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RESEARCH ARTICLE

Distributional patterns of Characiformes in the Chacoan Sub-region (Neotropical Region)

Padrões de distribuição de Characiformes na Sub-Região Chaquenha (Região Neotropical)

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Resumo A maior diversidade de peixes de água doce ocorre na Região Neotropical. Porém, há poucos estudos em Biogeografia Histórica incluindo um número representativo de espécies ou áreas de grande extensão geográfica. Seus padrões biogeográficos têm sido comparados com aqueles identificados para táxons de organismos terrestres, com o intuito de recuperar a história da biota Neotropical. A história geológica de rios e lagos costeiros do componente sudeste da Região Neotropical é predominantemente recente, apresentando complexidades bióticas singulares, que resultaram em grande diversidade ictiológica. Neste estudo, foi aplicado o método pan-biogeográfico de análise de traços, utilizando o *software Martitracks*, para identificar padrões de distribuição de Characiformes da Sub-região Chaquenha. Foram usadas 13.410 ocorrências referentes a 132 espécies nominais, que resultaram em 16 traços generalizados e um nó biogeográfico. Os Characiformes apresentaram padrões de distribuição concordantes com aqueles de outros táxons. Os padrões obtidos estão de acordo com o estado atual de conhecimento da história geológica da Sub-região Chaquenha e se ajustam aos Padrões Biogeográficos A, B e C formalmente reconhecidos, determinados por eventos geológicos antigos, intermediários e recentes, respectivamente.

Palavras-Chave: Characiformes, Biogeografia Histórica, análise de traços, Sub-região Chaquenha, Região Neotropical.

Abstract The greatest diversity of freshwater fishes occurs in the Neotropical Region. However, there are a few Historical Biogeography studies including a large amount of species or areas with a great geographical extension. Their distributional patterns have been compared with those identified for taxa of terrestrial organisms, with the purpose to recover the history of the Neotropical biota. The geological history of coastal rivers and lakes of the southeastern component of the Neotropical Region is mainly recent, showing singular biotic complexities, resulting in great ichthyological diversity. In this study, we applied the panbiogeographic method of track analysis using the *Martitracks* software to identify distributional patterns of Characiformes from the Chacoan Sub-region. We used 13,410 occurrences related to 132 nominal species, resulting in 16 generalized tracks and a single biogeographic node. The Characiformes showed distributional patterns matching with those of other taxa. The patterns obtained is according to the current state of knowledge about the geological history of the Chacoan Sub-region and fit in with the Biogeographic Patterns A, B and C, formally recognized, determined by ancient, intermediate, and recent geological events, respectively.

Keywords:Characiformes, Historical Biogeography, track analysis, Chacoan Sub-region, Neotropical Region.

Introduction

The greatest diversity of freshwater fishes occurs in the tropics, especially in the Neotropical Region (Helfman *et al.*, 2009). In absolute numbers, about 7,000 nominal species of fishes live in South and Central America (Albert & Reis, 2011), and globally one out of five known species occur in the Neotropical Region (Vari & Malabarba, 1998).

Characiformes is a diverse lineage of actinopterygian fish from the continental waters of Africa and the Americas (Betancur-R *et al.*, 2017). The clade comprises 24 families (Nelson *et al.*, 2016), from which four having more than 200 species distributed throughout Africa while the rest is found in the Americas, with about 2,300 species. The group comprises a great diversity of forms, behaviors and ecologies and includes the *piranhas*, *tetras*, *lambaris* and *dourados* so familiar to both fishermen and aquarists (Géry, 1977).

The richness of the Neotropical fish fauna has been the focus of some discussions and some efforts have been made in order to understand its origin and history. Several studies have presented evidence that speciation and genetic divergence of the Neotropical fish fauna is related to geological events between lowland water bodies and those of adjacent crystalline shields and involves process such as the catchment of rivers and headwaters (Ribeiro, 2006; Albert & Reis, 2011; Ribeiro & Menezes, 2015).

River systems in eastern part of Brazil, including river mouths such as São Francisco in Alagoas, have been considered important areas of endemism for fish (Menezes, 1996). A list drawn up by Bizerril (1994) included reference to possible vicariant events that would have promoted the differentiation of the ichthyofauna. Several authors (e.g., Menezes, 1988; Ribeiro, 2006; Buckup, 2011; Echeverry & Gallo, 2015; Ribeiro & Menezes, 2015) have discussed the historical relationship between geotectonic processes and differentiation of the ichthyofauna. Thus, although the history of southeastern Neotropical rivers and lakes is relatively recent from a geochronological point of view, they have unique and complex biotic history, which include outstanding ichthyological diversity (Albert & Reis, 2011).

Different tools of Historical Biogeography could be used to reconstruct and understand the history of isolation, divergence, and diversification of fish species. Panbiogeography is one approach to Historical Biogeography consisting of an amount of methods with the widest application (Heads, 2012; Morrone, 2015). It was founded and developed from studies realized by the Italian American Léon Camille Marius Croizat (1894-1982), with components of global fauna and flora. The results of applying his method were published in some works, such as *Panbiogeography* (Croizat, 1958) and *Space, Time, Form: The Biological Synthesis* (Croizat, 1964). Later, the panbiogeographic methodology was improved by several authors (Craw *et al.*, 1999; Grehan, 2011; Miranda & Dias, 2012) using statistics and exact algorithms.

The study presented here aims to identify distributional patterns of freshwater fishes, specifically characiforms, from the Chacoan Sub-region (Neotropical Region) applying panbiogeographic method of track analysis, and comparing the results with other taxa, including those that served as basis for the regionalization proposed by Morrone (2014).

