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# Systematics of *Spintherobolus* (Teleostei: Characidae: Cheirodontinae) from eastern Brazil

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Two eastern Brazilian freshwater fishes, *Spintherobolus ankoseion* and *S. leptoura*, are described as new species and *S. papilliferus* Eigenmann and *S. broccae* Myers are redescribed from larger population samples than were previously available. *Spintherobolus* is hypothesized to be the sister group of a clade within the subfamily Cheirodontinae, family Characidae and a cladogram of the relationships of the species of *Spintherobolus* to one another and to other cheirodontines is presented. Previously proposed relationships of *Spintherobolus* with the Bolivian characid *Grundulus bogotensis* and this latter species relationships with cheirodontine characids are rejected. A preliminary investigation of the phylogenetic relationships of the cheirodontine characids is discussed.

Dois peixes de água doce do leste brasileiro, *Spintherobolus ankoseion* e *S. leptoura*, são descritos como espécies novas. *Spintherobolus papilliferus* Eigenmann e *S. broccae* Myers são redescritos com base em amostragens maiores do que as disponíveis anteriomente. *Spintherobolus* é considerado grupo irmão de um clado dentro da subfamília Cheirodontinae, família Characidae, sendo apresentado um cladograma com as relações entre as espécies de *Spintherobolus* e destas com outros Cheirodontinae. Hipoteses previamente propostas de relações de parentesco entre *Spinterobolus* e o caracídeo Boliviano *Grundulus bogotensis*, bem como desta última espécie com outros Cheirodontinae, são investigadas e rejeitadas. As relações filogenéticas de Cheirodontinae são discutidas preliminarmente.

## Introduction

*Spintherobolus* Eigenmann (1911: 167), with *S. papilliferus* Eigenmann (1911: 167) as its type, was described as a new and anatomically unusual characid fish that, according to Eigenmann, bore tricuspid teeth in a single series on the dentary, premaxilla, and upper part of the maxilla. It also lacked an adipose fin, had a lateral line of one or two scales, a scaleless caudal fin, a very short scaleless anal fin, and "tactile papillae" reported as "excessively developed". This species (Fig. 1) was collected from Alto da Serra, a railroad station near a headwater tributary of the rio Tietê, a few kilometers east of Paranapiacaba, São Paulo, Brazil. A second, miniature species,

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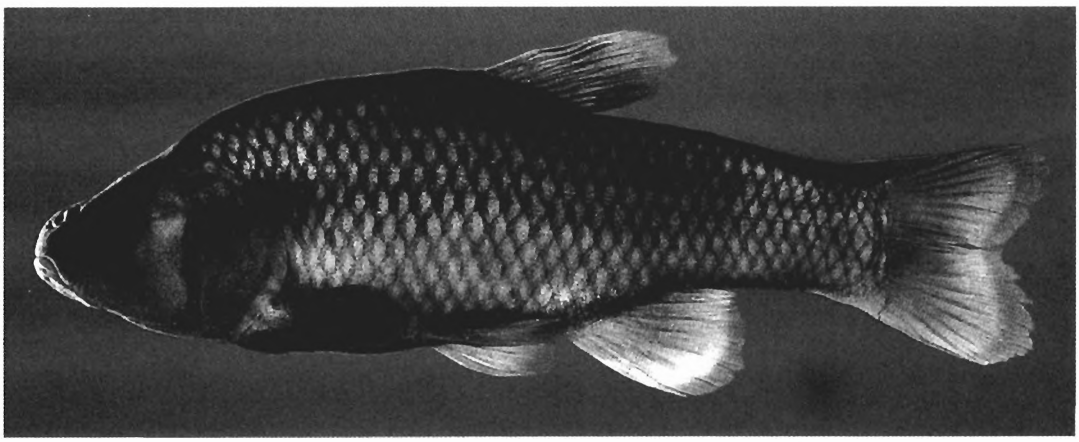


**Fig. 1.** *Spintherobolus papilliferus*, MZUSP 49408, adult male, 57.8 mm SL, Brazil, São Paulo.

*S. broccae* Myers (1925: 143) (Fig. 2) was described from aquarium specimens said to be collected from "Hills behind Rio de Janeiro". This species appeared occasionally in the aquarium trade, where it became known as *Phoxinopsis broccae* by Myers (1926: 273), Arnold & Ahl (1936: 107-108), Böhlke (1954: 31) and Sterba (1987: 119). Subsequently it became known as *Phoxinopsis typicus* Regan (1907: 262). The reasons for the adoption of *P. typicus* for *S. broccae* in some systematic and aquarium literature, for example Innes (1935: 130), Myers (1944: 186), and Géry (1977: 607), were explained by Böhlke (1954: 24-38). However, our examination of the holotype of *P. typicus* reveals that it must be considered a junior synonym of *Aphyocharax anisitsi* Eigenmann & Kennedy (1903: 517) and not a senior synonym of *S. broccae*. Therefore, *S. broccae* is a valid species. Travassos (1953), unfortunately mostly overlooked by subsequent authors, reviewed *Spintherobolus*, and pointed out a close relationship between *S. papilliferus* and *S. broccae* based on common possession of features such as the characteristic shape of the lower jaw. Some of these features we find to be synapomorphies diagnosing *Spintherobolus*. Travassos did not consider *S. broccae* a junior synonym of *P. typicus* even though he was unable to examine the type specimens of both species. Sarraf (1997) redescribed *S. broccae* from recently collected specimens and utilized that name for the species following Weitzman & Vari (1988) and Malabarba (1994). Sarraf (1997) also provided information about the differences between *S. broccae* and *S. papilliferus*.

We redescribe *Spintherobolus papilliferus* and *S. broccae* based on more specimens than were available to Travassos, describe two new species from coastal drainages east of the Serra Geral, provide new information on the distribution of neuromasts on the head and body of these fishes, present a hypothesis of the monophyly of the genus, review the phylogenetic relationships of *Spintherobolus* to other characids, discuss the phylogeny of the species, and comment on the distribution of the genus.

## Methods and materials

Counts and measurements were taken according to Fink & Weitzman (1974: 1-2). For counts recorded in the descriptions, the holotype is given first followed in parentheses by the mean, range and total number of specimens counted. Total vertebral counts include the five vertebrae of the Weberian apparatus. The preural vertebra (terminal half centrum), hypural bones, and associated vertebral elements, usually designated as $PU_1+U_1$, but not necessarily consisting only of those elements, were counted as one vertebral element. Vertebral and procurrent caudal fin-ray counts were taken from radiographs and from cleared Alizarin red and Alcian blue counter stained preparations. These preparations are called cleared and stained in the text or abbreviated c&s in lists of specimens.

Morphometric data for holotypes and other specimens are presented separately in the tables.

**Fig. 2.** *Spintherobolus broccae*, USNM 287324, adult male, 18.2 mm SL, Brazil, Rio de Janeiro.

All measurements other than standard length (SL) are expressed as a percentage of SL except subunits of the head which are recorded as a percentage of head length.

Basic descriptive statistics and statistical tests of null hypotheses of character similarities were computed using SigmaStat for DOS 1.01, 1993 and/or SigmaStat for Windows 95, 1995, Jandel Scientific. As is usually the case, meristic data taken from fish population samples fail to pass tests for normality and equal variance. In the present case none of the data sets from our population samples had normal distributions or equal variances. Thus among the species of *Spintherobolus* we elected to use nonparametric multiple comparison tests (Kruskal-Wallis one way analysis of variance on ranks) of the null hypotheses that the population samples are equal for particular characters. If this test indicated a significant difference among the species in question, all pairwise multiple comparisons of data from those species were done using Dunn's method for population samples of unequal size. Graphic representation corresponding to these tests are presented as Tukey box plots of ranked data laid on their sides so that geographical and other information could also be conveniently shown in the graphs. These were prepared using SigmaPlot 5.0 for DOS, 1992 or SigmaPlot 2.0 for Windows 95, 1995 in conjunction with SigmaStat for DOS as well as SigmaStat for Windows 95, 1995, Jandel Scientific. These graphs are presented to provide a visual representation of the tests performed for population similarity and dissimilarity as well as to show sample population structure. Such graphs better display the skewed or other nonparametric shapes of the meristic data of each population sample than do central tendency graphs that present the mean, standard deviation (or the 95 % confidence intervals) and the extremes. The graphs presented here display the sample median (= 50th percentile [mediana in Portuguese]) as a relatively thick vertical bar. This is the value for which no more than half of the data are smaller and no more than half are larger. The median is usually equal to the mean in parametric data sets, but in skewed population samples, i.e. nonparametric data sets this is not so. Although the median expresses different information than the mean, it is less likely to be influenced by extreme measurements than the mean and therefore is a better measure of central tendency in skewed data sets. The $25^{th}$ and $75^{th}$ percentiles are represented as the lateral borders of the box plots, and represent the values at which 25 % of the sample falls below and 25 % falls above the box borders. The $10^{th}$ and $90^{th}$ percentile points are represented by error bars and circles represent the $5^{th}$ and $95^{th}$ percentiles. When the minimum and maximum are respectively different from these, each is represented by an asterisk (*). When the data are skewed, for example when the count is 9 (n = 45) and 10 (n = 2) the median is 9, and only the fifth and the 95th percentile points will be calculated. Thus the data represented by the box plot and all other data can only be expressed by the median (plus a circle for the 5th percentile), except for the $95^{th}$ percentile

**Table 1.** Character data matrix for *Spintherobolus*, related cheirodontines, outgroup characids, and *Grundulus bogotensis*. Character numbers correspond to synapomorphies numbered in the text. State 0 corresponds to the plesiomorphic state and states 1-4 to the apomorphic conditions.

| Characters | 1-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 | 31-35 |
|---|---|---|---|---|---|---|---|
| Outgroup characids | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| *Grundulus bogotensis* | 00010 | 00000 | 00000 | 01114 | 00001 | 00000 | 00000 |
| *Odontostilbe fugitiva* | 11110 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| *Cheirodon* spp. | 11111 | 11110 | 00000 | 00000 | 00000 | 00000 | 00000 |
| *Odontostilbe piaba* | 11111 | 11111 | 11110 | 00000 | 00000 | 00000 | 00000 |
| *Spintherobolus papilliferus* | 11011 | 11110 | 00011 | 11113 | 11111 | 12111 | 10000 |
| *Spintherobolus broccae* | 11011 | 11111 | 11111 | 11211 | 11111 | 11100 | 01111 |
| *Spintherobolus ankoseion* | 11011 | 11111 | 11111 | 11112 | 11111 | 11000 | 01111 |
| *Spintherobolus leptoura* | 11011 | 11111 | 11111 | 11112 | 11111 | 11100 | 01111 |

which will be represented by a circle. All data utilized are expressed as integer values, for example fin-ray counts and vertebral counts, but in SigmaStat, although the medians are expressed in integer values, the percentiles are expressed as integers or part integer values. Various forms of skewed graphs are presented below and their alteration from a normal bell-shaped curve is a representation of the skewed nature of the population structures. In all cases where statistically significant differences are presented by the plots in our graphs as representative of nonparametric tests of data, we also ran a corresponding parametric test and found approximate agreement in terms of statistical significance.

Logarithmic scatter plots, their regression lines and the lines representing 95 % confidence intervals about the mean were prepared using the SigmaPlot programs cited above. The entire population sample for each character is shown on the linear plots simply to show the growth curves for given characters that are either sexually dimorphic or different among the species of *Spintherobolus*. Tests of differences between the sexes of a given species were performed using log transformed data and were done only on members of both sexes which had comparable standard lengths. These tests, when they indicated differences, are represented by logarithmic regression plots. These plots were prepared by transforming linear plots to base 10 log plots and scaling the axes back to the original millimeter notations but maintaining logarithmic dimensions. This places the plots in logarithmic form but still provides the reader some visual concept of the data points in terms of the original measured lengths. Regression lines and equations are given to present comparative approximations of the growth parameters of population samples of immature, sexually maturing, and mature fishes when possible. In no instances are regression lines, regression equations or covariance analyses to be construed as predictors of body shape beyond the data shown in the relevant plots. All regression statistics are based on the linear regression model. All confidence intervals in the plots are 95 % for the mean. Covariance analyses were omitted when the plots showed wide separation of 95 % confidence intervals from the 'opposing' mean regression lines of the two or more population samples being tested for similarities and differences. Influential outlying points were checked by re-examination of specimens. In regression analyses a series of diagnostic tests using SigmaStat were run to estimate the suitability of the data for the linear regression model. Data that failed these tests were not used in the analyses.

The synonymies are not inclusive. We cite only references first using different names for the taxa under consideration. However, when appropriate, we provide an abbreviated history of the name usage for each taxon.

In our discussions, comments on phylogeny are based on the concepts of phylogenetic systematics of Hennig (1966) as discussed by Wiley (1981), and more recently by Nelson (1994). Maddison et al. (1984) are followed for outgroup considerations. We follow Schaefer et al. (1989: 203-208) and Buckup (1993b: 332-336) in evaluating reductive characters as apomorphies in constructing hypothetical phylogenies.

We confine the use of the term autapomorphy to species, thus avoiding the confusion that arises when a character is considered an autapomorphy for a genus and a synapomorphy for its included species. Thus we use the term synapo-

morphy at all levels other than species. We use the term diagnosis for characters used to identify a taxon when those characters are synapomorphies or autapomorphies.

We provide an annotated, numbered apomorphy list consecutively diagnosing more inclusive to less inclusive clades. This list corresponds to the synapomorphies and autapomorphies of the matrix in Table 1, for phylogenetic analysis. State 1 in the matrix corresponds to the derived state of a given character or the first derived state of a multistate character. Multistate characters are numbered consecutively and each state is discussed in the text. Characters that are synapomorphies in a more inclusive clade but reversals in a less inclusive clade (or clades) are given a number the first time the character appears as an apomorphy. Reversals of characters that are apomorphies for less inclusive clades are given the same number that they had upon first appearance but the number is followed by R meaning reversal. Hypotheses of independent acquisition and reversal are based on the most parsimonious overall hypothesis of character distribution for the groups studied. The overall hypothesis presented here was constructed using PAUP (version 3.1.1; Swofford, 1993) and using the Branch and Bound algorithm. MacClade version 3.1 (Maddison & Madisson, 1992) was used to trace character evolution. The matrix of character distribution (Tab. 1) included data from all known species of *Spintherobolus*, putatively related cheirodontines, *Grundulus bogotensis* (Humboldt) previously hypothesized as related to *Spintherobolus* (Eigenmann, 1915: 20; Géry, 1977: 607), and outgroup characids. The first line of the matrix corresponds to a hypothetical characid outgroup of the Cheirodontinae and was used to hypothesize the polarity of the characters in the analysis. This hypothetical outgroup has the characters and character states found in the apparently plesiomorphic condition for American characids such as the species of *Brycon* Müller & Troschell and the species of the tetragonopterine characid genus *Astyanax* Baird & Girard, species hypothesized to be relatively plesiomorphic within the group of American characids thought suitable as an outgroup for the Cheirodontinae (Weitzman, 1962; Weitzman & Fink, 1983; Buckup, 1993a). *Grundulus bogotensis* was included to test previous hypotheses of its relationships to species of *Spintherobolus* (Eigenmann, 1915; Böhlke, 1954; Géry, 1977).

A list of material examined other than population samples of *Spintherobolus* species is given at the end of the text. Biogeographic principles follow Humphries & Parenti (1986). All photographs of fishes are from preserved specimens unless otherwise noted.

Specimens used in this study are deposited in the following museums and universities: BMNH, Natural History Museum, London; FMNH, Field Museum of Natural History, Chicago; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MNRJ, Museu Nacional, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; and USNM, National Museum of Natural History, Smithsonian Institution, Washington.

Abbreviations for organizations and institutions are given below in the Acknowledgments. Other abbreviations are as follows. HL, head length; LL, lateral line; SL, standard length; spm(s), specimen(s).

## Phylogenetic relationships of *Spintherobolus*

A hypothesis of the monophyly and phylogenetic relationships of *Spintherobolus* with other characiforms is necessary to develop a hypothesis of the phylogenetic relationships of the species within this characid clade (Fig. 3). Sarraf (1997) following Malabarba (1994) pointed out that *Spintherobolus* is monophyletic based on the presence of papillary neuromasts and several other anatomical features. Our hypothesis of phylogenetic relationships of *Spintherobolus* is based on a review of cheirodontine phylogeny by Malabarba (1994; in press). The major results of that research include diagnoses of other monophyletic assemblages of that subfamily. We herein summarize a hypothesis of relationships of *Spintherobolus* with *Cheirodon* Girard (sensu Casciotta et al., 1992), with a group of cheirodontines related to *Odontostilbe fugitiva* Cope, the generic type, and to another group of species related to *O. piaba* (Lütken). In our view *Odontostilbe*, as currently recognized, is both polyphyletic and paraphyletic. However, hypotheses of phylogenetic relationships among the species of *Cheirodon* and *Odontostilbe* are not discussed in depth here, but are the subject of a separate paper (Malabarba, in press).

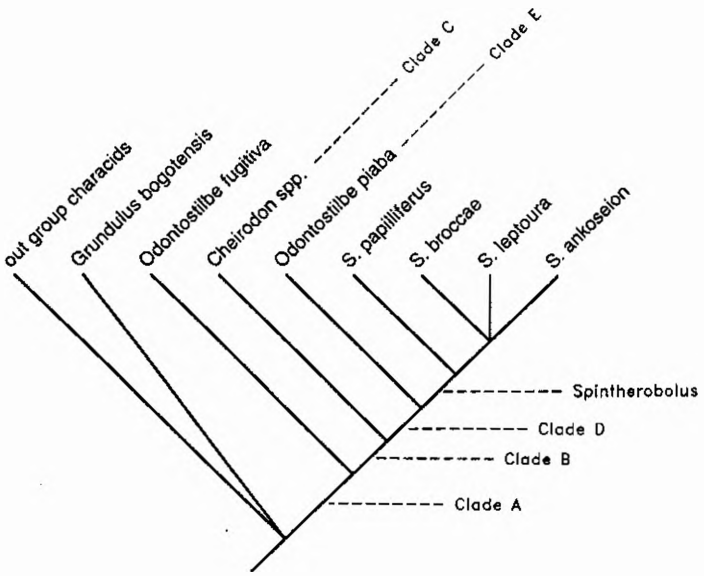



**Fig. 3.** A phylogeny of *Spintherobolus* and related cheirodontine taxa based on consensus tree of 3 equally parsimonious cladograms. Tree statistics: Tree Length = 49, Consistency Index = 0.796, Retention Index = 0.867.

Eigenmann (1915: 19-20) and Géry (1971: 161, 1977: 607) suggested that *Spintherobolus* is related to *Grundulus* Günther. Those authors and Böhlke (1954: 6, 19, 24-25) considered these genera cheirodontines because each has a single row of premaxillary teeth. However, all these authors recognized a putative polyphyletic nature for the Cheirodontinae as each defined it. Böhlke (1954: 24-25) reviewed the suggested relationship between *Spintherobolus* (recognized by him as *Phoxinopsis*) and *Grundulus* based on an examination of the types of *S. papilliferus* and *S. broccae* and the specimens of *Grundulus* listed below. Because he did not examine dissected or cleared and stained specimens, his conclusions were necessarily tentative. He recognized many differences in these two genera and, on the basis of a phyletic context, placed them in separate cheirodontine tribes.

Géry (1977: 607), again in a phyletic context, stated that *Spintherobolus* belongs to a "*Grundulus* group" of cheirodontines because it has a "lateral line perforating only 1-6 scales; adipose fin lacking; anal fin short; few interhemals; large suborbital reduced; etc." We find most of these characters reductive in the context of our phylogenetic analysis and cladogram (Fig. 3). Our analysis indicates that these reductive features are independently acquired by these two genera. Thus the features listed by Géry as phyletically significant are phylogenetically significant at different taxonomic levels than suggested by him. We find that *Grundulus* lacks the characters that diagnose the more restricted Cheirodontinae as recognized here and by Malabarba (1994; in press). *Grundulus* also lacks the synapomorphies that support the hypothesis that *Spintherobolus* is phylogenetically related to certain clades within the Cheirodontinae. Therefore, we hypothesize *Grundulus* to be allied to characids other than cheirodontines. At this time the relationships of *Grundulus* within the Characidae are unknown and the genus is placed incertae sedis within the family.

### Subfamily Cheirodontinae, Clade A

*Spintherobolus* species belong to a restricted Cheirodontinae as diagnosed phylogenetically by Malabarba (1994; in press). For purposes of hypothesizing the phylogenetic relationships of *Spintherobolus* we summarize his diagnosis using the first four characters listed below. The Cheirodontinae as diagnosed by these features is equivalent to Clade A in our cladogram.

(1) A pigmented humeral spot is absent. Preserved cheirodontines often appear to have a humeral spot but the darkened area in the humeral region is due to a muscle hiatus just lateral to the

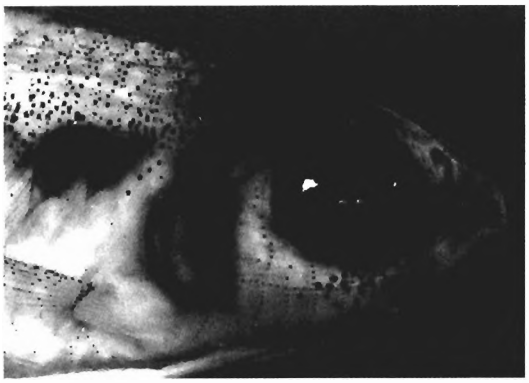


**Fig. 4.** *Spintherobolus broccae*, USNM 287324, adult male, 17.9 mm SL. Head and anterior body region, right side. Two pseudotympanums, black areas are located posterior to the dorsal portion of the opercular opening. The posterior pseudotympanum is homologous with the single pseudotympanum of other cheirodontines while the anterior pseudotympanum is found only in *Spintherobolus*. The small dark dots arranged in rows arer the neuromast pattern over the face and opercular region. In the region ventral to the pectoral fin a few neuromasts can be seen partly bordering the scales. Such neuromasts are also present in the dorsal or back region. However, these are sometimes hard to distinguish from the somewhat larger dark chromatophores that often have somewhat indistinct borders. The rows of neuromasts are especially clear in the infraorbital region and on the dentary.

