

ECOLOGY OF AMAZONIAN NEEDLEFISHES
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INTRODUCTION

The Amazon Basin has about 15 families and over 60 species of fishes whose relatives are mostly marine (Roberts, 1972 gives a slightly lower estimate for the species). Supposedly the freshwater forms were derived from marine taxa, or at least their ancestors were. The Belonidae, or needlefishes, are represented by at least 10 genera and 32 species in the oceans and freshwaters of the world (Collette, 1974b; Nelson, 1976). South America has four freshwater belonid genera, three (*Potamorhaphis*, *Pseudotylosurus* and *Belonion*) of which are endemic and one (*Strongylura*) that is worldwide in marine, estuarine and freshwaters (Collette, 1974b). In South America *Pseudotylosurus* appears to be the most widespread freshwater belonid genus, and is known from the Orinoco, Amazon and La Plata drainage systems and from rivers in the Guianas region (Collette, 1974c). *Pseudotylosurus microps* is found in the Orinoco and Amazon basins and in the Guianas; *P. eigenmanni* is known from the Paraná-Paraguay and upper Madeira areas (Collette, 1974c). *Potamorhaphis* is distributed in the Orinoco and Amazon basins and in the Guianas region; *P. petersi* is known from the Amazon and Orinoco basins, whereas *P. guianensis* is found in these two systems and in the Guianas (Collette, 1974a, 1982). The genus *Belonion* is known from the Orinoco and Amazon Basins; *B. dibranchodon* appears to be restricted to the Orinoco system, and likewise, *B. apodion* to the Amazon drainage (Collette, 1966).

Needlefishes are so-named because of their greatly elongate jaws and bodies (Fig. 1). Morphologically, however, they resemble an arrow more than a needle, and the analogy is also more correct. The anal and dorsal fins are relatively small and lie posteriorly, just as feathers do on an arrow. Species of *Pseudotylosurus* and *Potamorhaphis* reach at least 30 cm in total length, in contrast to *Belonion* whose largest members are only about 5 cm. *Belonion* is also strikingly different because only the lower jaw is greatly elongate, whereas in all other known belonids both jaws are well developed, at least in adults.

In this paper we offer the first information on the ecology of Amazonian needlefishes, and furthermore, relate this data to the morphological structure of the fishes, and their hypothesized phylogeny.

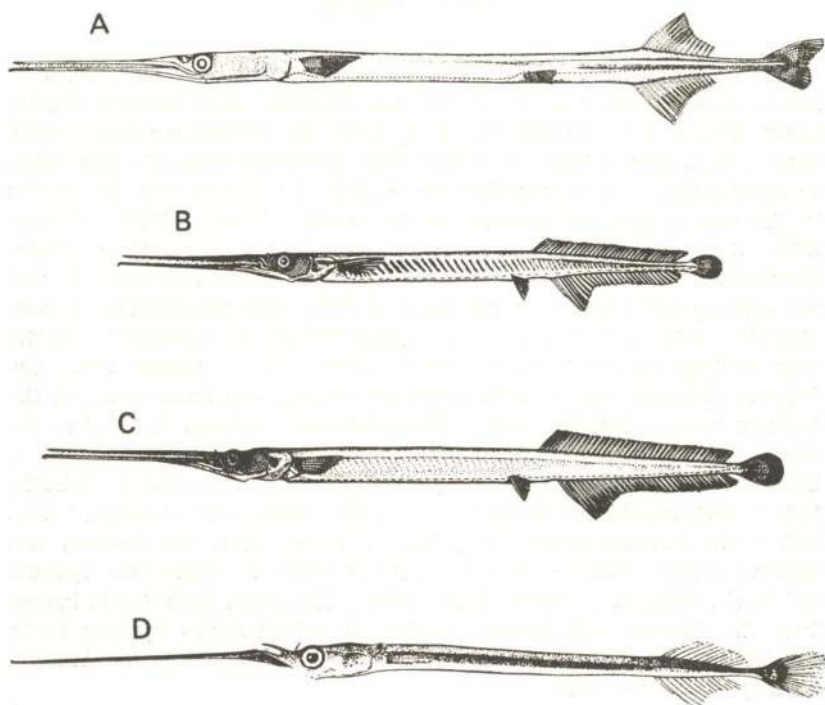


Figure 1 — A) *Pseudotylorus microps*, 18 cm; B) *Potamorrhaphis guianensis*, 10 cm; C) *Potamorrhaphis petersi*, 13 cm; D) *Belonion apodion*, 4 cm. From Collette (1966, 1974-a, 1974-c). Illustrations courtesy of Dr. Bruce Collette.

