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**THE FISHES OF THE BENI-MAMORÉ AND PARAGUAY BASINS,  
AND A DISCUSSION OF THE ORIGIN OF THE  
PARAGUAYAN FAUNA\***

BY

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The resemblance of the freshwater fish fauna of the La Plata to that of the Amazon basin has been known since the earliest collections were made in those regions. During the past fifty years the identification of a great amount of material taken from numerous localities in those river systems has further emphasized this similarity.

Jordan ('96) pointed out that the marshy character of the upland between the Tapajos and the Paraguay would permit the free movement of fishes between the two basins. Eigenmann ('06) and Eigenmann, McAtee, and Ward ('07) directed attention to the low nature of the divide between the Guaporé and some of the principal headwaters of the Paraguay and suggested this as a possible migratory route.

Haseman ('12) was unable to account for the remarkable similarity of the freshwater fish fauna in many of the smaller river basins whose headwaters are near those of the Amazon, by migration of forms now existent in the Amazon, and used the Paraguay and Amazon basins as examples to illustrate the hypothesis of parallel evolution as applied to the South American freshwater fish problem.

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Eigenmann and Eigenmann ('91), and Eigenmann ('09) compared the then known faunas of the La Plata and Amazonian systems. Eigenmann, McAtee, and Ward ('07) compared the rather completely known fauna of the Paraguay with that of the Amazon. No study, however, has been made of the relationship of the fauna of any of the northern affluents of the La Plata and southern affluents of the Amazon whose headwaters intermingle on the highlands of Matto Grosso. This has been due to a lack of knowledge of the nature of the complete fauna from any of the southern affluents of the Amazon. During the past twenty-five years the identification of large collections taken from the Beni, Guaporé, and Mamoré basins has made this region well known ichthyologically, and a comparison of the fauna of the Paraguay with that of the Beni-Mamoré is now possible.

The close similarity of the Beni-Mamoré to the Paraguay in size, physical, geographical, and geological features has given many environments that are practically identical. The two systems apparently differ only in respect to the smaller size and more tropical position of the former, and the slightly lower altitude of the latter. These similar conditions, the rich faunas of the two basins, and the lowland divide between them, which is older than the South American freshwater fish fauna, make a comparison of the two regions doubly interesting.

As yet the faunas of the Xingu, Tapajos, and Tocantins are imperfectly known.

This report was made as a part of the general plan for the study of the problem of the distribution of the South American freshwater fishes as outlined by Eigenmann ('06 and '09). The first intensive work under this plan was done in British Guiana, followed by Columbia, and the western slopes of the Andes. After exhaustive work in these regions, attention was turned to the problem on the eastern slope of the Andes, which had been started several years previously. Large collections had been made and were being identified, monographs were being prepared and the work was well under way at the time of Dr. Eigenmann's death on April 24, 1927.

The collections made by Dr. Carlos Ternetz in the Tocantins will greatly increase the knowledge of the fishes of that basin when they are studied. Dr. Ternetz, who was an unusually expert fish collector, collected for Dr. Carl H. Eigenmann from September 1923 to May 1925 in the Tocantins, Lower Amazon, Rio Negro, Cassiquiare and Orinoco. This is one of the largest fish collections to come out of South America and is probably second only to the Agassiz collections that were made during the Thayer Expedition to Brazil. The Ternetz collection was acquired by the California Academy of Sciences along with the entire Indiana University fish collection, and is now located in the Museum of that institution in San Francisco.



## PHYSICAL AND GEOLOGICAL FEATURES

The Beni-Mamoré drain an area slightly smaller than the Paraguay. Both rivers extend into the eastern slope of the Bolivian Andes. Each drains a part of the highlands of Matto Grosso and large parts of the Gran Chaco, which is the low broad plain of northern Argentina, Paraguay, and southeastern Bolivia. The Beni-Mamoré system extends farther south than any other part of the Amazonian system. Between 14 and 19 degrees it has the same latitude as the Paraguay.

The Beni-Mamoré system is composed of three large converging streams, the Beni, Mamoré, and the Guaporé. The Beni and the Mamoré have their sources in the Andes near La Paz and Cochabamba respectively. The Beni is fed chiefly by streams from the Andes, whereas the Mamoré receives many tributaries from the grassy plains of Bolivia. Both of the latter streams run across alluvial deposits of Quaternary age for the greater part of their course; then they flow over Archæan rocks at Cachuela Esperanza and Guajua Mirim. Below these falls, at Villa Bella, the streams unite to form the Madeira river. At this point the altitude is approximately 450 feet. Above the falls, the Beni and Mamoré rivers are navigable by steam launches to the foothills of the Andes. The Guaporé has its source on the highlands of Matto Grosso near some of the headwaters of the Paraguay and receives many short streams flowing from Serra dos Parecis.

The converging headwaters of the Paraguay after a short course over the level campos of the highlands of Matto Grosso drop quickly to an altitude of about 700 feet. In some streams this drop is completed not more than 100 miles from their sources. After the rivers leave the highlands, they are navigable by steam launches to the mouth of the La Plata. For the greater part of its course the Paraguay runs through swamps and marshes on alluvial deposits of Quaternary age. It joins the Parana at an altitude of about 150 feet. Many short tributaries are received from the east. Their sources are in the Triassic and Cretaceous formations of the southern extension of the highlands between the Parana and Paraguay rivers. From the west the Paraguay receives its longest and largest tributary, the Pilcomayo. It arises within a few miles of some of the Andean sources of the Mamoré, flows southeastward across the Gran Chaco to join the Paraguay near Asuncion.

The following quotations describe the highlands of Matto Grosso over which the fishes of the Amazon are supposed to have had access to the Paraguay:

Reclus ('95), page 252, says:

"The divide between the sources of the Guaporé and the headwaters of the Paraguay scarcely exceeds 1650 feet in altitude, and the Brazilian uplands appear to be connected with those of the Chiquitos territory only by a very narrow isthmus of ancient rocks. Here is the true geographical centre of South America.



