



Biogeography of Glandulocaudinae (Teleostei: Characiformes: Characidae) revisited: phylogenetic patterns, historical geology and genetic connectivity

NAÉRCIO A. MENEZES¹, ALEXANDRE C. RIBEIRO¹, STANLEY WEITZMAN² & RODRIGO A. TORRES³

¹Museu de Zoologia, Universidade de São Paulo, Caixa Postal 42594, 04218970 São Paulo, Brazil.
E-mail: naercio@usp.br; acribeiro@click21.com.br

²Division of Fishes, Department of Zoology, National Museum of Natural History, MRC 0159, PO Box 37012, Smithsonian Institution, Washington, D.C., 200013-7012, USA. E-mail: weitzman.stan@nmnh.si.edu

³Laboratório de Genômica Evolutiva e Ambiental, Departamento de Zoologia, Universidade Federal de Pernambuco, Centro de Ciências Biológicas, Av. Prof. Moraes Rego, s/n Cidade Universitária 50670-901 - Recife, PE – Brazil. E-mail: rodrigotorres@ufpe.br

Abstract

The biogeography of the Glandulocaudinae (former Glandulocaudini) is reviewed. The major pattern of diversification presented by this group of freshwater fishes can be clearly associated to the main aspects of the tectonic evolution of the southern portion of the Cis-Andean South American Platform. The phylogenetic relationships within the group suggest that the clade represented by *Lophiobrycon* is the sister-group of the more derived clade represented by the genus *Glandulocauda* and *Mimagoniates*. *Lophiobrycon* and *Glandulocauda* occur in areas of the ancient crystalline shield of south-eastern Brazil and their present allopatric distribution is probably due to relict survival and tectonic vicariant events. Populations of *Glandulocauda melanogenys* are found in contiguous drainages in presently isolated upper parts of the Tietê, Guaratuba, Itatinga, and Ribeira de Iguape basins and this pattern of distribution is probably the result of river capture caused by tectonic processes that affected a large area in eastern and southeastern Brazil. The species of *Mimagoniates* are predominantly distributed along the eastern and southeastern coastal areas, but *M. microlepis* is additionally found in the rio Iguaçú and Tibagi basins. *Mimagoniates barberi* occurs in both SW margin of the upper rio Paraná basin and the lower Paraguay and *Mimagoniates* sp. occurs in the upper Paraguay river basin. Tectonic activations of the Continental Rift of Southeastern Brazil along the eastern margin of the Upper Paraná basin promoted population fragmentation responsible of the present day distribution presented by *Glandulocauda melanogenys*. We hypothesize that occurrence of *Mimagoniates* along the lowland area around the Paraná basin was due to a single or a multiple fragmentation of populations along the W-SW border of the upper Paraná Basin, probably due to the major tectonic origin of the Chaco-Pantanal wetland foreland basins since the Miocene as well as Cenozoic tectonic activity along the borders of the upper Paraná basin, such as in the eastern Paraguay, in the Asunción Rift. Distributional pattern of *Mimagoniates* suggests that its initial diversification may be related to the tectonic evolution of the Chaco-Pantanal foreland basin system and a minimum age of 2.5 M.Y are proposed for this monophyletic group. Previous hypotheses on sea level fluctuations of the late Quaternary as being the main causal mechanism promoting cladogenesis and speciation of the group are critically reviewed. Phylogeographic studies based on molecular data indicate significant differences among the isolated populations of *M. microlepis*. These findings suggest that a much longer period of time and a paleogeographic landscape configuration of the Brazilian southeastern coastal region explain the present observed phylogenetic and biogeographic patterns.

Key words: Biogeography, Glandulocaudinae

Introduction

The subfamily Glandulocaudinae (former Glandulocaudini) consists of three genera: *Lophiobrycon*, *Glandulocauda* and *Mimagoniates* (Fig.1). The biogeography of these Neotropical fishes has been previously dis-

cussed by Weitzman *et al.* (1988) and Menezes & Weitzman (1990) focusing on the main biogeographic patterns within the genera *Glandulocauda* and *Mimagoniates*, to that date, the known representatives of the group. The description of *Lophiobrycon weitzmani* by Castro *et al.* (2003) provided new insights into the systematics of the Glandulocaudinae, since this taxon was considered by these authors as a basal lineage within the group, potentially informative of its initial diversification history. Recently, Ribeiro (2006), in a simplified view, used the biogeography of the Glandulocaudinae to discuss the biogeographic history of the Brazilian coastal rivers. Finally, Ribeiro *et al.* (2006) provided an additional distributional record for *Glandulocauda melanogenys*, previously known only from the upper rio Tietê basin and associated this new record with the geological mechanisms responsible for the capture of the upper rio Guaratuba from its ancient course to become a coastal tributary. Additional data on Glandulocaudinae distributional ranges has been also recently provided in the literature. Serra *et al.* (2007) recorded *Glandulocauda melanogenys* in the upper rio Itatinga basin, a coastal tributary of SE Brazil and Sant'Anna *et al.* (2006) reported the occurrence of *Mimagoniates microlepis* also in the upper rio Tibaji, a tributary of the Upper Paraná basin of SE Brazil.

The idea of reviewing the biogeography of the Glandulocaudinae came from the opportunity of adding new insights that resulted from recent and somewhat independent studies carried out by us. The systematics of the Glandulocaudinae is under review by NM and SW and additional new data on distributional ranges of species are going to be added. In addition, studies on the genetic connectivity of local populations of *Mimagoniates microlepis* throughout the southern coastal and upland drainages of Brazil, is an ongoing topic performed by RAT (Torres *et al.*, 2007). These new data suggest that the biogeographic history of the Glandulocaudinae is still more complex than previously suspected, and an update of the hypothesis proposed by Weitzman *et al.*, (1988), Menezes & Weitzman (1990), and Ribeiro (2006) is necessary.

Fortunately, the geological history of the South American continent has benefited from recent advances of the knowledge of intra plate tectonics which provide a unifying factor not only to geology itself, but help to clarify considerably the interpretation of biological distributional patterns. When coupled with phylogenetic information, the availability of geological information is crucial for understanding biogeographic patterns generated by the Neotropical ichthyofauna (Lundberg *et al.*, 1998; Ribeiro, 2006).

In this paper, we update the information on Glandulocaudinae biogeography in light of new geological, biological and molecular data. We conclude that Glandulocaudinae diversification is clearly associated with the main geotectonic events that have been acting on the southern region of South America and hope that our interpretations can be useful to future studies on Neotropical freshwater fish biogeography.

Material and methods

Data on the phylogenetic relationships among Glandulocaudinae and of geographic distribution of species were taken from recent papers dealing with the systematics of the group (Weitzman *et al.*, 1988; Menezes & Weitzman, 1990; Weitzman & Menezes, 1998; Castro *et al.*, 2003, and Weitzman *et al.*, 2005; Menezes & Weitzman in prep). The topology and polarity of characters are fully discussed in Menezes & Weitzman (in prep). New records on geographic distribution of species, and data on the tectonic evolution of the South American continent were obtained from the literature.

Interpretation of biogeographic patterns was made base on the construction of an area cladogram (Morrone & Crisci, 1995) and follow Nelson's (1985) concept of biogeography, as being the interrelationships or synthesis between biology and geology, in which synchronizations of biological and geological history is the basic tenet (Ribeiro, 2006). Our biogeographic analysis follows a "taxon history" approach as discussed by Hovenkamp (1997) which seeks to fit biotic diversity to the matrix of known Earth history. With this approach, we attempt to clarify earth history not in terms of area relationships, but in terms of sequences of vicariance events.

Molecular analysis were performed in specimens of *M. microlepis* from 10 different localities including the upper rio Iguaçu, the coastal plain of the Paraná, São Paulo and Santa Catarina states in SE-S Brazil. Vouchers were deposited and catalogued in the collection of Museu de História Natural do Capão da Imbuia (MHNCI), Curitiba, Brazil as follows: MHNCI 11703, 22 specimens, rio Ribeirão, Paranaguá, state of Paraná; MHNCI 11704, 1 specimen, basin of rio Acaraí, São Francisco do Sul, state of Santa Catarina; MHNCI 11705, 3 specimens, rio Mongaguá, Mongaguá, state of São Paulo; MHNCI 11706, 1 specimen rio Caierana, Piraquara, state of Paraná; MHNCI 11707, 1 specimen, rio da Várzea, Lapa, state of Paraná; MHNCI 11708, 3 specimens, rio Curralinho, Piraquara, state of Paraná; MHNCI 11709, 13 specimens, rio Piraquara, Piraquara, state of Paraná; MHNCI 11710, 1 specimen, rio Mergulhão, Antonina, state of Paraná; MHNCI 11711, 1 specimen, rio Água Verde, Canoinhas, state of Santa Catarina; MHNCI 11712, 20 specimens, ribeirão Caixa d'Água, Itariri, state of São Paulo. DNA was isolated from muscle samples using the methodology provided by Sambrook & Russell (2001).