STUDY AREA

The study area focuses on the Rio Negro and Rio Tefé in the state of Amazonas, Brazil (Fig. 2). The Rio Negro is a northern affluent of the Rio Solimões-Amazonas, and also its largest tributary. The Rio Tefé is a southern tributary of the Rio Solimões, and enters this river about 500 km upstream from its confluence with the Rio Negro. Both the Rio Negro and Rio Tefé are blackwater rivers, that is, they transport minimal sediment loads, but their waters are nevertheless dark because they are stained by humic acids. The organic compounds coloring the Rio Negro are derived from vegetation growing on white sands (podzolic soils) whose litter is incompletely decomposed, thus allowing run-off to carry humic acids into the streams and main river (Klinge, 1965; Klinge & Ohle, 1964). The origins of the humic acids in the Rio Tefé are unknown. The Rio Negro and Rio Tefé are extremely poor in nutrients, and are chemically very similar to rainwater (Gibbs, 1967, 1971; Sioli, 1967, 1968). Their pH's are usually below 5.0, though high acidity in itself does not appear to prevent herbaceous plant communities from developing, especially in floodplain areas where there have been recent tree and shrub die-offs. The invasion of aquatic macrophytes in these blackwater rivers appears to be a recent phenomenon, as neither Wallace (1853) nor Spruce (1908) reported them in the Rio Negro in mid-nineteenth century and local residents of the Rio Tefé told the first author that *Paspalum*, *Oryza* and other herbaceous taxa first appeared in this system about two decades ago. The floodplains of the Rio Negro and Rio Tefé are covered mostly by rainforest adapted to seasonal inundation.

Fish collections that were made by others but that were examined for this study included those from the lower Rio Solimões (Ilha Marchantaria), Rio Negro-Rio Solimões confluence (Paraná de Paracauá), lower Rio Japurá (exact locality unknown) and Rio Aripuanã (Igarapé do Castanhal). Further details will be given later in the paper (also Fig. 2).

MATERIALS AND METHODS

Most of the specimens examined for this study were captured by the first author while making fish collections in the Rio Negro and Rio Tefé during 1979 and 1980. There was no special effort made to catch belonids, but they were taken with seines, dipnets and rotenone while collecting other fishes. Most of our material is from the low water periods, as we had no success catching belonids in flooded forest, where they apparently go during the inundation season. All together 151 belonid specimens were examined for stomach contents (the breakdown by species, locality and number of specimens of each species examined are indicated on Fig. 2). Fifteen of the specimens were from uncatalogued

