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Research Paper

Patterns of Freshwater Fishes of the Caribbean Versant of Venezuela

key words: biogeographic provinces, coastal rivers, classification and ordination analyses, biodiversity, dispersion, hotspots

Abstract

We delineate local and regional biogeographic provinces that suggest patterns of species richness, and primary and secondary freshwater fish distributions along the Caribbean coast of Venezuela. We use presence-absence records and classification and ordination models. Patterns at local and regional scales varied markedly such that primary species dominated humid drainages and secondary species dominated arid drainages or transition provinces. Species rich areas, and the presence of narrowly endemic species correlate with patterns of historical isolation and hydrographic refuges. Patterns of species distributions across arid drainages suggest that close proximity of coastal marine drainages allows dispersion and exchange of species. This pattern is particularly evident among secondary species. Hotspots of species richness and endemisms are identified and are recommended as priorities for conservation.

1. Introduction

1.1. General Overview

South America contains perhaps the greatest species richness of freshwater fishes in the world. Major diversification, is seen in the enormous drainages of the Amazonas and Orinoco Rivers and also along both flanks of the Andes and in isolated slopes that flow directly to the sea (Malabarba *et al.*, 1998; Reis *et al.*, 2003). Biogeographic investigation has advanced rapidly and the current state of the art is seen in recent phylogeographic revisions of several groups (*e.g.*, Vari and Harold, 2001; Armbruster, 2003). Summaries of fish species richness and distribution patterns at regional (*e.g.*, lower Mesoamerica: Smith and Bermingham, 2005) or even continental levels (*e.g.*, South America: Hubert and Renno, 2006) are also appearing. Nevertheless, some drainages of relatively small regions have geologic or climatic histories that are not necessarily associated with the patterns of species richness and distribution recognized at larger scales. On the other hand, our taxonomic,

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distributional, and phylogenetic knowledge of Neotropical fishes remains at a gross scale (VARI and WEITZMAN, 1990; CUNHA RIBEIRO, 2006; ALBERT *et al.*, 2006).

Different geological processes have contributed to the conformation of fish fauna in the transandean slopes of northern South America. Regions were created with distinctive biota (biogeographical provinces), that in some cases are neither recognized nor well defined. Local extinctions and speciation account for the variations we observe that differ from the generally well-known history of major geologic events that have shaped the freshwater fish faunas. This is the case for the freshwater ichthyofauna of the Caribbean versant of Venezuela (CVV), where two faunas are currently recognized: Maracaibo and Caribbean (FERNÁNDEZ-YÉPEZ, 1970; MAGO-LECCIA, 1970; LASSO *et al.*, 2004). Biogeographical limits for these regions have never been clearly defined, and local variation remains undocumented. Thus the analyses of regional species distribution patterns have been limited. In addition to regional gradients, significant heterogeneity in the richness and distribution of species can occur at local and regional scales. Since the geologic and climatic history is known for a large part of northern South America, one only needs data on the richness and distribution of species to explain current biogeographic patterns. Prior to this study, the drainages of the CVV have been poorly collected and studied, and local variation in the freshwater fish fauna has not been described. Even less is known about the conservation status of fishes in this region. We carried out this study in order to elucidate local patterns of species richness and delineate more precisely the distribution of freshwater fishes along river drainages of the northern coast of Venezuela. This information allowed us to identify biogeographic patterns and entities and to establish their relationship to geologic and climatic processes at work in the CVV.

1.2. Genesis of the Caribbean Versants of Venezuela

During the Cenozoic, Andean and Guyana Shield drainages ran towards an immense delta on the Caribbean coast (VAN HOUTEN and TRAVIS, 1968). During Early Eocene, marine incursions covered many drainages of Venezuela in the region now known as the llanos. Between the Eocene and the Miocene, plate tectonics had already uplifted the central Andean range of Colombia (ERIKSON and PINDELL, 1993). In the region of Lake Maracaibo, a major south to north drainage, here called the proto-Orinoco, flowed toward its Caribbean delta. This drainage encompassed (at least) the eastern slopes of the central mountain range of Colombia and the western drainages of the Guyana Shield (KELLOGG, 1984; HOORN *et al.*, 1995; HOORN *et al.*, 2006; ITURRALDE-VINCENT and MACPHEE, 1999). LUNDBERG *et al.* (1998) state that "Prior to late Miocene, the foreland basin drained the vast region of western Amazonia, western Orinoco and Magdalena northward to the Caribbean". The continued uplift of the Andes in western Venezuela reoriented the course of the proto-Orinoco to the east. Evidence of the position of the proto-Orinoco and the alteration of its course towards the east are detected in sequences of fluvio-deltaic sediment deposits from the middle Eocene and late Miocene of northern Venezuela (DÍAZ DE GAMERO, 1996). Fluvio-deltaic sediments from the Late Miocene have been found in eastern Venezuela. During the Pliocene and Pleistocene such sediments were already registered near Trinidad Island (DÍAZ DE GAMERO, 1996).

The Oriental range of Colombia ended its major uplift in Early Pliocene (GREGORY-WODZ-ICKI, 2000) and differential movement of the Maracaibo microplate with respect to the South American plate prompted uplift of the Santa Marta massif and the Perijá range (KELLOGG, 1984). The Perijá mountains culminated their ascent during the Pliocene and completed the process isolating of the Lake Maracaibo Basin from the Magdalena (Fig. 1). Rotation of the Maracaibo microplate determined the genesis and rapid rise of the Venezuelan Andes in Late Pliocene (~8 Myr; MATTSON, 1984), thus finalizing separation of the Lake Maracaibo Basin from the Orinoco River (MACELLARI, 1984). The two west-east oriented mountain ranges of northern Venezuela have different histories. The central mountain range of the CVV had it's
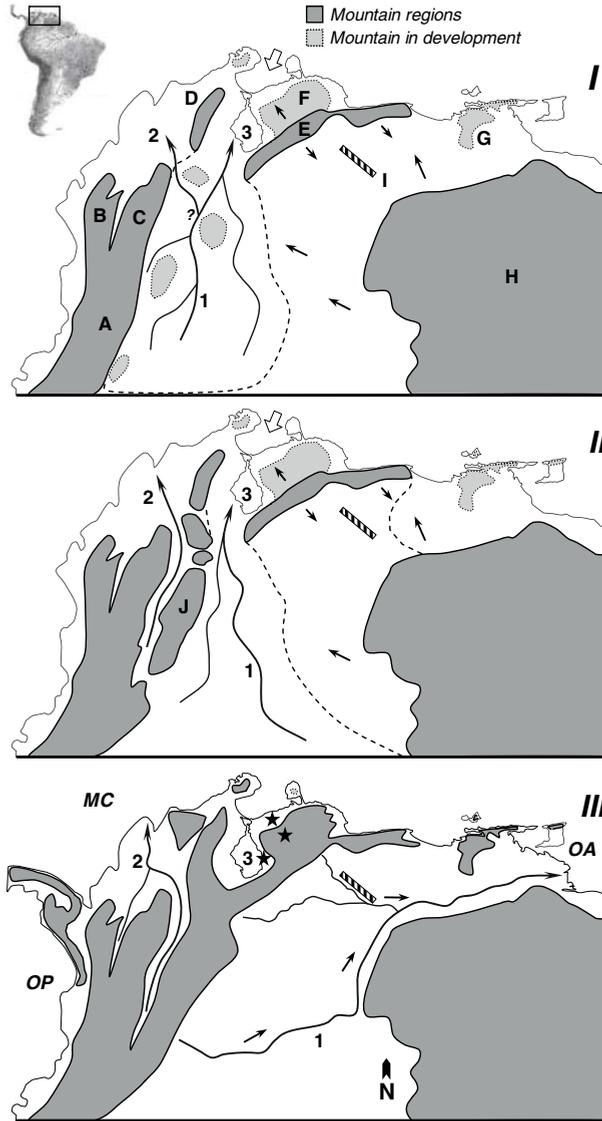
Figure 1. Paleohydrology of northern South America. I: between Late Oligocene and Early Miocene the Andes (A) formed the western (B) and central (C) mountains ranges, the Sierra of Perijá emerged (D) and Venezuelan Andes (E), all associated with the Coastal range, the Coro orogeny (F) and Tur-imiquire massif (G). The proto-Orinoco (1) was associated with the Magdalena slopes (2) and its delta was in the Maracaibo Lake basin (3). II: In mid-Miocene the Oriental range emerged (J). III: During the late Miocene and Holocene the Maracaibo basin was isolated and the Orinoco River took its current conformation. The white arrows and segmented lines show the marine incursions and their extent. The black arrows show the fluxes of sediments and the segmented bar the Baúl Arch (I). H: Guyana Shield, OP: Pacific Ocean, MC: Caribbean Sea and OA: Atlantic Ocean. The stars indicate the fish fossils and fluvial-deltaic sediments. Modified from HOORN *et al.*, (1995), GALVIS *et al.*, (1997) and HOORN (2006).

origin in the upper Cretaceous, much earlier than that of the Venezuelan Andes located to the south and separated from it by the Yaracuy depression (STEYERMARK, 1979; GONZÁLEZ DE JUANA *et al.*, 1980).

For the Venezuelan Caribbean coast the recent maximum lower limit for marine regression was 120 m below sea level (b.s.l.) during the pleniglacial period (18 ka), but another Holocene low point at 15 m b.s.l. is reported around 8 ka along the Venezuelan coast (RULL, 1999). Later, the marine level gradually ascended to reach its current level. During these lows large areas of the Gulf of Venezuela emerged (GALVIS *et al.*, 1997), and similar effects occurred all along the Caribbean coast. The Paria peninsula would have been connected with Trinidad Island and in turn with the outlets of the San Juan and Orinoco rivers. During the Neogene, important marine incursions occurred in the area that is now occupied by the Lake Maracaibo Basin (LOVEJOY *et al.*, 2006) and even extended to the south, reaching the northwestern Amazon floodplains. These incursions, may have allowed for the invasion of marine lineages such as stingrays, needlefish, manatee, and dolphins into the fluvial biodiversity of South America's large river basins, but probably caused extensive extinctions of the freshwater faunas in isolated coastal drainages. Other marine incursions have been recognized in more recent times, influenced by the alternation of glacial periods.

