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ORIGINAL ARTICLE

Biogeographical revision of Argentina (Andean and Neotropical Regions): an analysis using freshwater fishes

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ABSTRACT

Aim To provide an objective geographic framework displaying the distribution patterns of freshwater fishes from Argentina.

Location Argentina, southern South America.

Methods Parsimony analysis of endemicity (PAE) and similarity and cluster analyses were applied to presence and absence data on 440 fish species from 52 localities in Argentina. Both 50% majority consensus and strict consensus analyses were undertaken in the first case, and the Jaccard similarity index was used in the second.

Results Five ichthyogeographic provinces are described based on a PAE of the 52 localities. A cluster analysis provided similar results.

Main conclusions The following zoogeographic provinces are proposed for Argentine freshwater fish fauna following the International Code of Area Nomenclature: Andean Cuyan, Patagonian, Aymaran, Great Rivers and Pampean. The former two are placed within the Andean Subregion of the Austral Region, and the latter three within the Neotropical Subregion of the Holotropical Region. These provinces, based on results coinciding with PAE and cluster analysis, represent the first classification of Argentine provinces based on objective methods. Some small regions of endemism and some localities remain separated from the proposed regions. The new scheme includes valuable empirical information from previous schemes, and is in agreement with ecological zones and other environmental arrangements proposed earlier.

Keywords

Areas of endemism, Argentina, biogeography, freshwater fishes, ichthyogeographic provinces, limnology, Neotropics, PAE.

INTRODUCTION

Probably the greatest change in the zoogeography of South America was the division of the Neotropical Region into a north-eastern area, which retained the original name, and a south-western area, the Andean Region, belonging to the Holotropical and Austral kingdoms, respectively (Amorim & Tozoni, 1994; Morrone, 1996, 2002; Humphries & Parenti, 1999). Following the work of Eigenmann (1909), Ringuelet (1961, 1975) treated in considerable detail the distribution of fishes in South America, explicitly considering the relationship between the western part of Argentina and areas located in New Guinea and Australia.

There are numerous classifications for the distribution of the freshwater fishes of Argentina (see Table 1), as well as other wider biogeographical classifications of South America (see Crisci *et al.*, 1991a, b; Humphries & Parenti, 1999; Morrone, 2006). The majority of these classifications tend to be in agreement (Menni, 2004). However, the most popular system, that proposed by Ringuelet (1975), was challenged by Arratia *et al.* (1983), who considered that the Andean-Cuyan Province had stronger affinities with the Patagonian Province than with the Paranensean Province. Furthermore, Arratia *et al.* (1983) extended the western limit of the Paranensean fauna to the eastern slope of the Andes. These modifications of Arratia *et al.* (1983) coincide with an earlier

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Table 1 Zoogeographic studies referring to Argentine fishes.

Eigenmann (1909)	Mainly fishes from Patagonia
Lahille (1929)	Silversides, Argentine and Chilean geography
Mac Donagh (1934, 1938)	Geography of Argentinean fishes
Pozzi (1945)	Main ichthyogeographic regions
Ringuelet *et al.* (1967)	Fishes from Argentina
Géry (1969)	Ichthyogeography of South America
McDowall (1971a,b)	Distribution of galaxiids
Ringuelet (1975)	Geography and ecology of Argentinean fishes
Cabrera & Willink (1973)	Biogeography of Latin America including fish examples
Del Castillo (1986)	Numerical taxonomy applied to fish families distribution
Berra (2001)	Distribution of world freshwater fishes
Arratia *et al.* (1983)	Geography and ecology of Argentinean fishes
Vari (1988, 1991, 1992)	Biogeography of curimatid fishes
Schaefer (1991, 1997)	Biogeography of Hypoptopomatinae
Banarescu (1995)	Biogeography of fresh waters
Menni & Gómez (1995)	Disjunction and gradients
Menni *et al.* (1996)	Ecological patterns
Bonetto (1998)	Fishes from the Rio de la Plata basin
Almirón *et al.* (1997)	Border between subregions in Argentina
Arratia (1997)	Brazilian and Austral fishes
Dyer (1998, 2000)	Silversides geography
Malabarba *et al.* (1998)	Collected papers
Matthews (1998)	Global distribution of freshwater fishes
Morrone (2001)	Biogeography of Latin America and the Caribbean
Sivasundar *et al.* (2001)	Population and distribution of *Prochilodus*
López *et al.* (2002)	Ecoregions of Argentina
Baigún & Ferriz (2003)	Fishes of Patagonia
Cussac *et al.* (2004)	Distribution of galaxiids
Menni (2004)	Fishes & environments in Argentina
López & Miquelarena (2005)	Genera shared by Argentina and nearby countries
Menni *et al.* (2005)	Gradients in northwestern Argentina
Hubert & Renno (2006)	Biogeography of northern South America
Ruzzante *et al.* (2006)	Phylogeography of *Percichthys*

classification of Ringuelet (1961) for the entire Argentinean fauna.

In recent years there has been a sudden increase in the number of species descriptions of fishes in the Argentine territory. Important examples are the genus *Astyanax* within the characiforms (Miquelarena & Menni, 2005) and further discoveries in the north-eastern and north-western regions of the country. According to the recent survey by López & Miquelarena (2005), the freshwater fishes of Argentina are assigned to 183 genera comprising 438 described species. The latter number is a 398% increase over the number given by Géry (1969). Furthermore, several recent papers focusing on particular taxa and areas provide a much more accurate description of the geographic distribution of fishes than was previously available (for example Almirón *et al.*, 1992; Haro & Bistoni, 1996; del Barco, 1997; Haro *et al.*, 1998; Sverlij *et al.*, 1998; López *et al.*, 2001, 2003, 2005; Baigún & Ferriz, 2003; Monasterio de Gonzo, 2003; Cussac *et al.*, 2004; Menni, 2004; Butí & Cancino, 2005; Casciotta *et al.*, 2005; Liotta, 2005; López & Miquelarena, 2005; Menni *et al.*, 2005; Monasterio de Gonzo *et al.*, 2005).

Over the last 25 years, several research groups have worked on fish systematics, ecology and distribution, with extensive field work being carried out in many areas of Argentina. Their results have provided a large number of new records and new species, and in many cases communities and limnology were also studied. The information derived from these activities is summarized below.

1. Improvement in the knowledge of the fish fauna of central Argentina (Menni *et al.*, 1984; Casciotta *et al.*, 1989; Miquelarena *et al.*, 1990; Miquelarena & Menni, 1992; Ferriz, 1996; Haro & Bistoni, 1996).

2. Changes in the composition of the fish fauna of the Lagunas Encadenadas del Oeste, where richness increased to 18 species from 14 previously known (Miquelarena & López, 1995).

3. New information on the north-western region, which shows differences from pampasic assemblages fishes (Miquelarena & Aquino, 1995; Butí, 1999; Fernández & Schaefer, 2003; Fernández & Vari, 2004; Fernández & de Pinna, 2005; Menni *et al.*, 2005; Miquelarena & Menni, 2005).