"On the maps a continuous chain of mountains is traced between the Madeira and Tapajoz basins, then between the Tapajoz and Paraguay, and lastly between the Tapajoz and the Araguaya. Yet it is certain that this semi-circular ridge has but a fragmentary existence. The heights dominating the plains of the Upper Paraguay and its affluents are in reality merely the escarpments of a plateau disposed in horizontal or very slightly inclined strata, and eroded by the streams now descending towards the Amazons. The rampart itself has a mean elevation of no more than 1650 feet, and above the edge of the plateau rise a few isolated crests, attaining here and there a height of some 3000 feet.

"Thus the orographic system of the Matto Grosso watershed indifferently called 'cordilheria' or 'campos' dos Parexi, from the local tribe, presents a mountainous aspect, only as seen from the south. On this steep side the face of the escarpment is carved into rocky walls, sharp peaks, or needles. But on the opposite side, facing the Tapajoz and Zingu basins, nothing is seen except a long gently inclined slope gradually merging in the Amazonian plains."

On page 254 Reclus ('95) continues:

"Another remarkable phenomenon is the intermingling of its (Paraguay) farthest headstreams with those of the Amazon's affluents. The Jauru, former frontier stream between the Spanish and Portuguese possessions, approaches so near to the Guaporé that it was found easy to connect the two systems by an artificial canal. The Aguapehy affluent of the Jauru is separated from the Alegre, which joins the Guaporé near Matto Grosso, only by a narrow isthmus of slight elevation, and not more than half a mile wide. In 1772 a canal was cut through the divide, large enough to admit a six-oared boat, and other attempts to establish a permanent communication between the two waterways have failed only through lack of sufficient traffic to support such works."

Hartt ('70), pages 503-504, states:

"The rivers Xingu, Tapajos and Paraguay all take their rise in this plain within a few miles of one another near Diamantino, and the watershed is so low that wooden canoes ascend the Tapajos from Santarem, cross over, and embark on the Paraguay, descending to Villa Maria." This plain, according to Hartt, who quotes from Chandless, "has nothing of a mountainous character. It is simply a high range of country varying but little in its general elevation though deeply grooved by the valleys of the rivers."

#### DISTRIBUTIONAL DATA

In the following consideration the freshwater forms that are marine in character and, consequently, whose distribution does not depend upon fresh water are not included. Reference to the distribution list will show that only a very few such species exist.

The following table gives a summary of the fishes that are found in the Paraguay and the Beni-Mamoré basins:

	<i>Families</i>	<i>Genera</i>	<i>Species</i>
Taken from Beni-Mamoré . . . . .	21	141	275
Taken from Paraguay . . . . .	21	138	307
Common to Paraguay and Beni-Mamoré . . . . .	18	86	120
Common to Paraguay and entire Amazon . . . . .	21	122	176
Common to Beni-Mamoré and entire La Plata . . . . .	19	99	121
Taken from Paraguay but not from Beni-Mamoré . . . . .	3	52	187
Taken from Paraguay but not from Amazon basin . . . . .	0	16	131
Taken from Beni-Mamoré but not from La Plata . . . . .	3	42	154



The above table shows, as might be expected from the agreement in physical features, that the two basins are nearly equally rich in genera. The slightly larger Paraguay basin contains a few more species than the Beni-Mamoré.

*Beni-Mamoré Basin.* Three families, Cetopsidae, Astroblepidae, and Electrophoridae, are found in the Beni-Mamoré that have not been taken in the Paraguay. Cetopsidae have been reported from elsewhere in the La Plata and might be expected in the Paraguay. The Astroblepidae are strictly an Andean family, and a collection from the upper reaches of the Pilcomayo would undoubtedly contain representatives. The Electrophoridae contain a single genus which includes the electric eels; these forms seem not to be represented in the La Plata basin.

Of the 141 genera found in the Beni-Mamoré, 86, or 61 per cent, are found in the Paraguay; 13 of the remaining 55 genera are found elsewhere in the La Plata basin. Thus 99, or 70 per cent, of the genera are common to the Beni-Mamoré and La Plata basins. Of the 42 genera that have been found in the Beni-Mamoré that have not been found in the La Plata, *Acrobrycon*, *Hemibrycon*, and *Astroblepus* are Andean forms, and might be expected in the Andean headwaters of the Pilcomayo. Of the remaining 39 genera, 18 contain a single species; each of the remaining 21 genera contain fewer than ten species.

Of the 275 species found in the Beni-Mamoré, 120, or 43.6 per cent, have been taken in the Paraguay. Of the remaining 155 found in the Beni-Mamoré only a single species has been reported from elsewhere in the La Plata.

The above data indicate that the fishes of the Beni-Mamoré do not have free access to the Paraguay at the present time. The divide between the Guaporé and the Paraguay acts as a barrier to more than half of the specific fauna of the Beni-Mamoré.

The important genera that are found in the Beni-Mamoré system have had access to the La Plata system. This access seems to have been during relatively recent times, inasmuch as the genera which have been found in the Beni-Mamoré and not in the La Plata are, for the most part, small and unimportant. Sufficient time has elapsed, however, for the independent derivation of more than half of the specific fauna of the Beni-Mamoré.

It is interesting to note here, the relation of the fauna of the Beni-Mamoré to that of the Amazon. Five, or 3.5 per cent, of the genera, all of which contain a single species, and 54, or 19 per cent, of the species found in the Beni-Mamoré have not been found elsewhere in the Amazon basin.

*Paraguay Basin.* Eighteen families are common to the Paraguay and Beni-Mamoré basins. Three families, Hypophthalmidae, Aspredinidae, and Poeciliidae, have been taken from the Paraguay that





have not been found in the Beni-Mamoré. The first family is present, no doubt, somewhere in the Beni-Mamoré. The second family is represented by a single species in the Paraguay, *Dysichthys australe*, which Haseman ('11) considered synonymous with *Bunocephalus rugosus*. This species belongs to the Bunocephalidae, which is represented in the Beni-Mamoré. The third family should have been found somewhere in the Beni-Mamoré.