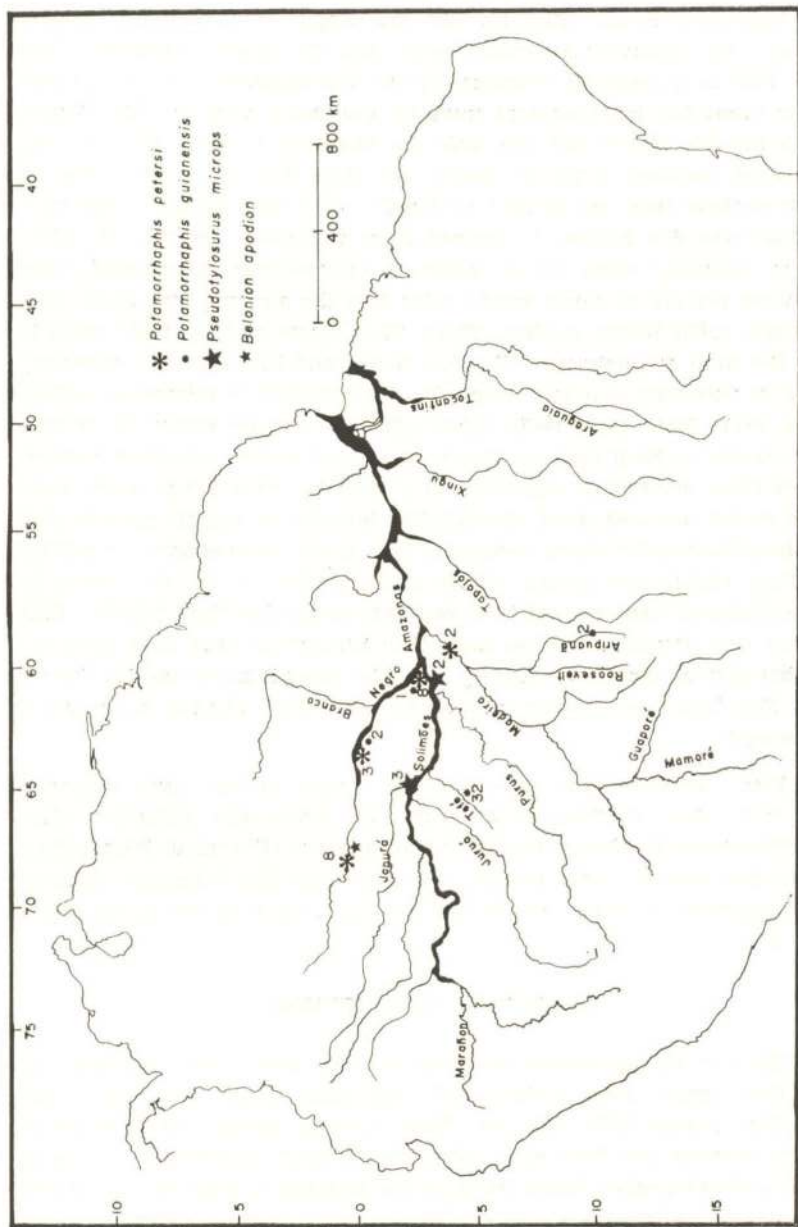


Figure 2 — Map of study area showing the sites at which each species was captured and the number of specimens examined.

collections deposited at the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus. Though more specimens for analysis would be desirable, the decision to publish the data at hand was based on the fact that no additional belonids could be obtained and that there is almost no information on the ecology of Amazonian needlefishes in the literature.

Both the stomachs and intestines of the belonids studied were analyzed for food contents. All food items were examined under a microscope. Analyses for *Potamorrhaphis* and *Pseudotylorus* were made by identifying, separating and counting all of the food items found. Because *Belonion* has a more diverse feeding behavior than the above two genera, three methods — occurrence, dominance and volume — were employed to study its food contents. Occurrence is calculated as the number of individuals in which a particular food item was present; likewise, dominance is calculated as the number of individuals in which a particular food item constituted the major part of the bulk. Volume is calculated from fullness multiplied by the percentages (expressed in intervals of .05 or .10) estimated to be the contributions of individual items found in the stomach and intestines. Thus, for example, an individual might be 50 percent full (fullness score of 50), of which 60 percent (.60) was zooplankton and 40 percent (.40) insect larvae; the volume for zooplankton and insect larvae would then be, respectively, 30 and 20. Mean fullness was calculated using all specimens, even those with empty stomachs.

RESULTS

Belonion apodion

A total of 80 specimens of *B. apodion* were analyzed for food contents. The specimens were collected at four different sites in the upper Rio Negro region; three of these were lakes located on island floodplains, and the fourth was a low-lying swampy area formed at the confluence of the Rio Urubaxi with the Rio Negro (see Fig. 2). In all three lake sites zooplankton was the major food item eaten, followed by insects (mostly larvae) or bryozoans (Tab. 1). At the Rio Urubaxi/Rio Negro swamp site, dipteran insect larvae accounted for the largest volume of food eaten, followed by zooplankton (Tab. 2). Mean fullnesses ranged between about 31 and 62 percent, with the highest two values for sites where zooplankton was the dominant food item eaten.