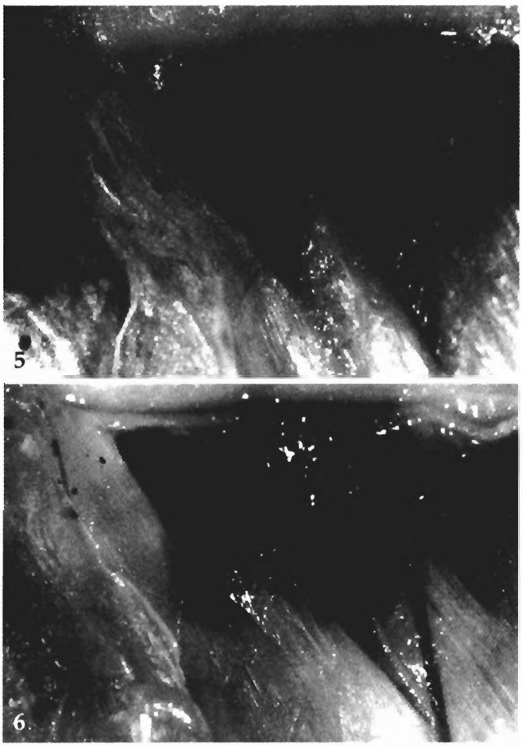



**Fig. 5.** *Spintherobolus ankoseion*, paratype, MCP 19253, adult female, 25.2 mm SL. Anterior and posterior pseudotympanal region of left side, anterior is to the left. The skin and scales were removed, exposing the muscles of the lateral body wall and the pleural ribs of the fifth and sixth vertebrae (first and second pleural ribs). The black, pigmented swimbladder walls (the actual pseudotympanums) of both the anterior and posterior pseudotympanal regions have been removed, showing the black interior of the swimbladder.

**Fig. 6.** *Spintherobolus leptoura*, paratype, MCP 19254, adult female, 25.4 mm SL. Anterior and posterior pseudotympanums of left side. The skin and scales were removed, exposing the muscles of the lateral body wall, pleural ribs of the fifth and sixth vertebrae (first and second pleural ribs), and the black, pigmented wall of the swimbladder. The larger black area to the right represents the pseudotympanum present in all cheirodontines, while the black area to the left is the area of the pseudotympanum characteristic of the species of *Spintherobolus*.

anterior portion of the swimbladder (Fig. 4). The swimbladder may have dark pigment on it, but this is not the same pigment that forms the humeral spot of the epidermis of other characiforms.

Absence of a humeral spot occurs in relatively few other characiform species, but none of these have all four of the characters listed here. This statement suggests that the lack of humeral spots in some other characiforms is homoplastic with regard to their absence in the Cheirodontinae. At this time we are unable to provide an analysis of the cladistic significance of the humeral spot and its absence in other characiforms because the phylogenetic significance of the distribution of its presence or absence is unstudied and unknown in nearly all of them. We can only suggest that the loss of this character occurred independently in certain outgroup characids.

(2) A characteristic hiatus occurs in musculature of the body wall in the area of the swimbladder between the first and second pleural ribs, exposing the swimbladder (Figs. 4-6). This hiatus is not a simple derived absence of musculature tissue, but a derived and organized feature of the body wall presumably making it more efficient in transmitting sound from the environment to the swimbladder, perhaps by avoiding interference from active muscle tissue. This hia-

**Fig. 7.** *Odontostilbe* sp., MCP 11136, adult male 37.0 mm SL. SEM photograph of a frontal view of the anterior three premaxillary teeth of the right side. Illustrated for each tooth are a pedicles and a flattened, expanded distal region bordered by approximately 10 tooth cusps. Scale marker = 100 μm.

tus is an organ called the pseudotympanum because the membranous wall of the swimbladder is exposed to fluid and some fat in the muscular hiatus. The absence of interference with sound transmission from active muscle tissue may increase the efficiency of that transmission from water external to the skin and scales to the wall of the swimbladder. From there sound is transmitted to the inner ear through the intermediate contact between the swimbladder wall and the Weberian apparatus. Also the absence of muscle tissue against the membranous swimbladder wall may allow that wall more freedom to respond to sound waves. Note: The species of *Spintherobolus* have two rather than one pseudotympanum and their posterior pseudotympanum (between the first and second pleural ribs) is homologous to that in all other species of the Cheirodontinae; see more detailed description in synapomorphy 21 below for *Spintherobolus*.

Among other characiforms, a pseudotympanum of different structure and presumably not homologous with that found in the Cheirodontinae is also found in the species of the Characinae. The implications of this are discussed by Malabarba (in press).

(3) Cheirodontine teeth have a proximal peduncle or pedicle and an expanded and compressed distal region bordered by a few to many cusps (Fig. 7). Note: In the case of the species of *Spintherobolus* the modification of this flattened, expanded distal portion into an essentially conical tooth is a secondary alteration according to the hypothesis of relationships presented here; see also apomorphy 3R below. Note that not all of these teeth in *Spintherobolus* are conical.

Somewhat similar teeth occur in *Piabucus* and *Iguanodectes*, genera referred to the tribe Iguanodectini of the Tetragonopterinae by Géry (1977). Even when these genera are entered in our analysis and their teeth are coded the same as those of the Cheirodontinae, these two genera are excluded from that subfamily in the most parsimonious cladogram.

(4) All cheirodontines have a single series of teeth on the premaxilla. This feature is discussed by Malabarba (in press) but it is not restricted to the Cheirodontinae and has appeared convergently many times in the Characidae and some other characiforms.

The Cheirodontinae consists of several major clades (Malabarba, 1994; in press). We treat only one of these, Clade B containing *Spintherobolus*, in detail in our cladogram (Fig. 3). We defer treatment of the other cheirodontine clades to Malabarba (in press). The species of *Spintherobolus* form a subgroup of clade B and share several derived features of the ventral procurrent caudal-fin rays not found in other characiforms, including other clade A cheirodontines. Other Clade A cheirodontines are represented in Figure 3 by *Odontostilbe fugitiva* Cope, the type species of *Odontostilbe*.

In addition to the species of *Spintherobolus* Clade B cheirodontines include the species of *Cheirodon* (sensu Casciotta et al., 1992) and are here labeled as Clade C in Figure 3. Some other species at present placed in the polyphyletic and paraphyletic *Odontostilbe* are here placed in Clade E in our cladogram and the earliest described species of this clade, *Odontostilbe piaba*, represents the included species our Figure 3.

### Tribe Cheirodontini, Clade B

Clade B cheirodontines have the following four synapomorphies.

(5) Twelve to twenty-eight ventral procurrent caudal-fin rays in both males and females. Outgroup cheirodontines and other outgroup characids have 5-11 ventral procurrent caudal-fin rays, except *Salminus* Agassiz in Spix & Agassiz, with 16 ventral procurrent caudal-fin rays

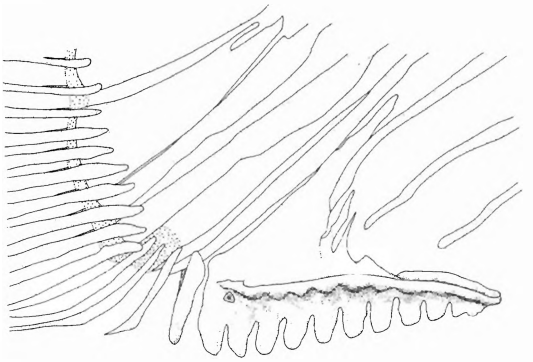


**Fig. 8.** *Spintherobolus ankoseion*, USNM 297935, adult male, 24.5 mm SL. Osteology of ventral procurrent caudal-fin rays and associated bony structures, anterior to right.

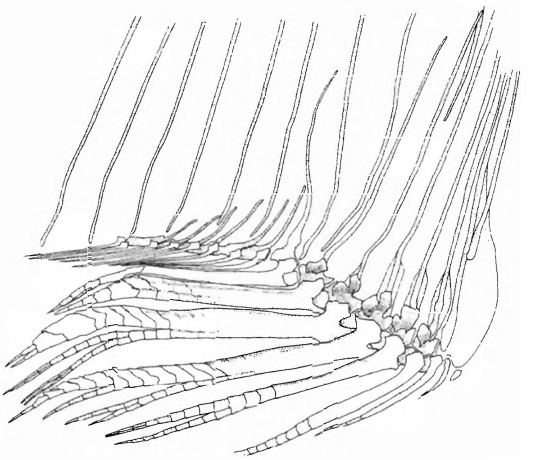


**Fig. 9.** *Spintherobolus ankoseion*, USNM 297935, adult male, 24.5 mm SL. Anal-fin rays and associated pterygiophores, left side, anterior to right.

according to Roberts (1969: 428-429). *Salminus* has no other synapomorphies listed here for the cheirodontine clades discussed.

(6) The ventral procurrent caudal-fin rays of males are elongate and the ray halves (see Weitzman, 1962: 40, discussion of the anal-fin ray halves) of each side are fused along their entire length. In most other characids and clade A cheirodontines the ray halves form a V shaped bone in frontal view with its two halves fused only distally, although in some, for example *Astyanax* cf. *bimaculatus* Linnaeus, the anterior two or three ray halves may be fused for 50 to 80 % of their distal length.

(7) The anterior-most ventral procurrent caudal-fin rays of the females have the proximal portions of their ray halves fused to each other, but retain an opening near their distal tips, giving a needle-like shape to these rays. Females of most outgroup characids and cheirodontines have the entire lengths of their ray halves separate.

(8) Several of the anteriormost ventral procurrent caudal-fin rays of males project through the muscles at which point they are covered only by extremely thin skin (often lost or nearly undetectable in preserved specimens). Thus they can be easily seen along the ventral margin of the caudal peduncle (Fig. 8). In other characids the anterior ventral procurrent caudal-fin rays are buried in the muscles and skin and are not visible along the ventral surface of the caudal peduncle.

(9) Males of Clade B cheirodontines have elongated hemal spines of four or more posterior caudal vertebrae (preural vertebrae), those anterior to the terminal half centrum and its processes. These are associated with the ventral procurrent caudal-fin ray supports (Fig. 8). Outgroup cheirodontines and characids have only the posterior one, two, or sometimes three caudal (preural) vertebrae directly articulating with the ventral procurrent caudal-fin rays.

### Clade D

Note: Cheirodontine Clade B includes Clade C, *Cheirodon*, the sister group to clade D which contains certain *Odontostilbe* species and its sister clade *Spintherobolus*. Although other than *Spintherobolus* the subclades of Clade B will be treated in detail by Malabarba (in press), we note here that 12 to 18 ventral procurrent caudal-fin rays occur in members of Clade D and that Clade C members have 17-28 ventral procurrent caudal-fin rays in both males and females, the most derived number for Clade B. See also certain comments about Clade E members in the discussion below.

Clade D is diagnosed by four synapomorphies of the sexually dimorphic anal-fin rays and one of the ventral procurrent caudal-fin rays of the males.

(10) In males the anterior branched anal-fin rays 1 through 5-8 are slab shaped and five to eight times more expanded in the sagittal plane than comparable rays in the females (Fig. 9). Sag-

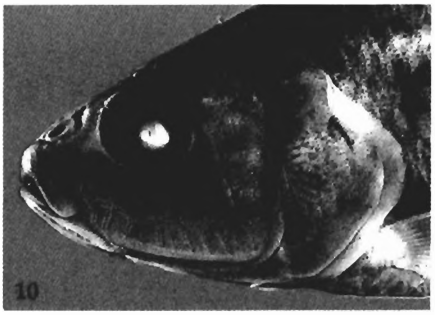


**Fig. 10.** *Spintherobolus papilliferus*, MNRJ 4237, female, 34.7 mm SL, head region, left side, Brazil, São Paulo, rio Ipiranga. Rows of neuromasts occur over the infraorbital, preopercular, and opercular region. These are distributed in shallow grooves that can be seen in the photograph. The neuromasts are also distributed on the scale borders posterior to the head and operculum but these are hard to distinguish from dark chromatophores in the photograph. A row of neuromasts along the ventral border of the dentary is hidden in a deep groove. The small dark dots arranged in rows are the neuromast patterns over the face and opercular region. In the region ventral to the pectoral fin a few neuromasts can be seen partly bordering the scales. Such neuromasts are also present in the dorsal or back region. However, these are sometimes hard to distinguish from the somewhat larger dark chromatophores that often have somewhat indistinct borders. The rows of neuromasts are especially clear in the infraorbital region.

**Fig. 11.** *Spintherobolus papilliferus*, MZUSP 51021, female 60.8 mm SL. Dorsum of head and back nearly to dorsal-fin origin. Neuromasts are present in the irregular grooves between the eyes and the supraoccipital region but these are nearly impossible to see in the photograph. A bilaterally distributed row of neuromasts runs along the long axis of the body between the nares. This row of neuromasts shows more clearly on the left side than on the right side of the top of the head.

ittal expansion of anal-fin rays in the males of other characiform groups is known, for example in *Nannostomus* Günther of the Lebiasinidae (Weitzman, 1966: 25) and *Bryconamericus* Eigenmann of the Characidae (Vari & Siebert, 1990: 520). However, the form of the expansion in clade D cheirodontines is unique in the extensive degree of sagittal expansion.

(11) The ray segments of the expanded anal-fin rays progressively fuse to one another as the male specimens become fully mature (Fig. 9). We know of no other characiforms having several ray segments so extensively fused in each ray, except for example some specialized glandulocaudines where the fusion is in the caudal fin, not the anal fin; see Weitzman & Fink (1985: 16-19).

(12) The proximal ends of the expanded anal-fin rays have their lepidotrich bases extended anteriorly (Fig. 9). These processes are associated with anal-fin muscles and ligaments and may be involved with a particular courtship/spawning activity restricted to Clade D cheirodontines. We have not found anal-fin rays similar to these in any other characiforms.

(13) Clade D cheirodontines have two to four (or sometimes five in Clade E) anal-fin ray hooks on the posterior borders of the hook bearing segments. Fifty percent of the males of *S. ankoseion* have anal-fin ray hooks. Hooks are occasionally present on the anal-fin rays of male *S. broccae* and *S. leptoura*. Only one of the 14 males of *S. broccae* in USNM 342064 had anal-fin hooks and only the holotype of *S. leptoura* had hooks. The anal-fin hooks found in *S. ankoseion*, *S. leptoura*, and *S. broccae* are extremely reduced in size and are limited to the second to the fourth segments of the first and second branched fin rays, but always with 2-4 hooks per segment. The single adult male *S. papilliferus* lacks anal-fin ray hooks, but because hook presence is occasional in the other species of *Spintherobolus* we are not certain of their absence in that species. A parsimonious analysis of all 14 synapomorphies considered so far, plus the next 14 for *Spintherobolus* might indicate that the possible absence of anal-fin ray hooks in some species of *Spintherobolus* would be a secondary loss. On the other hand, the samples are relatively small and the absence of hooks may represent reproductive seasonality. Outgroup cheirodontines have only one or two hooks per ray segment on the posterolateral border of the anal-fin rays.

(14) The adult males of species in Clade D have the distal ends of the ventral procurrent caudal-fin rays spatulate and rounded in profile (Fig. 8). In Figure 8 most of these rays are fused to one another. Although some other cheirodontine clades have ventral procurrent caudal-fin rays expanded sagittally, all have the distal ends of these rays acutely pointed.

**Discussion.** Species of *Spintherobolus* are most closely related to the monophyletic cheirodontine clade E which includes the following species of *Odontostilbe*: *O. piaba*, *O. notomelas* (Eigenmann), *O. calliura* (Boulenger), *O. kriegi* (Schindler), *O. microdon* Eigenmann, *O. micropterus* (Eigenmann). This clade also includes *Holoshesthes heterodon* Eigenmann. We briefly discuss Clade E here to more clearly explain the cheirodontine relationships of *Spintherobolus*. A presentation of hypothesized relationships within Clade E is deferred to later. The species of *Spintherobolus* and Clade E cheirodontines are united as Clade D in Figure 3.

All four anal-fin ray characters described above (10-13) are present in the three *Spintherobolus* species of Clade B, but they are not found in *S. papilliferus*. The 14 synapomorphies given above and the 14 given below support a hypothesis of phylogenetic relationships of *S. papilliferus* to Clade B cheirodontines and more specifically to the other species of *Spintherobolus*. A parsimonious interpretation of these character state changes indicates a secondary loss of these sexually dimorphic anal-fin features in *S. papilliferus*.

### *Spintherobolus* Eigenmann

*Spintherobolus* Eigenmann, 1911: 167 (type species: *S. papilliferus* Eigenmann, 1911: 167 by monotypy and original designation)

**Diagnosis.** Jaw teeth elongate and conical or tricuspid (Fig. 12); anterior ventral procurrent caudal-fin rays with proximal ends anterior to haemal spine of antepenultimate vertebrae fused to one another proximally; symphyseal dentary articulations are smooth, lacking intercalated folded bony surfaces common to most characids; neuromasts on head obvious and present in shallow channels and distributed on head in a characteristic manner in which one horizontal series in the infraorbital region is crossed by several more or less vertical series (Figs 4, 10 & 11);

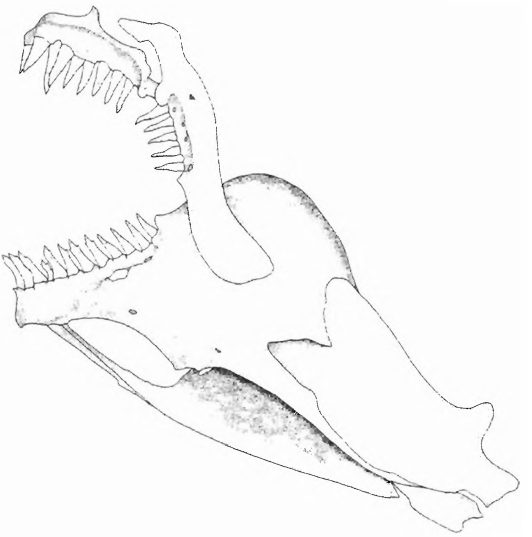


**Fig. 12.** *Spintherobolus ankoseion*, USNM 297935, adult male, 24.5 mm SL. Jaws & teeth.

dentary with a large anterior fenestra (Fig. 12) associated with large epidermal, papilla-like structure bearing several neuromasts; anterior pseudotympanum occurs anterior to first pleural rib (see character 21 below for detailed explanation).

**Monophyly of *Spintherobolus*.** The following 14 (15-27, 3R) synapomorphies indicate monophyly for *Spintherobolus*. *Spintherobolus* consists of two sister groups, one (a) containing *S. papilliferus* and the other (b) the remaining three species. This information is provided at this point to facilitate discussion of the fourteen synapomorphies described below.

(3R) The jaw teeth are elongate and conical or tricuspid. When tricuspid there are small lateral cusps near the distal apices of what are essentially teeth having an elongate pedicle and a slightly recurved apical cone (Fig. 12). The anterior dentary teeth of *Spintherobolus* have three small cusps. Teeth bearing these small cusps are more numerous than the strictly conical teeth present in the large species, *S. papilliferus*. The premaxillary teeth are usually conical, but in *S. papilliferus* they bear some very small lateral cusps in their somewhat laterally expanded distal portions. The maxillary teeth in all species are conical.

Tooth shape, tooth counts and the number of cusps have been extensively used for suggesting

cheirodontine and other characid relationships since Eigenmann (1915) used these features in cheirodontines and other small characids. As discussed by Weitzman & Fink (1983: 341-353), features such as numbers of rows of teeth, counts of the numbers of teeth in a particular jaw bone, the number of cusps in particular teeth, and the shape and form of the teeth and their cusps varies widely in various lineages of the American Characidae and provide data in support of phylogenetic hypotheses. However, as with many other characters, convergent evolution of such tooth features often cause problems in phylogenetic reconstruction, especially when teeth are not compared and described in enough detail to detect differences and similarities and are used for this purpose without the abundant use of other data.

Conical and tricuspid teeth are found in a number of American characids. The clades within the Cheirodontinae closest to *Spintherobolus* on the basis of other synapomorphies have five or more cusps, indicating that the low cusp number in *Spintherobolus* is derived. Some species belonging to other cheirodontine clades also have tricuspid teeth, but their teeth are never elongate and essentially conical in shape at their apices. For example, *Odontostilbe microdon* (Eigenmann, 1915: 80), *Cheirodon australe* Eigenmann (1927: 44), and *C. kiliani* Campos (1982: 154), although having tricuspid teeth, have these two secondary cusps large enough so that the teeth are broad and the cusps are more or less equal. This cusp number is here considered independently derived, not because of the different tooth shapes, but because of the numerous synapomorphies indicating these *Cheirodon* species belong to cheirodontine clades different from that of *Spintherobolus*.

(15) A complex, patterned series of exposed neuromasts are distributed on the head and body (Figs. 4, 10 & 11). All *Spintherobolus* species lack most latero-sensory canals on the head and body. Instead there are series of exposed neuromasts distributed often in shallow channels, in a pattern unique to *Spintherobolus* over the dorsal, ventral, and lateral surfaces of the head. The neuromasts also occur near the posterior border of the body scales and scales at the base of the caudal fin. The neuromast lines of the head for *S. broccae* were mapped by Sarraf (1997: figs. 2-4), but their terminology equivalents to these lines in other fishes, for example in Arratia & Huaquin (1995: fig. 13) were not attempted. The neuromast lines of the species of *Spintherobolus* are quite complex and an accurate comparative study of their homology and the nomenclatural equivalency of these lines with those of other characins, catfishes and other teleosts would require a comparative study of the nerve branches serving their neuromasts, a study beyond the scope of the present work. Such a study would perhaps be a useful source of synapomorphies suggesting a phylogeny of the species of *Spintherobolus*, but we hesitate to use the neuromast lines of *Spintherobolus* for this purpose without a detailed study of their anatomy and homology.

The neuromasts of *Spintherobolus* were first identified as "tactile papillae" by Eigenmann (1911: 167). We examined the surface of these organs at 200× but have no histological evidence to confirm that these are neuromasts. However, these organs are similar in gross anatomy to the neuromasts described for *Astyanax mexicanus* and histologically examined by Schemmel (1967). They are found distributed in a manner somewhat similar to those figured by Schemmel (1967: 266-267, figs. 4-5) along body scales of this species. In *Spintherobolus*, these organs are small, rounded, slightly elevated discs that are translucent or have a brown, orange, or red, color. The color intensity varies from collection to collection, ranging from no perceptible color to a relatively dark brown or red. The color possibly depends upon length of time in and the conditions of the preservative. It is also possible that the color is an environmental contaminant because specimens of some collections that have brown or red sediment caught in the mucus around their scales and fins are the ones that most often have colored neuromasts. The disc's color, when present, is due to several small, circular areas of color at the surface of the neuromast. These spots of color appear to correspond to sensory cells, each probably bearing a sensory filament. However, sensory filaments or cupulae are not detectable under a dissecting microscope.