Of the 138 genera found in the Paraguay 86, or 62.3 per cent, are also found in the Beni-Mamoré; 36 of the remaining 52 genera are found elsewhere in the Amazon basin. Thus 122, or 85.5 per cent, of the genera are common to the Paraguay and Amazon basins. Of the 16 genera that are found in the Paraguay that have not been taken anywhere in the Amazon, *Paravandellia*, *Mixobrycon*, *Bertonolus*, *Piabarchus*, and *Neofundulus* are each known from a single type specimen. *Mimagoniates*, *Vesicatrus*, *Branchioica*, and *Rivulichthys* contain single species from restricted localities. The remaining 7 genera are more or less widely distributed in the La Plata basin; one contains a single species; two contain two species; and four contain three species.

Of the 307 species found in the Paraguay 120, or 39 per cent, have been taken in the Beni-Mamoré. Of the remaining 187 species found in the Paraguay 56 have been found elsewhere in the Amazon. Thus a total of 176, or 57.3 per cent, of the species found in the Paraguay are also found somewhere in the Amazon basin. This leaves 131, or 43 per cent, that are found in the Paraguay basin but not anywhere in the Amazon.

The above data indicate that the Paraguay has not secured that part of its fauna which it has in common with the Amazon basin from the fauna now present in the Beni-Mamoré. Other parts of the Amazon have contributed to it. The Xingu, Tapajos, and Tocantins may have played as important roles as the Guaporé.

The few unimportant genera that are peculiar to the Paraguay indicate that its fauna was received relatively recently. But sufficient time has elapsed for the derivation of 43 per cent of its species.

The São Francisco and coastal streams may have contributed a few species to the Paraguay. This is indicated by the 35 species that are common to the Paraguay, the São Francisco and the coastal streams; of these only 15 have been taken from the Amazon basin.

#### ORIGIN OF THE FISHES OF THE PARAGUAY

The close resemblance of the fishes of the Paraguay to the enormous and diversified fauna of the Amazon indicates their origin from the Amazonian forms. Furthermore, the nature of the divide between the two basins indicates that the fishes of the Amazon basin have had access to the Paraguay basin.

Haseman ('12), however, considered the precipitous falls in the rivers leaving the plateau of Matto Grosso to have been effective



barriers to fish migration since the early Mesozoic epoch, except for certain generalized highland genera. This was before the present forms had evolved. Therefore, he was unable to explain the similarity of the Paraguayan fauna to that of the Amazon by migration. He explained the similarity of the Paraguayan fauna to that of the Amazonian by the hypothesis of "similar evolution in unconnected but similar environments" from a primitive and generalized highland stock which was present before the present configuration of the vast Amazonian region was attained. When the primitive and generalized forms reached the Paraguayan and Amazonian systems they were supposed to have undergone parallel evolution.

The geological history of the highlands of Matto Grosso and the Amazon basin, and the place of origin of the South American freshwater fish fauna indicate the Paraguayan fauna has reached that place only by migration through the Amazon valley and over the divide between the Amazon and the La Plata basins.

The highlands of Matto Grosso, where the headwaters of the Paraguay and the southern affluents of the Amazon take their origin, are Permian or older (Branner '19). Therefore some of the rivers which leave these highlands have flowed northward toward what is now the Amazon basin long before freshwater fishes were present in South America, probably before Cretaceous times.

The freshwater deposits of the late Tertiary period, which have been found along that part of the Amazon receiving the Madeira and Tapajos rivers, indicate a very low valley at that time. Agassiz ('68) considered the region between the highlands of Guiana and Brazil to have been below the sea before the Tertiary rise of the Andes. Haseman ('12) thought the Amazon basin had been above the sea since Permian times, and contained a westward flowing river until the Tertiary uplift of the Andes forced the water eastward. In either case it is rather certain that the Amazon basin was below sea level or very low during the latter part of the Mesozoic era. This was earlier than the establishment of any of the now existent genera of freshwater fishes.

The freshwater fish fauna of South America seems to have been derived from the north. Eigenmann ('09) stated that the distribution of the characinids and cichlids lent support to the Archhelenis theory. This theory gave the forms an origin from the hypothetical land bridge between Africa and South America, and has gained but little support among ichthyologists, who regard the similarity of the South American and African faunae as more superficial than real. Haseman ('12) gave the South American fish fauna a North American origin during the Miocene period. Evidence for this was based on *Priscacara*, a genus of fossil cichlids of doubtful relationship, which had been taken from Green River and Bridger Eocene of Wyoming and Utah. Nichols and Griscom ('17) considered the origin of the cichlids as probably marine during the Tertiary, and Nichols ('30) gave a northern origin to the catfishes and characinids.



Osborn ('10) considered the general South American fauna as having been derived from North America.

Fossil characinids belonging to the genera *Lignobrycon* and *Eobrycon*, which agree most closely with *Brycon*, *Henochilus*, and *Salminus*, have been found in the Tertiary deposits near São Paulo, Brazil, and a third fossil genus has been described from scales taken from the Tertiary deposits at Huacho, Peru. Probably no genera of characinids which exist now were present until after the beginning of the Tertiary period, when the freshwater fishes probably entered the Amazon basin. At the time they entered, the Amazon basin was being formed, and the fishes before reaching the Paraguay had to pass through the developing Amazon basin. Here adaptive radiation began in every conceivable direction. Before the entrance of the fishes the Tocantins, Tapajos, Xingu, and Madeira or similar streams flowed toward the Amazon, and their tributaries were cutting back into the ancient highlands of Brazil. These highlands were the divide between the La Plata and the Amazon basins long before the fishes entered South America. Therefore the fishes have never had anything but a highland route over which to enter the Paraguay. If it is true that the highlands are a complete barrier at the present time as Dr. Haseman attempted to show and the character of the fishes of the two slopes may indicate, then there must have been a time when the slopes were less precipitous. This, in fact, must have been the condition before the southern tributaries of the Amazon had cut back into the older and harder formations where waterfalls of considerable height now exist. In order to account for the similarity of the Paraguayan fauna to that of the Amazon under this condition it becomes necessary to assume that the barriers did not appear until the genera and species common to the two basins had evolved.