4. The presence of several genera shared between Bolivia and Argentina, supporting the north-western assemblage (López & Miquelarena, 2005; Menni *et al.*, 2005).

5. The faunal composition of many aquatic environments within the flood plains of the Paraguay River in north-eastern Argentina (Menni *et al.*, 1992).

6. A high rate of description of new species, many of which are apparently endemics, in north-eastern Argentina (López *et al.*, 2005).

7. New information on Argentine Mesopotamian fishes (López *et al.*, 2005), particularly in the Iberá swamps (Casciotta *et al.*, 2005).

We used the above-mentioned information to find geographical patterns among a large number of aquatic environments throughout southern South America. Based on this we propose a new zoogeographical classification for freshwater fishes from the Argentine territory.

MATERIALS AND METHODS

We analysed a total of 52 localities in Argentina, for which we obtained information on the composition of the fish fauna from the literature and from our own data. These localities were basins, individual streams and small water courses, and lentic environments. For each locality we assessed the presence or absence of 440 reported species, resulting in an absence/presence binary matrix of 440 species in 52 localities. The matrix is included in Appendix S1 (see Supplementary Material).

Numbers of localities in clades correspond to numbers in Fig. 4; *Jenynsia multidentata*, *Cnesterodon decemmaculatus* and *Odontesthes bonariensis* were excluded from the analysis because their distributions have been modified by aquaculture and other human activities.

In order to uncover potential biogeographical patterns, we examined the data using two techniques, namely parsimony analysis of endemicity (PAE) and multivariate (cluster) analysis.

Parsimony analysis of endemicity (PAE)

Parsimony analysis of endemicity is a method that aims to find similarities between areas based on natural patterns of distribution. PAE classifies localities, areas, or quadrats according to their shared taxa by means of a parsimony algorithm (see Rosen, 1988). The result is a hierarchical classification of the geographical units (Crisci *et al.*, 2000, 2003). For this purpose, we analysed the binary data matrix with PAUP (Swofford, 1998) using a heuristic search with 1000 random addition sequences.

Branch support is based on a bootstrap analysis (Felsenstein, 1985) and a decay analysis (Bremer, 1988), the former computed with PAUP and the latter performed by constructing a PAUP-command file in MacClade (Maddison & Maddison, 2001) and then performing a calculation in PAUP. In order to characterize the areas, the synapomorphies (= endemic species) for each area (= clade) were used. Non-endemic but very common species present in basins, streams or lentic habitats were considered in the descriptions of areas.

Multivariate analysis

Multivariate methods can be regarded as an alternative to PAE for classifying biotas. Assemblages can be identified subjectively by assessing how far the biota in one area corresponds to that in another, and thereby grouping areas accordingly. Some assemblages are closer in taxonomic composition, which can be expressed statistically in terms of cluster hierarchies or relative biotic distances. The resulting patterns are expressed in numerous ways, cluster diagrams being the most common (Rosen, 1988).

In order to perform the cluster analysis, we used the Jaccard association index to construct the similarity matrix (Hubalek, 1982; Murguía & Villaseñor, 2003) and UPGMA (unweighted pair-group method using arithmetic averages) was applied to obtain the clustering graph (dendrogram). Cluster analysis was performed using the program PAST (Hammer *et al.*, 2001). We also computed the co-phenetic coefficient (Sokal & Rohlf, 1962) to evaluate the degree of distortion of the analysis.

In order to compare groups between methods, we labelled clades with Roman numerals and clusters with capital letters and Arabic numbers (see below). The biogeographical classification obtained in this paper follows the International Code of Area Nomenclature (ICAN) (Ebach *et al.*, 2007).

RESULTS

Parsimony analysis of endemicity

Parsimony analysis of endemicity yielded 1196 trees with length (L) 1045 (consistency index (CI) = 34; retention index (RI) = 61). All of the most parsimonious trees were retained, but we present only the strict consensus and the majority-rule trees. The strict consensus tree and support statistics are shown in Fig. 1. Bootstrap values were moderate to high, with eight branches supported by more than 50%. Decay indexes were low, maximally equal to one.

The five main clades of localities can be identified in the strict consensus tree. One clade is formed by the Middle and Lower Paraná River, the Upper Paraná River, the Uruguay River, the Río de la Plata and its tributaries, the Paraná River Delta, the Bermejo River, the Pilcomayo River, the Formosean swamp zone, the Santa Fé swamp zone, and the Lower Paraguay River. A smaller clade contains the tributaries of the Paraná River in Misiones and the Iguazú River. The former clade presented a moderate bootstrap support value (64%), and the latter a high bootstrap support value (99%). A third clade contains the Chubut-Senguer, the Negro, Chico and Santa Cruz, and Deseado rivers, with a low bootstrap support value (< 50%). A fourth clade is formed by the tributaries of the Chilecito Valley, Abaucán-Salado River, tributaries of the Salar de Pipanaco, and Del Valle River and its tributaries, and rivers and creeks of the eastern slope of Mount Ambato. The fifth clade includes the Salí-Dulce and Juramento rivers in Salta, the Tercero, Cuarto and Carcarañá rivers in central Argentina, the Salado-Vallimanca, Segundo and Primero rivers, the Pampean basins of the Atlantic slope and the Southwestern Pampean basins, the Northwestern Córdoba rivers, and the Quinto and Chorrillos rivers. These last two clades have a very low decay index. The remaining localities are unresolved.

The 50% majority-rule consensus (Fig. 2) included, in Clade IV, several localities that were unresolved in the strict consensus. This clade is formed by the tributaries of the Llancanelo (brackish) lagoon and the Atuel, Diamante, San Juan, Jachal, Vinchina, Tunuyán, Desaguadero, Colorado, and Mendoza rivers, and has a high frequency of bipartitions. The clade of the strict consensus tree comprising the Chubut, Negro, Chico and Santa Cruz, and Deseado rivers is included in a major clade together with the Coyle, Gallegos and Chico del Sur rivers, the rivers and creeks from Tierra del Fuego, environments in the Malvinas Islands, and Isla de los Estados (Clade V). This clade shows a high frequency of bipartitions. Two clades of the strict consensus tree (Fig. 1) are grouped in a major clade together with the Dorado and del Valle rivers in Salta, showing 75% of bipartitions (= frequency of occurrence) (Clade I). Five localities are unresolved and will be discussed below. Endemic species for each area are shown in Table 2, and species supporting clades are shown in Table 3.

The detailed composition of clades resulting from the 50% majority consensus tree is as follows.