Forty-five primers (Operon Technologies series) were primarily tested in order to identify those with good amplification performances in terms of molecular variation and band clearness. Of those with good performances, the best six primers were selected (Table 1) focusing also for minimizing lab procedure efforts for reaching analytical robustness such as suggested by Telles *et al.* (2001) and Hollingsworth & Ennos (2004). RAPD reactions were performed at least twice in different days and with different brand reagents in a final volume of 15µl using a *Personal Eppendorf* termocicler following Almeida *et al.* (2001). The reactions were performed with an initial denaturation step of 4-min at 92° C, followed by more 40 cycles of 40 s of denaturation at 92° C, 1 min 30 s for annealing at 40° C, 2 min for extension at 72° C, and a final elongation step of 5min at 72° C. The PCR products were resolved by electrophoresis in 1.4% agarose gels immersed in TBE buffer and stained with ethidium bromide. After runs of approximately 4/5 h (80 V), the results were documented using an image capture system (Vilber Lourmat). The molecular weight of the fragments was estimated with a molecular marker ladder of 100bp (Invitrogen Inc.).

TABLE1. Primer sequences used in the present study.

Primers code	Sequence
OPA20	5' GTTGCGATCC 3'
OPAM07	5' AACCGCGGCA 3'
OPAM13	5' CACGGCACAA 3'
OPW5	5' GGCGGATAAG 3'
OPX04	5' CCGTACCGA 3'
OPX18	5' GACTAGGTGG 3'

The obtained results were converted into a binary matrix in which (0) was attributed to absence of band and (1) to its presence. Bayesian inference was performed with 1,000,000 generations of 4 Markov chains, and the posterior probabilities of branches were obtained computing the whole set of generations with *Mimagoniates lateralis* as outgroup. Isolation by distance among sampled regions was verified by Sperman correlation analysis (Statistica v. 6.0; Statsoft Inc.) comprising comparisons among the average genetic distances with the geographic distances (kms) estimated directly in a map as a straight line between sampled areas. The genetic distances were obtained by performing a Neighbor-Joining analysis (Saitou & Nei, 1987) using Paup* v.4.0b10 (Swofford, 2000).

Mapping of the Glandulocaudinae distribution in association with topographic and tectonics features were performed based on GIS databases (Hearn *et al.*, 2000; Bizzi *et al.*, 2001) in which layers of data were pre-

pared and added to the original database by direct geo-referencing of tectonic and geological maps available on literature for the area (Saadi, 1993; Saadi, *et al.*, 2002; Riccomini *et al.*, 2001; Berrocal & Fernandes, 1996).

Systematic background

Menezes & Weitzman (1990) performed a phylogenetic analysis of the Glandulocaudinae (former Glandulocaudini, then consisting of the genera *Glandulocauda* and *Mimagoniates*) primarily based on morphological data of the caudal organ, a complex structure in which modified caudal-fin scales, rays and associated hypertrophied glandular tissue are involved. Later on, Weitzman & Menezes (1998), included both genera in an overall analysis of representatives of all genera then assigned to the Glandulocaudinae, corroborating the monophyly of the group composed by both genera.

Castro *et al.* (2003) described *Lophiobrycon weitzmani* and reanalyzed Weitzman & Menezes's (1998) data base including the new genus as sister-group of *Glandulocauda* and *Mimagoniates*. Castro *et al.* (2003) interpreted the condition of the caudal-fin scales and associated caudal-fin rays in *Lophiobrycon* as relatively plesiomorphic (Fig. 1).

Recently, Weitzman *et al.* (2005) provided new evidence for the monophyly of *Lophiobrycon*, *Glandulocauda* and *Mimagoniates*. According to these authors, the subfamily Glandulocaudinae as previously recognized does not represent a natural group. *Lophiobrycon*, *Glandulocauda* and *Mimagoniates* differ from the remaining taxa previously included within the Glandulocaudinae by having the hypertrophied caudal-fin gland derived from modified "club cells", not the modified mucus cells reported for *Corynopoma riisei* and presumably present in other tribes of the former Glandulocaudinae. Also, Weitzman *et al.* (2005) pointed out that the derived scales and fin rays of the Stevardiinae and the restricted Glandulocaudinae were not homologous. These authors, thus, limited Glandulocaudinae to the genera *Lophiobrycon*, *Glandulocauda* and *Mimagoniates* and allocated the remaining taxa to the subfamily Stevardiinae.

Weitzman *et al.* (2005) also concluded that the caudal-fin scale arrangement in *Lophiobrycon* represents a plesiomorphic condition relatively to the other two genera. The authors confirmed the phylogenetic position of *Lophiobrycon* proposed by Castro *et al.* (2003) as the sister group of *Glandulocauda* and *Mimagoniates*. In Figure 2 we synthesize the current hypothesis of the Glandulocaudinae phylogenetic relationships as hypothesized by these previous contributions on the systematics of the group.

Geological background

The geological structure of the South American continent can be synthetically described as a Gondwanaland fragment which includes a set of five Arquean cratons (Amazonian, São Francisco, Rio de la Plata, São Luiz, and Luiz Alves) (Cordani *et al.*, 2000) surrounded by ancient Pre-Cambrian orogenic belts (both consisting of the crystalline shields) and associated sedimentary cover that form the South American Platform. The South American Platform interacts with the Nazca Plate to the west, creating the Andean orogenic belt.

Most of the South American platform rocky basement resulted from a set of paleo-continental amalgamation developed in response to the convergence of the São Francisco, Congo, and the Rio de La Plata cratons, during the Neoproterozoic to Early Paleozoic (between 0.9 to 0.5 Ga) originating the Eastern Gondwana supercontinent in the so-called Brazilian/Pan African orogenic cycle (Trouw *et al.*, 2000; Almeida *et al.*, 2000).

Within the Brazilian Platform, shields are, thus, constituted by rocks of the cratons and neighboring ancient orogenic belts resulted from the Brazilian/Pan African cycle. These sets of Precambrian rocks present

a structural inheritance of its collisional origin, along with one of the most conspicuous is the presence of a complex system of Precambrian rift and shear zones. This complex system of ancient rifts behave as weakness zones, more susceptible to undergo deformations due to subsequent tectonic reactivation events (Saadi, 1993 Saadi *et al.*, 2002, Riccomini & Assumpção, 1999). Since the Gondwanaland break-up (culminated approximately 90 M.Y.) reactivations along this set of Precambrian fracture zones have been driven the tectonic behavior of the entire platform. This is based on the concept of resurgent tectonics (Hasui, 1990 apud Suguio, 2001), in which ancient structures (faults and shear zones) become reactivated subsequently by more recent tectonic events. The evolution of the continental paleodrainage and relief is strongly controlled by resurgent tectonics (Saadi *et al.*, 2005).