The altitude of the streams on the highlands of Matto Grosso would not prevent the migration of lowland forms from the Amazonian system to the Paraguayan, because several collections from the eastern slopes of the Andes demonstrate that the lowland forms ascend those streams to an altitude of about 2500 feet.

In order to test whether the highlands had been a partial barrier the author attempted to analyze the physical effects of the divide by separating the fishes found in the Beni-Mamoré into strong and weak forms, based upon his South American collecting experience. These were then separated into those that had succeeded in getting across the divide and those that had not. The results showed that the weak forms were equally successful in crossing over. In like manner it was found that the Paraguay contained weak and strong swimming forms in equal proportion.

It is not known at present which tributaries of the Amazon offered the migratory path. Probably all that have headwaters near those of either the Paraguay or Parana have taken part. The large collection of fishes taken by Carlo Ternetz from the Rio Tocantins may



throw some additional light on the question of the time and manner in which the entire La Plata received its fishes.

### SUMMARY

The origin of the Paraguayan freshwater fish fauna can be explained by migration. It is not necessary to assume parallel evolution to account for the resemblance of the fauna of the Paraguay to that of the Amazon.

The fishes entered South America sometime during the Tertiary and crossed the low Amazon valley and a highland divide to enter the Paraguay. Other tributaries of the Amazon in addition to the Rio Guaporé seem to have been migratory paths.

The falls in the streams flowing from the highlands of Matto Grosso seem to be barriers to free migration at the present time; but the nature of the fishes of the two slopes indicate that the barrier is of recent origin.

### SYMBOLS USED IN DISTRIBUTIONAL LISTS

- in the first column indicates that the species is present in the Beni basin; | , that it is present in the Mamoré basin; + indicates that it is present in both basins.
- in the second column indicates that the species is present in the Paraguay basin.
- \* species peculiar to the Paraguay basin.
- \*\* genus and species peculiar to the Paraguay basin.
- † species peculiar to the Mamoré basin.
- †† genus and species peculiar to the Mamoré basin.
- ‡ species peculiar to the Beni.
- ‡‡ genus and species peculiar to the Beni.
- a species found in the Amazon basin without the Beni-Mamoré basin.
- A genus found in the Amazon basin.
- c species found in the coastal streams of southeastern Brazil.
- g species found in Guiana.
- m species found in the Magdalena basin.
- p species found in the La Plata basin but has not been taken in the Paraguay.
- P genus found in the La Plata but has not been taken in the Paraguay.
- s species found in the São Francisco.
- t species found in the Tocantins.
- W species widespread, i. e., in northwestern South America, Amazon basin, Paraguay, and coastal streams of southeastern Brazil.



# DISTRIBUTION OF FISHES IN THE PARAGUAY AND THE BENI-MAMORÉ SYSTEMS

	Beni- Mamoré	Paraguay		Beni- Mamoré	Paraguay
POTAMOTRYGONIDAE					
a <i>Potamotrygon hystrix</i> .....		—	a <i>Knodus moenkhausii</i> .....		—
a " <i>dumerilii</i> .....		—	* " <i>chapadae</i> .....		—
CLUPEIDAE					
a <i>Neosteus flavipinnis</i> .....	—		a " <i>breviceps</i> .....	+	
ENGRAULIDAE					
a <i>Anchovia olida</i> .....		—	† " <i>jacunda</i> .....	—	
" <i>brevirostris</i> .....	—		<i>Markiana nigripinnis</i> .....	—	—
SYNBRANCHIDAE					
W <i>Synbranchus marmoratus</i> .....	—	—	a <i>Gymnocorymbus thayeri</i> .....	—	
CHARACINIDAE					
CHEIRODONTINAE					
A <i>Phytocharax dentatus</i> .....	—	—	" <i>ternetzi</i> .....	+	—
" <i>anisitsi</i> .....	—	—	a <i>Thayeria obliquus</i> .....	—	
* " <i>rathbuni</i> .....		—	* <i>Hemigrammus ulreyi</i> .....	—	—
* " <i>paraguayensis</i> .....		—	s " <i>marginatus</i> .....	—	—
a " <i>pusillus</i> .....	+		* " <i>tridens</i> .....		—
a " <i>alburnus</i> .....	+		a " <i>lunatus</i> .....	+	—
* " <i>ipacarayensis</i> .....		—	a " <i>unilineatus</i> .....	—	—
* " <i>pappenheimi</i> .....		—	a " <i>ocellifer</i> .....	—	—
<i>Prionobrama paraguayensis</i> .....		—	a " <i>schmardae</i> .....	—	—
a " <i>fligerus</i> .....	+		a <i>Hyphessobrycon serpae</i> .....	—	—
a <i>Paragoniates alburnus</i> .....	—		g " <i>rosaceus</i> .....	—	—
* <i>Megalampodus megalopterus</i> .....		—	† " <i>hasemani</i> .....	—	—
† " <i>rogoaguae</i> .....	—		" <i>callistus</i> .....	+	—
** <i>Mixobrycon ribeiroi</i> .....		—	a " <i>agulha</i> .....	—	—
a <i>Parecbasis cyclolepis</i> .....	—		sa " <i>gracilis</i> .....	—	—
† <i>Microschemobrycon guaporensis</i> .....	—		" <i>santae</i> .....	—	—
sa <i>Cheirodon piaba</i> .....	—	—	" <i>anisitsi</i> .....	—	—
* " <i>microdon</i> .....		—	" <i>lutkeni</i> .....	—	—
† " <i>madeirae</i> .....	—		* " <i>maxillaris</i> .....	—	—
a <i>Holoshethes pequirá</i> .....	—	—	a† <i>Bryconacidnus ellisi</i> .....	—	
<i>Odontostilbe paraguayensis</i> .....	—	—	† " <i>hemigrammus</i> .....	—	
" <i>microcephala</i> .....	—	—	* <i>Astyanax alleni</i> .....		—
** <i>Mimagoniates barberi</i> .....		—	* " <i>pellegrini</i> .....		—
†† <i>Monotocheirodon pearsoni</i> .....	—		a " <i>abramis</i> .....	—	—
†† <i>Prodontocharax melanotus</i> .....	—		W " <i>bimaculatus</i> .....	+	—
p <i>Probolodus heterostomus</i> .....	—		a " <i>paraguayensis</i> .....	—	—
TETRAGONOPTERINAE					
<i>Tetragonopterus argenteus</i> .....	+	—	" <i>lineatus</i> .....	—	—
a <i>Moenkhausia jamesi</i> .....	—	—	* " <i>marionae</i> .....	—	—
sa " <i>sanctae-filomenae</i> .....	+	—	W " <i>fasciatus</i> .....	—	—
a " <i>grandisquamis</i> .....	—	—	a " <i>eigenmanniorum</i> .....	—	—
a " <i>dichoura</i> .....	+	—	† " <i>guaporensis</i> .....	+	—
a " <i>intermedia</i> .....	+	—	a <i>Ctenobrycon hauxwellianus</i> .....	+	—
a " <i>lepidura lepidura</i> .....	—	—	s <i>Psellogrammus kennedyi</i> .....	—	—
a " <i>gracilima</i> .....	—	—	<i>Astyanacinus moorii</i> .....	—	—
a " <i>colletti</i> .....	—	—	† " <i>multidens</i> .....	—	—
a " <i>copei</i> .....	—	—	A* <i>Deuterodon acanthogaster</i> .....		—
a " <i>ceros</i> .....	—	—	a <i>Bryconamericus exodon</i> .....		—
a " <i>cotinho</i> .....	+		" <i>iheringii</i> .....		—
			a " <i>alfredae</i> .....	—	—
			s " <i>stramineus</i> .....		—
			† " <i>bolivianus</i> .....	—	—
			a <i>Acrobrycon ipaniquianus</i> .....	—	—
			a <i>Hemibrycon huambonicus</i> .....	—	—
			† " <i>beni</i> .....	—	—
			ma <i>Creagrutus beni</i> .....	—	—
			†P <i>Piabina beni</i> .....	—	—
			** <i>Piabarchus analis</i> .....		—
			sga <i>Creatochanes affinis</i> .....	—	—
			† <i>Bryconops alburnoides</i> .....	—	—
			<i>Phenacogaster beni</i> .....	+	



