

Systematics of the Neotropical
Characiform Genus *Steindachnerina*
Fowler (Pisces: Ostariophysi)

RICHARD P. VARI

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ABSTRACT

Vari, Richard P. Systematics of the Neotropical Characiform Genus *Steindachnerina* Fowler (Pisces: Ostariophysi). *Smithsonian Contributions to Zoology*, number 507, 118 pages, 80 figures, 10 tables, 1991.—The genus *Steindachnerina* Fowler (1906) of the characiform family Curimatidae is defined as a monophyletic unit. Shared derived features of the gill arches and possibly in dorsal-fin pigmentation diagnose the genus. Derived features of the gill arches, buccopharyngeal complex, infraorbital series, palatine arch, and neurocranium, form of the prepelvic region of the body, details of pigmentation, and meristic features define monophyletic subunits of *Steindachnerina* or are autapomorphic for species.

Steindachnerina has three junior synonyms *Curimatorbis*, *Crucentina*, and *Rivasella*, all described by Fernández-Yépez (1948). Twenty-one species are recognized in *Steindachnerina*: *S. amazonica* (Steindachner, 1911) of the Rio Tocantins; *S. argentea* (Gill, 1858) of Trinidad, the Río Orinoco, and coastal rivers of northern Venezuela; *S. atratoensis* (Eigenmann, 1912b) of the Río Atrato; *S. bimaculata* (Steindachner, 1876) of the Rio Amazonas and Río Orinoco; *S. binotata* (Pearson, 1924) of the Río Madeira; *S. biornata* (Braga and Azpelicueta, 1987) of the Río de La Plata basin and the coastal rivers of Uruguay and southern Brazil; *S. brevipinna* (Eigenmann and Eigenmann, 1889) of the Río Uruguay, Río Paraguay, and lower Río Paraná, and possibly the upper Río Xingu; *S. conspersa* (Holmberg, 1891) of the Río Paraguay and lower Río Paraná; *S. dobula* (Günther, 1868a) of the western Amazon basin; *S. elegans* (Steindachner, 1874) of the coastal rivers of eastern Brazil; *S. fasciata* (Vari and Géry, 1985) of the Río Madeira basin; *S. gracilis* Vari and Vari (1989) of the Río Tocantins; *S. guentheri* (Eigenmann and Eigenmann, 1889) distributed from Guyana through the Río Orinoco basin, and the Andean piedmont to northern Bolivia; *S. hypostoma* (Boulenger, 1887a) of the Amazon basin; *S. insculpta* (Fernández-Yépez, 1948) of the upper Río Paraná; *S. leucisca* (Günther, 1868) of the Amazon basin; *S. notonota* (Miranda-Ribeiro, 1937) of northeastern Brazil; *S. planiventris* Vari and Vari (1989) of the Amazon basin; *S. pupula*, new species, endemic to the Río Orinoco; *S. quasimodoi* Vari and Vari (1989) from the Río Yavari (Río Javari); and *S. runa*, new species, from Surinam, French Guiana, and Brazil. A key to the species of *Steindachnerina* is provided.

Nineteen species and subspecies are placed into synonymy in this study. *Curimatus leuciscus bolivae* described by Eigenmann and Ogle (1908) and *Allenina pectinata* Fernández-Yépez (1948) are placed into the synonymy of *Steindachnerina leucisca*. *Curimatus trachystetus* Cope (1878), *C. bimaculatus sialis* Eigenmann and Eigenmann (1889), *Prochilodus pterostigma* Fowler (1913), *Curimatus semiornatus* Steindachner (1914), and *Curimata melaniris* Fowler (1940) are all placed into the synonymy of *Steindachnerina bimaculata*. *Curimata stigmata* Vari (1987) is a synonym of *Curimata biornata*. *Curimatus nitens* Holmberg (1891) and *Curimatus nigrotaenia* Boulenger (1902) are placed into the synonymy of *Steindachnerina brevipinna*. *Curimatus nasus* Steindachner (1882), *Curimata hypostoma hastata* Allen (in Eigenmann and Allen, 1942), *Curimata niceforoi* Fowler (1943a), and *Prochilodus stigmaturus* (Fowler, 1911), are all considered synonyms of *Steindachnerina dobula*. *Steindachnerina guentheri* has four junior synonyms: *Curimatus morawhannae* Eigenmann (1912a), *Curimatus issororoensis* Eigenmann (1912a), *Curimatus metae* Eigenmann (1922), and *Curimata robustula* Allen (in Eigenmann and Allen, 1942). *Curimatus elegans bahiensis* Eigenmann and Eigenmann (1889) is placed into the synonymy of *Steindachnerina elegans*.

The phylogenetic biogeography of *Steindachnerina* indicates numerous cases of large-scale, secondary dispersal during the evolution of the genus. The basal speciation events within *Steindachnerina* predate the final uplift of the Andes. A major part of the speciation within the genus predates the formation of the Amazon basin and apparently occurred outside of the Río Amazonas system or in peripheral portions of the basin. The previous occurrence of a *Steindachnerina* species within the Río Magdalena system of Colombia and its subsequent extinction is hypothesized based on phylogenetic and distributional data.

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Systematics of the Neotropical Characiform Genus *Steindachnerina* Fowler (Pisces: Ostariophysii)

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Introduction

The genus *Steindachnerina* Fowler of the family Curimatidae occurs in the vast majority of the myriad drainage systems that weave across the expansive lowlands of tropical and subtemperate South America. Of the 21 species of *Steindachnerina* recognized in this study, 20 occur in rivers to the east of the main Andean Cordilleras, with several species occurring as far south as central Argentina. The western and northern versants of the Andes together constitute a much smaller region, portions of which are desert or near desert. Not unexpectedly, only two species of *Steindachnerina* are known to occur within the resulting relatively depauperate fish fauna of that region; both in river systems draining into the Caribbean Sea. *Steindachnerina argentea* Gill, a species widespread in western Trinidad and through the Río Orinoco basin, also inhabits the Río Tocuyo and Río Tuy systems, small, widely separated river basins of the coastal versant of northern Venezuela. Much further to the west, the Río Atrato system of northwestern Colombia is inhabited by the endemic *S. atratoensis* (Eigenmann). *Steindachnerina* is unknown in the other river systems entering the Caribbean Sea along northern South America, most notably the Río Magdalena and the rivers of the Lago Maracaibo basin, which are inhabited by curimatids of the genera *Potamorhina* Cope, *Curimata* Bosc, and *Cyphocharax* Fowler. *Steindachnerina* is also absent in the numerous, typically swift-flowing rivers draining into the Pacific Ocean from southern Costa Rica to northern Peru,

which have species of the curimatid genera *Pseudocurimata* Fernández-Yépez and *Cyphocharax* in their faunas.

Members of *Steindachnerina* occur in diverse aquatic habitats spanning the spectrum from the lentic backwaters of lowland flood-plains to the more rapidly flowing courses on the lower slopes of the Andean piedmont, Guiana and Brazilian shields, and Atlantic coastal ranges. In those habitats adults of *Steindachnerina* feed on a broad spectrum of different types of algae (Nomura and Taveira, 1979; de Godoy, 1975) and organic detritus (Saul, 1975). These very abundant food sources support large populations of different, often sympatric, species of *Steindachnerina*. At least the more common *Steindachnerina* species participate in the large-scale annual migrations of mixed schools of fishes that occur in most South American river systems (e.g., upper Rio Paraná, de Godoy, 1975).

Despite the occurrence of species of *Steindachnerina* across most of lowland South America, and the increasing abundance of population samples of the genus in systematic collections, the taxonomy of the nominal forms united in *Steindachnerina* in this study has been problematical. The numerous nominal species in the Curimatidae and the broad geographic distribution of many of those species complicated the problem of species recognition for those authors who limited their studies of the family and its subunits to within political boundaries, or who focused their research efforts on subcontinental regions. Previous studies of the species of *Steindachnerina* were additionally hampered by the numerically and geographically limited samples of many nominal forms. The samples of some nominal species of *Steindachnerina* (e.g., *S. amazonica*) are still unsatisfactory, and the fish fauna of many regions of the continent, especially of the major tributaries of the Rio Amazonas, remains relatively poorly collected. An additional problem confronting early researchers, particularly those who did not have access to type series, was the absence of critical information needed for identification in many original species

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descriptions. In several instances these descriptions were so brief that it was impossible to recognize that some nominal species were actually closely related to the other taxa herein assigned to *Steindachnerina*. The supraspecific classification of the species of *Steindachnerina* was similarly pervaded by uncertainty. The problems noted above relative to the question of species recognition together with the less rigorous methodologies available to many previous researchers also hampered efforts to elucidate the supraspecific natural groups within the Curimatidae, in other words monophyletic assemblages in the strict sense of that term.

The most recent broadly encompassing treatment of the Curimatidae was that of Fernández-Yépez (1948). The classification of species within Fernández-Yépez's Curimatinae (the Curimatidae of this study) differs in numerous instances from the generic assignments of those species recently proposed by Vari (1989a:7-9). For purposes of this discussion I will leave aside for the moment the questions associated with the five nominal species of *Steindachnerina* (sensu lato) that Fernández-Yépez was forced to retain insertae sedis in *Curimata* as a consequence of his lack of available material. Even in the absence of those species a number of incongruities manifest themselves when the species of *Steindachnerina* of this study are overlain on the phylogenetic framework proposed by Fernández-Yépez (1948, fig. 2). The most obvious of these problems is that the members of *Steindachnerina* of the present study are components of six of the fifteen genera of the tribe Curimatini of Fernández-Yépez. The finer generic subdivision of Fernández-Yépez would not per se constitute a problem if those six genera together constituted a monophyletic group. However, under his classification five of the six genera included additional curimatid species lacking the shared derived features proposed by Vari (1989a) as diagnostic for *Steindachnerina*. Furthermore, nearly all of those additional species instead demonstrate synapomorphies characteristic of other lineages within the Curimatidae, and thus were reassigned by Vari (1989a, tables 2, 3) to the hypothesized monophyletic clades *Pseudocurimata*, *Curimata*, and *Curimatella*. A few of these extraneous species were, in turn, placed by Vari (1989a, tables 2, 3) in the questionably natural genus *Cyphocharax*, not known to be characterized by any uniquely derived features.

The inconsistencies between the classification put forward by Fernández-Yépez (1948) and that proposed by Vari (1989a) are to a degree reflective of the differing methodologies used by those authors. Fernández-Yépez (1948) recognized a number of genera and suprageneric taxa, either explicitly or by default, on degrees of overall similarity or difference. That system does not critically examine the correlation, or lack thereof, between recognized supraspecific taxa and hypothesized evolutionary lineages. Phylogenetic systematics, the methodology used in Vari (1989a) and the present study, in contrast, requires that taxa reflect the hypothesized evolutionary history of the included species. In other words, that they be natural or

monophyletic in the strict sense of those terms. The common application of that more rigorous criterion in phylogenetic studies of fishes postdates Fernández-Yépez's effort by over two decades.

The uncertainties about species identity and geographic distribution discussed above, along with a lack of an explicit hypothesis on the intrageneric evolutionary history of the clade as defined by Vari (1989a) demonstrate the need for a revisionary and phylogenetic reanalysis of *Steindachnerina*. The present study has three major aims: first, to determine the recognizable species in the lineage and their distinguishing characters; second, to analyze the morphological variation within *Steindachnerina* and advance a hypothesis of the evolutionary history within the clade; and third, to delimit the known geographic distributions of the recognized forms and put forward an hypothesis of the historical biogeography of the genus.