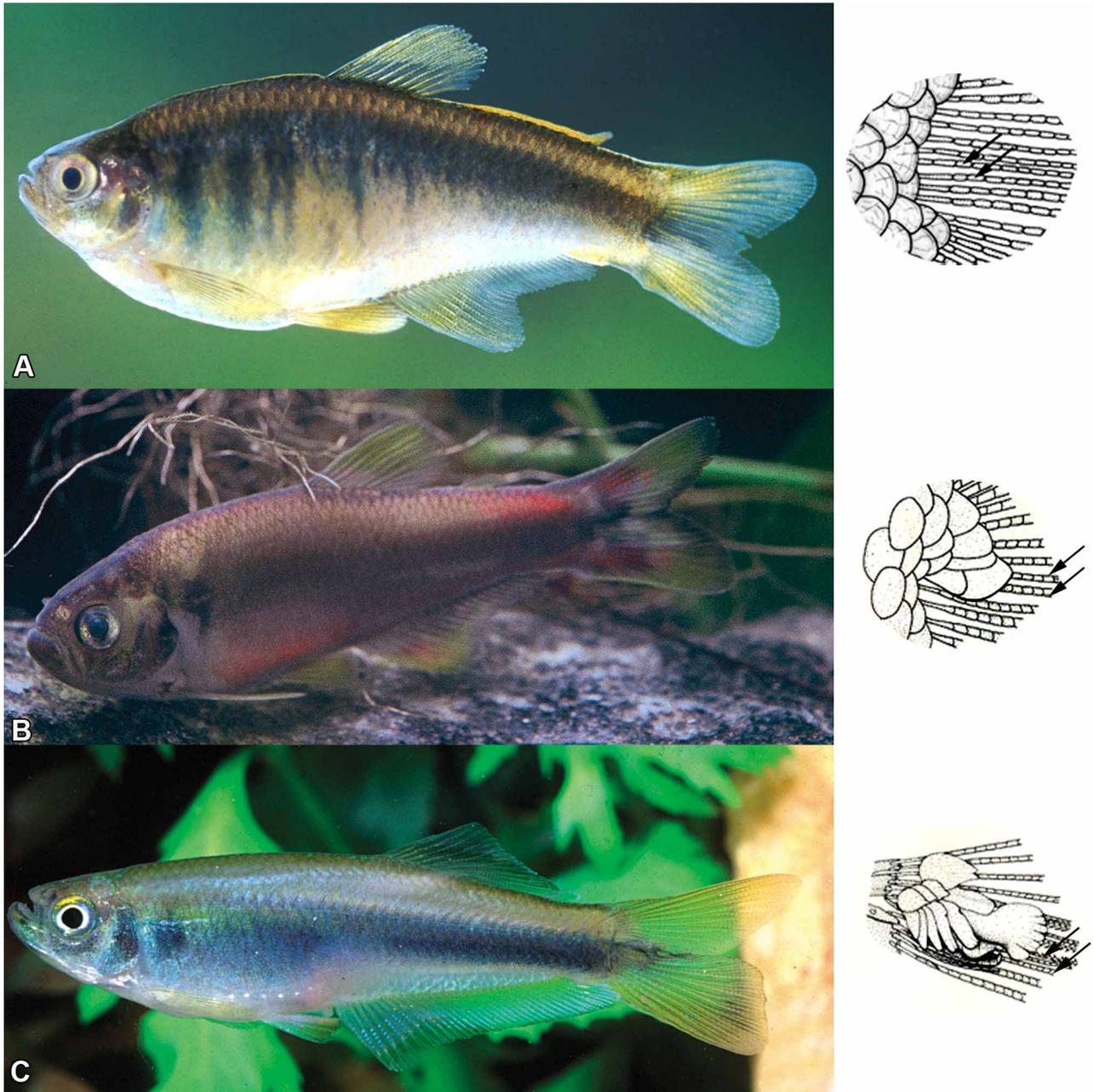
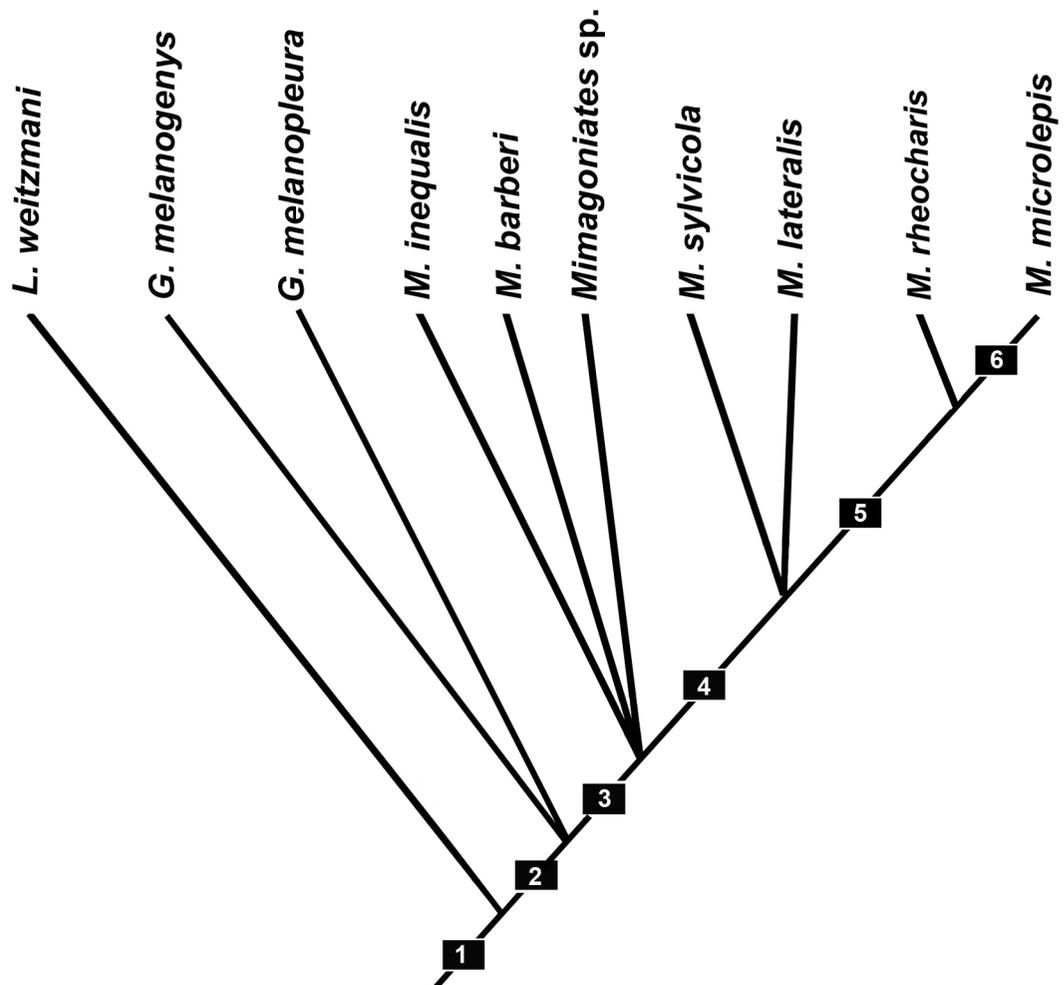


FIGURE 1. Representatives of the Glandulocaudinae and their caudal organs. A) *Lophiobrycon weitzmani*; paratype , LIRP 4338, photo by R.M.C. Castro; B) *Glandulocauda melanogenys*, uncatalogued specimens, collected at Estação Biológica de Boracéia, Rio Guaratuba basin, photo by J.C. Nolasco C) *Mimagoniates microlepis*, photo by R.L. Corte. Arrows indicate the caudal-fin rays 11 and 12. (modified from Menezes & Weitzman, 1990 and Castro *et al.* 2003).



1- Caudal-gland cells consisting on specialized club cells. Modified caudal-fin squamation derived from dorsal-fin caudal lobe.

2- Modified caudal-fin squamation well-developed, extending over the caudal-fin membrane along region of glandular tissue.

3- Caudal-fin ray pump present. Gland cells concentrated around pump opening.

4- Caudal-fin pump chamber well developed.

5- Hooks at least on caudal-fin 10-11.

6- Hooks strongly developed on caudal-fin rays 8-12.

FIGURE 2. Cladogram showing the phylogenetic relationship of the Glandulocaudinae.

Along the distributional range encompassed by the Glandulocaudinae (Fig.3), which includes the upper Paraná basin in the Brazilian highlands and adjacent Paraguay and coastal rivers lowlands, this system of rifted zones played a major role in the landscape evolution through time. Tectonic reactivations along these ancient geological structures since the break-up of the Gondwanaland have been extensively reported in the specialized geological scientific literature.

In the following sections, we associate the main events of the South American tectonic history acting at the southern portion of the continent in a biogeographic reconstruction of the Glandulocaudinae. Our reconstruction considers the recent advances on intra-plate tectonics and the known tectonic behavior of the South American continent.