	Beni- Mamoré	Paraguay		Beni- Mamoré	Paraguay
** <i>Vesicatrurus legatus</i> .....		—			
** <i>Bertonolus paraguayensis</i> .....		—			
BRYCONINAE					
A* <i>Brycon microlepis</i> .....		—			
* " <i>hilarii</i> .....		—			
CHALCININAE					
* <i>Chalcinus paranensis</i> .....		—			
a " <i>angulatus</i> .....	—	—			
a " " <i>curtus</i> .....	—	—			
a " <i>albus</i> .....	—	—			
†† <i>Clupeacharax anchoveoides</i> .....	—	—			
STETHAPRIONINAE					
* <i>Ephippicharax orbicularis paraguayensis</i> .....		—			
Pa <i>Stethaprion crenatus</i> .....	—	—			
a <i>Brachychalcinus copei</i> .....	—	—			
" <i>retrospina</i> .....		—			
IGUANODECTINAE					
A <i>Piabucus melanostomus</i> .....		—			
GLANDULOCAUDINAE					
<i>Pseudocorynopoma doriae</i> .....		—			
† <i>Gephyrocharax major</i> .....	—	—			
SERRASALMONINAE					
a <i>Serrasalmus nattereri</i> .....		—?			
* " <i>ternetzi</i> .....		—			
" <i>marginatus</i> .....		—			
a " <i>spilopleura</i> .....	+	—			
a " <i>humeralis</i> .....	+	—			
† " " <i>gracilior</i> .....		—			
† " <i>hollandi</i> .....		—			
a " <i>elongatus</i> .....		—			
a <i>Colossoma brachypomus</i> .....		—			
" <i>mitrei</i> .....		—			
a <i>Mylossoma aureum</i> .....	+	—			
a " <i>duriventris</i> .....	+	—			
* " <i>paraguayensis</i> .....		—			
* " <i>ocellatum</i> .....		—			
† <i>Metynnis guaporensis</i> .....		—			
a " <i>roosevelti</i> .....	+	—			
* " <i>otluquensis</i> .....		—			
* " <i>mola</i> .....		—			
a " <i>maculatus</i> .....		—			
a " <i>hypsauchen</i> .....		—			
a <i>Myleus setiger</i> .....		—			
<i>Myloplus levis</i> .....		—			
a " <i>rubripinnis</i> .....		—			
a <i>Catopryon mento</i> .....	+	—			
CYNODONTINAE					
a <i>Cynodon gibbus</i> .....		—			
a " <i>vulpinus</i> .....		—			
CHARACINAE					
a <i>Charax gibbosa</i> .....		—			
" <i>argentea</i> .....		—			
" <i>squamosus</i> .....		—			
* " <i>caliurus</i> .....		—			
a <i>Roestes molossus</i> .....		—			
a <i>Roeboides microlepis</i> .....		—			
* " <i>prognathus</i> .....		—			
a " <i>affinis</i> .....	—	—			
" <i>bonariensis</i> .....		—			
* " <i>descalvadensis</i> .....		—			
a <i>Eucynopotamus kneri</i> .....	—	—			
m " <i>magdalenae</i> .....		—			
a " <i>humeralis</i> .....		—			
c <i>Salminus maxillosus</i> .....		—			
a " <i>hilarii</i> .....	—	—			
ACESTORRHAMPHINAE					
a <i>Acestrorhynchus falcatus</i> .....	+	—			
Ac <i>Acestrorhamphus hepsetus</i> .....		—			
ERYTHRININAE					
W <i>Hoplias malabaricus</i> .....	—	—			
W <i>Hoplerythrinus unitaeniatus</i> .....	—	—			
a <i>Erythrinus erythrinus</i> .....		—			
GASTEROPELECIDAE					
a <i>Thoracocharax stellatus</i> .....	—	—			
ANOSTOMIDAE					
P† <i>Anostomus gracilis</i> .....		—			
a " <i>proximus</i> .....		—			
a <i>Curimata spilurus</i> .....	—	—			
* " <i>gillii</i> .....	—	—			
a " <i>nasus</i> .....	—	—			
* " <i>conspersus</i> .....	—	—			
* " <i>nigrolaenia</i> .....	—	—			
c " <i>elegans</i> .....	—	—			
" " <i>nitens</i> .....	—	—			
a " <i>bimaculatus</i> .....		—			
c " <i>gilberti</i> .....	—	—			
a " <i>rutiloides</i> .....	—	—			
† " <i>binotatus</i> .....	—	—			
† " <i>esperanzae</i> .....	—	—			
† " <i>pearsoni</i> .....	—	—			
s <i>Prochilodus reticulatus</i> .....	—	—			
a " <i>nigricans</i> .....	—	—			
s " <i>argenteus</i> .....	—	—			
c " <i>scrofa</i> .....	—	—			
" <i>lineatus</i> .....	—	—			
† " <i>beni</i> .....	—	—			
a <i>Anodus latior</i> .....		—			
a " <i>laticeps</i> .....		—			
a <i>Leporinus striatus</i> .....	—	—			
a " <i>frederici</i> .....	—	—			
a " <i>obtusidens</i> .....	—	—			
a " <i>trifasciatus</i> .....	—	—			
a " <i>eques</i> .....	—	—			
a " <i>affinis</i> .....	—	—			