Many of the neuromasts are located in shallow epidermal channels of *Spintherobolus*, especially on the head. The distribution pattern of these organs is approximately the same in all four species except that there are more vertical channels on the cheek (infraorbital region) in *S. papilliferus* than in the other species (Figs. 10-11). Laterally on the cheek a longitudinal curved neuromast channel extends from the posterior border of

maxilla to the posterior margin of preopercle. From this channel, at intervals, extend more or less vertical channels, each dorsally reaching the ventral margin of the orbit, and ventrally reaching to near the ventral border of the preopercle. The opercle has an anterior, vertical linear channel near the posterior preopercular border. Posterior to this the opercle bears a series of shallow channels containing neuromasts. Dorsally on the head these organs are mainly distributed in somewhat irregular transverse grooves between the orbits and in two small longitudinal channels between the nares (Fig. 11). There is a well-developed ventrally facing skin flap extending posteriorly from the area between the dentary and maxilla to the posteroventral end of the preopercle. This flap partly covers an elongate groove running along its length. The groove with its neuromasts has several medially directed branches. The dentary bears ventral grooves containing neuromasts, these being numerous in the gular area between the two halves of the dentary. Two to six vertically aligned neuromasts are located near the posterior border of many of the body scales. Although many of the scales bear neuromasts, they are not present on all scales. We were unable to detect any repetitive pattern of distribution of neuromasts on the body scales. See Arratia & Huaquin (1995) for citation of much of the literature on fish neuromasts.

What appear to be similar organs, also with complex patterns of distribution on the head, accompanied by an absence of laterosensory canals, were described by Poll & Lambert (1964a: 337, 1964b: 407) for certain species of the African citharinid characiform *Neolebias* Steindachner, 1894. These organs were identified as "lignes d'organes sensoriels ponctiformes". Note: Although Poll & Lambert used *Congocharax* Matthes, 1964 for the generic name of those species of *Neolebias* readily showing the neuromasts, we follow Vari (1979: 330) in recognizing *Congocharax* as a junior synonym of *Neolebias* even though Poll & Gosse (1982: 5) provided ample evidence of the different features that can be used to distinguish these nominal genera. We do this because recognition of *Congocharax* would make *Neolebias* paraphyletic according to the phylogenetic evidence provided by Vari and not contradicted by additional data extracted from Poll & Gosse and cladistically analyzed along with the data from Vari.

As pointed out by Sarraf (1997: 30), similar organs are found in the species of *Phenacogaster* and *Roeboides* Günther. These were called "cervical pit-lines" by Géry (1972: 10-11). Although cervical is a word referring to a neck, these structures are located in shallow channels mostly on the head and putatively assigned as a synapomorphy uniting these two genera by Malabarba & Lucena (1995: 342). We examined these structures in species of these two genera and found they have the same apparent gross anatomy and sometimes the same color characteristics as those of *Spintherobolus*, but with different distributional patterns on the head and body. We agree with Sarraf (1997) that these patterns are independently derived in *Spintherobolus* on the one hand and *Phenacogaster* and *Roeboides* on the other. The surface neuromasts of the laterosensory system and their characteristic distributional patterns found in some species of *Neolebias*, represent similar but apparently also independently derived features from those present in *Spintherobolus* or *Phenacogaster* and *Roeboides*. As Vari (1979: 329) has shown, the species of *Neolebias* bearing apparent neuromasts have a derived position in a clade of African characiforms. The exposed neuromasts described for *Astyanax mexicanus* by Schemmel (1967) seems to be also independently derived from those present in *Spintherobolus* (compare the neuromast distributional pattern of *A. mexicanus* in Schemmel (1967: 267, fig. 5) and of *Spintherobolus* species; Figs. 4, 10). None of these outgroup characiform taxa bearing obvious neuromasts and discussed above have all the synapomorphies listed for the Cheirodontinae.

Böhlke (1954: 25) reported "rows of papillae" on the head of *Crenuchus spilurus* and suggested this genus should be examined when considering the relationships of either *Spintherobolus* or *Grundulus*. We have examined the heads of several specimens of *C. spilurus* and fail to find structures that we can confidently identify as being similar to the organs we tentatively identify as neuromasts. There are, however, scattered small papillose structures having a central depression or opening. These might be taste buds, but histological examination is needed to confirm such an identification. The Crenuchinae is phylogenetically related to the Characidiinae and both placed in the Crenuchidae by Buckup (1993a: 229; in press) and we found no evidence to contradict Buckup's hypothesis or suggest that *Crenuchus* is a cheirodontine.

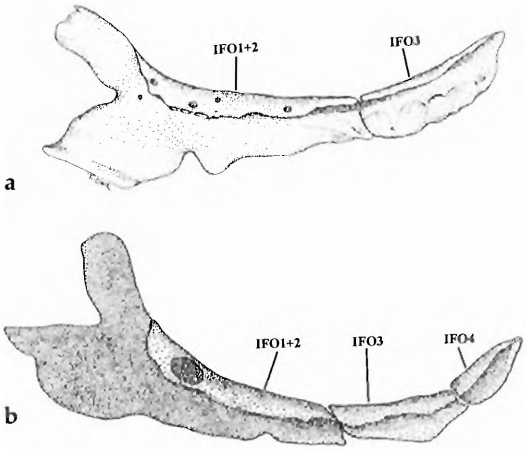



**Fig. 13.** *Spintherobolus ankoseion*, infraorbital bones. **a**, USNM 297935, adult female, 24.6 mm SL; **b**, USNM 297935, adult male, 24.5 mm SL.

(16) The dentary has a large anterior fenestra (Fig. 12). Associated with this fenestra is a large epidermal, papilla-like structure surrounded by a deep groove that has its deep internal portion lodged in the dentary fenestra. The external surface of this papilla bears several exposed neuromasts. The ventral face of the dentary bone, posterior to the fenestra is concave (more so in *S. papilliferus* than the other species; see also the dentary characters noted below under the synapomorphies that hypothesize subgroup b in Figure 3). We suggest the fenestra and the associated nervous and supporting tissues are a derived sensory organ and consider all to be one complex character.

Travassos (1953: 506) first noted the fenestra, but not the associated modified soft tissue. He considered the fenestra to demonstrate a close relationship between *S. broccae* and *S. papilliferus*. All four species examined herein have this feature, which is absent in other cheirodontines or characids examined by us.

(17) The adipose fin is absent. The adipose fin loss in *Spintherobolus* is unique within the monophyletic subfamily Cheirodontinae as recognized by us; see also Malabarba (in press). We suggest the absence of an adipose fin in *Spintherobolus* and *Grundulus* is homoplastic because of the relationships hypothesized here for *Spintherobolus*. Eigenmann (1915: 4, 14) briefly discussed the lack of an adipose fin in *Grundulus* and *Spintherobolus* and, in part, used this feature to unite these genera in a phyletic group. Géry (1977: 607) followed Eigenmann in this regard.

Adipose fin loss has occurred several times within hypothesized independent clades of characiforms, for example the Characinae (*Priocharax* Weitzman & Vari), Xenurobryconini (*Iotabrycon* Roberts, *Xenurobrycon* Myers & P. Miranda-Ribeiro, and *Tyttocharax* Fowler), the Gasteropelecidae (*Carnegiella* Eigenmann), and the Lebiasinidae (some species of *Nannostomus* Günther); see also discussion by Weitzman & Ortega (1995: 147). In these genera the absence of an adipose fin is correlated with small to miniature size. The absence of an adipose fin in the American characiforms is not always associated with miniature size. For example the large species of *Lebiasina*, family Lebiasinidae, and species of the Erythrinidae lack an adipose fin. The American characid genus *Hasemania* Ellis was for the most part defined as being like *Hyphessobrycon* Durbin but without an adipose fin. As currently conceived *Hasemania* (Géry, 1977: 518) lacks miniature species. We agree with Géry (1977: 518) that this genus is probably polyphyletic.

(18, state 1) The infraorbital bones (Fig. 13a-b) are somewhat variable, but some are always reduced in size and number and others possibly fused. They are usually altered as follows. One large bony element is located in the usual characid position of infraorbital 2. In some specimens (Fig. 13a-b) this bone has an anterodorsal portion that is in the position of infraorbital 1of other characids and a posterior part that may represent infraorbital 2. Thus this bony element may consist of infraorbital 1 and 2 fused to each other. In some specimens this is the only infraorbital bone present. Another infraorbital, much reduced in size and apparently absent in *S. broccae* (18, state 2; see diagnosis under *S. broccae*), is placed in the position of infraorbital 3 (Fig. 13a). Infraorbitals 4 through 6 are almost always absent, at least as ossifications, but in one specimen of *S. ankoseion* a fourth infraorbital bone appears to be present (Fig. 13b). A well developed antorbital is present in the ventro-lateral wall of the nasal capsule.

Although reductions in the size and apparent loss of infraorbitals are observed in some cheirodontines, for example *Cheirodon australe* Eigenmann, no other cheirodontines have the infraorbitals with the anatomy described here for *Spintherobolus*. A reduction of the posterior infraorbital bones also occurs in *Grundulus bogotensis* (Humboldt) but in that species infraorbital 2

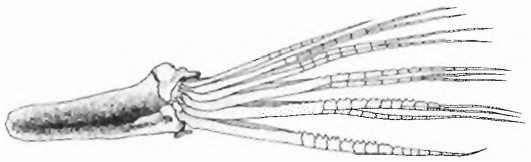


**Fig. 14.** *Spintherobolus ankoseion*, USNM 297935, adult male, 24.5 mm SL. Pelvic girdle and fin.

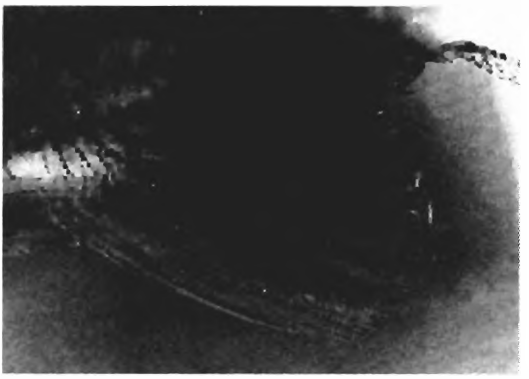


**Fig. 15.** *Spintherobolus leptoura*, USNM 346386, adult male, paratype, 21.8 mm SL. Anal fin, lateral view, left side, showing the distribution of pigment pattern on the fin and the derived nature of branched rays 2 through 5.

and a large infraorbital 3 are well ossified.

Infraorbital bone reduction and apparent loss are common in small and miniature characiforms of divergent clades; see Weitzman & Fink (1983) and Weitzman & Fink (1985) for documentation. However, *S. papilliferus* and *G. bogotensis* are both comparatively large and were in part suggested as related by shared infraorbital loss by Eigenmann (1915: 5-6, 14) and Géry (1977: 607). Although the pattern of infraorbital loss in these species differs, this would not preclude considering such loss a synapomorphy for the two species. However, *Grundulus* lacks the synapomorphies uniting the species of *Spintherobolus* to the Cheirodontinae.

(19) There are one unbranched and five to six branched pelvic-fin rays. The outgroup number of pelvic-fin rays in the Characidae is i,7, and, with rare exceptions, this count is found in all outgroup cheirodontine species. The count in *Spintherobolus* is i,5 or i,6 in *S. papilliferus* and is always i,5 in the other three species. This is a derived reductive feature for the species of *Spintherobolus* (Fig. 14).

A low pelvic-fin ray count occurs in certain miniature or small sized characiforms, for example *Carnegiella* (see Weitzman, 1960: 217) and *Priocharax* Weitzman & Vari (1987: 614), and one might therefore expect a low pelvic-fin ray count in a small species such as *S. broccae*. However, *S. papilliferus* although not especially small (to at least 60.8 mm SL) has a low pelvic-fin ray count. *Grundulus bogotensis*, also not especially small (to at least 67.0 mm SL) also has a somewhat reduced number of pelvic-fin rays, i,6.

(20) The anal fin has iii-iv unbranched and 9-16 branched rays (Figs. 9, 15). The number of anal-fin rays in the Characidae is quite variable. The primitive state, however, can be hypothesized as having at least more than 15 branched rays as found in the apparently most primitive American characid species such as the species of *Brycon* Müller & Troschell. Among the cheirodontine species the number of branched anal-fin rays varies from 16 to 24. *Spintherobolus* thus has a derived, reduced number and we suggest this as a synapomorphy uniting the species of the genus. A reduced number of anal-fin rays also occurs in the Chilean species of *Cheirodon* (*C. australe* Eigenmann, *C. galusdae* Eigenmann (12-15 branched rays), *C. pisciculus* Girard, *C. kiliani* (9-13)) but this is independently derived according to the hypothesis of cheirodontine relationships proposed herein. *Grundulus bogotensis* also has a reduced number of anal-fin rays, iv,11-12, but again evolved independently of *Spintherobolus*, based on its lack of synapomorphies of clades A to D.

Branched anal-fin rays in *Spintherobolus* varies from 13-16 ($\bar{x}$ = 14.1; state 1) in *S. broccae*, 11-14 in *S. ankoseion* and *S. leptoura* ($\bar{x}$ = 12.6 for both species; state 2), and 9-10 ($\bar{x}$ = 9.1; state 3) in *S. papilliferus*. We considered these three ranges and their means as different states in our analysis because all were significantly different and can thus be hypothesized as having a different genetic basis. All three states are derived according to outgroup comparison. *Grundulus bogotensis* also has a small number of anal-fin rays (11-12) and has been suggested as closely related to the species of *Spintherobolus* by Géry (1977: 607), but again, its anal fin is different from those of the species of *Spintherobolus* in that the anal fin in *G. bogotensis* lacks the derived features of the anal-fin rays in the males of the species of *Spintherobolus* described here. Also, the anal-fin pterygi-

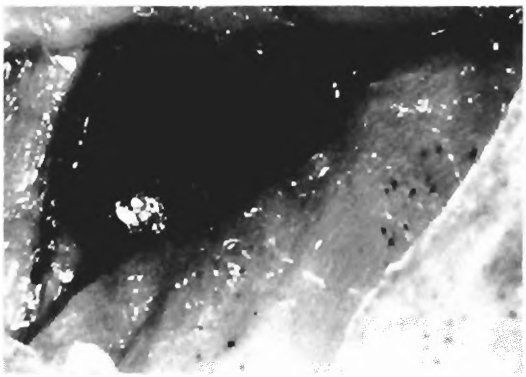


**Fig. 16.** *Spintherobolus papilliferus*, MZUSP 49408, adult female, 50.4 mm SL. Area of the anterior and posterior pseudotympanums of left side, anterior is to the right. The skin and scales were removed, exposing the muscles of the lateral body wall, pleural ribs of the fifth and sixth vertebrae (first and second pleural ribs), and the black, pigmented wall of the swimbladder. The larger black area to the left represents the pseudotympanum present in all cheirodontines. The somewhat obscured apical black area in the right upper part of the photograph is the area of the anterior pseudotympanum characteristic of the species of *Spintherobolus*. However, in adult *S. papilliferus* the anterior pseudotympanum is, in part, obscured by muscle tissue.

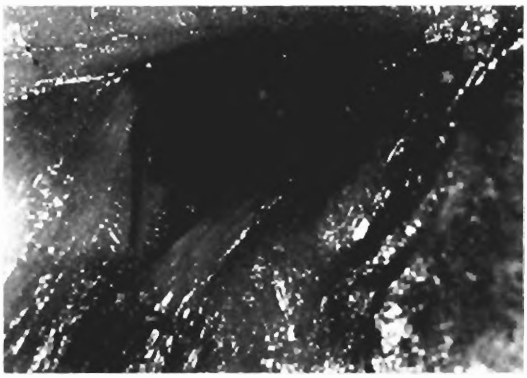


**Fig. 17.** *Spintherobolus papilliferus*, MZUSP 51022, juvenile, 23.9 mm SL. Anterior and posterior pseudotympanums of left side, anterior is to the right. The skin and scales were removed, exposing the muscles of the lateral body wall, pleural ribs of the fifth and sixth vertebrae (first and second pleural ribs), and the black, pigmented wall of the swimbladder. The larger black area to the left represents the pseudotympanum present in all cheirodontines, while the black area to the right is the area of the anterior pseudotympanum characteristic of the species of *Spintherobolus*.

ophores of *Grundulus* appear derived in that they are all short, having no elongate anterior pterygiophores as found in the species of *Spintherobolus* and in most characids. Thus the reduced number of anal-fin rays in *Grundulus bogotensis* seems to be derived, but based on morphology not homologous to the condition found in *Spintherobolus* species. The most parsimonious hypothesis in the global analysis indicates state 3 (9-10) anal fin rays, is an autapomorphy for *S. papilliferus*. State 1 (13-16 branched rays) is a synapomorphy for *Spintherobolus* with an additional reduction of 13-14 branched rays (state 2), as synapomorphic for *S. ankoseion* and *S. leptoura* is equally parsimonious with the hypothesis that state 2 is a synapomorphy for *Spintherobolus* together with an increase (state 1) as an autapomorphy for *S. broccae*.

(21) An anterior pseudotympanum lies anterior to the first pleural rib. This pseudotympanum consists of a muscle hiatus lateral to the anterior portion of the swimbladder. The juveniles of *S. papilliferus* and all specimens of the other three species display both pseudotympanums (Figs. 4-6, 16). However, in adult *S. papilliferus* the anterior pseudotympanum is partially filled by muscular tissue and is relatively obscure but still present (Fig. 17).

A posterior pseudotympanum is situated between the first and second pleural ribs in all cheirodontines including the species of *Spintherobolus* but all other cheirodontines lack the anterior pseudotympanum. The presence of a muscle hiatus anterior to first pleural rib has been also observed in *Atopomesus pachyodus* Myers, *Paracheirodon axelrodi* (Schultz), and an unidentified species of *Axelrodia* Géry. However, these species do not have all of the synapomorphies shared by species of the Cheirodontinae. Thus these three species are excluded from that subfamily and relationships with *Spintherobolus*.

(22) In adult males the anterior ventral procurrent caudal-fin rays, those that have their proximal ends inserted anterior to the haemal spine of the antepenultimate vertebrae, are fused to one another proximally (Fig. 8). Fusion begins with sexual maturation only in males. Among characiforms this character is unique to species of *Spintherobolus*, although one species of undescribed cheirodontine not closely related to *Spintherobolus* also has some fusion among its ventral procurrent rays.

(23) The anterior ventral procurrent caudal-fin rays of males have reduced proximal portions, not rising above the area of fusion between the rays, while the posterior dorsal portions of these rays are fused into a flat compressed plate that inserts between the hemal spine of the preural vertebrae (Fig. 8). The ventral procurrent caudal-fin rays posteriorly associated with the hemal spine of pu3, pu2, and pu1 (parhypural) are separate. The proximal portions of the anterior, ventral procurrent caudal-fin rays in males of *Spintherobolus* species are reduced or lost during sexual maturation. In young specimens and females of *Spintherobolus* and other Characidae these portions are ossified and well-developed.

(24) The symphyseal dentary joint surfaces are smooth oval articular surfaces, lacking the intercalated and folded bony surfaces found in other characiforms. The articulation is supported by tough ligamentous tissue. A similar condition was found in the cheirodontine *Pseudocheirodon arnoldi* (Boulenger), a species that otherwise displays none of the synapomorphies of *Spintherobolus* and clade B cheirodontines.

(25) Lateral line reduced to 2-6 perforated scales. Lateral line reduction or loss has been used for defining cheirodontine and other characid genera since Eigenmann (e.g. 1915, 1917). Weitzman & Fink (1983: 391-394) discussed laterosensory reduction in small characids and noted that its loss is often correlated with small size and that the condition has evolved repeatedly in small characids. They also suggested that such reductive characters are phylogenetically significant at some level, but in practice can sometimes prove problematic for use as synapomorphies.

In *Spintherobolus* we found lateral-line reduction to be a synapomorphy for the species of the genus according to the most parsimonious distribution of the 35 characters used in our analysis of cheirodontine and other characids. Lateral-line counts range from 2-6 in *Spintherobolus* species (mean 3.7 in *S. broccae*, 4.0 in *S. leptoura* and *S. ankoseion*, 4.6 in *S. papilliferus*). In the nearest clade to *Spintherobolus*, the *O. piaba* group, the means in lateral-line range from 6.5-9.2. In the next closest clade, the species of *Cheirodon*, the means range from 6.7-8.8. No other cheirodontines have the reduced number of pored scales in *Spintherobolus*. *Grundulus* also has a small number of perforated lateral-line scales (5-6), but this appears independently derived according to the most parsimonious hypothesis of our data.

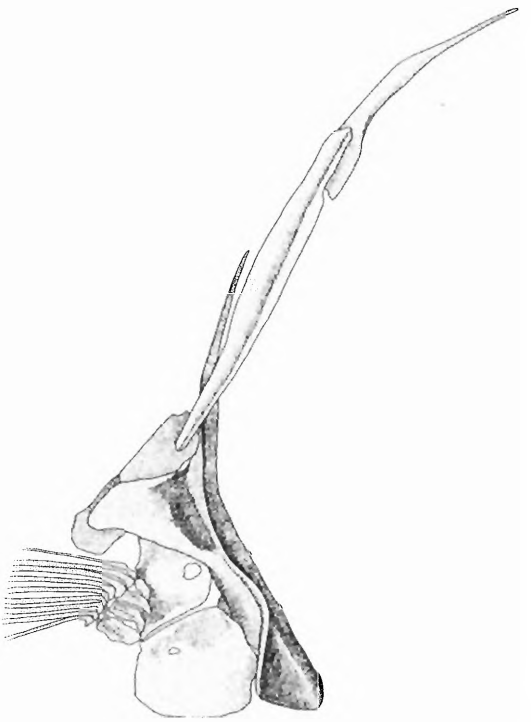


**Fig. 18.** *Spintherobolus ankoseion*, USNM 297935, adult male, 24.5 mm SL. Osteology of pectoral girdle.

(26) The coracoid bone of the pectoral girdle of *Spintherobolus* is reduced in length, and more or less discoid in shape (Fig 18). In all other cheirodontines and characids examined by us the coracoid is either derived in other ways, for example in the gasteropelecids (Weitzman, 1954: 225), or elongate and similar to that described by Weitzman (1962: 41) for *Brycon meeki* Eigenmann & Hildebrand.

(27, state 1) The eyes of species of *Spintherobolus* are small and derived compared to other cheirodontines. *Spintherobolus broccae* has a mean eye diameter of 28.7 %, *S. leptoura* a mean of 27.2 %, *S. ankoseion* a mean of 27.6 %, and *S. papilliferus* a mean of 21.3 % compared to head length. Cheirodontine outgroups related to *Spintherobolus* have relatively large eyes, 33.9-40.3 % HL in clade C (*Cheirodon*) and 35.4-41.0 % of head length in clade E (*O. piaba* and related species) and many American characids have an eye size ranging from about 25 to 35 % HL (Weitzman et al., 1994: 55). Small eye size is apparently a reductive synapomorphy for *Spintherobolus*.