At two of the sites, cladocerans (especially *Bosminopsis* and *Bosmina*) were the principal zooplankton eaten, while at the other two rotifers were. Copepods were only found in specimens from two sites, and then in only small quantities. The large number of insects found in the Rio Urubaxi/Rio Negro specimens were mostly pupae of Diptera, but there was also a considerable number of winged adults.

A Mean Fullness: 62 percent		12 specimens: 35-41 mm SL		
FOOD ITEMS		Occurrence	Dominance	Volume
ZOOPLANKTON				
1. <i>Bosminopsis deitersi</i> (Cladocera) ...	9	3	159	
2. <i>Bosmina</i> spp. (Cladocera)	9	1	134	
3. Calanoida (Copepoda)	1	—	15	
4. Cyclopoida (Copepoda)	3	—	15	
5. <i>Keratella</i> sp. (Rotifera)	8	2	168	
6. <i>Lecane</i> sp. (Rotifera)	3	—	7	
7. Other Rotifera	8	—	7	
Sub-total of zooplankton	—	6	505	
INSECTS				
1. Formicidae	1	1	60	
2. Other insects	1	1	20	
Sub-total of insects	—	2	80	
OTHER FOOD ITEMS				
1. Bryozoa	4	2	165	
EMPTY	3	—	—	
Total Volume	—	—	750	
B Mean Fullness: 31 percent		4 specimens: 35-49 mm SL		
FOOD ITEMS		Occurrence	Dominance	Volume
ZOOPLANKTON				
1. <i>Bosminopsis deitersi</i> (Cladocera) ...	1	—	1	
2. Unidentified Cladocera	1	1	50	
3. Unidentified Rotifera	1	—	1	
Sub-total of zooplankton	—	1	52	
OTHER FOOD ITEMS				
1. Bryozoa	1	—	2	
2. Detritus	2	2	70	
Sub-total of other food items	—	2	72	
EMPTY	1	—	—	
Total Volume	—	—	124	
C Mean Fullness: 62 percent		2 specimens: 31-43 mm SL		
FOOD ITEMS		Occurrence	Dominance	Volume
ZOOPLANKTON				
1. <i>Lecane</i> sp. (Rotifera)	2	1	95	
INSECTS				
1. Unidentified	1	1	30	
EMPTY	—	—	—	
Total Volume	—	—	125	

TABLE 2

Stomach and intestine content analyses of Belonion apodion captured in a low-lying swampy area at the confluence of the Rio Urubaxi and Rio Negro. A total of 62 specimens, ranging between 31 and 44 mm standard length (as measured from the tip of the upper jaw to the hypurals) were examined. Mean fullness was 42 percent.

FOOD ITEMS	Occurrence	Dominance	Volume
ZOOPLANKTON			
1. <i>Bosminopsis deitersi</i> (Cladocera) ...	23	—	79
2. <i>Bosmina spp</i> (Cladocera)	6	—	18
3. Chydoridae (Cladocera)	3	—	13
4. Ephyipia (Cladocera)	1	—	5
5. Calanoida (Copepoda)	1	—	2
6. Cyclopoida (Copepoda)	1	—	1
7. <i>Keratella sp.</i> (Rotifera)	6	1	59
8. <i>Lecane sp.</i>	20	—	42
9. Unidentified Rotifera	15	—	51
Sub-total of zooplankton	—	1	270
INSECTS			
1. Diptera (pupae)	52	46	1405
2. Diptera (winged adults)	16	9	487
3. Unidentified insects	5	4	105
Sub-total of insects	—	59	1997
OTHER FOOD ITEMS			
1. Bryozoa	13	1	113
2. Acarinae	1	—	1
3. Detritus	22	1	181
4. Phytoplankton	3	—	28
Sub-total of other food items	—	2	323
EMPTY	—	—	—
Total Volume	—	—	2590

TABLE 1 (Left)

Stomach and intestine content analyses of Belonion apodion captured in three lakes of the upper Rio Negro. A) inland lake near Barcelos; B) inland lake near Tapuruquara; C) inland lake near mouth of Rio Arirará. SL standard length.