	Beni- Mamoré	Paraguay		Beni- Mamoré	Paraguay
a <i>Leporinus hypselonotus</i> .....		—	AUCHENIPTERIDAE		
ca " <i>conirostris</i> .....		—	a <i>Trachelyopterus coriaceus</i> .....	—	—
a " <i>fasciatus</i> .....	—	—	a <i>Centromochlus heckelii</i> .....	—	—
a " <i>y-ophorus</i> .....	—	—	a " <i>intermedius</i> .....	—	—
a " <i>maculatus</i> .....	—	—	a " <i>aulopygius</i> .....	—	—
a <i>Rhytiodus microlepis</i> .....	—	—	a <i>Trachycorystes ceratophysus</i> .....	+	—
† <i>Laemolyta fasciata</i> .....	—	—	sa " <i>galeatus</i> .....	+	—
a <i>Psectrogaster curviventris</i> .....		—	ca " <i>striatulus</i> .....	—	—
a " <i>ciliatus</i> .....		—	a <i>Auchenipterichthys thoracatus</i> .....		—
a <i>Curimatella alburnus</i> .....		—	a <i>Auchenipterus nuchalis</i> .....	—	—
* " " <i>australis</i> .....	—	—	* " <i>nigripinnis</i> .....	—	—
* " <i>rehni</i> .....	—	—	† <i>Tetranematichthys quadrifilis</i> .....		—
a <i>Schizodon fasciatus</i> .....	—	—	<i>Entomocorus benjamini</i> .....		—
* " <i>borelli</i> .....	—	—	DORADIDAE		
a " <i>dissimilis</i> .....	—	—	a <i>Pterodoras granulatus</i> .....		—
s " <i>isognathus</i> .....	—	—	as <i>Platydoras costatus</i> .....	+	—
a <i>Lahilliella nasutus</i> .....	—	—	a <i>Acanthodoras cataphractus</i> .....	—	—
HEMIODONTIDAE			a " <i>spinosissimus</i> .....	+	—
a <i>Parodon suborbitalis</i> .....	—	—	a <i>Amblydoras hancocki</i> .....	+	—
s " <i>tortuosus</i> .....	—	—	a <i>Anadoras weddellii</i> .....	—	—
* " <i>gestri</i> .....	—	—	* <i>Oxydoras kneri</i> .....	—	—
s " <i>hilarii</i> .....	—	—	a <i>Trachydoras nattereri</i> .....	—	—
<i>Apareiodon affinis</i> .....	—	—	a " <i>paraguayensis</i> .....	—	—
a <i>Hemiodus unimaculatus</i> .....		—	a " <i>atripes</i> .....	—	—
a " <i>semitaeniatus</i> .....		—	a <i>Doras punctatus</i> .....	—	—
a " <i>microlepis</i> .....	—	—	a " <i>eigenmanni</i> .....	—	—
* <i>Anisitsia othonops</i> .....	—	—	a <i>Opsodoras humeralis</i> .....	—	—
sa " <i>notata</i> .....		—	a <i>Astrodoras asterifrons</i> .....	—	—
A <i>Nannostomus stignasemion</i> .....		—	a <i>Leptodoras linnelli</i> .....	—	—
ca <i>Characidium fasciatum</i> .....	—	—	* <i>Rhinodoras d'Orbignyi</i> .....	—	—
* " <i>lateralis</i> .....	—	—	AGENEIOSIDAE		
† " <i>bolivianum</i> .....	—	—	m <i>Ageneiosus dentatus</i> .....		—
a <i>Pyrhulina australis</i> .....	—	—	a " <i>brevifilis</i> .....	—	—
† " <i>beni</i> .....	—	—	† " <i>madeirensis</i> .....	—	—
RHAMPHICHTHYIDAE			a " <i>valenciennesi</i> .....	—	—
a <i>Rhamphichthys rostratus</i> .....	—	—	HYPOPHTHALMIDAE		
W <i>Hypopomus brevirostris</i> .....	—	—	a <i>Hypophthalmus edentatus</i> .....	—	—
a " <i>arledi</i> .....		—	PIMELODIDAE		
p <i>Gymnorhamphichthys hypostomus</i> .....		—	a <i>Callophysus macropterus</i> .....	—	—
APTERONOTIDAE			c <i>Pimelodella serrata</i> .....	—	—
a <i>Sternarchus albifrons</i> .....	—	—	a " <i>cristata</i> .....	—	—
a <i>Odontosternarchus sachsii</i> .....		—	a " <i>gracilis</i> .....	+	—
GYMNOTIDAE			a " <i>mucosa</i> .....	—	—
W <i>Gymnotus carapo</i> .....	—	—	a " <i>roccae</i> .....	—	—
W <i>Sternopygus macrurus</i> .....	—	—	a " <i>buckleyi</i> .....	—	—
W <i>Eigenmannia virescens</i> .....	—	—	a " <i>griffini</i> .....	—	—
a " <i>troscheli</i> .....		—	* " <i>laticeps</i> .....	—	—
ELECTROPHORIDAE			a " <i>australis</i> .....	—	—
a <i>Electrophorus electricus</i> .....		—	* " <i>notomelas</i> .....	—	—
			* " <i>meeki</i> .....	—	—
			* " <i>megalaria</i> .....	—	—
			a <i>Pinirampus pirinampu</i> .....	—	—
			a <i>Luciopimelodus platanus</i> .....	—	—