SYSTEMATIC PROCEDURES

This paper continues a series of publications that deal with aspects of the phylogeny, taxonomy, distribution, and historical biogeography of curimatid characiforms (Vari, 1982a, 1982b, 1983, 1984a, 1984b, 1987, 1988, 1989a, 1989b, 1989c, 1989d; Vari and Castro, 1988; Vari and Géry, 1985; Vari and Nijssen, 1986; Vari and Vari, 1989). Vari (1989a) advanced an hypothesis of generic-level relationships within the Curimatidae. That study and the phylogenetically more encompassing scheme of familial relationships for the Curimatidae and proximate relatives (Prochilodontidae, Anostomidae, and Chilodontidae) put forward by Vari (1983) are herein used as the phyletic framework for the outgroup analyses and polarity hypotheses of discretely variable characters within *Steindachnerina*. Discussions of the theory and methods of polarity determination can be found in Wiley (1981), Watrous and Wheeler (1981), and Maddison et al. (1984).

The hypothesis of evolutionary relationships within *Steindachnerina* is derived following the principles of phylogenetic systematics first formalized by Hennig (1950, 1966) and since discussed and refined by a variety of authors (see Wiley, 1981 for a summary). In that system, recognized taxa must be monophyletic in including all descendants of an hypothesized common ancestor (the holophyletic of some authors). Monophyletic groups are defined on the basis of the most parsimonious hypothesis of relationships derived from the distribution of shared derived (synapomorphic) characters. The general scientific principle of parsimony, the proposal of the hypothesis of the phylogenetic history of a group that necessitates the fewest assumptions about character transformation is preferred and utilized in this study. The use of this principle is not meant to imply that evolutionary mechanisms are necessarily always parsimonious. Neither is there an underlying assumption that convergencies (homoplasies) are relatively rare. Rather, parsimony is judged to be the best

inferential principal for such analyses (see Beatty and Fink, 1979; Wiley, 1981, for further discussions of this topic).

METHODS AND MATERIALS

Measurements were made with dial calipers and data recorded to tenths of a millimeter. Counts and measurements were made on the left side of specimens whenever possible. Lateral-line scales were counted from the supracleithrum to the hypural joint. Counts of midlateral scales posterior to the hypural joint include all pored scales in that series. Counts of total vertebrae were usually taken from radiographs with supplementary information derived from cleared and stained specimens. In counts of vertebrae the fused $PU_1 + U_1$ is considered a single bone, and the vertebrae incorporated into the Weberian apparatus are counted as four elements. The numbers in parentheses that follow a particular vertebral count are the numbers of radiographed and cleared and stained specimens with that count.

Subunits of the head are presented as proportions of head length (HL). Head length itself and measurements of body parts are given as proportions of standard length (SL). Greatest depth of the body was taken at the origin of the dorsal fin. In the counts of median- and pelvic-fin rays, the unbranched fin rays are indicated by lower case roman numerals, and the branched fin rays as arabic numerals. The observed range in the values of each count and proportional measurement is presented first, followed by the value of the holotype or lectotype for a particular count or measurement, when available, in square brackets. When the recognized species of *Steindachnerina* have junior synonyms, the available morphometric and meristic data for the type series of all the conspecific nominal species is presented in tabular form. In those cases the data in the brackets in the species description are for the holotype or lectotype of the senior synonym.

The "Material Examined" section of each species account is arranged in the following sequence: number of specimens of the species examined (in parentheses, the number of specimens forming the basis for the meristic and morphometric data, and the range of standard lengths (in mm) for these specimens), collection locality of specimens, institutional abbreviation, catalog number, number of specimens in the lot (in parentheses, the number of specimens in the lot from which counts and measurements were taken if less than the total number of specimens, and the standard lengths (in mm) of those individuals). Geographic descriptors are in the sequence of country (capitalized) then state, province, department or district (in italics), followed by more specific locality data. Information on collectors and date of collection of examined specimens is presented only in the case of the type series of the species described in this paper.

Concepts of characiform families used in this paper are those of Greenwood et al. (1966) with three modifications. The Cynodontidae of those authors is considered a tribe in the

Characidae rather than a distinct family following Howes (1976). The Ichthyboridae of Greenwood et al. is considered a synonym of an expanded Distichodontidae in line with the results of Vari (1979). The common names presented are those found in the literature, although such terminology is not standardized across the entire range of the species. In the synonymies for each species, localities are presented as in the original citation, followed by the corrected or modern equivalent, in parentheses, if that differs.

OSTEOLOGICAL MATERIAL EXAMINED.—Osteological preparations were cleared and counterstained for cartilage and bone using a modification of the method outlined by Taylor and Van Dyke (1985). Previously cleared specimens stained solely with alizarin Red-S were supplemental sources of osteological data. Osteological terminology follows that used in Vari (1989a:5). Drawings were made with a Zeiss microscopic camera lucida.

The following cleared and stained specimens of *Steindachnerina* are the basis for osteological text illustrations and/or specific observations noted in the text. Measurements, in mm, are standard lengths (SL).

- Steindachnerina amazonica* (Steindachner), USNM 298161, 1 specimen, ~57.5 mm; Brazil, Goiás, Rio Paina, tributary of Rio Maranhão, upper Rio Tocantins system.
- Steindachnerina argentea* (Gill), USNM 285663, 2 specimens, 79.5–83.5 mm; Trinidad, Northern Trinidad, Arouca River, just north of Churchill to Roosevelt Highway.
- Steindachnerina atratoensis* (Eigenmann), USNM 220199, 1 specimen, 59.3 mm; Colombia, Choco, Río Pavarando, tributary of Río Salaquí.
- Steindachnerina bimaculata* (Steindachner), USNM 251450, 2 specimens, 61.5–75.4 mm; Peru, Loreto, Río Amazonas, opposite Tabatinga, Brazil.
- Steindachnerina binotata* (Pearson), USNM 301960, 1 specimen, 89.6 mm; Peru, Madre de Dios, Río Tambopata, near Puerto Maldonado.
- Steindachnerina biornata* (Braga and Azpelicueta), USNM 285194, 1 specimen, paratype of *Curimata stigmata* Vari, 66.3 mm; Brazil, Rio Grande do Sul, Rio Jacuí, at bridge on road between Santa Maria and Vera Cruz.
- Steindachnerina brevipinna* (Eigenmann and Eigenmann), USNM 287022, 2 specimens, 70.2–76.2 mm; Brazil, Rio Grande do Sul, Sanga das Águas Frias, off Rio Uruguai.
- Steindachnerina conspersa* (Holmberg), USNM 232224, 1 specimen, 83.2 mm; Paraguay, Presidente Hayes, off Trans-Chaco Highway at km 50.
- Steindachnerina dobula* (Günther), USNM 295173, 2 specimens, 62.8–68.2 mm; Peru, Madre de Dios, Parque Nacional Manú, Río Manú system.
- Steindachnerina elegans* (Steindachner), USNM 297903, 1 specimen, 78.5 mm; Brazil, Bahia, Rio Pardo.
- Steindachnerina elegans* (Steindachner), USNM 297004, 2 specimens, 47.0–53.5 mm; Brazil, Rio Jequitinhonha, at km 205 on road between Salto da Divisa and Jacinto.
- Steindachnerina fasciata* (Vari and Géry), USNM 270377, 1 specimen, paratype of *Curimata fasciata* (Vari and Géry), 72.3 mm; Brazil, Território de Rondônia, Rio Romari near Nova União Município de Ouro Preto do Oeste.
- Steindachnerina gracilis* Vari and Vari, USNM 293034, 2 specimens, paratypes, 62.5–63.5 mm; Brazil, Goiás, Rio Araguaia, Aruanã.
- Steindachnerina guentheri* (Eigenmann and Eigenmann), USNM 298035, 2 specimens, 46.5–72.0 mm; Peru, Madre de Dios, Parque Nacional Manú, Río Manú system.
- Steindachnerina guentheri* (Eigenmann and Eigenmann), USNM 263978, 61.5–70.0 mm; Peru, Madre de Dios, Río Tambopata system.

- Steindachnerina hypostoma* (Boulenger), USNM 167802, 1 specimen, 82.7 mm; Peru, Río Huallaga.
- Steindachnerina hypostoma* (Boulenger), USNM 261493, 1 specimen, 76.8 mm; Peru, Ucayali, Pucallpa.
- Steindachnerina insculpta* (Fernández-Yépez), USNM 295272, 1 specimen, 68.7 mm; Brazil, São Paulo, Represa de Volta Grande, Miguelópolis.
- Steindachnerina leucisca* (Günther), USNM 261520, 2 specimens, 87.5–89.5 mm; Peru, Ucayali, Río Ucayali, Masisea.
- Steindachnerina notonota* (Miranda-Ribeiro), USNM 297907, 1 specimen, 73.2 mm; Brazil, Ceará, reservoir on Rio Acarau.
- Steindachnerina notonota* (Miranda-Ribeiro), USNM 220202, 2 specimens, 51.2–75.1 mm; Brazil, Ceará, reservoir at Pentecostes.
- Steindachnerina planiventris* Vari and Vari, USNM 267987, 2 specimens, paratypes, 63.2–64.3 mm; Brazil, Território de Rondônia, Rio Machado, Santo Antonio.
- Steindachnerina pupula*, new species, USNM 194177, 1 specimen, 79.1 mm; Venezuela, Estado Barinas, Río Las Palmas.
- Steindachnerina quasimodoi* Vari and Vari, USNM 293042, 2 specimens, paratypes, 72.0–93.9 mm; Peru, Loreto, Río Javari, near Petropolis.
- Steindachnerina runa*, new species, USNM 300000, 1 specimen, paratype, 87.1 mm; Surinam, Brokopondo, Marowijne or Gran Creek, 63 km S of Afobaka.

The observations on osteological characters in outgroups to *Steindachnerina*, both within the Curimatidae and within other taxa in the Characiformes, are based on the specimens cited in Vari (1989a:10, 11).

ABBREVIATIONS

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions and collections are used.

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CM	Carnegie Museum, Pittsburgh (fish collections now at FMNH)
FMNH	Field Museum of Natural History, Chicago
GC	Personal collection of Jacques Géry; no register numbers
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus
IU	Former Indiana University collections, now dispersed to various repositories
KU	University of Kansas, Museum of Natural History, Lawrence
LACM	Los Angeles County Museum of Natural History
MAC	Ministerio de Agricultura y Cria, Caracas (collections now at MBUCV)
MBUCV	Museo de Biología, Universidad Central de Venezuela, Caracas
MCP	Museu de Ciências da Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre
MCZ	Museum of Comparative Zoology, Cambridge
MNRJ	Museu Nacional, Rio de Janeiro
MHNG	Muséum d'Histoire Naturelle, Geneva
MNHN	Muséum National d'Histoire Naturelle, Paris
MHN-USM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NMW	Naturhistorisches Museum Wien, Vienna
NRM	Naturhistoriska Riksmuseet, Stockholm

ROM	Royal Ontario Museum, Toronto
SU	Stanford University, collections now at CAS
UFPB	Universidade Federal da Paraíba, João Pessoa, Brazil
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	Former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
USP-RP	Universidade de São Paulo, Ribeirão Preto, Brazil
ZMA	Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Amsterdam
ZMUC	København Universitet, Zoologisk Museum, Copenhagen
ZUEC	Zoologia, Universidade Estadual de Campinas, Campinas, Brazil

TEXT AND FIGURE ABBREVIATIONS.—The following abbreviations are used in the text figures and text:

AE	anterior extension of ventral process of third hypobranchial (H_3)
AI	area of attachment on mesopterygoid of ligament between mesopterygoid and vomer
ALP	anterior lobulate processes of buccopharyngeal complex
APF	anterior posteromedian flap of buccopharyngeal complex
ASMQF	anterior section of metapterygoid-quadrate fenestra
BB	basibranchial
BH	basihyal
BHC	basihyal cartilage
BHTP	basihyal tooth-plate
CART	cartilage
CF	cranial fan
DLF	dorsolateral flange of second infrapharyngobranchial (PB_2)
E	epibranchial
EB	epiphyseal bar
ECT	ectopterygoid
FR	frontal
GA	gill arch
H	hypobranchial
HL	head length
HY	hyomandibula
IL	insertion area on H_3 of ligament between second and third hypobranchials (H_2 and H_3)
IO	infraorbitals
LF	lateral fold of buccopharyngeal complex
LPGA	lobulate processes of buccopharyngeal complex on anteroventral surface of first and second gill arches
ME	mesethmoid
MES	mesopterygoid
MET	metapterygoid
METR	metapterygoid ridge
MF	medial fold of buccopharyngeal complex
P	parietal
PB	infrapharyngobranchial
PE	posterior extension of ventral process of third hypobranchial (H_3)
PLP	posterior lobulate process of buccopharyngeal complex
POP	preopercle
PPF	posterior posteromedian flap of buccopharyngeal complex
PSMQ	posterior section of metapterygoid-quadrate fenestra
PU ₁	first preural centrum
QU	quadrate
SOC	supraoccipital
SYM	symplectic
U ₁	first ural centrum

UL	upper lip
UP ₅	fifth upper pharyngeal tooth plate
VLF	ventrolateral flange of second infrapharyngobranchial (PB ₂)
VPH ₃	ventral process of third hypobranchial (H ₃)

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Character Description and Analysis

The synapomorphies diagnosing *Steindachnerina* and the recognizable monophyletic subunits of the genus are discussed in this section. Hypothesized generic and intrageneric synapomorphies are numbered sequentially on the cladogram of Figure 11 to simplify the visualization of their distribution within the proposed phylogenetic scheme. The numbering of synapomorphies and autapomorphies in the following character descriptions and analyses, and in the subsequent "Synapomorphy List and Phylogenetic Reconstruction" section corresponds to that numbering system. Those derived characters are also cross-referenced in the "Character Summary" of the Appendix. For purposes of uniformity and clarity the characters autapomorphic for species of *Steindachnerina* are highlighted as a "SYNAPOMORPHY" in the following text. Those shared derived features having a phylogenetic distribution incongruent with the arrived at phylogeny, both those occurring in two lineages within *Steindachnerina* or found in a subunit of the genus and an outgroup within the Curimatidae, are discussed under "Convergent Characters."

Additional information on some of the derived features congruent with the hypotheses of the monophyly of *Steindachnerina* and of clades within the genus is in some instances found in cited publications focusing on questions of intrafa-

mial (Vari, 1989a) or intrageneric relationships within the Curimatidae (Vari, 1982a; 1984a; 1989b; 1989c; 1989d).

BUCCOPHARYNGEAL COMPLEX

Vari (1989a:31–33) provided a broad overview of the major modifications of the fleshy lining of the dorsal portion of the buccopharyngeal region found within the Curimatidae. Outgroup comparisons both to the proximate sister taxa to the Curimatidae (the families Prochilodontidae, Chilodontidae, and Anostomidae) (Vari, 1983) and other more distantly related families of characiforms support the hypothesis that the soft tissues lining the dorsal and dorsolateral surfaces of the buccopharyngeal region primitively have the form of a thin, smooth, mucosal layer. That simple lining continues without interruption posteriorly to the margin of the anterior gill slit. This simple hypothesized plesiomorphous condition is modified in diverse fashions within the Curimatidae.

Vari (1989a:31) applied the term buccopharyngeal complex to all of the diverse elaborations of the soft tissues of the dorsal portions of the buccopharyngeal region found within the Curimatidae. The overall buccopharyngeal complex of curimatids is readily subdivided, in turn, into several discrete components that demonstrate hypothesized derived modifications at diverse supra- and sub-generic levels of universality. Given the different taxonomic levels at which the different components of the buccopharyngeal complex provide phylogenetically useful information, it is most efficient to structure the following discussion and analysis around its four major anatomical subunits. These are: (1) the anteriormost portion of the buccopharyngeal complex situated on the roof of the oral cavity; (2) the posterior lobulate processes located in the buccopharyngeal cavity ventral of the orbits; (3) the fleshy posteromedial flaps located in the region immediately anterior of the area of attachment of the first gill arch to the ventral surface of the neurocranium; and (4) the lobulate processes on the medial portions of the anteroventral surfaces of the first and second gill arches.

ROOF OF THE ORAL CAVITY.—Only two genera in the Curimatidae, *Curimatopsis* and *Potamorhina*, have a smooth, thin layer of soft tissue lining the roof of the oral cavity that is equivalent to the hypothesized primitive condition for that region discussed in the immediately preceding section. The remaining genera of the family, *Psectrogaster*, *Curimata*, *Pseudocurimata*, *Curimatella*, *Steindachnerina*, and *Cyphocharax*, possess a variety of derived, often complex, modifications of the mucosal tissues of the roof of the oral cavity. The elaborations of that tissue layer manifest themselves at several levels of complexity within the family; the simplest of which consists of three relatively small, longitudinally aligned, thin folds on the roof of the cavity. One of the folds is located along the dorsal midline, and is flanked laterally by a fold to each side. This relatively simple system of three weakly developed folds on the roof of the oral cavity is the ontogenetic, and

evidently phylogenetic, basal bauplan from which develop other, varying more elaborate, forms of that component of the buccopharyngeal complex in other curimatid lineages (see discussion in following paragraphs). The common possession of elaborations of the soft tissues on the roof of the oral cavity, either in the form of three weakly developed folds, or as further derived conditions of those structures, was hypothesized by Vari (1989a:31) to be a synapomorphy for the clade consisting of *Psectrogaster*, *Curimata*, *Pseudocurimata*, *Curimatella*, *Steindachnerina*, and *Cyphocharax*.

Two subunits within the clade formed by those seven genera possess notably more elaborate forms of the anterior portion of the buccopharyngeal complex. The first of these, common to all the species of *Curimata* as redefined by Vari (1989b), has the three thin folds on the roof of the oral cavity typical of curimatid outgroups expanded into a series of large, fleshy flaps flanked by a series of associated smaller, secondary fleshy folds (see Vari, 1989a, fig. 28; 1989b, fig. 8). The second elaborate form of the anterior portion of the buccopharyngeal complex within the Curimatidae is found in the majority of the species in *Steindachnerina*. These species are, however, characterized by a different, evidently nonhomologous, type of modification of that portion of the buccopharyngeal complex. Five of the species of *Steindachnerina*, *S. argentea*, *S. bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata*, possess the three simple, thin, longitudinal folds on the roof of the oral cavity common to the proximate outgroups to the genus in the Curimatidae (Figure 1). The remaining members of the genus (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) have that portion of the buccopharyngeal complex considerably more developed, albeit to different degrees. The least pronounced of these last modifications of the primitive intrageneric condition is unique to *Steindachnerina biornata*, which retains three folds on the roof of the oral cavity as occur in *S. argentea*, *S. bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata*. In *S. biornata*, however, the folds are enlarged into much thickened, pendulous flaps extending much further ventrally into the oral cavity than in the last five species. These enlarged flaps in *S. biornata* are superficially reminiscent of the fleshy flaps on the roof of the oral cavity in the species of *Curimata*. The large flaps in *Steindachnerina biornata* are, however, simpler than those of the species of *Curimata*, most obviously in their lack of the secondary folds on the three primary flaps that are characteristic of *Curimata* (Vari, 1989a:31, 32, fig. 28; Vari, 1989b, fig. 8). Vari (1989a:33) noted, furthermore, that under the overall most parsimonious scheme of phylogenetic relationships within the Curimatidae the elaborations of the anterior portion of the buccopharyngeal complex in *Curimata* and *Steindachnerina* are hypothesized to be independently evolved modifications of the three simple folds found in most other genera within the Curimatidae.

The three fleshy flaps on the roof of the oral cavity in *S.*

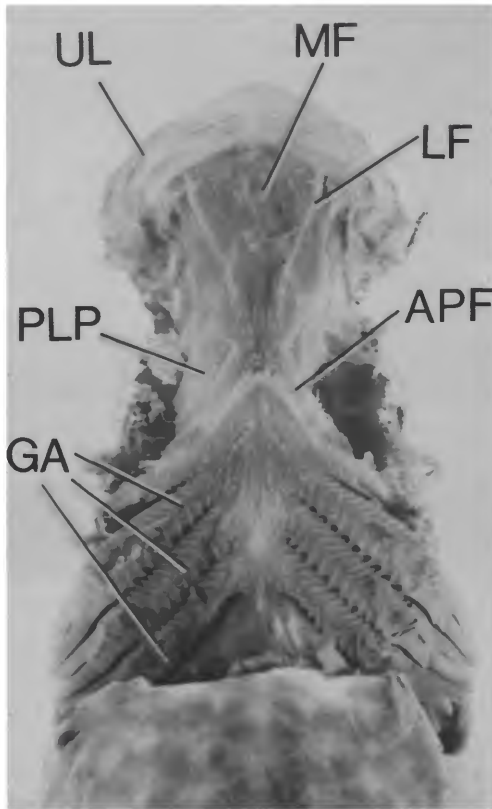


FIGURE 1.—Roof of the buccopharyngeal region and anterior portion of the gill arches of *Steindachnerina leucisca*, USNM 261520; ventral view showing buccopharyngeal complex (hyoid apparatus, ventral portion of gill arches, eyes, and associated tissues removed).

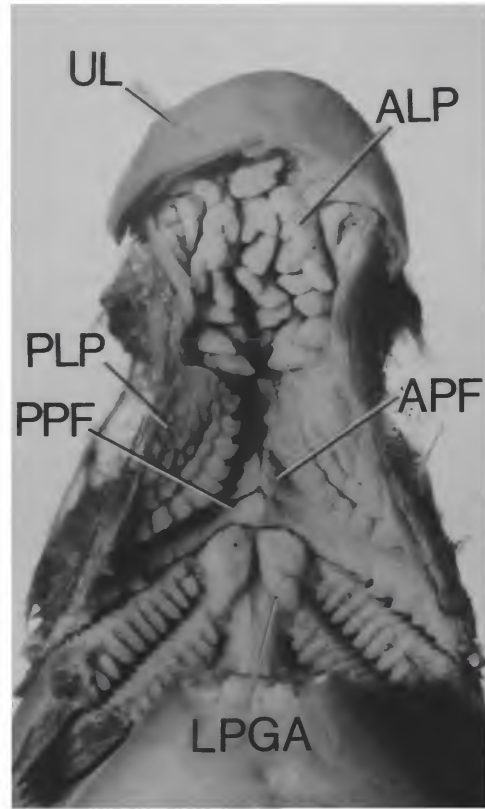


FIGURE 2.—Roof of the buccopharyngeal region and anterior portion of the gill arches of *Steindachnerina hypostoma*, USNM 261493; ventral view showing buccopharyngeal complex (hyoid apparatus, ventral portion of gill arches, eyes, and associated tissues removed).

biornata are, in turn, morphologically intermediate between the weakly developed folds present in *S. argentea*, *S. bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata*, and the more elaborate forms of the complex in *S. amazonica*, *S. atratoensis*, *S. brevipinna*, *S. dobula*, *S. elegans*, *S. fasciata*, *S. gracilis*, *S. guentheri*, *S. hypostoma*, *S. insculpta*, *S. notonota*, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa*. All of those fifteen species have varying numbers of secondary fleshy lobulate bodies extending from the three thick fleshy flaps dangling ventrally into the oral chamber. *Steindachnerina atratoensis* is unique among these species in having only one series of small lobulate bodies situated on the anterior portions of the three primary folds. The other fourteen species in this assemblage (*amazonica*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) have the mucosal tissues of the roof of the oral cavity remarkably expanded to form a close-set mass of distinctly lobulate, occasionally terminally bifid, fleshy processes extending ventrally into the buccal cavity (Figure 2,

ALP). Ontogenetic series including specimens of a broad size range are available for only some of the species (*brevipinna*, *elegans*, *guentheri*, *hypostoma*, and *pupula*) in this assemblage of 14 species. That material indicates that at least in those species the lobulate processes arise as outgrowths of three simple fleshy flaps comparable to those in adults of *S. biornata*. Furthermore, in those developmental series the number of lobulate bodies, their size, and the complexity of their overall shape increase ontogenetically. This progressive ontogenetic elaboration is congruent with a hypothesis of the derived nature of the lobulate bodies. That polarity hypothesis agrees with that based on outgroup comparison for these fourteen species of *Steindachnerina*.