Materials and Methods

The panbiogeographic method of track analysis used here delineates the individual tracks of each taxon that are drawn as line graphs on maps. These are superimposed to determine generalized tracks and the intersecting localities (nodes) between generalized tracks. This method involves the following steps: 1) map each taxon by connecting localities as a minimum length line graph; 2) recognizing similar individual tracks that have overlapping localities as a generalized track; 3) recognizing nodes in areas where two or more generalized tracks meet; 4) map the individual and generalized tracks, and the nodes (Heads, 2004; Morrone, 2004).

The individual track is the basic unit of the study. It is a line that connects the locations (geographical coordinates of each geographic locality) for the distribution of a species or a supraspecific taxon. This line is formed from the union of points by the minimum distance connecting all points (Grehan, 2011). The Generalized Track (GT) is the overlap of two or more individual tracks, which indicates that they have common ancestral range subject to the same vicariant events (geological, tectonic, or climatic) (Craw, 1988; Craw *et al.*, 1999; Morrone, 2004; Grehan, 2011), or they represent a common path of dispersion (*i.e.*, geodispersion), or isolated dispersion events (Morrone & Crisci, 1995; Craw *et al.*, 1999; Nihei & Carvalho, 2005). Additionally, they can also indicate putative areas of endemism (Morrone, 2004; Nihei & Carvalho, 2005).

We named the “Generalized Tracks” in this study as GT - n, where “n” is an integer. For those subunits that are inserted in major GTs, we used GT n1-n2.

Nodes are represented here as the intersection of two or more generalized tracks (Craw *et al.*, 1999; Crisci *et al.*, 2003). According to Grehan (2011), the nodes represent the intersection of different ecologies, phylogenies, as well as distributions. Nodes can also be characterized as areas of biological endemism, phylogenetic diversity, limits of geographic or phylogenetic distribution and geographical disjunction. The nodes correlate the biological characteristics with the origin and/or geological process that formed the biotas (Heads, 1989; Crisci *et al.*, 2003; Nihei & Carvalho, 2005).

Species included in this work were selected based on geographic data (“type locality” and “distribution”) from Buckup & Menezes (2007) and records from freshwater bodies (*Arroio, Bacia, Baía, Córrego, Lago, Lagoa, Laguna, Riacho, Rio* and *Tributário*) of the hydrographic regions according to ANA (2015). The 132 species selected for analysis are listed in the Appendix.

We used maps of hydrographic regions available in http://www3.ana.gov.br/portal/ANA/aguas-no-brasil/panorama-das-aguas/copy_of_divisoes-hidrograficasand http://portal1.snirh.gov.br/ana/apps/webappviewer/index.html?id=9cc5900ceb0d4c279305d43197980dd8 (accessed in July 25th, 2015).

The geographical data used to estimate the distribution of taxa and to perform track analysis were obtained from the database of the following collections: The Academy of Natural Sciences Fish Collection (ANSP-Ichthyology, Philadelphia, Pennsylvania, United States); Fish Collection of the Departamento de Zoologia e Botânica, Universidade Estadual Paulista (DZSJRP-Pisces, São José do Rio Preto, São Paulo, Brazil); Coleção Ictiológica da Universidade Federal do Espírito Santo (CIUFES, Vitória, Espírito Santo, Brazil); Coleção Ictiológica do Acervo Biológico da Amazônia Meridional, Campus Sinop, Universidade Federal de Mato Grosso (ABAM, Sinop, Mato Grosso, Brazil); Coleção Zoológica Delta do Parnaíba – Pisces, Universidade Federal do Piauí (CZDP-Pisces, Parnaíba, Piauí, Brazil); Laboratório de Ictiologia do Grupo de Ecologia Aquática, Universidade Federal do Pará (GEA, Belém, Pará, Brazil); Coleção de Peixes INPA, Instituto Nacional de Pesquisas da Amazônia (INPA-Peixes, Manaus, Amazonas, Brazil); Coleção de Peixes do Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Campus Ribeirão Preto (LIRP, Ribeirão Preto, São Paulo, Brazil); Coleção de Peixes do Museu de História Natural Capão da Imbuia (MHNCI–Peixes, Curitiba, Paraná, Brazil); Coleção Científica da Divisão de Peixes do Museu de Zoologia, Universidade Estadual de Feira de Santana (MZFS, Feira de Santana, Bahia, Brazil); Subcoleção Ictiológica do Campus Parnaíba daUniversidade Estadual do Piauí (UESPI PHB, Parnaíba, Piauí, Brazil); Coleção de Peixes do Laboratório de Ictiologia Sistemática da Universidade Federal do Tocantins (UNT, Porto Nacional, Tocantins, Brazil); Zoneamento Ecológico Econômico do Acre – Ictiofauna (ZEE-ICTIO, Rio Branco, Acre, Brazil); Museum of Comparative Zoology, Harvard University (HU-Zoo, Cambridge, Massachusetts, United States); Coleção de Peixes, Instituto Nacional da Mata Atlântica (INMA), Museu de Biologia Prof. Mello Leitão (MBML-Peixes, Santa Teresa, Espírito Santo, Brazil); Coleção de Peixes, Pontifícia Universidade Católica do Rio Grande do Sul (MCP-Peixes, Porto Alegre, Rio Grande do Sul, Brazil); Museu de Zoologia da Universidade Estadual de Londrina, Coleção de Peixes (MZUEL-Peixes, Londrina, Paraná, Brazil); Coleção de Peixes do Museu de Zoologia da Universidade de São Paulo (MZUSP - São Paulo, São Paulo, Brazil); US-Animalia, National Museum of Natural History, Extant Specimen and Observation Records, Smithsonian Institution (NMNH-Animalia, Washington, DC, United States); Coleção de Peixes, Universidade Federal do Rio de Janeiro (NUPEM/UFRJ, Macaé, Rio de Janeiro, Brazil); Coleção Ictiológica do Nupélia, Universidade Estadual de Maringá (NUP, Maringá, Paraná, Brazil); Coleção de Peixes, Universidade Federal do Rio Grande do Sul (UFRGS - Porto Alegre, Rio Grande do Sul, Brazil); Coleção de Peixes do Museu de Zoologia da Universidade Estadual de Campinas (ZUEC-PIS, Campinas, São Paulo, Brazil); Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul (ZUFMS-PIS, Campo Grande, Mato Grosso do Sul, Brazil); Coleção Ictiológica do Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ, Rio de Janeiro, Rio de Janeiro, Brazil).

