

MINIATURIZATION IN SOUTH AMERICAN FRESHWATER FISHES; AN OVERVIEW AND DISCUSSION

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Abstract.—Miniature species within the South American freshwater fish fauna are listed and their phylogenetic and ecological distribution is analyzed. Criteria used in identifying miniature South American freshwater fishes are briefly discussed and eighty-five such fishes of five ordinal groups, Clupeiformes, Characiformes, Siluriformes, Cyprinodontiformes and Perciformes, are listed. Approximately eighty-eight percent of these miniatures are characiforms and siluriforms, all primary division ostariophysan fishes. Phylogenetic information on the relationships of these miniatures indicates that such species have arisen in the freshwaters of South America about sixteen times within the Characiformes, twelve in Siluriformes, four in the Cyprinodontiformes and once each in the Clupeiformes and Perciformes. Miniatures of most groups occur in lentic or slow-flowing waters, but the one pimelodid and some trichomycterid catfish miniatures are cryptobenthic in swift-flowing streams.

Resumo.—Peixes miniatura de água doce da América do Sul são definidos e uma lista contendo 85 espécies miniatura, pertencentes à cinco diferentes ordens de teleosteos, é fornecida. Peixes miniatura de água doce sul americanos são arbitrariamente definidos como aqueles que, até onde se sabe, não excedem 26 milímetros de comprimento padrão, sendo que a maioria atinge a maturidade sexual com menos de 20 milímetros de comprimento padrão. As espécies incluídas entre estes limites tem em comum vários caracteres pedomórficos (reduativos) quando comparadas com táxons relacionados. Duas espécies miniatura são conhecidas dentre os Clupeiformes, 49 dentre os Characiformes, 26 dentre os Siluriformes, cinco dentre os Cyprinodontiformes e três dentre os Perciformes. Aproximadamente 88% destes peixes miniatura são Ostariophysa da divisão primária.

A informação disponível sobre as relações filogenéticas da maioria dos peixes miniatura é de qualidade questionável; no entanto, nós provisoriamente estimamos que espécies miniatura surgiram independentemente pelo menos 34 vezes na fauna de peixes de água doce da América do Sul; 16 dentre os Characiformes, 12 dentre os Siluriformes, quatro dentre os Cyprinodontiformes e uma única vez dentre os Clupeiformes e dentre os Perciformes.

A informação sobre a ecologia de peixes miniatura é também escassa mas, como seria de se esperar no caso de peixes diminutos, a maioria ocorre em águas lênticas ou de fluxo lento. No entanto, um pimelodídeo miniatura e alguns tricomicterídeos miniatura são criptobênticos em riachos de fluxo rápido.

The South American freshwater fish fauna is one of the most diverse in the world, with numerous species unknown to science being continually discovered, and a large percentage of the fauna still undescribed (Böhlke et al. 1978). The early collectors and researchers engaged in studies of the ichthyofauna of that continent failed to appreciate the degree of this diversity, particularly among smaller species, and as a consequence often focused on the more obvious species of larger adult body size (Myers 1947: 13–14). Subsequent research by various authors has resulted in a better appreciation of the large number of species of smaller body size, but it is only in the last few decades that a number of species of very small size as adults have been described. The pace of description of such miniature species has quickened in the last decade and recent collecting efforts in various regions of South America revealed the existence of many interesting miniature species (Stewart 1985, 1986; M. Weitzman 1985; Weitzman & Fink 1985; Géry & Uj 1986; Weitzman 1986, 1987; Fernandez & Weitzman 1987; Weitzman & Vari 1987). The comparative studies associated with the description of some of those species (Weitzman & Vari 1987) disclosed that the number of miniature species is much greater than commonly recognized. Indeed, during the twelve decades that have passed since the Thayer Expedition about 85 freshwater South American species (Table 1) that are miniature as adults, or not known to exceed 25 to 26 mm in standard length in nature, have been described from the freshwaters of South America.

In the present paper we discuss the phylogenetic distribution of miniatures in the Neotropical freshwater ichthyofauna, and provide an estimate of the number of miniaturization events within this fauna. The available information on the ecology of South American miniature fishes is summarized, and we evaluate a previous concept of the predominance of secondary freshwater fishes among the miniature

species known from South American drainages.

Miniature Fishes in South American Freshwaters

The range in body sizes among fishes, bony and cartilaginous, is remarkable, covering the spectrum from diminutive fishes under 26 mm standard length (SL), such as those discussed in this paper, to species such as the whale shark which achieves lengths of over 12 m and possibly up to 21.4 m (Campagno 1981). Whereas the larger species of fishes are typical of open waters, particularly in marine environments, smaller species, especially miniatures, are usually, although not exclusively, associated with more complex substrates and ecosystems. This correlation is reflected in the ichthyofaunas of South American streams and rivers, and of Indo-Pacific coral reefs, which are the most diverse in the freshwater and marine environments respectively. Correlated with that high species diversity is the presence in those habitats of a large number of species of small fishes of approximately 25 to 70 or 80 mm SL as adults, together with many miniature species. In Table 1 we list 85 nominal species not known to exceed 26 mm SL, many of which are known to mature at under 20 mm SL. These are considered to be miniature fishes in this paper. Although the term "miniature" implies a very small body size, our primary criterion for distinguishing miniature fishes is not solely size related. Rather it involves the presence in such miniatures of a large number of apparently paedomorphic morphological features including the degree of development of the laterosensory canal system of the head and body, reductions in the number of fin rays and body scales, and a diminution of the sculpturing on the surface bones of the head. Such paedomorphic features in fishes are commonly referred to as reductive in the systematic ichthyological literature and are considered to be due to

Table 1.—Miniature Neotropical freshwater fishes arranged by order, family and some cases by subfamilies and tribes following sequence of discussion in text. Species arranged alphabetically within families, subfamilies or tribes. Maturity is given as minimum known body length at maturity. Maximum is maximum known body length.