The modifications of the anterior portion of the buccopharyngeal complex thus manifest themselves at three levels of complexity within *Steindachnerina*. Each of the increasingly elaborate modifications of this system is considered synapomorphic for the involved species possessing it. The expansion of the thin folds on the roof of the oral cavity either into thick

flaps (*biornata*) or beyond that condition into thickened flaps bearing lobulate ventral processes is a shared derived feature for sixteen species of *Steindachnerina* (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 21). The possession of one or more rows of lobulate fleshy bodies on the ventral surface of the three thick flaps on the roof of the oral cavity represents a synapomorphy for fifteen species of the genus (*amazonica*, *atratoensis*, *brevipinna*, *dobula*, *elegans*, *gracilis*, *fasciata*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 26). Finally, the presence of multiple series of highly developed, sometimes terminally bifid, lobulate fleshy structures on the anterior portion of the buccopharyngeal complex is a shared derived feature common to fourteen members of the *Steindachnerina* (*amazonica*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 30).

POSTERIOR LOBULATE PROCESSES.—The soft tissues of the roof of the buccopharyngeal cavity situated posterior of the fleshy flaps and/or lobulate bodies discussed in the immediately preceding section also undergo diverse alterations within *Steindachnerina*. One of the most pronounced of these modifications involves the elaborations of the soft tissues of the portion of the buccopharyngeal complex located ventral and ventromedial of the orbit. In *Curimatopsis*, *Potamorhina*, and *Psectrogaster*, that portion of the buccopharyngeal mucosae has the form of a convex surface lined with a smooth, thin, soft mucosal tissue layer, a condition similar to that common to outgroups to the Curimatidae. That portion of the buccopharyngeal region in the remaining curimatid genera (*Curimata* (see Vari, 1989a, fig. 28), *Pseudocurimata*, *Steindachnerina*, *Curimatella*, and *Cyphocharax*) is thickened into a distinct fleshy pad situated ventral of each orbit. In their simplest condition, these paired structures, termed the posterior lobulate processes of the buccopharyngeal complex by Vari (1989a:33), are delimited medially by a roughly semicircular series of small to moderately sized, fleshy, ventrally directed, finger-like projections. These projections form the margin of a patch of proportionally smaller fleshy papillae that extend laterally from the medial semicircular series of enlarged papillae to the lateral margin of the buccopharyngeal cavity (Figure 1). Such relatively simple, moderately developed posterior lobulate processes occur throughout *Curimata*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax*, but within *Steindachnerina* they are found only in *S. argentea*, *S. conspersa*, *S. bimaculata*, *S. leucisca*, and *S. binotata*. The remaining species of *Steindachnerina* (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) have the fleshy processes that form the pads more highly developed. These sixteen species have both particularly well-developed

lobulate bodies along the median margin of each posterior lobulate processes and relatively larger papillae across the entire ventral surface of each pad (Figure 2, PLP). Such highly developed fleshy bodies on the posterior lobulate processes are unique to these curimatids among all examined characiforms, and are thus hypothesized to represent a synapomorphy for that assemblage of species (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 22).

ANTERIOR POSTEROMEDIAN FLAP (APF).—Two distinctly triangular, fleshy flaps on the roof of the buccopharyngeal region are associated with the possession of posterior lobulate processes in the majority of curimatids. These structures, the anterior and posterior posteromedian flaps (Figures 1 and 2, APF and PPF), situated posteromedial to the lobulate processes, are most highly developed along the dorsal midline and taper progressively laterally. The anterior posteromedian flap (APF) has a smooth or slightly crenulate posterior margin in outgroups to *Steindachnerina* within the Curimatidae. That simple condition is, in turn, typical of all species of *Steindachnerina* with the exception of *S. argentea*, *S. bimaculata*, *S. binotata*, *S. conspersa*, and *S. leucisca*. Instead, these five species have a series of relatively small, discrete, fringe-like, fleshy processes along the posterior margin of the flap (Figure 1, APF). In light of the unique nature of the structures in those five species both within the Curimatidae and among examined outgroups they are hypothesized to be a synapomorphy for this subunit of *Steindachnerina* (SYNAPOMORPHY 5).

LOBULATE PROCESSES OF FIRST AND SECOND GILL ARCHES (LPGA).—The fleshy lining of the buccopharyngeal region in the region where the first and second gill arches articulate with the ventral portion of the neurocranium is typically smooth and simple in examined characiforms and among most curimatids. Within *Steindachnerina* this simple morphology of the mucosal tissues in this region is limited to *S. argentea*, *S. bimaculata*, *S. binotata*, *S. conspersa*, and *S. leucisca* (Figure 1). All other members of the genus have the soft tissues of the anteroventral surface of the proximate sections of the first and second gill arches expanded into a series of moderately to well-developed fleshy papillae. This series of closely packed papillae extends without interruption across the anteromedial portions of the first and second gill arches, forming a longitudinally ovoid fleshy mound (Figure 2, LPGA). The ovoid mounds of papillae on each side of the gill arches are, however, distinctly separated from each other medially by an area of smooth, grossly unmodified soft tissue. In light of their unique nature among examined characiforms, these structures are hypothesized to be a shared derived character for the species of *Steindachnerina* that possess them (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 23).

The various modifications described in the immediately preceding sections form very elaborate fleshy complexes on the roof of the buccopharyngeal region. In the majority of species of *Steindachnerina* the resultant complex extends from immediately posterior to the upper lip posteriorly onto the anterior portions of the dorsal sections of the gill arches (e.g., *S. hypostoma*, Figure 2). Vari (1989a:33) notes that histological examinations of the elaborate fleshy modifications of the lining of the roof of the buccopharyngeal region in various groups of curimatids revealed that those structures have large concentrations of mucus producing cells in their surface layers. That unusual concentration of mucus producing tissues led him to propose that the entire buccopharyngeal complex may be an adaptation associated with the microphagous feeding habits of curimatids.

Reid (1982) describes an evidently analogous mucosal system among Old World cyprinid ostariophysans, and proposes that the highly developed buccopharyngeal modifications in those groups (the vomero-palatine organ of Reid's terminology) serves to produce large amounts of precipitating mucus that traps ingested particles, in particular aufwuchs (a conglomerate of algae, perizoon communities, fungi, inorganic matter, and detritus). Similar particle precipitating systems repeatedly appear to have evolved independently; also having been reported in fishes in the family Cichlidae (Moriarty et al., 1973), in addition to the Cyprinidae and Curimatidae, and outside of fishes it is known to occur in some anuran tadpoles (Wasserzug, 1972).

Vari (1989a:33) notes that limited field observations during low water levels on a few curimatid species in the rivers of Surinam (not including any species of *Steindachnerina*) suggest that one of the major feeding modes in some members of the family involves picking aufwuchs from the substrates of rivers and streams. Similar feeding behavior also has been reported for one curimatid species of the genus *Cyphocharax* in the Pantanal of Brazil by Sazima (1986:55; 1988:191). Aufwuchs is relatively abundant in Neotropical freshwaters even during low water periods. Furthermore, as Goulding et al. (1988:64) point out, during high water levels the area covered by aufwuchs dramatically increases both as the waters cover a greater land surface and as a consequence of the inundation of tree trunks, limbs, and leaves in flooded rainforests.

Detailed studies of the diets of species of *Steindachnerina* are only available for two species of the genus, both with distributions limited to the eastern portions of Brazil. Azevedo et al. (1938:487-489) in their study of *Steindachnerina notonota* (identified by those authors as *Curimatus elegans*) note that the species ingested "microscopic algae" of various families, inorganic matter, and presumably accidentally, some insect parts. Nomura and Taveira (1979:332) were able to identify at least twenty-four different types of filamentous and microscopic algae in the stomachs of *S. insculpta* (their *Curimatus elegans*). de Godoy (1975:591), in a less finely resolved analysis of stomach contents, also finds that such

algae were major food items for the same species (identified by him as *Pseudocurimata elegans*). None of these studies critically examines the contribution of the other components of the aufwuchs, the perizoon communities and fungi, to the stomach contents of these curimatids.

It is neither clear how the algal material found in the stomachs of *S. notonota* and *S. elegans* is selected by the species, nor are there any observations on the method by which the buccopharyngeal complex assists in preliminary processing of these ingested food items. The limited data on the food habits of species of *Steindachnerina* is nonetheless compatible with a hypothesis that the well-developed buccopharyngeal complex in the species of *Steindachnerina* serves as a particle precipitating, mucus producing system. The data are too sparse, however, to provide any insight into how the particular modifications of the buccopharyngeal complex in the various subgroups of *Steindachnerina* might correlate with the selection and utilization of different types and sizes of food items.

BRANCHIAL ARCHES

The ossifications, cartilages, diverse connective tissues, and muscles that contribute to the branchial arches form a very complex system that demonstrates a significant degree of variation within the Curimatidae and proximate outgroups. This variation provides a great deal of phylogenetically useful information pertinent to hypotheses of the relationships of the Curimatidae to other member of the Characiformes (Vari, 1983), with respect to generic relationships within the Curimatidae (Vari, 1989a) and for the elucidation of intrageneric phylogenies in the family (e.g., *Curimata*, Vari, 1989b). Over three-quarters of the species of *Steindachnerina* possess varying complex, grossly obvious modifications of the soft mucosal tissues of the buccopharyngeal region (see immediately preceding discussion under "Buccopharyngeal Complex"). Those modifications, which presumably function in initial food item manipulation, are paralleled by restructurings of components of both the dorsal and ventral portions of the gill arches, the second stage food item processing system. The various components of the gill arches will be treated individually in the following sections in order to facilitate the discussion and visualization of the phylogenetic distribution of the numerous derived features.

DORSAL PORTIONS OF BRANCHIAL ARCHES.—Two of the four synapomorphies advanced by Vari (1989a:58) as distinguishing *Steindachnerina* within the Curimatidae involve modifications of components of the dorsal portions of the branchial arches. An additional series of modifications serving to characterize subunits of the genus have also been discovered during this study.

First Infrapharyngobranchial (PB₁): Vari (1989a:25) notes that the relative proportions of the cartilaginous versus ossified portions of the first infrapharyngobranchial in *Steindachnerina* differ from those in other curimatid genera.

Contrary to the condition in outgroups, the species of *Steindachnerina* have the proximal cartilaginous portion of the element particularly well developed proportional to the distal ossified portion of the element that extends dorsolaterally and is joined by connective tissue to the ventral surface of the neurocranium. This shift in the relative proportions of the ossified and cartilaginous components of the first infrapharyngobranchial is thus considered a synapomorphy for the species of *Steindachnerina* (see Vari (1989a:25) for a more detailed discussion) (SYNAPOMORPHY 1).

First Epibranchial (E_1): A single autapomorphic modification of the first epibranchial has been discovered in one species of *Steindachnerina* (*quasimodoi*) during the course of this study. In all the species of *Steindachnerina* the uncinat process of the first epibranchial has a relatively elongate flange extending posteriorly along the posterodorsal margin of the process. In larger individuals of the genus that flange is, in turn, reinforced anterobasally by a weakly developed low ridge. That additional basal process serves as the area of attachment for various ligamentous tissue bands extending dorsally to the ventral surface of the neurocranium. *Steindachnerina quasimodoi* has that low ridge along the anterolateral surface of the uncinat process of E_1 markedly expanded into a very well-developed, triangular process extending anteriorly over the concave central trough that runs the length of the dorsal surface of E_1 . Such a large secondary process arising from the uncinat process of *S. quasimodoi* is hypothesized derived given its unique nature both within *Steindachnerina* and across the Curimatidae (SYNAPOMORPHY 44).