The geographical coordinates were obtained from the Global Biodiversity (GBIF,

2016) and the Species Link (SPLINK, 2016). We used only "original" (those defined by the collectors) and "not suspect" coordinates (those that coincide with the names of the municipalities registered in the collection).

For the construction of generalized tracks and nodes, tools from *Martitracks* (Echeverría-Londoño & Miranda-Esquivel, 2011) were used. The following parameters were established: c = 2; r = 2.5 (lmin), 3 (lmax), 4 (lmax.line); and m = 0.8 (min-SI). Where "c" is the Cut Value that eliminates the redundant points of the analysis; "r" is the Congruence Rule that checks whether the individual tracks are congruent with each other; "m" - min-Sl is a Similarity Index (minimum congruence).

Firstly, the default parameters [c = 0.25; r = 0.25 (lmin), 0.50 (lmax), 0.75 (lmax.line); and m = 0.85 (min-SI)] were used, but they generated uninformative results. For this reason, we modified them based on the simulation made by Ferrari *et al.* (2013), who used the data provided by Moreira *et al.* (2011). This simulation generated similar results to those found in the manual analysis performed by Moreira *et al.* (2011). Also, Echeverría-Londoño & Miranda-Esquivel (2011) tested the application with data from Alzate *et al.* (2008), with the same parameters herein used, as well as by Ferrari *et al.* (2013)

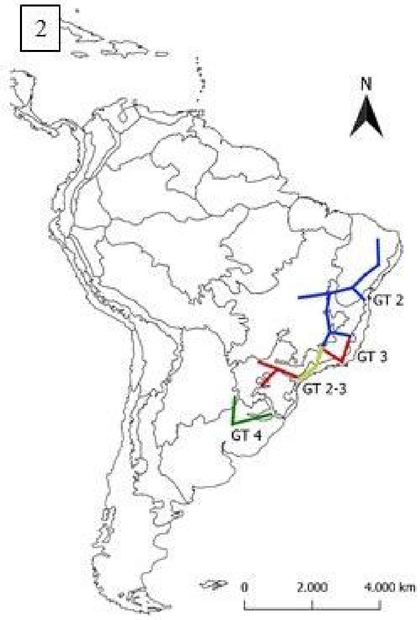
The map in shapefile format of the Neotropical Region (Morrone, 2014) for the presentation of the results was available in Löwenberg-Neto (2014). We used the software QGIS 2.18 (QGISBRASIL, 2017) for plot and analyze the tracks and nodes.

Track analysis was applied to 13,410 geographic coordinates for 132 species. After each figure (Figs. 1-9) there is a description of the generalized tracks and their biogeographic location.

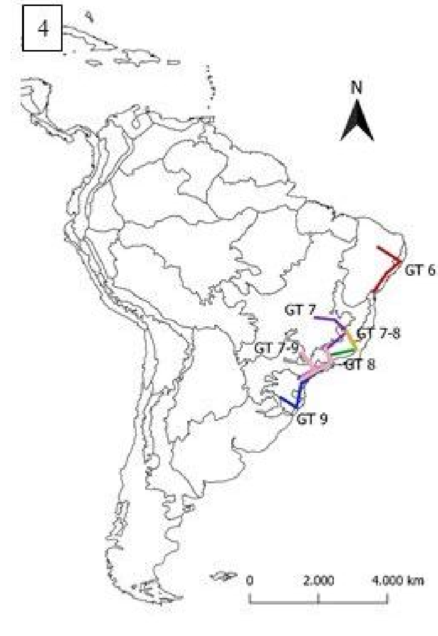
Results

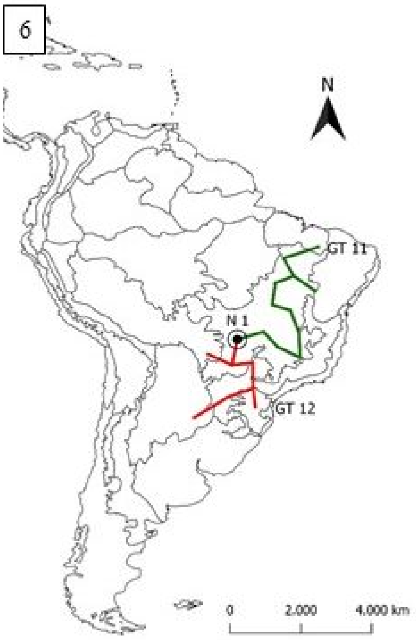
From the analysis of 13,410 geographic data for 132 species, 16 generalized tracks and one node were obtained. The maps with the GTs and nodes and their description are shown below.