1.3. Ichthyofauna

South America's ichthyofauna was already modern and diverse by Late Miocene (MALABARBA *et al.,* 1998). Early Miocene marine transgressions greatly affected the Caribbean coast. The freshwater proto-Orinoco delta, from which large river fishes such as *Phractocephalus* and *Colossoma* are known as fossils was transformed as estuarine and marine environments penetrated far inland and abutted the Andes (LUNDBERG and AGUILERA, 2003; DAHDUL, 2004). The rise of the Mérida range isolated the Lake Maracaibo and Magdalena Basins (LOVEJOY *et al.*, 2006; ALBERT *et al.*, 2006), leaving the region vulnerable to mass extinctions, but also permitted subsequent vicariant speciation. The coastal mountains east of the Maracaibo Basin also played a role. For example, the Unare River drainage, only recently isolated from the Orinoco, has the same species of *Austrofundulus* found in the Orinoco Basin, but different species are found in the Tucacas region of the Aroa River drainage, and the Lake Maracaibo Basin (HRBEK *et al.*, 2005). KASPER and LARUE (1986) using sediment data from Barbados have hypothesized that the Orinoco Delta flowed into the Caribbean through the region of present day Rio Unare.

Initial contributions to the biogeography of the continental fishes of northern South America consider the fish fauna of the Lake Maracaibo Basin to be different from the remainder of the Caribbean drainages (*e.g*, EIGENMANN, 1920; SCHULTZ, 1949; GÉRY, 1969; GALVIS *et al.*, 1997), but more similar to that of the Magdalena drainage of northern Colombia and related to the Orinoco biota. In the coastal drainages of Venezuela, FERNÁNDEZ-YÉPEZ (1970) identified and arranged the drainages as hydrographic complexes according to the ichthyofauna present. Along similar lines, MAGO-LECCIA (1970) proposed seven hydrographic provinces and presented lists of species for each. His classification divided the CVV into Caribbean and Lake Maracaibo drainages according their faunas, but didn't determine their relationships.

A listing of the continental ichthyofauna of Venezuela, including secondary freshwater fishes tolerant of salinity and occuring in brackish environments or deltas, has been summarized by LASSO *et al.* (2004). These authors recognized 177 species from the Lake Maracaibo Basin and 194 from those rivers draining to the Caribbean Sea. They listed a high number of species for the Gulf of Paria drainage (158 sp.) and a low number for Lake Valencia (32 sp.). They also recognized the dominance of Siluriformes and Characiformes in both. On the other hand some species in the CVV have disjunct distributions, and in some cases, species of the same genus not known to occur together elsewhere (*e.g*., *Gephyrocharax*)

do occur sympatrically in transition zones. Some drainages have unexpectedly high species richness and endemism, but most areas of the CVV have relatively depauperate freshwater fish faunas (TAPHORN and LILYESTROM, 1984; VARI and HAROLD, 2001; LASSO *et al.*, 2004; PROVENZANO and MILANI, 2006; RODRÍGUEZ-OLARTE *et al.*, 2006, 2007).

2. Methods

2.1. Attributes of Hydrographic Drainages

For this work we studied all drainages of the CVV from the Perijá Mountains in the west to the Paria peninsula in the east. The endorheic drainage of Lake Valencia was included because of the occurrence of species shared with Caribbean drainages. For comparison we also included the Ranchería River drainage of northeastern Colombia, drainages along the southern slopes of the Paria peninsula, and the San Juan River drainage just north of the Orinoco Delta. The islands of Trinidad (4996 km^2) and Margarita (1020 km^2) were also included. Since biogeographic analyses should consider extensive areas (ALBERT *et al.*, 2006), the smallest drainages (< 1000 km^2) were combined with larger adjacent drainages of the basin. These drainage groups were considered here as one drainage and were designated with the name of the drainage of greatest size. The grouping and division of drainages was established using geologic and neotectonic maps of Venezuela (BELTRÁN, 1993; HACKLEY *et al.*, 2006), as well as relief, area, and altitude (CIET, 2005; LEHNER *et al.*, 2006). Bathymetric depths for the coast of Venezuela were obtained from the international bathymetric chart of Caribbean Sea and Gulf of Mexico (http://www.ngdc.noaa.gov).

Drainages were as follows (Fig. 2): (1) Ranchería, (2) Limón [including the drainages of the Guajira peninsula], (3) Palmar-Apón, (4) Santa Ana, (5) Catatumbo, (6) Escalante, (7) Chama [including Mucujepe], (8) Tucaní [with Río Frío, Tucanizón, Arapapuey and Caus], (9) Motatán, (10) Misoa, (11) Pueblo
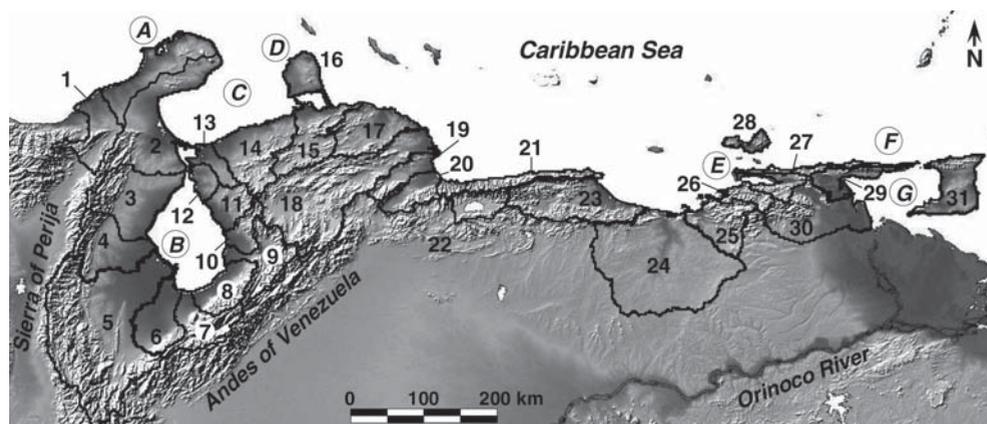

Figure 2. Basins of Caribbean versant of Venezuela (CVV) considered in this study: (1) Ranchería, (2) Limón [including the drainages of the Guajira peninsula], (3) Palmar-Apón, (4) Santa Ana, (5) Catatumbo, (6) Escalante, (7) Chama [including Mucujepe], (8) Tucaní [with Río Frío, Tucanizón, Arapapuey and Caus], (9) Motatán, (10) Misoa, (11) Pueblo Viejo, (12) Mene [with Tamare and Aurare], (13) Cocuiza [including Palmar], (14) Maticora [with Borojo, Zazárida and Urumaco], (15) Mitare [with Coro], (16) peninsula of Paraguaná, (17) Hueque [with Ricoa and Cristo], (18) Tocuyo [including Tucurere], (19) Aroa, (20) Yaracuy [with Urama], (21) Central Coast [it contains several very small drainages], (22) Lake Valencia,(23) Tuy [with Curiepe, Capaya and Guapo], (24) Unare, (25) Neverí, (26) Manzanares, (27) Cariaco [including several small drainages of the Cariaco gulf], (28) Margarita Island, (29) Paria [with several small drainages of the gulf of Paria], (30) San Juan [with Guarapiche] and the (31) Trinidad Island. Geographical features: Guajira Peninsula (A), Lake Maracaibo (B), Gulf of Venezuela (C), Paraguaná Peninsula (D), Araya Peninsula (E), Paria Peninsula (F) and Gulf of Paria (G).

Viejo, (12) Mene [with Tamare and Aurare], (13) Cocuiza [including Palmar], (14) Maticora [with Borojo, Zazárida and Urumaco], (15) Mitare [with Coro], (16) peninsula of Paraguaná, (17) Hueque [with Ricoa and Cristo], (18) Tocuyo [including Tucurere], (19) Aroa, (20) Yaracuy [with Urama], (21) Central Coast [it contains several very small drainages], (22) Valencia, (23) Tuy [with Curiepe, Capaya and Guapo], (24) Unare, (25) Neverí, (26) Manzanares, (27) Cariaco [including several small drainages of the Cariaco gulf], (28) Margarita Island, (29) Paria [with several small drainages of the gulf of Paria], (30) San Juan [with Guarapiche] and (31) Trinidad Island. Humidity of drainages was determined using AGRIMED (2004) and EWEL *et al.*, (1976). The arid classification is defined by high temperatures and low or very low precipitation. Arid drainages were the Ranchería, Cocuiza, Matícora, Mitare, Paraguaná, Hueque, Ricoa, Tocuyo, Unare, Neverí, Manzanares, Cariaco and Margarita Island; all others were classified as humid.

2.2. Data on the Ichthyofauna

The coverage of fish samples from the CVV is extensive. For many of the drainages of the CVV historical records are available: Maracaibo tributaries were reported on in large part by TAPHORN and LILYESTROM (1984). Andean slopes of central and west-central CVV were studied by RODRÍGUEZ-OLARTE *et al.* (2006, 2007), and most of the eastern coastal drainages have also been studied. The data quality is assumed to be adequate for this study because LASSO *et al.*, (2004) and others have recently standardized taxonomic usage and reviewed all principal fish collections in Venezuela. We used 12155 records of freshwater fishes from the collections of CPUCLA (Colección Regional de Peces, Universidad Centroccidental Lisandro Alvarado), MCNG (Museo de Ciencia Naturales Guanare, Universidad de los Llanos), MHNLS (Museo de Historia Natural La Salle), EBRG (Estación Biológica de Rancho Grande) and ICN-UNC (Instituto de Ciencias Naturales, Universidad Nacional de Colombia) and of the databases of the California Academy of Sciences (http://www.calacademy.org) and FishBase (http://www.fishbase.net). General references were used to update the identification of these records when possible (REIS *et al.*, 2003; LASSO *et al.*, 2004) and was supplemented with local lists. Arbitrary epithets were included for those species without taxonomic description. We consider endemic species as those restricted in distribution to one province or subprovince inside the CVV. The species with occurrence only in drainages or subprovinces outside of the CVV (*e.g.*, San Juan) were considered restricted because their general distribution was not determined for this study. Since our interest was to recognize the patterns of distribution for the strictly freshwaters fishes, we did not consider those species or peripheral groups that occurred in environments with marine influence or known to be amphidromous, such as (among others) many species of Gobiidae, Ariidae and Gerreidae.

For several drainages of the CVV, long term and complete records of freshwater fishes do not exist. Taxonomic problems within some genera also hindered correct consideration of some species. Although the absence of a particular species from one river might be due to differences in sampling type or effort, we assume that the absence of a species from our larger categories such as a drainage or group of drainages does truly reflect the absence of that species from the unit under consideration. Unique records were considered doubtful and were excluded if they were disjunct from the rest of the species in the distribution recognized by experts; nevertheless, such exclusions also were based on the recognized revision of the potential distribution for species, as well as their tolerance to salinity. For some possibly valid species (*e.g.*, *Hoplias teres*, Erythrinidae) no records exist, and so they were recorded as present only from the type locality. For others (*e.g.*, *Caquetaia kraussii*, Cichlidae) no verified museum records exist that support a possible natural disjunct distribution. A matrix was made containing binary registers of presence-absence for 34 families and 270 of strictly freshwater species (see Table 1).