Second Infrapharyngobranchial (PB_2): Vari (1989a:25) notes that the second infrapharyngobranchial in the species of *Steindachnerina* is distinctive in the way in which it articulates with the anterior portion of the third infrapharyngobranchial (PB_3). Among curimatids the relative position of these two elements is such that the lateral surface of the anterior section of PB_3 lies against the medial surface of the midsection of PB_2 . Those elements are additionally joined together by loose connective tissues bands. Although the two infrapharyngobranchials in outgroup curimatids are typically in close contact, neither of the proximate surfaces of the two elements in members of the family is restructured to reinforce the joint. All species of *Steindachnerina* have, in contrast, a varyingly developed, but distinct depression on the medial surface of the anterior portion of the second infrapharyngobranchial. That depression receives the lateral articular surface of the anterior portion of the third infrapharyngobranchial and is delimited dorsally and ventrally by longitudinally aligned bony flanges termed by Vari (1989a:25) the dorsolateral (DLF) and ventrolateral (VLF) flanges respectively (Figure 3). Although a process evidently comparable to the DLF occurs on the second infrapharyngobranchial in the species of curimatid genus *Psectrogaster*, the structure in that genus is hypothesized homoplastic relative to the somewhat similar DLF process in the species of *Steindachnerina* both within the most parsimoni-

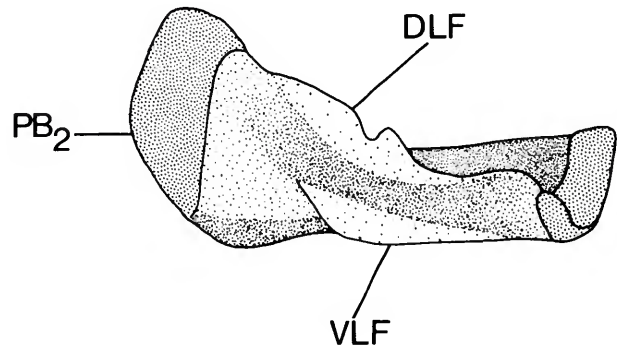


FIGURE 3.—*Steindachnerina hypostoma*, USNM 167802, second infrapharyngobranchial, right side, posterior view, medial to left (denser patterned stippling represents cartilage).

ous hypothesis of intrafamilial phylogenetic relationships (Vari, 1989a:60), and within the intrageneric phylogeny proposed herein for *Steindachnerina*. The presence of the distinct depression on the medial surface of the second infrapharyngobranchial that receives the anterolateral portion of the third infrapharyngobranchial and the associated flanking bony processes are thus hypothesized to together constitute a synapomorphy for the species of *Steindachnerina* (SYNAPOMORPHY 2).

Five species of *Steindachnerina* (*argentea*, *bimaculata*, *binotata*, *consersa*, and *leucisca*) have relatively shallow depressions on this surface of PB_2 with the dorsolateral and ventrolateral flanges in these species obvious, although not pronounced. In contrast, the depression and associated flanges on PB_2 are particularly well developed in the remaining 16 species of *Steindachnerina* (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*). As a consequence, the trough formed by the articular depression and associated flanges is particularly pronounced in that assemblage (Figure 3). That further development of the articular depression on the second infrapharyngobranchial beyond the condition in the remaining members of the genus is, in turn, considered a synapomorphy for that assemblage of 16 species (SYNAPOMORPHY 24).

Fifth Upper Pharyngeal Tooth-plate (UP_5): Vari (1989b) describes a transversely expanded form of the fifth upper pharyngeal tooth-plate in a small subunit of *Curimata*, and hypothesized that the pronounced widening of the main body of this ossification was derived relative to the narrower form of that element typical for other curimatids. In that discussion Vari notes that a similarly expanded UP_5 also characterized an unspecified subunit of *Steindachnerina*.

A relatively narrow, moderately twisted form of the fifth upper pharyngeal tooth-plate occurs in *Pseudocurimata*,

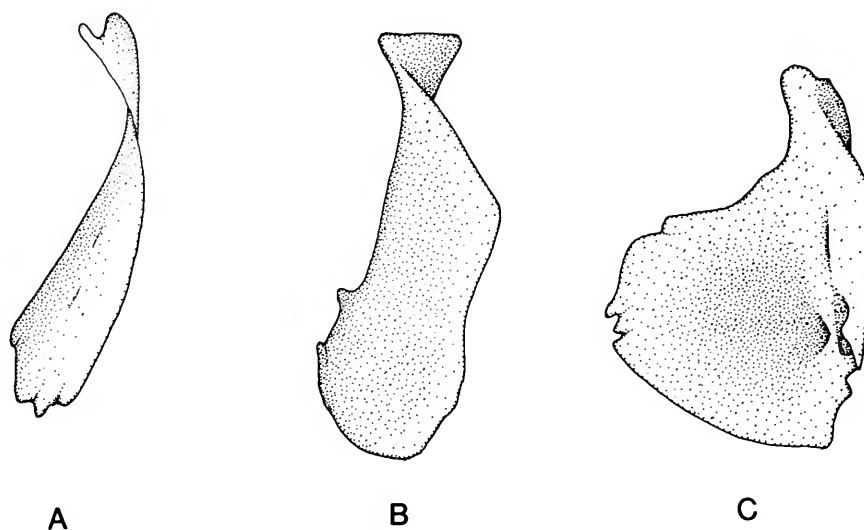


FIGURE 4.—Fifth upper pharyngeal tooth plate of (A) *Steindachnerina conspersa*, USNM 232224, (B) *Steindachnerina guentheri*, USNM 298035, and (C) *Steindachnerina hypostoma*, USNM 167802; left side, ventral view, anterior to top, medial to left.

Cyphocharax, and *Curimatella*, the proximate outgroups to *Steindachnerina* in the terminal polytomy within the Curimatidae recognized by Vari (1989a:57, 58). That narrow condition of the fifth upper pharyngeal tooth-plate is also typical of *Psectrogaster* the sister group to the clade formed by the four cited genera, and is thus hypothesized plesiomorphous for *Steindachnerina*. A narrow form of UP₅ comparable to that in outgroups is found in six species of *Steindachnerina* (*argentea*, *bimaculata*, *binotata*, *biornata*, *conspersa*, and *leucisca*) (Figure 4A). In the remaining 15 members of the family (*amazonica*, *atratoensis*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) the fifth upper pharyngeal tooth-plate is expanded transversely to differing but notable degrees. Furthermore, that ossification in those species has the pronounced longitudinal twisting characteristic of the less-derived form of the bone within the genus (Figure 4A) either greatly reduced (Figure 4B) or nearly completely eliminated (Figure 4C). In 14 of the 15 cited species of *Steindachnerina* the transverse widening of UP₅ is carried only to a moderate degree (Figure 4B), whereas the expansion is particularly pronounced in *S. hypostoma* (Figure 4C). The unique nature of the expansion of UP₅ to varying degrees in a subunit of *Steindachnerina*, both relative to the narrow form of the bone in the other six members of the genus and among proximate outgroup curimatids, is congruent with the hypothesis that it is synapomorphic for the 15 species possessing it (*amazonica*, *atratoensis*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*,

guentheri, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 27). The very wide form of the fifth upper pharyngeal tooth-plate unique to *S. hypostoma* is, in turn, considered an autapomorphy for that species (SYNAPOMORPHY 46).

As noted in the previous paragraph, Vari (1989b) describes a similar transverse expansion of the fifth upper pharyngeal tooth-plate within a subclade of the lineage that he recognizes as *Curimata*. The common occurrence of that derived feature in a subunit of *Curimata* and a clade within *Steindachnerina* is considered to be the result of independent acquisition of that feature on the basis of the most parsimonious phylogenetic hypothesis at the suprageneric level among curimatids (Vari, 1989a:57, 58), and within the intrageneric phylogenies of both *Curimata* (Vari, 1989b), and *Steindachnerina*.

VENTRAL PORTIONS OF BRANCHIAL ARCHES.—*Third Hypobranchial* (H₃): The typical form of the third hypobranchial among characiforms is a dorsoventrally flattened, ventrally unelaborated element without any distinct processes extending from the main body of the bone. Vari (1989a) notes that the third hypobranchial in all members of the Curimatidae differs from that generalized characiform morphology of that element in having the anteroventral portion of the element expanded ventrally into a discrete, longitudinally aligned process that is intimately associated with and ligamentously joined to the lateral surface of the connective tissue covering the ventral aorta. Those ventral processes of H₃, in turn, bear anterior and posterior extensions extending longitudinally along the con-

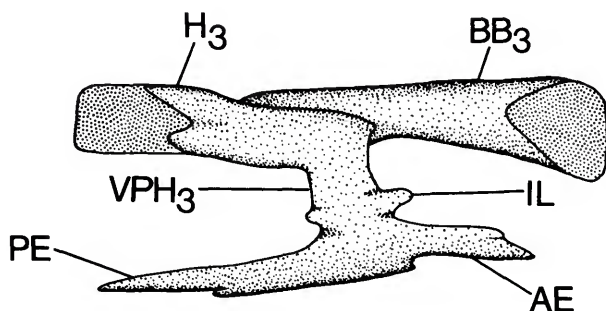


FIGURE 5.—*Steindachnerina hypostoma*, USNM 167802, third basibranchial and third hypobranchial; right side, lateral view, anterior to right (denser patterned stippling represents cartilage).

nective tissues surrounding the ventral aorta (Figure 5, and Vari, 1989a, fig. 23, AE and PE respectively). The anterior extension of the ventral process of the third hypobranchial also serves as the area of attachment of a discrete ligament connecting that process and the ventral surface of the second hypobranchial (H_2). Two further modifications of the ventral process of the third hypobranchial are synapomorphic for *Steindachnerina* or subunits of the genus, and another is autapomorphic for one of the species.

The species of *Steindachnerina* differ from all other curimatids in the morphology of the portion of the ventral process of the third hypobranchial that serves as the point of attachment on that element for the ligament connecting the ventral portions of the second and third hypobranchials. Most curimatids have that portion of the ventral process unelaborated or have only a slightly raised process in the area where the ligament attaches (e.g., *Curimata cyprinoides*, Vari, 1989a, fig. 23, IL). The species of *Steindachnerina*, in contrast, have a distinct bony process extending anteriorly from the anterodorsal surface of the ventral process of the third hypobranchial (e.g., *Steindachnerina hypostoma*, Figure 5, IL). This well-developed secondary process on the ventral process of the third hypobranchial is hypothesized to be a synapomorphy for the members of the genus given its unique nature in that lineage among examined characiforms (SYNAPOMORPHY 3).

Vari (1989b) notes that a species-pair within *Curimata* (*roseni* and *inornata*) is characterized by a discrete anterolateral spur on the anterior extension of the ventral process of the third hypobranchial. The process in the two species is, however, situated distinctly more anteriorly along the anterior extension of that ossification than is the expansion of the process in the species of *Steindachnerina*. This difference raises questions about the homology of the processes within the two genera. The hypothesis of the non-homology of the processes on the anterior extension of H_3 in *Steindachnerina*, on the one hand, and *Curimata roseni* and *C. inornata* on the

other, is also congruent with the most parsimonious hypothesis of intrafamilial relationships (Vari, 1989a) and of relationships within *Curimata* (Vari, 1989b). The common occurrence of the possibly homologous structure in the two genera is thus considered to be at most a homoplasy.

The anterior extension of the ventral process of the third hypobranchial is progressively tapered anteriorly in outgroups to *Steindachnerina* within the Curimatidae (e.g., *Curimata cyprinoides*, Vari, 1989a, fig. 23, AE), and also in the majority of members of the genus (e.g., *Steindachnerina hypostoma*, Figure 5, AE). Four species of *Steindachnerina* (*bimaculata*, *conspersa*, *binotata*, and *leucisca*) have the anterior portion of the process rather subdivided into two distinct, blunt-tipped, terminal processes. Given the simpler forms of the anterior portion of the anterior extension in other curimatids, the possession of this restructuring of that section of the ossification in those four species is considered a synapomorphy for that lineage (SYNAPOMORPHY 7).