Name, author, date	Maturity	Maximum	Reference
Clupeiformes			
Engraulidae			
<i>Amazonsprattus scintilla</i> Roberts, 1984	19.0	19.5	Roberts 1984:318
<i>Anchoviella manamensis</i> Cervigón, 1982	17.5	25.0	Cervigón 1982:220
Characiformes			
Lebiasinidae			
<i>Nannostomus anduzei</i> Fernandez & Weitzman, 1987	11.2	16.2	Fernandez & Weitzman 1987:165
<i>Nannostomus marginatus</i> Eigenmann, 1909	17.0	23.0	Weitzman & Cobb 1975:25
<i>Nannostomus minimus</i> Eigenmann, 1909	16.0	23.0	Weitzman & Cobb 1975:21
Characidae			
Characinae			
<i>Priocharax ariel</i> Weitzman & Vari, 1987	11.8	17.1	Weitzman & Vari 1987:642
<i>Priocharax pygmaeus</i> Weitzman & Vari, 1987	?	16.4	Weitzman & Vari 1987:642
Glandulocaudinae			
<i>Iotabrycon praecox</i> Roberts, 1973b	14.2	21.8	Weitzman & Fink 1985:105
<i>Scopaeocharax atopodus</i> (Böhlke, 1958)	17.8	22.0	Weitzman & Fink 1985:107
<i>Scopaeocharax rhinodus</i> (Böhlke, 1958)	19.2	25.0	Weitzman & Fink 1985:107
<i>Tytocharax cochui</i> (Ladiges, 1950)	<16.0	22.0	Ladiges 1950:308; Weitzman & Fink 1985:108, 110
<i>Tytocharax madeirae</i> Fowler, 1913	13.5	17.5	Weitzman & Fink 1985:108
<i>Xenurobrycon heterodon</i> Weitzman & Fink, 1985	13.6	20.1	Weitzman & Fink 1985:88; Weitzman 1987:113
<i>Xenurobrycon macropus</i> Myers & Ribeiro, 1945	12.0	19.8	Weitzman & Fink 1985:7, 75
<i>Xenurobrycon polyancistrus</i> Weitzman, 1987	11.0	13.1	Weitzman 1987:113
<i>Xenurobrycon pteropus</i> Weitzman and Fink, 1985	13.5	13.8	Weitzman & Fink 1985:85
Tetragonopterinae			
<i>Axelrodia lindeae</i> Géry, 1973	?	20.6	Géry 1973:111
<i>Axelrodia riesei</i> Géry, 1966	?	16.7	Géry 1966:112
<i>Axelrodia stigmatias</i> (Fowler, 1913)	?	20.5	Géry 1966:117
<i>Cheilodon luelingi</i> Géry, 1964	?	17.6	Géry 1964:19
<i>Hemigrammus tota</i> Durbin, 1909	?	21.0*	Durbin 1909:60
<i>Hypheobrycon amandae</i> Géry & Uj, 1986	16.0	19.5	Géry & Uj 1986:59
<i>Hypheobrycon cataleptus</i> (Durbin, 1909)	?	18.0*	Durbin 1909:55
<i>Hypheobrycon diancistrus</i> Weitzman, 1977	23.2	23.9	Weitzman 1977:349, 351
<i>Hypheobrycon elachys</i> Weitzman, 1985	12.0	17.9	Weitzman 1985:800

Table 1. — Continued.

Name, author, date	Maturity	Maximum	Reference
<i>Hypheobrycon flammieus</i> Myers, 1924	14.5	25.0	M. Weitzman pers. comm.
<i>Hypheobrycon georgetii</i> Géry, 1961b	14.4	16.7	Géry 1961b:124
<i>Hypheobrycon gracilior</i> Géry, 1964	?	21.5	Géry 1964:12
<i>Hypheobrycon grieni</i> Hoedemanni, 1957	14.2	25.7	M. Weitzman pers. comm.
<i>Hypheobrycon loretoensis</i> Ladiges, 1938	?	24.0	Géry 1961a:35
<i>Hypheobrycon minimus</i> Durbin, 1909	?	21.0*	Durbin 1909:68
<i>Hypheobrycon minor</i> Durbin, 1909	?	25.0*	Durbin 1909:65
<i>Hypheobrycon tukunai</i> Géry, 1965a	19.0	20.6	Géry 1965a:25
<i>Megalamphodus rogoaguai</i> Pearson, 1924	16.5	23.0	Pearson, 1924:33; personal observation
<i>Microhemobrycon elongatus</i> Géry, 1973	?	25.0	Géry 1973:97
<i>Oxybrycon parvulus</i> Géry, 1964	?	15.7	Géry 1964:16
<i>Paracheirodon innesi</i> (Myers, 1936)	17.2	22.2	Personal observation
<i>Paracheirodon simulans</i> (Géry, 1963)	17.0	19.6	Weitzman & Fink 1983:358
<i>Spintherobolus broccae</i> Myers, 1925a**	17.6	23.5	Myers 1925a:144; personal observation
<i>Tytobrycon dorsimaculatus</i> Géry, 1973	19.0	20.5	Géry 1973:118
<i>Tytobrycon hamatus</i> Géry, 1973	14.1	16.9	Géry 1973:129
<i>Tytobrycon spinosus</i> Géry, 1973	17.0	20.5	Géry 1973:121
<i>Tytobrycon xerini</i> Géry, 1973	17.7	22.6	Géry 1973:126
Characidiinae			
<i>Elachocharax geryi</i> Weitzman & Kanazawa, 1978	?	15.5	Weitzman & Kanazawa 1978:173
<i>Elachocharax junki</i> (Géry, 1971)	?	22.4	Weitzman & Géry 1981:892
<i>Elachocharax miopterus</i> Weitzman, 1986	?	13.9	Weitzman 1986:738
<i>Elachocharax pulcher</i> Myers, 1927	?	22.1	Weitzman & Géry 1981:890
<i>Jobertina bahiensis</i> (Almeida, 1971)	16.0	23.3	Almeida 1971:112
<i>Jobertina eleotrioides</i> Géry, 1960	?	21.0	Géry 1960:4
<i>Klausewitzia aphanes</i> Weitzman & Kanazawa, 1977	13.0	16.5	Weitzman & Kanazawa 1977:151, 158
<i>Klausewitzia ritae</i> Géry, 1965b	<20.0	25.0	Géry 1965b:199
Siluriformes			
Trichomycteridae			
Trichomycterinae			
<i>Trichomycterus hasemani</i> Eigenmann, 1914	?	18.0*	Eigenmann 1918b:326
<i>Trichomycterus santaeritae</i> Eigenmann, 1918b	?	24.0*	Eigenmann 1918b:341
<i>Trichomycterus johnsoni</i> Fowler, 1932	?	16.0	Fowler 1932:368
Glanapteryginae			
<i>Pygidianops eigenmanni</i> Myers, 1944	?	23.0	Myers 1944:593

Table 1.—Continued.