To recognize patterns of distribution of tolerance to salinity, matrices were made for primary and secondary species. The dispersion of primary freshwater fishes that are physiologically intolerant of saline conditions requires direct connections between drainages, either by lowland anastomosis, capture of headwaters, or extraordinary events of flooding (UNMACK, 2001). Secondary fishes have a relatively high tolerance of saline environments and therefore face no barriers to dispersal throughout the coastal drainages. These are considered attributes that can explain the presence and distribution of fish fauna throughout of CVV. Salt tolerance was assigned according to STIASSNY and RAMINOSOA (1994), or the occurrence of the species in estuaries and outlets of the rivers to the sea according to the available records.

Table 1.   List of freshwater fish species registered in the CVV and in neighboring basins. Salinity tolerance (T) is expressed as either primary (1) or secondary (2) taxa. Subprovinces: Perijá-Andes (I), Eastern Zulia (II), Falcón (III), Tocuyo-Yaracuy (IV), Tuy-Valencia (V), Neverí-Cariaco (VI), Caribbean Atlantic (VII) and Trinidad Island(VIII). Other entities: Ranchería basin in the Magdalena province (M) and Guajira territory (It) inside the subprovince Perijá-Andes.

Families	T	Species	M	It	I	II	III	IV	V	VI	VII	VIII
Auchenipteridae	1	*Ageneiosus pardalis*	–	1	1	–	–	–	–	–	–	–
Anostomidae	1	*Leporinus* cf. *friderici*	–	–	–	–	–	–	1	–	–	1
Anostomidae	1	*Leporinus muyscorum*	1	–	–	–	–	–	–	–	–	–
Anostomidae	1	*Leporinus* cf. *striatus*	1	–	–	–	–	–	–	–	–	–
Anostomidae	1	*Schizodon corti*	–	1	1	–	–	–	–	–	–	–
Apteronotidae	1	*Apteronotus leptorhynchus*	–	–	1	–	–	–	–	–	–	–
Apteronotidae	1	*Apteronotus* n. sp.	–	–	–	–	–	1	–	–	–	–
Apteronotidae	1	*Apteronotus cuchillo*	–	–	1	1	–	–	–	–	–	–
Apteronotidae	1	*Apteronotus cuchillejo*	–	–	1	–	–	–	–	–	–	–
Aspredinidae	1	*Aspredinichthys filamentosus*	–	–	–	–	–	–	–	–	1	1
Aspredinidae	1	*Aspredinichthys tibicen*	–	–	–	–	–	–	–	–	1	1
Aspredinidae	1	*Aspredo aspredo*	–	–	–	–	–	–	–	–	1	1
Aspredinidae	1	*Bunocephalus amaurus*	–	–	–	–	–	–	1	1	–	–
Aspredinidae	1	*Dupouyichthys sapito*	–	1	1	–	–	–	–	–	–	–
Aspredinidae	1	*Hoplomyzon atrizona*	–	–	1	–	–	–	–	–	–	–
Aspredinidae	1	*Platystacus cotylephorus*	–	–	–	–	–	–	–	–	1	1
Aspredinidae	1	*Xiliphius kryptos*	–	–	1	–	–	–	–	–	–	–
Astroblepidae	1	*Astroblepus chotae*	–	–	1	–	–	–	–	–	–	–
Astroblepidae	1	*Astroblepus orientalis*	–	–	1	–	–	–	–	–	–	–
Astroblepidae	1	*Astroblepus phelpsi*	–	–	1	–	–	–	–	–	–	–
Atherinopsidae	1	*Atherinella venezuelae*	–	–	–	–	–	–	1	–	–	–
Auchenipteridae	1	*Trachelyopterus peloichthys*	–	1	1	1	–	–	–	–	–	–
Auchenipteridae	2	*Pseudauchenipterus nodosus*	–	–	–	–	–	–	–	–	1	1
Auchenipteridae	2	*Trachelyopterus galeatus*	–	–	–	–	–	–	1	–	–	1
Auchenipteridae	1	*Trachelyopterus insignis*	1	–	–	–	–	–	–	–	–	–
Callichthyidae	2	*Callichthys callichthys*	–	–	–	–	–	–	–	–	1	1
Callichthyidae	1	*Corydoras aeneus*	–	–	–	–	–	1	1	–	–	1
Callichthyidae	2	*Hoplosternum littorale*	–	–	–	–	–	–	1	–	1	1
Callichthyidae	2	*Hoplosternum magdalenae*	–	1	1	1	–	1	–	–	–	–
Callichthyidae	2	*Megalechis thoracata*	–	1	1	1	–	1	–	–	–	1
Cetopsidae	1	*Pseudocetopsis motatanensis*	–	1	1	–	–	–	–	–	–	–
Cetopsidae	1	*Pseudocetopsis orinoco*	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Aphyocharax alburnus*	–	–	–	–	–	–	1	1	–	–
Characidae	1	*Astyanax bimaculatus*	–	–	–	–	–	1	1	1	1	1
Characidae	1	*Astyanax* cf. *caucanus*	1	–	–	–	–	–	–	–	–	–
Characidae	2	*Astyanax viejita*	1	1	1	1	1	1	1	–	–	–
Characidae	2	*Astyanax magdalenae*	–	1	1	1	–	–	–	–	–	–
Characidae	1	*Astyanax metae*	–	–	–	–	–	1	1	1	1	–
Characidae	1	*Astyanax venezuelae*	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Brycon moorei*	1	–	–	–	–	–	–	–	–	–
Characidae	1	*Brycon polylepis*	–	1	1	–	–	–	–	–	–	–
Characidae	1	*Brycon unicolor*	–	1	1	–	–	–	–	–	–	–
Characidae	1	*Bryconamericus alpha*	–	–	–	–	–	1	1	–	–	–
Characidae	1	*Bryconamericus loisae*	–	1	1	1	1	1	1	–	–	–
Characidae	1	*Bryconamericus beta*	–	–	–	–	–	–	–	–	1	–
Characidae	1	*Bryconamericus cismontanus*	–	–	–	–	1	1	1	–	–	–
Characidae	1	*Bryconamericus charalae*	–	–	–	–	–	1	–	–	–	–

Table 1.   (continued)

Families	T	Species	M	It	I	II	III	IV	V	VI	VII	VIII
Characidae	1	*Bryconamericus deuterodonoides*	–	–	–	–	1	1	1	–	–	–
Characidae	1	*Bryconamericus meridae*	–	–	1	–	1	–	–	–	–	–
Characidae	1	*Bryconamericus motatanensis*	–	–	1	–	–	–	–	–	–	–
Characidae	1	*Bryconamericus* sp. Alto Tocuyo	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Bryconamericus yokiae*	–	–	–	–	–	–	1	–	–	–
Characidae	1	*Bryconamericus lassorum*	–	–	–	–	–	–	–	–	1	–
Characidae	1	*Cheirodontops geayi*	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Corynopoma riisei*	–	–	1	–	–	–	1	1	–	1
Characidae	1	*Creagrutus affinis*	1	–	–	–	–	–	–	–	–	–
Characidae	1	*Creagrutus bolivari*	–	–	–	–	–	1	1	–	–	–
Characidae	1	*Creagrutus crenatus*	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Creagrutus hildebrandi*	–	1	1	1	1	–	–	–	–	–
Characidae	1	*Creagrutus hysginus*	–	–	–	–	–	–	–	1	1	–
Characidae	1	*Creagrutus lassoi*	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Creagrutus lepidus*	–	–	–	–	–	1	–	–	–	–
Characidae	1	*Creagrutus maracaiboensis*	1	–	1	–	–	–	–	–	–	–
Characidae	1	*Creagrutus melasma*	–	–	–	–	–	1	1	1	1	–
Characidae	1	*Creagrutus paralacus*	–	–	1	–	–	–	–	–	–	–
Characidae	1	*Creagrutus taphorni*	–	–	–	–	–	1	1	–	–	–
Characidae	1	*Ctenobrycon spilurus*	–	–	–	–	–	–	1	–	1	–
Characidae	1	*Cynopotamus venezuelae*	–	1	1	–	–	–	–	–	–	–
Characidae	1	*Gephyrocharax melanocheir*	1	–	–	1	1	1	–	–	–	–
Characidae	1	*Gephyrocharax valencia*	–	–	–	–	1	1	1	1	1	–
Characidae	1	*Gephyrocharax venezuelae*	–	1	1	1	1	1	–	–	–	–
Characidae	1	*Gilbertolus maracaiboensis*	–	1	1	1	–	–	–	–	–	–
Characidae	1	*Gymnocorymbus thayeri*	–	–	–	–	–	–	–	1	1	1
Characidae	1	*Hemibrycon guppyi*	–	–	–	–	–	–	–	–	–	1
Characidae	1	*Hemibrycon jabonero*	1	1	1	1	1	1	–	–	–	–
Characidae	1	*Hemibrycon metae*	–	–	–	–	–	1	1	1	1	–
Characidae	1	*Hemibrycon taeniurus*	–	–	–	–	–	–	–	1	–	1
Characidae	1	*Hemigrammus unilineatus*	–	–	–	–	–	–	–	–	1	1
Characidae	1	*Hemigrammus* sp. Trinidad	–	–	–	–	–	–	–	–	–	1
Characidae	1	*Hyphessobrycon* cf. *axelrodi*	–	–	–	–	–	–	–	–	1	1
Characidae	1	*Hyphessobrycon bentosi*	–	–	–	–	–	–	–	–	1	–
Characidae	2	*Hyphessobrycon fernandezi*	–	–	–	–	–	1	1	–	–	–
Characidae	1	*Hyphessobrycon* cf. *inconstans*	1	–	–	–	–	–	–	–	–	–
Characidae	2	*Hyphessobrycon sovichthys*	–	1	1	1	1	1	1	–	–	–
Characidae	1	*Markiana geayi*	–	–	–	–	–	–	–	–	1	–
Characidae	1	*Moenkhausia pittieri*	–	–	–	–	–	–	1	–	–	–
Characidae	1	*Mylossoma acanthogaster*	–	1	1	–	–	–	–	–	–	–
Characidae	1	*Nanocheirodon insignis*	–	–	1	1	–	1	–	–	–	–
Characidae	1	*Odontostilbe pulcher*	–	–	–	–	–	1	1	–	1	1
Characidae	1	*Paragoniates alburnus*	–	–	–	–	–	–	–	–	1	–
Characidae	1	*Phenagoniates macrolepis*	–	1	1	1	–	–	–	–	–	–
Characidae	2	*Roeboides dayi*	1	–	–	–	–	–	–	–	–	–
Characidae	2	*Roeboides dientonito*	–	1	1	1	1	1	1	1	1	1
Characidae	1	*Saccoderma melanostigma*	1	1	1	1	1	–	–	–	–	–
Characidae	1	*Salminus affinis*	1	–	–	–	–	–	–	–	–	–
Characidae	1	*Serrasalmus neveriensis*	–	–	–	–	–	–	1	1	–	–
Characidae	1	*Triportheus elongatus*	–	–	–	–	–	–	–	–	1	1
Characidae	1	*Xenagoniates bondi*	–	–	–	–	–	–	–	–	1	–
Cichlidae	2	*Aequidens latifrons*	1	–	–	–	–	–	–	–	–	–