One final modification of the third hypobranchial is autapomorphic for *Steindachnerina hypostoma*. In all other curimatids the medial margins of the ventral processes on H_3 that bracket the lateral surface of the ventral aorta are distinctly separated from each other medially. In that generalized condition the intervening space along the ventral surface of the ventral aorta is filled by various connective tissues layers (see Vari, 1989a, fig. 23). In *S. hypostoma*, in contrast, the ventral processes of the third hypobranchial are very distinctive in being fused along the ventral midline, resulting in a single ossification that envelops the ventral and lateral surfaces of that portion of the ventral aorta. Such a fusion is unique to *S. hypostoma* among examined characiforms (SYNAPOMORPHY 47) and thus hypothesized autapomorphic for the species.

BASIHIAL AND BASIHIAL TOOTH-PLATE

The unpaired, median basihyal, the most anterior element of the hyoid arch, extends forward from between the paired dorsal hypohyals toward the symphysis of the dentaries. In characiforms the basihyal consists of a cartilaginous core, more extensive in juveniles, that is partially enveloped to differing extents posteroventrally, posterolaterally, and anteroventrally by a curved sheath of bone. The central and posterior sections of the dorsal surface of the cartilaginous core of the element are usually overlain in characiforms by an independent, sheet-like ossification, the basihyal tooth-plate, which is tightly applied to the dorsal surface of the underlying cartilaginous core of the basihyal. Despite its name, the basihyal tooth-plate does not bear any dentition in characiforms.

The complex formed by the conjoined basihyal and basihyal tooth-plate demonstrates a notable degree of variation within the Curimatidae, both in the overall form of the cartilaginous and ossified portions of the basihyal, and in the presence or absence of the basihyal tooth-plate. The continuum between those diverse morphological plans does not, except in one

instance, permit the ready recognition of discrete character-states within the family. That single exception involves the form of the complex consisting of the basihyal and basihyal tooth-plate in *Steindachnerina*. Among the majority of curimatids the overall form of these conjoined elements ranges from an elongate structure with slightly divergent lateral margins to an elongate, somewhat triangular element with moderately diverging, but nearly straight, lateral margins (see Vari, 1989a, fig. 33A). The species of *Steindachnerina* alternatively have the anterior portion of the bone-cartilage complex greatly expanded laterally with an accompanying pronounced angle in the margins of the complex approximately midway along its longitudinal length (Figure 6). This lateral expansion is most pronounced in the anterior cartilaginous portion of the basihyal, which is many times wider than the posterior section of the ossification (Figure 6, BHC). In some individuals of various species the anteriorly widened portion of the basihyal is flanked laterally on one or both sides by much smaller subsidiary cartilage bodies. The pronounced widening of the anterior portion of the basihyal in *Steindachnerina* is paralleled by a similar, albeit not as extensive, expansion of the overlying basihyal tooth-plate (Figure 6, BHTP). In light of their unique nature within the Curimatidae, these lateral expansions of the anterior portion of the basihyal and associated basihyal tooth-plate are jointly considered a synapomorphy for the species of *Steindachnerina* (SYNAPOMORPHY 4).

Although not approximated within the Curimatidae outside

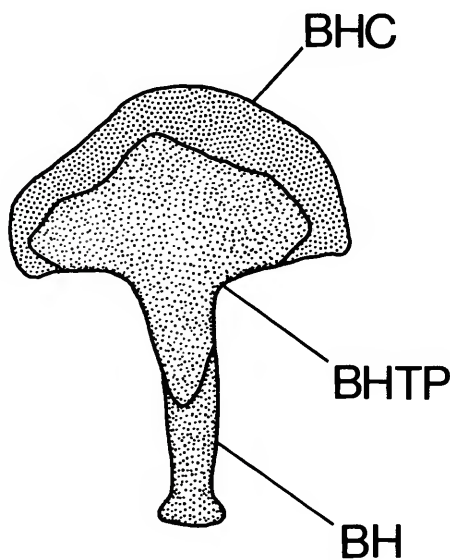


FIGURE 6.—*Steindachnerina bimaculata*, USNM 261450, basihyal and basihyal tooth-plate; dorsal view, anterior at top (denser patterned stippling represents cartilage).

of *Steindachnerina*, a lateral expansion of the anterior portions of the basihyal and basihyal tooth-plate is common to the three genera of the family Prochilodontidae (*Ichthyoelephas* Posada Arango, *Prochilodus* Agassiz, and *Semaprochilodus* Fowler) that together constitute the hypothesized sister group to the Curimatidae (Vari, 1983:47, 48; 1989a:51, 52). As illustrated for *Ichthyoelephas* by Roberts (1973:219, fig. 23), the ossified portions of the basihyal-basihyal tooth-plate complex in prochilodontids (the basihyal of Roberts' figure) are anteriorly expanded in a fashion comparable to that in the species of *Steindachnerina*. The various synapomorphies for the Curimatidae discussed by Vari (1983:48; 1989a:52, 53) and numerous shared derived features in agreement with the placement of *Steindachnerina* within the generic-level hypothesis of relationships within the Curimatidae (Vari, 1989a) are congruent with the hypothesis that the widened complex formed by the basihyal and basihyal tooth-plate in *Steindachnerina* and the Prochilodontidae are independent acquisitions of that feature. The alternative hypothesis, that the common possession of such a basihyal complex in those two lineages represents the retention of the condition common to the ancestor of the Curimatidae and Prochilodontidae, would require the repeated independent loss of that feature in a series of curimatid lineages, and is thus far less parsimonious.

PALATINE ARCH

The four elements of the palatine arch, the palatine, ectopterygoid, mesopterygoid, and metapterygoid, possess a number of modifications within the Curimatidae (Vari, 1989a:43–47). Among the members of *Steindachnerina*, however, only two of those ossifications, the mesopterygoid and metapterygoid, show restructurings useful in proposing a hypothesis of intrageneric relationships.

MESOPTERYGOID (MES).—The morphology of the mesopterygoid typical of the clade consisting of *Psectrogaster*, *Steindachnerina*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax* is characterized by a number of modifications. Two of these alterations are very distinctive, the mode by which the mesopterygoid is suspended from the neurocranium (Vari, 1989a:44, 45), and the ventral expansion of that ossification into the mesopterygoid-quadrate fenestra with the resultant subdivision of that opening into anterior and posterior portions (Vari, 1989a:45; Figure 7, ASMQR and PSMQR respectively). Within *Steindachnerina* the dorsal and posterodorsal portions of the mesopterygoid undergo further modifications that apparently serve to reinforce the area of the mesopterygoid onto which the vomer to mesopterygoid ligament attaches.

As noted by Vari (1989a:44, 45), the mesopterygoid in the clade consisting of *Psectrogaster*, *Steindachnerina*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax* is notably restructured relative to the condition in outgroups, both within and outside of the Curimatidae. The form of the mesopterygoid in the other genera within that clade thus serves as the best approximation

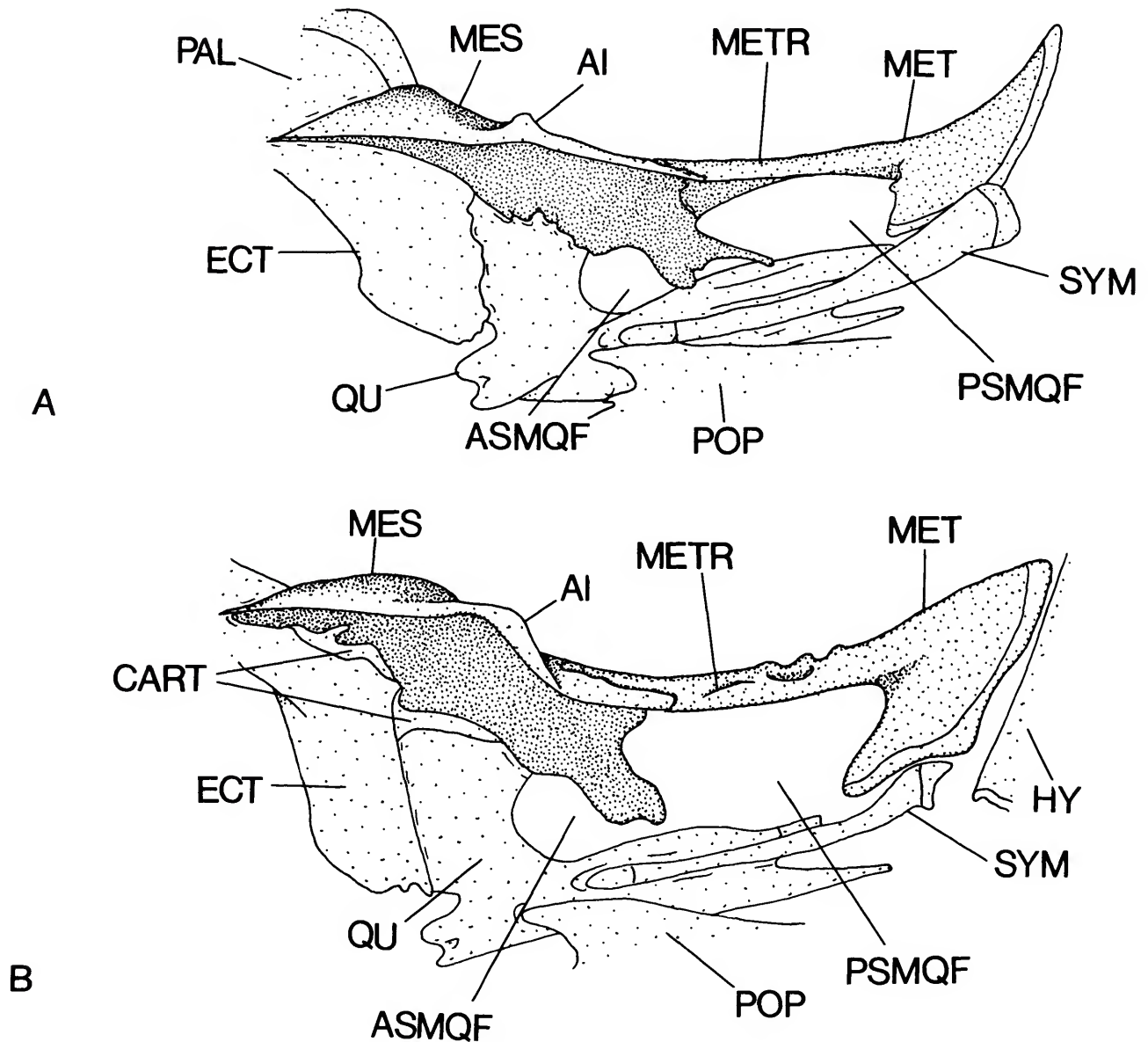


FIGURE 7.—Mesopterygoid and metapterygoid and adjoining elements of (A) *Steindachnerina binotata*, USNM 301960, and (B) *Steindachnerina runa*, USNM 300000; right side, medial view, anterior to left. Proximate portions of neighboring bones outlined and lightly stippled.

of the ancestral condition of the ossification within *Steindachnerina*. In those four genera the region of the mesopterygoid onto which the mesopterygoid-vomer ligament attaches is relatively simple, with the process for the attachment of the ligament (Figure 7, AI) lying in the same general plane as the rest of the medial section of the ossification. The ventral surface

of that process in the outgroup taxa is also relatively smooth. In *Psectrogaster*, *Pseudocurimata*, *Curimatella*, and *Cyphochax* the portion of the mesopterygoid extending posteriorly from the process for the attachment of the ligament to the irregular articulation with the metapterygoid is relatively thin vertically in a medial view (Figure, 7A, MET).