Pseudotyllosurus microps

No specimens of *P. microps* were obtained from the Rio Negro or Rio Tefé, though Collette (1974c) has examined specimens from the confluences of the Rio Negro with the Rio Solimões and the Rio Negro with the Rio Branco. The species is probably rare or absent in blackwaters in the mid-western/central Amazon. For comparative purposes, six specimens from the INPA collection were examined. Five of these contained fish in their stomachs. All five prey specimens had their heads bitten off, and these were also found in the stomachs. The prey to predator ratio (based on standard length) for the five prey specimens was the following: 11, 16, 18, 22 and 24 percent (mean = 18.2). None of the prey could be identified to genus because of digestion, but at least two of the quintet were characins.

Potamorrhaphis guianensis

Of the 42 specimens of *P. guianensis* examined, 32 were from the Rio Tefé, three from the Rio Negro, two from the Rio Aripuanã and one, from the INPA collection, was without any information. The specimens ranged between 15 and 29 cm in standard length. Fourteen of the specimens examined had empty stomachs and intestines, while all of the others, with one exception, contained only insects (Tab. 2). The unusual individual contained a 34 mm *Nannostomus* sp., but since both species were captured in the same seining, it may have been swallowed while in the net. Of the 60 individual insects eaten by 27 specimens of *P. guianensis*, 48 were ants (mostly winged forms), while the others identified included an aquatic hemipteran and an adult odonatan. One spider had also been eaten.

Potamorrhaphis petersi

Of the 24 specimens of *P. petersi* examined, 19 were from the Rio Negro, two were from the Rio Aripuanã and two unlabeled specimens were from the INPA collection. The specimens ranged between 15 and 26 cm in standard length. Insects had the highest occurrence, and were found in eight of the specimens. Winged ants were the most important insects eaten, and were found in five of the specimens; the only other insect identified was an orthopteran eaten by one individual. Fish had been eaten by six of the *P. petersi* examined. Prey that could be identified were a larval *Crenicichla* sp. (31 mm standard length), an *Apistogramma* sp. (21 mm standard length) and two characins (both 12 mm standard length). The prey to predator length ratio (based on standard length) was the following: 7,8 and 16 percent (mean = 10.3). One of the characins had its head bitten off, while the other prey were found whole in the stomachs.

TABLE 3

Stomach content analyses of Potamorrhaphis guianensis and P. petersi
P. guianensis

FOOD ITEM	OCCURRENCE	TOTAL PREY INDIVIDUALS
Formicidae	19	48
Hemiptera (aquatic)	1	1
Odonata (adult)	1	1
Unidentified insects	9	9
Arachnids	1	1

P. petersi

Formicidae	5	7
Orthoptera	1	1
Unidentified insects	2	2
Fish		
<i>Crenicichla</i> sp.	1	1
<i>Apistogramma</i> sp.	1	1
characins	2	2
Unidentified	1	1

DISCUSSION

The two most salient characteristics of belonid morphology are elongate, tubular bodies and greatly extended jaws (or jaw in the case of *Belonion*). We hypothesize that the arrow-like morphology of *Potamorrhaphis* and *Pseudotyllosurus* is an adaptation for high velocity strikes at prey. On numerous occasions the first author has observed *Potamorrhaphis* striking at what must have been prey (though the prey were never seen in the water). The same strike pattern was observed on all occasions, which was this. *Potamorrhaphis* never attacked head-on, but usually at about a 90 to 150 degree angle, as measured from either eye. All strikes observed were launched from a stationary position, and not when the fish was swimming. The impression is that *Potamorrhaphis* do not actively pursue prey, but wait for them to pass or fall into the water, at which time they strike. This is always close to the shore and near the surface. Before striking, *Potamorrhaphis* recurve their bodies (much like a bow) and then shoot (like an arrow) towards the prey. The recurvature of their bodies, before striking, would appear to give them the muscular tension needed to strike at high velocity. The strikes are so fast that the first author was never sure what the fishes were attacking. In the case of prey that are other fishes, the advantage of

high speed strikes is obvious: to capture the animal before it defects the potential predator. In the case of the insect-eating *Potamorrhaphis* species, high speed strikes may be necessary to get food items that are intensively attacked by many other fishes as well, as the prey (mostly ants) present few obstacles to their capture once they have fallen in the water. Belonids appear to feed only during the day, and at night remain stationary near the shore, usually aligning themselves with submerged roots, branches or other vegetation. In the case of *Strongylura timucu* in the mangrove swamps of São Paulo, southeastern Brazil, Sazima and Uieda (1979) suggest that body alignment with submerged vegetation is protective resemblance and an adaptation against avian predators. The Rio Negro and Rio Tefé have low biomasses of piscivorous birds, and thus body alignment of belonids with vegetation, if it is anti-predatory in nature, must be an adaptation against fishes and perhaps caimans.

