

# Fishes and environment in northwestern Argentina: from lowland to Puna<sup>★</sup>

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## Abstract

The fish fauna and its relationships with physiography and climate were studied in northwestern Argentina from 21°30' S to 26°30' S and 63°30' W to 65°50' W, an area about 10,276 km<sup>2</sup>. Along a southeast–northwest gradient, the Chaco forest at low altitudes gives way to the Yungas cloud forest in highlands, and then, to an increasing desertic landscape, with xerophytic vegetation and scarce rainfall along the Grande River. Finally, extreme desert conditions prevail in the most northern part at the Puna plateau. Water chemistry was sampled from sites from 400 to over 3800 m a.s.l. In all 3278 fish specimens of 52 species were collected. Previous lists included 84 species. Only 19 were shared, meaning that 40 species are new for the area and/or particular localities, including 7 reports from Aguas Calientes. These results increase by one third the number of species in northwestern Argentina. The fish fauna was represented by eurytopic species of Paranensean genera as *Astyanax*, *Bryconamericus* and other characoids, mixed with locally distributed siluriforms. Under extreme climatic conditions, species of *Trichomycterus* predominate. Species assemblages show a combination of a large number of species typical of, sometimes endemic to or rather abundant in, the area, combined with a few species of Paranensean character. Fish assemblages were clearly defined by faunistic composition and distribution related with physiography and climate traits. A significant negative correlation is observed between both species number and abundance, and increasing altitude, and positive relationships exist with mean annual temperature and other climate traits. Diversity values (Shannon index) agree with the described pattern of increasing impoverishment of the fish fauna of northwestern Argentina, along gradients of increasing altitude and dryness and decreasing temperature.

## Introduction

In Northwestern Argentina the distribution of fishes shows two main wide-scale patterns. One is the extension into the area of the eastern 'Paranensean' fauna, referring to organisms typically associated with the middle and lower Parana River. The other pattern is the presence of several

endemic species, or species with restricted distributions (Gaston, 1997), often related with endorrheic basins. Some species occur more frequently, or in larger abundance, than in areas to the south or east (Ringuelet, 1975; Arratia et al., 1983; Menni et al., 1992). For instance, perciforms (*Aequidens*, *Crenicichla* and *Geophagus*), synbranchids (*Synbranchus*) and lepidosirenids (*Lepidosiren*) are not represented in western Salta (Arratia et al., 1983).

Arratia & Menu Marque (1984) reviewed the fish fauna from the Grande River, and found that

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*Trichomycterus boylei* and *T. roigi* inhabit the upper course of the Grande River while *T. alterus*, *Corydoras micracanthus* (not seen since the original description), *Astyanax eigenmanniorum*, *Astyanax fasciatus*, *Moenkhausia intermedia* and *Psellogramus kennedyi* live only below 2100 m a.s.l.

*Odontostilbe microcephala*, *Astyanax bimaculatus paraguayensis* (= *A. asuncionensis*), *Odontostilbe hastata* (now in *Saccoderma*) and *Parodon tortuosus* (= *P. nasus*) inhabit Las Piedras River. *Serrapinus piaba* is reported from an unnamed creek of the San Francisco basin. *Ixinandria steinbachi* has been reported from the Aguas Negras River, in the Calilegua highlands (near our locality 8) and from the Rosario River, 48 km from Salta City, at 2210 m a.s.l. (Fernández, 1996b). None of these species has been found south of 30° S in western Argentina (Arratia et al., 1983).

Ringuet et al. (1967b) reported 70 species, many of them from Luna Muerta and Hickman (23°13' S, 63°34' W) in eastern Salta and Rio Piedras in southern Salta, which explains the strong Paranensean composition of his records and the absence of many of the species reported here.

Until now, the fish fauna of northwestern Argentina consists of 84 species (Ringuet et al., 1967a; Ringuet, 1975; Arratia et al., 1983, Menni et al., 1992; Menni et al., 1998). In the zoogeographic scheme of Ringuet (1975), the area is included in the Andino-Cuyana Province of the Andean Dominion. In contrast, Arratia et al. (1983) and Arratia & Menu Marque (1984) emphasized its Paranensean traits and extended the Parano-platensean Province to include it.

The area studied here shows marked climatic, vegetative, physiographic and environmental differences occurring over relatively short distances. Eastward, in the Chaco plain, relative richness appears related with climatic factors. This is suggested by the abundance of species and individuals in the wetter (eastern) part of the Formosa Province floodplain of the Paraguay River, as compared with the impoverished, dry western section, associated with the markedly seasonal Pilcomayo River (Menni et al., 1992). Although species composition of the eastern and western zones are rather similar and probably dependant on histor-

ical factors, there are 41 species in the western zone, versus 79 in the eastern zone, with 31 species found in both zones. The families Gymnotidae, Hemiodontidae, Crenuchidae, Trichomycteridae, Lebiasinidae and Aspredinidae are absent in western Formosa (Menni et al., 1992), but some of them are present again in the study area in the provinces of Salta and Jujuy. A creek from the San Francisco River basin, influenced by thermal sources, is inhabited by 16 fish species that have lethal and acclimatization temperatures correlated with high water temperature (Menni et al., 1998).

The aim of this paper is to use the landscape gradients of the area to explore the relationships of the fish fauna with regular changes in physiographic and climate variables. This ecological approach (Bayley & Li, 1996) is based on an improved knowledge of faunistic composition, which shows a considerable increase of the fish richness, and allows us to define assemblages of species characteristics of northwestern Argentina, and to establish their distribution patterns.

## Study area

Field work was carried out in the area from 21°30' S to 26°30' S and 63°30' W to 65°50' W in Argentina, roughly corresponding to the provinces of Salta and Jujuy (Fig. 1). Sampled localities were related with the Grande River (Jujuy), the San Francisco (mainly in Salta) and Juramento (Salta) river basins, but these last two rivers were not sampled. The higher western part is under arid Andean-Punean climate, and the eastern part under Tropical Highland climate (Köppen System).

The San Francisco River, with 122 m<sup>3</sup> s<sup>-1</sup> mean discharge (Secretaría de Obras Públicas, 2000), empties into the Bermejo River and through this river into the Paraguay-Paraná basin. The Juramento River reaches the lower course of the Paraná through the Salado River. These links are related with the occurrence of Paranensean fishes in northwestern Argentina, though the two areas have fairly distinct fauna (Ringuet, 1975; Menni et al., 1998).

