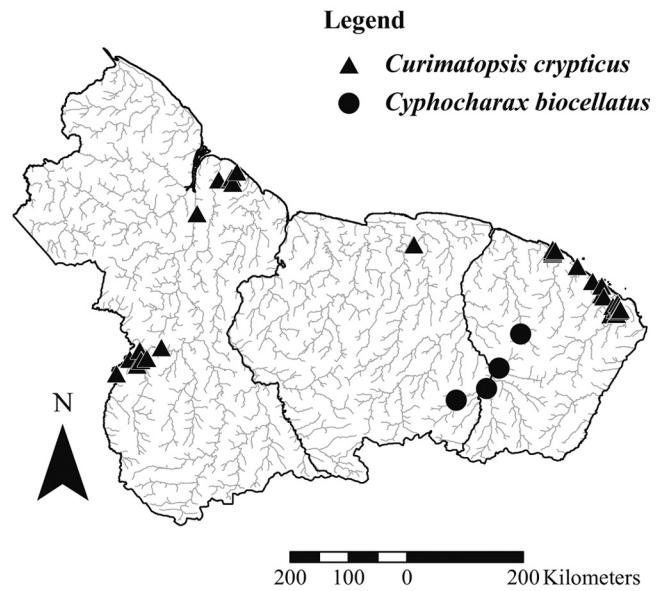


Appendix Figure 18. - Distribution map of *Curimatopsis crypticus* (triangles) and *Cyphocharax biocellatus* (circles).
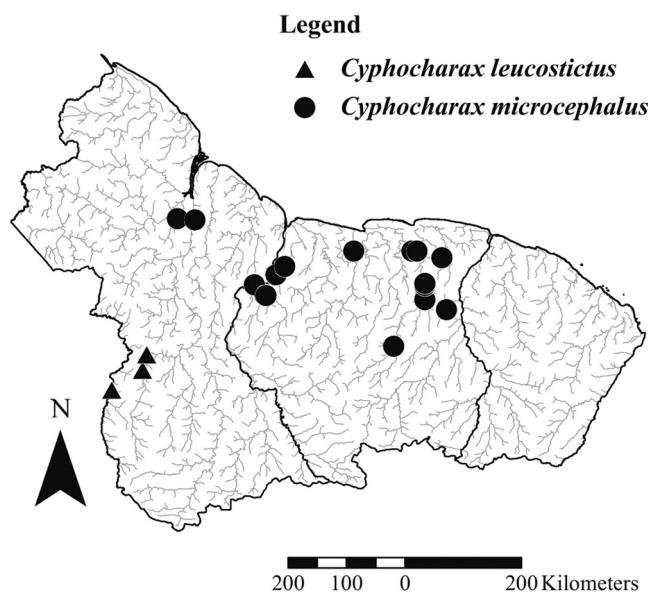


Appendix Figure 19. - Distribution map of *Cyphocharax leucostictus* (triangles) and *C. microcephalus* (circles).
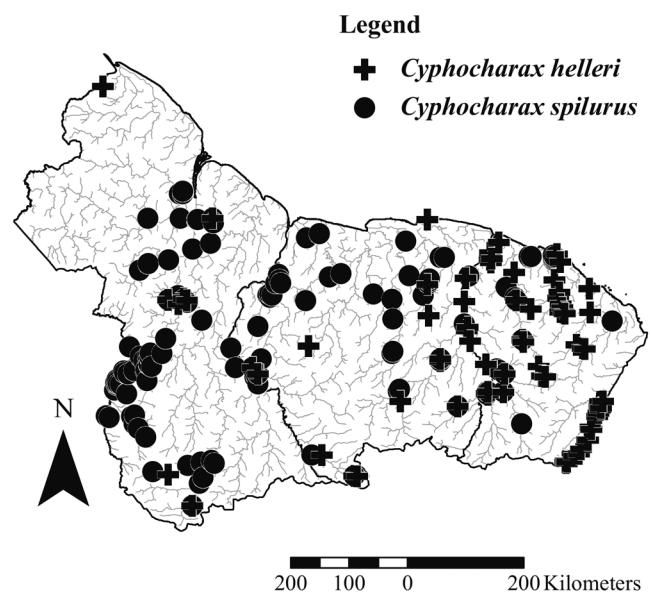