Table 1.   (continued)

Families	T	Species	M	It	I	II	III	IV	V	VI	VII	VIII
Cichlidae	2	*Aequidens pulcher*	–	1	1	1	1	1	1	1	1	1
Cichlidae	2	*Apistogramma guttata*	–	–	–	–	–	–	–	–	1	–
Cichlidae	2	*Apistogramma hoignei*	–	–	–	–	–	–	–	–	1	–
Cichlidae	2	*Astronotus* sp.	–	–	–	–	–	–	–	–	1	–
Cichlidae	2	*Caquetaia kraussii*	–	1	1	1	1	–	–	–	–	–
Cichlidae	2	*Caquetaia umbrifera*	1	–	–	–	–	–	–	–	–	–
Cichlidae	2	*Cichlasoma orinocense*	–	–	–	–	–	–	1	–	1	–
Cichlidae	2	*Cichlasoma taenia*	–	–	–	–	–	–	1	1	1	1
Cichlidae	2	*Cleithracara maronii*	–	–	–	–	–	–	–	–	1	1
Cichlidae	2	*Crenicichla frenata*	–	–	–	–	–	–	–	1	1	1
Cichlidae	2	*Crenicichla geayi*	–	–	–	–	–	1	1	1	1	–
Cichlidae	2	*Crenicichla saxatilis*	–	–	–	–	–	–	–	1	1	1
Cichlidae	2	*Geophagus steindachneri*	1	1	1	–	–	–	–	–	–	–
Crenuchidae	1	*Characidium boavistae*	–	1	1	–	–	–	–	–	–	–
Crenuchidae	1	*Characidium chupa*	1	1	1	–	–	1	1	1	1	–
Ctenoluciidae	2	*Ctenolucius hujeta*	1	1	1	1	1	–	–	–	–	–
Curimatidae	1	*Curimata cyprinoides*	–	–	–	–	–	–	–	–	1	–
Curimatidae	2	*Cyphocharax aspilos*	–	1	1	1	–	–	–	–	–	–
Curimatidae	1	*Cyphocharax magdalenae*	1	–	–	–	–	–	–	–	–	–
Curimatidae	1	*Cyphocharax spilurus*	–	–	–	–	–	–	1	–	1	–
Curimatidae	2	*Potamorhina laticeps*	–	1	1	–	–	–	–	–	–	–
Curimatidae	1	*Steindachnerina argentea*	–	–	–	–	–	1	1	1	–	1
Doradidae	1	*Doraops zuloagai*	–	1	1	–	–	–	–	–	–	–
Doradidae	1	*Rhinodoras thomersoni*	–	–	1	–	–	–	–	–	–	–
Erythrinidae	1	*Erythrinus erythrinus*	–	–	–	–	–	–	–	–	1	1
Erythrinidae	1	*Hoplerythrinus cinereus*	–	–	–	–	–	–	–	–	–	1
Erythrinidae	1	*Hoplerythrinus unitaeniatus*	–	–	–	–	–	–	–	–	1	1
Erythrinidae	2	*Hoplias malabaricus*	1	1	1	1	1	1	1	1	1	1
Erythrinidae	1	*Hoplias teres*	–	–	1	–	–	–	–	–	–	–
Gasteropelecidae	1	*Gasteropelecus maculatus*	1	–	1	1	–	–	–	–	–	–
Gasteropelecidae	1	*Gasteropelecus sternicla*	–	–	–	–	–	–	–	–	1	1
Gymnotidae	1	*Gymnotus carapo*	–	–	–	–	–	–	1	–	1	1
Heptapteridae	1	*Cetopsorhamdia picklei*	–	–	1	–	–	–	–	–	–	–
Heptapteridae	1	*Cetopsorhamdia* sp.	–	–	–	–	–	1	–	–	–	–
Heptapteridae	1	*Cetopsorhamdia* sp. *Rancheria*	1	–	–	–	–	–	–	–	–	–
Heptapteridae	1	*Imparfinis nemacheir*	–	1	1	–	–	–	–	–	–	–
Heptapteridae	1	*Pimelodella cristata*	–	–	–	–	–	1	1	–	1	–
Heptapteridae	2	*Pimelodella odynea*	–	1	1	1	1	1	–	–	–	–
Heptapteridae	1	*Pimelodella* sp. *Rancheria*	1	–	–	–	–	–	–	–	–	–
Heptapteridae	1	*Pimelodella tapatapae*	–	–	–	–	–	–	1	–	–	–
Heptapteridae	1	*Rhamdella* sp. *San Juan*	–	–	–	–	–	–	–	–	1	–
Heptapteridae	1	*Rhamdia foina*	–	–	–	–	–	–	–	–	1	–
Heptapteridae	1	*Rhamdia humilis*	–	–	–	–	–	–	1	–	–	–
Heptapteridae	1	*Rhamdia guatemalensis*	1	1	1	1	–	–	–	–	–	–
Heptapteridae	1	*Rhamdia quelen*	–	–	–	–	1	1	1	1	1	1
Hypopomidae	1	*Brachyhypopomus diazi*	–	–	–	–	–	1	–	–	–	–
Hypopomidae	1	*Brachyhypopomus occidentalis*	–	1	1	1	–	–	–	–	–	–
Lebiasinidae	1	*Piabucina erythrinoides*	–	1	1	1	1	1	–	–	–	–
Lebiasinidae	1	*Pyrrhulina lugubris*	–	–	–	–	–	–	–	–	1	–
Loricariidae	1	*Ancistrus brevifilis*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Ancistrus gymnorhynchus*	–	–	–	–	–	1	–	–	–	–
Loricariidae	1	*Ancistrus triradiatus*	–	–	–	–	–	1	–	–	1	–

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Table 1.   (continued)

Families	T	Species	M	It	I	II	III	IV	V	VI	VII	VIII
Loricariidae	1	*Ancistrus maracasae*	–	–	–	–	–	–	–	–	–	1
Loricariidae	1	*Ancistrus martini*	–	–	1	1	–	–	–	–	–	–
Loricariidae	1	*Chaetostoma anomalum*	–	–	1	–	–	1	–	–	–	–
Loricariidae	1	*Chaetostoma guairense*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Chaetostoma machiquense*	–	–	1	1	–	–	–	–	–	–
Loricariidae	1	*Chaetostoma milesi*	–	–	–	–	–	1	–	–	–	–
Loricariidae	1	*Chaetostoma nudirostre*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Chaetostoma pearsei*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Chaetostoma sovichthys*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Chaetostoma stanni*	–	–	–	–	–	1	–	–	–	–
Loricariidae	1	*Chaetostoma tachiraense*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Chaetostoma venezuelae*	–	–	–	–	–	–	–	–	1	–
Loricariidae	1	*Chaetostoma yurubiense*	–	–	–	–	–	1	–	–	–	–
Loricariidae	1	*Chaetostoma* sp. *Trinidad*	–	–	–	–	–	–	–	–	–	1
Loricariidae	1	*Cordylancistrus nephelion*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Cordylancistrus perijae*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Cordylancistrus* sp. *Rancheria*	1	–	–	–	–	–	–	–	–	–
Loricariidae	1	*Crossoloricaria venezuelae*	–	1	1	–	–	–	–	–	–	–
Loricariidae	1	*Dasyloricaria filamentosa*	–	1	1	–	1	–	–	–	–	–
Loricariidae	2	*Dolichancistrus cobrensis*	–	1	1	1	–	–	–	–	–	–
Loricariidae	1	*Farlowella acus*	–	–	–	–	–	1	1	–	–	–
Loricariidae	1	*Farlowella curtirostra*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Farlowella mariaelenae*	–	–	–	–	–	1	1	–	–	–
Loricariidae	1	*Farlowella martini*	–	–	–	–	–	1	–	–	–	–
Loricariidae	1	*Farlowella taphorni*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Farlowella venezuelensis*	–	–	–	–	–	–	–	–	1	–
Loricariidae	1	*Farlowella vittata*	–	–	–	–	–	–	1	1	1	–
Loricariidae	1	*Hemiancistrus maracaiboensis*	–	1	1	–	1	–	–	–	–	–
Loricariidae	1	*Hypostomus emarginatus*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Hypostomus hondae*	1	1	1	–	1	–	–	–	–	–
Loricariidae	1	*Hypostomus pagei*	–	–	–	–	–	1	–	–	–	–
Loricariidae	1	*Hypostomus plecostomoides*	–	–	–	–	–	–	1	–	1	–
Loricariidae	1	*Hypostomus plecostomus*	–	–	–	–	1	1	1	–	1	–
Loricariidae	1	*Hypostomus robinii*	–	–	–	–	–	–	–	–	–	1
Loricariidae	1	*Hypostomus villarsi*	–	1	–	–	–	–	–	–	–	–
Loricariidae	2	*Hypostomus watwata*	–	1	1	1	1	1	–	1	1	–
Loricariidae	1	*Lamontichthys maracaibero*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Lasiancistrus guacharote*	–	–	1	1	–	–	–	–	–	–
Loricariidae	1	*Lithogenes valencia*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Loricaria cataphracta*	–	–	–	–	–	–	–	–	1	–
Loricariidae	1	*Loricariichthys brunneus*	–	–	–	–	–	–	1	1	–	–
Loricariidae	1	*Pseudancistrus* sp. *Tuy*	–	–	–	–	–	–	1	–	–	–
Loricariidae	1	*Pterygoplichthys multiradiatus*	–	–	–	–	–	–	–	–	1	–
Loricariidae	1	*Pterygoplichthys zuliaensis*	–	–	1	–	–	–	–	–	–	–
Loricariidae	1	*Rineloricaria caracasensis*	–	–	1	–	–	–	1	–	–	–
Loricariidae	1	*Rineloricaria magdalenae*	1	1	1	1	–	–	–	–	–	–
Loricariidae	1	*Rineloricaria rupestris*	–	–	1	–	1	1	–	–	–	–
Loricariidae	1	*Spatuloricaria lagoichthys*	–	1	1	–	–	–	–	–	–	–
Loricariidae	1	*Spatuloricaria phelpsi*	–	1	1	–	–	–	–	–	–	–
Loricariidae	1	*Sturisoma aureum*	1	–	–	–	–	–	–	–	–	–
Loricariidae	1	*Sturisoma kneri*	–	1	1	1	1	–	–	–	–	–
Loricariidae	1	*Sturisomatichthys leightoni*	–	–	1	–	–	–	–	–	–	–