With 28.7 m<sup>3</sup> s<sup>-1</sup> mean discharge, the Grande River is an important aquatic environment, being a permanent stream in a dry area. It runs south through the deep valley called Quebrada de

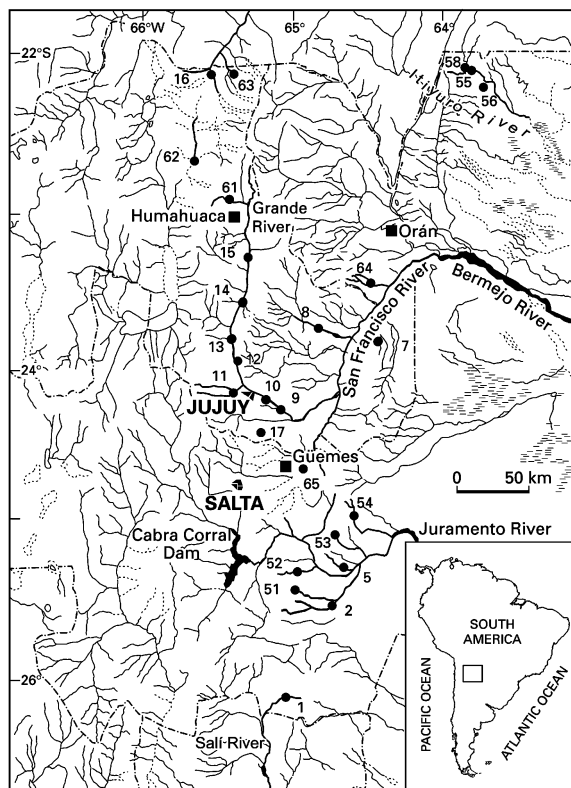


Figure 1. Localities sampled in northwestern Argentina during the years 1987, 1988 and 1991. Some courses remain dry most of the year. The \* indicates that water chemical data are available. 1, La Candelaria. 2, Metán River. 5, tributary creek to the Juramento River. 7, creek NE of the Aguas Calientes creek. 8\*, ponds of the Duraznal River. 9\* Pacara Creek. 10, creek before Huaico Mora Creek. 11, Barcaza Creek. 12\*, tributary creek of the Grande River. 13, small artificial channel in Tumbaya. 14, tributary creek of the Grande River at Tilcara. 15\*, creek in Quebrada Colorada. 16, creek south from La Quiaca. 17, creek near La Ciénaga Dam. 51, Río de las Conchas. 52, Piedras River. 53, Las Cañas River. 54\*, river near Las Víboras. 55\*, dam over the Itiyuro River. 56\*, Capiazuti River. 58\*, Itiyuro River. 61\*, Grande River. 62, Río de Abra Pampa. 63\*, creek at Yavi. 64\*, Sanjón Seco Creek. 65\*, Saladillo Creek. Basin of each locality are given in Figure 3.

Humahuaca, turning east at about 24°20' S to meet the San Francisco River, from which it is separated along most of its course by the Oriental Highlands. The upper course of the Grande River crosses arid country. At about 1000–1400 m a.s.l. there are seasonal rains, and the fish fauna is more diversified, with Paranensean elements (Arratia & Menu Marque, 1984).

In southeastern Salta, the Juramento River, also known as the Salado or Salado del Norte

River, with  $29.5 \text{ m}^3 \text{ s}^{-1}$  mean discharge, results from the confluence of numerous tributaries from the southwestern part of the province. At present the Cabra Corral and Las Tunas dams interrupt its course. Through a single tributary, the Juramento River receives two major rivers, the Metán River and the Las Cavas or Las Cañas River. The Juramento River basin is a complex fluvial system covering 24 000 km<sup>2</sup>. East of the studied area, the Juramento River runs through 1500 km of arid Chaco plain to the lower Paraná. The Itiyuro and Capiazuti rivers in northeastern Salta are currently endorheic basins, although these rivers possibly flow into the Bermejo River under exceptional flooding circumstances. The sources of the Itiyuro River are in Bolivia, at 21°43' S and 63°44' W. About 65 km in length, the river enters Argentina at 22°S following a NW–SE general direction, meets the Icuá Creek, and after 15 km ends in swamps between Tonono and Bobadal. The 1500 km<sup>2</sup> basin is between 400 and 600 m a.s.l., and has a tropical climate that is moderated by its altitude.

Considering the studied area from East to West, xerophytic bush and forest of the lower part are replaced by cloud forest at higher altitudes, followed by dry highlands and finally by the Puna desert (Cabrera 1951, 1971, 1976). Climatic differences between low altitudes at Orán in northern Salta and Güemes in central Salta against Humahuaca in the dry highland are shown in Figure 2.

### Material and methods

Sampling was conducted at 14, 10 and 2 localities studied during 1987, 1988 and 1991, respectively (Figs. 1 and 3). Results from 21 stations at the thermal creek in Aguas Calientes (Jujuy) during the same sampling periods were reported elsewhere (Menni et al. 1998). Collection locations were the shores of large rivers, small streams (>5 m width) or creeks (<5 m width). Fish samples were obtained during the day, using a seine net 10 m length and 1 m height, with 20 mm mesh size in the wings and 10 mm mesh size in the cod end. Hand nets were used at the same time to obtain as many species and individuals as possible, as indicators of their relative abundance (Winemiller,

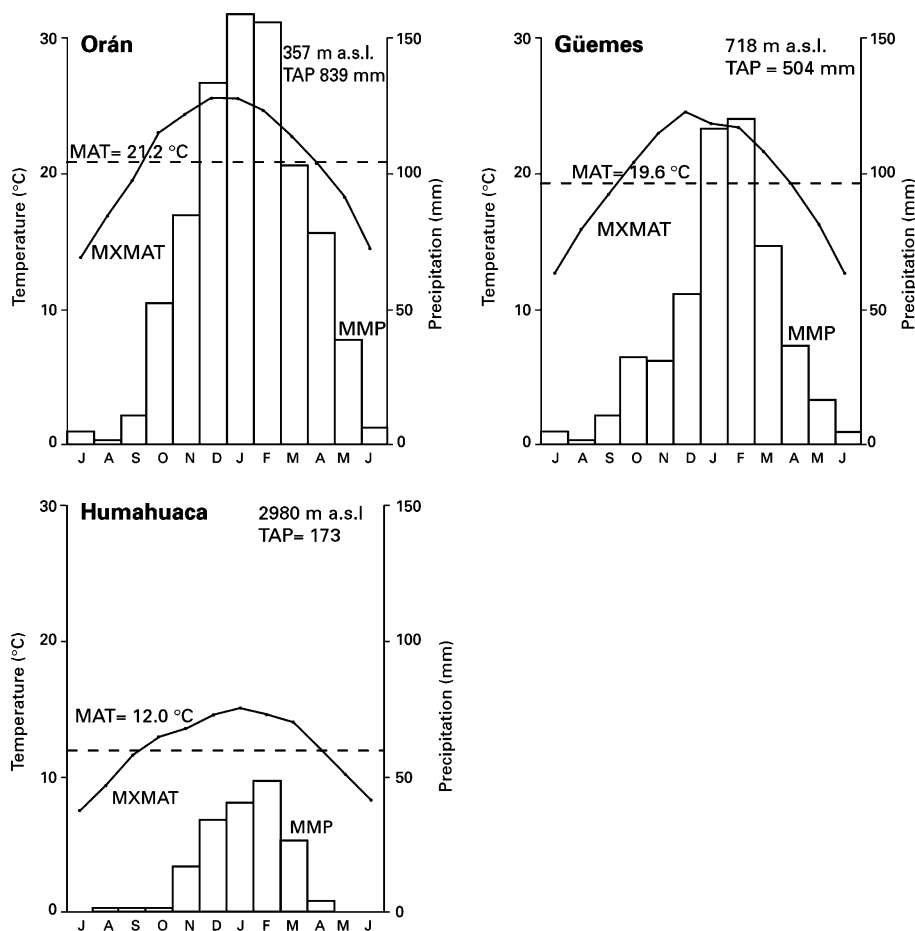


Figure 2. Climatograms of Orán (Yunga jungle area), Güemes (wet lowland) and Humahuaca (dry Puna area). MAT: mean annual temperature (dashes), MXMAT: maximum mean annual temperature (solid line), TAP: total annual precipitation, MMP: Mean monthly precipitation (bars). (Data from the Servicio Meteorológico Nacional, Argentina).