Name, author, date	Maturity	Maximum	Reference
Vandeliinae			
<i>Paravandellia bertonii</i> (Eigenmann, 1918a)	?	24.0*	Eigenmann 1918b:368
<i>Paravandellia magdalenae</i> (Miles, 1943a)	?	22.0	Miles 1943b:369
<i>Paravandellia oxyptera</i> A. Miranda-Ribeiro, 1912	?	23.0	P. Miranda-Ribeiro 1947:4
Tridentinae			
<i>Miuroglanis platycephalus</i> Eigenmann & Eigenmann, 1889	?	17.0*	Eigenmann & Eigenmann 1889:56
<i>Tridensimilis brevis</i> (Eigenmann & Eigenmann, 1889)	?	21.0*	Eigenmann & Eigenmann 1889:54
<i>Tridensimilis venezuelae</i> Schultz, 1944	?	20.5	Schultz 1944:267
<i>Tridentopsis pearsoni</i> Myers, 1925b	18.0	23.0	Myers 1925b:86
<i>Tridentopsis tocantinsi</i> LaMonte, 1939	?	23.0	LaMonte 1939:1
Sarcoglanidinae			
<i>Malacoglanis gelatinosus</i> Myers & Weitzman, 1966	18.2	19.9	Myers & Weitzman 1966:282
<i>Sarcoglanis simplex</i> Myers & Weitzman, 1966	?	19.6	Myers & Weitzman 1966:279
Loricariidae			
<i>Microlepidogaster lophophanes</i> (Eigenmann & Eigenmann, 1889)	?	18.0	Eigenmann & Eigenmann 1889:42
Callichthyidae			
<i>Aspidoras brunneus</i> Nijssen & Isbrücker, 1976b	?	21.3	Nijssen & Isbrücker 1976b:116
<i>Aspidoras carvalhoi</i> Nijssen & Isbrücker, 1976b	?	25.4	Nijssen & Isbrücker 1976b:116
<i>Aspidoras pauciradiatus</i> Weitzman & Nijssen, 1970	?	23.2	Weitzman & Balph 1979:10-11
<i>Corydoras gracilis</i> Nijssen & Isbrücker, 1976a	?	23.2	Nijssen & Isbrücker 1976a:91
<i>Corydoras habrosus</i> Weitzman, 1960a	15.5	20.1	Weitzman 1960a:141-145
<i>Corydoras hastatus</i> Eigenmann & Eigenmann, 1888	18.2	20.1	Personal observation
<i>Corydoras pygmaeus</i> Knaack, 1966	18.3	23.7	Nijssen & Isbrücker 1986:52, personal observation
Aspredinidae			
<i>Dupouyichthys sapito</i> Schultz, 1944	?	23.0	Schultz 1944:245; Stewart 1985:10
<i>Hoplomyzon papillatus</i> Stewart, 1985	?	16.9	Stewart 1985:8
Scoloplacidae			
<i>Scoloplax dicra</i> Bailey & Baskin, 1976	?	13.8	Bailey & Baskin 1976:5, 7
Pimelodidae			
<i>Horiomyzon retropinnatus</i> Stewart, 1986	23.3	23.3	Stewart 1986:50
Cyprinodontiformes			
Poeciliidae			
Fluviophylacinae			
<i>Fluviophylax pygmaeus</i> (Myers & Carvalho), in Myers, 1955	12.5	22.0	Roberts 1970:10, Weitzman 1982:191

Table 1.—Continued.

Name, author, date		Maturity	Maximum	Reference
Pociliinae				
Pociliini				
	<i>Pocilia hasemani</i> (Henn, 1916)	?	23.0	Jacobs 1969:287
	<i>Pocilia minor</i> (Garman, 1895)	9.5	15.0	K. Hartel pers. comm.
Heterandriini				
	<i>Neoheterandria elegans</i> Henn, 1916	16.5	18.0	Henn 1916:118
Cnesterodontini				
	<i>Phallotorynus jucundus</i> von Ihering, 1930	14.9	24.9	C. Ferraris pers. comm.
Perciformes				
Eleotrididae				
	<i>Microphilypnus amazonicus</i> Myers, 1927	?	17.1	Personal observation***
	<i>Microphilypnus macrostoma</i> Myers, 1927	?	20.0	Myers 1927:135***
	<i>Microphilypnus ternetzi</i> Myers, 1927	?	20.0	Myers 1927:134***

* Total length taken from cited literature.

** Research in progress by the senior author indicates that *Spintherobolus broccae* Myers (1925a) is not a synonym of *Phoxinopsis typicus* Regan (1907) as proposed by Myers in Anonymous (1970).

*** The largest *Microphilypnus* specimen examined (of an unidentified species) is 25.5 mm SL.

the loss of terminal stages in the developmental sequence. Myers (1958:29) discussed various characters commonly demonstrating paedomorphic features in South American freshwater fishes, and those features will be discussed and evaluated in greater detail in a future paper. For the purposes of this paper, the miniature South American fishes listed in Table 1 satisfy either of two criteria. They are either species which mature sexually at under 20 mm SL and may sometimes reach somewhat larger sizes, or species for which maturity data are unknown but which are not reported to exceed 25 to 26 mm SL in the wild. Species examined by us or reported in the literature as getting larger than that size, even though they may mature at lengths somewhat shorter than 20 mm SL are not included. This cut-off point for "miniatures" is arbitrary and the listing is meant as a preliminary guide to future studies of miniature fishes in South America rather than as a definitive enumeration of such species.

The size limitation used in the present study was adopted because all listed species that have been examined in detail which mature under 20 mm SL, and do not grow to longer than 25 to 26 mm SL, have in common numerous apparently paedomorphic morphological reductions. A few species in Table 1 are known to somewhat exceed 26 mm SL when raised and kept in aquaria. These include *Corydoras habrosus* Weitzman, *Paracheirodon innesi* (Myers), *Hyphessobrycon flammeus* Myers, *Hyphessobrycon griemi* Hoedemann, and *Hyphessobrycon loretoensis* Ladiges. Some of these species may exceed this length in nature, but that remains unconfirmed. Geisler & Annibal (1984:77-78) have discussed aquarium versus wild lengths for *Paracheirodon axelrodi* (Schultz), a fish that exceeds our size limit, but which displays paedomorphic features (Weitzman & Fink 1983:354-357). Geisler & Annibal believed that individuals of this species rarely live more than one year in the wild, and that poor nutrition in its

natural habitat further limits the adult size of the species. Most miniatures probably live less than one year in the wild, perhaps considerably less.