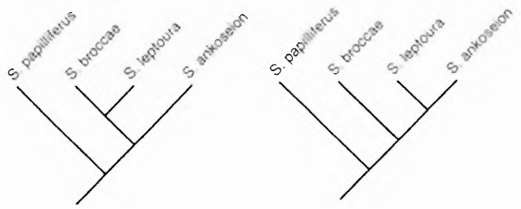



**Fig. 19.** Alternate cladograms of the relationships of the species of *Spintherobolus*.

(28) Relatively short pectoral-fin lengths are characteristic of males of *S. broccae* (15.2-18.7, $\bar{x}$ = 16.9 % SL), *S. leptoura* (15.6-17.9, $\bar{x}$ = 16.9 % SL), and *S. papilliferus* (15.7-16.6, $\bar{x}$ = 16.1 % SL). The males of *S. ankoseion* have relatively long pectoral fins (18.2-20.8, $\bar{x}$ = 19.0 % SL) and the outgroup clades C and E also have relatively long pectoral fins, 17.0-20.9, $\bar{x}$ = 18.5 % SL and 19.6-21.7, $\bar{x}$ = 20.2 % SL respectively.

The distribution of this feature is ambiguous in three equally most parsimonious cladograms based on other characters (Figs. 3, 19a-b). First, in all three cladograms this feature may be considered a synapomorphy for hypothesizing the monophyly of *Spintherobolus*, but with a reversal to a longer pectoral fin in *S. ankoseion*, requiring two steps in each. However, in the cladogram having *S. broccae* and *S. leptoura* united as sister species (Fig. 19a) another, two step, equally parsimonious hypothesis is supported by the data. This hypothesis indicates that a short pectoral fin was independently acquired in *S. papilliferus* and in the clade uniting *S. broccae* and *S. leptoura* (Fig. 19a). In this hypothesis the character of short pectoral fin does not support *Spintherobolus* as a clade.

**Etymology.** *Spintherobolus* comes from the Greek spinther meaning spark and obelos, to spit. Eigenmann (1915: 19) stated "emitting small sparks, referring to the appearance of yellow neuromasts on the head".

### Key to species of *Spintherobolus*

1 - Branched anal-fin rays 11-16 (Fig. 20); vertebrae 32-34 (Fig. 21); scales in a longitudinal series 31-33 (Fig. 22); horizontal eye diameter longer than snout length; coastal Atlantic drainages, east of Serra Geral. .. 2

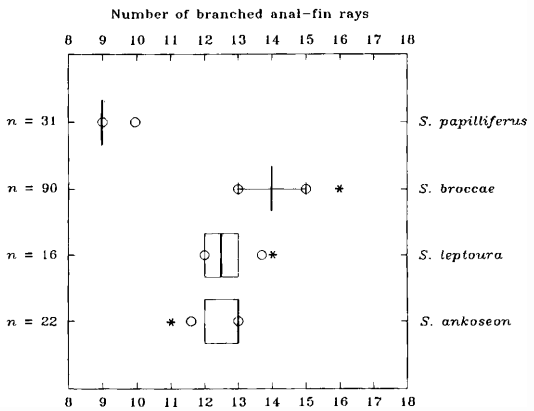



**Fig. 20.** Tukey box plots of the number of branched anal-fin rays in species of *Spintherobolus*. Visual comparison of these box plots shows that the anal-fin ray counts of *S. papilliferus* are obviously different from all other species. Also, although there is overlap, the counts of *S. broccae* are obviously significantly different from those of *S. leptoura* and *S. ankoseion*. However, there were no significant differences between the counts of *S. leptoura* and *S. ankoseion* when subject to a Mann-Whitney rank-sum test.

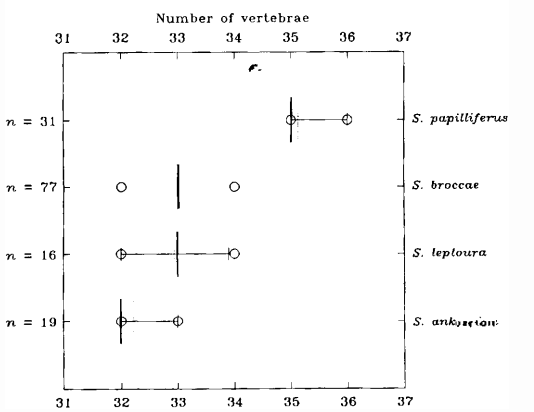



**Fig. 21.** Tukey box plots of the number of vertebrae in species of *Spintherobolus*. Visual comparison of these box plots shows that the vertebral counts of *S. papilliferus* are obviously different from all other species. Those of *S. broccae* and *S. leptoura* are not significantly different and those of *S. ankoseion*, although overlapping with those of *S. broccae* and *S. leptoura* are significantly different from these two species when subject to Mann-Whitney rank-sum tests (T = 398, P < 0.001 and T = 246, P < 0.001 respectively).

- Branched anal-fin rays 9, rarely 10; vertebrae 35-36; scales in a longitudinal series

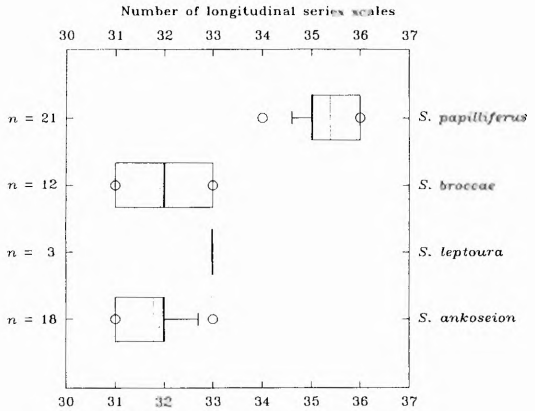



**Fig. 22.** Tukey box plots of the number of longitudinal series scales in species of *Spintherobolus*. Visual comparison of these box plots shows that these scale counts of *S. papilliferus* are obviously different from all the other species. The counts of *S. leptoura* may be different from those of *S. broccae* and *S. ankoseion*, but the available counts for *S. leptoura* are too few (3) for useful statistical comparisons. The counts of *S. broccae* and *S. ankoseion* are not significantly different.

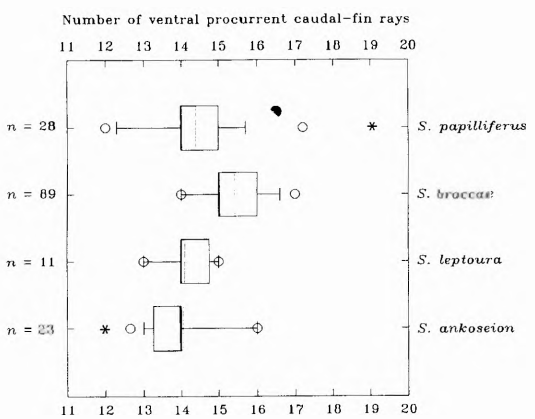



**Fig. 23.** Tukey box plots of the number of procurrent caudal-fin rays in species of *Spintherobolus*. Significant differences were not found between *S. papilliferus* and *S. leptoura*, between *S. leptoura* and *S. ankoseion*, and between *S. papilliferus* and *S. ankoseion*. However, significant differences using Mann-Whitney rank sum tests were found between *S. papilliferus* and *S. broccae* ($T$ = 984, $P < 0.001$), between *S. broccae* and *S. leptoura* ($T$ = 195, $P = < 0.001$), and between *S. broccae* and *S. ankoseion* ($T$ = 604, $P = < 0.001$).

34-36; horizontal eye diameter shorter than snout length; headwaters of rio Tietê, upper rio Paraná drainage. ..... *S. papilliferus*

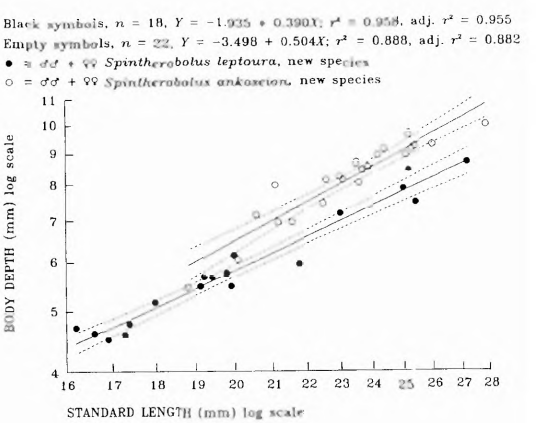



**Fig. 24.** Graph of body depth as a function of standard length for *Spintherobolus leptoura* (black symbols) and *S. ankoseion* (empty symbols). Axes are logarithmic. Note that the 95 % confidence intervals in lengths of about 21 to 28 mm SL do not overlap with the means of the of the compared species indicating a significant difference in these size ranges. These growth pattern differences are used to separate these species in the key and text.

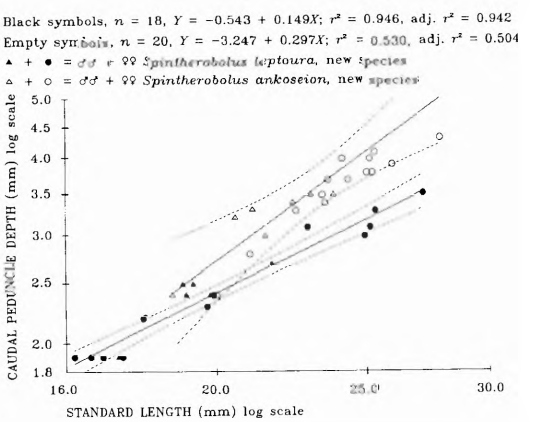



**Fig. 25.** Graph of caudal peduncle depth as a function of standard length for *Spintherobolus leptoura* (black symbols) and *S. ankoseion* (empty symbols). Axes are logarithmic. Note that the 95 % confidence intervals in lengths of about 21 to 27 mm SL do not overlap with the means of the compared species indicating a significant difference in these size ranges. These growth pattern differences are used to separate these species in the key and text.

2. - Branched anal-fin rays 11-14, usually 12-13, $\bar{x}$ = 12.6 for both species; ventral procurrent caudal-fin rays 12-16, $\bar{x}$ = 14.0 for *S. ankoseion* and 14.1 for *S. leptoura* (Fig. 23); third infraorbital bone present. ..... 3

- Branched anal-fin rays 13-16, usually 14-15, $\bar{x}$ = 14.1; ventral procurrent caudal-fin rays 14-17, $\bar{x}$ = 15.4; third infraorbital absent; Rio de Janeiro region and area near Santos, São Paulo). ..... *S. broccae*

3. - Body depth of specimens of both sexes between about 21.0 and 28.0 mm SL 32.4-38.5 % SL, $\bar{x}$ = 35.8 % (Fig. 24); male body depth regardless of body length 29.3-37.9 % SL, $\bar{x}$ = 34.2 %; male caudal-peduncle depth 12.8-15.6 % SL, $\bar{x}$ = 14.8 % (Fig. 25); freshwaters around Baia de Paranaguá, Paraná south to Barra do Sai, Santa Catarina. ..... *S. ankoseion*
- Body depth of specimens of both sexes between about 21.0 and 28.0 mm SL 27.5-33.7 % SL, $\bar{x}$ = 31.0 % (Fig. 24); male body depth regardless of body length 26.6-29.7 %, $\bar{x}$ = 28.3; male caudal peduncle depth 11.0-13.1 % SL, $\bar{x}$ = 12.3 % (Fig. 25); rio Quilombo, rio Ribeira de Iguape drainage, São Paulo. ..... *S. leptoura*

### Subgroup a

There is only one species in subgroup a. See apomorphy list below for features separating this species from all others in the genus. This species also lacks the synapomorphies listed below in Subgroup b for three species of *Spintherobolus*.

### *Spintherobolus papilliferus* Eigenmann
(Figs. 1, 26-28)

*Spintherobolus papilliferus* Eigenmann, 1911: 167, pl. 5 figs. 1-4 (new species description, type locality: Alto da Serra, São Paulo, Brazil, holotype: CM 2582, now FMNH 104802; 4 paratypes: CM 2583, now FMNH 54918 and CAS[SU] 17520)

**Specimens examined.** All from Brazil, São Paulo, upper rio Tietê drainage. FMNH 104802, holotype, immature; 34.1 mm SL; FMNH 54918, 3 paratypes, immature, 20.2, 30.5, 30.7 mm SL; CAS-SU 17520, 1 paratype, juv., 28.5 mm SL (note: FMNH specimens mixed and holotype not separately labeled; see Discussion section below); Alto da Serra, 4 Aug 1908, J. D. Haseman. – MZUSP 51022, 17, all immature, 16.7-24.6 mm SL; Parana-piacaba and Campo Grande; 24 Mar 1967, S. P. Werner. – MZUSP 49408, 1 male 57.8 mm SL, 2 females, 50.3-50.4 mm SL, 1 female, c&s, 45.0 mm SL; "last creek on road to Paranapiacaba"; 20 Mar 1980, R. M. C. Castro. – MZUSP 51021, 1, female, 60.8 mm SL; rio Ipiranga; January 1929, H. Luederwöldt. – MNRJ 6260, 1, female, 35.8 mm SL (same specimen in Travassos, 1953: 506, fig. 1). – MNRJ 4237, 1 male, 34.5 mm SL, 4 females, 32.8-36.5 mm SL; rio Ipiranga; date unknown but probably before 1931, A. Couto de Magalhães.

**Diagnosis.** The following five autapomorphies (20, state 3; 27, state 2; 29; 30; 31) distinguish *S. papilliferus* from all other species of the genus. Also three anal-fin reversals (10R, 11R, 12R) help distinguish this species.

(20, state 3) Branched anal-fin rays 9-10. This is the lowest count for this fin known for the Cheirodontinae. The other three species of *Spintherobolus* have 11-16 branched anal-fin rays.

(27, state 2) The eyes of *S. papilliferus* (18.4-26.0, $\bar{x}$ = 21.3 % HL, n = 31) are the smallest of the four species of *Spintherobolus*. The eyes of *Spintherobolus ankoseion* (24.6-30.1, $\bar{x}$ = 27.6 %, n = 22), those of *S. broccae* (24.5-32.7, $\bar{x}$ = 28.7 %, n = 70), and those of *S. leptoura* (23.2-30.3, $\bar{x}$ = 27.2 %, n = 18) are significantly larger relative to head length than those of *S. papilliferus* and are not significantly different from each other. See also discussion of apomorphy 27, state 1, above.

(29) The caudal peduncle length of *S. papilliferus* is long, being 23.8-24.6 % SL ($\bar{x}$ = 24.2 %) in males and 21.3-27.0 % SL ($\bar{x}$ = 23.9 %) in females. The other three species have caudal peduncle lengths between 11.5-21.5 % SL. This demonstrates that almost no overlap occurs between *S. papilliferus* and the other species of *Spintherobolus* except in an occasional female. In species of outgroup clade E the caudal peduncle length varies between 11.0-19.6 % SL and the ranges of the means extend from 14.3-15.2 % SL.

(30) Large adult size. Mature adults of *S. papilliferus* reach at least 60.8 mm SL (a mature female) and 57.8 mm SL (a mature male). Another male 34.5 mm SL had developing secondary sexual characters. Specimens of *S. broccae*, *S. leptoura* and *S. ankoseion* are fully mature by at least 18 mm SL and adult males were recorded to reach 23.1 mm SL (*S. ankoseion*) while adult females reach 27.9 mm SL (*S. ankoseion*). Adults of outgroup clade E species are only known to range approximately between 20-40 mm SL.

**Fig. 26.** *Spintherobolus papilliferus*, MZUSP 51021, female 60.8 mm SL, Brazil, São Paulo, rio Ipiranga.
**Fig. 27.** *Spintherobolus papilliferus*, MZUSP 49408, adult female, 50.3 mm SL, Brazil, São Paulo, near Paranapiacaba.
**Fig. 28.** *Spintherobolus papilliferus*, FMNH 54918, holotype, 34.1 mm SL. Brazil, São Paulo, Alto da Serra, near Paranapiacaba.

(31) *Spintherobolus papilliferus* has a high vertebral count of 35-36. Compare vertebral counts of the species of *Spintherobolus* in Figure 21. Species of its sister subgroup b have 32-34 vertebrae and species in outgroup clade E are known to have 32-34 vertebrae.

(10R) The anal-fin rays of adult males are not expanded in a sagittal plane. See apomorphy 10, clade D, for outgroup condition and its taxonomic distribution.

(11R) Segments of anal-fin rays of adult males are not fused. See apomorphy 10, clade D, for outgroup state and its taxonomic distribution.

**Table 2.** Morphometrics of *Spintherobolus papilliferus*. Table includes measurements of all examined specimens. Values for the holotype are given separately.

| | holotype | males | | | | females | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | n | low | high | mean | n | low | high | mean |
| Standard length [mm] | 34.1 | 2 | 34.5 | 57.8 | 46.2 | 30 | 16.7 | 60.8 | 27.7 |
| **Percentage of standard length** | | | | | | | | | |
| Snout to anal-fin origin | 61.0 | 2 | 61.7 | 63.3 | 62.5 | 30 | 58.7 | 67.3 | 62.2 |
| Snout to dorsal-fin origin | 54.3 | 2 | 51.9 | 52.2 | 52.0 | 29 | 50.9 | 58.2 | 54.4 |
| Snout to pelvic-fin origin | 47.5 | 2 | 42.0 | 47.4 | 44.7 | 30 | 44.1 | 50.0 | 46.9 |
| Dorsal-fin base length | 9.4 | 2 | 9.6 | 12.3 | 10.9 | 29 | 9.4 | 12.4 | 11.1 |
| Anal-fin base length | 11.4 | 2 | 12.5 | 12.6 | 12.5 | 30 | 10.4 | 14.2 | 12.5 |
| Caudal peduncle length | 27.0 | 2 | 23.8 | 24.6 | 24.2 | 30 | 21.3 | 27.0 | 23.9 |
| Caudal peduncle depth | 12.9 | 2 | 13.3 | 15.4 | 14.4 | 30 | 11.4 | 15.8 | 13.3 |
| Depth at dorsal-fin origin | 29.6 | 2 | 28.7 | 31.8 | 30.3 | 29 | 26.4 | 32.2 | 28.8 |
| Dorsal-fin length | - | 2 | 22.5 | 24.3 | 23.4 | 27 | 17.0 | 27.4 | 23.1 |
| Pelvic-fin length | 12.9 | 2 | 14.5 | 15.9 | 15.2 | 29 | 11.4 | 15.9 | 13.3 |
| Pectoral-fin length | 10.9 | 2 | 15.7 | 16.6 | 16.1 | 29 | 10.9 | 16.5 | 14.0 |
| Bony head length | 29.3 | 2 | 28.7 | 29.8 | 29.2 | 30 | 26.8 | 32.0 | 30.2 |
| **Percentage of head length** | | | | | | | | | |
| Snout length | 24.0 | 2 | 24.4 | 25.3 | 24.8 | 29 | 18.3 | 29.4 | 23.3 |
| Upper jaw length | 20.0 | 2 | 20.2 | 20.9 | 20.6 | 29 | 16.0 | 23.0 | 19.5 |
| Horizontal eye diameter | 26.0 | 2 | 19.2 | 20.2 | 19.7 | 29 | 18.4 | 26.0 | 21.4 |
| Least interorbital width | 25.0 | 2 | 31.3 | 31.4 | 31.4 | 29 | 22.4 | 32.0 | 26.9 |

(12R) An anterior extension of the proximal end of the lepidotrichia of the anal-fin rays of males is absent. See apomorphy 12, clade D, for the outgroup state.

**Description.** Morphometric data are summarized in Table 2. The reduced anal fin and lack of an adipose fin in part give this species a rather unusual body shape for a characid. Body compressed, moderately elongate. Predorsal body profile convex with short concavity at nape followed by relatively steep convexity. This more strongly developed in large specimens (above 50 mm SL). Body profile gently convex behind nape to dorsal-fin origin and along dorsal-fin base. Body profile nearly straight between terminal base of dorsal-fin and caudal-fin origin. Ventral profile of head gently convex. Belly profile between pectoral and pelvic fins straight or slightly convex. Profile between pelvic-fin origin and anal-fin origin slightly concave. Body profile along anal-fin base nearly straight or slightly concave. Caudal peduncle elongate with dorsal and ventral profiles nearly straight.

Snout prominent, blunt, and rounded. Dorsal profile of head straight to slightly concave. Mouth terminal, angled posteroventrally. Maxilla short, not reaching line drawn vertically through anterior margin of eye. Eyes smaller than snout length.

Dorsal-fin rays, ii,9 in all specimens. Dorsal-fin origin near midbody distance. Adipose fin absent.

Anal-fin rays iii,10 (anterior unbranched rays iii in 29 specimens and 2 specimens with a fourth vestigial anterior element detectable in radiographs; 29 specimens with 9 branched anal-fin rays; holotype and one other specimen with 10 branched rays; Fig. 20). Profile of anal fin rounded, with tip of all branched rays ending at more or less vertical imaginary line along posterior border of anal-fin base. Anal fin without hooks in two males presumably large enough to be mature. Only one fully adult male examined and its anal-fin rays longer than those of females. Anal-fin origin at vertical line drawn through origin of posteriormost dorsal-fin ray.

Pectoral-fin rays i,13 (branched rays 10-13, $\bar{x}$ = 11.1, n = 20). Pectoral fin large, rounded, posterior tips of longest pectoral-fin rays extend to nearly pelvic-fin origin.

Pelvic-fin rays i,6 (branched rays 5-6, $\bar{x}$ = 5.8, n = 22). Pelvic fins of adult male reaching beyond anal-fin origin but not reaching that fin's origin in females. Largest male with very short, truncated hooks located on ventromedial surface of pelvic-fin rays. These occur along one third of un-

branched ray and about half of proximal length of first four branched rays.

Principal caudal-fin rays 10/9 (9/9 in one specimen, $\bar{x}$ = 18.9, n = 28). Dorsal procurrent caudal-fin rays 14 (range = 11-15, $\bar{x}$ = 13.0, n = 24). Ventral procurrent caudal-fin rays 15 (range = 12-17, $\bar{x}$ = 14.2, n = 26; Fig. 23). Ventral procurrent caudal-fin rays of males strong and well-developed, with proximal extremities fused, slab shaped and expanded in sagittal plane. Last five caudal vertebrae (including posterior half centrum) supporting caudal fin and procurrent rays, with enlarged and modified hemal spines. These five caudal vertebrae thus equal precaudal vertebrae by definition. Anteriormost 10 ventral procurrent fin rays of mature males fused, with lateral processes inserted among muscle fibers and skin of this region.

Scales cycloid. Lateral line with 3-6 perforated scales ($\bar{x}$ = 4.6, n = 19). Scales in longitudinal series 34-36 ($\bar{x}$ = 35.4, n = 19; Fig. 22). Scale rows between dorsal-fin origin and longitudinal series (series continuous with perforated scales) 6-7 ($\bar{x}$ = 6.3, n = 19) and between this scale series and pelvic-fin origin, 5-6 ($\bar{x}$ = 5.6, n = 19). Predorsal scales from occipital process to dorsal-fin origin 12-15, irregular and difficult to count accurately, with 12-15 scales. Scale rows around caudal peduncle, 18 in all specimens. No modified scales on caudal-fin or scale sheath along anal-fin base.