	Beni-Mamoré	Paraguay		Beni-Mamoré	Paraguay
W <i>Pseudopimelodus zungaro</i> .....	—	—	** <i>Branchioica bertonii</i> .....	—	—
* " <i>coltoides</i> .....	—	—	a <i>Urinophilus erythrurus</i> .....	—	—
a " <i>acanthocheira</i> .....		—	† <i>Vandellia hasemani</i> .....	—	—
* " <i>variolosus</i> .....	—	—	†† <i>Tridentopsis pearsoni</i> .....	—	—
W <i>Rhamdia sebae</i> .....		—	a <i>Pseudostegophilus nemurus</i> .....	—	—
a " <i>kneri</i> .....	—	—			
a " <i>micayi</i> .....	—	—	CETOPSIDAE		
W " <i>quelen</i> .....	+	—	Pa <i>Cetopsis candiru</i> .....	—	—
† <i>Nannorhamdia guttatus</i> .....	—	—	a " <i>plumbeus</i> .....	—	—
†P <i>Imparfinis bolivianus</i> .....	—	—			
†P <i>Rhamdella rusbyi</i> .....	—	—	ASTROBLEPIDAE		
a <i>Pimelodus ornatus</i> .....	—	—	† <i>Astroblepus longiceps</i> .....	—	—
" <i>albicans</i> .....	—	—			
W " <i>clarias</i> .....	+	—	CALLICHTHYIDAE		
S " <i>valenciennis</i> .....	—	—	W <i>Callichthys callichthys</i> .....	+	—
a " <i>altipinnis</i> .....		—	W <i>Hoplosternum thoracatum</i> .....	+	—
a <i>Platynematichthys punctulatus</i> .....		—	W " <i>littorale</i> .....	—	—
A* <i>Nannoglanis hoehnei</i> .....	—	—	a " <i>melampterum</i> .....	—	—
a <i>Phractocephalus hemilioplerus</i> .....		—	A* <i>Chaenothorax eigenmanni</i> .....	—	—
a <i>Sciades pictus</i> .....	—	?	s <i>Corydoras nattereri</i> .....	—	—
a <i>Hemisorubim platyrhynchus</i> .....		—	" <i>microps</i> .....	—	—
Asa <i>Pseudoplatystoma coruscans</i> .....	—	—	" <i>virescens</i> .....	—	—
ma " <i>fasciatum</i> .....	—	—	a " <i>armatus</i> .....	—	—
W <i>Sorubim lima</i> .....	+	—	" <i>australis</i> .....	—	—
a <i>Sorubimichthys planiceps</i> .....		—	" <i>aeneus</i> .....	—	—
<i>Iheringichthys labrosus</i> .....	—	—	" <i>flaveolus</i> .....	—	—
* " <i>megalops</i> .....	—	—	* " <i>aurofrenatus</i> .....	—	—
†† <i>Pteroglanis manni</i> .....	—	—	* " <i>polystictus</i> .....	—	—
m <i>Cetopsorhamdia nasus</i> .....	—	—	* " <i>paleatus</i> .....	—	—
a <i>Platysilurus barbatus</i> .....	—	—	† " <i>latus</i> .....	—	—
a <i>Cheirocerus eques</i> .....	—	—			
a <i>Heptapterus mustelinus</i> .....	—	—	LORICARIIDAE		
			PLECOSTOMINAE		
BUNOCEPHALIDAE			a <i>Plecostomus plecostomus</i> .....	—	—
* <i>Bunocephalus doriae</i> .....	—	—	s " <i>macrops</i> .....	—	—
" <i>iheringii</i> .....	—	—	s " <i>commersonii</i> .....	—	—
* " <i>rugosus</i> .....	—	—	s " <i>vaillanti</i> .....	—	—
† " <i>depressus</i> .....		—	* " <i>ternetzi</i> .....	—	—
† " <i>bifidus</i> .....	—	—	ca " <i>robinii</i> .....	—	—
			cs " <i>wuchereri</i> .....	—	—
ASPREDINIDAE			c " <i>auroguttatus</i> .....	—	—
A* <i>Dysichthys australe</i> .....	—	—	* " <i>borellii</i> .....	—	—
			a " <i>latirostris</i> .....		—
			* " <i>variostrictus</i> .....	—	—
			a " <i>verres</i> .....	—	—
PYGIDIIDAE			a " <i>emarginatus</i> .....	—	—
† <i>Pygidium barbouri</i> .....	—	—	† " <i>popoi</i> .....	—	—
† " <i>fassli</i> .....	—	—	† " <i>bolivianus</i> .....	—	—
a " <i>hasemani</i> .....	—	—	† <i>Ancistrus montanus</i> .....	—	—
a " <i>rivulatum</i> .....	+	—	a " <i>bufonius</i> .....	—	—
" <i>eichorniarum</i> .....	—	—	a " <i>cirrhosus</i> .....	—	—
a " <i>borellii</i> .....	—	—	a " <i>dubius</i> .....	—	—
" <i>corduense</i> .....	—	—	a " <i>hoplogenyus</i> .....	—	—
sa " <i>brasiliense</i> .....	—	—	† " <i>megalostomus</i> .....	—	—
* " <i>johnsoni</i> .....	—	—	†P <i>Rhinelepis levis</i> .....	—	—
* <i>Homodiaetus anisitsi</i> .....	—	—	a <i>Hemiancistrus vittatus</i> .....	—	—
A* <i>Ochmacanthus batrachostoma</i> .....	—	—	a <i>Pseudancistrus barbatus</i> .....	—	—
** <i>Paravandellia oxyptera</i> .....	—	—	a <i>Xenocara gymnorhynchus</i> .....	—	—