The apparent paedomorphic nature of miniature species in Table 1 at maturity, and the reductive nature of some characters are recognized within the context of the developmental sequences of the characters in apparently related outgroups maturing at longer lengths. The phylogenetic hypotheses available for most taxa are of an imprecise nature. Thus the documentation of paedomorphosis with respect to proximate sister groups involves general rather than specific phylogenetic comparisons. Precise information on morphology and size at maturity is not available for some taxa, a number of which are known only from limited series. In those instances we extrapolate that the correlations between a body size under 25 to 26 mm SL and the presence of paedomorphic features that are characteristic of other more inclusive taxa also applies to the species we have been unable to examine critically. It is also necessary to note that maturity data are absent for a number of the listed species. It is possible that future studies may reveal that adults of some of these taxa achieve sizes greater than the cut-off used to delimit miniatures in this paper.

The size criterion for miniatures in this study is not completely satisfactory when applied to some unlisted species with elongate bodies. For example the trichomycterid catfishes *Typhlobelos ternetzi* Myers and *Glanapteryx anguilla* Myers, have small heads displaying many paedomorphic features of miniatures, although the fishes exceed 30 mm SL. Similarly *Tomeurus gracilis* Eigenmann, an elongate poeciliid, is in many ways a miniature fish, but we have examined both males and females of 26.5 mm SL from Surinam (USNM 225463), and as a consequence do not include the species in our list. These three species are in actuality elongate miniatures in which the head length, but not body length agrees with that

of the species in Table 1. The concept of an elongate miniature is perhaps even more appropriate for the South American freshwater needlefishes of the genus *Belonion* Collette. Collette (1966:9, 15–21) in his description of the genus and contained species detailed numerous reductive characters for the genus relative to outgroup needlefishes involving the epipleurals, fourth upper pharyngeal tooth bones, laterosensory canal system and other features. Although *Belonion dibranchodon* Collette matures at 24.5 mm SL and members of the genus reach 41.8 mm SL (Collette 1966:12–13), the species are very elongate. In fishes of such shapes it might be more appropriate to compare species on the basis of the bony head length (exclusive of the elongate lower jaw in *Belonion*) rather than focusing on standard length. In such a framework more species such as *Belonion dibranchodon* would be listed as miniatures. A criterion of size using such a portion of the body with numerous paedomorphic features could be similarly used to delimit miniature species regardless of their actual standard length.

Although the data from *Belonion* and some characiform groups suggests that some alternative standard for miniature fishes might be appropriate, morphological data on paedomorphic features are unfortunately largely absent for many relatively small species of some major groups of South American freshwater fishes (e.g., Gymnotiformes, Cichlidae) slightly longer than 26 mm SL. Similarly there is a paucity of data on how and whether paedomorphic characters correlate with standards such as absolute head size in most groups. Thus for the sake of consistency we prefer to use standard rather than head length or another measurement as the benchmark for our discussion until more data are available.

If the concept of miniature fishes of this paper can be extended to other groups of fishes, then the majority of the miniature fishes, in both freshwater and marine environments, have been described within the

last 40 years. Böhlke & Robins (1968), Jewett & Lachner (1983), Lachner & Karnella (1978, 1980), Winterbottom (1983), and Winterbottom & Emery (1981, 1986) provide many examples of miniature marine gobies, and references in those publications will lead to other descriptions of such species. Springer (1983), in describing a new miniature species of western Pacific goby, has documented several skeletal modifications, of which some appear paedomorphic to us. More recently Whitehead and Teugels (1985) have described apparently paedomorphic features in *Sierrathrissa leonensis* Thys van den Audenaerde a species of African freshwater clupeid that reaches a slightly greater length, 26.7 mm SL, than the 26 mm SL limit on miniature fishes. Finally, Roberts (1986:332–340) reported many similar reductions in a miniature Asian cyprinid, *Danionella translucida* Roberts (1986:233).

Phylogenetic Lineages of South American Freshwater Fishes

The large number of species of miniature fishes within the South American freshwater ichthyofauna is striking, but a true sense of the possible significance of this phenomenon can only be achieved by examining miniaturization within a phylogenetic framework. In other words, in which major groups of fishes is miniaturization found, and how many times has it independently evolved?

Not surprisingly, the two largest groups of South American fishes, the ostariophysan orders Characiformes and Siluriformes, account for the vast bulk (88%) of the miniatures, while the Clupeiformes, Cyprinodontiformes and the Perciformes which are less speciose on that continent cumulatively include only about 12% of the miniatures. These five orders are each monophyletic and the evolution of miniatures in each of these clades has clearly proceeded independently. The question of how many times miniatur-



Fig. 1. *Amazonsprattus scintilla* Roberts, a miniature clupeiform fish, family Engraulidae, from the Amazon basin, AMNH 57371, 24.3 mm SL; Brazil, state of Amazonas, Rio Urubaxi, tributary of Rio Negro, south of east end of Ilha Tamaquari (01°32'N, 64°59'W).

ization has evolved within each lineage cannot be answered with the same precision, but we will address the issue to the extent possible within the context of available phylogenetic data. We must preface our general discussion with the observation that there are relatively few rigorous phylogenetic studies of components of the South American freshwater fish fauna, and many traditionally accepted taxa have not been critically reviewed with respect to their possible monophyly. In light of this lack of precision we conservatively do not hypothesize multiple miniaturization events within a genus unless phylogenetic data indicate that reduced size and its attendant paedomorphic features have independently evolved more than once in the taxon.

Only two species of miniature clupeiformes are described from South American freshwaters. Roberts (1984:321) withheld judgement on the phyletic associations of *Amazonsprattus* Roberts (Fig. 1), but further study by Gareth Nelson (pers. comm.) indicates that it is a member of the Engraulidae, as is *Anchoviella* Fowler, the other South American clupeiform genus with a described miniature species. A phylogenetic hypothesis that would provide insight into the relationships of the two miniature South American engraulids is not available, and currently it is not appropriate to hypothesize more than a single evolutionary miniaturization event in the group.

Interestingly no miniature species are known to occur in ten of the twelve Neotropical characiform families recognized by Greenwood et al. (1966:395–396), although in at least one, the Gasteropelecidae, there are several species of *Carnegiella* Eigenmann displaying numerous apparently paedomorphic features (Weitzman 1954, 1960b). Many of the characiform families without known miniatures demonstrate marked morphological adaptations for specialized feeding methods (e.g., Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae, Vari 1983:7–33, 43–46; in press), which may be incompatible functionally with a pronounced reduction in overall body size. Miniatures are rather found only in the Lebiasinidae and Characidae among the South American characiforms. Within those families the miniatures are distributed among eighteen genera, one lebiasinid and seventeen characid, most of which are poorly understood in terms of intrageneric phylogenetic relationships.