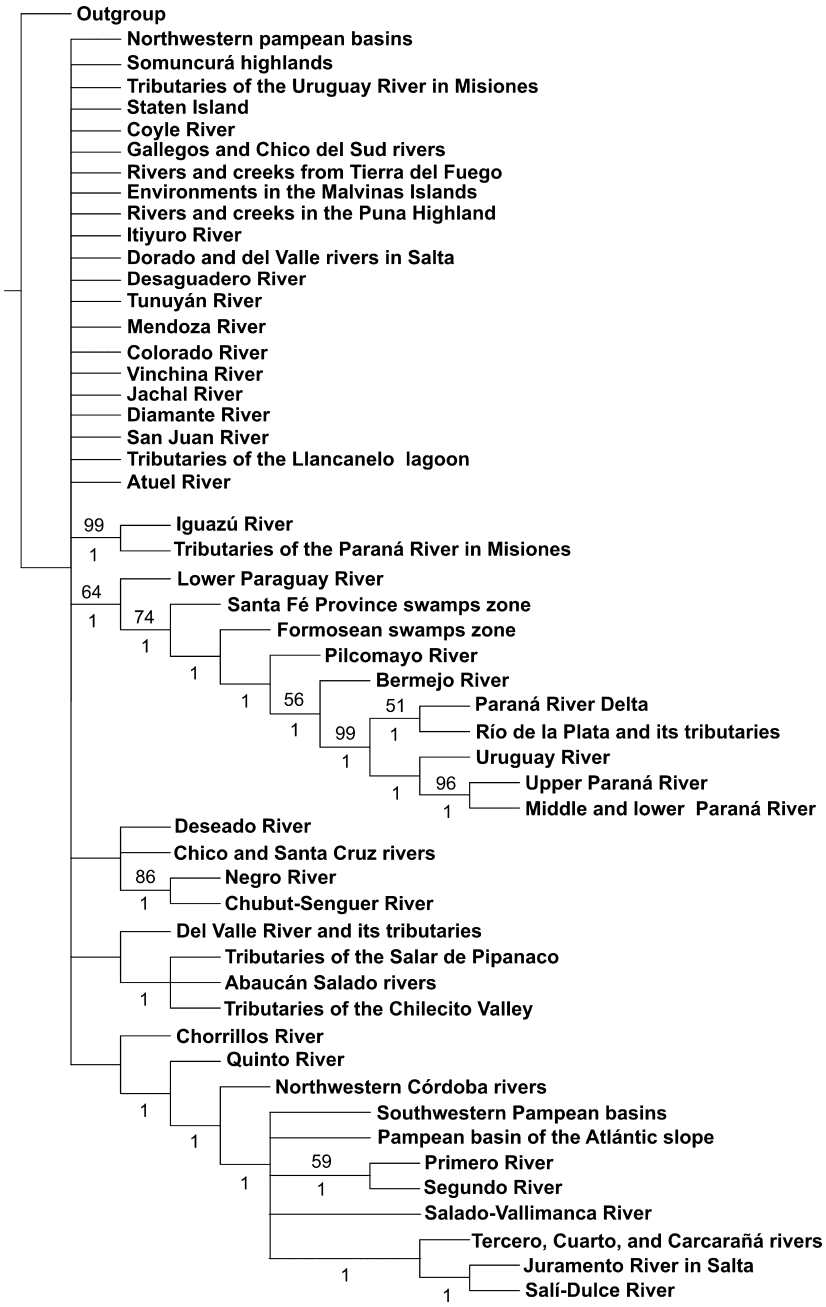

Figure 1 Strict consensus tree of 1196 trees (L = 1045; CI = 34; RI = 61) obtained from parsimony analysis of endemicity (PAE). Bootstrap values are shown above the branches with values > 50%; decay index values are shown below the branches with values > 0.

Clade I

31. Middle and Lower Paraná River
30. Upper Paraná River
34. Uruguay River
33. Rio de la Plata and its tributaries
32. Paraná River delta
38. Bermejo River
37. Pilcomayo River
35. Formosean swamp zone
36. Santa Fé Province swamp zone
39. Lower Paraguay River
40. Iguazú River
41. Tributaries of the Paraná River in Misiones
51. Dorado and Del Valle rivers in Salta

All these environments belong to the Río de la Plata basin, and are part of the Subtropical Potamic Axis (López *et al.*, 2002). The expansion of the Paranensean fauna in all these environments have been extensively discussed and demonstrated previously (Ringuelet, 1975; Vari, 1988; Schaefer, 1997; Menni, 2004).