1996; Galacatos et al., 1996). Collecting effort was as uniform as the various environments allowed, and was carried out until no variation in catch was observed. In all 3278 specimens were obtained (Appendix A). Several species have not yet been conclusively identified and one new species of the siluriform genus *Rhamdella* (Heptapteridae) from the Itiyuro basin has been described (Miquelarena & Menni, 1999).

Altitudes were obtained from charts published by the Servicio Geográfico Militar and general climate traits (temperature and rainfall) were calculated after data from the Servicio Meteorológico Nacional (1985) (Table 1). Values of 12 water chemistry variables were obtained from 12 localities just before fishes were collected (Table 2).

Analyses were performed at the former Chemistry Laboratory of the Instituto de Limnología de La Plata following American Public Health Association (1989) techniques. A basic data matrix of 52 fish species by 26 localities was constructed (Table 3). Similarity matrices were calculated using the Jaccard index for geographical distribution and the Morisita index for abundance distribution (Hubalek, 1982; Matthews et al., 1994). The Pearson's correlation coefficient applied to abundance was utilized to confirm the analysis based on the Morisita index. Normality and homoscedacity were tested using the Kolmogorov–Smirnov and Levene tests respectively (Rohlf & Sokal, 1995). In the analysis, altitude was ln transformed. A cluster analysis using Q and R modes was performed

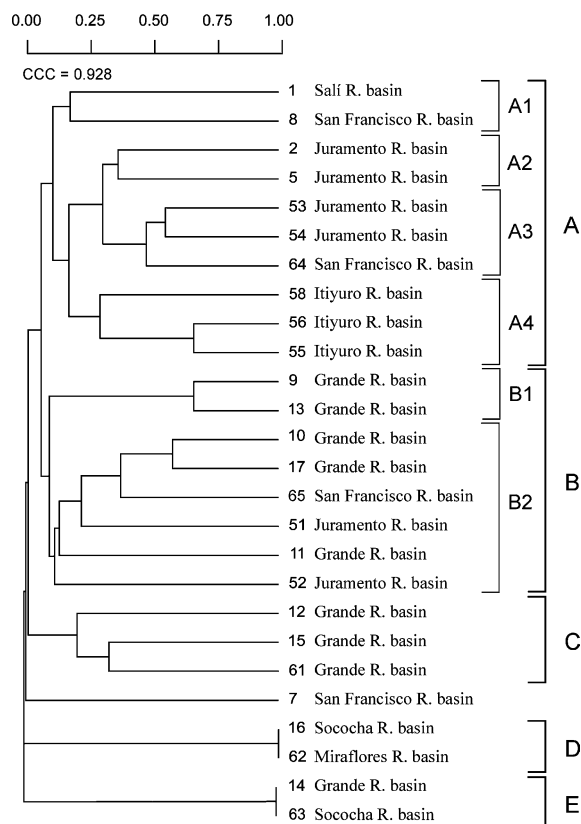


Figure 3. Cluster (UPGMA) of localities (OUT's) resulting from the Jaccard matrix of 26 localities by 52 species CCC = cophenetic correlation coefficient. River basins are indicated for each locality. Main cluster are labeled with capital letters, adding a number in subclusters.

using the unweighted pair group method using arithmetic averages (UPGMA). The cophenetic correlation coefficients (CCC) showed very low distortion in the clusters (Sokal & Rohlf, 1962). The Shannon index ( $H'$ ) was calculated for all stations and was modified as  $H' + 1$  to eliminate zero values in correlation analysis.

Correlations were calculated among climatic variables, including different measurements of temperature and rainfall, conductivity and total dissolved solids as water chemistry indicators, altitude, the conductivity/altitude ratio, number of species, number of individuals and the Shannon index. The statistical programs STATISTICA 5.1 (Statsoft®1999) and NTSYS 1.8 (Applied Bio-statistic®1993) were used. Localities 7 and 61 were not considered in this analysis because fishing effort was different in the former, and water

chemistry in the second was obviously influenced by human activity.

## Results

A total of 3278 individuals representing 53 species of fishes were collected. Best represented were the orders Characiformes with 5 families (Parodontidae, Anostomidae, Erythrinidae, Characidae and Crenuchidae), and the Siluriformes also with 5 families (Pimelodidae, Heptapteridae, Trichomycteridae, Callichthyidae and Loricariidae). The Cyprinodontiformes were represented by 2 families (Anablepidae and Poeciliidae) and the Perciformes by one (Cichlidae) (Table 3).

### *Fishes from the Grande and the San Francisco river basins in Jujuy*

The rather abundant *Trichomycterus roigi* was the only species obtained in northeastern Jujuy at Tilcara (Loc. 14, 2461 m a.s.l.) and Yavi (Loc. 63, 3440 m a.s.l.), near the Bolivian border. The unnamed creek in Yavi is a typical rhithron with rather clear water, rocky bottom, and strong current, with low content of total dissolved solids.

*Trichomycterus cf. boylei* was found in localities along the Grande River from over 2000 to 3693 m a.s.l. *Trichomycterus catamarcensis*, *Jenynsia maculata* and *Trichomycterus cf. spagazzinii* were collected in Loc. 12, a creek from the eastern slope of the Quebrada de Humahuaca. *Trichomycterus cf. rivulatus*, similar to a Bolivian species, lives in the Miraflores River or Río de Abra Pampa (Loc. 62, 3484 m a.s.l.) and in a creek near La Quiaca (Loc. 16, 3442 m a.s.l.).

On the eastern side of the sierra about at the latitude of Loc. 14, three localities from the San Francisco River basin housed different species. Only *Astyanax cf. eigenmanniorum* was obtained at Loc. 7. *Bryconamericus thomasi*, *Aphyocharax* sp., *Trichomycterus corduvensis* and *Hypostomus* sp. B were obtained in Loc. 8. Ten species from the comparatively large Saladillo River (Loc. 64), show dominance of fishes as *Astyanax lineatus* and *A. bimaculatus*, belonging to Paranensean genera.