	Beni- Mamoré	Paraguay		Beni- Mamoré	Paraguay
a <i>Pterygoplichthys multiradiatus</i> .....	—	—	ACHIRIDAE		
* " <i>anisitsi</i> .....	—	—	a <i>Achirus lineatus</i> .....		—
* " <i>juvens</i> .....	—	—	" <i>jenynsii</i> .....		—
* " <i>gigas</i> .....	—	—			
a " <i>lituratus</i> .....	—	—	SCIAENIDAE		
a <i>Cochliodon cochliodon</i> .....	—	—	* <i>Plagioscion ternetzi</i> .....		—
			a " <i>auratus</i> .....	—	—
HYPLOPTOPOMATINAE			<i>Pachyurus bonariensis</i> .....		—
a <i>Hypoptopoma joberti</i> .....	—	—	a " <i>schomburgkii</i> .....		—
* " <i>inexpectatum</i> .....	—	—	<i>Pachypops trifilis</i> .....	—	—
a <i>Olocinlus vittatus</i> .....	—	—			
			CICHLIDAE		
LORICARIINAE			A* <i>Chaetobranchopsis australis</i> .....		—
* <i>Loricaria parva</i> .....	—	—	a <i>Chaetobranchus flavescens</i> .....	—	—
a " <i>phoxocephala</i> .....	—	—	a <i>Cichla ocellaris</i> .....	+	—
" <i>catamarcensis</i> .....	—	—	a <i>Acaropsis nassa</i> .....	+	—
a " <i>maculata</i> .....	—	—	a <i>Astronotus ocellatus</i> .....	+	—
a " <i>typus</i> .....	—	—	a <i>Aequidens tetramerus</i> .....	+	—
a " <i>lanceolata</i> .....	—	—	c " <i>portalegrensis</i> .....	+	—
c " <i>anus</i> .....	—	—	a " <i>vittatus</i> .....	+	—
" <i>labialis</i> .....	—	—	a " <i>dorsigera</i> .....	+	—
a " <i>cataphracta</i> .....	—	—	" <i>paraguayensis</i> .....	—	—
a " <i>carinata</i> .....	—	—	† " <i>guaporensis</i> .....	—	—
* " <i>apeltogaster</i> .....	—	—	† " <i>awani</i> .....	—	—
" <i>laticeps</i> .....	—	—	a <i>Cichla bimaculatum</i> .....	+	—
* " <i>macrodon</i> .....	—	—	a " <i>severum</i> .....	+	—
* " <i>platycephala</i> .....	—	—	a <i>Mesonauta festivum</i> .....	+	—
* " <i>hoehnei</i> .....	—	—	<i>Crenicara maculata</i> .....	—	—
c " <i>nigricauda</i> .....	—	—	† " <i>altispinosa</i> .....	—	—
* " <i>cacerensis</i> .....	—	—	A* <i>Batrachops ocellatus</i> .....		—
† " <i>beni</i> .....	—	—	" <i>semifasciatus</i> .....		—
a <i>Homiodontichthys acipenserinus</i> .....	—	—	a <i>Crenicichla lepidota</i> .....	+	—
a <i>Farlowella oxyrhynchus</i> .....	—	—	" <i>simoni</i> .....	—	—
a " <i>kneri</i> .....	—	—	a " <i>saxatilis</i> .....	—	—
* " <i>jauruensis</i> .....	—	—	a " <i>cyanota</i> .....	—	—
† " <i>acestrichthys</i> .....	—	—	a " <i>reticulata</i> .....	+	—
A* <i>Sturisoma robustum</i> .....	—	—	a " <i>macrophthalma</i> .....	+	—
a " <i>barbatum</i> .....	—	—	a " <i>lugubris</i> .....	—	—
a " <i>rostrata</i> .....	—	—	a " <i>lenticulata</i> .....	—	—
			a " <i>johanni</i> .....	—	—
CYPRINODONTIDAE			a " <i>vittata</i> .....	—	—
<i>Rivulus balzanii</i> .....	—	—	<i>Apistogramma trifasciatum</i> .....	—	—
a " <i>punctatus</i> .....	—	—	* " <i>corumbae</i> .....		—
† " <i>beniensis beniensis</i> .....	—	—	* " <i>borellii</i> .....		—
† " <i>lacustris</i> .....	—	—	* " <i>ritensi</i> .....		—
† " <i>rogoaguae</i> .....	—	—	a " <i>agassizi</i> .....	—	—
** <i>Neofundulus paraguayensis</i> .....	—	—	a " <i>ortmanni</i> .....	—	—
** <i>Rivulichthys rondoni</i> .....	—	—	a " <i>taeniatum</i> .....	+	—
			a " <i>pertense</i> .....	—	—
POECILIIDAE			† " <i>trifasciatum</i> .....		—
<i>Cnesterodon decemmaculatus</i> .....	—	—	maciliensi.....	—	—
c <i>Phalloceros caudimaculatus</i> .....	—	—	a <i>Geophagus surinamensis</i> .....	—	—
* <i>Pamphorichthys hasemani</i> .....	—	—	a " <i>cupido</i> .....	+	—
ca <i>Poecilia vivipara</i> .....	—	—	a " <i>jurupari</i> .....	+	—
c <i>Jenynsia lineata</i> .....	—	—	* " <i>balzani</i> .....		—
			c " <i>braziliensis</i> .....		—
BELONIDAE			A <i>Nannacara hoehnei</i> .....		—
a <i>Tylosurus amazonicus</i> .....	—	—			
a <i>Potamorhaphis guianensis</i> .....	—	—			



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