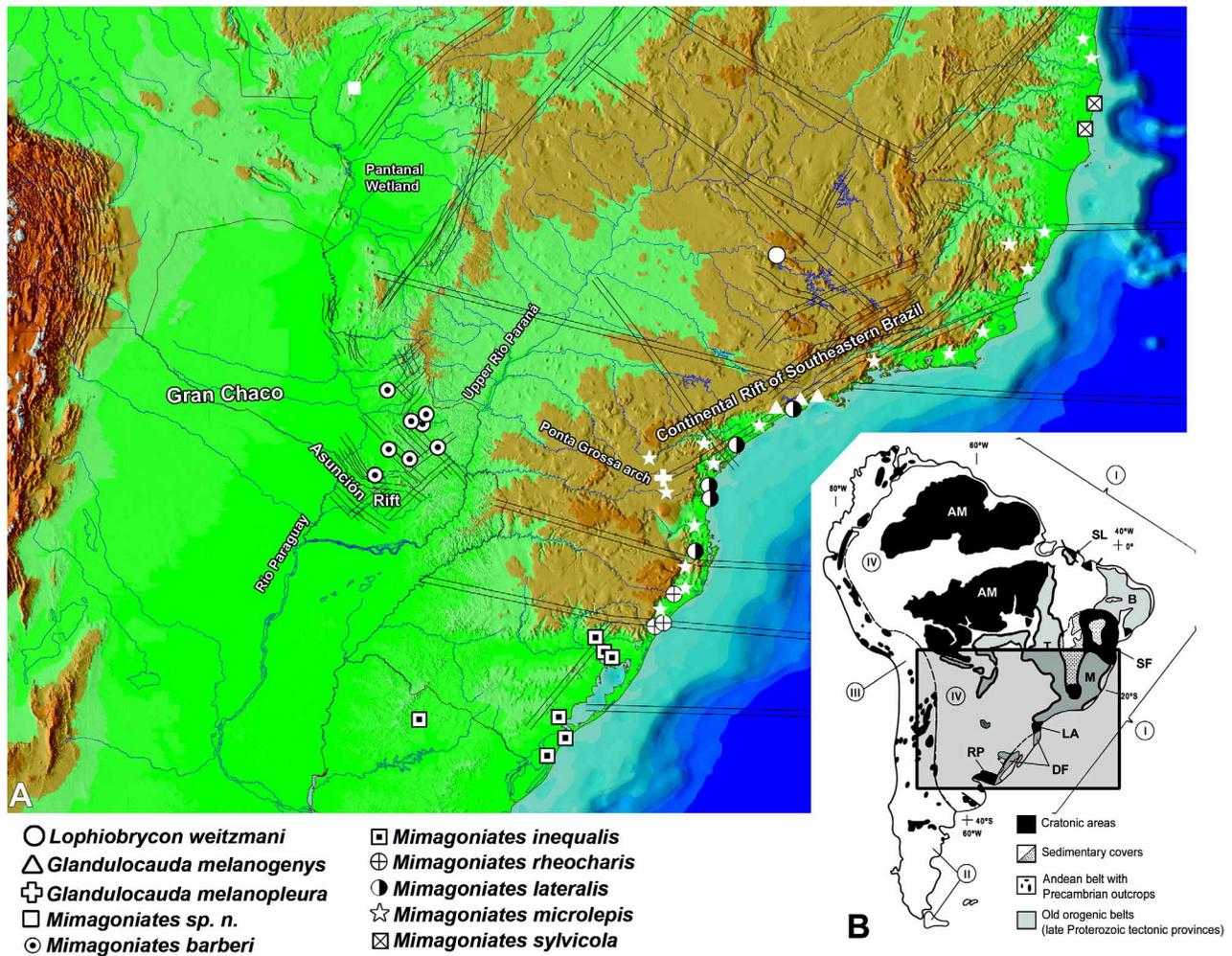


FIGURE 3. A) Distribution of the Glandulocaudinae and the topographic and tectonic features of SE South America. Double lines corresponds to the main axes of Quaternary tectonics in the area (according to Saadi, 1993; Saadi *et al.*, 2002 and Riccomini *et al.* 2001) B) The same area showed within the context of major tectonic provinces of South American Platform. I – South American Platform; II – Patagonian massif; III – Andean orogenic belt; IV – foreland basins; AM = Amazon craton; SL = São Luis craton; SF = São Francisco craton; LA = Luiz Alves craton; RP = Rio de la Plata craton; B = Borborema province; T = Tocantins province; M = Mantiqueira province; DF = Dom Feliciano belt. (Modified from Cordani *et al.*, 2000).

Results

Biogeographic history

The upper Paraná highlands and the initial diversification of the Glandulocaudinae. An area cladogram based on the phylogeny of the Glandulocaudinae (Fig.4) indicates that initial diversification of the group took place at the upper rio Paraná basin. The area cladogram also shows a pattern of fragmentations from this

ancient drainage area of the Brazilian crystalline shield into lineages that evolved in the neighboring lowland, including the Paraguay basin and the coastal drainages of SE South America, where the group become more widespread and diversified.

Lophiobrycon weitzmani, the less derived member of the group, is endemic to headwater streams in the middle stretch of the rio Grande drainage in the upper rio Paraná basin. The hypothesis that the present day upper portion of the Paraná Basin is an ancient biogeographic area is strongly supported by geological evidences. As proposed by Cox (1989) discussed by Potter (1997) and mentioned by Ribeiro (2006), the present configuration of the Paraná basin is a heritage of the main tectonic processes of the Gondwanaland break-up. The uplift of large megadomes in the center of the main Afro-Brazilian rift axis configured most of the present day shape of the Upper Paraná, upper São Francisco and Uruguay rivers basins. The upper portion of the rio Paraná basin probably had its major shape since the Cretaceous. Drainage readjustments have occurred, of course, but probably acting mostly at the eastern and western basin margins due to more recent tectonic events, which will be discussed later in this paper. We postulate, according to the current phylogenetic information, that the ancient Brazilian Crystalline Shield highland drained by the Paleo upper Paraná basin is the local of initial diversification of the Glandulocaudinae.

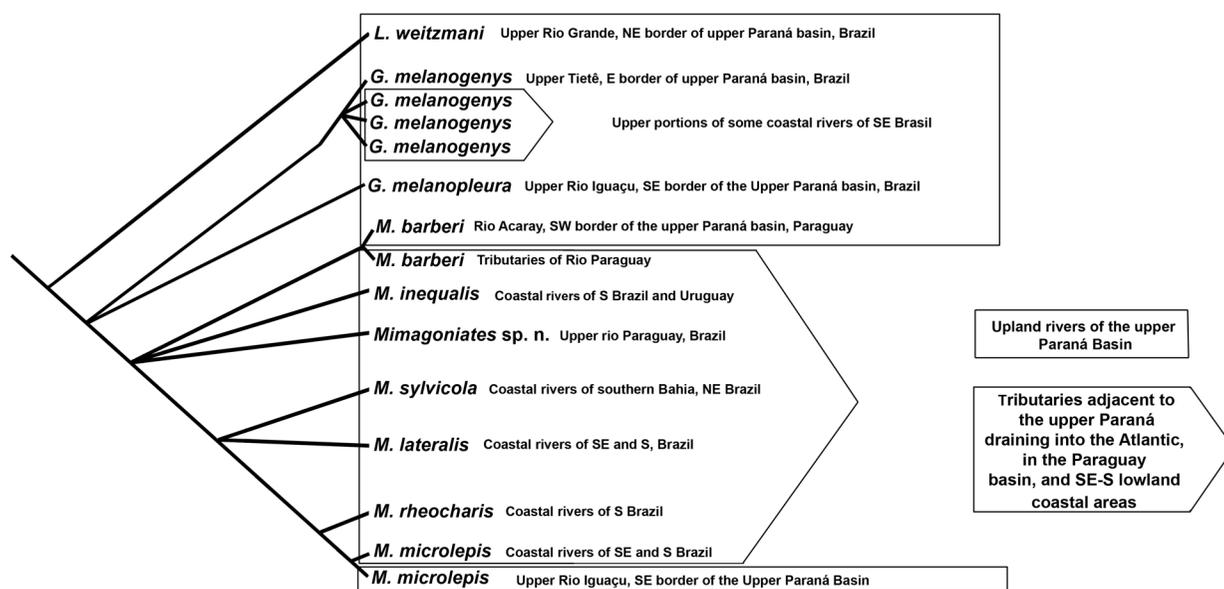


FIGURE 4. Area cladogram based on the current phylogeny of the Glandulocaudinae.

The second most plesiomorphic genus is *Glandulocauda*. *G. melanopleura* is only known from the upper Rio Iguaçu, (a major tributary of the Rio Paraná basin), and this distribution is congruent with the hypothesis of initial diversification of the group in the upper Paraná. Despite draining to the lower stretch of the rio Paraná, the upper portion of the Iguaçu basin are clearly historically related the upper Paraná basin. Such biogeographic relationships is expressed by conspicuous faunal similarities between the upper Iguaçu and adjoining areas, such as the Paranapanema (tributary of the upper Paraná) and Ribeira de Iguape (a large coastal river of SE-S Brazil) (Ribeiro, 2006). Such biogeographic relationships were hypothesized as being the result of intense river captures among neighboring areas, driven by the tectonic activity of the Ponta Grossa Arch along the Cenozoic, which acts as divide between such basins (Ribeiro, 2006).

Tectonic reactivations along the eastern border of the upper Paraná and the history of *Glandulocauda melanogenys*. *Glandulocauda melanogenys*, on the other hand, is slightly more widespread and its distributional pattern requires additional explanation. Populations of *Glandulocauda melanogenys* underwent secondary trans-basin vicariance and this species is also reported from coastal rivers adjoining the upper Paraná: upper portions of the coastal Rio Guaratuba, Itatinga, and Ribeira de Iguape in SE Brazil. Ribeiro *et*

al. (2006) demonstrate how the Quaternary tectonic activity of ancient faults located at the eastern border of the Paraná basin caused the capture of an ancient upper stretch of the Rio Tietê and its ichthyofauna, including *Glandulocauda melanogenys* by the River Guaratuba, a small coastal river of southeastern Brazil. The fish fauna of the upper rio Guaratuba is the same as that of the adjoining upper Rio Tietê of the Paraná basin and different from the typical fish fauna of Brazilian coastal drainages (Ribeiro *et al.*, 2006). A morphotectonic analysis of the upper rio Guaratuba basin carried out by the authors of this paper demonstrate how the upper rio Guaratuba, an ancient tributary of the Paraná basin, was captured and became a coastal river.