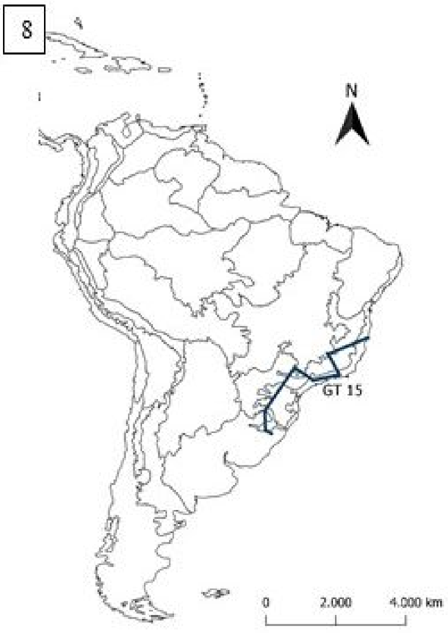

1
N
GT 1
0
2.000
4.000 km


2
N
GT 2
GT 3
GT 2-3
GT 4
0
2.000
4.000 km


3
N
GT 5
0
2.000
4.000 km


4
N
GT 6
GT 7
GT 7-8
GT 7-9
GT 8
GT 9
0
2.000
4.000 km





Figures 1-9 - Generalized tracks and nodes of Characiformes.

- GT1 composed of *Apareiodon affinis, A. ibitiensis, A. vittatus, A. vladii, A. itapicuruensis, A. hasemani, A. davisi, A. piracicabae* and *Parodonhilari,* located in Cerrado (Chacoan); Atlantic and Parana Forest (Parana);
- GT2 composed of *Curimatella lepidura, Cyphocharax gilbert, Psectrogaster rhomboides, P. saguiru, Steindachnerina elegans* and *S. notonota*, located in Caatinga and Cerrado (Chacoan); Atlantic and Parana Forest (Parana);
- GT3 composed of *Cyphocharax modestus, C. nagelii, C. vanderi, C. santacatarinae* and *Steindachnerina insculpta,* located in Atlantic, Parana Forest and Araucaria Forest (Parana);
- GT2-3 formed by line segment in common between GT2 and GT3. Located in Atlantic and Parana Forest (Parana);
- GT4 composed of *Cyphocharax saladensis, C. spilotus, C. voga* and *Steindachnerina biornata,* located in Chacoan and Pampean (Chacoan), Araucaria Forest (Parana);
- GT5 composed of *Prochilodus argenteus, P. costatus, P. hartii, P. vimboides, P. brevis* and *P. lineatus,* in Madeira (South Brazilian), Caatinga, Cerrado (Chacoan), Atlantic and Parana Forest (Parana);
- GT6 composed of *Characidium bahiense* and *C. bimaculatum,* crossing in Caatinga (Chacoan) and Atlantic (Parana);
- GT7 composed of *Characidium alipioi, C. fasciatum, C. grajahuense, C. interruptum, C. japuhybense, C. lagosantense, C. lauroi* and *C. schubarti,* crossing Cerrado (Chacoan), Atlantic and Parana Forest (Parana);
- GT8 composed of *Characidium timbuiense* and *C. vidali,* located in Parana Forest (Parana);
- GT9 composed of *Characidium lanei, C. oiticicai, C. pterostictum, C. occidentale, C. orientale, C. rachovii, C. serrano and C. tenue,* located in Atlantic and Araucaria Forest (Parana);
- GT7-8 formed by line segment in common between GT7 and GT8 e located in Atlantic and Parana Forest (Parana);
- GT7-9 formed by line segment in common between GT7 and GT9, located in Atlantic, Parana Forest and Araucaria Forest (Parana);
- GT10 composed of *Bryconferox, B. insignis, B. nattereri, B. opalinus, B. orthotaenia* and *Henochilus wheatlandii,* crossing Cerrado (Chacoan), Atlantic and Parana Forest (Parana);
- GT11 composed of *Galeocharax gulo, Phenacogaster calverti, P. franciscoensis* and *Roeboides xenodon,* spanning through Pará (Boreal Brazilian), Cerrado (Chacoan).
- GT12 composed of *Charax stenopterus* e *Galeocharax knerii* spanning Rondônia (South Brazilian), Cerrado, Chacoan (Chacoan), Parana Forest and Araucaria Forest (Parana);
- N1 formed by GT11 and GT12 located in Cerrado (Chacoan).
- GT13 composed of *Acinocheirodon melanogramma, Serrapinnus heterodon, Serrapinnus piaba, Compsura heterura* and *Kolpotocheirodon theloura,* crossing Caatinga, Cerrado (Chacoan) and Parana Forest (Parana);
- GT14 composed of *Cheirodon ibicuhiensis, C. interruptus, Heterocheirodon jacuiensis, Macropsobrycon uruguayanae, Serrapinnus calliurus, S. notomelas, Spintherobolus leptoura, S. papilliferus* and *S. ankoseion,* crossing Cerrado, Pampa (Chacoan), Atlantic, Parana Forest and Araucaria Forest (Parana);

- GT15 composed of *Diapoma speculiferum, D. terofali, Mimagoniates inequalis, M. lateralis, M. microlepis, M. rheocharis, M. sylvicola, Planaltina glandipedis, Pseudocoryno pomadoriae* and *P. heterandria,* crossing Pampean (Chacoan), Atlantic, Parana Forest and Araucaria Forest (Paraná);
- GT16 composed of *Triportheus guentheri* and *T. signatus,* crossing Cerrado (Chacoan) and Parana Forest (Parana);

Discussion

Overall, the generalized tracks and nodes found here were corroborated by distributional patterns of dipterans *Cyrtoneurina*, *Cyrtoneuropsis* and *Bitoracochaeta* (Carvalho *et al.*, 2003) and *Polietina* (Nihei & Carvalho, 2005); hymenopteran *Bombus* (Abrahamovich*et al.*, 2004); and coleopteran Entimini (Romo & Morrone, 2011), as follows:

1. GTg and GTf of *Cyrtoneurina* (cf. Carvalho *et al.,* 2003) match GT2-3 of Curimatidae and GT7-9 of Crenuchidae.
2. GTt of *Cyrtoneuropsis* (cf. Carvalho *et al.,* 2003) is congruent to GT2 of Curimatidae and GT11 of Characinae; GTu and GTvto GT2-3 of Curimatidae, GT7-9 of Crenuchidae, and GT15 of Glandulocaudinae.
3. GT CDE of *Bithoracochaeta* (cf. Carvalho *et al.,* 2003) match GT2-3 of Curimatidae, GT7-9 of Crenuchidae, GT15 of Glandulocaudinae.
4. GT7 of *Bombus* (cf. Abrahamovich *et al.,* 2004) match GT2-3 of Curimatidae, GT7-9 of Crenuchidae, GT 5 of Prochilodontidae, GT 14 of Cheirodontinae, GT 15 of Glandulocaudinae.
5. GT2 of *Polietina* (cf. Nihei & Carvalho, 2005) is congruent to GT6 of Crenuchidae and GT2 of Curimatidae; GT3 of *Polietina*(cf. Nihei & Carvalho, 2005) match GT6 de Crenuchidae; the line segment formed by GT 4 and 6 de *Polietina* (cf. Nihei & Carvalho, 2005) match GT 5 of Prochilodontidae; line segment formed by GT 5 and 7 of *Polietina* (cf. Nihei & Carvalho, 2005) match GT 7-9 of Crenuchidae; GT 7 of *Polietina* (cf. Nihei & Carvalho, 2005) match GT 2-3 of Curimatidae, GT 14 of Cheirodontinae (Characidae), GT 15 of Glandulocaudinae.
6. GT b Entimini (cf. Romo & Morrone, 2011) match GT2-3 and GT3 of Curimatidae, GT7-9 of Crenuchidae, GT9 of Crenuchidae, GT14 of Cheirodontinae (Characidae), GT 15 of Cheirodontinae (Characidae).

Carvalho *et al.* (2003) discussed possible vicariant events that could have shaped the distribution of Muscidae (Diptera) with reference to Amorim & Pires (1996). The authors emphasized the connection between the Parnaíba and Paraná basins, which occurred in the Late Cretaceous. GT 11 and GT 12, and N1 of Characinae (Characidae) (Fig. 6) were formed from the overlapping of localities of rivers and streams of the Paraná and Parnaíba basins. Throughout its history, the Parnaíba River has also been connected with other rivers in northeastern Brazil, such as the São Francisco River (Ribeiro, 2006).Due to these connections, the hydrographic basins of northeastern Brazil allowed a faunal interchange resulting in a diverse ichthyofauna (Ribeiro, 2006). In the present work, the GT 16 formed by Triportheinae species (Fig. 9) joins localities or streams that flow from the Parnaíba River to the São Francisco River.

Congruence found in the southeast of the Brazilian coast between GT 2, GT 2-3, GT 7-9, GT 15 and literature data is probably related to the rise of Serra da Mantiqueira (Amorim & Pires, 1996; Carvalho *et al.*, 2003) or Serra do Mar (Ribeiro, 2006). New studies are necessary to confirm this spatial correlation shaped by the uplift of both mountains.

Comparing the distributional patterns of fish with the results obtained by Nihei & Carvalho (2005) for *Polietina*, it is clear that there is congruence in the distribution between Crenuchidae, Curimatidae, Prochilodontidae, Cheirodontinae (Characidae), Glandulocaudinae (Characidae) and the cited Diptera.

Generalized tracks may indicate ancestral range subject to the same vicariance events or isolated dispersion events. If phylogenetically supported, the generalized track indicates an area of endemism or the preexistence of an ancestral biota (Nihei & Carvalho, 2005). Phylogenetically supported tracks are those formed by sister species or closely related species. According to phylogenetic studies, it was found that:

- Melo *et al.* (2016) recognized the following relationships: (*Prochiloduscostatus, P. lineatus*) + (*P. argenteus*, *P. hartii*).These species is in GT5;
- In the composition of GT10 of Bryconinae (Characidae) there are *Bryconferox* and *B. insignis* that are sister species (Hilsdorf *et al.*, 2008);
- In the composition of GT14, there are *Cheirodon interruptus* and *Serrapinnus calliurus*, which are sister species, according to Mirande (2010);
- GT15 has in its composition *Mimagoniates lateralis*, *M. microlepis* and *M. sylvicola* which, according to the cladogram presented by Menezes & Weitzman (2009) the relationship between these species is not fully understood, but they belong to the same clade.

According to Nihei & Carvalho (2005), generalized tracks formed by sister species or closely related species are relevant to understanding the history of species diversification. It should be noted here that the generalized tracks mentioned above are formed by species belonging to the same group of species or clade or are sister species. It is likely that the areas in which these tracks are identified have an effective historical determination in the speciation.

There is biogeographic congruence between Entimini and Curimatidae, Crenuchidae, Cheirodontinae (Characidae) in the Atlantic and Paraná Forest provinces in southeastern Brazil (see figures 2, 4 e 7). As for the distribution of Entimini, Romo & Morrone (2011) mention that the establishment of the Savana Corridor (Schmidt

& Inger, 1951; Prado & Gibbs, 1993; Morrone, 2006; Romo & Morrone, 2011) or Diagonal of Open Formations (Vanzolini, 1963; Romo & Morrone, 2011) along the Chacoan Sub-region (north-central Argentina, southern Bolivia, central-western Paraguay, Uruguay and central-northeast Brazil) (Morrone, 2006), would have been an important vicariant event for the fauna of the Brazilian Sub-region and Chacoan Sub-region.