Clade II

46. Salí-Dulce River
50. Juramento River in Salta
45. Tercero, Cuarto and Carcarañá rivers
47. Salado-Vallimanca River

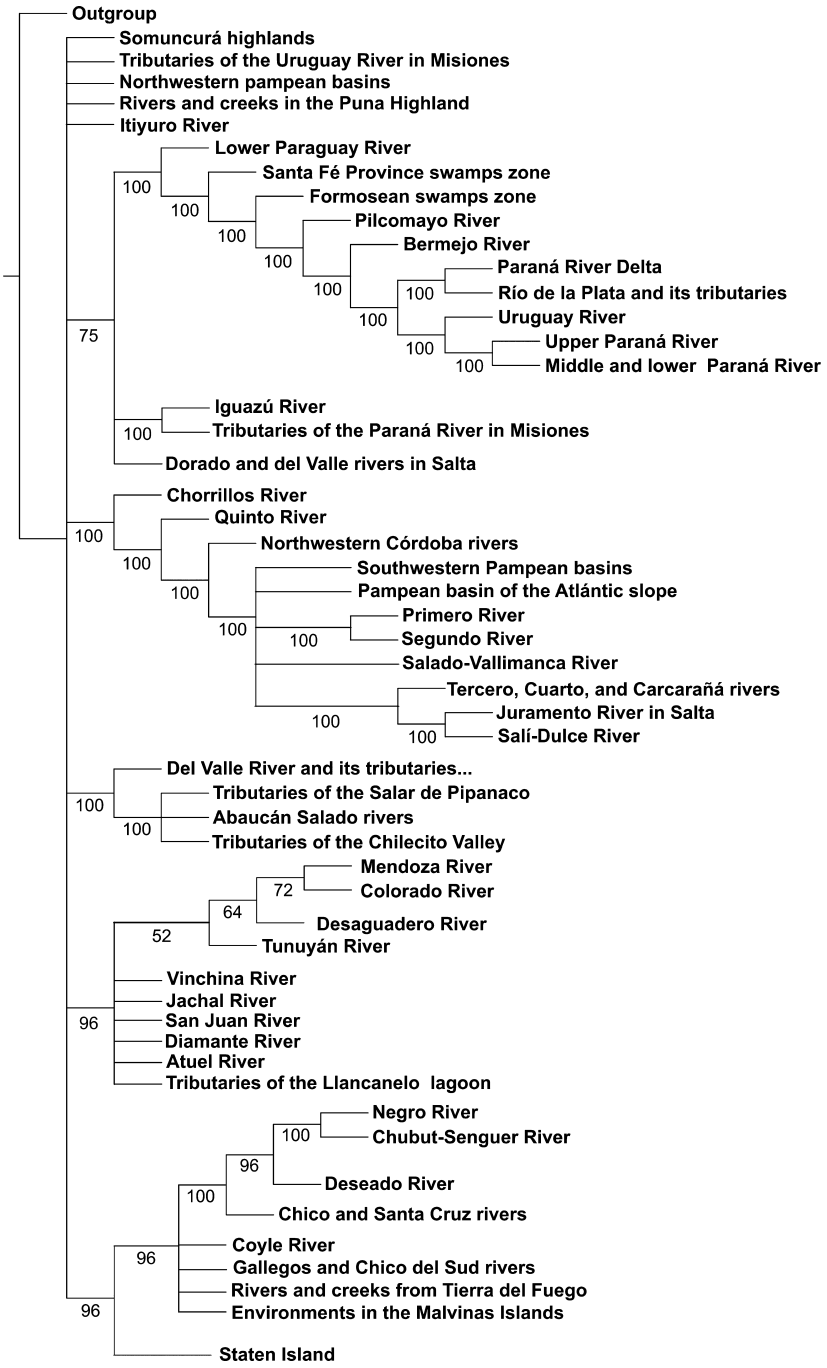

Figure 2 50% majority-rule consensus tree of 1196 trees (L = 1045; CI = 34; RI = 61) obtained from parsimony analysis of endemicity (PAE). Frequencies of occurrence are shown above the branches.

44. Segundo River
43. Primero River
49. Pampean basin of the Atlantic slope
48. South-western Pampean basins
42. North-western Córdoba rivers
28. Quinto River
27. Chorrillos River

This clade somewhat exceeds the area usually attributed to the Pampasic fishes. This name is usually applied to taxa inhabiting the typical 'lagunas' (lakes of third order) and rivers from the wet Pampa (Pampasia Bonaerense, in the sense of Ringuelet, 1975). In a strict geological sense, the Pampean Zone reaches up to the Pampean Highland (Frenguelli, 1946; Tonni & Cione, 1997). This clade grouped the most important rivers in central Argentina, of which the Tercero, Cuarto, Carcarañá and Juramento are connected with the Paraná River at present, whereas the Primero, Segundo and Salí-Dulce were connected with the Paraná River in the past. There are other endorrheic basins, such as the Quinto and Chorrillos rivers. The Pampean basin of the Atlantic slope includes small creeks that flow into the Atlantic Ocean and others that disappear into coastal sand dunes.

Table 2 List of endemic species corresponding to each of the proposed zoogeographic provinces.

	Andeancuyan	Patagonian	Aymaran	Pampean	*Great Rivers*
Olivaichthys cuyanus	X				
Silvinichthys mendozensis	X				
Trichomycterus heterodontus	X				
Olivaichthys mesembrinus		X			
Rhamdella aymarae			X		
Trichomycterus belensis			X		
Bryconamericus eigenmanni				X	
Astyanax cordovae				X	
Austrolebias robustus				X	
Astyanax hermosus				X	
Characidium borellii				X	
Silvinichthys bortayro				X	
Pimelodus argenteus					X
Megalonema argentina					X
Apteronotus ellisi					X
Xyliphius barbatus					X
Pimelodus absconditus					X
Rhamphichthys hahni					X
Hyphessobrycon wajat					X
Xyliphius lombarderoi					X
Corydoras carlae					X
Brochiloricaria chauliodon					X
Hemmigramus mattei					X
Hyphessobrycon igneus					X
Pimelodus brevis					X
Bryconamericus uporas					X
Loricariichthys edentatus					X
Astyanax latens					X
Tridentopsis cahuali					X
Astyanax leonidas					X
Astyanax ita					X
Bryconamericus ika					X
Astyanax troya					X
Astyanax tupi					X
Bryconamericus agna					X
Bryconamericus mennii					X
Bryconamericus sylvicola					X
Gymnogeophagus che					X
Oligosarcus menezesi					X

Clade III

23. Tributaries of the Salar de Pipanaco
24. Abaucán-Salado River
25. Tributaries of the Chilecito Valley
26. Del Valle River and its tributaries, rivers and creeks of the eastern slope of Mount Ambato.

These localities are all endorrheic basins in the provinces of Catamarca and La Rioja, within a mostly desert landscape.

Clade IV

6. Mendoza River
9. Colorado River
8. Desaguadero River
7. Tunuyán River
1. Vinchina River
3. Jachal River
5. San Juan River
2. Diamante River
4. Atuel River
10. Tributaries of the Llancanelo brackish lagoon

These are environments of north-western Argentina between 28°30′ S and 35°20′ S and centred about 68–69 W. *Trichomycterus heterodontus* and *Hatcheria macraei* have been reported from the Vinchina River, an endorrheic course in La Rioja province (Arratia *et al.*, 1983; López *et al.*, 2002; Menni, 2004). The rest of the rivers in the list are tributaries of the Desaguadero River, which collects most rivers of the area. Originally, and in some periods during the present, the Desaguadero River flowed into the Colorado River (Mazza, 1961).

Table 3 List of species supporting clades (see Fig. 2).

Clades	Synapomorphies
(Upper Paraná River, Middle and Lower Paraná River)	*Hyphessobrycon auca*; *Hyphessobrycon elachys*; *Hyphessobrycon eques*; *Hypophthalmus oremaculatus*; *Hypostomus meleagris*; *Ituglanis eichorniarum*; *Laetacara dorsigera*; *Leporinus elongatus*; *Metynnis mola*; *Potamorrhaphis eigenmanni*; *Pterolebias bokermanni*; *Rineloricaria lanceolata*
(Río de la Plata, Paraná River Delta)	*Phalloptychus januarius*; *Pimelodus brevis*; *Rhamdella jenynsii*
(Uruguay River, (Upper Paraná River, Middle and Lower Paraná River))	*Apistogramma trifasciata*; *Hypostomus alatus*; *Hypostomus luteomaculatus*; *Rhamphychthys hahni*; *Paraloricaria agastor*
(Uruguay River, Upper Paraná River, Middle and Lower Paraná River, Río de la Plata, Paraná River Delta)	*Ageneiousus inermis*; *Ramnogaster melanostoma*; *Rhinelepis strigosa*; *Schizodon platae*
(Bermejo River, Uruguay River, Upper Paraná River, Middle and Lower Paraná River, Río de la Plata, Paraná River Delta)	*Megalonema platanum*; *Oxydoras kneri*; *Potamotrygon brachyura*; *Raphiodon vulpinus*
(Pilcomayo River, Bermejo River, Uruguay River, Upper Paraná River, Middle and Lower Paraná River, Río de la Plata, Paraná River Delta)	*Pterodoras granulosus*
(Formosean swamps zone, Pilcomayo River, Bermejo River, Uruguay River, Upper Paraná River, Middle and Lower Paraná River, Río de la Plata, Paraná River Delta)	*Bergiaria westermanni*
(Santa Fe swamps zone, Formosean swamps zone, Pilcomayo River, Bermejo River, Uruguay River, Upper Paraná River, Middle and Lower Paraná River, Río de la Plata, Paraná River Delta)	*Odontostilbe pequira*; *Sorubim lima*; *Triportheus nematurus*
(Iguazú River, Tributaries of the Paraná River in Misiones)	*Astyanax leonidas*; *Crenicichla gaucho*; *Hypostomus derbyi*; *Hypostomus myersi*; *Imparfinis hollandi*; *Trichomycterus davisi*
(Primero River, Segundo River)	*Astyanax cordovae*
(Negro River, Chubut-Senguer River, Deseado River, Chico and Santa Cruz Rivers, Coyle River, Rivers and creeks from Tierra del Fuego, Gallegos and Chico del Sur Rivers, Environments in the Malvinas Islands)	*Galaxias plate*
(Negro River, Chubut-Senguer River, Deseado River, Chico and Santa Cruz Rivers, Coyle River, Rivers and creeks from Tierra del Fuego, Gallegos and Chico del Sur Rivers, Environments in the Malvinas Islands, Staten Island	*Galaxias maculatus*