Also from the San Francisco River basin are localities 10, 17, 65, 51, 11 and 52. Several of these

Table 1. Altitude and climate variables in northwestern Argentina

LOC	ALTITUDE	MAT	MXMAT	MIMAT	TA	PDY	TAP
64	367	21.0	27.3	15.4	11.8	357	101.7
8	465	18.0	26.9	14.9	12.0	136	99.6
5	555	21.0	26.6	14.4	12.2	890	97.7
56	565	22.0	26.6	14.4	12.2	825	97.5
55	600	22.0	26.5	14.2	12.2	900	96.7
58	600	22.0	26.5	14.2	12.2	900	96.7
52	723	17.7	26.1	13.6	12.4	870	94.0
65	734	19.6	26.1	13.6	12.4	504	93.8
54	780	21.0	25.9	13.3	12.5	912	92.8
53	789	20.0	25.9	13.4	12.5	791	92.6
1	815	18.9	25.8	13.2	12.6	1036	92.1
2	858	21.0	25.6	13.0	12.7	879	91.1
51	858	17.7	25.6	13.0	12.7	869	91.1
17	1150	16.6	24.7	11.5	13.1	785	84.8
9	1200	16.0	24.5	11.3	13.2	121	83.7
10	1259	16.0	24.3	11.0	13.3	121	82.5
11	1303	16.8	24.2	10.8	13.4	866	81.5
12	2094	16.6	21.6	6.8	14.7	550	64.4
13	2094	15.0	21.6	6.8	14.7	500	64.4
14	2461	13.8	20.4	5.0	15.3	134	56.5
15	2642	12.0	19.8	4.1	15.6	173	52.6
63	3440	9.4	17.2	0.2	16.9	305	35.3
16	3442	9.4	17.1	0.2	16.9	305	35.3
62	3484	13.1	17.0	0.0	17.0	586	34.4
61	3693	12.0	16.3	-1.0	17.3	208	29.8

LOC – locality number. MAT – mean annual temperature; MXMAT – maximum mean annual temperature; MIMAT – minimum mean annual temperature; TA – temperature amplitude (all in C); TAP – rainfall; PDY – rainfall days by year (in mm). (Data from the Servicio Meteorológico Nacional; Argentina).

localities display a high number of species for the area (9–18) in different combinations.

#### *Fishes from the Juramento River basin*

We sampled 6 localities from the Juramento River basin. Fishes from the Metán River (Loc. 2), and from a creek that empties into the left bank of the Juramento River near Tararipa (Loc. 5), added considerably to the Juramento River fish fauna. In the Río de las Conchas (Loc. 51), a tributary of the Metán River, northward of the city of Metán, *Astyanax lineatus*, *Bryconamericus thomasi*, *Trichomycterus cf. spgazzinii* and *Hypostomus* sp. C were captured.

*Ixinandria steinbachi* and *Trichomycterus cf. spgazzinii* were obtained from the Las Piedras

River (Loc. 52), about 10 km north of Metán, which is probably the locality mentioned by Ringuélet (1975) or very close to it. *Astyanax bimaculatus*, *Odontostilbe microcephala*, *Characidium* sp., *Bryconamericus thomasi*, *Parodon carrikeri*, *Acrobrycon tarijae* and *Astyanax eigenmanniorum* were obtained from the Las Cañas River (Loc. 53), above the left bank of the Juramento River. With the exception of the two species of *Astyanax*, the same species also occurred at Las Víboras (Loc. 54), together with *Loricaria tucumanensis* and *Trichomycterus spgazzinii*.

#### *Fishes from the Itiyuro basin*

At the bottom of the weir of the Itiyuro dam (Loc. 55), we found *Characidium* sp. (very abundant),

Table 2. Physical-chemical traits of waters in environments from northwestern Argentina

Locality	TDS	COND	CO <sub>3</sub> <sup>2-</sup>	CO <sub>3</sub> H <sup>-</sup>	Cl <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	Na <sup>+</sup>	K <sup>2+</sup>	Ca <sup>2+</sup>	Mg <sup>2+</sup>	pH	COD
8	400	348	0	194.1	7.1	95.2	32	1.9	63.6	6.4	7.20	2.5
54	610	533	9.8	271.3	21.3	120.8	51.2	3.2	43.6	32.7	8.48	5.6
64	700	760	24.0	258.6	107.8	76.8	162.9	3.9	23.4	18.2	8.79	9.0
55	760	755	4.9	253.9	31.2	252.3	77.0	4.4	92.9	24.5	8.34	5.6
56	900	877	0	338.5	31.9	299.9	108.1	4.6	96.1	18.8	8.16	8.0
58	750	759	9.8	233.9	35.5	263.3	77.0	3.6	5.4	23.0	8.33	5.6
9	60	65	0	30.5	3.6	13.1	3.0	1.1	56.2	5.2	6.86	9.0
65	1210	1253	4.8	165.9	400.0	215.9	341.4	5.3	29.5	11.6	8.53	10.2
12	190	174	0	110.9	7.1	14.8	22.0	1.0	38.0	4.8	6.89	3.5
15	350	369	0	155.3	14.2	86.6	35.0	2.9	156.7	13.9	7.22	5.3
61	1150	1085	0	169.2	71.0	494.5	99.1	6.7	32.3	33.0	8.14	2.0
63	300	353	14.7	72.2	66.1	57.0	43.2	6.1	–	5.0	8.90	5.6

Localities ordered as resulting from cluster analysis of presence/absence of species. TDS–total dissolved solids (mg l<sup>-1</sup>)–COND–conductivity (μS cm<sup>-1</sup>); COD; chemical oxygen demand (mg O<sub>2</sub> l<sup>-1</sup>). Ions in mg l<sup>-1</sup>.

*Astyanax lineatus*, *Hypostomus* sp. B and *Trichomycterus barbouri*. A large number of individuals of *Characidium* sp. were observed in the wall of the weir (about 3 m high), out of the water and exposed to the sun, though the surface they occupied was occasionally splashed by water. This behavior was described in detail by Zamprogno et al. (1989) from a Brazilian waterfall (see also Buckup et al., 2000). Five hundred meters down river of the dam, in an area with large boulders (Loc. 58) we obtained *Astyanax bimaculatus*, *Odontostilbe microcephala*, *Characidium* sp., *Rhamdella aymarae* and *Trichomycterus barbouri*. From the Capiazuti River between Aguaray and Campo Durán (Loc. 56), we obtained *Astyanax bimaculatus*, *Odontostilbe microcephala*, *Characidium* sp., *Astyanax* sp. C and *Trichomycterus barbouri*, three of these shared with Loc. 58.

Nine species were captured in Locality 1 of the Salí River basin, an endorheic system ending in a hypersaline lake. Only *Heptapterus mustelinus* and *Oligosarcus bolivianus* were obtained in Loc. 9, a relatively high mountain stream, and the same species and *Astyanax* sp. B in a manmade channel at Tumbaya (Loc. 13).

#### Localities and species clustering

Both localities and the species found in each of them are ordered in Table 3 according results from the cluster analysis. Analyses of similarity of

localities based on presence/absence of species provided well-defined clusters (Fig. 3). Main locality clusters were labeled with capital letters and minor clusters identified by numbers (e.g. A1, B2 ...). The main cluster A comprises localities along the western border of the Chaco plain and from the Itiyuro River basin. Fish composition in locality 55 is somewhat different because it is the weir of the Itiyuro dam. In the cluster A1 the southernmost Loc. 1 (La Candelaria) and 8 (small pools related with the Duraznal River of the San Francisco River basin) has a relatively low similarity with clusters A2 and A3 (mainly localities from the Juramento river basin) and A4 (Itiyuro basin).