Table 1. (continued)

Families	T	Species	M	It	I	II	III	IV	V	VI	VII	VIII
Nandidae	1	*Polycentrus schomburgki*	–	–	–	–	–	–	–	–	1	1
Parodontidae	1	*Parodon apolinari*	–	–	–	–	–	1	–	–	–	–
Parodontidae	1	*Parodon suborbitale*	1	1	1	–	–	–	–	–	–	–
Pimelodidae	1	*Brachyplatystoma vaillantii*	–	–	–	–	–	–	–	–	1	1
Pimelodidae	2	*Cheirocerus abuelo*	–	1	1	1	–	–	–	–	–	–
Pimelodidae	2	*Hypophthalmus marginatus*	–	–	–	–	–	–	–	–	1	–
Pimelodidae	1	*Megalonema psammium*	–	1	1	–	–	–	–	–	–	–
Pimelodidae	1	*Perrunichthys perruno*	–	–	1	–	–	–	–	–	–	–
Pimelodidae	1	*Pimelodus blochii*	–	–	–	–	–	–	–	–	1	–
Pimelodidae	2	*Pimelodus coprophagus*	–	1	1	–	1	–	–	–	–	–
Pimelodidae	1	*Pimelodus grosskopfii*	–	1	1	–	–	–	–	–	–	–
Pimelodidae	1	*Pimelodus navarroi*	–	–	1	–	1	–	–	–	–	–
Pimelodidae	1	*Platysilurus malarmo*	–	–	1	–	–	–	–	–	–	–
Pimelodidae	1	*Sorubim cuspicaudus*	–	–	1	1	–	–	–	–	–	–
Poeciliidae	2	*Micropoecilia picta*	–	–	–	–	–	–	1	–	1	1
Poeciliidae	2	*Poecilia boesemani*	–	–	–	–	–	–	–	–	–	1
Poeciliidae	2	*Poecilia caucana*	1	1	1	1	1	1	1	–	–	–
Poeciliidae	2	*Poecilia dauli*	–	–	–	–	–	1	–	–	–	–
Poeciliidae	2	*Poecilia koperi*	–	–	–	–	1	1	1	–	–	–
Poeciliidae	2	*Poecilia parae*	–	–	–	–	–	–	–	–	1	–
Poeciliidae	2	*Poecilia reticulata*	–	1	1	–	1	1	1	1	1	1
Poeciliidae	2	*Poecilia sphenops*	–	–	–	–	1	1	1	1	–	–
Poeciliidae	2	*Poecilia vivipara*	–	–	–	–	1	1	1	–	1	1
Poeciliidae	2	*Pseudolimia heterandria*	–	–	–	1	–	1	1	–	–	–
Poeciliidae	2	*Tomeurus gracilis*	–	–	–	–	–	–	1	–	1	–
Potamotrygonidae	1	*Potamotrygon yepezi*	–	1	1	–	–	–	–	–	–	–
Potamotrygonidae	2	*Potamotrygon orbignyi*	–	–	–	–	–	–	–	–	1	–
Prochilodontidae	1	*Ichthyoelephas longirostris*	1	–	–	–	–	–	–	–	–	–
Prochilodontidae	2	*Prochilodus mariae*	–	–	–	–	–	–	–	–	1	–
Prochilodontidae	1	*Prochilodus reticulatus*	1	1	1	1	–	–	–	–	–	–
Pseudopimelodidae	1	*Batrochoglanis acanthochiroides*	–	–	1	–	1	–	–	–	–	–
Pseudopimelodidae	1	*Microglanis iheringi*	–	–	–	–	–	–	1	–	1	–
Pseudopimelodidae	1	*Microglanis poecilus*	–	–	–	–	–	–	–	–	1	–
Pseudopimelodidae	1	*Pseudopimelodus* sp. *Maracaibo*	1	1	1	–	–	–	–	–	–	–
Pseudopimelodidae	1	*Batrochoglanis mathisoni*	–	–	–	–	–	1	–	–	–	–
Pseudopimelodidae	1	*Pseudopimelodus bufonius*	–	–	–	–	–	–	–	–	1	–
Rivulidae	2	*Austrofundulus goajira*	1	1	–	–	–	–	–	–	–	–
Rivulidae	2	*Austrofundulus leohoignei*	–	–	–	–	–	1	–	–	–	–
Rivulidae	2	*Austrofundulus leoni*	–	1	1	1	–	–	–	–	–	–
Rivulidae	2	*Austrofundulus limnaeus*	–	1	1	1	1	–	–	–	–	–
Rivulidae	2	*Austrofundulus transilis*	–	–	–	–	–	–	1	–	–	–
Rivulidae	2	*Gnatholebias zonatus*	–	–	–	–	–	–	1	–	1	–
Rivulidae	2	*Rachovia brevis*	1	1	–	–	–	–	–	–	–	–
Rivulidae	2	*Rachovia hummelincki*	1	1	–	1	1	–	–	–	–	–
Rivulidae	2	*Rachovia maculipinnis*	–	–	–	–	–	–	1	–	–	–
Rivulidae	2	*Rachovia pyropunctata*	–	1	1	1	–	–	–	–	–	–
Rivulidae	2	*Rivulus deltaphilus*	–	–	–	–	–	–	–	–	1	–
Rivulidae	2	*Rivulus hartii*	–	–	–	–	–	1	1	1	1	1
Rivulidae	2	*Rivulus marmoratus*	–	1	–	–	–	–	–	–	–	–
Sciaenidae	1	*Pachypops fourcroi*	–	–	–	–	–	–	–	–	1	–
Sciaenidae	1	*Plagioscion magdalenae*	1	–	–	–	–	–	–	–	–	–
Sciaenidae	1	*Plagioscion squamosissimus*	–	–	–	–	–	–	–	–	1	–

Table 1.   (continued)

Families	T	Species	M	It	I	II	III	IV	V	VI	VII	VIII
Sciaenidae	1	*Plagioscion auratus*	–	–	–	–	–	–	–	–	1	–
Sternopygidae	1	*Distocyclus goajira*	–	–	1	–	–	–	–	–	–	–
Sternopygidae	1	*Eigenmannia virescens*	1	1	1	1	–	–	1	–	–	–
Sternopygidae	1	*Sternopygus macrurus*	–	–	1	–	–	–	1	–	1	–
Sternopygidae	1	*Sternopygus pejeraton*	1	1	1	1	–	–	–	–	–	–
Synbranchidae	2	*Ophisternon aenigmaticum*	–	–	–	–	–	–	–	–	–	1
Synbranchidae	2	*Synbranchus marmoratus*	1	1	1	1	1	1	1	1	1	1
Trichomycteridae	1	*Ochmacanthus* cf. *alternus*	–	–	–	–	–	–	1	–	–	–
Trichomycteridae	1	*Trichomycterus arleoi*	–	–	–	–	–	1	–	–	–	–
Trichomycteridae	1	*Trichomycterus emanuelli*	–	–	1	–	–	–	–	–	–	–
Trichomycteridae	1	*Trichomycterus* cf. *bogotense*	–	–	–	–	–	1	–	–	–	–
Trichomycteridae	1	*Trichomycterus maracaiboensis*	–	1	1	–	–	–	–	–	–	–
Trichomycteridae	1	*Trichomycterus meridae*	–	–	1	–	–	–	–	–	–	–
Trichomycteridae	1	*Trichomycterus mondolfi*	–	–	–	–	–	–	1	–	–	–
Trichomycteridae	1	*Trichomycterus spelaeus*	–	1	–	–	–	–	–	–	–	–
Trichomycteridae	1	*Trichomycterus* sp. Tocuyo	–	–	–	–	–	1	–	–	–	–
Trichomycteridae	1	*Trichomycterus* sp. San Juan	–	–	–	–	–	–	–	–	1	–
Trichomycteridae	1	*Tridensimilis venezuelae*	–	–	1	–	–	–	–	–	–	–

2.3. Classification and Ordination

Drainages of the peninsula of Paraguaná and Margarita Island were not included in the multivariate analyses because we didn't have appropriate historical records and their reported species richness was very poor. To classify and compare relationships among the ichthyofaunas, two UPGMA cluster analyses (KREBS, 1999) were applied, using coefficients of Jaccard similarity and Euclidean dissimilarity. These analyses are effective for the biogeographic resolution and comparison of the dendrograms generated (*e.g.*, UNMACK, 2001; SMITH and BIRMINGHAM, 2005). In the first analysis, the matrix of presence-absence and the Jaccard coefficient was used. For the second analysis, the Euclidean coefficient was used based on data from the initial matrix but transformed into continuous variables by means of a correspondence analysis (CA). The CA method simplifies the presence-absence matrix. It extracts significant patterns from the first ordination axis and locates the noise in the remaining axes, where the biogeographic information remaining can be considered as irrelevant (LEGENDRE and LEGENDRE, 1998; SMITH and BIRMINGHAM, 2005). To test natural groupings in the data, each original matrix was compared with a matrix of ultrametric values derived from the original data to obtain cophenetic correlations. If two matrices show the same groups, a high cophenetic correlation exists, indicating a low distortion of the data (ROHLF and FISHER, 1968). The cluster analyses were applied by means of the PC-ORD 4.25 software (McCUNE and MEFFORD, 1999) and the cophenetic correlations with the program PAST 1.58 (HAMMER *et al.*, 2001).

To compare clusters, a non metric multidimensional scaling analysis (NMS) was developed based on the same coefficients and using the program PC-ORD. The initial coordinates for NMS were generated by a previous detrended correspondence analysis (DCA). In the NMS, relative distortion of the original data was evaluated by the stress average values; these diminished until appropriate values to represent the ordination in the fewest possible dimensions were obtained. As a test of goodness-of-fit the determination coefficient (r^2) was determined among distances of the space generated by the ordination and the distances of the real space; this coefficient indicates the adjusted measure of the data with respect to the multidimensional model applied, acceptable values being above 0.60 (HAIR *et al.*, 1999). The r^2 were generated in raw scale of the axes but the graphics were ordered from minimum to maximum scale for better understanding; also, all ordination graphics were rotated for easier comparison. Finally, the orthogonality was determined to check the statistical independence among the produced axes (McCUNE and MEFFORD, 1999).