Elongate jaws of Amazonian fishes that are at least superficially similar to those of *Potamorrhaphis* and *Pseudotylosurus* are only found in the characin genera *Boulengerella* and *Ctenolucius* (family Ctenoluciidae). All Amazonian fishes with pincer-like jaws are carvororous (*Boulengerella* has been studied by the first author — Goulding, in prep.). In contrast to ctenoluciids, belonids take smaller prey, and this behavior is also suggested by needlefishes' finer and more elongate jaws. In the Rio Negro and Rio Tefé, *Potamorrhaphis* and *Boulengerella* inhabit the same biotopes (shore zones of deep and shallow waters) and small groups of both taxa are often encountered intermixed. The different feeding behaviors of these two taxa perhaps largely explain why they are able to live together. *Potamorrhaphis*, however, have been found in the stomach contents of *Boulengerella*, and thus any notion of protective mimicry appears to carry little weight in this case.

The genus *Belonion* is the most aberrant of all belonids because adults have a small upper jaw, which makes them resemble half-beaks (Hemiramphinae) more than adult needlefishes. Collette (1966) suggested that *Belonion* is a neotenic form because most belonids go through a "halfbeak" stage during ontogeny, and furthermore, that *Belonion* is not closely related to *Potamorrhaphis* of the extant needlefishes. The small insect larvae and zooplankton accounting for most of the diet of *B. apodion* are the same types of foods that one would imagine for young belonids. Unfortunately, we were unable to find any larval *Potamorrhaphis* or *Pseudotylosurus*, to verify this assumption. Furthermore, it has not been shown that larval *Pseudotylosurus* and *Potamorrhaphis* go through a "halfbeak" stage. In any case, we hypothesize that the shortened upper jaw of *B. apodion*, in addition to the small size of the fish, is an adaptation for feeding on zooplankton and small insect larvae. Zooplankton and insect larvae probably enter the mouth of *B. apodion* through suction, in great contrast to the physical manipulation of prey by adult *Potamorrhaphis* and *Pseudotylosurus*. The short upper jaw in *B. apodion* — and in the juvenile stages of other belonids as well — allows a suction current to flow freely through the mouth (an elongate upper jaw would prevent this).

Potamorhaphis differs from *Pseudotyllosurus*, *Belonion* and *Strongylura* in its more elongate dorsal and anal fins (see Fig. 1). In the Rio Negro, *Potamorhaphis* were often observed in waters along deep shore zones (the bounce bank) where the current was fairly swift. Collette (1974b), reviewing the biotopes of where *Strongylura hubbsi* was captured in Central America, gives the impression that the species inhabits mostly quiet waters. The same seems to be true of *B. apodion* in the Rio Negro. The exact biotopes of *Pseudotyllosurus* have not been reported. The evidence, as far as it goes, seems to suggest that the more elongate dorsal and anal fins of *Potamorhaphis* may help with stabilization in the fast waters that the species inhabits, or at least which some populations do. It should be pointed out, however, that *Boulengerella* also inhabit these lotic biotopes, but that they have relatively small dorsal and anal fins, perhaps because they are stronger swimmers than belonids.

Amazonian belonids have a diverse feeding spectrum and evidence at least two types of behavior that are unknown for other fishes of the region. First, is the decapitation habit of *Pseudotyllosurus microps*. *Pseudotyllosurus microps* bites the heads of its prey, and at least one specimen of *Potamorhaphis petersi* had done the same. This behavior would appear to be for killing the prey and/or eliminating its widest part, and not for shortening its length before ingestion, though it certainly serves all these functions. It would be instructive to know whether *P. microps* strikes at the head region of the prey — killing its victim instantly, as it were — or alternatively, grasps the fish in any manner possible, and then manipulates it in the jaws until it can be decapitated.