Locality clusters A2 and A3 share the presence of *Astyanax bimaculatus*, *Odontostilbe microcephala*, *Characidium* sp., *Bryconamericus thomasi*, *Parodon carrikeri* and *Acrobrycon tarijae*, which are components of a northwestern fauna. Some Paranensean species such as *Cnesterodon decemmaculatus*, *Rhamdia quelen*, *Pimelodus albicans* and the rather eurytopic *Bryconamericus iheringi*, mixed with species of *Loricaria*, *Rineloricaria* and *Oligosarcus bolivianus*, of northwestern character, occur further south at locality 2. The typical Pampasic species *Hoplias malabaricus* and *Rhamdia quelen* occur at locality 5. In cluster A4 (Itiyuro River basin), the same northwestern species, *Astyanax bimaculatus*, *Odontostilbe microcephala* and *Characidium* sp. were found together with, in





different combinations, the endemic *Rhamdella aymarae*, *Hypostomus* sp. B, *Trichomycterus barbouri* (in all three localities), *Astyanax* sp. C and *Odontostilbe* sp. B.

In the large cluster B, most stations have a different combination of northwestern species than that found in cluster A. These species are *Astyanax lineatus*, *Heptapterus mustelinus*, *Oligosarcus bolivianus* and *Jenynsia maculata* plus Paranensean species like *Rhamdia quelen*, and *Corydoras* cf. *paleatus*. In addition, a particular group of species is found in Loc. 65. Several of these species are herein recognized for the first time as components of the northwestern fauna, namely, *Microglanis cottoides*, *Rineloricaria* cf. *catamarcensis*, *Rineloricaria* sp., *Trichomycterus* cf. *barbouri* and three species of *Hypostomus*.

Localities of cluster B correspond to a central sector at high and middle altitudes around Jujuy and Salta cities. All of them, except locality 13, are under a subtropical-highland climate with abundant rains. These localities belong to the San Francisco River basin. The southern sector includes localities with similar traits, but related with the Juramento River basin (Loc. 51 and 52).

A smaller but well-defined group is formed by *Trichomycterus* cf. *boylei* in cluster C, grouped with *Trichomycterus catamarcensis*, *T.* cf. *spgazzinii* and *Jenynsia maculata* in Loc. 12 and ‘*Bryconamericus*’ sp. and *Trichomycterus alterus* in Loc. 15. *Jenynsia maculata*, *J. alternimaculata* and *J. pygogramma* are endemic of northwestern Argentina (Ringuelet et al. 1967a; Ghedotti 1998). These localities are transitional places showing a clear South to North impoverishment gradient, as well as decreasing Paranensean influence. The southernmost locality of the cluster (Loc. 12) includes four species: *Jenynsia maculata*, *Trichomycterus* cf. *spgazzinii*, *T.* cf. *boylei* and *T. catamarcensis*. Intermediate locality 15 includes ‘*Bryconamericus*’ sp., *Trichomycterus alterus*, and *T.* cf. *boylei*. *Trichomycterus* cf. *boylei* is the only species at the northern most locality (Loc. 61) and is the only species found in all three stations. The remaining localities, in the most northwestern part of the sampled area, cluster together based on the presence of *Trichomycterus* cf. *rivulatus* (cluster D) and *T. roigi* (cluster E).

## Ecology

Values of water chemistry traits are given in Table 2. About half of the stations (41.7%) have water in the hypohaline interval ( $< 0.5 \text{ g l}^{-1}$ ) and the other half (58.3%) in the oligohaline interval ( $0.5\text{--}5 \text{ g l}^{-1}$ ) (in the sense of Ringuelet et al., 1967b). Localities with lower content of total dissolved solids are situated in the western part of the sampled area and mainly at high altitudes. Locality 61 (Tres Cruces) is an exception, probably due to pollution by cattle. Values of pH were high. Values of chemical oxygen demand, which are low compared with other places in Argentina (Menni et al., 1996), are particularly low in small highland creeks.

A single locality from the San Francisco River basin (Loc. 8) and all of the sampled localities from the Grande River basin lacked  $\text{CO}_3^-$  and had low values of  $\text{Mg}^{2+}$ . The Itiyuro River basin had high values of  $\text{CO}_3\text{H}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$ .

Highest values of chemical oxygen demand were observed at Sanjón Seco and Saladillo rivers. These are streams over 5 m width, larger than other localities, with richer fauna and direct tributaries of the San Francisco River. Median values correspond to medium size streams in the relatively dry but forested area in northern Salta, where litter is probably washed to the rivers. The Saladillo creek has the highest values of  $\text{Cl}^-$  and  $\text{Na}^+$ , a feature acknowledged in its name.

Neither species richness nor number of individuals was uniform among localities. The former values ranged from 1 to 20 species and the latter from 5 to 533 individuals per locality (Table 3). High number of species and high calculated diversities were common in wet areas at lower altitude. Fewer species and lower diversity values were found in dryer places at higher altitude. The highest number of species and individuals were found at localities of the clusters A2 and A4 (Fig. 3, Table 3).

The impoverished nature of the fish fauna becomes evident in the most northward localities, where usually only a single species was obtained per station: *Trichomycterus roigi* at Tilcara and Yavi (Loc. 14 and 63), *T.* cf. *boylei* at Loc. 61 (Grande River near Tres Cruces), *T.* cf. *rivulatus* at localities 62 (Miraflores River) and Loc. 16 (creek

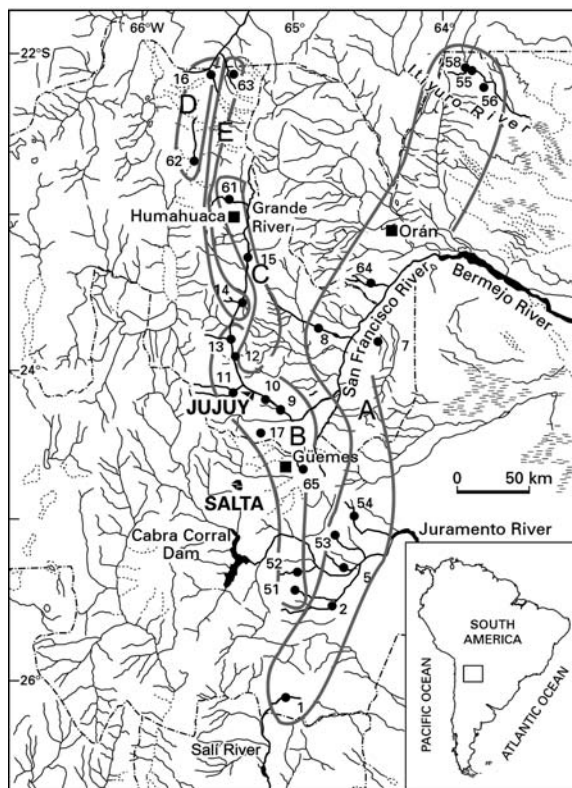


Figure 4. Patterns of localities distribution based in the cluster analysis of 26 localities by 52 species Jaccard matrix. Areas of clusters labeled with capital letters as in Figure. 3.

south of La Quiaca). Localities 61, 62 and 63 are in the Puna Plateau, under harsh dry conditions, at 3693, 3440 and 3442 m a.s.l. In Yavi *T. roigi* occurs in relatively rich populations (see also Fernández, 1996a). However, a few kilometers northward of Tilcara, at Quebrada Colorada (Loc. 15), there are three species (*Trichomycterus cf. boylei*, *T. alterus* and '*Bryconamericus*' sp.).