All jaw teeth with expanded basal pedicle and more or less conical along their length, but with slightly expanded distal tip. Distal conical part of dentary teeth with small medial and small lateral cusps. Middle cusp relatively large, elongate and slender. Anterior premaxillary teeth also with one cusp on each side, these extremely reduced and almost imperceptible. Maxillary teeth conical with somewhat laterally expanded distal conical portion. There are 8 premaxillary, 7 maxillary and 12 dentary teeth in one cleared and stained specimen, 45.0 mm SL.

Vertebrae 35-36 ($\bar{x}$ = 35.1, n = 30; Fig. 21).Branchiostegal rays 4. Two rays attached nearly together on midventral surface of anterior ceratohyal, one on posteroventral lateral surface of anterior ceratohyal, and one on the mid-ventrolateral surface of posterior ceratohyal, in one cleared and stained specimen.

**Color in alcohol.** The color description of preserved adults given below was taken from specimens collected within the last 17 years. The color pattern of the juvenile types of *S. papilliferus* are somewhat faded but essentially the same as that of the more recently collected adult specimens. See Figures 1, 10, 11, 26, 27, & 28 for the preserved color patterns of adult males and females. The dorsal and lateral parts of the body are pale to medium brown, and pale yellowish brown ventrally. No obvious discrete lateral body stripes, bands, or blotches are present. In the photographs of a male and female, there appears to be a dark humeral spot just posterior to the more dorsal region of the opercular flap. This is not due to an increase number or size of the dark chromatophores. It is rather the area of the anterior and posterior pseudotympanums where the muscles of the lateral body wall are thin or absent. Black pigment coating the swimbladder can be seen through the skin and appears dark in the photograph.

The scale borders, especially their posterior borders are covered by a relatively wide band of dark chromatophores, producing a reticulate pattern over the body. These chromatophores are darker and perhaps more numerous dorsally making the belly region relatively pale and the back region relatively dark. What looks like a caudal spot in Figure 27 of the female is an artifact of lighting in taking the photograph. No area of any scale is free of dark chromatophores and the central region of all scales thus appears pale brown.

The pectoral and pelvic fins of the female are hyaline with a few scattered dark chromatophores. The pectoral fins of the male are relatively dark, with numerous dark chromatophores scattered over both the dorsal and ventral surfaces. The male's pelvic fins are lighter, much like those of the female. The dorsal fin has a scattering of dark chromatophores, which are more concentrated in the mid-dorsal region of the fin. The anal and caudal fins are hyaline with a thin scattering of small dark chromatophores over the rays and membranes. The patterns appearing in the caudal- and anal-fin photographs are due to the relative thickness of the fin and how it reflects and refracts light, not to pigment patterns. The head is pale brown around the mouth and on the ventral surface of the snout, jaws, and opercular region. The dorsal surface of the snout, between the eyes, the dorsum of the cranium and the nape are all dark brown. The head area posterior to the circumorbitals and extending ventrally from the parietal region across the dorsal

opercular region is pale brown in both sexes.

Color in life unknown.

**Sexual dimorphism.** Males and females are not easily distinguished externally, having a similar body shape and color pattern (Figs. 1, 26, 27). External sexually dimorphic features are not extensively developed. The ventral procurrent caudal-fin rays of males are fused to each other, more developed than those of females, and have lateral processes. These rays are embedded deep into the scales and skin in this species and can be only identified after dissection or osteological preparation. The presence of small hooks on the pelvic fins is the clearest external sexually dimorphic feature found in this species. The pelvic fin reaches the anal-fin origin in males, but not in females.

**Status of the holotype.** Eigenmann (1911: 167) described *S. papilliferus* based on five specimens, the holotype, CM 3582, and four paratypes (designated cotypes by Eigenmann), CM 3583. We found five specimens labeled as paratypes, four in FMNH 54918, and one in CAS-SU 17520. We find that according to the labels in both jars FMNH 54918 originally contained five specimens, and one was subsequently transferred to SU 17520. However, Ibarra & Stewart (1987: 81) stated that the holotype was missing and five paratypes were present. Since they do not give FMNH museum numbers we are uncertain of the meaning of their statement. However, the holotype must be one of the five specimens present in the CAS and FMNH collections. Eigenmann gave the total length of the holotype as 41 mm and the paratypes as ranging from 25-39 mm in total length. Unfortunately all the specimens now have damaged caudal fins, but we identify the largest in the FMNH collection as the holotype (Fig. 28). Its general body shape and color pattern also fit well with that published in Eigenmann (1911: pl. 5 fig.1; 1915: pl.3 fig. 1).

**Conservation note.** Menezes and Weitzman are extensively documenting the location of the Alto da Serra type locality near the head waters of the rio Grande da Serra, a tributary of the rio Tietê in the vicinity of Campo Grande and Paranapiacaba, State of São Paulo. The known collecting sites for this species have been altered by pollution and commercial use, especially that of the rio Ipiranga in the city of São Paulo where the fish is apparently extinct. We have examined one large female 60.8 mm SL (MZUSP 51021; Figs. 11, 26) collected in 1929 from this locality that has grooves on the top of the head that are deeper than any other specimen examined. This specimen also has 33 vertebrae rather than the 35-36 found in all other specimens of *S. papilliferus*. The young specimens we have from rio Ipiranga have the usual number of vertebrae found in *S. papilliferus* and because they are young, their cephalic grooves are not well-developed. The absence of more adult, mature specimens of *S. papilliferus* from the rio Ipiranga locality and with only one mature male and three mature females of this species from the rio Grande da Serra locality prevent us from investigating further the possibility that the large specimen from rio Ipiranga might be a different species.

At present *S. papilliferus* may survive only in the rio Grande da Serra, near Paranapiacaba and Campo Grande. This area is next to the storage and transfer yards of the Rede Ferroviária Federal S. A (Brás) where it crosses the summit of the Serra do Mar (locally called the Serra de Paranapiacaba) between the cities of São Paulo and Santos. This area lies near the Reserva Biológica de Paranapiacaba where *S. papilliferus* may still exist. No extensive search has been made for this species in the Paranapiacaba region, but recent collection trips to the immediate vicinity of Paranapiacaba and Campo Grande failed to produce this fish.

### Subgroup b

**Diagnosis.** This clade consists of *S. broccae*, *S. ankoseion*, and *S. leptoura*. These species are united in subgroup b by the following synapomorphies:

(32) The ray segments of the posterior branch of the second through fifth anal-fin rays of fully adult males are thickened and have a characteristic somewhat asymmetrical chevron shape in lateral profile (Figs. 9, 15). These segments are all part of a complex of anal-fin modifications as follows. Adult males have the second through fifth branched anal-fin rays large, thickened and elongate, especially in their proximal portions that are not or only partly divided into segments. The second through the fourth of these rays are especially large and the posterior branch of the first division of each ray is much larger than the anterior division and more or less maintains the

size and strength of the proximal portion of the ray. The thickened, characteristically chevron shaped ray segments are present on these posterior branches. The posterior distal half of these ray segments are curved and extend posteriorly and distally, giving the segment its asymmetrical chevron shape. The apex of this curved portion of each segment is angular with its distal sharp process pointing more or less distally, towards the distal tip of its fin-ray. These segments sometimes bear very small hooks that appear more like small, knob-like processes.

The ray segments are relatively rectangular, either short or elongate, in other characids. The shape of these segments in the species of subgroup a is unknown elsewhere among characiforms.

(33) The pterygiophore of the sixth branched anal-fin ray in both males and females is directed dorsally, away from the fifth which is directed anteriorly and in parallel with the pterygiophores anterior to it (Fig. 9). The sixth pterygiophore is not parallel with those posterior to it, rather its proximal end is convergent with the one posterior. The pterygiophore just posterior to that of the sixth branched ray has its proximal end butting or nearly butting between the proximal tip and the mid length of the sixth pterygiophore. This characteristic osteological pattern is associated with the change at this point from elongate, anterior lobe anal-fin rays to short, posterior rays in both sexes. It also is at the dividing point between the thickened and the usual characiform rays of the anal fin in the males. All other, more posterior anal-fin pterygiophores are parallel and dorsoanteriorly directed. We have seen this feature in no other characiforms.

(34) A black pigmented area lies ventral to the eyes (Figs. 2, 4, 29-37). No other cheirodontines, including *S. papilliferus*, have such spots.

(35) A longitudinal stripe occurs on the body dorsal to the anterior lobe of the anal-fin and extends onto the short posterior branched anal-fin rays (Figs. 2, 29-37). No similar pattern occurs on other cheirodontine characids.

**Diagnosis.** These species differ from *S. papilliferus* in having the following features. Some of these features are not synapomorphies for these three species because they are clade D synapomorphies or a slight modification of them. We describe them here in order to clearly distinguish the subgroup b species of *Spintherobolus* from *S. papilliferus*. The large branched anal-fin rays, two through five, of the males are slab shaped and expanded in the sagittal plane (Figs. 9, 15). The proximal ends of the these rays have their lepidotrich bases extending anteriorly so that they insert between the lepidotrichia of the next anterior ray. The number of branched anal-fin rays is 11-16, versus 9-10 in *S. papilliferus*. The number of vertebrae is 32-34, versus 35-36 in *S. papilliferus*. The number of scales in a longitudinal series is 31-33, versus 34-36 in *S. papilliferus*).

**Discussion.** The relationships among the *Spintherobolus* species of subgroup b are difficult to hypothesize because no clear synapomorphies grouping any two of these three species were found. Below we discuss our attempt to polarize certain characters we found useful for distinguishing *Spintherobolus* species, but not for their diagnosis into clades.

The number of ventral procurrent caudal-fin rays is significantly greater (range 14-17, $\bar{x}$ = 15.4) for *S. broccae* than for *S. ankoseion* (range 12-16, $\bar{x}$ = 14.0) and *S. leptoura* (range 13-15, $\bar{x}$ = 14.1). See Figure 23 for a visual and nonparametric statistical expression of the differences and similarities among the species of *Spintherobolus*. The number of these elements in the sister clade formed by *S. papilliferus* (12-19, $\bar{x}$ = 14.4) and the next outgroup, clade E (9-18) includes all the ranges for *Spintherobolus* subgroup b species and the two states found in *Spintherobolus* cannot be polarized.

The vertebral count of *S. ankoseion* (32-33, $\bar{x}$ = 32.2) is significantly different from that of *S. broccae* (32-34, $\bar{x}$ = 33.0) and *S. leptoura* (32-34, $\bar{x}$ = 33.9). See Figure 21 for a nonparametric statistical expression of the differences and similarities among the species of *Spintherobolus*. The range of vertebral numbers observed in these three *Spintherobolus* species is included in the range of the outgroup clade E and cannot be polarized. The high count in the sister species, *S. papilliferus* (35-36, $\bar{x}$ = 35.1) is derived and an autapomorphy for that species; see apomorphy 31 above.

Body depth and caudal peduncle depth, although distinctive for *S. leptoura* and presented as a distinguishing feature for that species below, cannot be polarized because all ranges found in the species of *Spintherobolus* are found in outgroup clades C and E.

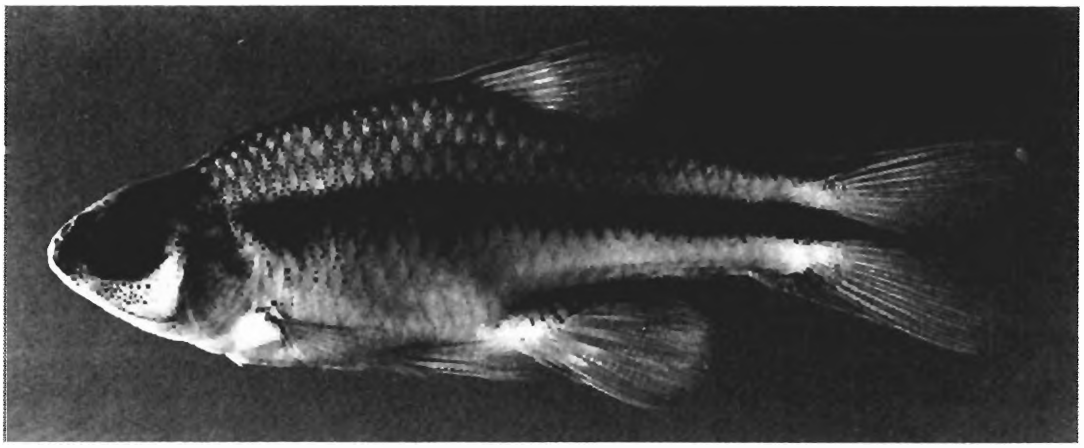


**Fig. 29.** *Spintherobolus ankoseion*, MZUSP 35430, holotype, male, 23.1 mm SL, Brazil, Santa Catarina, Barra do Sai.

Another character, anal-fin origin located relatively far anteriorly, appears to be a synapomorphy uniting *S. broccae* and *S. leptoura*, but we have not entered it in our analysis because the differences among states between the clades are small and the amount of data relatively limited. More data will be necessary to determine the significance of this feature.

We found only two *Spintherobolus* features useful for distinguishing species that can also be polarized. These are the number of branched anal-fin rays, synapomorphy 20, and the pectoral-fin length relative to SL, synapomorphy 28. However, the results of their analysis provides three equally parsimonious cladograms for subgroup b *Spintherobolus* species.

### *Spintherobolus ankoseion*, new species
(Figs. 29-31)

**Holotype.** MZUSP 35430, male, 23.1 mm SL; creek in the forest, near Barra do Sai, between Barra do Sai and Itapema, northern Santa Catarina, Brazil; 22 Dec 1985, W. Costa.

**Paratypes.** MZUSP 51024, 2 males, 22.5-23.0 mm SL, 9 females, 22.6-26.0 mm SL; MCP 19253, 1 male, 20.6 mm SL, 3 females, 24.4-27.9 mm, same data as holotype. The following paratypes are all from Paraná: Brazil: MZUSP 51025, 1, male, 21.1 mm SL; praia de Guaratuba, 5 km north of Matinhas; 4 Dec 1975, P. S. Santos Filho. – USNM 297935, 1 male, c&s, 23.1 mm SL, 1 female, c&s, 23.3 mm SL, 1 female, 23.6 mm SL, 1 juv., 13.0 mm SL; rio da Praia, near Guaratuba; 18 Feb 1988, R. M. C. Castro. – USNM 297936, 2 males, 18.8-21.6 mm SL, 2 females, 20.1-21.1 mm SL; unnamed blackwater stream crossing road "Elisio Pereira Alves Filho" about 15 km from road BR-277, SW of Paranaguá; 20 Feb 1988, R. M. C. Castro.

**Diagnosis.** This species is distinguished by the low vertebral count 32-33, $\bar{x}$ = 32.2, versus 32-34, $\bar{x}$ = 33.0 for *S. broccae* and 32-34, $\bar{x}$ = 32.9 for *S. leptoura* (Fig. 21); a larger preanal distance in males, 61.3-63.9 % SL, $\bar{x}$ = 62.6, versus for *S. broccae* 55.9-61.5, $\bar{x}$ = 59.7, and *S. leptoura* 57.3-61.9, $\bar{x}$ = 58.9. Although some overlap occurs in these ranges, Mann-Whitney rank sum tests presented in caption of Figure 21 indicate significant differences at the 0.05 level of probability. Other differences among these species are expressed in the diagnoses of the other species.

**Description.** Morphometric data are summarized in Table 3. Body compressed, moderately elongate. Predorsal body profile convex with concavity at nape. Body profile along dorsal-fin base posteroventrally inclined, becoming straight or slightly concave between dorsal and caudal fins. Ventral body profile gently convex between tip of mandible and pelvic fins. Belly profile convex between pelvic and anal fins in females and slightly concave in males. Body profile along anal-fin base slightly concave in females and slightly convex in anterior lobe in males and concave in their posterior lobe. Ventral profile of caudal pedun-

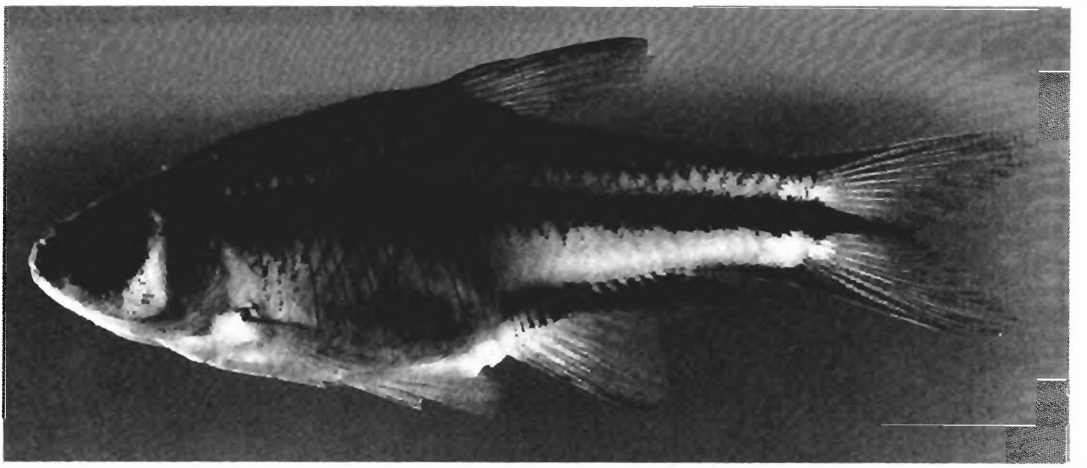


**Fig. 30.** *Spintherobolus ankoscion*, MCP 19253, paratype, female 27.9 mm SL, Brazil, Santa Catarina, Barra do Sai.

cle concave in females, with a keel formed by prominent ventral procurrent caudal-fin rays.

Snout shorter than eye diameter. Mouth terminal, angled posteroventrally; maxilla short, not reaching line drawn vertically through anterior margin of eye.

Dorsal-fin rays ii,9 (branched rays 8-9, $\bar{x}$ = 8.9). Dorsal-fin origin near midbody. Adipose fin absent.

Anal-fin rays iv,13 (anterior unbranched rays iii-iv, $\bar{x}$ = 3.2, n = 22; branched rays 11-13, $\bar{x}$ = 12.6, n = 22; Fig. 20). Profile of anterior lobe of anal fin of males large and rounded (Fig. 9). Distal tip of largest rays not reaching posteriorly beyond distal tip of posterior anal-fin rays; distal border of posterior anal-fin lobe concave. Anal-fin profile of females with distal border deeply concave, each ray decreasing in length from posterior unbranched ray to 6th branched ray. Anal-fin origin at vertical line drawn through dorsal-fin posterior basal termination. Three of six males examined have hooks on anal-fin rays. Hooks extremely reduced in size, occurring on posterior face of 2 to 6 segments of posterior branch of first and sometimes first and second branched anal-fin rays. Each segment bears two to three hooks on each side. Branched anal-fin rays 1-5 of males enlarged; branched rays two to four even more developed, reaching more than five times wider than more posterior rays. These rays with a posterior process on anteroproximal face of each lepidotrich. These processes are extensions of rays

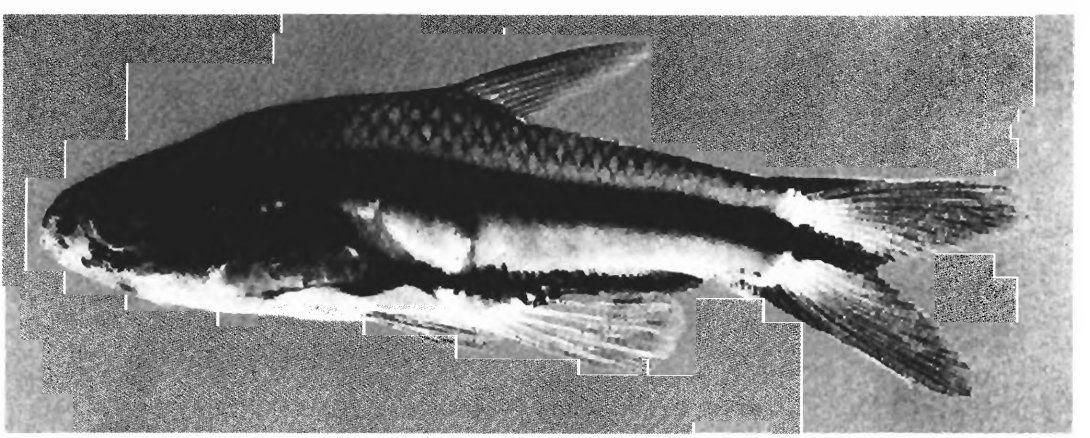


**Fig. 31.** *Spintherobolus ankoscion*, USNM 297936, adult male, SL uncertain. Brazil, Paraná, southwest of Paranaguá.

**Table 3.** Morphometrics of *Spintherobolus ankoseion*. Table includes measurements of all type specimens. Values for the holotype are given separately.

| | holotype | males | | | | females | | |
|---|---|---|---|---|---|---|---|---|
| | | n | low | high | mean | n | low | high | mean |
| Standard length [mm] | 23.1 | 7 | 18.8 | 23.1 | 21.5 | 16 | 13.0 | 27.9 | 23.4 |
| **Percentage of standard length** | | | | | | | | | |
| Snout to anal-fin origin | 62.3 | 7 | 61.3 | 63.9 | 62.6 | 16 | 60.0 | 63.5 | 62.0 |
| Snout to dorsal-fin origin | 56.3 | 7 | 53.2 | 57.8 | 55.6 | 16 | 53.2 | 59.0 | 55.8 |
| Snout to pelvic-fin origin | 48.9 | 7 | 41.3 | 48.9 | 44.6 | 16 | 40.4 | 45.4 | 42.9 |
| Dorsal-fin base length | 9.5 | 7 | 9.0 | 12.6 | 10.8 | 16 | 10.2 | 13.6 | 11.4 |
| Anal-fin base length | 21.7 | 7 | 21.3 | 23.8 | 22.0 | 16 | 20.7 | 26.5 | 22.9 |
| Caudal peduncle length | 15.1 | 7 | 16.5 | 19.1 | 17.2 | 16 | 13.4 | 17.7 | 16.3 |
| Caudal peduncle depth | 12.9 | 7 | 12.8 | 15.6 | 14.8 | 16 | 11.9 | 16.5 | 14.7 |
| Depth at dorsal-fin origin | 35.5 | 7 | 29.3 | 37.9 | 34.2 | 16 | 29.2 | 38.5 | 35.4 |
| Dorsal-fin length | 28.6 | 7 | 26.6 | 30.8 | 29.0 | 16 | 27.0 | 30.3 | 28.5 |
| Pelvic-fin length | 19.1 | 7 | 18.5 | 21.8 | 19.9 | 16 | 13.4 | 19.9 | 17.8 |
| Pectoral-fin length | 20.8 | 6 | 18.2 | 20.8 | 19.0 | 16 | 13.9 | 19.7 | 17.5 |
| Bony head length | 28.6 | 6 | 28.4 | 30.1 | 29.1 | 16 | 27.2 | 31.5 | 28.8 |
| **Percentage of head length** | | | | | | | | | |
| Snout length | 19.7 | 6 | 19.0 | 24.2 | 21.0 | 16 | 17.5 | 23.4 | 21.1 |
| Upper jaw length | 15.5 | 6 | 15.2 | 20.0 | 18.4 | 16 | 14.8 | 21.9 | 18.5 |
| Horizontal eye diameter | 5.8 | 6 | 24.6 | 27.4 | 26.2 | 16 | 25.0 | 31.0 | 28.2 |
| Least interorbital width | 28.8 | 6 | 27.0 | 30.0 | 28.3 | 16 | 24.7 | 29.9 | 26.7 |

two to four, each inserted between lepidotrichia of next anterior ray. Each bony ray segment of posterior branch of branched rays 2 to 4, and sometimes also rays 1 and 5, not squarish like other branches of same ray, but with the posteroventral angle acute and elongated to distal tip of that fin ray. Segments of branched fin rays 2 to 4 are progressively fused to each other.