Appendix Figure 20. - Distribution map of *Cyphocharax helleri* (crosses) and *C. spilurus* (circles).
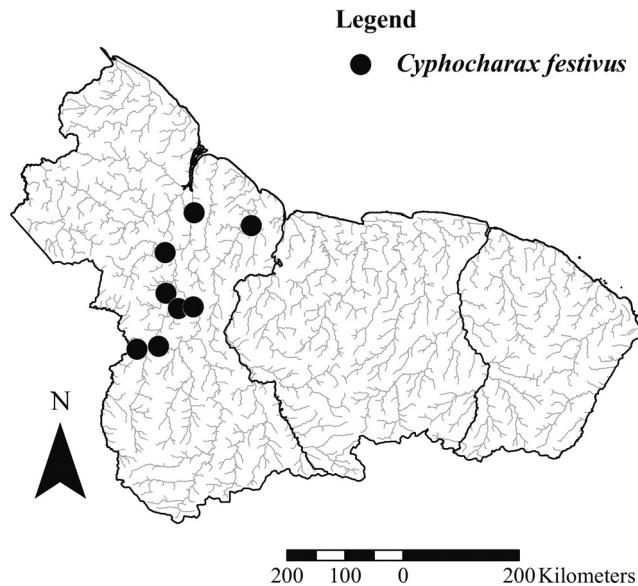
Appendix Figure 21. - Distribution map of *Cyphocharax festivus* (circles).
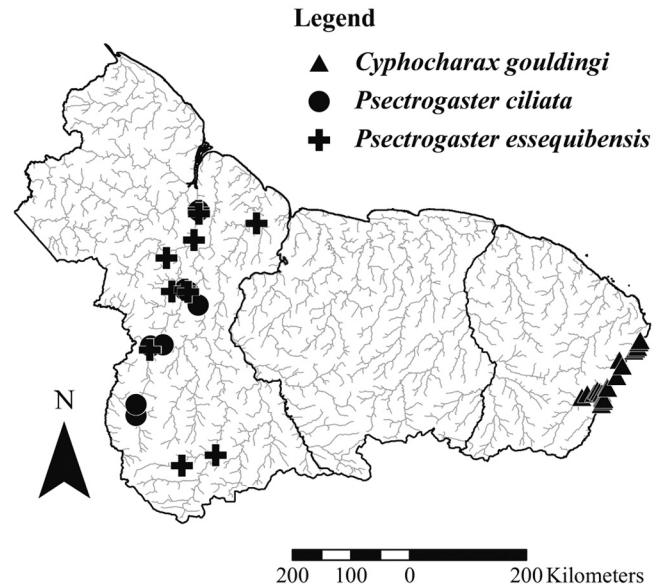


Appendix Figure 22. - Distribution map of *Cyphocharax gouldingi* (triangles), *Psectrogaster ciliata* (circles) and *P. essequibensis* (crosses).
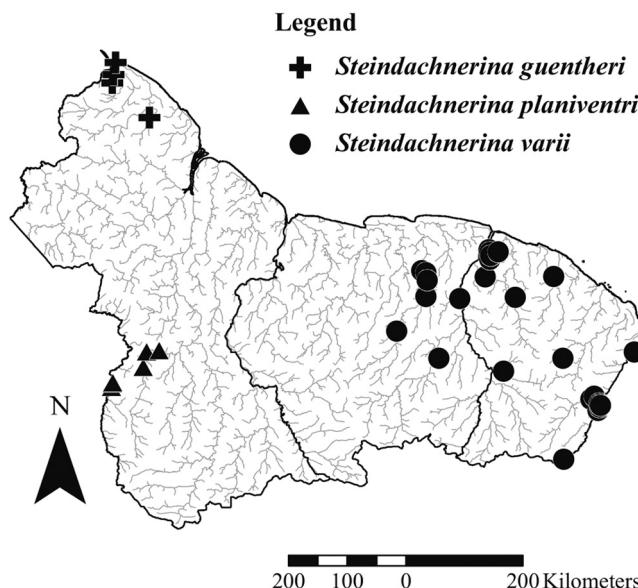


Appendix Figure 23. - Distribution map of *Steindachnerina guentheri* (crosses), *S. planiventris* (triangles) and *S. varii* (circles).
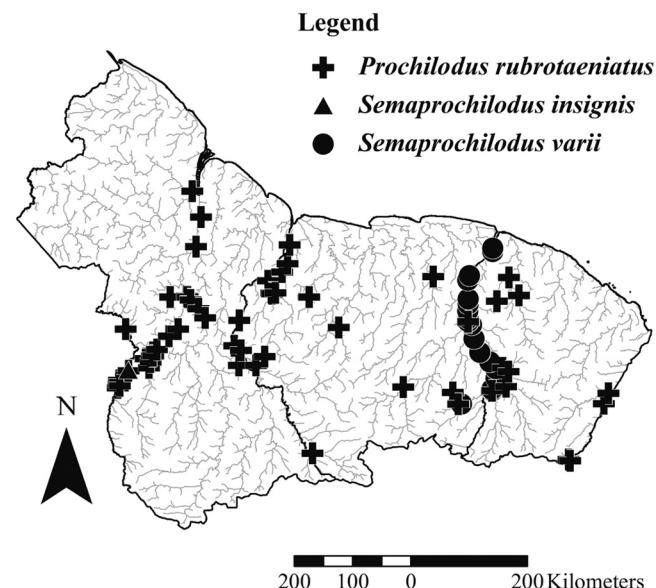


Appendix Figure 24. - Distribution map of *Prochilodus rubrotaeniatus* (crosses), *Semaprochilodus insignis* (triangle) and *Semaprochilodus varii* (circles)