The general clustering patterns show two longitudinal fringes (Fig. 4). The eastern fringe includes localities from the Itiyuro River basin in northeastern Salta, from the San Francisco River basin, and from the Juramento River basin, which conform the cluster A. The western fringe includes four areas. The wetter, richer southern area, includes all the localities of the cluster B. Northward, localities are ordered in a SE to NW gradient, with progressively higher altitudes and dryer climate, resulting in clusters C, D and E.

When species richness (the number of species) at lower altitudes, as found at localities of clusters

A2, A3 and B2, was compared with that of localities in the highland country (clusters D and E), an impoverishment was observed with increasing altitude and along the SE/NW direction. A high negative correlation was observed between altitude and both the number of species and of individuals (Rhode 1992) (Figs. 5 and 6). Values of the Shannon diversity index closely agreed with the pattern observed for richness and numbers of individuals, being higher in wetter low areas, and lower in dry, high altitude areas. Values ranged from 1.31 to 2.65 in localities near the San Francisco River, and from 0.35 to 3.01 in localities related with the Juramento River. Values from 0.59 to 2.08 were obtained from the lower section of the Grande River. Following that river up to the North, diversity decreased rapidly with increasing altitude and dryness, with values of 0.65 near Huacalera (Loc. 15) and 0.0 in Tilcara, near Tres Cruces, in the Abra Pampa River, near La Quiaca and in Yavi. These localities, inhabited by a single species, are physically controlled communities, partly in the sense of Sanders (1979).

#### Landscape and the fish fauna

Correlations among community traits, altitude, water chemistry indicators and climatic variables were highly significant in most cases (Table 4). Conductivity did not significantly relate to variables describing temperature and rainfall, but showed a high correlation with species number and consequently was correlated with diversity. Number of species was highly correlated with all the examined climatic and environmental variables except rainfall. Number of individuals correlated

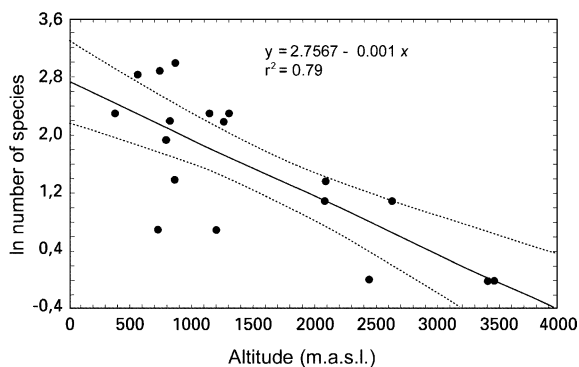


Figure 5. Regression line of species number as related to altitude.

Table 4. Correlation values among climatic and water chemistry factors, number of species and individuals, the Shannon index ( $H' + 1$ ) and the conductivity/altitude ratio

	Ln Altitude	COND	TDS	COND	$H' + 1$	MAT	MXMAT	MIMAT	TA	PDY	TAP	N <sup>0</sup> . sp
COND	-0.5517											
	N = 11											
<b>TDS</b>	-0.5928	-0.9926**										
	N = 11	N = 11										
COND	-0.8202**	0.8711**	0.8647**									
	N = 11	N = 11	N = 11									
$H' + 1$	-0.5721**	0.6997*	0.7129*	0.7265*								
	N = 24	N = 11	N = 11	N = 11								
MAT	-0.9040**	0.5954	0.6521*	0.7612**	0.6035**							
	N = 24	N = 11	N = 11	N = 11	N = 24							
MXMAT	-0.9652**	0.5132	0.5666	0.7412**	0.6447**	0.9134**						
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24						
MIMAT	-0.9651**	0.5132	0.5666	0.7412**	0.6451**	0.9132**	0.9999**					
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24	N = 24					
TA	0.9651**	-0.5132	-0.5666	-0.7413**	-0.6446**	-0.9133**	-0.9999**	-0.9999**				
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24	N = 24	N = 24				
PDY	-0.9652**	0.5132	0.5666	0.7413**	0.6450**	0.9133**	0.9999**	0.9999**	-0.999**			
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24	N = 24	N = 24	N = 24			
TAP	-0.4349**	0.5080	0.5628	0.4199	0.3965	0.6176**	0.4724*	0.4724**	-0.4724*	0.4724*		
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24	N = 24	N = 24	N = 24	N = 24		
N <sup>0</sup> . Sp.	-0.4861*	0.7866**	0.7744**	0.6900*	0.9041**	0.5472**	0.5266**	0.5266**	-0.5261**	0.5265**	0.3601	
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24	N = 24	N = 24	N = 24	N = 24	N = 24	
N <sup>0</sup> . IND	-0.5392**	0.4544	0.4499	0.4772	0.4351**	0.5843**	0.4966*	0.4967*	-0.4965*	0.4967*	0.3841	0.5722**
	N = 24	N = 11	N = 11	N = 11	N = 24	N = 24	N = 24	N = 24	N = 24	N = 24	N = 24	N = 24

Abbreviations as in Table 2.

\*  $p < 0.05$ , \*\*  $p < 0.01$ . N – sample size.

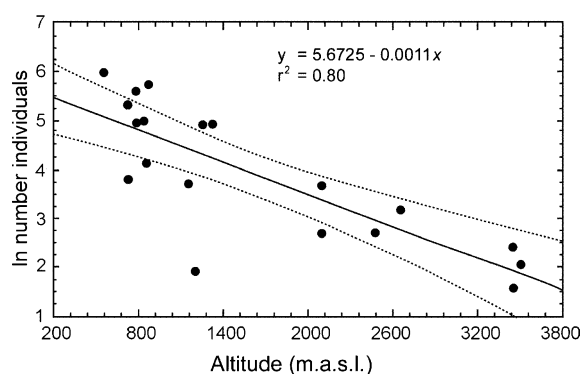


Figure 6. Regression line of number of individuals as related to altitude.

closely with altitude and mean annual temperature, which themselves were strongly correlated. The regression line between altitude and number of species (Fig. 5) is a synopsis of the relationship among number of species and environmental variables.

## Discussion

In the studied environments, water chemistry is characterized by high values of  $\text{CO}_3\text{H}^-$  and  $\text{SO}_4^{2-}$  and/or high values of  $\text{Cl}^-$  and  $\text{Na}^+$ . High values of  $\text{SO}_4^{2-}$  are uncommon in other places of Argentina (Bonetto & Lancelle, 1981; Menni et al., 1984; Menni et al., 1988; Menni et al., 1992; Menni et al., 1996; Bonetto et al., 1998). Localities from the eastern wet fringe show homogeneous high values of  $\text{CO}_3\text{H}^{2-}$  as well as high values of  $\text{SO}_4^{2-}$  and homogeneous values of total dissolved solids and conductivity.

Prior to this study, 84 species of fish were known from Northwestern Argentina. Fifty-nine species were collected during this survey, including 7 species only found at Aguas Calientes (Menni et al. 1998). As only 19 of these species were reported from this region previously, 40 species are new for the area and/or particular localities. The presence of *Trichomycterus catamarcensis* in locality 12 is only the second report of the species. These results increase by one-third the number of species in northwestern Argentina, which is now 124. This figure represents about 39% of the number of freshwater fishes known from the entire country.