Regarding this work and the fish distribution studied here, it should be considered that only distributional patterns of the Chacoan Sub-region were analyzed, therefore, there is no possibility to assess the impact of the emergence of the Savanna Corridor for characiformes. A broader study would be necessary for this analysis and there is a possibility that this event, like so many other events, will have a reduced impact on the distribution of fish, given the recurrence of "headwater capture" and the connections between the large hydrographic basins (Lundberg *et al.*, 1998; Ribeiro, 2006; Albert & Reis, 2011).

For the GTs 4, 12, 13 and 16 and node N1, no similar examples were found in the literature, due to probably the lack of collections and studies (Morrone, 2004). There is also the possibility that the incongruity is the result of particularities of the analyzed taxon. In this sense, many of the species of bony fish that contributed to the tracks and node may have a unique evolutionary history or linked to the histories of the rivers that shelter them. A possible lack of exact biological information for these species in these mentioned tracks and node difficult to make any argument to improve the biogeographic understanding. The incongruity may be related to the program used for the analysis of tracks, such as Ferrari *et al.* (2013) stated that the subjective definition of parameters can lead to an imprecise analysis.

In the Late Cretaceous, large clades of Neotropical ichthyofauna, including Characiformes, had already diversified, as shown by Lundberg *et al.* (1998). Although the oldest record of characiform in South America is from the late Campanian/early Maastrichtian (~83 to 72 Mya) (Gayet, 1991), probably the diversification of this clade occurred before the final separation of Africa and South America, also considering the gaps in the fossil record. This means that the history of the largest clades of bony fish occurred before the emergence of modern rivers or their present geography and catchment relationships (Lundberg *et al.*, 1998).

The geological history of the Neotropical Region, specifically in the crystalline shield and coastal drainages (Chacoan Sub-region), resulted in three distinct biogeographic patterns (Ribeiro 2006).

Pattern A: coastal rivers of Brazil are inhabited by taxa that have an ancient biogeographic history (Stiassny & Pinna, 1994; Ribeiro, 2006) dating from the Cretaceous, with the diversification of an endemic ichthyofauna. They are old taxa with few species and restricted geographic distribution. The Characiformes has its origin by at least in the Cretaceous (Brito *et al.*, 2007; Albert & Reis, 2011) with a minimum fossil age of 83 to 72 Mya (Gayet, 1991). This coastal pattern applies to the Crenuchidae (GT 6, 7, 8 and 9, Fig. 4).

Pattern B: generic level relationships between the endemic ichthyofauna of coastal drainages with the crystalline shield (Ribeiro, 2006). None of the taxa sampled here show this relationship.

Pattern C: is the result of faunal exchange between the rivers of the crystalline shield and the coastal drainages (Ribeiro, 2006). The distribution along the lines of the Pattern C can be corroborated by the generalized tracks that connect or that are present in hybrid areas, which are areas that have undergone neotectonics processes that have led to fauna exchange. Through the examples of hybrid areas given by Ribeiro (2006) and the generalized tracks, it is noticed that there is Pattern C in:

- In the region that includes the Upper Uruguay River, Jacuí and the Patos Lagoon System (Rio Grande do Sul, Brazil) and Negro and Salado (Argentina). In this area were found GT4 Curimatidae (Fig. 2).

- In the region that includes the Alto Rio Tietê, Ribeira de Iguape, the tributaries of the Paraná Basin, Rio Iguaçu and Rio Paranapanema. In this area are: GT3 from Curimatidae (Fig. 2) and GT14 from Cheirodontinae (Fig. 7).

- The region that includes the northern portion of the Paraná basin, São Francisco, Paraíba do Sul, Itapicuru, Itapemirim, and the mouth of the Rio Doce. In this area were found: the GT 1 of Parodontidae (Fig. 1); GT2 Curimatidae (Fig. 2); GT 10 Bryconinae (Fig. 5); GT 13 from Cheirodontinae (Fig. 7); GT 15 from Glandulocaudinae (Fig. 8).

- The region that includes the São Francisco River and the Parnaíba River: GT 16 from Triportheinae (Fig. 8).

In addition to the areas mentioned above, we have:

- The region that extends from the Paraná River Basin to the Parnaíba River: The GT 11 and GT 12, and the N1 of Characinae (Fig 6) were formed from the overlapping of localities of rivers and streams of the Paraná basin and of Parnaíba basin. Thus indicating a previous connection of these, as previously mentioned (Amorim & Pires, 1996).

- The region from the Paraná Basin to the Amazon (Lundberg *et al.*, 1998): GT 5 of Prochilodontidae (Fig. 3) links Amazonas to the tributaries of the Paraná, Rio São Francisco, Paraíba do Sul. There is a possibility that group took advantage of sea level changes throughout history. The distribution may be related to the connection of the Paraná River with the Amazon River, through the Paraná Sea (Lundberg *et al.*, 1998).

According to Ribeiro (2006), the distributional patterns A, B and C are consequences of old, intermediate, and recent geological events, respectively.

According to the hypothesis that corroborates Pattern A, cladogenetic events are related to the origin of the first drains that flowed into the Atlantic Ocean. Coastal rivers were structurally oriented by megadomes, major flaws and grabens. Ribeiro (2006) stated that this is the case about the rivers that were established in the megadomes Mantiqueira-Angola and Brazil-Niger, where a fault system was responsible for structuring the drainage pattern.