The system of ancient faults (mostly Pre-Cambrian in age) present at the eastern border of the Paraná Basin controlled, during the Cenozoic, the installation and deformation of the Continental Rift of Southeastern Brazil (CRSB) that includes a succession of taphrogenic basins or grabens (Riccomini *et al.*, 2004). This large fault system has been identified by geologists as the region with the most pronounced neotectonic activity in Brazil (Riccomini & Assumpção, 1999; Saadi, *et al.* 2005). This mega rift system extending from the Brazilian states of Santa Catarina in the south, to Rio de Janeiro, to the north, underwent deformation periodically due to tectonic reactivation (Riccomini *et al.*, 2004). As exemplified by the rio Guaratuba, several ancient headwater portions of the eastern margin of the Paraná Basin have been captured and became part of direct Atlantic tributaries (Ribeiro, 2006). Two other populations of *Glandulocauda melanogenys* were recently discovered. One in the upper portions of rio Ribeira de Iguape at Juquiá, São Paulo and another one in rio Itatinga, a tributary of rio Itapanhaú in Parque das Neblinas, a biological reserve, draining directly to the Atlantic Ocean (Serra *et al.*, 2007). The upper portions of the two rivers are captured stretches that primitively drained to the Paraná basin before the tectonic reactivation of the CRSB that caused drainage rearrangements in the area. The capture of the Rio Guaratuba was inferred by Ribeiro *et al.* (2006) to be of Late Pleistocene-Holocene in age which coincides with the last phases of tectonic reactivations of the CRSB (Riccomini *et al.*, 2004). Probably, the same reactivation event of the CRSB is the causal mechanism that promoted cladogenesis between the other populations of *Glandulocauda melanogenys* from their sister-groups at the eastern border of the Paraná Basin.

Plesiomorphic Glandulocaudinae lineages as relicts. Despite evolving initially in the upper Paraná, representatives of the two basalmost genera do not display a widespread distribution along the basin. The distribution ranges of *Lophiobrycon* and *Glandulocauda* are suggestive of being relict of a previously more widespread ancestor from the upper rio Paraná. *Lophiobrycon weitzmani* and the two known *Glandulocauda* species are from with high altitudes associated with first and second order clear water streams. Such kinds of environmental requirements could be a causal explanation of the present day relict disjoint distributions of *Lophiobrycon weitzmani*, *Glandulocauda melanogenys* and *Glandulocauda melanopleura*, at the edges of the upper Paraná Basin, along Serra da Canastra and Serra do Mar stretches respectively.

The upper rio Paraná basin is an area under major anthropogenic activity, including urbanization and agricultural practices. Recent collecting efforts aiming at an inventory of the ichthyofauna along the upper Paraná basin (Castro *et al.*, 2003; Castro *et al.*, 2004; Castro *et al.*, 2005) did not produce additional records of *Lophiobrycon* and *Glandulocauda* species and attempts to collect again *Lophiobrycon weitzmani* in the type locality were fruitless (ACR, personal observation). The rate of human interference on first to second order streams in the area where *Lophiobrycon* and *Glandulocauda* occur certainly make the species of these genera endangered.

Reaching lowlands: the origin of the neighboring drainages around the upper Paraná highlands. *Mimagoniates* is the most speciose genus within the Glandulocaudinae. In a basal lineage there are a set of species that are reported from outside the limits of the upper Paraná, where we speculate the initial evolution of the Glandulocaudinae might have taken place. This set of species, (*M. inequalis*, from the coastal Lagoa dos Patos and Lagoa Mirim; *M. barberi* from tributaries of rio Paraguay; and *Mimagoniates sp.* from the upper rio Paraguay) appear in a basal polytomy, with limited possibilities of area interrelationships inferences. Cladogenesis between these lineages are probably of great antiquity (we speculate at least 2.5 MY; see discus-

sion below), and an historical reconstruction is probably of great complexity due to the mega geomorphologic and tectonic events have acted in this region since the Tertiary: the Andean orogeny, local neotectonic reactivations and marine transgressions.

The Paraguay river basin is an area under major influence of the Andean orogeny that has taken place along the western margin of South America from the Cretaceous to the present (McQuarrie *et al.*, 2005; Uba *et al.*, 2006). Since the Miocene, the influences of the Andean uplift in this region have been quite pronounced, controlling the long-term evolution of the Chaco-Pantanal foreland basins (Assine, 2004; Uba *et al.*, 2006). Foreland basin systems develop as a result of flexural warping of the lithosphere in response to supralithospheric and sublithospheric orogenic wedging. Lithospheric flexure under static loads generates down-bending flexure proximal to the orogen, which migrates as the load advances. This system of interconnected foreland basin, the Chaco and Pantanal, formed during the late Cenozoic in response to Nazca-South American plate convergence and its related eastward interaction with the Brazilian shield (Uba *et al.*, 2006). There are evidences, according to Assine (2004) that, during the Cretaceous and afterwards, the western border of the upper Paraná basin extended westward much over the longitudes of the present day Pantanal Wetland. The area represented the natural extension of present day Brazilian crystalline shield into the W-SW, acting as divides between drainages of the upper Paraná and the Chaco basin. During the least compressive event along the Andean belt (~ 2.5 MY.) flexural subsidence associated with fault reactivation on its borders originated the Pantanal Wetland (Assine, 2004) and configure the present day divide between the western margins of the upper Paraná and upper Paraguay. The occurrence of *Mimagoniates* sp., from a tributary of the upper Paraguay should be associated with the major hydrographic change represented by the origin of the Pantanal Wetland foreland basin that captured the western tributaries of the upper Paraná to its tectonically active depression.

Concomitantly, the eastward migration of the Chaco basin's depocenter since the Miocene (McQuarrie *et al.*, 2005; Uba *et al.*, 2006) in association with tectonic reactivations along the divides of both basins probably also provide drainage captures due to base level changes or direct deviation of streams, from the SW margin of the upper Paraná to lower Paraguay basin.

The occurrence of *M. barberi* in both the SW border of the upper Paraná as well as in the lower portions of the Paraguay basin suggests that invasion of the Paraguay lowlands might have occurred, indeed, via fragmentation of populations along the W-SW border of the upper Paraná. The region of the eastern Paraguay, from where *Mimagoniates barberi* is known is an area of major Cenozoic tectonic activity. Eastern Paraguay lies in an intercratonic region which includes the westernmost side of the Paraná Basin of Brasil. It is bounded by an anticlinal structure, the Asuncion Arch, separating the Paraná Basin (East) from the Gran Chaco Basin (West) (Antonini *et al.*, 2005). A conspicuous tectonic feature, the Asunción rift, developed in this region thanks to Cenozoic reactivation of a system of NW-SE trending faults (Riccomini *et al.*, 2001). Major geomorphologic features such as the Yparacarái Lake developed under the tectonic control of the Asunción rift (Riccomini *et al.*, 2001). These systems of rifts are today tectonically and seismically active (Berrocal & Fernandes, 1996) and such activity certainly promote constant drainage rearrangements between the upper Paraná basin and the neighboring eastern Paraguay and explain the fragmentation of populations of *M. barberi* in both upper Paraná and tributaries of the Paraguay basin.

Without a resolved phylogeny within the species of *Mimagoniates* from the Paraguay basin, it is not possible to speculate about the sequence of cladogenetic events there. Hypothesis on the occurrence of *Mimagoniates* on the Paraguay basin as being a single or a multiple event of peripheral fragmentation from populations of the Paraná basin needs resolution of the phylogenetic relationships of basal *Mimagoniates* lineages.

Diversification along Brazilian coastal drainages and the occurrence of *Mimagoniates microlepis* in the upper Iguazu and upper Tibagi. Most of the *Mimagoniates* species are found in restricted stretches along the coastal area ranging from southern Bahia to Uruguay. *M. sylvicola* is so far known only from south-

ern Bahia, *M. lateralis* is confined to the area between Santos, São Paulo and Santa Catarina, *M. rheocharis* occurs from Santa Catarina to northern Rio Grande do Sul and *M. inequalis* is found in the rio Guaíba basin and a few streams in coastal Uruguay. *Mimagoniates microlepis* is the most widespread species, occurring from southern Bahia to northern Rio Grande do Sul and additionally also occurs in the upper Iguaçú and Tibagi rivers (Santana *et al.* 2006), SE border of the upper Paraná basin.

Weitzman *et al.* (1988) and Menezes & Weitzman (1990) discuss the distributional patterns of this set of species and concluded that sea level fluctuations of the late Pleistocene could explain the dispersion of a common ancestor between potentially connected coastal rivers along the emerged continental platform. The rise of sea level thus, promoted isolation of these dispersed populations in the upper stretches of these coastal rivers, which became isolated and speciation occurred. Within the discussion of Weitzman *et al.* (1988) and Menezes e Weitzman (1990) the pattern of distribution of *M. microlepis*, the most widespread species, occurring also in the upper Rio Iguaçú, an upland river from the Rio Paraná basin, is the most intriguing. It was hypothesized that the two isolated populations of *M. microlepis* could be explained by river capture, but the authors were cautious about this possibility and also suggested the possibility of introduction by man as an alternative explanation. Indeed, the two populations of *M. microlepis* are isolated by high scarps typical of the precipitous front of Serra do Mar in S Brazil.