Lebiasinids show a considerable range in overall standard lengths with *Pyrhulina* Valenciennes and *Lebiasina* Valenciennes each having species reaching 100 mm SL, and species of *Piabucina* Valenciennes growing to about 200 mm SL. The three species of *Nannostomus* Günther listed in Table 1 are members of a genus of 15 species that includes numerous species of about 25 to 35 mm SL and it is not surprising that

several miniatures are found in that taxon. According to Weitzman (1964:152–153) *Nannostomus* forms a derived clade within the Lebiasinidae. That hypothesis along with the larger body sizes in the lebiasinid outgroups, and the small but not minute body size of other *Nannostomus* species indicates that the minute size of the miniature *Nannostomus* is derived. Attempts to resolve the relationships within *Nannostomus* have not proved feasible (Weitzman & Weitzman 1982:417–419; Fernandez & Weitzman 1987:165). In the absence of that data we are unable to reasonably hypothesize whether the miniaturization process in that genus has occurred one, two, or three times, but conservatively assume that it took place only once.

The absence of reliable hypotheses of relationships among the vast majority of subfamilies and genera in the Characidae similarly does not permit us to advance any critically evaluated hypothesis on the exact number of evolutionary events represented by the occurrence of miniatures in 17 genera within the family. These genera are currently assigned to four subfamilies, Characinae, Glanduloaudinae, Tetragonopterinae (including Cheirodontinae) and Characidiinae. We prefer not to recognize a Cheirodontinae separate from the Tetragonopterinae in light of the difficulties in advancing an unambiguous diagnosis of the Cheirodontinae that were discussed by Fink & Weitzman (1974:1), Géry (1977:543) and particularly Weitzman & Fink (1983:341–353).

The uncertainties associated with hypotheses of the exact phylogenetic relationships of *Priocharax* Weitzman & Vari within the Characinae were discussed by Weitzman & Vari (1987:648–651). Nonetheless, the data demonstrate that the two species form a monophyletic group within the Characinae, a putative group of typically larger size fishes, although some taxa (*Gnathocharax* Fowler, *Heterocharax* Eigenmann and *Hoplocharax* Géry) are in the

25 to 35 mm SL size range. Thus, the minute size of the *Priocharax* species is considered to be the consequence of a single ancestral miniaturization.

The next two subfamilies, the Glanduloaudinae and Tetragonopterinae (including Cheirodontinae), both of which contain many miniatures, are apparently closely related groups, neither of which has, however, been shown to be monophyletic (Weitzman & Fink 1983:341–346; Weitzman et al. in Weitzman & Fink 1985:112–117). The phylogenetic relationships of the miniature glanduloaudine genera *Iotabrycon* Roberts, *Xenurobrycon* Myers & Miranda-Ribeiro, *Scopaeocharax* Weitzman & Fink, and *Tytocharax* Fowler (Table 1) were analyzed phylogenetically by Weitzman & Fink (1985:12–70) who hypothesized with considerable evidence that they form a monophyletic unit. The sister taxon to that assemblage, the genus *Argopleura* Eigenmann, has adults that range from 35 to 53 mm SL and the miniaturization in the four cited xenurobryconin genera is apparently the product of a single evolutionary event.

Few tetragonopterine genera have been the subject of comparable studies, and for most it is only possible to tentatively presume monophyly for multispecific taxa. One exception is the genus *Paracheirodon* Géry hypothesized to be monophyletic by Weitzman & Fink (1983:347–357), but of uncertain phylogenetic relationships within the Tetragonopterinae. The genus consists of three species, *P. simulans* Géry and *P. innesi*, both miniatures, and *P. axelrodi* which reaches an adult size of 33.1 mm SL in the wild, although Geisler & Annibal (1984:32) report an old aquarium specimen that reached 51.0 mm SL. Thus the genus evidently represents a single evolutionary shift to reduced body size with subsequent miniaturization. The hypothesis of the monophyly of *Paracheirodon* as proposed by Weitzman & Fink has been challenged by Géry (1984:59) and Géry & Mahnert (1986:49) who maintain that *P. simulans* belongs

to the large tetragonopterine genus *Hyphessobrycon* Durbin. A reanalysis of the data of Géry (1984) and Géry & Mahnert (1986) by Weitzman & Fink (1987) has reconfirmed the placement of *P. simulans* in the monophyletic clade *Paracheirodon*.

The lack of information on phylogenetic relationships within and among the remaining tetragonopterine taxa containing miniatures precludes any indepth critical discussion of the number of times that miniaturization arose among these taxa. We prefer to take a conservative course and assume that miniatures in genera with two or more species arose from single ancestral miniaturization events. That assumption may be disproved when the necessary phylogenetic studies are undertaken, indicating multiple independent miniaturization events in some of the taxa. Alternatively, such analyses may also reveal presently unsuspected sister group relationships between some of the genera, with a consequent reduction in the number of hypothesized miniaturization events. The involved tetragonopterine genera and the number of included species (in parentheses) are as follows: *Hyphessobrycon* (12), *Tyttobrycon* Géry (4), *Axelrodia* Géry (3), *Oxybrycon* Géry (1), *Megalampodus* Eigenmann (1), *Microschemobrycon* Eigenmann (1), *Cheirodon* Girard (1), *Hemigrammus* Gill (1), and *Spintherobolus* Eigenmann (1) (Fig. 2). Although we only count the miniature species of *Hyphessobrycon* as being the result of a single ancestral miniaturization, the genus is relatively speciose (over 60 nominal species) and includes a number of species in the 26 to 35 mm SL range (Weitzman 1977:355–356; M. Weitzman 1985:805) increasing the likelihood that miniaturization may have occurred multiple times in the genus. It has also been suggested that *Hyphessobrycon* may be polyphyletic (Weitzman & Fink 1983:342), a possibility that further complicates the question of the number of miniaturization events in the genus. All species of *Tyttobrycon* are minia-

tures (Géry 1973:117) as is the case with *Axelrodia* (Géry 1965a:31–35, 1966:111–118, 1973:111–115) and *Oxybrycon* (Géry 1964:15). *Microschemobrycon*, in contrast, contains a number of species of 30 to 35 mm SL (Eigenmann 1915:53; Géry 1973:86–101, 1977:598).