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In this work the biogeographic domains are considered extensive areas, like the regional drainages or groups of drainages (*e.g.*, Lake Maracaibo) with very few shared species or very low similarity with respect to other drainages or entities, usually less than 25%. The provinces represent medium sized groups of drainages with faunas that have a similarity between 25 and 50%. At the local level, the subprovinces were considered minor entities, as isolated drainages or small groups of drainages, with a high proportion (generally above 75%) of shared species and high similarity. Territories inside the subprovinces were defined as drainages or groups of drainages where extremes in species richness were found. The designations of some entities and their geographical borders were supported by their location relative to geographic barriers. From patterns detected here using species richness and distribution of freshwater fishes, the presence of endemics, and the past and recent geologic and climatic events of the history of northern South America, biogeographic entities were defined.

3. Results

Of all the families (34) the Characidae (64 sp.) and Loricariidae (55 sp.) contributed nearly 45% of the total richness (Table 1). Just a few families (6) surpassed ten species, among them the Cichlidae, Rivulidae and Heptapteridae; 25 families were found with five or fewer species. The largest numbers of Characidae species were found in the Tocuyo, Aroa and Tuy
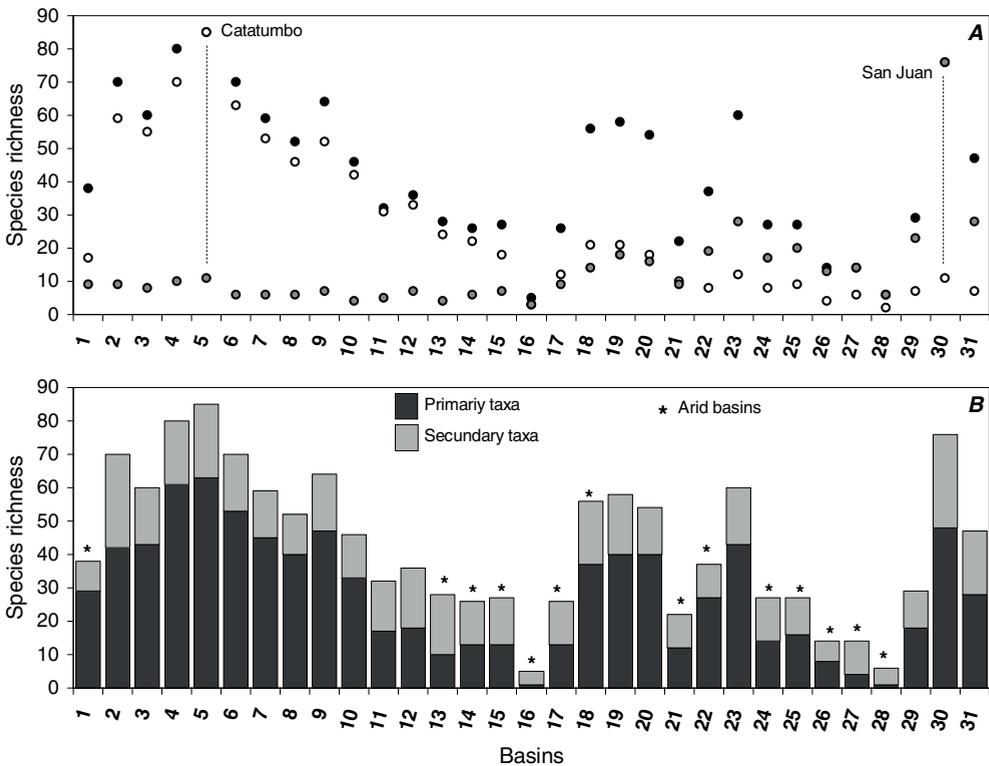

Figure 3. Species richness arranged in geographical order: from west to east (numbers refering to each basins are same as in Fig. 2). A: black circles denote total species richness, white circles species richness of Catatumbo drainage (85 sp.) that also occurred in other basins; grey circles denote the same for the San Juan drainage (79 sp.). B: the richness of primary and secondary taxa is shown and their relationships with climatic conditions of drainages (arid and humid).

drainages; Loricariidae was best represented in the drainages of Lake Maracaibo. Species richness was high (Fig. 3a) in Lake Maracaibo drainages and a few others such as Aroa and San Juan. Drainages from the geographical extremes of CVV with more richness, such as Catatumbo (East) and San Juan (West), had many species shared with other drainages of the CVV. For both primary and secondary species, humid drainages usually had more species than arid. In most drainages, more primary species (206 sp. in total) were present on average (~66%), than secondary species (64 sp.) but these proportions changed to nearly 50% each in small, arid drainages (Fig. 3b).
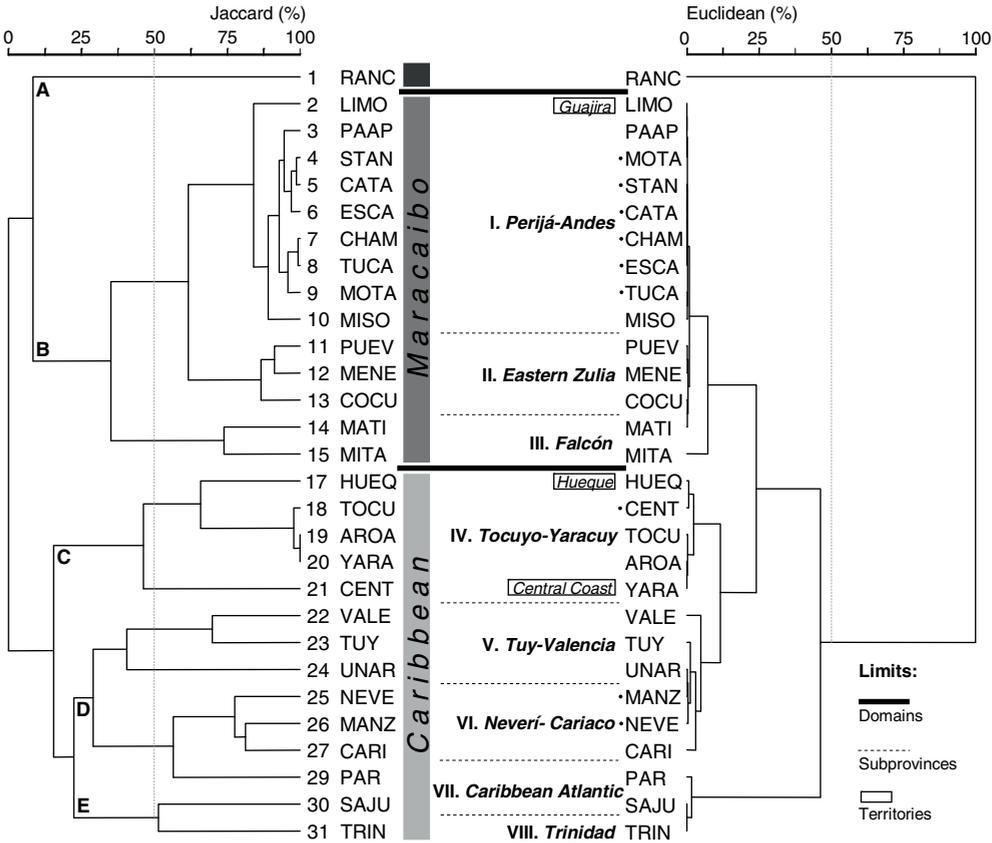

Figure 4. General relationships among ichthyofaunas of the CVV and adjacent basins. The UPGMA dendrograms compared are based on Jaccard ($r = 0.95$) and Euclidean ($r = 0.81$) coefficients. The arrangement of basins obtained in the dendrogram on the left correspond to the geographical sequence from West (Ranchería: 1 RANC) to East (Trinidad Island: 33 TRIN). Basins 16 and 28 were not included in multivariate analysis (see Methods). Limits between the biogeographic entities are represented by lines. Black circles show basins with different geographical arrangement corresponding to the coefficients. Vertical bars indicate the domains (Magdalena, Maracaibo and Caribbean). The provinces are A: Magdalena, B: Maracaibo, C: Western Caribbean, D: Central Caribbean and E: Eastern Caribbean. Inside the subprovinces [Perijá-Andes (I), Eastern Zulia (II), Falcón (III), Tocuyo-Yaracuy (IV), Tuy-Valencia (V), Neverí-Cariaco (VI), Caribbean Atlantic (VII) and Trinidad (VIII)] some transitional territories were defined (Guajira, Hueque and Central Coast). The numbers assigned to each basin are same as in Figure 2.
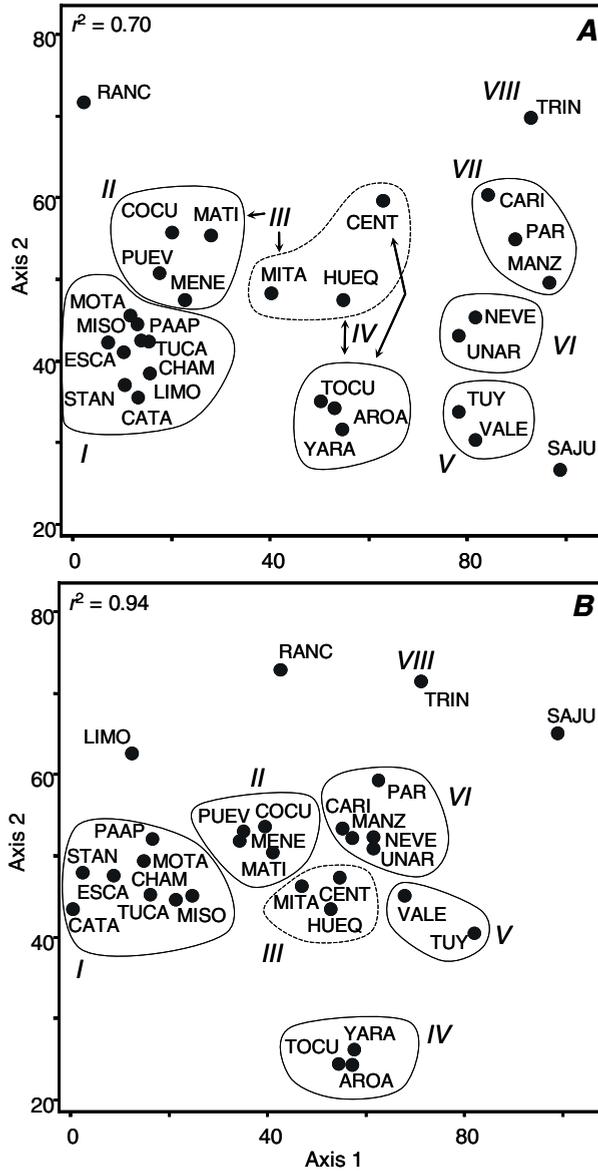
Figure 5.   NMS ordinations based on Jaccard (A) and Euclidean (B) coefficients describing groups of basins with similar faunas (subprovinces: I–VIII). Dashed lines group the transitional basins at the borders of subprovinces. The arrangement of most basins and their groups was related to the geographical sequence and agreed with the cluster dendrograms generated. Basin codes are same as those presented in Figure 4.
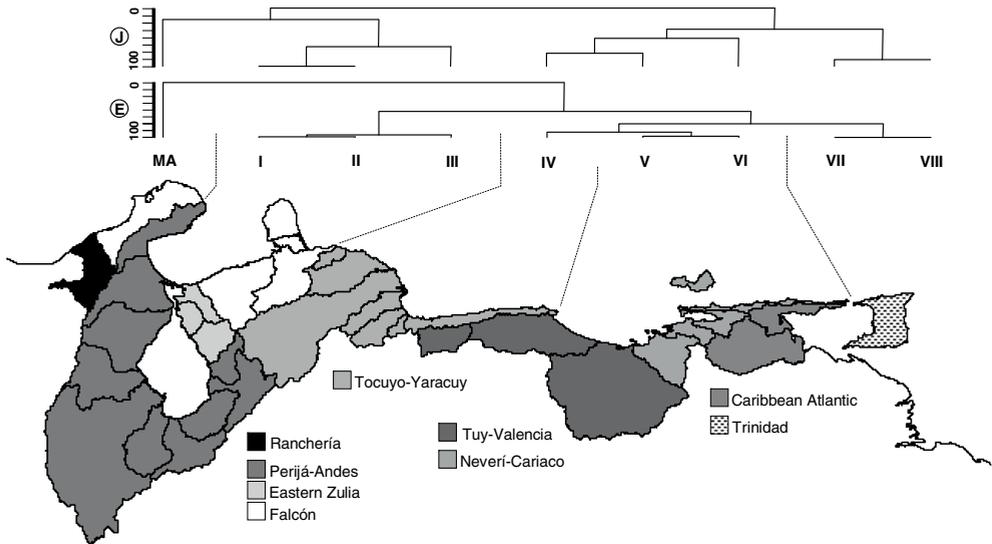
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Figure 6.   Biogeographic subprovinces detected in CVV (I–VIII) compared with true geographic conformation of hydrological basins using cluster analyses, Jaccard (J) and Euclidean (E) coefficients. MA: Magdalena (Ranchería drainage).