*Trichomycterus roigi*, known from several localities in western and northwestern Salta and western and southwestern Jujuy, is a high altitude fish, living from about 1000 m a.s.l in the Grande River to 4300 a.s.l. in water below 24C (Arratia et al., 1983; Fernández, 1996a). We found this species near the Bolivian border, in a clear water stream with low temperature, without vegetation. This environment is similar to the type locality of the species in the rhithron area of the Pastos Chicos River, an endorheic basin with torrential floods associated with intense summer rains (Arratia & Menu Marque, 1984). Lack of competitors probably explains the large number of individuals caught at Yavi. As trichomycterids in highland creeks in Cordoba, *T. roigi* inhabits below small irregular stones (Menni et al., 1984). Although there are warm water species of Trichomycteridae, most species from Argentina were described as "Andean" because they inhabit clear cold stream waters (Ringuelet et al., 1967a, Ringuelet 1975, Arratia et al., 1983), as did the several species reported here.

The fish fauna is represented in each environment by particular combinations of wide ranging eurytopic species (within the area), such as *Bryconamericus thomasi* (occurring in 38.4% of localities), *Characidium* sp. (34.6%), and *Astyanax bimaculatus*, *Odontostilbe microcephala* and *Heptapterus mustelinus* (30.7% each), mixed with locally distributed, sometimes isolated, trichomycterids. *Trichomycterus* cf. *boylei* and *T. roigi* were nearly as abundant as the above-mentioned dominant species. *Astyanax lineatus*, *Acrobrycon tarija* and *Jenynsia maculata* are also abundant in some localities.

*Characidium* sp. was most abundant in a dam on the Itiyuro River, near the type locality of the endemic *Rhamdella aymarae*. Localities from this basin share homogeneous high conductivity and high  $\text{CO}_3\text{H}^-$ ,  $\text{SO}_4^{2-}$  and  $\text{Ca}^{2+}$  values.

Small seasonal courses in the Quebrada de Humahuaca, usually inhabited only by trichomycterids, lack  $\text{CO}_3^{2-}$  and have  $\text{CO}_3\text{H}^-$  values lower than Itiyuro basin localities. *Trichomycterus* cf. *boylei* lives only at this group of stations.

The Pacara creek, in a high wet mountainous area, is markedly oligotrophic. Only *Heptapterus mustelinus* and *Oligosarcus bolivianus* live there. The latter species, which occurs both in Bolivia

and Argentina, is an 'Andean element' of the ten 'plateau species group' occurring in medium to high altitudes (200–1500 m a.s.l.) (Menezes, 1988). The presence of these species in both a high-energy oligotrophic stream (Loc. 9) and a slow flowing man-made channel at high altitude (Loc. 13) suggests wide ecological tolerances.

Some environments, particularly the Saladillo Creek (Loc. 65) and the Itiyuro basin, show some traits in common with the stream influenced by thermal sources in Aguas Calientes, Jujuy (Menni et al., 1998). Because of its thermal traits, this stream differs from localities considered here in the composition of the fish fauna, the relative number of species, and the high number of some of them, in many cases well over the total number collected in the rest of localities together. For example, 1241 specimens of *Astyanax bimaculatus* were collected in Aguas Calientes, while 297 were obtained from all remaining localities.

Species richness is relatively high at medium altitudes in the wet area about 24°10' S, where the Grande River turns East to join the San Francisco River. This was a zone with rich natural vegetation and heavily flowing creeks around Jujuy and Güemes. These richness values are, nevertheless, rather lower than those found in localities of the Paraguay – Paraná rivers basins (Cordiviola de Yuan, 1980, Cordiviola de Yuan & Pignalberi de Hassan, 1981, 1985; Menni et al., 1992). Indeed, they are below the number of species that may be found in some lotic environments related with the Río de la Plata at 36° S (50 species, Almirón et al., 2000). Some variation in local assemblages richness is expected, because many species in regional pools cannot find appropriate habitat at all stream sites (Casciotta et al., 1989; Hugueny & Paugy, 1995; Matthews, 1998).

Correlation analysis among faunistic traits (number of species and individuals), general climate traits (temperature and rainfall), altitude, and water chemistry indicators (conductivity and total dissolved solids) strongly support the relationship among faunistic traits and these environmental factors. Species number is positively correlated with most variables, excepting total rainfall, with correlation higher for water chemistry factors. Number of individuals is more correlated with altitude and temperature-related variables. With the exception of rainfall, the

Shannon index correlated significantly with most variables, suggesting that diversity depends from both climatic and water chemistry factors. Altitude may be used as a summary variable.

Cluster analysis, based in both presence – absence of species and their abundance, show that localities and species have a clear pattern of latitudinal distribution, related with physiography, climate and water chemistry.

In conclusion, from a systematic point of view, the considerable increase in the number of species now known to be present in the studied area, clearly indicates that this fish fauna forms a well defined and complex northwestern group, different from both the Pampasian and Middle Paraná River faunas. From an ecological point of view, the bulk of the information (Ringuelet, 1975; Arratia et al., 1983; Menni et al., 1984, 1992, 1996, 1998), related general climate and ecological traits with composition and distribution of fishes, including distribution patterns related with general climate (Ringuelet, 1975; Menni et al., 1992) or altitude and rain (Arratia et al., 1983). Herein, we show that in an area with well-defined ecological gradients in northwestern Argentina, different environments along these gradients exhibited consistent differences in the number of fish species inhabiting them and their density. Both richness and diversity gradually decreased along a latitudinal gradient, related with decreasing temperature and rainfall with increasing altitude. Particular fish communities were found to be related with these environmental variables.

#### Acknowledgements

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## Appendix A

Reference material deposited in the fish collection at the Instituto de Limnología de la Plata (ILPLA). Number of specimens between parenthesis.

*Parodon carrikeri*: Loc. 2, ILPLA 1482, (6); Loc. 53, ILPLA 1503, (29); Loc. 54, ILPLA 1455, (4); Loc. 64, ILPLA 1499, (2); Loc. 65, ILPLA 1434, (2); *Leporellus* cf. *vittatus*: Loc. 64, ILPLA 1502, (1). *Hoplias malabaricus*: Loc. 5, ILPLA 1460, (2). *Astyanax bimaculatus*: Loc. 2, ILPLA 1477, (28); Loc. 5, ILPLA 1459, (147); Loc. 53, ILPLA 1507, (1); Loc. 56, ILPLA 1449, (2) Loc. 58, ILPLA 1512, (7); Loc. 64, ILPLA 1493, (58). Loc. 65, ILPLA 1424, (60). *Astyanax eigenmanniorum*: Loc. 5, ILPLA 1468, (1); Loc. 10, ILPLA 1519, (7); Loc. 53, ILPLA 1508, (1); Loc. 64, ILPLA 1498, (1). *Astyanax* cf. *eigenmanniorum*: Loc. 2, ILPLA 1488, (4). *Astyanax lineatus*: Loc. 2, ILPLA 1487, (2); Loc. 10, ILPLA 1515, (43); Loc. 17, ILPLA 1443, (2). Loc. 51, ILPLA 1446, (34); Loc. 55, ILPLA 1471, (1); Loc. 64, ILPLA 1496, (122); Loc. 65, ILPLA 1423, (85). *Astyanax* cf. *lineatus*: Loc. 5, ILPLA 1467, (21). *Astyanax* sp. A: Loc. 5, ILPLA 1466, (3). *Astyanax* sp. B: Loc. 13, ILPLA 1513, (12). *Astyanax* sp. C: Loc. 55, ILPLA 1473, (1). Loc. 56, ILPLA 1452, (1); Loc. 65, ILPLA 1437, (1); *Bryconamericus iheringi*: Loc. 1, ILPLA 1526, (16); Loc. 2, ILPLA 1490, (34).