The last characid subfamily to be considered and one containing eight described miniatures in three genera (*Elachocharax* Myers, *Klausewitzia* Géry and *Jobertina* Pellegrin) is the Characidiinae. Once again the information on relationships within the subfamily is limited, with only *Elachocharax* having been the subject of phylogenetic treatment (Weitzman & Géry 1981; Weitzman 1986). *Elachocharax* is hypothesized to be monophyletic with four known species, all miniatures, and the reduced adult size assumed to be a consequence of a single evolutionary event. The situation in *Klausewitzia* is more equivocal, with the two described species, both of which are miniatures, perhaps united by a single character, the presence of a maxillary tooth, a character that may be either plesiomorphous or a derived reversal (Weitzman & Kanazawa 1977:157–159).

The phylogenetic problems associated with *Jobertina* and the evidently most closely related genus, *Characidium* Reinhardt are complex and we neither have data on whether *Jobertina* is monophyletic nor on whether the two known miniatures are sister species. We can only note that some of the species of *Characidium* achieve adult body sizes of over 110 mm SL and that the reduced size of the two *Jobertina* species is apparently a derived feature. Miniaturization in the Characidiinae is thus counted as having occurred three times, once each in *Elachocharax*, *Klausewitzia* and *Jobertina*. We note, however, that most of the miniature species of these genera have in common various features (e.g., elongate pectoral fin rays, Weitzman & Kanazawa 1978:160) that may represent synapomorphies for those taxa. If that is the case, miniaturiza-



Fig. 2. *Spintherobolus brocuae* Myers, a miniature characiform fish, family Characidae, from southeastern Brazil, USNM 287324: (A) mature female, 22.0 mm SL, (B) mature male, 18.5 mm SL; Brazil, state of Rio de Janeiro, small tributary of Rio Macacu, about 1–2 km from town of Cachoeiros de Macacu (approx. 22°29'S, 42°41'W).

tion may have arisen only once in the Characidiinae, but the problem requires more study.

Phylogenetic analyses of South American freshwater siluriform families and genera are very rare. According to present classifications (Myers 1944, Myers & Weitzman 1966, Bailey & Baskin 1976, Isbrücker 1980, Stewart 1985) the miniature siluriforms listed in Table 1 are distributed among six family group taxa, although some authors disagree on the placement of *Scoloplax* Bailey and Baskin. Under all the classificatory schemes, miniatures are found in the Aspredinidae, Callichthyidae, Loricariidae, Pimelodidae and Trichomycteridae. *Scoloplax*, originally placed in the Loricariidae by Bailey & Baskin (1976), was removed from that family by Isbrücker (1980) who

placed it in the monotypic Scoloplacidae. That shift fails to elucidate the phylogenetic relationships of the single contained species, but that classification is followed for the purposes of this discussion since the alternative proposed alignment is no more satisfactory.

The eight genera of miniature Trichomycteridae are found in five subfamilies, Trichomycterinae (*Trichomycterus* Valenciennes), Glanapterygiinae (*Pygidianops* Myers), Vandelliinae (*Paravandellia* Miranda-Ribeiro), Tridentinae (*Tridensimilis* Schultz, *Miuroglanis* Eigenmann & Eigenmann, and *Tridentopsis* Myers (Myers 1944: 599) (Fig. 3)) and Sarcoglanidinae (*Sarcoglanis* Myers & Weitzman, and *Malacoglanis* Myers & Weitzman (Myers & Weitzman 1966:279)). The Trichomycterinae

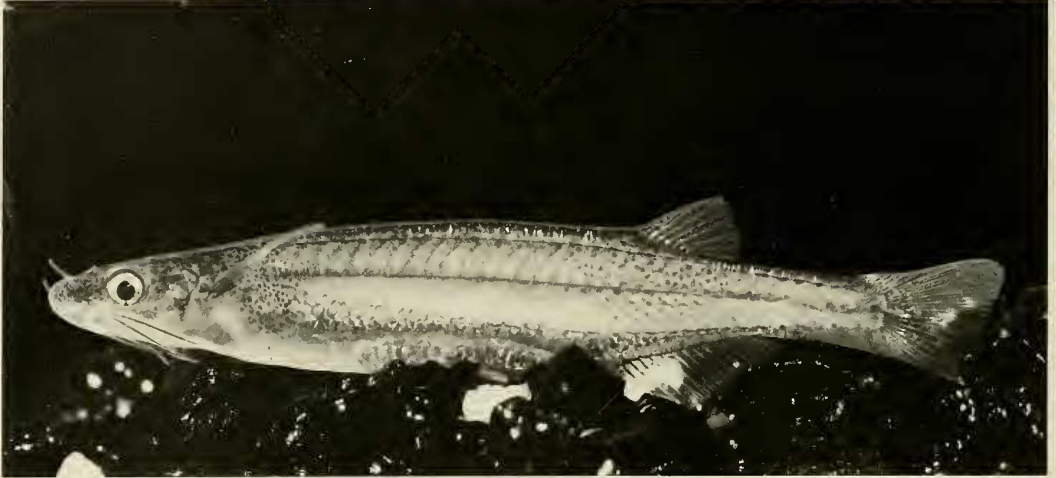


Fig. 3. *Tridentopsis* sp., a miniature South American siluriform fish, family Trichomycteridae, 23.8 mm SL; aquarium specimen, no definite collecting locality information.

contains species ranging from 16.0 to over 260 mm SL as adults (Eigenmann 1918b: 286, 326; Fowler 1932:368). The phylogenetic relationships of the three described miniatures of that subfamily are unresolved and we assume that they represent a single miniaturization event. Four subfamilies contain only miniatures (Sarcoglanidinae) or mostly miniatures and small species (Glanapteryginae, Vandelliinae, Tridentinae) but belong to separate and divergent clades within the Trichomycteridae (J. N. Baskin, pers. comm.) and thus represent distinct miniaturization events. Miniaturization in the Trichomycteridae thus arose at least five times.

Miniature species in the Callichthyidae are limited to three species of *Aspidoras* von Ihering and four species of *Corydoras* Lacépède. Although Weitzman & Balph (1979: 16–18) raised questions about the distinctiveness of these genera, they noted (1979: 20) that reduced size in *Corydoras* and *Aspidoras* was apparently independently derived. The relationships of the four miniature *Corydoras* species are unresolved and the genus is very speciose raising the possibility that miniaturization arose several times in that taxon. We prefer nonetheless

to be conservative and to hypothesize only a single miniaturization within each genus. Miniaturization is consequently considered to have arisen at least twice in the Callichthyidae.