The UPGMA dendrogram based on the Jaccard distance generated an arrangement of drainages very similar to the real geographic arrangement (Fig. 4). The exclusion of records from drainages adjacent to the CVV didn't modify this order nor its magnitude. Borders of the CVV corresponded with the geographical borders estimated initially. Three major entities, here called domains, with great differences among their fish faunas were recognized. These faunas have their approximate boundaries within the pairs of drainages of Ranchería-Limón, Mitare-Hueque and Cariaco-Paria. Smaller distances in the dendrograms reflect drainages with more similar faunas, like in drainages of Lake Maracaibo. The ichthyofaunas of drainages, that flow to the Caribbean Sea, formed ordered groups but with lower similarity. Relationships recognized by cluster analyses using both coefficients produced similar distributions of drainages, but the Euclidean coefficient presented weaker evidence of arrangement at levels of lower dissimilarity (Fig. 4), such as the Maracaibo Lake drainages. The cophenetic correlations for the dendrograms based on Jaccard ($r = 0.95$) and Euclidean ($r = 0.81$) distances indicated a high adjustment of the data. In both dendrograms, groups of drainages with a higher degree of faunal similarity were identified. The cluster for primary taxa also had good fit of data (Jaccard: $r = 0.96$; Euclidean: $r = 0.83$); as well as that applied to the secondary taxa (Jaccard, $r = 0.91$; Euclidean: $r = 0.87$). These clusters coincided in the general arrangement of relationships among faunas, but arrangements using only secondary taxa showed some differences in the arrangement of some drainages.

Ordinations based on Jaccard similarity ($r^2 = 0.70$; orthogonality = 96%; stress = 10.8) discriminated different entities for the ichthyofauna (Fig. 5a), showing two general groups of drainages: one grouped Sierra Perijá with Andean drainages and another for those drainages located in the eastern coast of Lake Maracaibo. Isolated drainages, or groups of drainages, previously documented to have low richness and considered transitional, were also detected (Mitare, Hueque and Ricoa). Some contiguous drainages to the Caribbean Sea showed well defined arrangements (*e.g.*, Tocuyo, Aroa and Yaracuy), but to the east of the CVV the arrangement was less clear, describing only pairs of drainages (*e.g.*, Tuy and Valencia).

Table 2. Biogeographic entities recognized in CVV and their principal drainages. * = recognized as hotspots. ** = basins not included in multivariate analyses. *** = entity proposed.

Domains	Provinces	Subprovinces	Drainages (number assigned)
Magdalena	Magdalena	Ranchería	Ranchería (1)
Maracaibo	Maracaibo	**I.** Perijá-Andes*	Limón (2), Palmar-Apón (3), Santa Ana (4), Catatumbo (5), Escalante (6), Chama (7), Tucaní (8), Motatán (9), Misoa (10)
		II. Eastern Zulia	Pueblo Viejo (11), Mene (12), Cocuiza (13)
		III. Falcón	Maticora (14), Mitare (15), Paraguaná (16**)
Caribbean	Western Caribbean	**IV.** Tocuyo-Yaracuy*	Ricoa and Hueque (17), Tucurere and Tocuyo (18), Aroa (19), Yaracuy (20), Central Coast (21)
	Central Caribbean	**V.** Tuy-Valencia*	Lake Valencia (22), Tuy (23), Unare (24)
		VI. Neverí-Cariaco	Neverí (25), Manzanares (26), Cariaco (27), Margarita island (28**)
	Eastern Caribbean	**VII.** Caribbean Atlantic	Paria (29), San Juan (30)
		VIII. Trinidad	Trinidad (31)
Atlantic	Orinoco***	Delta***	Rivers and channels associated with Orinoco delta

(Left margin, vertical text: **CARIBBEAN VERSANT OF VENEZUELA**)

Drainages with fauna less related to the biota of CVV were clearly separate (Ranchería, San Juan and Trinidad Island). Likewise, ordination based on the Euclidean measure ($r^2 = 0.94$; orthogonality = 99%; stress = 12.9; Fig. 5b) showed narrower groupings and fewer divisions. In this ordination, relationships were shown to overlap, such as the isolation of some drainages (*e.g.*, Limón) but with clear relationship with two or more groupings: those of the drainages of Sierra of Perijá, Andean and the eastern coast of Lake Maracaibo. In the same trend, drainages with less related faunas were isolated.

Ordination for the primary taxa based on Jaccard measure ($r^2 = 0.60$; orthogonality = 92%; stress = 18.1) showed a similar pattern to that generated in the ordination for all taxa, while the ordination with base in the Euclidean measure ($r^2 = 0.92$; orthogonality = 99%; stress = 16.9) presented a less dispersed arrangement of the drainages. The secondary taxa only showed dispersed ordination in the drainages when the Jaccard coefficient was used ($r^2 = 0.84$; orthogonality = 87%; stress = 19.6) but with better defined relationship using the Euclidean measure ($r^2 = 0.91$; orthogonality = 83%; stress = 13.5).

Two domains converge completely in the CVV: Maracaibo and Caribbean (Fig. 6), being bordered by the Magdalena domain to the east and Atlantic domain to the west. The eastern edge of the Magdalena domain (Ranchería drainage) has an ichthyofauna that showed
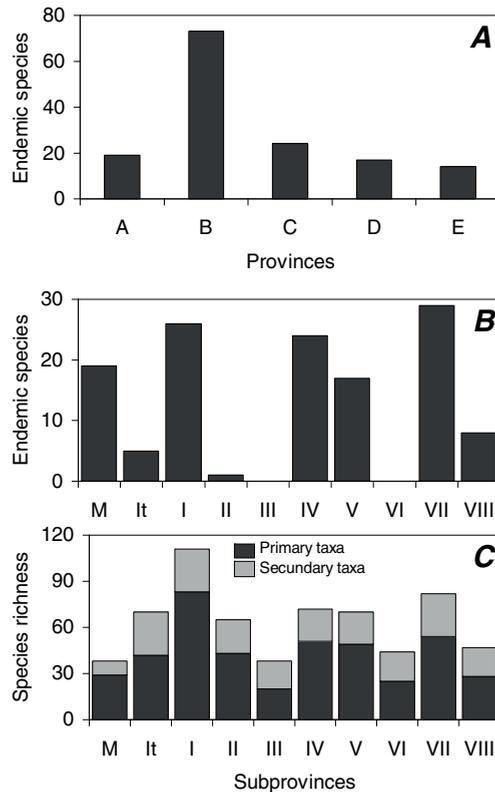
Figure 7. Variation and composition of species richness in the biogeographic provinces: A: endemic species in the Magdalena (A: only Ranchería drainage), Maracaibo (B), Western Caribbean (C), Central Caribbean (D) and Eastern Caribbean (E) provinces. B: endemic species in the subprovinces: Ranchería basin in the Magdalena province (M), Guajira territory (It) in the border of the Perijá-Andes subprovince, Perijá-Andes (I), Eastern Zulia (II), Falcón (III), Tocuyo-Yaracuy (IV), Tuy-Valencia (V), Neverí-Cariaco (VI), Caribbean Atlantic (VII) and Trinidad (VIII). C: species richness for primary and secondary taxa in the same provinces.

a very low relationship with the Maracaibo domain. The few shared species between the Limón and Ranchería drainages suggest that the latter is part of the Magdalena domain. The low similarity of the Ranchería drainage suggests that the north-eastern drainages of the Lake Maracaibo represent a transition zone. Five biogeographic provinces are recognized (Table 2): Magdalena (A), Maracaibo (B), and Western (C), Central (D) and Eastern Caribbean (E) and show remarkable differences in the number of endemic species (Fig. 4, 7a).