*Bryconamericus thomasi*: Loc. 2, ILPLA 1491, (37). Loc. 5, ILPLA 1469, (21); Loc. 17, ILPLA 1441, (15); Loc. 51, ILPLA 1447, (8); Loc. 53, ILPLA 1509, (4); Loc. 64, ILPLA 1500, (2); Loc. 65, ILPLA 1435, (2). '*Bryconamericus*' sp.: Loc. 11, ILPLA 1415, (39). Loc. 15, ILPLA 1524, (1). *Oligosarcus bolivianus*: Loc. 2, ILPLA 1479, (2). Loc. 5, ILPLA 1464 (6); Loc. 9, ILPLA 1522, (6); Loc. 10, ILPLA 1520, (1); Loc. 13, ILPLA 1514, (2); Loc. 17, ILPLA 1438, (1); Loc. 65, ILPLA 1433, (2). *Acrobrycon tarijiae*: Loc. 2, ILPLA 1476, (80); Loc. 5, ILPLA 1458, (24); Loc. 53, ILPLA 1505, (24); Loc. 54, ILPLA 1453, (109). *Acrobrycon* cf. *tarijiae*: Loc. 5, ILPLA 1465, (1); Loc. 64, ILPLA 1501, (5). *Odontostilbe microcephala*: Loc. 1, ILPLA 1418, (5); Loc. 2, ILPLA 1475, (68);; Loc. 53, ILPLA 1504, (145); Loc. 54, ILPLA 1452, (1); Loc. 54, ILPLA 1457, (1); Loc. 58, ILPLA 1510, (15); Loc. 64, ILPLA 1497, (9). *Odontostilbe* sp. A: Loc. 11, ILPLA 1413, (2). *Odontostilbe* sp. B: Loc. 55, ILPLA 1492, (1). *Aphyocharax* sp.: Loc. 8, ILPLA 1409, (2). *Characidium* sp.: Loc. 1, ILPLA 1420, (1); Loc. 2, ILPLA 1481, (2); Loc. 5, ILPLA 1461, (22). Loc. 53, ILPLA 1506, (24); Loc. 54, ILPLA 1454, (6); Loc. 55, ILPLA 1470, (800); Loc. 56, ILPLA 1450, (4); Loc. 58, ILPLA 1511, (2); Loc. 64, ILPLA 1495 (23). *Microglanis cottoides*: Loc. 65, ILPLA 1427, (6). *Pimelodus albicans*: Loc. 2, ILPLA 1474, (3). *Heptapterus mustelinus*: Loc. 1, ILPLA 1525, (3); Loc. 2, ILPLA 1480, (1); Loc. 9, ILPLA 1523, (1); Loc. 10, ILPLA 1516, (49); Loc. 11, ILPLA 1416, (1); Loc. 11, ILPLA 1528, (1); Loc. 17, ILPLA 1439, (9); Loc. 65, ILPLA 1425, (15); *Pimelodella* cf. *gracilis*: Loc. 2, ILPLA 1478, (16). *Rhamdia quelen*: Loc. 5, ILPLA 1462, (9); Loc. 10, ILPLA 1518, (4); Loc. 17, ILPLA 1444, (1); Loc. 65, ILPLA 1426, (7). *Trichomycterus alterus*: Loc. 15, ILPLA 1395, (2). *Trichomycterus barbouri*: Loc. 55, ILPLA 1388, (22); Loc. 56, ILPLA 1389, (3); Loc. 58, ILPLA 1390, (3). *Trichomycterus* cf. *barbouri*: Loc. 5, ILPLA 1392, (1); Loc. 65, ILPLA 1391, (7). *Trichomycterus corduvensis*: Loc. 1, ILPLA 1408, (6); Loc. 8, ILPLA 1404, (63). *Trichomycterus* cf. *corduvensis*: Loc. 10, ILPLA 1400, (1). *Trichomycterus* cf. *boylei*: Loc. 12, ILPLA 1385, (3); Loc. 15, ILPLA 1386, (19); Loc. 61, ILPLA 1384, (163). *Trichomycterus* cf. *rivulatus*: Loc. 16, ILPLA 1405, (5); Loc. 62, ILPLA 1406, (8). *Trichomycterus roigi*: Loc. 14, ILPLA 1394, (15); Loc. 63, ILPLA

1393, (127). *Trichomycterus spegazzinii*: Loc. 64, ILPLA 1399, (2). *Trichomycterus cf. spegazzinii*: Loc. 12, ILPLA 1397, (27); Loc. 17, ILPLA 1407, (1); Loc. 51, ILPLA 1401, (20); Loc. 52, ILPLA 1402, (42); Loc. 65, ILPLA 1396 (6). *Trichomycterus cf. weyrauchi*: Loc. 11, ILPLA, 1387, (8). *Trichomycterus catamarcensis*: Loc. 12, ILPLA 1398, (2). *Lepthoplosternum pectorale*: Loc. 2, ILPLA 1483, (1). *Corydoras cf. paleatus*: Loc. 10, ILPLA 1517, (22); Loc. 11, ILPLA 1412, (3); Loc. 17, ILPLA 1442, (4); Loc. 65, ILPLA 1436, (1). *Loricaria tucumanensis*: Loc. 2, ILPLA 1485, (3); Loc. 54, ILPLA 1456, (1); Loc. 64, ILPLA 1494, (4). *Ixinandria steinbachi*: Loc. 11, ILPLA 1414, (11); Loc. 17, ILPLA 1440, (2); Loc. 52, ILPLA

1403, (3); Loc. 65, ILPLA 1431, (1). *Rineloricaria* sp.: Loc. 2, ILPLA 1484, (3). *Rineloricaria cf. catamarcensis*: Loc. 1, ILPLA 1421, (7); Loc. 65, ILPLA 1432, (1). *Hypostomus* sp. A: Loc. 65, ILPLA 1429, (1). *Hypostomus* sp. B: Loc. 1, ILPLA 1417, (24); Loc. 5, ILPLA 1463, (59); Loc. 8, ILPLA 1410, (6); Loc. 55, ILPLA 1472, (1); Loc. 65, ILPLA 1428, (7). *Hypostomus* sp. C: Loc. 1, ILPLA 1422, (2); Loc. 2, ILPLA 1486, (1); Loc. 65, ILPLA 1430, (1). *Jenynsia maculata*: Loc. 1, ILPLA 1419, (74); Loc. 10, ILPLA 1521, (2); Loc. 11, ILPLA 1411, (66); Loc. 12, ILPLA 1527, (7); Loc. 17, ILPLA 1445, (3). *Cnesterodon decemmaculatus*: Loc. 2, ILPLA 1489, (1).