Two miniatures, one each in *Hoplomyzon* Myers and *Dupouyichthys* Schultz, occur in the Aspredinidae. According to Stewart (1985:4) the species occur in separate monophyletic taxa containing other small species. Thus miniatures are presumed to have arisen twice in the Aspredinidae. There is only one described miniature in the Pimelodidae, *Horiomyzon retropinnatus* Stewart (1986), and a single such species is tentatively identified for the Loricariidae, *Microlepidogaster lophophanes* (Eigenmann & Eigenmann). As noted above, the phylogenetic relationships of *Scoloplax*, the only genus of the Scoloplacidae, are the subject of some controversy, but under either proposed classification it probably represents an independent miniaturization event since no miniatures are known in likely sister groups to that genus. In summary miniatures have arisen at least twelve times in the South American members of the Siluriformes.

The five miniature species in the Cyprin-

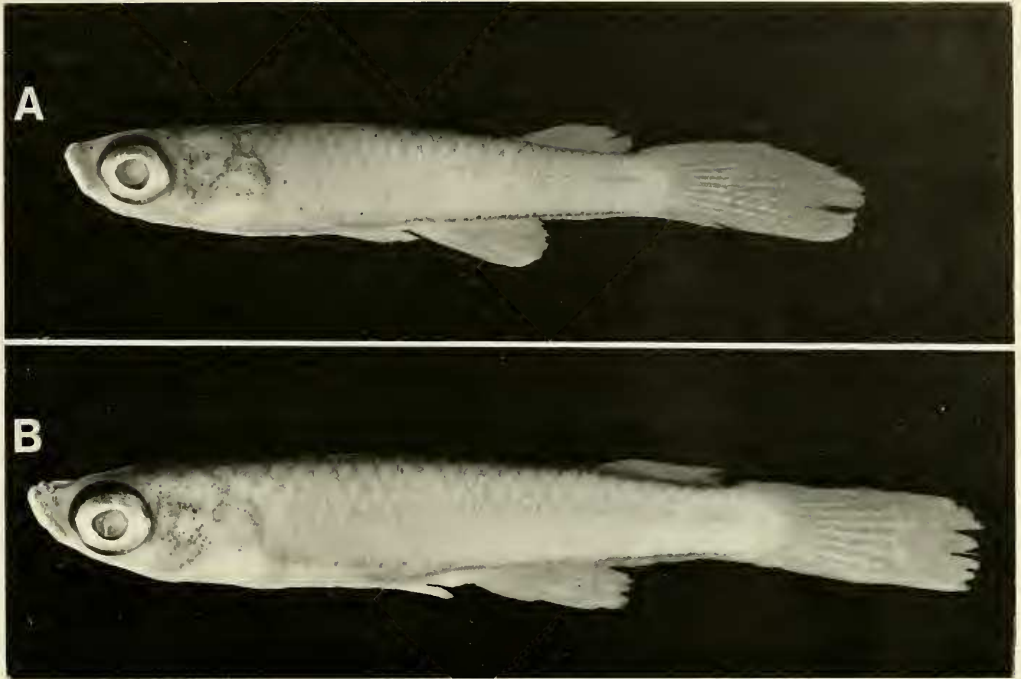


Fig. 4. *Fluviphylax pygmaeus* (Myers & Carvalho), a miniature cyprinodontiform fish, family Poeciliidae, from the Amazon basin, USNM 227730: (A) mature male, 10.3 mm SL, (B) mature female, 13.1 mm SL; Brazil, state of Amazonas, Rio Negro, Lago Sirola, Anavilhanas Archipelago (approx. 03°10–15'N, 60°40–45'W).

idontiformes belong to two subfamilies of the Poeciliidae according to Parenti (1981: 451, 463). *Fluviphylax pygmaeus* (Myers & Carvalho) (Fig. 4) is the only described member of the Fluviphylacinae and is an independent evolution to small size. The four other diminutive cyprinodontiform species are distributed in three tribes of the Poeciliinae in the classification proposed by Rosen & Bailey (1963:3, 39, 61, 116). The two species of *Poecilia* Bloch & Schneider are placed in the Poeciliini, *Neoheterandria* Henn in the Heterandriini, and *Phallotorynus* Henn in the Cnesterodontini. If these tribes represent monophyletic groups, then miniatures have evolved at least three times in the Poeciliidae and a total of four times in the Cyprinodontiformes.

The final miniatures known in the South American freshwater ichthyofauna, the electrids of the genus *Microphylipnus* Myers (Fig. 5) have not been studied since described by Myers (1927). Although of un-

certain relationship to other members of that family, and not shown to be monophyletic, they represent at least one evolutionary miniaturization event.

On the basis of present information we can reasonably estimate that miniaturization within the South American freshwater fish fauna has taken place independently sixteen times in the Characiformes, on at least twelve occasions in the Siluriformes, in four instances in the Cyprinodontiformes and once in each of the Clupeiformes and Perciformes, for a total of about thirty-four events.

Ecology of South American Miniature Freshwater Fishes

There are currently 85 described species of miniature or putatively miniature fishes from forested regions of South America (Table 1), a number that will undoubtedly increase. Fewer miniature fish species have

A



B

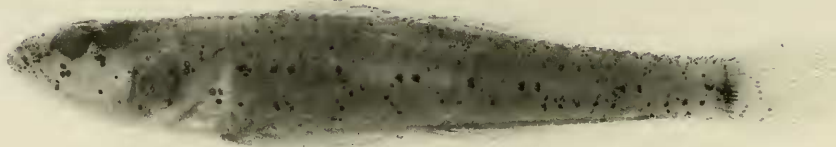


Fig. 5. *Microphilypnus* sp., a miniature perciform fish, family Eleotrididae, from the Amazon basin, USNM 290836: (A) mature male, 20.8 mm SL, (B) mature female, 21.7 mm SL; Brazil, state of Amazonas, Rio Urubaxi, tributary of Rio Negro, south of east end of Ilha Tamaquari (01°32'N, 64°59'W).

been reported from other tropical freshwater regions. If we use the same standard for a miniature, approximately one dozen miniature fish species are known from the freshwaters of Africa (Daget et al. 1984, 1986) and a comparable number seem to have been reported from the Asiatic tropics, totals admittedly likely to increase in the future. Reasons for the current differences in the numbers of miniature species from the three continental tropical regions are obscure. In part the larger number of miniatures in South American freshwaters may simply reflect the richness of the overall fish fauna on that continent; however, our knowledge of the ichthyofauna is so poor (Böhlke et al. 1978:667–670) that it is premature to speculate further at this time.