Ribeiro (2006) discussed the presence of *Mimagoniates microlepis* in the upland rivers of the rio Iguaçú and concluded that this occurrence is an evidence that diversification of *Mimagoniates* species along coastal drainages could not be causally related to the sea level changes of the late Pleistocene, as previously proposed by Weitzman *et al.* (1988). The reason for such conclusion is that, from the late Pleistocene to the present, the physiography of the Serra do Mar coastal range was exactly the same as observed today. The degree of tectonic uplift necessary to send back to the upland a faunal component once isolated in lowland coastal rivers are unlikely to occur if we consider the present stepped physiography of Serra do Mar of southeastern and south Brazil represented by abrupt scarps. According to Ribeiro (2006) the tectonic activity in the Ponta Grossa resulted in captures from coastal rivers to upland areas in a paleogeographic scenario that was anterior to sea level changes of the late Pleistocene. Our results of molecular analysis presented herein add new support to this hypothesis.

According to the topology of the Bayesian molecular phylogeny (Fig. 5) an additional historical event may be related to the rise of the lineage inhabiting the Iguaçú headwaters. In this analysis several highly supported clades may be identified which are probably associated with true vicariant process occurring along coastal drainages, especially between the three main sampled areas: coastal plains of the states of São Paulo, Paraná and Santa Catarina (Figure 5). These areas may correspond to ancient coastal sub basins draining an exposed continental Platform presently submerged. According to Justus (1990), there is, in the offshore area of the Brazilian state of Rio Grande do Sul a huge fluvial fan, the Rio Grande fan, composed of about 900 m of sediments from upper Miocene to lower Pliocene. The presence of the Rio Grande fan suggests a large period of time in which the Brazilian continental platform was exposed. There are also, evidences of complex Quaternary submersed fluvial systems along the southeastern and southern Brazilian continental platform (Abreu & Calliari, 2005). Speciation along coastal drainages, thus, did not necessarily occur associated with sea level changes of the late Pleistocene. If the present distribution pattern presented by the more plesiomorphic *Mimagoniates* lineages such as *Mimagoniates* sp. and *M. barberi* are related to the tectonic evolution of the Chaco-Pantanal foreland basin, a minimum age of about 2.5 MY can be attributed to *Mimagoniates*. This estimated minimum age provide an alternative scenario for the diversification of the group and provide a much longer period of time in which diversification along the coastal drainages took place.

Additional data from genetic distances (GTR – General Time Reversible molecular model) contrasted with geographic distances, demonstrate that there was no statistical support for putative isolation by distance (Figures 5 and 6), suggesting that the present day geographic configuration is not relevant to explain phylogenetic patterns, which are, more likely, causally related to paleogeographic cladogenetic events.

With respect to the discussion above, the molecular intraspecific phylogeny showed herein suggests that the diversification of *Mimagoniates microlepis* within the Iguaçú basin seems to have occurred during a later historical event. In terms of temporal colonization, based on the obtained results it seems that the expansion of the species along the study area has occurred from North to South and then reaching the Iguaçú headwaters.

Ribeiro (2006) reviewed the geological and tectonic histories of the Brazilian coastal region and discusses in detail the upper Iguaçú area. According to Ribeiro (2006), ichthyologists have been identifying for a long time, the presence of a mixed ichthyofauna between coastal rivers and two main areas of the adjacent upland Paraná Basin: the upper rio Tietê and the upper Iguaçú.

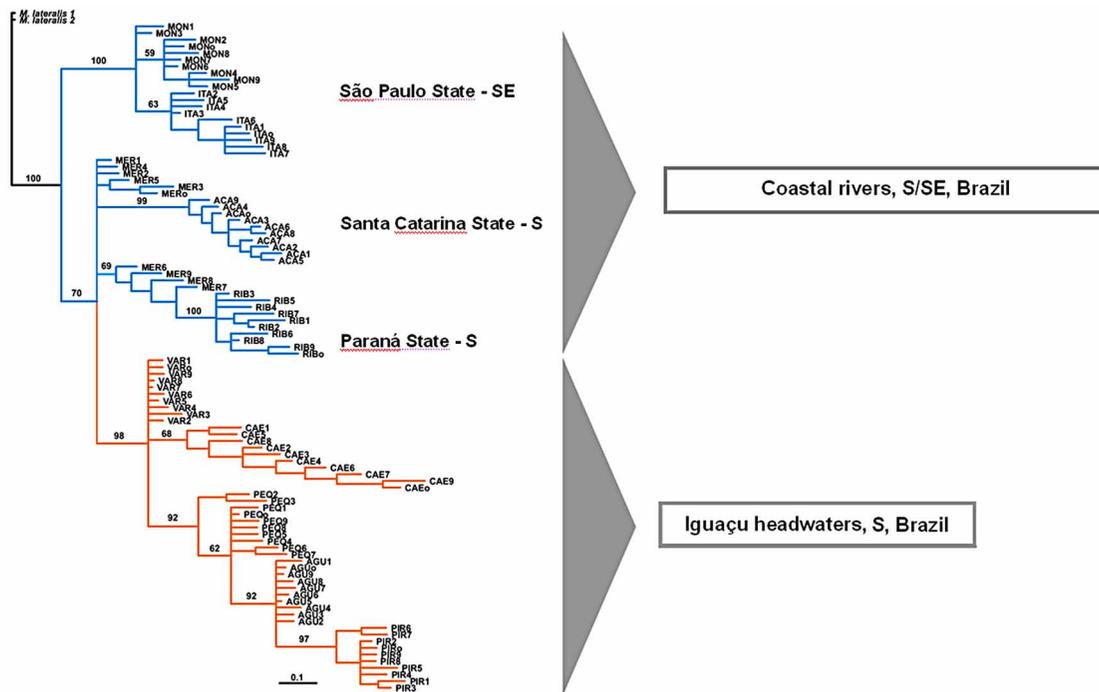


FIGURE 5. Bayesian cladogram showing the phylogenetic relationships among populations of *Mimagoniates microlepis* from SE and S Brazil. Orange branches represent samples from rio Iguaçú basin. Blue branches represent streams from the coastal area. Numbers in branches indicates the posterior probabilities of the clusterings for GTR distances, obtained by Monte Carlo Markov Chains. Sampled localities are the follow: PIR= rio Piraquara, Piraquara, state of Paraná; CAE= rio Caerana, Piraquara, state of Paraná; PEQ= rio Pequeno, São José dos Pinhais, state of Paraná; VAR= rio da Várzea, Lapa, state of Paraná; AGU= rio Água Verde, Canoinhas, state of Santa Catarina; MER= rio Mergulhão, Antonina, state of Paraná; RIB= rio Ribeirão, Paranaguá, state of Paraná; MON= rio Mongaguá, Mongaguá, state of São Paulo; ITA= rio Caixa d'Água, Itariri, state of São Paulo; ACA= tributary of rio Acaraí, São Francisco do Sul, state of Santa Catarina. For each locality, 10 specimens were sampled and are indicated by numbers 0-9.

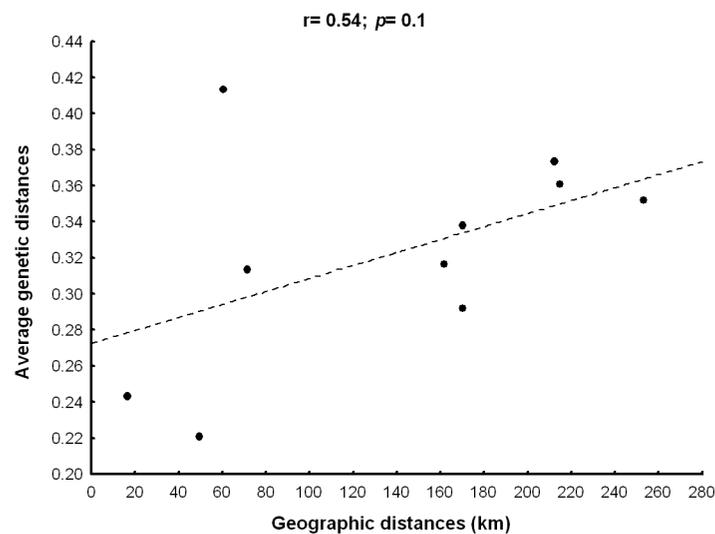


FIGURE 6. Spermann correlation between average genetic distances (GTR) and geographic distances showing no statistical support among variables.

The area corresponding to the divides between the Upper Iguacú, Ribeira de Iguape and Paranapanema, headwaters, correspond to a prominent geological feature: the Ponta Grossa Arch. The arch consists of an uplift of the crystalline basement along the southeastern portion of the Paraná Basin (Petri & Fulfaro, 1983). The Ponta Grossa Arch displays an intricate system of deep faults and fractures that was supposed to be the main conduit of the immense Cretaceous flow of lava over the Paraná Basin known as Serra Geral Formation, which left a large system of dykes of intrusive magma. Some authors have pointed out that the Ponta Grossa Arch has a general tendency to uplift (Almeida & Carneiro, 1998) and underwent tectonic activity during the Cenozoic (Almeida & Carneiro, 1998). The tectonic activity of the Ponta Grossa Arch could have resulted in a particularly accelerated fluvial dynamic events between adjacent drainage systems, accelerating faunal exchange between them. Vertical movements between faulted blocks and erosive evolution of rivers along such rifts promote mixing between adjacent drainages, and likely explain the faunal exchanges that occurred between the coastal drainages such as the Ribeira de Iguape, and the uplands Iguaçú and Paranapanema rivers.