Clade V

11. Negro River
13. Chubut-Senguer River
14. Deseado River
15. Chico and Santa Cruz rivers
16. Coyle River
18. Gallegos and Chico del Sur rivers
17. Rivers and creeks from Tierra del Fuego
19. Environments in the Malvinas Islands
20. Isla de los Estados.

All of these are Patagonian rivers in a strict geographic sense. The Colorado River, although geographically usually considered the northern border of Patagonia, is included in Clade IV.

Unresolved localities

The north-western Pampean basins, Somuncurá highlands, the tributaries of the Uruguay River in Misiones, the rivers and creeks in the Puna Highlands, and the Itiyuro River resulted in a basal polytomy in the PAE and were not included in any of our provinces.

North-western Pampean basins (29): These basins include lakes and ponds, with a relatively high salinity and long desiccation periods. They have a small fish fauna composed of *Cheirodon interruptus, Austrolebias nonoiuliensis* and *Rhamdia quelen*. In this area, Pampean assemblages are clearly recognizable in completely new communities that developed following an increase in rainfall and temperature in areas that were dry half a century ago (Gómez *et al.*, 2004; Gómez & Menni, 2005).

Somuncurá Highlands (12): The Somuncurá plateau is a peculiar environment in the centre of northern Patagonia, with small streams inhabited by a few species. The endemic characid *Gymnocharacinus bergi,* apparently related to *Bryconamericus* (Géry, 1978; Miquelarena *et al.*, 2005), lives in the Valcheta creek. This creek is fed by thermal springs that maintain a high water temperature suitable for *G. bergi* (Menni & Gómez, 1995). This species has been separated from the rest of the subtropical fauna at least since the desertification of the Pampean region in Miocene times (Vucetich & Verzi, 1999; Ortiz-Jaureguizar & Cladera, 2006).

Jenynsia multidentata has been reported from the Valcheta Creek, the Paja Alta Creek and the Curicó pond, and

Cnesterodon decemmaculatus from the Curicó pond only. *Oncorrhynchus mykiss* and *Salvelinus fontinalis* have been introduced in several places in the basin (Ortubay *et al.*, 1997), but high temperatures exclude them from the area where *G. bergi* lives.

The degree of endemism in the highlands is also high for other groups, especially amphibians and reptiles among the vertebrates (Cei, 1969). Considering the possible relationships of *G. bergi* with other characiform subfamilies, this area is certainly an enclave of the Great Rivers Province.

Tributaries of the Uruguay River in Misiones and nearby localities (52): The most north-eastern section of Argentina in the state of Misiones is a particularly complex area (Roig & Cei, 1961; Cabrera & Willink, 1973; López *et al.*, 2002). It has been considered part of the Alto Paraná Province (Ringuelet, 1975; Vari, 1988). In recent times this area has been the richest source of new species, most of them still endemic to isolated small basins. New species include *Astyanax ojiara, Astyanax saguazu, Astyanax paris, Bryconamericus ytu, Rineloricaria missioneira, Hypobrycon poi* and *Australoheros tembe*. Some species initially described as endemics were later found in nearby countries (Miquelarena & Menni, 2005). In the cluster analysis, the tributaries of the Uruguay River in Misiones appear to be related to the Cluster C fauna, at a low level of similarity.

Itiyuro River (21): This river, with sources in Bolivia, belongs to an endorrheic basin, but may reach the Bermejo River during the heaviest floods. Its ichthyofauna, recently described (Menni *et al.*, 2005), includes several species with clear Paranensean relationships, although *Trichomycterus barbouri* and the endemic *Rhamdella aymarae* are not among these.

Rivers and creeks in the Puna Highland (22): These are water courses of the rithron type, mainly under strong physical conditions in dry highlands. Five species were considered in the matrix, including *Bryconamericus thomasi* and *Jenynsia maculata*, which have rather restricted distributions in north-western Argentina, and *Trichomycterus belensis*, which occurs only in a tributary creek of the Laguna Blanca in Catamarca.

Multivariate analysis

The dendrogram (Fig. 3) derived from the application of the Jaccard index presents five groups (A1, A2, B, C1 and C2). Cluster C1 groups the localities defined in the majority-rule consensus cladogram as Clade I, with the exception of the Dorado and del Valle rivers in Salta. This cluster is related to Cluster C2. Cluster C2 includes the localities defined in the strict and 50% majority-rule consensus cladograms as Clade II, except for the inclusion of the Dorado and Del Valle rivers in Salta and the exclusion of the Chorrillos and Quinto rivers, which are in Cluster B.

Cluster A1 includes the same localities as Clade IV, and Cluster A2 includes the same localities as Clade V of the 50% majority-rule consensus cladogram. Cluster B, however, corresponds to Clade III, but does not include the Itiyuro River, rivers and creeks in the Puna Highland, far to the north, or the Chorrillos and Quinto rivers and the north-western Pampean basins.

Clusters B, C1 and C2 appear to be related and are separate from clusters A1 and A2, which form another main cluster. These relationships among groups are the same as those proposed by Arratia *et al.* (1983).

The five unresolved localities of the PAE clustered as follows: the tributaries of the Uruguay River in Misiones are related to the Great Rivers and Pampean provinces (Cluster C) at a very low level, and the Somuncurá Plateau joins the other clusters at the lowest level of similarity. The north-western Pampean basins, the rivers and creeks in the Puna Highland, and the Itiyuro River clustered (Cluster B) with Aymaran Province localities.

DISCUSSION

At present there are few cladistic hypotheses available for the freshwater fishes of Argentina. In spite of this, there are some very detailed biogeographical analyses available in which Argentine species have been included. Vari (1988, 1991, 1992) and Vari & Weitzmann (1990), for example, provided biogeographical analyses of curimatid fishes and other taxa. Schaefer (1991, 1997, Hypoptopomatinae and *Otocinclus*) also discussed the species present in Argentina and their areas of distribution. Dyer (1998), who studied the phylogeny of South American silversides, provided further evidence for the separation of *Odontesthes hatcheri* from Patagonia from the remaining species with more northern distributions. Ghedotti (1998) provided a phylogeny of the genus *Jenynsia*, but stated that the biogeographic patterns derived from his study should be considered only as preliminary.