The diversity and composition of the miniature fish fauna in South America was previously discussed by Roberts (1973a: 247–248), who stated that “Excepting the

catfishes, all diminutive (Amazonian) species are secondary freshwater fishes and belong to groups whose presence can be thought of as ‘marginal.’” More recently (1984:320) he has further suggested that “In the Amazon, where community structure of freshwater fishes may be more complex than anywhere else, minute body size seems to have arisen primarily in response to biotic factors.” He continued that, “this in my opinion, is the general reason why so many of the smallest Amazonian fishes belong to secondary freshwater fish groups which in terms of relative numbers of species represent an insignificant fraction of the fauna.” He also notes that miniatures in various other groups may be discovered in the future. Secondary freshwater fishes as defined by Myers (1937:344–345) are those fishes belonging to teleost groups ordinarily of marine or euryhaline habit, or those groups with members commonly entering

an euryhaline habitat. In South American freshwaters the known miniatures belong to five major groups, three of which, the Cyprinodontiformes, Clupeiformes and Perciformes (only Eleotrididae) are secondary freshwater fish groups according to Myers' concepts. The other two groups, the Characiformes and Siluriformes are primary freshwater groups, that is teleost groups typically of freshwater habits. Of the 85 listed species of South American miniatures, about 88% belong to the primary freshwater groups, the characiforms and siluriforms (Table 1). The secondary freshwater groups, cyprinodontiforms, clupeiforms, and perciforms in contrast, together represent only ten of the 85 miniature freshwater fishes known from South America (Table 1). Increased collecting with specialized techniques, and future revisionary studies may change the relative contribution of these major taxonomic units to the fauna of miniature fishes. Current data indicate, however, that contrary to Roberts, it is the primary rather than secondary freshwater groups that predominate among miniature fishes of the Amazon basin, the area of occurrence of the majority of characiform and siluriform fishes listed in Table 1.

The degree to which ecological factors (? the biotic factors of Roberts (1984:320)) show a correlation with, and may have been involved in the evolution of miniature fishes in South American freshwaters is difficult to determine at this time. The possibility that acidic waters of low productivity may result in reduced poring of the laterosensory system of the body, and perhaps of overall body size was noted by Collette (1962:179–191) relative to the North American percid fish *Etheostoma fusiforme* Girard. Black acidic waters are quite common in South America, and many of the species listed in Table 1 occur in that environment (pers. observ.). In-depth studies of the ecology of most freshwater fishes in South America are rare and very little is known about the habits or life histories of small and miniature

freshwater fishes in that region. The reasons for this lack of information about miniatures are myriad, many revolving around the diminutive size of the species in question. Such species are not often noted while making general collections. Those sampling efforts are, furthermore, usually not focused at the microhabitat level necessary to delimit those ecological parameters possibly idiosyncratic to miniature species.

Miller (1979:271–274) briefly discussed the habitats of small fishes, but did not specifically refer to miniatures as defined herein. Our own observations and the limited pertinent literature reveal one general ecological parameter common to many miniatures—their repeated occurrence in still or slow-flowing shallow waters. This association is not unexpected given the difficulties small or miniature fishes have in maintaining position in a rapidly moving water column. Miniature Neotropical fishes living in less turbulent habitats are detailed below. This listing is based on personal observations supplemented by personal communications and literature information.

Among the miniature clupeiforms, only *Amazonsprattus scintilla* Roberts is known to live in still or slow-flowing waters. The more speciose characiform miniatures we have seen in, or which have been reported from that habitat include the characidiines *Elachocharax mitopterus* Weitzman & *Elachocharax pulcher* Myers, the characines *Priocharax ariel* Weitzman & Vari and *Priocharax pygmaeus* Weitzman & Vari, the glandulocaudines *Xenurobrycon polyancistrus* Weitzman (Weitzman 1987:118–119), species of *Tytocharax* Fowler (Saul 1975: 111; D. J. Stewart, pers. comm.), and *Iotabrycon praecox* Roberts (Roberts 1973b: 501–502), the tetragonopterine *Hyphessobrycon elachys* M. Weitzman (1985:799), and the lebiasinids *Nannostomus anduzei* Fernandez & Weitzman and *N. marginatus* Eigenmann. The siluriform species *Corydoras hastatus* Eigenmann & Eigenmann (Myers 1953:269; I. Sazima, pers. comm.)

and *Scoloplax dicra* Bailey & Baskin (R. M. C. Castro, pers. comm.) also are found in that habitat. The cyprinodont *Fluviphylax pygmaeus* (Myers & Carvalho) has been observed at or near the water surface by us and others in still waters, attached and detached floating meadows, and slow-flowing river margins both with and without plant cover (Weitzman 1982:193–195). An unidentified species of *Microphylipnus* of the Eleotrididae has been observed in quiet waters of small and large rivers, usually on or near the bottom, both over sand and mud, in areas with and without plant cover (C. J. Ferraris, Jr., pers. comm.). It is likely that the remaining miniatures in these groups will also share comparable habitats.

The catfish family Trichomycteridae has many members parasitic on the gills of large fishes, and perhaps as a consequence of that unusual habit does not neatly fit the above characterization of the habitats of miniatures. During feeding the miniature parasitic trichomycterids (e.g., *Paravandellia bertonii* Eigenmann (A. Miranda-Ribeiro 1923: 11–12) and *P. magdalenae* Miles (1947:99) attach to the gills of larger fishes, a feeding habit that also serves to insulate them from the currents of the surrounding stream. *Trichomycterus santaeritae* Eigenmann (1918b:341; see also Eigenmann 1911:350, locality number 56) of the Trichomycterinae and *Malacoglanis gelatinosus* Myers & Weitzman (1966:286) of the Sarcoglanidinae both live in relatively still waters, and their morphology indicates that they are not parasitic. As noted by Eigenmann (1918b: 269) most non-parasitic members of the Trichomycterinae (=Pygidiinae of Eigenmann), in contrast, live in moderately to swiftly flowing streams, but avoid the water currents by being cryptobenthic. Thus on a microhabitat level the two species of *Trichomycterus* listed in Table 1 can be considered to inhabit water conditions typical of other miniatures.

Stewart (1985) noted that although the miniature catfish species of Aspredinidae

live in streams with strong currents, they are actually benthic, occupying an area of reduced current flow. The same is apparently true for the one pimelodid catfish species in Table 1 (Stewart 1986:48).

Although we note an association of miniature fishes with still or slow-flowing waters, this does not imply that such environmental parameters have been the prime selective agents for miniaturization, a process that undoubtedly is the result of many different factors. Further studies are necessary to determine the generality of the correlation between still waters and miniatures, and to study the degree to which these relate to physical environmental parameters.

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