Recently, Sant'Anna *et al.* (2006) reported the occurrence of *Mimagoniates microlepis* in the upper rio Tibagi, a left tributary of the rio Paranapanema, upper Paraná drainage. This new record corroborates the hypothesis of intense faunal exchange between drainages in the region of the Ponta Grossa Arch. *Mimagoniates microlepis* thus, occurred secondarily in the upper Rio Iguaçú as well as in the upper Rio Tibagi throughout tectonic uplift in the Ponta Grossa arch that promote capture from ancient coastal rivers into the upper Paraná basin. This hypothesis is strongly corroborated by the genetic conectiveness results shown herein (Figure 5) that conclude that populations of *M. microlepis* from the upper Iguaçú is a highly supported monophyletic lineage, more closely related to populations from coastal rivers of Paraná and Santa Catarina, S Brazil. The new record of *M. microlepis* mentioned by Sant'Anna *et al.* (2006), on the other hand, suggests that this population could be the sister group of that from the Iguaçú or from other unidentified coastal river, probably the adjacent Ribeira de Iguape which are very spatially close to Tibagi. The occurrence of *Mimagoniates microlepis* in both Upper Iguaçú and Tibagi might be, thus, independent events of faunal interchange between the coastal rivers and the upland area. Phylogeographic studies including the population of *Mimagoniates microlepis* from the upper Tibagi are necessary for testing this hypothesis.

Concluding remarks and questions to future investigation. The Glandulocaudinae, a group of the highly diversified Neotropical fish fauna, has fascinated ichthyologists through time, for both scientific and aesthetical reasons. The degree of morphological and behavioral specialization shared by these fishes are stimulating for evolutionary research. The distributional patterns of glandulocaudin fishes are also of great value for understanding the main biogeographic patterns of freshwater fishes in the southern portion of the South American continent. We conclude that initial diversification of the group occurred in the Brazilian Highlands drained by the paleo-upper Paraná Basin. Present day diversification of the group is tentatively explained by cladogenetic events associated with the main geological events that took place in the South American continent that led to peripheral fragmentation of ancestral populations at the edges of the Paleo-upper Paraná : 1) The uplift of the Andean cordilleras and its tectonic influences along the western margin of the Upper Paraná basin throughout the evolutionary history of the Chaco-Pantanal foreland basins including the tectonic history of the Asunción Rift in Eastern Paraguay; 2) the Quaternary tectonic history of the eastern border of the Upper Paraná basin, an area under the influence of the Continental Rift of Southeastern Brazil and its tectonic reactivation events; 3) Sea level changes of the late Pleistocene and the possibility of faunal dispersion along the Brazilian coastal river along the exposed portions of the continental platform; and 4) tectonic activity at the Ponta Grossa Arch, an area under recent tectonic uplift that likely promoted mixing between coastal rivers and adjacent upland eastern tributaries of the upper rio Paraná.

Future investigations on Glandulocaudinae systematics may help to clarify the phylogenetic relationships of basal *Mimagoniates* lineages providing useful data for understanding the sequence of fragmentation that led to present day distribution of lowland species. Phylogeographic studies based on mtDNA sequences associated with the most modern analytical tools such as haplotype network and coalescence analysis within *M.*

microlepis and *M. barberi* also provide useful information about the biogeographic history of the populations now occurring in the upper Paraná and the lower Paraguay basins. Finally, future phylogenetic analysis of taxa with similar distributional patterns can provide additional data to support our views, including details of other areas, not encompassed by present day Glandulocaudinae distributional patterns.

Acknowledgments

The authors are financially supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), through grants to NM (Proc. 304576/2006-9) and to ACR (Proc. 140488/2004-9). Support to molecular analyses were provided to RAT by Programa Prodoc/Capes and Finep, Ministries of Education and Science and Technology, Brazilian Federal Government. Collecting permits were issued by Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (processo Ibama 02001.002040/99-61)

Literature cited

- Abreu, J.G.N. & Calliari, J.L. (2005) Paleocanais na plataforma continental interna do Rio Grande do Sul: evidências de uma drenagem fluvial pretérita. *Revista Brasileira de Geofísica*, 23(2), 123–132.
- Almeida, F.S., Fungaro, M.H.P. & Sodr , L.M.K. (2001) RAPD and isoenzyme analysis of genetic variability in three allied species of catfish (Siluriformes: Pimelodidae) from the Tibagi River, Brazil. *Journal of Zoology*, 253, 113–120.
- Almeida, F.F.M. & Carneiro, C.D.R. (1998) Origem e evolu o da Serra do Mar. *Revista Brasileira de Geoci ncias*, 28(2), 135–150.
- Almeida, F.F.M., Brito Neves, B.B. & Carneiro, C.D.R. (2000) The origin and evolution of the South American Platform. *Earth-Science Reviews*, 50(2000), 77–111.
- Antonini, P., Gasparon, M., Comin-Chiaramonti, P. & Gomes, C.B. (2005) Post-Paleozoic magmatism in Eastern Paraguay: Sr-Nd-Pb isotope compositions. pp57–69 In: Comin-Chiaramonti, P. & C. B. Gomes (Eds.) Mesozoic to Cenozoic alkaline magmatism in the Brazilian Platform. Edusp, S o Paulo, 750p.
- Assine, M.L. (2004) A bacia sedimentar do Pantanal Mato-Grossense. Pp. 61–74 In: Mantesso-Neto, V., Bartorelli, A., Carneiro, C.D.R. & Brito-Neves, B.B. (Eds.). Geologia do continente Sul-Americano: Evolu o da obra de Fernando Fl vio Marques de Almeida. S o Paulo, Editora Beca, 673p.
- Berrocal, J. & Fernandes, C.C. (1996) Seismicity in Paraguay and neighboring regions. Pp.57–66 In: Comin-Chiaramonti, P. & Gomes, C.B. (Eds.) Alkaline magmatism in central-eastern Paraguay: relationships with coeval magmatism in Brazil. Edusp, S o Paulo, 458p.
- Bizzi, L.A., Schobbenhaus, C., Gonalves, J.H., Baars, F.J., Delgado, I.M., Abram, M.B., Neto, R.L., Matos, G.M.M. & Santos, J.O.S. (2001) Geology, Tectonics and Mineral Resources of Brazil: *Geographic Information System (GIS) and maps at the 1:2500000 scale*. CPRM, Bras lia, 4 CD-Rom. ISBN: 85-7499-006-X.
- Castro, R.M.C., Ribeiro, A.C., Benine, R.C. & Melo, A.L.A. (2003) *Lophobrycon weitzmani*, a new genus and species of glandulocaudine fish (Characiformes: Characidae) from the rio Grande drainage, upper rio Paran  system, south-eastern Brazil. *Neotropical Ichthyology*, 1(1): 11–20.
- Castro, R.M.C., Casatti, L., Santos, H.F., Ferreira, K.M., Ribeiro, A.C., Benine, R.C., Dardis, G.Z.P., Melo, A.L.A., Stopiglia, R., Abreu, T.X., Bockmann, F.A., Carvalho, M., Gibran, F.Z. & Lima, F.C.T. (2003) Estrutura e composi o da ictiofauna de riachos do Rio Paranapanema, sudeste e sul do Brasil. *Biota Neotropica*, S o Paulo, 3(1):1–31.
- Castro, R.M.C., Casatti, L., Santos, H.F., Melo, A.L.A., Martins, L.S. F., Ferreira, K.M., Gibran, F.Z., Benine, R.C., Carvalho, M., Ribeiro, A. C., Abreu, T. X., Bockmann, F. A., Pelic o, G. Z., Stopiglia, R. & Langeani, F. (2004). Estrutura e composi o da ictiofauna de riachos da bacia do Rio Grande no Estado de S o Paulo, sudeste do Brasil. *Biota Neotropica*, S o Paulo, 4(1), 1–39.
- Castro, R.M.C., Casatti, L., Santos, H.F., Vari, R.P., Melo, A.L.A., Martins, L.S.F., Abreu, T.X., Benine, R.C., Gibran, F. Z., Ribeiro, A.C., Bockmann, F.A., Carvalho, M., Pelic o, G.Z., Ferreira, K.M., Stopiglia, R. & Akama, A. (2005) Structure and composition of the stream ichthyofauna of four tributary rivers of the upper Rio Paran  basin, Brazil. *Ichthyological Exploration of Freshwaters*, M nchen, 16(3), 193–214.
- Cordani, U.G., Sato, K., Teixeira, W., Tassinari, C.C.G. & M.A.S. Basei, M.A.S. (2000) Crustal evolution of the South American platform. Pp. 19–40. In: Cordani, U. G., E. J. Milani, A. Thomaz-Filho, & D. A. Campos (Eds). Tectonic