Pectoral-fin rays i,8 (branched rays 7-11, $\bar{x}$ = 8.9). Posterior tip of longest pectoral-fin ray extends posterior to pelvic-fin origin in both males and females. Pelvic-fin rays i,5. Tip of largest ray reaching posteriorly beyond anal-fin origin in males, but not reaching that point in females. Pelvic fin of males bearing hooks on ventromedial face of unbranched ray and three (rarely two) following branched rays. Hooks present along their entire length, except for third branched ray which has hooks, when present, along only half this ray's length. Two hooks present on each ray segment, only on medialmost branch.

Principal caudal-fin ray count 10/9. Dorsal procurrent caudal-fin rays 11 (9-11, $\bar{x}$ = 10.0, n = 22). Ventral procurrent caudal-fin rays, 12 (12-16, $\bar{x}$ = 14.0, n = 22). Ventral procurrent caudal-fin rays of males large, with their proximal tips fused, slab shaped and expanded in sagittal plane. Four to five terminal caudal (preural) vertebrae (including posterior half centrum) support caudal-fin rays and ventral procurrent rays, with enlarged and modified hemal spines. Those ventral procurrent rays anterior to hemal spine of antepenultimate vertebra fused to each other and with lateral bony processes between muscles and skin. Anteriormost ventral procurrent rays with proximal tips absent.

Scales cycloid. Lateral line with 4 perforated scales (4-5, $\bar{x}$ = 4, n = 22). Scales in lateral series, 33 (31-33, $\bar{x}$ = 31.8, n = 19; Fig. 22). Scale rows between dorsal-fin origin and lateral-line series 5 (5-6, $\bar{x}$ = 5.5, n = 21), and between lateral line and pelvic-fin origin 6 (4-6, $\bar{x}$ = 5.3, n = 21). Scale rows around caudal peduncle 14 (n = 19). No modified scales on caudal fin. Scale sheath along anal-fin base absent.

Teeth. All jaw teeth with a basal pedicle and somewhat laterally expanded distal conical cusp. Anterior dentary teeth tricuspid, but each with single cusp laterally and posteriorly. Premaxillary and maxillary teeth all conical. Premaxillary teeth 8, maxillary teeth 5-6 and dentary teeth 12-13 in two c&s specimens.

Vertebrae. 32 (32-33, $\bar{x}$ = 32.2, n = 19; Fig. 21). Branchiostegal rays 4 in two cleared and stained specimens. Arranged as in *S. papilliferus*.

**Color in alcohol.** See Figures 29-30 for the preserved color patterns adult males and females which are approximately the same and very close to that of *S. broccae*. A discrete lateral body stripe extends from just dorsal to the dorsalmost part of the gill opening to the caudal peduncle where it continues onto the caudal fin as a solid dark wedge with its apex covering the two middle caudal-fin rays. In the photographs of a male and female, there appears to be a dark humeral spot just posterior to the more dorsal region of the opercular flap. This is the area of the anterior and posterior pseudotympanums and the black pigment coating the swimbladder can be seen through the skin. The dark chromatophores of the lateral stripe occur in this area but they are not increased in size or number and do not form a humeral spot.

The scale borders are covered by a double or, in some areas a triple row of dark chromatophores above the lateral stripe, giving the dorsal part of the body a reticulate pattern. The median scale row along the back from the nape to the caudal fin is very dark, nearly black, and the scales do not have pale centers as they do in most of the dorsal body region. The abdomen and sides ventral to the lateral stripe are pale cream color or yellowish (the color of preserved muscle tissue) and the scale borders of one or two horizontal scale rows just ventral to the lateral stripe have dark chromatophores in one or two rows. The posterior termination of the caudal peduncle, both dorsal and ventral to the lateral stripe, is white, without dark pigment of any kind.

The pectoral and pelvic fins of both sexes are hyaline with a few scattered dark chromatophores, especially on the anterior undivided ray of both fins. The dorsal fin is mostly hyaline except for its anterior dorsal border where the anterior undivided rays and the first branched ray have numerous dark chromatophores. The rays posterior to these dark rays progressively lose the dark chromatophores. The caudal fin is hyaline with a thin scattering of small dark chromatophores over the rays and membranes, especially those of the dorsal parts of the dorsal lobe of the male. A second dark, relatively broad stripe covers some of the muscular mid-base of the fin and extends posteriorly to completely cover the short anal-fin rays that follow the large, elongate, anterior anal-fin lobe. The anterior lobe of the fin, distal to its muscular base, is hyaline except for the unbranched rays.

The head is pale brown around the mouth with a scattering of dark chromatophores over the ventral surface of the snout, jaws, and opercular region. In the photographs (Figs. 29-30), the snout region, especially the jaws, is somewhat overexposed and the dark chromatophores do not show well. The dorsal surface of the snout and the area between the eyes are pale brown, while the dorsum of the cranium and the nape are dark brown. The head area posterior to the eye and extending ventrally from the parietal region to the preopercle and branchiostegal rays is white. The circumorbital region ventral to the eye is dark, with a series of dark chromatophores, giving producing dark spot ventral to the eye. The opercular region is dark dorsally and pale brown to white ventrally in both sexes.

**Color in life.** See Figure 31 of a male photographed immediately after capture. Life colors are very much like those in preservative except that the dark stripes are black, the abdominal region bluish white and the two white spots at the posterior termination of the caudal peduncle are intense white with very pale orange just anterior to them. The distal half of the caudal-fin rays are greenish brown to almost pale orange. The dorsal fin bears the same colors. The pelvic and pectoral fins are hyaline except for the anterior unbranched rays which are darkened with the black chromatophores. The procurrent rays are black, at least in the male. The dorsal surface of the snout and head is dark brown to black, except for the nares which are translucent much like most of the body lacking black pigment.

**Sexual dimorphism.** Males and females can be externally recognized by the anal-fin shape; compare Figures 29 and 30. The distal profile of this fin is deeply concave with the anterior lobe comparatively acutely angled in females. In males the anterior lobe is rounded in profile and the distal border of this lobe extends further posteriorly than in females. Not all males have hooks on the anal fin but all have hooks on the pelvic-fin rays and large branched anal-fin rays 1 to 5. Males have a keel along ventral profile of caudal peduncle, formed by the ventral procurrent caudal-fin rays.

**Etymology.** The name *ankoseion* is from the Greek ankos, a mountain valley or glen and eïon, a beach and is given in reference to the fact that

**Fig. 32.** *Spintherobolus broccae*, USNM 287324, adult male 18.9 mm SL, Brazil, Rio de Janeiro, Cachoeira de Macacu.
**Fig. 33.** *Spintherobolus broccae*, USNM 287324, adult female 20.8 mm SL, Brazil, Rio de Janeiro, Cachoeira de Macacu.

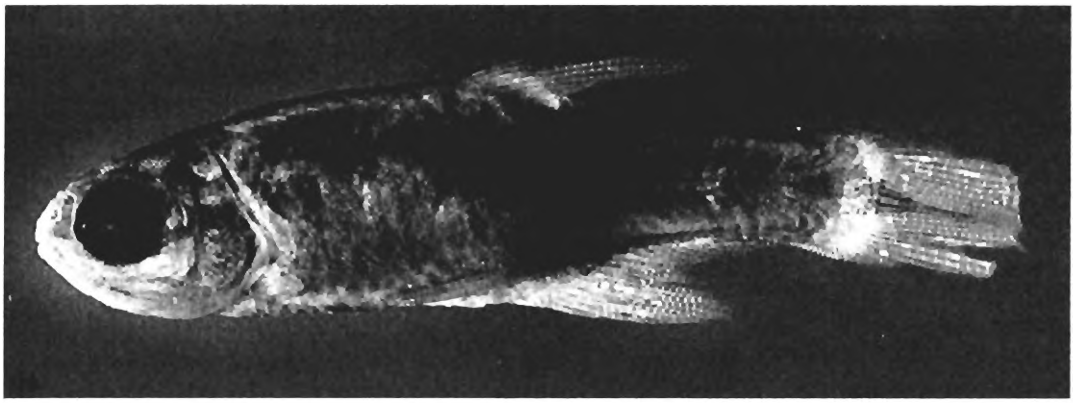
this species lives between the coastal mountains and the sea. A noun in apposition.

**Ecological notes.** This species, like the others in subgroup b, lives in the lower elevations of coastal blackwater streams that drain the surrounding forests.

### *Spintherobolus broccae* Myers
(Figs. 2, 32-35)

*Spintherobolus broccae* Myers, 1925: 143, 2 figs. (new species description, type locality: hills behind Rio de Janeiro, holotype: CM 7979a (now FMNH 58863), one paratype: CM 7980a, five additional spms in author's collection, # 56, three of these are USNM 92959, but 1 spm missing; see also CAS-SU 24073 below)

**Specimens examined.** USNM 92959, 2 males, paratypes, 20.0-20.3 mm SL; near Rio de Janeiro (city), Rio de Janeiro, Brazil; 1924, R. Brocca. – CAS-SU 24073, 1 male, 20.3 m SL; paratype; Brazil, Rio de Janeiro, near Rio de Janeiro; 1924; R. Brocca & Salathe, 1924. – USNM 342062, 1 male, 19.2 mm SL, 3 females, 21.5-22.1 mm SL; 5 km East of Sampaio Correa, Saquarema; 27 Nov 1979, C. Cruz, S. Weitzman et al. – USNM 287324, 1 male, c&s, 18.2 mm SL, 2 females, c&s 18.3-19.0 mm SL; 13 males, 17.1-18.9 mm SL, 27 females, 17.5-20.9 mm SL; MCP 19196, 4 males, 17.5-17.9 mm SL, 3 females, 17.4-18.9 mm SL; rio Macacu, near town of Cachoeiras de Macacu,



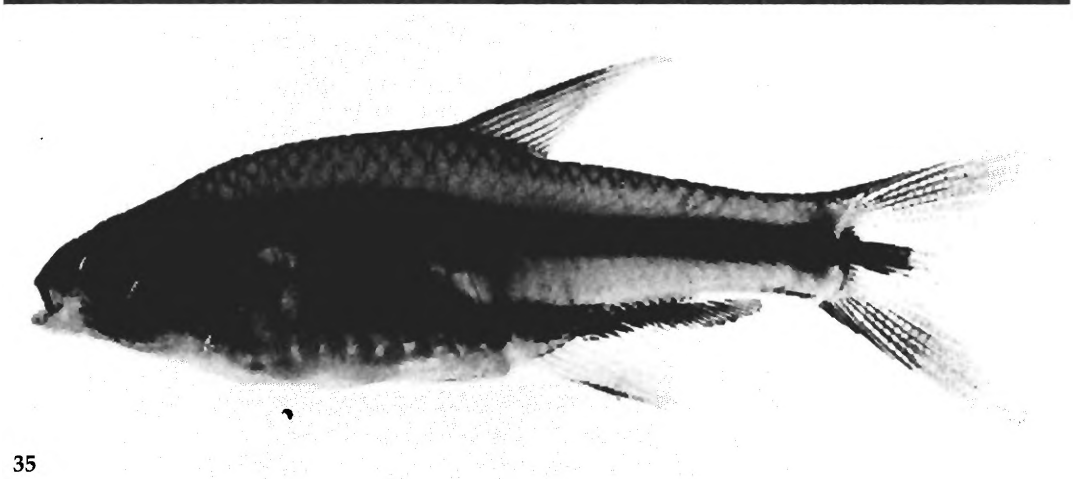


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**Fig. 34.** *Spintherobolus broccae,* USNM 92959, paratype, adult male 20.3 mm SL, Brazil, vicinity of Rio de Janeiro.
**Fig. 35.** *Spintherobolus broccae,* USNM 297997, adult female, SL uncertain, Brazil, São Paulo, Bertioga.

small tributary about 1-2 km from town, highway bridge over stream; 27 Nov 1979, C. Cruz, S. Weitzman et al. – MNRJ 8796, 3 males, 18.1-18.4 mm SL, 3 females, 18.0-18.5 mm SL, 6 immature, 13.6-17.4 mm SL; swamp or marshy area near Imbarié, Baixada Fluminense; 4 Aug 1954, L. Travassos et al. – MNRJ 6264, 62, adults + immature, 14.6-18.8 mm SL; old road to Petrópolis, about 1-2 km from new road to Petrópolis, Raiz da Serra, Rio de Janeiro; 28 Sep 1942, L. Travassos et al. – USNM 342064, 13 males, 18.6-22.4 mm SL, 10 females, 20.1-22.9 mm SL, 1 (c&s), 19.4 mm SL; Estacion Ecologia, Universidade Federal Rural do Rio de Janeiro, at km 43 on the road from Rio de Janeiro to São Paulo; 15 Dec 1972, E. Izecksohn et al. – USNM 297997, 3 females, 20.8-25.6 mm SL, 21 young males, 16.4-18.8 mm SL, 214 immature, 13.0-20.1 mm SL; unnamed clear water stream crossing road SP-98 at km 94, northwest of Bertioga; 23 Feb 1988, R. M. C. Castro.

**Diagnosis.** This miniature species lacks infraorbital bone 3. The other miniature species, *S. ankoseion* and *S. leptoura*, as well as the non-miniature *S. papilliferus* have the third infraorbital bone well ossified and, in addition, have significantly lower anal-fin ray counts (Fig. 20) and ventral procurrent caudal-fin ray counts (Fig. 23). Although statistically significant, there is overlap in these counts (see counts given below), especially in the ventral procurrent caudal-fin ray count, and species determination using these counts must be made by examining population samples, not in-

**Table 4.** Morphometrics of *Spintherobolus broccae*. Table includes measurements of specimens from USNM 287324 USNM 342062, USNM 342064 and MCP 19196.

| | males | | | | females | | | |
|---|---|---|---|---|---|---|---|---|
| | n | low | high | mean | n | low | high | mean |
| Standard length [mm] | 31 | 17.1 | 22.4 | 18.8 | 40 | 17.5 | 22.9 | 19.8 |
| **Percentage of standard length** | | | | | | | | |
| Snout to anal-fin origin | 31 | 55.9 | 61.5 | 59.7 | 40 | 57.8 | 63.9 | 60.5 |
| Snout to dorsal-fin origin | 31 | 51.3 | 59.5 | 56.2 | 40 | 52.6 | 60.6 | 55.7 |
| Snout to pelvic-fin origin | 31 | 36.2 | 44.7 | 42.2 | 40 | 39.8 | 44.7 | 42.1 |
| Dorsal-fin base length | 31 | 9.0 | 14.0 | 10.8 | 40 | 9.1 | 12.0 | 11.0 |
| Anal-fin base length | 31 | 18.8 | 26.7 | 23.4 | 40 | 19.9 | 26.5 | 23.7 |
| Caudal peduncle length | 31 | 12.4 | 19.1 | 15.7 | 40 | 13.1 | 17.7 | 15.4 |
| Caudal peduncle depth | 31 | 12.6 | 15.1 | 13.8 | 40 | 11.2 | 14.9 | 13.1 |
| Depth at dorsal-fin origin | 31 | 29.2 | 32.8 | 30.5 | 40 | 28.1 | 35.1 | 30.8 |
| Dorsal-fin length | 31 | 22.4 | 29.9 | 26.9 | 39 | 22.1 | 30.3 | 26.1 |
| Pelvic-fin length | 31 | 16.4 | 20.7 | 18.4 | 38 | 13.5 | 19.5 | 16.9 |
| Pectoral-fin length | 29 | 15.2 | 18.7 | 16.9 | 38 | 12.9 | 18.3 | 15.6 |
| Bony head length | 31 | 25.4 | 30.4 | 28.6 | 38 | 25.6 | 30.3 | 28.3 |
| **Percentage of head length** | | | | | | | | |
| Snout length | 31 | 17.0 | 23.6 | 20.3 | 39 | 17.6 | 21.8 | 19.9 |
| Upper jaw length | 31 | 17.3 | 23.6 | 21.0 | 39 | 17.2 | 25.0 | 21.6 |
| Horizontal eye diameter | 31 | 26.3 | 32.7 | 29.1 | 33 | 24.5 | 32.1 | 28.3 |
| Least interorbital width | 31 | 26.8 | 34.6 | 29.7 | 33 | 25.0 | 30.8 | 28.1 |

dividual specimens. However, specimens bearing overlapping anal-fin ray counts are uncommon.

(18, state 2) Infraorbital 3 absent. This is an autapomorphy for *S. broccae*. See apomorphy 18 for a discussion of infraorbital loss in species of *Spintherobolus*.

The anal-fin ray count for *S. broccae* is 13-16, $\bar{x}$ = 14.1 versus 11-14, 12.6 for both *S. ankoseion* and *S. leptoura*. The ventral procurrent caudal-fin ray count for *S. broccae* is 14-17, $\bar{x}$ = 15.4, versus 12-16, $\bar{x}$ = 14.0 for *S. ankoseion* and 13-15, $\bar{x}$ = 14.1 for *S. leptoura*. These relatively high counts for *S. broccae* relative to all other species of *Spintherobolus* appears autapomorphic for this species.

**Description.** Morphometric data are summarized in Table 4. Body compressed, moderately elongate. Predorsal body profile slightly convex. Body profile along dorsal-fin base posteroventrally inclined, becoming straight or slightly convex between dorsal and caudal fins in females and nearly straight to slightly convex in males. Ventral profile convex from anterior tip of mandible to pelvic-fin origin. Belly profile slightly convex between pelvic-fin and anal-fin origin in females, slightly concave in males. Body profile along anal-fin base concave in females; slightly convex at anterior anal-fin lobe of males and concave along posterior short finned section Ventral profile of caudal peduncle concave ir females. Keel formed by prominent ventral pro current caudal-fin rays of males makes ventra profile of caudal peduncle nearly straight bu inclined ventrally in a posterior direction.

Snout short, shorter than eye diameter. Mouth terminal, gape angled posteroventrally; maxilla short, not reaching line drawn vertically through anterior margin of eye.

Dorsal-fin rays, ii,8-9 ($\bar{x}$ = 8.9, n = 28). Dorsal fin origin behind midbody. Adipose fin absent.

Anal-fin rays iii-iv,13-16 (unbranched rays $\bar{x}$ = 3.1, n = 88; branched rays $\bar{x}$ = 14.1, n = 90) Anterior lobe of anal fin of males rounded, long er than posterior lobe, concave. Anal fin in fe males deeply concave, decreasing in size from posterior unbranched ray to sixth branched ray following rays all of equal size. Anal-fin origin a vertical line drawn through origin of most poste rior dorsal-fin ray in females and at vertical line drawn through middle of dorsal-fin base in males Hooks in anal-fin rays rare among examined males. When present, hooks much reduced in size, found on posterior face of two to six bony segments of posterior branch of first and some times second branched rays. When present, each ray segment bears two to three hooks on each

side. Anal-fin rays one through five in males large, second to fourth branched rays more than five times thicker in sagittal dimension than following rays. These large rays with a process on anteroproximal face of each lepidotrich, these being projections of rays two through four, each inserted between lepidotrichia of next anterior ray. Each bony ray segment of posterior branch of branched rays two through four and sometimes also the first and fifth rays, not relatively square like other branches of same ray, but with their posteroventral angle acute and elongate, angled towards distal tip of that fin ray. Segments of branched fin rays two and four progressively fused to each other.

Pectoral-fin rays i,8-10 ($\bar{x}$ = 8.6, n = 36). Posterior tip of longest pectoral-fin rays extending beyond pelvic-fin origin in both males and females. Pelvic-fin rays i,5 in all counted specimens (n = 36). Tip of largest ray reaching to or beyond anal-fin origin of males, but not reaching that fin in females. Pelvic-fin rays of males with hooks on unbranched ray and 2 or 3 branched rays, 2 each bone segment. Hooks on ventromedial face and along all length of unbranched to second branched ray and along half length of third branched ray.

Principal caudal-fin rays count usually 10/9 (one specimen 10/10 and one specimen 9/9, n = 85). Dorsal procurrent caudal-fin rays 9-13 ($\bar{x}$ = 11.0, n = 86). Ventral procurrent caudal-fin rays 14-17 ($\bar{x}$ = 15.4, n = 89). Ventral procurrent caudal-fin rays of males large, well-developed, with their proximal tips fused, slab shaped and expanded in sagittal plane. Four to five most posterior caudal vertebrae (including posterior 'half centrum') supporting principal caudal-fin rays and procurrent rays, with enlarged and modified hemal spines. Those elements anterior to the hemal spine of antepenultimate vertebra fused to each other and with lateral bony projections between muscles and skin. Anteriormost ventral caudal procurrent rays with proximal tips absent or abbreviated in length.

Scales cycloid. Lateral line with 2-4 perforated scales ($\bar{x}$ = 3.4, n = 34). Scales in a lateral series, 31-33 ($\bar{x}$ = 31.8, n = 23). Scale rows between dorsal-fin origin and lateral-line series, 4-6 ($\bar{x}$ = 5.0, n = 31), and between lateral line and pelvic-fin origin, 4-5 ($\bar{x}$ = 4.7, n = 31). Scale rows around caudal peduncle, 14 in all specimens (n = 31). No modified scales on caudal fin. Scale sheath along anal-fin base absent.

Teeth. All jaw teeth with a basal pedicle and laterally expanded conical distal tip. Anteriormost dentary teeth tricuspid followed lateroposteriorly by conical teeth. Premaxillary and maxillary teeth conical. Premaxillary teeth 5-7, maxillary teeth 5-8 and dentary teeth 5-8 in four c&s specimens.

Vertebrae 32-34 ($\bar{x}$ = 33.0, n = 88). Branchiostegal rays 4 in four cleared and stained specimens, with same attachments as in *S. papilliferus*.