The Pattern B suggests an interchange of fauna between the crystalline shield and coastal rivers across the Cenozoic. The continuous erosive retraction on the east limit of the platform was responsible for the transfer of fauna from the rivers of the central plateau to the rivers of the coastal plains. With taxa undergoing subsequent diversification in both the coastal plain and plateau drainages. The tectonism, through reactivations and movements of large blocks, led to the capture of hydrographic systems. This has an impact on the distributional patterns of aquatic biotas (Ribeiro, 2006).

The geological mechanism associated with the Pattern C refers to the concept of Neotectonics (Saadi, 2013). According to recent models, the widespread rift system and other crustal discontinuities present along the Atlantic coast of South America act as areas of weakness more prone to tectonic activity and deformations (Saadi *et al.*, 2002). Several hydrological anomalies are probably related to tectonic activations, most importantly the stream capture (Cobbold *et al.*, 2001).

The areas where the Pattern C occurs have been identified as active tectonic areas, some of which have a recent activity of approximately 1.6 MA (Saadi *et al.*, 2002). This is what occurs in the crystalline shield of southeastern Brazil, which shares a mixed fauna with the drainages of the coastal plain such as, for example, the area that includes the headwaters of the Ribeira do Iguape, Iguaçu and Paranapanema rivers and the upper Tietê. It is important to note that in this area we find the GT3 from Curimatidae (Fig. 2) and the GT14 from Cheirodontinae (Fig. 7).

The generalized tracks in the regions of Paranapanema, Iguaçu and Ribeira do Iguape can be explained by the presence of the Ponta Grossa Arch. It has a general tendency to uplift (Almeida &Carneiro, 1998) and suffered tectonic activity during the Cenozoic (Almeida & Carneiro, 1998; Souza & Souza, 2002). The arc's tectonic activity may have resulted in a change in the fluvial dynamics of the area, accelerating the faunal exchange between water bodies, such as the coastal part of Ribeira do Iguape and the plateau portions of Iguaçu and Paranapanema. The distributional pattern of Curimatidae (Fig. 2) and Cheirodontinae (Fig. 7) may be a consequence of this.

The idea of southeastern Brazil being a tectonically active area (Cobbold *et al.*, 2001) is supported by complex distributional patterns that include the Pattern C. This tectonic activity explains why the Paraná Basin has contributed more to the development of ichthyofauna coastal drainage, exemplified by the patterns of Parodontidae (Fig. 1), Curimatidae (Fig. 2), Bryconinae (Fig. 5), Cheirodontinae (Fig. 7) and Glandulocaudinae (Fig. 8).

The tectonic control over the distributional patterns of fish fauna in coastal and plateau drainages is a recurrent process, suggesting a high degree of faunal exchange between basins (Ribeiro, 2006). The mixed nature of hydrographic basins has already been noted by Costa (2001), who indicated headwaters as effective areas of faunal exchange. The same tectonic process that allowed the interchange between Brazilian coastal rivers with neighboring drainages probably also occurred between basins located in the interior of the continent in the crystalline shield. This pattern is found in Characinae (Fig. 6), which occurs in the crystalline shield and joins the Paraná and São Francisco rivers.

The distributional patterns of ichthyofauna in the Neotropical Region are related to multiple factors: changes in the sea level (Weitzman *et al.*, 1988); retraction of the east limit (Ribeiro & Menezes, 2015); old and recent historical events; and, mainly, the capture of rivers, headwaters, or entire hydrographic systems.

It was found that the same clade can present different and conflicting distributional patterns. This is possible if we consider the premise that the fish fauna of the Neotropical Region is modern, and that the main groups of fish have a minimum Cretaceous age (Brito *et al.*, 2007).

Conclusion

Through tracks analysis it was possible to identify that the distributional patterns of characiformes from Chacoan Subregion fit into the Patterns A, B and C already described in the literature.

The patterns found are corroborated by others presented by different taxa with different dispersion capacities, but which may have something in common when compared to their histories.

In addition, the results indicate that the history of Neotropical fish and the rivers that shelter them is intricate and of great complexity, resulting from ancient and recent geological processes, from the setting of a watercourse to the interaction between them through headwaters capture, streams, rivers, and even entire hydrographic systems.

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APPENDIX- Fish species included in this study.