- evolution of South America. 31st International Geological Congress. Rio de Janeiro, *Academia Brasileira de Ciências, e Departamento Nacional da Produção Mineral (DNPM)*, 856p.
- Cox, K.G. (1989) The role of mantle plumes in the development of continental drainage patterns. *Nature*, 342, 873–876.
- Hearn, P.Jr., Here, T, Schruben, P., Sherrill, D., LaMar, C. & P. Tsushima, (2000) Global GIS Database: Digital Atlas of Central and South America. *U.S. Geological Survey, Digital Data Series DDS-62-A*.
- Hollingsworth, P.M. & Ennos, R.A. (2004). Neighbour joining trees, dominant markers and population genetic structure. *Heredity*, 92, 490–498.
- Hovenkamp, P. (1997) Vicariance events, not areas, should be used in biogeographical analysis. *Cladistics*, 13, 67–79.
- Justus, J.O. (1990) Hidrografia. Pp. 189–218 *In: Mesquita, O.V. (coordenador). Geografia do Brasil, Região Sul. IBGE, Rio de Janeiro, 420 p.*
- Lundberg, J.G., L.G. Marshall, J. Guerrero, B. Horton, M.C.S.L. Malabarba & F. Wesselingh. (1998) The stage for Neotropical fish diversification: A history of tropical South American rivers. Pp 13–48. *In: Malabarba, L.R., R.E. Reis, R.P. Vari, Z.M.S. Lucena & C.A.S. Lucena (Eds.). Phylogeny and classification of Neotropical fishes. Porto Alegre, Edipucrs, 603p*
- McQuarrie, Horton, N., Zandt, B.K., Beck, G.S. & DeCelles, P.G. (2005). Lithospheric evolution of the Andean fold-thrust belt, Bolivia, and the origin of the central Andean plateau. *Tectonophysics*, 399 (2005). 15– 37.
- Menezes, N.A. & Weitzman, S.H. (1990) Two new species of *Mimagoniates* (Teleostei: Characidae: Glandulocaudinae), their phylogeny and biogeography and a key to the glandulocaudinae fishes of Brazil and Paraguay. *Proceeding of the Biological Society of Washington*, 103(2), 380–426.
- Menezes, N.A. & Weitzman, S.H. (in preparation). Systematics of the neotropical fish subfamily Glandulocaudinae (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology*.
- Morrone, J. & Crisci, J.V. (1995) Historical Biogeography: Introduction to Methods. *Annual Review in Ecology and Systematics* 26:373–401.
- Nelson, G. (1985) A decade of challenge the future of biogeography. *Earth Sciences History*, 4(2): 187–196.
- Petri, S. & Fúlvaro, V.J. (1983) Geologia do Brasil. São Paulo, *Edusp*, 631p.
- Potter, P.E. (1997) The Mesozoic and Cenozoic paleodrainage of South America: A natural history. *Journal of South American Earth Sciences*, 10(5–6), 331–344.
- Ribeiro, A.C. (2006) Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotropical Ichthyology*, 4(2), 225–246.
- Ribeiro, A.C., Lima, F.C.T., Riccomini, C. & Menezes, N.A. (2006) Fishes of the Atlantic Rainforest of Boracéia: testimonies of the Quaternary fault reactivation within a Neoproterozoic tectonic province in Southeastern Brazil. *Ichthyological Exploration of Freshwaters*, 17(2), 157–164.
- Riccomini, C., Velázquez, V.F. & Gomes, C.B. (2001) Cenozoic lithospheric faulting in the Asunción Rift, eastern Paraguay. *Journal of South American Earth Sciences* 14:625–630.
- Riccomini, C. & Assumpção, M. (1999). Quaternary tectonics in Brazil. *Episodes*, 22(3), 221–225.
- Riccomini, C.L., Sant’Anna, G. & Ferrari, A.L. (2004) Evolução geológica do rift continental do sudeste do Brasil. Pp. 383–405. *In: Mantesso-Neto, V., Bartorelli, A., Carneiro, C.D.R. & Brito-Neves, B.B (Eds.). Geologia do continente Sul-Americano: Evolução da obra de Fernando Flávio Marques de Almeida. São Paulo, Editora Beca, 673p.*
- Saadi, A. (1993) Neotectônica da plataforma brasileira: esboço e interpretações preliminares. *Geonomos* 1(1):1–15.
- Saadi, A., Machette, M.N., Haller, K.M., Dart, R.L., Bradley, L. & Souza, A.M.P.D. (2002) Map and database of Quaternary faults and lineaments in Brazil. *U.S. Geological Survey, Open-File Report 02-230*. (available at <http://pubs.usgs.gov/of/2002/ofr-02-230>).
- Saadi, A., Bezerra, F. H. R., Costa, R. D., Igreja, H. L. S. & Franzinelli, E. (2005) Neotectônica da Plataforma Brasileira Pp. 211 – 234. *In: Souza, C. R. G., Suguio, K., Oliveira, A. M. S. & Oliveira, P.E. (Eds.). Quaternário do Brasil. Ribeirão Preto, Holos, 378p.*
- Saitou N. & M. Nei, M. (1987) The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, 4, 406–425.
- Sambrook J. & D.W. Russell, D.W. (2001) *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.
- Sant’Anna, J.F.M., Almeida, M.C., Vicari, M.R., Shibatta, O.A., & Artoni, R.F. (2006) Levantamento rápido de peixes em uma lagoa marginal do rio Imbituva na bacia do alto rio Tibagi, Paraná, Brasil. *Publicações da UEPG, Ciências, Biologia e Saúde*, Ponta Grossa, 12 (1): 39–46.
- Serra, J.P., Carvalho, F.R & Langeani, F. (2007). Ictiofauna do rio Itatinga in Parque das Neblinas, Bertioga, Estado de São Paulo: composition and biogeography. *Biota Neotropica*, 7(1), 131–136. Available at <http://www.biotaneotropica.org.br/v7n1/pt/abstract?article+bn01707012007>
- Swofford, D.L. (2000). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods) Version 4.0b4a. *Sinauer Associates*, Sunderland, Massachusetts.
- Suguio, K. (2001) Geologia do Quaternário e mudanças ambientais: (passado + presente = futuro?). *Paulo’s comuni-*

- Telles, M.P.C., Monteiro, M.S.R., Rodrigues, F.M., Soares T.N., Resende, L.V., Amaral, A.G. & Marra, P.R. (2001) Marcadores RAPD na análise de divergência genética entre raças de bovinos e número de locos necessários para a estabilidade da divergência estimada. *Ciência Animal Brasileira*, 2(2), 87–95.
- Torres, R.A., Motta, T.S., Nardino, D.N., Adam, M.L. & Ribeiro, J. (2007) Chromosomes, RAPDs and evolutionary trends of the Neotropical fish *Mimagoniates microlepis* (Teleostei: Characidae: Glandulocaudinae) from coastal and continental regions of the Atlantic forest, Southern Brazil. *Acta Zoologica* 88: (Doi: 10.1111/j.1463-6395.2007.00314.x)
- Trouw, R., Heilbron, M., Ribeiro, Pacifullo, A.F., Valerino, C.M., Almeida, J.C.H, Tupinambá, M & Andreis, R.R. (2000) The central segment of the Ribeira Belt. Pp. 287–310 in Cordani, U.G., Milani, E.J, Thomaz-Filho, A. & Campos, D.A. (eds.), Tectonic evolution of South America. 31st *International Geological Congress*. Rio de Janeiro.
- Uba, C. E., Heubeck, C. & Hulka, C. (2006) Evolution of the late Cenozoic Chaco foreland basin, Southern Bolivia. *Basin Research* 18, 145–170.
- Weitzman, S.H. & Menezes, N.A. (1998) Relationships of the tribes and genera of the Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new genus, *Chrysobrycon*. Pp. 171–192. In: Malabarba, L. R., Reis, R.E., Vari, R.P. Lucena, Z.M.S. & C. A. S. Lucena, C.A.S. (Eds.). Phylogeny and classification of Neotropical fishes. Porto Alegre, *Edipucrs*, 603p.
- Weitzman, S.H., Menezes, N.A. & Weitzman, M.J. (1988) Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distribution of other freshwater fishes in eastern and southeastern Brazil. Pp. 379–427. In: Vanzolini, P.E., & W. R. Heyer (Eds.). Proceedings of a workshop on Neotropical distribution patterns. Rio de Janeiro. *Academia Brasileira de Ciências*, 488 p.
- Weitzman, S. H., Menezes, N.A., Evers H. & Burns, J.R. (2005) Putative relationships among inseminating and externally fertilizing characids, with a description of a new genus and species of Brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae). *Neotropical Ichthyology*, 3(3).329–360.