The morphology of the posterior portion of the mesopterygoid in *Psectrogaster*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax* is thus hypothesized primitive when it occurs within seven species of *Steindachnerina* (*argentea*, *atratoensis*, *bimaculata*, *binotata*, *biornata*, *conspersa*, and *leucisca*). In the remaining 14 species in the genus (*amazonica*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) the posterodorsal and posterior portions of the mesopterygoid are altered. Those species have the region of the mesopterygoid proximate to the process onto which the mesopterygoid-vomer ligament attaches more convoluted than in the outgroups. That portion of the ossification is, furthermore, thickened vertically relative to the hypothesized plesiomorphic condition within the genus (Figure 7B). The restructuring of the dorsal portions of the mesopterygoid in those 14 species is paralleled by the presence of a distinct ridge along the ventromedial margin of the portion of the ossification proximate to the process. This group of species also has the posteromedial portion of the ossification adjoining the irregular area of articulation with the metapterygoid vertically thickened (Figure 7B). The increased convolution of the dorsal portion of the mesopterygoid is not approximated elsewhere in the family and that restructuring is thus considered a synapomorphy for 14 species of *Steindachnerina* (*amazonica*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 31). A posterior thickening of the mesopterygoid also occurs in three species of *Curimata* (*mivartii*, *cerasina*, and *aspera*). That thickening is, however, hypothesized to have arisen more than once among curimatids within the context of the overall familial phylogeny (Vari, 1989a:50), and within the hypothesis of phylogenetic relationships within *Curimata* (Vari, 1989b) and that for *Steindachnerina* proposed herein. The thickening of the posterior portion of the mesopterygoid is thus hypothesized as a synapomorphy for those 14 species of *Steindachnerina* (*amazonica*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (SYNAPOMORPHY 32). (Note: The abbreviation AI used by Vari (1989a, fig. 41) in the illustration of the mesopterygoid and associated elements indicates the area of insertion of the discrete ligament extending from that region to the ventral surface of the neurocranium.)

METAPTERYGOID (MET).—Vari (1983:28) hypothesized that a distinct horizontal ridge extending at least part way along the medial surface of the metapterygoid is a synapomorphy for the members of the Curimatidae. In a subsequent paper (Vari, 1989a:45, 46) he proposes that the extension of the ridge across the entire length of the mesopterygoid is a synapomorphy for the clade consisting of *Curimata*, *Psectrogaster*, *Steindachnerina*, *Pseudocurimata*, *Curimatella*, and *Cyphocharax*. The anterior portion of the metapterygoid and the associated metapterygoid ridge in most of these cited genera is only

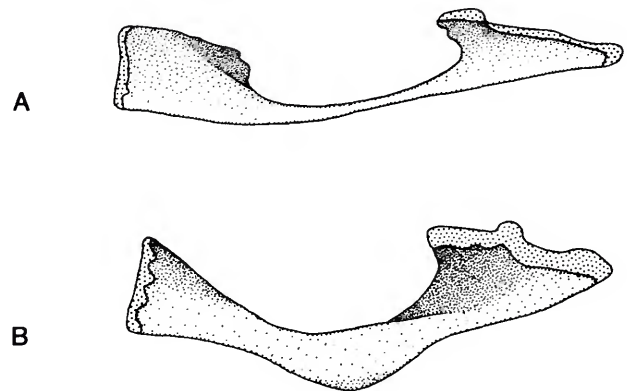


FIGURE 8.—Metapterygoid of (A) *Steindachnerina bimaculata*, USNM 261450, and (B) *Steindachnerina quasimodoi*, USNM 293042; right side, dorsal view, anterior to left (dense patterned stippling represents cartilage).

moderately developed vertically, the condition also common to about half of the species within *Steindachnerina* (*amazonica*, *argentea*, *atratoensis*, *bimaculata*, *binotata*, *biornata*, *conspersa*, *fasciata*, *guentheri*, *leucisca*, and *notonota*). The remaining species of the genus (*brevipinna*, *dobula*, *elegans*, *gracilis*, *hypostoma*, *insculpta*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) have the anterior portion of the metapterygoid considerably vertically thickened. That expanded region of the bone is continuous anteriorly with the comparably expanded posterior portion of the mesopterygoid (Figure 7B).

The metapterygoid in the second subunit of *Steindachnerina* just cited also has its overall morphology modified relative to the condition typical for curimatids. In most members of the family the medial margin of the metapterygoid is straight or only slightly convex medially when it is examined from a dorsal view (Figure 8A). That generalized form of metapterygoid is found within *Steindachnerina* in eleven species (*amazonica*, *argentea*, *atratoensis*, *bimaculata*, *binotata*, *biornata*, *conspersa*, *fasciata*, *guentheri*, *leucisca*, and *notonota*). The other ten species in the genus (*brevipinna*, *dobula*, *elegans*, *gracilis*, *hypostoma*, *insculpta*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) are characterized by a pronounced medial curvature of the middle section of the metapterygoid when the bone is examined from a dorsal view (Figure 8B). This alteration of the overall form of the ossification is unique to those taxa within the Curimatidae and thus hypothesized derived.

Although the two just-discussed features of the metapterygoid, the anterior expansion and the medial curvature of the element, are most parsimoniously hypothesized to be derived on the basis of the conditions of the element in the outgroups to *Steindachnerina*, one of them, the greater vertical development of the anterior portion of the bone, also occurs elsewhere within

the Curimatidae. Vari (1989a:46) also proposes that the anterior thickening of the metapterygoid is a synapomorphy for the genus *Curimata*. Within the overall most parsimonious hypothesis of intrafamilial relationships among curimatids (Vari, 1989a) and that proposed herein of intrageneric relationships within *Steindachnerina*, the common occurrence of that feature in all the species of *Curimata* and a subunit of *Steindachnerina* is hypothesized to be independently derived. Furthermore, the species of *Curimata* do not demonstrate the medial curvature of the metapterygoid common to the noted subunit of *Steindachnerina*. The vertical expansion of the anterior portion of the metapterygoid in ten species of *Steindachnerina* (*brevipinna*, *dobula*, *elegans*, *gracilis*, *hypostoma*, *insculpta*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) is thus considered a synapomorphy for that clade (SYNAPOMORPHY 34). The medial curvature of the medial portion of the ossification in those same species is also hypothesized to be a shared derived feature for the same taxa (SYNAPOMORPHY 35) albeit homoplastically present in the species of *Curimata*.

INFRAORBITALS

The most common arrangement of the infraorbital series within the Curimatidae and proximate outgroups (Prochilodontidae, Anostomidae, and Chilodontidae) is a series of six infraorbitals, each of which bears a varying complex segment of the laterosensory canal system. The infraorbital series has a number of modifications within the Curimatidae, with one of the more notable being the reduction in the number of elements, evidently independently, in two lineages of curimatids that possess a number of evidently pedomorphic reductive features (Vari, 1989a:62, 63; see also discussion in Weitzman and Vari, 1988). Although the number of infraorbitals does not vary

within *Steindachnerina*, a subunit of the genus demonstrates another reductive trend involving a significant shift in the relative sizes and form of the fourth and fifth infraorbitals, with an associated increase in the size of the third infraorbital.

THIRD AND FOURTH INFRAORBITALS (IO_3 and IO_4).—Among most species of *Steindachnerina* and within sequential outgroups to that genus in the Curimatidae, the third infraorbital (IO_3) (the “great suborbital” and “second suborbital” of some authors; see discussion in Weitzman and Fink, 1983:392) is the largest element in the series. That element in *Steindachnerina* is a moderate-sized ossification situated along the ventral border of the orbital rim (Figure 9A). The smaller fourth infraorbital (IO_4) is situated posterodorsal to IO_3 and forms the posteroventral rim of the orbit, with the dorsal margin of the third infraorbital being approximately twice as long as the anterior edge of the fourth.

Four species of *Steindachnerina* have the relative proportions and forms of the third and fourth infraorbitals markedly altered relative to the just described generalized state. In *Steindachnerina bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata* (Figure 9B) the third infraorbital is notably expanded posteriorly. As a consequence, in these four species the ossification extends posteriorly and posterodorsally into the region plesiomorphically occupied by the anterior and anteroventral sections of the fourth infraorbital. The fourth infraorbital, in turn, is both proportionally shortened vertically and narrowed horizontally resulting in an overall triangular element with reduced anterior and posterior plate-like processes extending from the tubular laterosensory canal segment. The expansion of IO_3 and the associated reduction of IO_4 is reflected in the fact that the orbital margin of the third infraorbital in those four species is about three rather than two times the length of the anterior margin of the fourth infraorbital. Given the condition

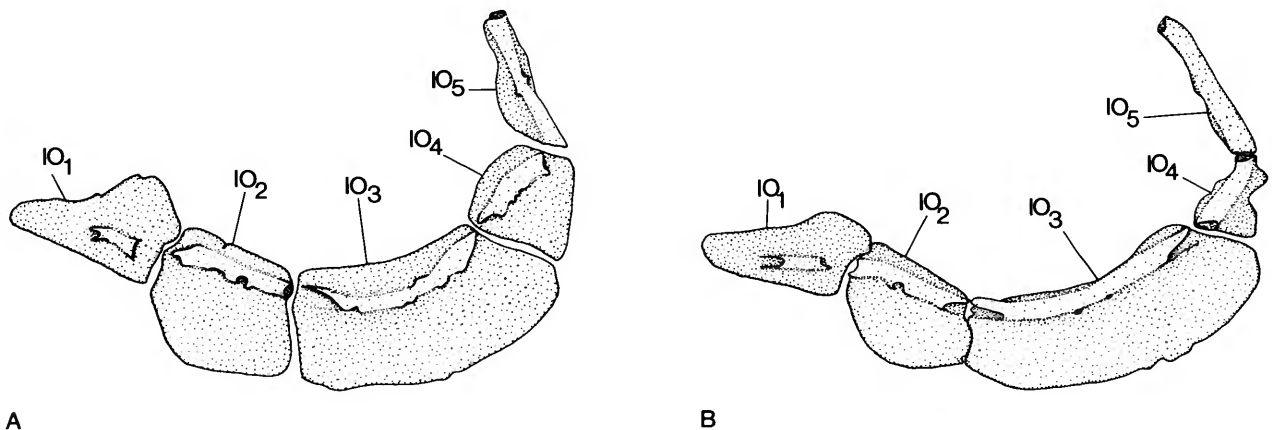


FIGURE 9.—First through fifth infraorbitals of (A) *Steindachnerina brevipinna*, USNM 287022, and (B) *Steindachnerina leucisca*, USNM 261520; left side.

of these elements in the cited outgroups, the changes in the relative proportions and shapes of the third and fourth infraorbitals respectively are considered to represent two synapomorphies for the lineage consisting of *S. bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata* (SYNAPOMORPHIES 8 and 9).

FIFTH INFRAORBITAL (IO₅).—The fifth infraorbital in outgroups to *Steindachnerina* and in the vast majority of species in that genus consists of a tubular ossification flanked by definite plate-like processes along its anterior and posterior margins (see Vari, 1989a, fig. 35). Within *Steindachnerina* the posterior process on IO₅ is typically less developed than in many curimatids, but the majority of species in the genus have an anterior plate-like process that extends to, or nearly to, the posterior margin of the orbit (Figure 9A). The exceptions to that generalization are *Steindachnerina bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata* (Figure 9B), which lack the plate-like anterior extension of the tubular laterosensory canal segment of the fifth infraorbital typical of other species of *Steindachnerina*, or have only small anterior flanges on that structure. The absence of a well-developed plate-like ossification on the anterior margin of IO₅ is hypothesized derived given the presence of a well-developed process on the element in outgroups to the four species clade both within and outside of *Steindachnerina*. Within the final intrageneric phylogeny that feature represents a synapomorphy for *S. bimaculata*, *S. conspersa*, *S. leucisca*, and *S. binotata* (SYNAPOMORPHY 10).