**Color in alcohol.** See Figure 2, 32-33 for the approximately equivalent preserved color patterns of adult males and females. A discrete lateral body stripe extends from just dorsal to the dorsalmost part of the gill opening to the caudal peduncle where it continues onto the caudal fin as a very solid dark wedge with its apex covering the two middle caudal-fin rays. In the photographs of a male and female, there appears to be a dark humeral spot just posterior to the more dorsal region of the opercular flap. This is not a humeral spot. Instead it is the area of the anterior and posterior pseudotympanums and the black pigment coating the swimbladder is visible through the skin.

The scale borders are covered by a single row of dark chromatophores above the lateral stripe, giving the dorsal part of the body a reticulate pattern. The abdomen and sides ventral to the lateral stripe is pale cream color or yellowish (the color of preserved muscle tissue) and the scale borders are devoid of dark chromatophores. The posterior termination of the caudal peduncle, both dorsal and ventral to the lateral stripe, is white, without dark pigment of any kind.

The pectoral and pelvic fins of both sexes are hyaline with a few scattered dark chromatophores, especially on the anterior undivided ray of both fins. The dorsal fin is mostly hyaline except for its anterior dorsal border where the anterior undivided rays and the first branched ray have numerous dark chromatophores. The rays posterior to these dark rays progressively lose the dark chromatophores except distally where the posterior tip of the second and often the third branched rays have many dark chromatophores. The caudal fin is hyaline with a thin scattering of small dark chromatophores over the rays and membranes, especially those of the dorsal parts of the dorsal lobe of the male. The anterior base of the anal-fin is the origin of a second dark, relatively broad stripe which cov-

ers the muscular anterior base of the fin and extends posteriorly to almost completely cover the short anal-fin rays that follow the large, elongate, anterior anal-fin lobe. The anterior lobe of the fin, distal to its muscular base, is hyaline except for the distal tip of the first branched ray.

The head is pale brown around the mouth with a scattering of dark chromatophores over the ventral surface of the snout, jaws, and opercular region. In the photographs (Figs. 2, 4, 32-33), the snout region, especially the ventral part of the jaws, is overexposed and the dark chromatophores do not show. The dorsal surface of the snout and the area between the eyes are pale brown, while the dorsum of the cranium and the nape are dark brown. The head area posterior to the eye and extending ventrally from the parietal region to the preopercle and branchiostegal rays is white. The circumorbital region ventral to the eye is dark, with a series of dark chromatophores, giving the impression of a spot ventral to the eye. The opercular region is dark dorsally and pale brown to white below in both sexes.

**Color in life.** See Figure 35 of a female, taken immediately after capture, from near Bertioga, São Paulo. Life colors are very much like those in preservative except that the dark stripes are black, the abdominal region bluish white and the two white spots at the posterior termination of the caudal peduncle are yellowish to white. The body is translucent greenish yellow. The black chromatophores anterior, dorsal and posterior to the pseudotympanums are expanded and the area they occupy is black; those posterior to this are somewhat contracted and the lateral stripe remains less dense until approximately the anterior end of the caudal peduncle where the black chromatophores are again expanded and the stripe appears black. The black spot ventral to the eye is quite dark with expanded black chromatophores. The premaxilla and maxilla are black. The dentary is white except for scattered black chromatophores in its anterior region. The relatively hyaline regions of the caudal fins are pale reddish and a bit of this color also occurs on the anterior two branched rays of the anal fin.

**Sexual dimorphism.** Males and females can be recognized externally by the anal fin-shape; compare Figures 32 and 33. The anal fin of the females is deeply concave and divided into a prominent anterior lobe that has a rather straight posterodistal border and a narrow posterior lobe made up of relatively short fin rays. The anal fin of males is very similar except the anterior lobe has a rounded or circular posterior border. Not all males have hooks on the anal fin but all of them have hooks on the pelvic-fin rays and anal-fin rays one through five enlarged. Males have a keel in the ventral profile of the caudal peduncle. This is formed by the ventral procurrent fin rays. The ventral procurrent rays of female are unmodified.

**Discussion.** *Spintherobolus broccae* was described as a new species by Myers (1925:143) from aquarium specimens and the species was previously misidentified as *Hasemania bilineata* Ellis (1911: 1950) by Rachow (1924: 601). Meinken (1929a-b) provided the history of the species discovery and importation. Myers (1925: 144) considered *S. broccae* and *Phoxinopsis typicus* Regan (1907: 262) possibly generically the same and Myers (1926: 273) was apparently convinced of this for, he listed the species as *P. broccae* in his list of tropical fish names published by Innes. However, he had not seen Regan's type of *P. typicus* and the illustrations of the two species, Regan (1907: 262) and Myers (1925: 144, pl. 10), although not exactly the same, look similar enough so that the distinctness of the species was justifiably questionable, especially since Regan's drawing was a hasty sketch. It wasn't until Innes (1935: 130), on the advice of G. S. Myers, listed the species as *P. typicus*, that *S. broccae* came to be considered a junior synonym of *P. typicus*. Nearly all subsequent aquarium fish literature considered the species to be *P. typicus*.

Travassos (1953: 512) recognized the species as *S. broccae*. Böhlke (1954: 30-31) tentatively recognized *P. typicus* and *S. broccae* as distinct species and he included these two nominal species and *S. papilliferus* in *Phoxinopsis*. His reasons for doing this were based on information received from G. S. Myers sometime before 1953. According to Böhlke, "Prof. G. S. Myers a number of years ago sent a paratype of his *Spintherobolus broccae* to the late J.R. Norman of the British Museum (Natural History) for comparison with Regan's type of *Phoxinopsis typicus*. Dr. Myers has informed me that after a point by point comparison of the two specimens (including the teeth, which are very important characters) Norman concluded that they were specifically identical". Myers must have sent a paratype to Norman

soon after publication of the original description because the catalog number of the specimen is BMNH 1925.10.19.1 (Eschmeyer & Ferraris, pers. comm.). This is corroborated by Myers (1926: 273) wherein he used the generic name *Phoxinopsis* rather than *Spintherobolus*.

In 1973 Böhlke wrote to SHW that he examined the type of *P. typicus* and found it to be an *Aphyocharax* Günther, 1868. Later the holotype of *P. typicus* was borrowed by SHW and identified as *Aphyocharax anisitsi* Eigenmann & Kennedy (1903: 517). Thus *S. broccae* is not a junior synonym of *P. typicus*, but *P. typicus* is a junior synonym of *A. anisitsi* and *Phoxinopsis* is a junior synonym of *Aphyocharax*.

*Spintherobolus broccae* and *A. anisitsi* are very different fishes and it is difficult to understand how Norman confused the two. If young specimens of *A. anisitsi* are compared with comparable sized adult female specimens of *S. broccae*, about 18-20 mm in SL, they appear somewhat similar in body shape and fin position, but not in color and certainly not in their teeth and mouth shapes. The three paratypes we have seen of *S. broccae* (USNM 92959, CAS 24073) are now faded and have lost their dark markings. If they had lost these when Norman examined his specimen, the type of *P. typicus* and the paratype of *S. broccae* would have had no striking color pattern differences. Although both species have relatively elongate and somewhat similar jaw teeth, those of *S. broccae* are more slender. Furthermore the gape of *S. broccae* is wide and the toothed portions of the dentary and the premaxilla extend laterally almost at right angles to the long axis of the head and body. In *A. anisitsi* the mouth opening is narrow, the snout conical, and the toothed portions of the premaxillae and dentaries are curved posteriorly.

Sarraf (1997: 28) recorded the principal caudal-fin ray count as i,18,i. This produces a principal ray count of 20 rather than 19. Yet when we counted the principal caudal-fin rays in figure 8 of Saraaf (1997) we counted 10/9 which is equivalent to nearly all of the counts given above in our description of *S. broccae* and would be i,17,i for a total 19 in Sarraf's method of counting. The dorsal-fin ray count was recorded ii,8 by Sarraf (1997: 28). We found the number to be ii,9 in most specimens, and found ii,8 as an unusual count ($\bar{x}$ = 8.9, n = 28).

**Ecological notes.** Myers (1944: 186) reported specimens from "behind the beach of Sernambetiba" to live in dark-brown swamp waters. SHW has taken this species (USNM 287324, MCP 19196) in somewhat brown acid waters of a stream in the forests surrounding the town of Cachoeiras de Macacu, Rio de Janeiro and from clear waters of a stream draining into lagoa Saquarema (USNM 34206). The area around lagoa Saquarema was at one time at least partly forested, but this is no longer true. Nevertheless, *S. broccae* has survived in the region. The species appears to be present in somewhat acid waters in relatively lowland areas, in both swamps and slow moving streams, to the north and south of the city of Rio de Janeiro, but only in areas where the streams remain unpolluted.

### *Spintherobolus leptoura*, new species
(Figs. 36-37)

**Holotype.** MZUSP 41854, male, 19.1 mm SL; rio Quilombo, fazenda Dalila, Registro, São Paulo, Brazil; 16 Feb 1990, M. Damato & O. Oyakawa.

**Paratypes.** MZUSP 51023, 2 males, 17.2-19.6 mm SL, 7 immature – females, 16.2-27.2 mm SL, 1 male, c&s, 19.9 mm SL, 1 female, c&s, 25.2 mm SL; USNM 346386, 1 male, 21.8 mm SL, 2 immature – females, 16.2-25.0 mm SL; MCP 19254, 1 male, 18.9 mm SL; 2 immature – females, 16.6-25.4 mm SL; collected with holotype.

**Diagnosis.** Most elongate and slender species, adult males differing from other small species by caudal peduncle depth and body depth (Figs. 24, 25, 38). Body depth in *S. leptoura* 26.6-29.7, $\bar{x}$ = 28.3 % SL, versus 29.3-37.9, $\bar{x}$ = 34.2 in *S. ankoseion* (Fig. 24), and 29.2-32.8, $\bar{x}$ = 30.5 in *S. broccae*. Caudal peduncle depth in *S. leptoura* 11.0-13.1, $\bar{x}$ = 12.3 % SL, versus 12.8-15.6, $\bar{x}$ = 14.8 in *S. ankoseion*, and 12.6-15.1, $\bar{x}$ = 13.8 in *S. broccae*. Although these ratios overlap in juveniles, they do not in adult males and females as demonstrated by Figures 24 and 25.

**Description.** Morphometric data are summarized in Table 5. Body compressed and relatively elongate. Predorsal body profile slightly convex with a slight concavity at nape. Body profile along dorsal-fin base posteroventrally inclined becoming straight or slightly concave between dorsal

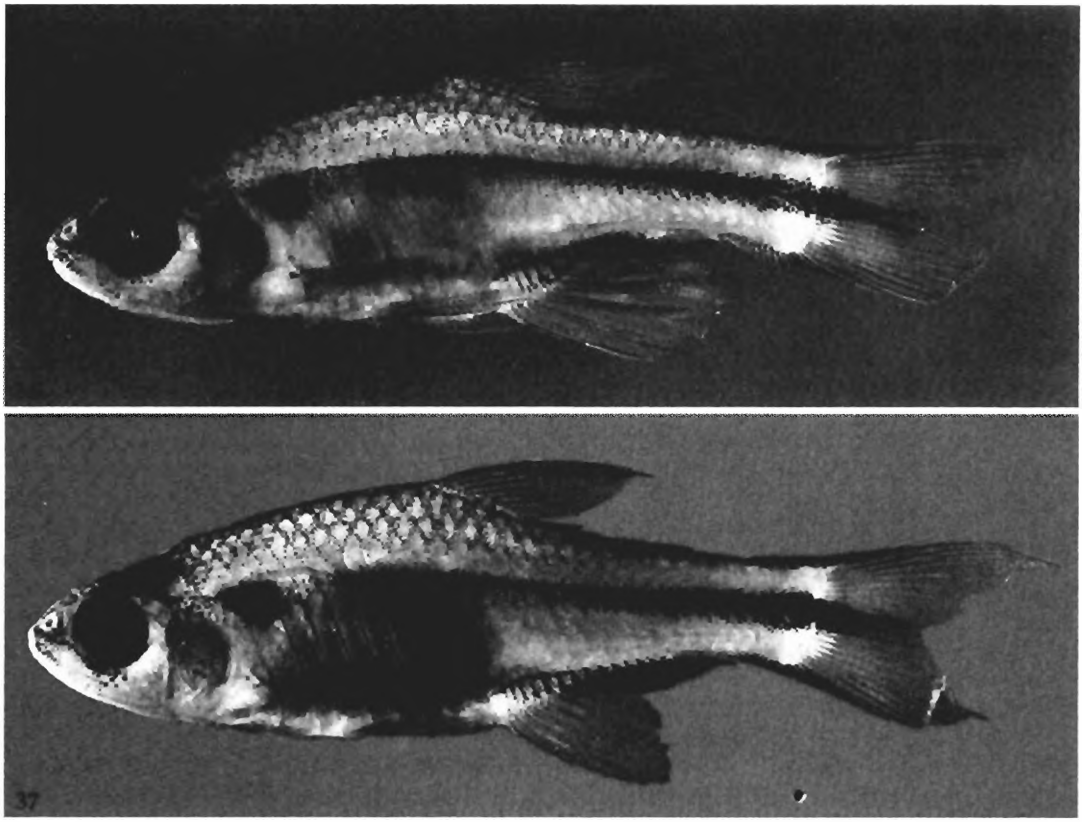

**Fig. 36.** *Spintherobolus leptoura*, MZUSP 41854, holotype, adult male 19.1 mm SL, Brazil, São Paulo, fazenda Dalila, Registro.
**Fig. 37.** *Spintherobolus leptoura*, MZUSP 41854, paratype, adult female 25.0 mm SL, Brazil, São Paulo, fazenda Dalila, Registro.

and caudal fins in females and nearly straight to slightly convex in males. Ventral profile from tip of mandible to pelvic-fin origin convex and slightly concave between pelvic- and anal-fin origins. Entire body profile along anal-fin base concave in females. This same profile convex in anterior anal-fin lobe of males. Remaining posterior anal-fin body profile nearly straight and continuous with straight or nearly straight caudal peduncle profile. Ventral profile of caudal peduncle somewhat concave in females, but straight and slightly serrated in males because of prominent ventral procurrent caudal-fin rays.

Snout short, shorter than eye diameter. Mouth terminal, angled posteroventrally; maxilla reaching line drawn vertically through anterior margin of eye.

Dorsal-fin rays, ii,9 in all specimens. Dorsal-fin origin slightly posterior to midbody. Adipose fin absent.

Anal-fin rays iii,14 (anterior unbranched rays iii-iv, $\bar{x} = 3.1$, n = 16; branched anal-fin rays 12-14, $\bar{x} = 12.6$, n = 16). Anterior lobe of anal fin of males strongly developed, rounded profile. Distal tip of longest (and largest) rays reaching posteriorly beyond distal tip of most posterior anal-fin rays. Distal profile of posterior anal-fin lobe concave. Distal profile of entire anal fin in females concave, with length of first 6 branched rays decreasing in size and posterior rays smaller, nearly of equal size. Branched anal-fin rays 1-5 of males very large, and rays 2 to 4 most enlarged and best developed, becoming more than 5 times wider than following posterior rays. Rays 2-4 with a process on anteroproximal face of each

lepidotrich. Processes inserted between lepidotrichia of next anterior ray. Each bony ray segment of posterior branch of branched rays 2 to 4, and sometimes also first and fifth branched rays, not rectangular as other branches of same ray, but all with a posteroventral acute and elongate angle extending towards distal tip of that fin ray. Segments of branched fin rays 2 to 4 progressively fused to each other. Holotype only specimen with hooks. These on two segments of first branched ray. Hooks extremely reduced, with 2 or 3 hooks on posterior face of both segments.

Pectoral-fin rays i,9 (branched rays 8-11, $\bar{x}$ = 8.9, n = 14). Posterior tip of longest pectoral-fin ray extended beyond pelvic-fin origin in both males and females. Pelvic-fin rays, i,5 in all counted specimens (n = 18). Tip of longest ray reaching to or beyond anal-fin origin in both sexes. Pelvic fin of males with short, wide-based hooks on ventromedial face of unbranched ray and first two branched rays (one male had them on first to third branched rays) along almost their total length.

Principal caudal-fin ray count 10/9. Dorsal procurrent caudal-fin rays 9 (7-10, $\bar{x}$ = 8.8, n = 9). Ventral procurrent caudal-fin rays, 15 (13-15, $\bar{x}$ = 14.1, n = 10). Ventral procurrent caudal-fin rays of males strongly-developed, with their proximal tips fused, slab shaped, and expanded in a sagittal plane. Four or five posteriormost caudal (preural) vertebrae (including posterior half centrum) supporting caudal fin and procurrent rays

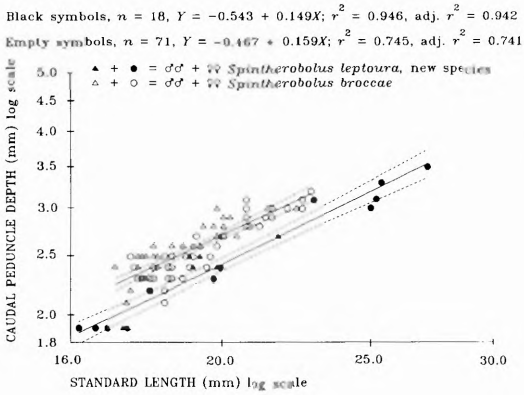


**Fig. 38.** Graph of caudal peduncle depth as a function of standard length of *Spintherobolus leptoura* (black symbols) and *S. broccae* (empty symbols). Axes are logarithmic. Note that the 95 % confidence intervals in lengths of about 18 to 24 mm SL do not overlap with the means of these of the compared species indicating a significant difference in these size ranges. Comparison of these growth patterns are discussed under the diagnosis of *S. leptoura*.

**Table 5.** Morphometrics of *Spintherobolus leptoura*. Table includes measurements of all type specimens. Values for the holotype are given separately.

| | holotype | males | | | | females | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | n | low | high | mean | n | low | high | mean |
| Standard length [mm] | 21.8 | 6 | 17.3 | 21.8 | 19.5 | 12 | 16.2 | 27.2 | 20.9 |
| **Percentage of standard length** | | | | | | | | | |
| Snout to anal-fin origin | 58.7 | 6 | 57.3 | 61.9 | 58.9 | 12 | 58.6 | 62.2 | 60.5 |
| Snout to dorsal-fin origin | 56.0 | 6 | 53.8 | 56.0 | 55.3 | 12 | 53.5 | 57.0 | 55.5 |
| Snout to pelvic-fin origin | 44.5 | 6 | 42.2 | 44.5 | 43.4 | 12 | 37.4 | 45.1 | 41.6 |
| Dorsal-fin base length | 11.3 | 6 | 11.3 | 12.5 | 11.7 | 12 | 9.6 | 12.9 | 11.5 |
| Anal-fin base length | 21.1 | 6 | 21.1 | 22.9 | 21.9 | 12 | 21.0 | 24.0 | 22.8 |
| Caudal peduncle length | 18.4 | 6 | 16.7 | 21.5 | 18.8 | 12 | 15.2 | 18.1 | 16.3 |
| Caudal peduncle depth | 12.4 | 6 | 11.0 | 13.1 | 12.3 | 12 | 9.5 | 13.5 | 11.8 |
| Depth at dorsal-fin origin | 27.5 | 6 | 26.6 | 29.7 | 28.3 | 12 | 26.6 | 33.7 | 29.9 |
| Dorsal-fin length | 25.7 | 6 | 22.5 | 28.6 | 26.4 | 12 | 23.0 | 29.4 | 26.2 |
| Pelvic-fin length | 20.2 | 6 | 17.8 | 20.2 | 18.8 | 12 | 14.2 | 19.0 | 17.0 |
| Pectoral-fin length | 17.9 | 5 | 15.6 | 17.9 | 16.9 | 10 | 14.6 | 19.0 | 16.3 |
| Bony head length | 28.9 | 6 | 28.9 | 30.4 | 29.3 | 12 | 26.1 | 30.2 | 28.2 |
| **Percentage of head length** | | | | | | | | | |
| Snout length | 19.5 | 6 | 19.0 | 22.4 | 19.9 | 12 | 18.9 | 23.2 | 20.9 |
| Upper jaw length | 19.5 | 6 | 19.0 | 21.4 | 19.9 | 12 | 18.4 | 22.9 | 21.0 |
| Horizontal eye diameter | 27.0 | 6 | 25.9 | 28.1 | 26.9 | 12 | 23.2 | 30.3 | 27.4 |
| Least interorbital width | 27.0 | 6 | 26.3 | 29.3 | 27.5 | 12 | 25.5 | 30.3 | 27.9 |

and bearing large, modified hemal spines. Those elements anterior to hemal spine of antepenultimate vertebra fused to each other and having lateral bony processes between muscles and skin. Proximal tips of anterior ventral procurrent rays undeveloped.

Scales cycloid. Lateral line with 4 perforated scales (n = 10). Scales in longitudinal series 33 (n = 3). Scale rows between dorsal-fin origin and lateral-line series 5 (n = 6), and between lateral-line series and pelvic-fin origin 5 (4-5, $\bar{x}$ = 4.5, n = 6). Scale rows around caudal peduncle 14 in all countable specimens (n = 2). No modified scales on caudal fin. Scale sheath along anal-fin base absent.

Teeth. All jaw teeth with basal pedicle and somewhat laterally expanded distal conical cusp. Anterior dentary teeth tricuspid but each with single cusp laterally and posteriorly. Premaxillary and maxillary teeth all conical. Premaxillary teeth 7-8, maxillary teeth 5-6 and dentary teeth 10-11 in 2 c&s specimens.

Vertebrae 33 (range = 32-34, $\bar{x}$ = 32.9, n = 16). Branchiostegal rays 4 in two cleared and stained specimens, arranged as in other species.

**Color in alcohol.** See Figures 36-37 for the approximate preserved and similar color patterns of adult males and females. A discrete lateral body stripe extends from just dorsal to the dorsalmost part of the gill opening to the caudal peduncle where it continues onto the caudal fin as a very solid dark wedge with its apex covering the two middle caudal-fin rays. The dark stripe consists of a dusting of dark chromatophores anterior to the pseudotympanum area and this continues posterior to this, merging with the dark lateral stripe that becomes dense with dark chromatophores external to the dorsal region of the abdomen. This stripe increases in width, and density posteriorly to the base of the caudal fin. In the photographs of a male and female (Fig. 36-37), there appears to be a dark humeral spot just posterior to the more dorsal region of the opercular flap. This is the area of the anterior and posterior pseudotympanums and the black pigment coating the swimbladder can be seen through the skin, appearing black in the print.