In the subprovinces detected (I: Perijá-Andes, II: Eastern Zulia, III: Falcón, IV: Tocuyo-Yaracuy, V: Tuy-Valencia, VI: Unare-Cariaco, VII: Caribbean-Atlantic and VIII: Trinidad; Table 2), important differences in the number of endemic species was seen (Fig. 4, 7b). The Perijá-Andes subprovince has the highest endemism as well as general species richness. The second subprovince with greater richness and endemism was Tocuyo-Yaracuy. The Caribbean-Atlantic subprovince, bordering with CVV, had the largest number of species. Many of the latter species are not restricted to the drainages of Paria and San Juan, but are also reported from other drainages of the Orinoco Basin and Atlantic coasts. Some

subprovinces have no endemic species. On the other hand, the occurrence of primary and secondary taxa at the level of subprovinces (Fig. 7c) maintained a similar proportion, registering more secondary species in the subprovinces comprised of arid drainages, but also in those of smaller size.

4. Discussion

4.1. Hydrographic Refuges

Results suggest that some drainages and zoogeographic entities of the CVV with high species richness, considered here as hydrographic refugia, are a result of orographic and climatic differences. The Aroa and Yaracuy drainages are in the path of humidity-laden trade winds blowing in from the sea. During extremely dry periods of the past, associated with the glacial maxima, coastal mountains receiving higher rainfall would become hydrographic refuges in an otherwise parched landscape. Thus, areas found today to contain relatively high species richness and endemism may be the result of this process. This could also explain the high richness and endemism observed in the Tuy drainage (Fig. 8). A similar refuge might have occurred in the plains and slopes of the southern portion of the Lake Maracaibo Basin. That area has very high precipitation as a result of the collision of moisture – carrying winds with the mountain ranges (HUBER and FRAME, 1988).

Given the geologic history of the CVV, areas with higher endemism and species richness could be the result of regional disturbances such as marine incursions and local mountain orogeny. These could have promoted vicariance and permitted allopatric species to survive in relatively stable aquatic environments on mountain slopes receiving unusually high amounts of rain (COLINVAUX, 1998). Refuges of higher rainfall (HAFFER, 1997; NORES, 1999) would
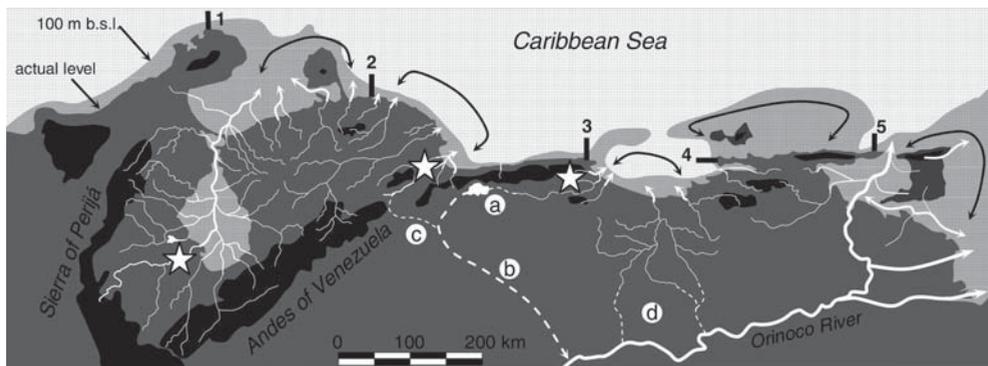

Figure 8. Geophysical processes structuring biogeography in the CVV. Sea level was estimated to have been around 120 meters lower 18000 years ago, permitting connections among the lower courses of regional drainages. Our data indicate that there were connections between the Valencia and Tuy basins (a), as well as with the Orinoco basin (b), and possibly with the Yaracuy basin (c). Headwaters of Unare basin would have been connected with the Orinoco drainage (d). Dispersion (black arrows) along the coast would be more intense in contiguous basins (*e.g.* Lake Maracaibo) or between proximate deltas or river mouths, but limited by deep trenches in the continental marine platform in some sectors: Guajira peninsula (1), north coast of subprovince IV (2), basins of Central Coast territory (3) and the flanks of Araya and Paria peninsulas (4 and 5). Hotspots are recognized in hydrographic refuges (stars) inside subprovinces I, IV and V: floodplains South of Lake Maracaibo, Aroa and Yaracuy basins and Tuy basin.

have split species into populations isolated by surrounding arid conditions, just as marine incursions in the Pleistocene would have created isolated populations in the highlands. Species surviving in isolation would later be able to disperse to neighbouring drainages when conditions became more acceptable to such dispersion. Higher species riches still exists today in the areas of the CVV that may have been humid refugia during the Pleistocene.

4.2. *The Dispersion of Freshwater Fishes*

Primary species dominated almost all drainages studied. Drainages with the lowest proportion of primary species are those with significant marine influence, where regional and ancestral drainage patterns limit the flow from highlands and foothills. In the CVV and contiguous drainages, the taxa with intolerance to salinity are mainly Characiformes and Siluriformes (see Table 1); while the secondary taxa are represented principally by Cichlidae, Poeciliidae, Rivulidae and Synbranchidae. The dispersion of freshwater fishes in drainages with contiguous floodplains is recognized, but can also occur all along the marine coasts, either because the fish can tolerate salinity, or because they can take advantage of freshwater plumes that can extend for considerable distances into the sea from the mouths of rivers.

On the other hand, this type of dispersion can vary with terrestrial and submarine platform geomorphology, creating a selectively permeable barrier to the dispersion of species. This is evident in several sectors where steep mountain slopes extend to the coast in contrast to areas where the bathymetry is shallow (Fig. 8). In the CVV we found three distinct sectors with these features: the flanks of the Sierra of San Luis in Falcón state, the small drainages of the Coastal range and the flanks of the Turimiquire massif and the Araya Peninsula. In these sectors the seawater is deep, contrary to the shallow coast that is common in most of the CVV. Such features are associated with the changes detected in the richness and composition of primary and secondary species. This suggests that the dispersion of many taxa along the marine coast is limited to certain sections of CVV, mainly those with contiguous drainages and/or with shallow bottoms near their mouths. Since there are only a few rivers with high discharge of fresh water directly to the sea (*e.g.*, Tocuyo, Tuy, Unare), dispersion of fishes through freshwater plumes is more probable contiguous rivers with mouths located along shallow shores. Among Lake Maracaibo drainages, this type of dispersion would be facilitated because rivers empty into a mostly freshwater lake.

The occurrence of primary taxa of the Orinoco Basin in drainages to the East of the CVV may be due to the enormous territory occupied by the Orinoco delta, its proximity to the San Juan drainage, and its influence in the Gulf of Paria. It could also be due to dispersion via freshwater plumes and the drift due to the north equatorial current and the seasonal changes in salinity produced by outflow of the Orinoco River. The Orinoco River discharges around 31000 m^3 sec^{-1} of freshwater into Atlantic Ocean and its plume can exceed an area of 160 000 km^2, *i.e.*, a surface that annually covers the east and southeastern portion of the Caribbean Sea (CHUANMIN *et al.*, 2004). In the eastern CVV and in contiguous rivers, records of freshwater fishes suggest that dispersion from the Orinoco biota occurs more commonly than the reverse process and that this phenomenon is more important in the Eastern Caribbean and Trinidad subprovinces. This sort of dispersion has only minor current importance to the rest of the CVV. However, in the ancient and recent past the Orinoco River acted as a main agent of dispersion at several points of the CVV (ALBERT *et al.*, 2006), but regional processes (*e.g.*, isolation, desiccation, extinction, etc.) reduced the influence of the Orinoco biota. These fish distributional breaks, also recognized among the biogeographic entities detected, might be a result of historical variations in the sea level.

In the Caribbean region, about 18000 years ago, the sea level dropped to 120 m below its current level and then began to ascend gradually (RULL, 1999). Earlier marine regressions are also recognized in the Caribbean Sea during the Pleistocene, when sea levels

dropped to about 45 meters below sea level (ZELLMER, 1979). Along the coast of northern South America these marine regressions would have created a common river channel for all the drainages of Lake Maracaibo. Explaining this likely process would have fastened the sharing of fish species between the floodplains and foothills of those drainages. Similar events would have occurred within most of the contiguous drainages throughout of the CVV. Previously isolated drainages, such as the peninsula of Paraguaná and Margarita Island may have been in contact with continental drainages. At those times, drainages that flow into the gulf of Paria, including the western drainages of Trinidad Island, would have had common drainages. Thus, in the recent past, an important exchange of species could have occurred across the Venezuelan coast, making dispersion possible even for primary species, but the same newly dispersed fish communities would be subjected later to the climatic conditions of the drainages.

4.3. Areas of Higher Species Richness in CVV

A hotspot is defined as an area that ranks particularly high for species diversity, endemism, rarity and/or intensity of threat (REID, 1998). Hotspots can be designed for continental regions, such as the Tropical Andes of South America, which includes a large part of the CVV, within these, the term hotpoints has been proposed for smaller areas of high species diversity or endemism (ZANFORLIN et al., 2007). Some drainages of the CVV qualify as hotpoints by having high species richness, high levels of endemism, and ever-increasing anthropogenic threats. First among these is the Maracaibo province which is the most speciose with 111 species, 73 (66%) of which are endemic. Within the Maracaibo province, the Perijá-Andes subprovince, had the highest richness (105 sp.) and endemism (26 sp., 25%), and so is considered an important hotspot and a conservation priority. In the Caribbean domain, richness at a local level is much lower than in the Maracaibo domain. The Western Caribbean province contains many low diversity drainages (Hueque and Central Coasts territories); therefore, the relatively high richness (72 sp.) and endemism (24 sp) in central drainages of the Tocuyo-Yaracuy subprovince (Aroa and Yaracuy) suggest that it is also a hotspot. The Tuy drainage, in the Central Caribbean province, represents the third hotspot of the CVV (60 sp., 17 (28%) endemic); however, this diversity no longer seems exceptional if grouped with the adjacent Valencia and Unare drainages (Tuy-Valencia subprovince (Table 2).

The Venezuelan Caribbean coast contains several protected areas, as well as some relatively undisturbed regions; however, these are small and most of the drainages have suffered strong and widespread anthropogenic impacts, especially along major waterways. Those areas identified herein as hotspots face high risks of development from agriculture, industry and urbanization. Major rivers like Catatumbo, Yaracuy and Tuy are already heavily impacted and in many cases significant reductions of fish stocks and even presumed extinctions have been reported (BISBAL, 1988; RODRÍGUEZ and ROJAS-SUÁREZ, 1999; LÓPEZ-ROJAS and BONILLA-RIVERO, 2000; MARN, 2001; PROVENZANO et al., 2003; FAJARDO et al., 2005). Except for the existence of the few protected areas, no conservation plans exist for the preservation of freshwater fishes in the CVV, hence, they must be considered at risk, and of high priority for conservation.

5. Acknowledgements

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