The second unusual feature of belonid feeding is found in the zooplankton eaten by *Belonion apodion*. Unlike other adult zooplanktivorous fishes, *B. apodion* consumes significant quantities of rotifers (rotifers are relatively rare in the oceans, thus the statement pertains mostly to freshwater communities). Rotifers are among the smallest metazoan animals, and those found in *B. apodion* stomach and intestine contents were less than 0.1 mm in length. This may be compared to copepod and cladoceran lengths which exceeded 0.3 mm. It is generally assumed that zooplankton feeding fishes do not capture rotifers because their small size allows them to pass through gillrakers and thus out through the gills. Because *B. apodion* lacks fine, numerous gillrakers, there is no reason to believe that it is a filter feeder. More likely, it pecks at individual zooplankton and, because of its very small size, is able to take rotifers that are too diminutive to be captured in quantities by larger fishes.

Based on Collette's (1974a, 1974b, 1974c, 1976, 1982) extensive work on freshwater belonid taxonomy and morphology, we have constructed a cladogram suggesting phylogenetic relationships of Amazonian needlefishes (Fig. 3). The feeding behavior of four of the five Amazonian species is also indicated on the cladogram. We have found little information

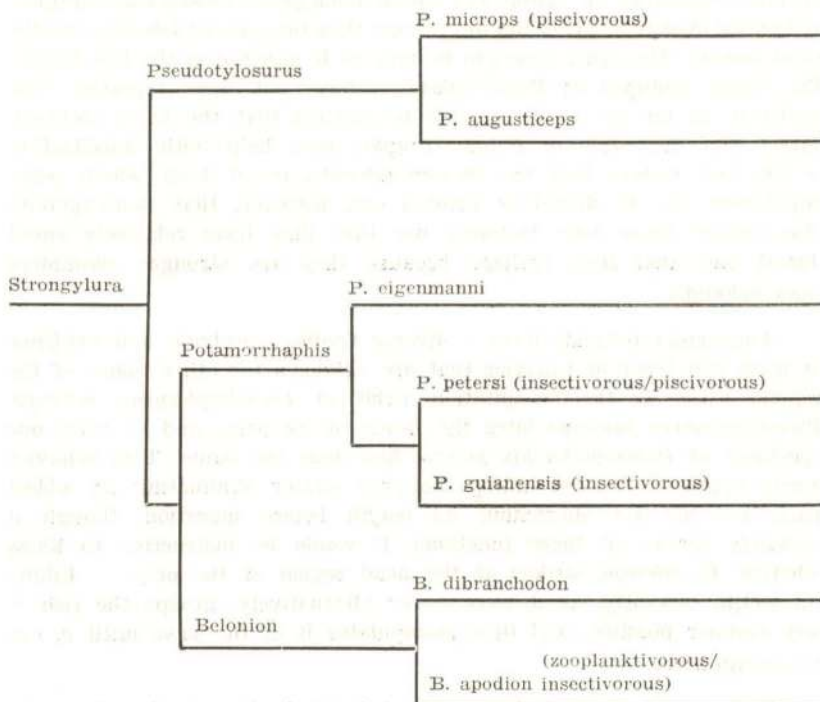


Figure 3 — Dendrogram suggesting the phylogenetic relationships of South American freshwater needlefishes (Belonidae).

on the feeding behavior of *Strongylura*, hypothetically the most primitive freshwater belonid genus of South America (Collette, 1966), though Sazima & Uieda (1979) state that *S. timucu*, a brackish water species, feeds on fish and shrimp. Nevertheless, it appears safe to hypothesize that the most primitive forms (that is, most closely related to marine ancestral taxa) are largely piscivorous (as suggested by our limited data on *Pseudotylosurus microps*). The other phylogenetic line, which led to *Potamorrhaphis* and *Belonion*, evolved feeding habits partially (*P. petersi*), largely (*P. guianensis*) or totally (*B. apodion*) outside of piscivory. If there is a trophic trend in Amazonian belonid phylogeny, then it has been from piscivory to insectivory and zooplanktivory.

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