As a result of the application of objective criteria to evaluating the relationships and similarity among fish localities in Argentina, we obtained five clades, roughly equivalent to the provinces proposed previously (Ringuelet, 1975; Arratia *et al.*, 1983), with some differences in details and some hierarchical changes. The most important differences are the definition of the Aymaran Province and the extension of the Pampean Region. The existence of the former province was foreseen by Menni (2004) and Menni *et al.* (2005), who mentioned the traits of the fish fauna from north-western Argentina and discussed its ecology. The Pampean Region in the sense of this paper includes a northern section evidently related to tributaries of the Paraná River.

Our results confirm the traditional extension of the Andean Cuyan and Patagonian provinces. The former one is extended to the Atlantic Ocean with the inclusion of the Colorado River.

The resulting classification in which provinces correspond to clades derived from the PAE of 50% majority consensus is shown in Fig. 4.

Systematic biogeography

Kingdom AUSTRAL (Kuschel, 1969)

Region ANDEAN (Shannon, 1927)

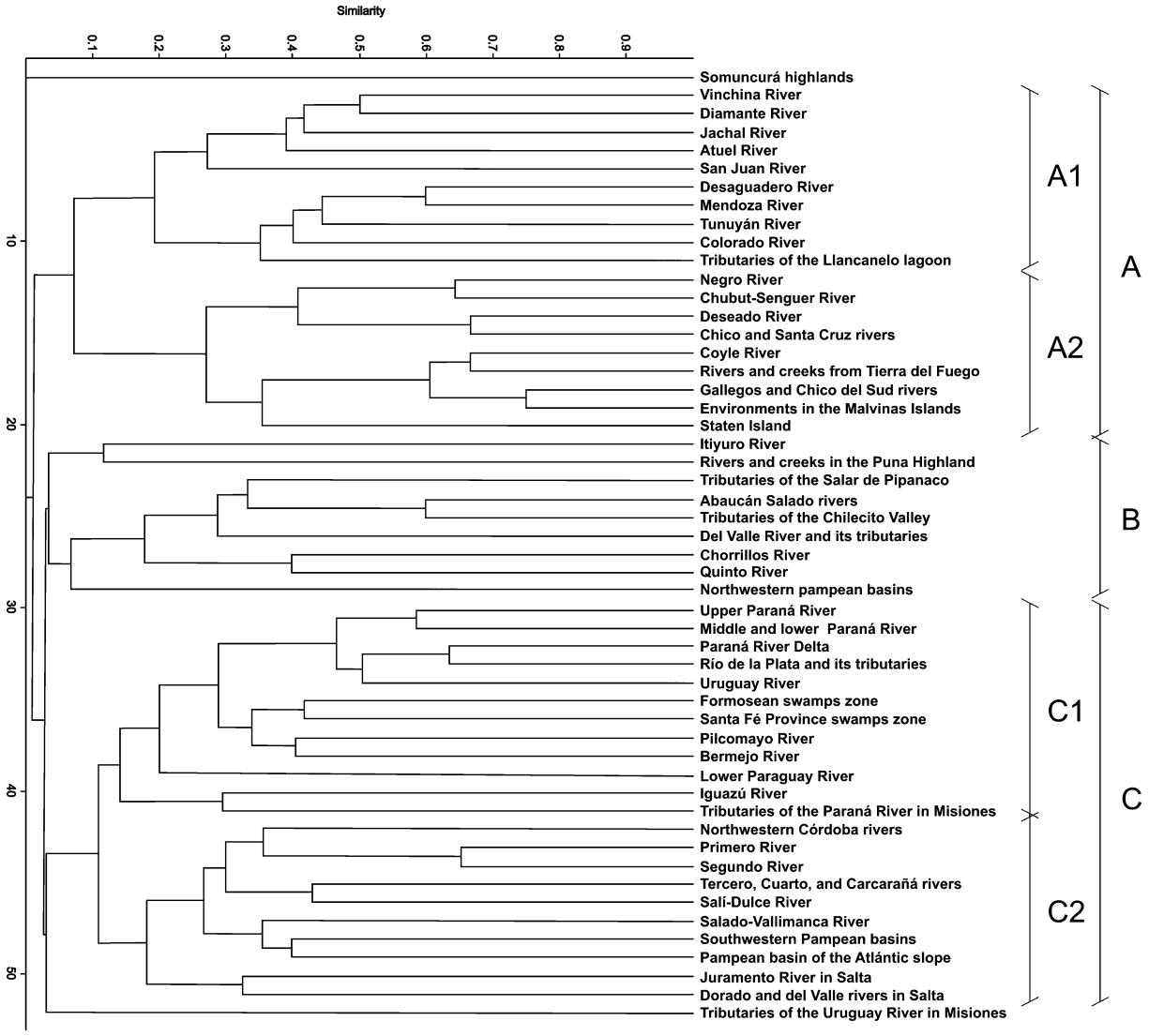

Figure 3 Cluster analysis (UPGMA: unweighted pair-group method using arithmetic averages) resulting from the Jaccard matrix of 52 localities by 440 species. Cophenetic correlation value = 0.90. A, B and C: main areas. Provinces: C1, Great Rivers; C2, Pampean; B, Aymaran; A1, Andean Cuyan; A2, Patagonian.

Province Andean Cuyan (Clade IV)

Type locality: Mendoza River (32°49′ S, 70°03′ W to 32°22′ S, 68°15′ W).

Diagnosis: Our results, in agreement with those of Arratia *et al.* (1983), indicate that the Vinchina Bermejo River, the northernmost limit of *Hatcheria macraei* and *Trichomycterus heterodontus*, is the northern end of the Andean Cuyan Province. *Hatcheria macraei* occurs in all localities of the Andean Cuyan Province, but also occurs in the western part of Patagonia and the lowest Colorado, Negro and Chubut rivers, reaching 47°30′ S, 72° W (Eigenmann, 1909).

Description: As suggested by Arratia *et al.* (1983), the PAE gave evidence of two groups of localities within the province. One includes the Vinchina-Bermejo River in La Rioja, the Jachal and San Juan rivers in San Juan Province, and the Atuel River, the Diamante Pond and the Llancanelo Lake in Mendoza. The other comprises the Desaguadero, Mendoza, Tunuyán and Colorado rivers. The cluster analysis provides a similar topology, but joins the Llancanelo Lake with the second group. In the PAE, the former group appears as a polytomy, and corresponds to the poorest habitats in the province. The second group includes the richest environments. In this area the most common species, besides *H. macraei*, are *Olivaichthys cuyanus*, *Percichthys trucha* and *Cheirodon interruptus*, the latter with clear Paranensean relationships and a well-known eurytopic species (Menni *et al.*, 1996).