- **CHARACIFORMES** – **Parodontidae**: *Apareiodon affinis* (Steindachner, 1879), *A. davisi* (Fowler, 1941), *A. hasemani* Eigenmann, 1916, *A. ibitiensis* Campos, 1944, *A. itapicuruensis* Eigenmann & Henn, 1916, *A. piracicabae* (Eigenmann, 1907), *A. vittatus* Garavello, 1977, *A. vladii* Pavanelli, 2006 and *Parodon hilarii* Reinhardt, 1866; **Curimatidae**: *Curimatella lepidura* (Eigenmann & Eigenmann, 1889), *Cyphocharax gilbert* (Quoy & Gaimard, 1824), *C. modestus* (Fernández-Yépez, 1948), *C. nagelii* (Steindachner, 1881), *C. saladensis* (Meinken, 1933), *C. santacatarinae* (Fernández-Yépez, 1948), *C. spilotus* (Vari, 1987), *C. vanderi* (Britski, 1980), *C. voga* (Hensel, 1869), *Psectrogaster rhomboids* Eigenmann & Eigenmann, 1889, *P. saguiru* (Fowler, 1941), *Steindachnerina biornata* (Braga & Azpelicueta, 1987), *S. elegans* (Steindachner, 1874), *S. insculpta* (Fernández-Yépez, 1948) and*S. notonota* (Miranda Ribeiro, 1937); **Prochilodontidae:** *Prochilodus argenteus* Agassiz, 1829, *P. brevis* Steindachner, 1874, *P. costatus* Valenciennes, 1850, *P. hartii* Steindachner, 1874, *P. lineatus* (Valenciennes, 1836) and *P. vimboides* Kner, 1859; **Anostomidae:** *Leporellus vittatus* (Valenciennes, 1850), *Leporinus aguapeiensis* Campos, 1945, *L. amblyrhynchus* Garavello & Britski, 1987, *L. bahiensis* Steindachner, 1875, *L. conirostris* Steindachner, 1875, *L. copelandii* Steindachner, 1875, *L. crassilabris* Borodin, 1929, *L. elongates* Valenciennes, 1850, *L. garmani* Borodin, 1929, *L. lacustris* Campos, 1945, *L. marcgravii* Lütken, 1875, *L. melanopleura* Günther, 1864, *L. mormyrops* Steindachner, 1875, *L. obtusidens* Valenciennes, 1836, *L. octofasciatus* Steindachner, 1915, *L. paranensis* Garavello & Britski, 1987, *L. piau* Fowler, 1941, *L. reinhardti* Lütken, 1875, *L. steindachner i*Eigenmann, 1907, *L. striatus* Kner, 1858, *L. taeniatus* Lütken, 1875, *L.thayeri* Borodin, 1929, *Schizodon australis* Garavello, 1994, *S. intermedius* Garavello & Britski, 1990, *S. jacuiensis* Bergman, 1988, *S. knerii* (Steindachner, 1875) and *S. nasutus* Kner, 1858; **Crenuchidae:** *Characidium alipioi* Travassos, 1955, *C. bahiense* Almeida, 1975, *C. bimaculatum* Fowler, 1941, *C. fasciatum* Reinhardt, 1866, *C. interruptum* Pellegrin, 1909, *C. japuhybense* Travassos, 1949, *C. lagosantense* Travassos, 1947, *C. lanei* Travassos, 1967, *C. lauroi* Travassos, 1949, *C. occidentale* Buckup& Reis, 1997, *C. oiticicai* Travassos, 1967, *C. orientale* Buckup& Reis, 1997, *C. pterostictum* Gomes, 1947, *C. rachovii* Regan, 1913, *C. schubarti* Travassos, 1955, *C. Serrano* Buckup& Reis, 1997, *C. tenue* (Cope, 1894), *C. timbuiense* Travassos, 1946, *C. vestigipinne* Buckup& Hahn, 2000 and *C. vidali* Travassos, 1967; **Characidae – Bryconinae:** *Bryconferox* Steindachner, 1877, *B. hilarii* (Valenciennes, 1849), *B. insignis* Steindachner, 1877, *B. nattereri* Günther, 1864, *B. opalinus* (Cuvier, 1819), *B. orthotaenia* Günther, 1864 and *Henochilus wheatlandii* Garman, 1890; **Characidae – Characinae:** *Charax stenopterus* (Cope, 1894), *Galeocharax gulo* Cope, 1870, *G. knerii* Steinachner, 1875, *Phenacogaster calverti* (Fowler, 1941), *P. franciscoensis* Eigenmann, 1911 and *Roeboides xenodon* (Reinhardt, 1851); **Characidae – Cheirodontinae:** *Acinocheirodon melanogramma* Malabarba & Weitzman, 1999, *Cheirodon ibicuhiensis* Eigenmann, 1915, *C.*

interruptus (Jenyns, 1842), *Compsuraheterura* Eigenmann, 1915, *Heterocheirodon jacuiensis* Malabarba & Bertaco,1999, *Kolpotocheirodon figueiredoi* Malabarba, Lima & Weitzman, 2004, *K. theloura* Malabarba & Weitzman, 2000, *Macropsobrycon uruguayanae* Eigenmann, 1915, *Serrapinnus calliurus* (Boulenger, 1900), *S. heterodon* (Eigenmann, 1915), *S. notomelas* (Eigenmann, 1915), *S. piaba* (Lütken, 1875), *Spintherobolu sankoseion* Weitzman & Malabarba, 1999, *S. broccae* Myers, 1925, *S. leptoura* Weitzman & Malabarba, 1999 and *S. papilliferus* Eigenmann, 1911; **Characidae – Glandulocaudinae:** *Diapoma speculiferum* Cope, 1894, *D. terofali* Géry, 1964, *Glandulocauda melanogenys* Eigenmann, 1911, *G. melanopleura* Eigenmann, 1911, *Hysteronotus megalostomus* Eigenmann, 1911, *Mimagoniates inequalis* Eigenmann, 1911, *M. lateralis* Nichols, 1913, *M. microlepis* Steindachner, 1877, *M. rheocharis* Menezes & Weitzman, 1990, *M. sylvicola* Menezes & Weitzman, 1990, *Planaltina britski* Menezes, Weitzman & Burns, 2003, *P. glandipedis* Menezes, Weitzman & Burns, 2003, *Pseudocoryno pomadoriae* Perugia, 1891 and *P. heterandria* Eigenmann, 1914; **Characidae – Iguanodectinae:** *Piabucus melanostomus* Holmberg, 1891; **Characidae – Serrasalminae:** *Myleus altipinnis* (Valenciennes, 1850), *M. micans* (Lütken, 1875), *Myloplustiete* (Eigenmann & Norris, 1900), *Pygocentrus piraya* (Cuvier, 1819), *Serrasalmus brandti* (Lütken, 1875) and *S. marginatus* Valenciennes, 1836; **Characidae – Stethaprioninae:** *Orthospinus franciscensis* (Eigenmann, 1914); **Characidae – Tetragonopterinae:** *Tetragonopterus chalceus* Spix & Agassiz, 1829; **Characidae – Triportheinae:** *Lignobrycon myersi* (Miranda Ribeiro, 1956), *Triportheus guentheri* (Garman, 1890) and *T. signatus* (Garman, 1890).