The scale borders above the lateral dark stripe are covered by a single row of dark chromatophores, giving the dorsal part of the body a reticulate pattern. Just ventral to the stripe the scale borders continue to be dark for about one to one half the width of a scale row. The belly and sides ventral to the lateral stripe are pale cream color or yellowish (the color of preserved muscle tissue) and the ventrolateral surface of the abdomen may be covered with dark chromatophores of varying density. The posterior termination of the caudal peduncle, both dorsal and ventral to the lateral stripe, is white, without dark pigment of any kind, except for the procurrent caudal-fin rays in this region which are covered with dark chromatophores.

The pectoral and pelvic fins of both sexes are hyaline with scattered dark chromatophores, especially on the anterior undivided ray of both fins. The dorsal fin is more or less hyaline except for its anterior dorsal border where the anterior undivided rays and the first and second branched rays have numerous dark chromatophores. The rays posterior to these dark rays progressively have fewer dark chromatophores distally. The caudal fin is hyaline, especially for the proximal one third of its length. There is a thin scattering of small dark chromatophores over the rays and membranes, especially along their distal length. A second longitudinal dark, but relatively broad stripe covers the muscular anterior base of the fin and extends posteriorly to almost completely cover the short anal-fin rays that follow the large, elongate, anterior anal-fin lobe. The anterior lobe of the anal fin, distal to its muscular base is hyaline except for the basal one third the distal tips of the anterior unbranched and the first two branched rays. These are covered with dark chromatophores.

The head is pale brown around the mouth with a scattering of dark chromatophores over the ventral surface of the snout, jaws, and opercular region. The snout region, especially the jaws possess a scattering of dark chromatophores. The dorsal surface of the snout and the area between the eyes are pale brown, while the dorsum of the cranium and the nape are dark brown. The head area posterior to the eye and extending ventrally from the parietal region to the preopercle and branchiostegal rays is white except for some dark chromatophores in the dorsal region of the opercle. The circumorbital region ventral to the eye is dark, with a series of dark chromatophores, giving the impression of a spot ventral to the eye when these chromatophores are expanded. The opercular region is dark dorsally and pale brown to white below in both sexes.

**Color in life.** Life colors have not been recorded, but we expect that life colors are very much like those in preservative except that the dark stripes are usually black, the abdominal region white and the two white areas at the posterior termination of the caudal peduncle are intense white.

**Sexual dimorphism.** The sexes are easily identified externally by the shape of anal fins (Figs. 36-37). The distal border of the anal fin of females is concave and the anterior lobe has an acute distal tip. When this lobe is depressed it does not reach the posterior termination of the fin. The anterior lobe of the anal fin of males is largely rounded, with the tip of largest rays reaching beyond the tip of last anal-fin rays. The shape of first to fifth branched anal-fin rays, the modified ventral procurrent caudal-fin rays and the presence of hooks in the pelvic fins are also characteristic for males.

**Etymology.** The word *leptoura* is from the Greek leptos meaning small, thin or delicate and oura, Greek for tail. The name is given in reference to the relatively slender caudal peduncle of this species. A noun in apposition.

**Ecological notes.** We have no ecological information about this species.

### Geographic distribution of *Spintherobolus*

The distribution of *Spintherobolus* remains something of an enigma. The three species of subgroup b are known to occur in freshwaters at relatively low elevations (below 100 meters), along the Atlantic coast, east of the Serra Geral formation in drainages of the Baixada Fluminense, i.e. the lowlands around and to the east and west of the Baia de Guanabara, Rio de Janeiro (*S. broccae*); the lowlands around Santos, São Paulo (again *S. broccae*); the lowlands around the rio Ribeira de Iguape, São Paulo (*S. leptoura*); and the lowlands around the Baia de Paranaguá, Paraná, southward to the lowlands surrounding Barra do Sai, northern Santa Catarina (*S. ankoseion*). The sister group of subgroup b, subgroup a, contains only one species, *S. papilliferus*, and is known only from the headwaters of the westward flowing rio Tietê, at elevations above 700 meters.

The phylogenetic biogeography of the fishes of the rio Tietê, other upper rio Paraná drainages and the coastal streams of the Atlantic forest region east of the Serra Geral remains essentially unknown (Weitzman et al., 1988). The fauna of these areas, especially that of the rio Tietê, was extensively compared by Langeani (1989) in an unpublished thesis. His discussion was based on faunal similarities and dissimilarities and he clearly recognized that the absence of phylogenies prevents the presentation of phylogenetic biogeographical hypotheses. He recognized the fish fauna of the rio Tietê as distinct from other rivers of the rio Paraná drainage and from that of the coastal rivers to the east. There are a large number of endemic species in the rio Tietê as well as some endemics found in the coastal drainages to the east, but there are almost no cladograms that allow useful biogeographic discussions of these distributions. The phylogenetic relationships of *Spintherobolus* presented here allows some consideration, albeit minimal, of the biogeographic significance of the distribution of its species.

Outgroups for *Spintherobolus* are clade E and C cheirodontines. Thus an area cladogram must take into account the total distribution of the species in clade E. These species, at present mostly placed in *Odontostilbe*, are distributed in the Amazon (*O. micropterus*), São Francisco (*O. piaba*), and the Paraná-Paraguay drainages (*O. calliura, O. kriegi, O. notomelas, O. microdon*, and *Holoshesthes heterodon*) so we hypothesize that the relationships of the species of *Spintherobolus* are to the west of the crest of the Serra Geral.

None of the several fishes listed by Langeani (1989: 188) as endemic to the rio Tietê headwater stream, the rio Grande da Serra, has been found in the rio Paraiba do Sul which has its headwaters just to the north of the origin of the rio Grande da Serra or to the east in the ribeirão Mogi, a coastal stream originating just east of the crest of the Serra Geral in this area. However, these streams need thorough surveys to fully identify their fish fauna. Some species of the coastal drainages were listed by Langeani (1989: 189) as present in the rio Tietê headwaters. Some of these such as *Hyphessobrycon bifasciatus* Ellis could have entered the Tietê basin by stream capture from the rio Paraiba do Sul to the north or less likely because of the steepness of the terrain, from the ribeirão Mogi to the east. However, all this is speculation. What is important here is that apparently the species of *Spintherobolus*, as we know them today, may have had a common ancestor that lived in the rio Tietê head waters and in the coastal

drainages to the east. That an ancestral species of *Spintherobolus* may have reached the rio Tietê drainage via stream capture from the ribeirão Mogi by the rio Grande da Serra cannot be known but is a possibility.

One fossil characid species, *Astyanax unicus* Travassos & Santos, has been found by M. C. S. L. Malabarba (1998) to be the only known species of a sister group of *Spintherobolus* as presently proposed rather than a species of *Astyanax*. The fossil species has been registered for the Tremembé Formation, the lacustrine unit of the Taubaté Basin. The Taubaté Basin is situated in eastern São Paulo, extending its greater axis (approximately 173 km) in a NE-SW direction along the valley of Paraíba do Sul River. Relationships of the fossil species to *Spintherobolus* seems to suggest ancient connections between the rio Tietê and Coastal drainages through the ancient valley of rio Paraiba (M. C. S. L. Malabarba, in press).

We have not proposed a phylogeny for the coastal species of *Spintherobolus*. These are closely related lowland species at present isolated from one another by portions of the Serra Geral that come steeply down to the Atlantic Ocean, preventing lowland interchange of freshwaters even during flood periods. It seems likely that these species have been isolated in this way for a time sufficient for them to have evolved their distinct characteristics recorded above. Some other coastal lowland species, apparently related to each other, have similar distributions, for example *Hyphessobrycon flammeus* Myers is from the Baixada Fluminense and *H. griemi* Hoedeman is from the lowlands around the rio Ribeira de Iguape, São Paulo and the lowlands around the Baia de Paranaguá, Paraná as reported by Weitzman et al. (1988: 419-420). These distributions and the speciation through isolation of formerly widespread species are possibly fostered by changes in sea level as discussed by Weitzman et al. (1988: 414-419).

**Comparative material.** In addition to the specimens of *Spintherobolus* listed above, the following list of specimens was examined for this study. Other cheirodontine specimens reported by Malabarba (1994) formed the basis for the outgroup comparison. These are not listed here and will be reported by Malabarba (in press).

*Charax caudimaculata*: USNM 295596, 6, 53.3-80.7 mm SL; Parque Nacional Manu, Madre de Dios, Peru. *Coptobrycon bilineata*: FMNH 54383, holotype of *Hasemania bilineata*, 33.2 mm SL; Alto da Serra, São Paulo, Brazil. *Cheirodon ortegai*: MZUSP 25993, 3, 25.9-31.1 mm SL; Lobococha, Masisea, Provincia Coronel Portill, Ucayali, Peru. *Crenuchus spilurus*: USNM 225487, 10, 27.2-36.6 mm SL; Koekwie Kreek, Nickerie, Suriname. *Grundulus bogotensis*: USNM 79212, 17, 23.7-53,6 mm SL; Chapiners, Colombia. *Hasemania hanseni*: MZUSP uncat., 5, 24.8-20.4 mm SL; small pool near Formosa, Distrito Federal, Brazil. *H. melanura*: FMNH 54384, holotype, 27.7 mm SL; Porto União, rio Iguaçu, Paraná, Brazil. *Odontostilbe fugitiva*: MZUSP 42854, 484; rio Machado, near its mouth, Amazonas, Brazil. *Odontostilbe* sp.: MCP 11136 1, 37.0 mm SL, c&s; rio Piratini, Fazenda dos Hinz, distrito de Coimbra, Santo Ângelo, Rio Grande do Sul, Brazil. *O. piaba*: MCP14007, 21 + 4 c&s; rio São Francisco, under bridge of highway 262, Moema, Minas Gerais, Brazil. *Phenacogaster pectinatus*: USNM 263945, 6, 34.5-39.7 mm SL; Reserva Natural de Tombopata, Madre de Dios, Peru. *P. megalostictus*: USNM 225192, 13, 18.9-30.2 mm SL; stream near camp Angoemara, Nickerie District, Surinam. *Roeboides paranensis*: USNM 326341, 44, 35.6-56.3 mm SL; rio Paraguai, Cáceres and vicinity, Mato Grosso, Brazil. *R. guatemalensis*: USNM 78729, 7, 39.1-83.7 mm SL; Missimbi, Empire, Panama.

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## Literature cited

Arnold, J. P. & E. Ahl. 1936. Fremdländische Süsswasserfische. Braunschweig, 592 pp.

Arratia, G. & L. Huaquin. 1995. Morphology of the lateral line system and of the skin of diplomystid and certain primitive loricarioid catfishes and systematic and ecological considerations. Bonn. Zool. Monogr., 36: 1-108.

Böhlke, J. E. 1954. Studies on the phylogeny and systematics of fishes of the family Characidae. Unpubl. Dissertation, University Microfilms, Ann Arbor, v + 209 pp.

Buckup, P. A. 1993a. The monophyly of the Characidiinae, a neotropical group of characiform fishes (Teleostei: Ostariophysi). Zool. J. Linn. Soc., 108: 225-245.

— 1993b. Phylogenetic interrelationships and reductive evolution in neotropical characidiin fishes (Characiformes, Ostariophysi). Cladistics, 9: 305-341.

— In press. Phylogeny of characiform fishes and the relationships of the Characidiinae (Teleostei: Ostariophysi). In L. R. Malabarba, R. E. Reis & R. P. Vari (eds.), Phylogeny and classification of neotropical fishes. Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre.

Campos, H. 1982. Systemática del género *Cheirodon* (Pisces: Characidae) en Chile con descripción de una nueva especie. Análisis de multivarianza. Stud. Neotrop. Fauna Env., 17: 129-162.

Eigenmann, C. H. 1911. New characins in the collections of the Carnegie Museum. Ann. Carnegie Mus., 8: 164-181.

— 1915. The Cheirodontinae, a subfamily of minute characid fishes of South America. Mem. Carnegie Mus., 7: 1-99, pls. 1-17.

— 1917. Eighteen new species of fishes from northwestern South America. Proc. Amer. Philos. Soc., 56: 673-689.

— 1927. The fresh-water fishes of Chile. Mem. Mus. Comp. Zool., 43: 1-102.

Eigenmann, C. H. & C. H. Kennedy. 1903. On a collection of fishes from Paraguay. Proc. Acad. Nat. Sci. Philad., 55: 497-537.

Ellis, M. D. 1911. On the species of *Hasemania*, *Hyphessobrycon*, and *Hemmigrammus* collected by J. D. Haseman for the Carnegie Museum. Ann. Carnegie Mus., 8: 148-163, pls 1-3.

Fink, W. L. & S. H. Weitzman. 1974. The so-called cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). Smithson. Contr. Zool., 172: 1-46.

Fowler, H. W. 1948. Os peixes de água doce do Brasil (1.ª entrega). Arq. Zool. Estado São Paulo, 6: 1-204.

— 1950. Os peixes de água doce do Brasil (2.ª entrega). Arq. Zool. Estado São Paulo, 6: 205-404.

Géry, J. 1971. Une sous-famille nouvelle de poissons characoïdes sud-américains: les Geisleriinae. Vie et Milieu, Ser. C, 22: 153-166.

— 1972. Corrected and supplemental descriptions of certain characoid fishes described by Henry W. Fowler, with revisions of several of their genera. Stud. Neotop. Fauna, 7: 1-35.

— 1977. Characoids of the World. T. F. H. Publications, Neptune City, New Jersey, 672 pp.

Günther, A. 1868. Diagnoses of some new freshwater fishes from Surinam and Brazil in the collection of the British Museum. Proc. Zool. Soc. London, 4: 475-481.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana, 263 pp.

Humphries, C. & L. R. Parenti. 1986. Cladistic biogeography. Oxford Press Monographs on Biogeography, 2: i-xi + 1-98.

Ibarra, M. & D. J. Stewart. 1987. Catalogue of the type specimens of recent fishes in Field Museum of Natural History. Fieldiana Zool., N. S., 35: 1-112.

Innes, W. T. 1931. Goldfish varieties and tropical aquarium fishes. 14th edition. Innes, Philadelphia, 316 pp.

— 1935. Exotic aquarium fishes. Innes, Philadelphia, 463 pp.

Langeani, F. 1989. Ictiofauna do altocurso do rio Tietê (SP): taxonomia. Mestre em Ciências, Dissert. Inst. Bioc. Univ. São Paulo, vii + 231 pp.

Maddison, W. P., M. C. Donoghue & D. R. Maddison. 1984. Outgroup comparison and parsimony. Syst. Zool., 33: 83-103.

Maddison, W. P. & D. R. Maddison. 1992. MacClade. Analysis of phylogeny and character evolution. Version 3.1. Sinauer Associates, Sunderland, MA.

Malabarba, L. R. 1994. Systemática e filogenia de Cheirodontinae (Ostariophysi: Characiformes: Characidae). Dissert. Inst. Bioc. Univ. São Paulo, vii + 287 pp.

— In press. Characters and major clades of the Cheirodontinae (Ostariophysi: Characiformes: Characidae). In L. R. Malabarba, R. E. Reis & R. P. Vari (eds.), Phylogeny and classification of neotropical fishes. Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre.

Malabarba, L. R. & Z. M. S. Lucena. 1995. *Phenacogaster jancupa*, new species, with comments on the relationships and a new diagnosis of the genus (Ostariophysi: Characidae). Ichthyol. Explor. Freshwaters, 6: 337-344.

Malabarba, M. C. S. L. 1998. *Megacheirodon*, a new genus of characiform fish (Ostariophysi: Characidae) from Tremembé Formation, Tertiary of São Paulo, Brazil. Ichthyol. Explor. Freshwaters, 8: 193-200.

— In press. Phylogeny of fossil Characiformes and paleobiogeography of the Tremembé Formation, São Paulo, Brazil. In L. R. Malabarba, R. E. Reis & R. P. Vari (eds.), Phylogeny and classification of neotropical fishes. Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre.

Meinken, H. 1929a. *Spintherobolus broccae* Myers. Blätter für Aquarien- und Terrarienkunde, 40: 19-21.

— 1929b. Die Importen des Jahres 1928. Pp.24-72 in M. Günter, Taschenkalender für Aquarien- und Terrarienfreunde 1929. Wenzel, Braunschweig, pp. 1-205.

Myers, G. S. 1925. Description of a new cheirodontine characin from Rio de Janeiro. Ann. Carnegie Mus., 16: 143-144.

— 1926. Alphabetical list of aquarium fishes, their breeding habits, care etc. Pp. 264-283 in W. T. Innes, Goldfish varieties and tropical aquarium fishes. 9th edition. Innes, Philadelphia [not seen; reference from Rachow, 1943: 798 and authorship confirmed by Myers, 1970: 25. We examined this list, unaltered, in Innes, 1931: 286-296].

— 1944. Field notes on fishes of the vicinity of Rio de Janeiro (part 1). The Aquarium, Philadelphia, 13: 185-186.

— 1970. Annotated chronological bibliography of the publications of George Sprague Myers (to the end of 1969). In: Anonymous, Festschrift for George S. Myers in honor of his sixty-fifth birthday. Proc. Calif. Acad Sci., Ser. 4, 38 (2): i-vii + 1-437.

Nelson, G. J. 1994. Homology and systematics. Pp. 101-149 in B. K. Hall, Homology the hierarchical basis of comparative biology. Academic Press, San Diego.

Poll, M. & J. P. Gosse. 1982. Réhabilitation des genres *Congocharax* Matthes, 1964 et *Dundocharax* Poll, 1967 (Pisces, Distichodontidae) mis en synonymie par R. P. Vari, 1979, avec *Neolebias* Steindachner, 1894. Bull. Inst. R. Sci. Nat. Belg., 54 (2): 1-8.

Poll, M., & J. Lambert. 1964a. *Congocharax gossei* sp. n. du Gabon (Ogooué) (Pisces, Citharinidae). Rev. Zool. Bot. Afr., 70: 336-340.

— 1964b. Au sujet *Barbus miolepis* Blgr. et des espèces voisines ou synonymes (Pisces, Cyprinidae). Rev. Zool. Bot. Afr., 70: 405-411.

Rachow, A. 1924. *Hasemania bilineata*. Wochenschrift für Aquarien- und Terrarienkunde, Braunschweig, 18: 601 [Not seen; based on Rachow, 1943: 798].

— 1943. *Phoxinopsis broccae* (G. S. Myers). Pp 798-808 in M. Holly, H. Meinken & A. Rachow, Die Aquarienfische in Wort und Bild. Lieferung 77/78. Kernen, Stuttgart.

Regan, C. T. 1907. Descriptions of two new characinid fishes from Argentina. Ann. Mag. Nat. Hist., Ser. 7, 19: 261-263.

Roberts, T. R. 1969. Osteology and relationships of the families of characoid fishes, particularity the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenolucius*, and *Acestrorhynchus*. Proc. Calif. Acad. Sci., 36: 391-500.

Sarraf, A. 1997. Redescription and distribution of *Spintherobolus broccae* Myers (Characiformes: Characidae). Rev. Fr. Aquariol. Herpet., 24: 27-30.

Schaefer, S. A., S. H. Weitzman, & H. A. Britski. 1989. Review of the neotropical catfish of the genus *Scoloplax* (Pisces: Loricarioidea: Scoloplacidae) with comments on reductive characters in phylogenetic reconstruction. Proc. Acad. Nat. Sci. Philad., 141: 181-211.

Schemmel, C. 1967. Vergleichende Untersuchungen an den Hautsinnesorganen ober- und unterirdisch lebender *Astyanax*-Formen – ein Beitrag zur Evolution der Cavernicolen. Ztschr. Morph. Tiere, 61: 255-316.

Sterba, G. 1987. Süsswasserfische der Welt. Urania-Verlag, Leipzig, 915 pages.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1.1, Smithsonian Institution, Washington, D.C.

Travassos, H. 1952. Catálogo dos gêneros e subgêneros da subordem Characoidei (Actinopterygii – Cypriniformes). Dusenia, 3: 225-250.

— 1953. Fauna do Distrito Federal. III. Sôbre o gênero "*Spintherobolus*" Eigenmann, 1911 (Cypriniformes-Characoidei). An. Acad. Bras. Ciênc., 25: 505-517.

Vari, R. P. 1979. Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea). Bull. Br. Mus. Nat. Hist., Zool., 36: 261-344.

Vari, R. P. & D. J. Siebert. 1990. A new unusually sexually dimorphic species of *Bryconamericus* (Pisces: Ostariophysi: Characidae) from the Peruvian Amazon. Proc. Biol. Soc. Wash., 103: 516-524.

Weitzman, S. H. 1954. The osteology and the relationships of the South American characid fishes of the subfamily Gasteropelecinae. Stanford Ichthyol. Bull., 4: 213-263.

— 1960. Further notes on the relationships and classification of the South American characid fishes of the subfamily Gasteropelecinae. Stanford Ichthyol. Bull., 7: 217-239.
— 1962. The osteology of *Brycon meeki*, a generalized characoid fish, with an osteological definition of the family. Stanford Ichthyol. Bull., 8: 1-77.
— 1966. Review of South American characid fishes of subtribe Nannostoma. Proc. U. S. Natn. Mus., 119 (3538): 1-56.
— 1997. Comments on miniature freshwater fishes with an introduction to the tetras of the glandulocaudine tribe Xenurobryconini. Trop. Fish Hobbyist, 45 (5): 136-154.
Weitzman, S. H. & S. V. Fink. 1985. Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). Smithson. Contr. Zool., 421: 1-121, figs. 1-81.
Weitzman, S. H., S. V. Fink, A. Machado-Allison & R. Royero. 1994. A new genus and species of Glandulocaudinae (Teleostei: Characidae) from southern Venezuela. Ichthyol. Explor. Freshwaters, 5: 45-64.
Weitzman, S. H. & W. L. Fink. 1983. Relationships of the neon tetras, a group of South American freshwater fishes (Teleostei, Characidae), with comments on the phylogeny of the New World characiforms. Bull. Mus. Comp. Zool., 150: 339-395.
Weitzman, S. H., N. A. Menezes & M. J. Weitzman. 1988. Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes, Characidae) with comments on the distributions of other freshwater fishes in eastern and southeastern Brazil. Pp. 379-427 in P. E. Vanzolini & W. R. Heyer (eds.), Proceedings of a workshop on neotropical distribution patterns. Academia Brasileira de Ciências, Rio de Janeiro.
Weitzman, S. H. & H. Ortega. 1995. A new species of *Tyttocharax* (Teleostei: Characidae: Glandulocaudinae: Xenurobryconini) from the Rio Madre de Dios basin of Peru. Ichthyol. Explor. Freshwaters, 6: 129-148.
Weitzman, S. H. & R. P. Vari. 1987. Two new species and a new genus of miniature characid fishes (Teleostei: Characiformes) from northern South America. Proc. Biol. Soc. Wash., 100: 640-652.
— 1988. Miniaturization in South American freshwater fishes; an overview and discussion. Proc. Biol. Soc. Wash., 101: 444-465.
Wiley, E. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. Wiley, New York, vi + 439 pp.

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