Mac Donagh (1950) noted the presence of the freshwater eel *Synbranchus marmoratus* in the area, but the first formal report from San Juan is also the most western one in Argentina (Murúa & Acosta, 1997; Gómez, 2001).

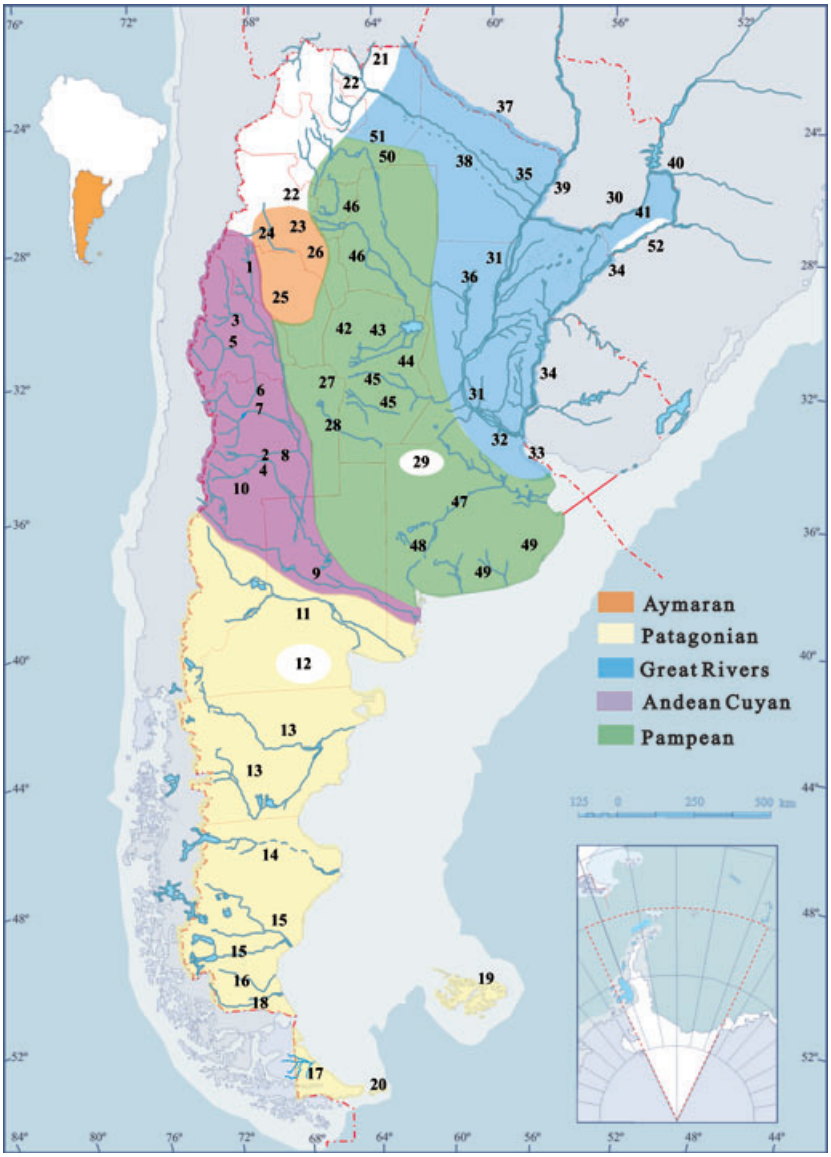

Figure 4 Ichthyological provinces of Argentina resulting from a parsimony analysis of endemicity (PAE) 50% majority-rule consensus tree of a matrix of 52 localities by 440 species. Numbers of localities correspond to lists in the text. Areas in white correspond to unresolved localities.

Synbranchus marmoratus is the fish with the widest distribution in South America; therefore, its presence far to the south is not surprising. However, its genetic and caryotypic variation is large (Torres *et al.*, 2005), suggesting that it may include more than one evolutionary lineage.

The Andean Cuyan Province shares with the Aymaran Province *Hatcheria macraei, Cheirodon interruptus, Trichomycterus borellii, Jenynsia pygogramma.*

The Andean Cuyan Province shares with the Patagonian Province *Odontesthes hatcheri, Percichthys trucha, Hatcheria macraei, Olivaichthys viedmensis* and *Percichthys colhuapiensis.*

The Andean Cuyan Province shares several species with the Great Rivers Province, namely *Cheirodon interruptus, Trichomycterus borellii, Synbranchus marmoratus, Mugil liza, Oligosarcus jenynsii* and *Astyanax eigenmanniorum*. Differing in the species shared with Patagonia, these species are in general widely distributed through the other provinces. The Andean Cuyan Province shares with the Pampean Province *Astyanax eigenmanniorum, Cheirodon interruptus, Synbranchus marmoratus, Jenynsia pygogramma, Oligosarcus jenynsii, Trichomycterus borellii* and *Mugil liza.*

Province Patagonian (Clade V)

Type locality: Negro River (39°00′ S, 68°00′ W to 41°02′ S, 62°47′ W).

Diagnosis: This is the best defined province because of the presence of osmeriform fishes of the family Galaxiidae. In all available classifications, it includes southern Argentina and southern Chile (Ringuelet, 1975; Arratia *et al.*, 1983). Here we refer only to the Argentine section. The northern border of the province in Argentina may be conflictive, because the Colorado River, which Almirón *et al.* (1997) considered a transitional area, appears as a part of the Andean Cuyan Province in our analysis.

Description: Excluding introduced salmonids, 21 fish species occur in Patagonia (Menni, 2004), considering recent data on *Percichthys* (López-Arbarello, 2004) and the presence of *Corydoras paleatus* (possibly introduced) in the northern part (Baigún *et al.*, 2002).

Arratia *et al.* (1983) considered Patagonia to be divided into two large faunistic regions separated by the Chubut River. Both the PAE and the cluster analyses show a division between a cluster including the Negro, Chubut-Senguer, Deseado, and Chico and Santa Cruz rivers, which are localities with a relatively larger number of species, and another one including the Coyle River, Tierra del Fuego, Gallegos and Chico del Sur rivers, Isla de los Estados and Malvinas Islands which are poorer. The northern cluster includes two species of *Galaxias*, two species of *Aplochiton*, the Patagonian silverside *Odontesthes hatcheri* and *Percichtys trucha* in all localities considered. There are also *Hatcheria macraei* in the Negro, Chubut-Senger and Deseado rivers, *Olivaichthys viedmensis* in the Negro and Chubut-Senguer rivers, *O. mesembrinus* in the Chubut-Senguer River, and *Percichthys colhuapiensis* in the Negro and Chubut-Senguer rivers.

In the southern area, *Galaxias maculatus* occurs in all five localities, and *G. platei* occurs in four of them. *Aplochiton zebra* and *A. taeniatus* occur in the Malvinas Islands, the former also in Tierra del Fuego, and the second also in the Gallegos and Chico del Sur rivers.

Galaxias maculatus, being present in all of them, is the widely distributed species. The Negro and Senguer rivers are much more diverse than the others, having nine species each, with eight species shared. The Patagonian Province shares with the Aymaran Province only *Hatcheria macraei*. With the Great Rivers and Pampean provinces it only shares *Corydoras paleatus*, which is a recent observed presence and could be an anthropic introduction.

Discussion: The formal placement of the Andean Cuyan and Patagonian provinces as divisions of a larger group (Andean Region) followed the proposal of Arratia *et al.* (1983), who considered them, together with the Chilean Province, as part of the Austral Subregion (=Andean *sensu* Morrone, 1996).

The Colorado River has been considered more closely related to the Paranensean area than to Patagonia, on the basis of several Paranensean species found there relatively recently (Almirón *et al.*, 1997). On the basis that *Trichomycterus* and *Hatcheria macraei* are shared with localities in the Clade IV, our analysis suggests a closer relationship of the Colorado River with rivers from middle Western Argentina.

The Andean Cuyan Province shares with the Patagonian Province the family Percichthyidae. At a specific level they share *Percichthys trucha* and *P. colhuapiensis*. *Percichthys trucha* ranges from the system Colorado-Desaguadero (Jachal River, 30°30′ S) to Colhue Huapi Lake, and *P. colhuapiensis* ranges from the same lake northwards to Tulumayá and Puente de Fierro Lake in Mendoza. Patagonia has an endemic Percichthydae, *P. laevis* (López-Arbarello, 2004). Note that if there were only a single species of *Percichthys* (Ruzzante *et al.*, 2006) these differences would not exist. These provinces share the siluriform genus *Olivaichthys*, with *O. cuyanus* being endemic to the Andean Cuyan Region. *Olivaichthys mesembrinus* is a Patagonian endemic. *Olivaichthys viedmensis* is common to both provinces, which also share the Atherinopsidae *Odontesthes hatcheri*.

Kingdom HOLOTROPICAL (Rapoport, 1968)
Region NEOTROPICAL (Sclater, 1858)

Province Aymaran (Clade III)

Type locality: Tributaries of the Salar de Pipanaco (28°07′ S, 66°25′ W).

Diagnosis: Clade III includes four localities in middle Western Argentina, in a rather mountainous and dry area. These localities do not have endemic species, but share two species of *Trichomycterus,* namely *T. corduvensis* and *T. alterus*, plus two other less common species.

Description: With the Pampean Province the Aymaran Province shares *Trichomycterus barbouri, T. corduvensis, T. alterus, T. borellii, Heptapterus mustelinus, Bryconamericus iheringii, B. rubropictus, Rhamdia quelen, Rineloricaria catamarcensis*, *Cheirodon interruptus* and *Jenynsia pygogramma.* With the Great Rivers Province it shares *Rhamdia quelen, Heptapterus mustelinus, Bryconamericus iheringii, Cheirodon interruptus, Trichomycterus corduvensis, T. alterus, T. barbouri, T. borellii, Rineloricaria catamarcensis* and *Bryconamericus rubropictus.*

Province Great Rivers (Clade I)

Type locality: Middle Paraná River (27°18′ S, 58°36′ S to 32°07′ S, 60°37′ W).

Diagnosis: This province corresponds to the large subtropical region defined by the Argentinean Mesopotamia (the area between the Paraná and Uruguay rivers) and adjacent areas. In the sense used here, the province is more restricted than the Parano Platense Province of either Ringuelet (1975) or Arratia *et al.* (1983). This difference is a result of the extension of the Pampean Province in our analysis.

Description: There are 394 fish species in the Great Rivers Province, which is by far the richest of Argentina. Ninety-one (23.1%) are shared with the Pampean Province. In the Great Rivers Province, *Salminus brasiliensis, Prochilodus lineatus* and *Synbranchus marmoratus* occur in all localities. The first two species, which are typical migratory species, have a close trophic relationship. *Eigenmannia virescens, Roeboides bonariensis, Loricariicthys melanocheilus, Astyanax abramis, Hoplias malabaricus, Pimelodus maculatus, Pimelodella gracilis, Astyanax bimaculatus, A. fasciatus, Odontostilbe pequira, Pimelodus albicans* and *Pygocentrus nattereri* occur in most of the localities. Three localities are much richer than the others, namely Upper Paraná, Middle and Lower Paraná and the Paraná Delta. The Bermejo River, in spite of its not having been much explored, also has a considerable number of species.

Province Pampean (Clade II)

Type locality: Chascomús Lake (35°36′ S, 58°02′ W).

Diagnosis: The 'pampasic fishes' in the sense of Ringuelet (1975) are those of the Salado-Vallimanca River, the Southwestern Pampean basins and the Pampean basins of the Atlantic slope. Fishes of rivers of Córdoba are very similar to those of the Salado area (Menni, 2004). The small fauna from the Pampean basins of the Atlantic slope (Casciotta *et al.*, 1999) is a subset of the Pampean fauna, living in small rivers at the border of the impoverished area limiting with Patagonia. The Sierra de la Ventana highlands at 38°S 62°W, inhabited by several Paranensean species (Menni *et al.*, 1988), belong to this province. According to our analysis, this province differs from the Pampasic Dominion *sensu* Ringuelet (1961) in that it includes several localities placed north of the Pampasic Dominion. *Astyanax eigenmanniorum, Bryconamericus iheringii, Cheirodon interruptus* and *Synbranchus marmoratus* are the species present in most localities, in agreement with well-known evidence (Menni, 2004). The first three are very eurytopic species (Menni *et al.*, 1996). Note that in north-western Córdoba there are 11 species (including the most abundant of the Pampasic Province), but that the remaining pampasic species are absent. The faunistic similarity between rivers in Córdoba and the Paraná River is well known (Haro & Bistoni, 1996).

Description: There are 134 species in the Pampean Province. Of these, the following do not occur in the Great Rivers Province: *Cheirodon interruptus*, *Bryconamericus eigenmanni*, *Trichomycterus tenuis*, *Jenynsia pygogramma*, *J. maculata*, *Astyanax hermosus*, *Characidium borellii*, *Crenicichla vittata*, *Austrolebias nonoiuliensis*, *A. robustus*, *Silvinichthys bortayro* and *Hatcheria macraei.*

In the cluster analysis this province is clearly delimited and related to the Great Rivers Province.

CONCLUSIONS

Using quantitative methods we identified five zoogeographic provinces for Argentine freshwater fish fauna: Andean Cuyan, Patagonian, Aymaran, Great Rivers, and Pampean. These provinces represent the first classification of Argentine ichthyogeographic provinces based on objective methods. Our results confirm the traditional extension of the Andean Cuyan and Patagonian provinces, but the former is extended to the Atlantic Ocean with the inclusion of the Colorado River. The Aymaran Province is defined for the first time, and the Pampean Province is extended to the north.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Original data matrix of 52 Argentinean localities by 440 freshwater fish species.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365.2699.2008.01904.x (This link will take you to the article abstract).

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