A previously reported derived feature of the infraorbital series within *Steindachnerina* should be commented on at this point. Vari (1989a:37) notes that *Steindachnerina binotata* was purportedly characterized by the absence of a laterosensory canal segment in the first infraorbital; an evidently paedomorphic reduction also present homoplastically in all species of *Curimatopsis* and some species of *Cyphocharax*. That observation was based on a single, relatively small individual of *Steindachnerina binotata*, the only then available cleared and counterstained specimen of the species. Examination of a series of subsequently captured larger specimens has revealed that a laterosensory canal segment is indeed present in the first infraorbital of larger individuals of *S. binotata*.

CRANIAL FONTANELS

One of the major features in the neurocranium of many characiforms is the prominent dorsomedian cranial fontanel that, at their maximum degree of development, extend from the supraoccipital to the mesethmoid. Such extensive openings occur within some Neotropical members of the Characidae (e.g., *Brycon* Müller and Troschel, Weitzman, 1962, fig. 2; *Creatochanes* Günther (= *Bryconops* Kner), Alexander, 1964, fig. 2; *Pygocentrus* Müller and Troschel, and *Serrasalmus* Lacépède, Machado-Allison, 1985, figs. 6, 13; *Oligosarcus* Günther (as *Paroligosarcus* Amaral Campos and Trewavas), Menezes, 1969, fig. 64), and the New World families

Hemiodontidae (e.g., *Hemiodus* Müller, Roberts, 1974, fig. 1) and Chilodontidae. Among African characiforms, elongate fontanel typify the Citharinidae (e.g., *Citharinus* Cuvier, Daget, 1962, fig. 7) and some members of the Distichodontidae (e.g., *Xenocharax* Günther, Daget, 1960, fig. 7; see also Vari, 1979:290). Less-pronounced apertures are found in some members of the Characidae both in the Neotropics (e.g., *Salminus* Agassiz, Roberts, 1969, fig. 9) and Old World (e.g., *Alestes* Müller and Troschel, Myers, 1929, fig. 1), the Anostomidae (e.g., *Pseudanos* Winterbottom, Winterbottom, 1980, fig. 53), and most members of the Old World family Distichodontidae (e.g., *Nannaethiops* Günther, Daget, 1965, fig. 7; see also Vari, 1979:290). The fontanel are greatly reduced or absent in various characiform groups including the Lebiasinidae (Weitzman, 1964, fig. 2), Erythrinidae (Gregory, 1933, fig. 68), and Gasteropelecidae (Weitzman, 1954, fig. 2).

The presence and absence of the dorsomedian cranial fontanel within various subunits of the Characiformes, and the diverse degrees of development of the apertures, when present, makes it impossible to generalize at this time on the condition of the opening primitive for the order. Nonetheless, data from proximate outgroups to *Steindachnerina*, both within the Curimatidae and outside of that family, allows us to reasonably advance a hypothesis about the plesiomorphic condition within the genus. In the Prochilodontidae, the hypothesized sister clade to the Curimatidae, an elongate fontanel occurs in *Prochilodus* and *Semaprochilodus*, which together include the vast majority of species in the family. The opening is somewhat reduced in *Ichthyoelephas*, the least speciose prochilodontid genus (see Roberts, 1973, fig. 2). Extensive dorsomedian cranial fontanel extending from the supraoccipital to the mesethmoid also characterize all curimatid genera outside of *Steindachnerina* and most members of the genus. The occurrence of extensive cranial fontanel in sequential proximate outgroups to *Steindachnerina*, both within and outside of the Curimatidae, is congruent with the hypothesis that such a condition is plesiomorphic within the genus. In the hypothesized plesiomorphic bauplan among curimatids the anterior two-thirds of the relatively extensive dorsomedian cranial fontanel is bordered laterally by distinctly separated frontals that are only in contact medially through the epiphyseal bar. The medial margins of the frontals anterior to the epiphyseal bar are either parallel to each other or only converge very gradually anteriorly. The anterior portion of the fontanel is, in turn, formed by a distinct notch on the posteromedial border of the medially situated mesethmoid.

Within *Steindachnerina* such an hypothesized plesiomorphic form of the cranial fontanel occurs in all species of the genus with the exception of *S. quasimodoi*, *S. gracilis*, *S. planiventris*, and *S. hypostoma*. In those species both the mesethmoid and frontals are enlarged relative to the condition in outgroups, resulting in a reduction in the size of the fontanel. Those four species have the posteromedial portion of the mesethmoid expanded posteriorly into a triangular process

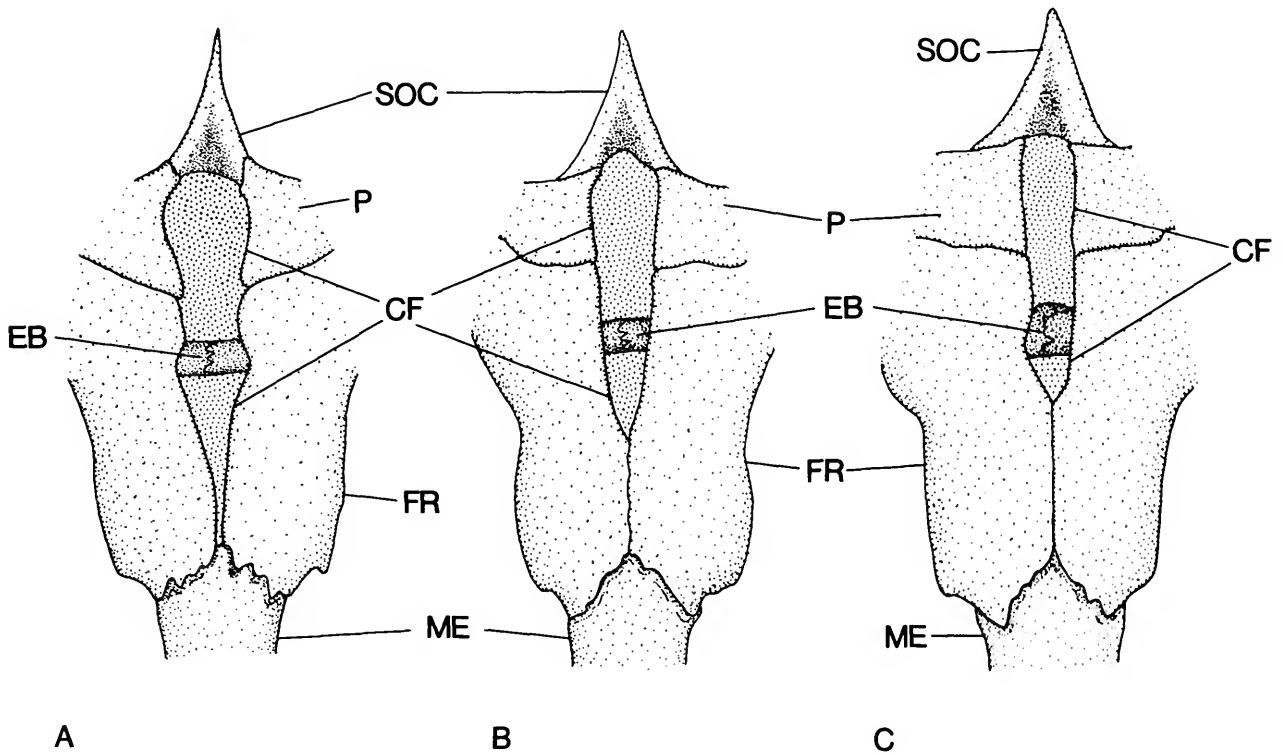


FIGURE 10.—Dorsal view of dorsomedian cranial fontanel and neighboring portions of proximate bones of (A) *Steindachnerina quasimodoi*, USNM 293042, 76.0 mm SL; (B) *Steindachnerina planiventris*, USNM 267987, 62.1 mm SL; and (C) *Steindachnerina hypostoma*, CAS 63192 (Formerly IU 15825), 82.0 mm SL. Cranial fontanels indicated by denser patterned stippling.

extending between the anteromedial margins of the frontals (Figure 10, A to C) rather than retaining the median indentation typical of other curimatids. In *S. quasimodoi* the margins of the frontals bordering the fontanel are somewhat expanded medially relative to the outgroup conditions, and as a consequence are only separated from each other anteriorly by a slight gap (Figure 10A). *Steindachnerina gracilis*, *S. planiventris* (Figure 10B), and *S. hypostoma* (Figure 10C), in turn, have the frontals further expanded medially resulting in a broad line of contact between the contralateral frontals, a condition most pronounced in *S. hypostoma*.

These various modifications of the mesethmoid and frontals are hypothesized to represent synapomorphies at various levels of inclusiveness. The posterior development of the mesethmoid and the medial expansions of the anterior portions of the frontals, at least to some degree, are each considered synapomorphies for *S. quasimodoi*, *S. gracilis*, *S. planiventris*, and *S. hypostoma* (SYNAPOMORPHIES 40 and 41). The further medial expansion of the anterior sections of the frontals beyond the condition in *S. quasimodoi* is, in turn, hypothesized to be a

synapomorphy for *S. gracilis*, *S. planiventris*, and *S. hypostoma* (SYNAPOMORPHY 45). The extensive medial contact between the frontals found in *S. hypostoma* beyond the condition in any other curimatid is hypothesized to be an autapomorphy for that species (SYNAPOMORPHY 48).

PIGMENTATION

Species of the majority of genera within the Curimatidae do not show many marked differences in the pigmentation patterns observable in preserved specimens. *Steindachnerina* is in many ways the most notable exception to that generalization, with a relatively significant amount of intrageneric variation of the dark pigmentation on the body and median fins. Furthermore, much of this intrageneric variation is quite discrete and thus readily applicable to phylogenetic analyses.

Four members of *Steindachnerina* (*leucisca*, *binotata*, *bimaculata* and *consersa*) have distinctive patterns of dark pigmentation along the mid-dorsal surface of the body in the region between the posterior margin of the head and the origin

of the dorsal fin. In each of these species there is a well-developed, dark, longitudinally elongate, mid-dorsal spot of dark pigmentation situated slightly posterior of the tip of the supraoccipital spine. These four species also have a very distinct saddle-shaped dark spot straddling the dorsal midline immediately anterior to the origin of the dorsal fin. The possession of both of these pigmentation patches are unique to the lineage consisting of *S. leucisca*, *S. binotata*, *S. bimaculata*, and *S. conspersa* within the Curimatidae, and thus are hypothesized to represent synapomorphies for the clade composed of these four species (SYNAPOMORPHIES 11 and 12). A subgroup of that assemblage, *Steindachnerina bimaculata*, *S. binotata*, and *S. leucisca*, is characterized by a distinctive pattern of one or more longitudinal series of small dark spots on the lateral and dorsolateral surfaces of the body in adults of the species (Figures 12, 15, 24). These spots vary in number and intensity between and within the three species, but the presence of such spots is not approximated elsewhere within the Curimatidae. Thus, the possession of such spots is hypothesized to be a derived feature supporting an hypothesis that the species are each other's closest relatives (SYNAPOMORPHY 14).

One of the more distinctive pigmentation features common to multiple species of *Steindachnerina* is the varyingly developed pattern of dark pigmentation associated with the scales along at least the posterior portion of the lateral line (see photographs under species descriptions). This dark pigmentation is distinct from the underlying midlateral stripe of dusky pigmentation found in many members of the genus. A superficial, dark, midlateral pigmentation pattern is very obvious in adults of ten members of the genus (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *elegans*, *fasciata*, *guentheri*, *insculpta*, *notonota*, and *runa*). Some of these species have the pigmentation developed into a broad, dark, midlateral stripe, and all of these taxa have some expansion of the dark pigmentation along the caudal peduncle. A less obvious, but evidently homologous, pattern of dark pigmentation is typically present to some degree in juveniles of *S. hypostoma* (Figure 26) and juveniles and adults of *S. quasimodoi*, *S. planiventris*, and *S. gracilis*. No indication of the stripe has been found in examined specimens of *S. pupula*, and such pigmentation only occurs in rare individuals of *S. dobula*. Given the absence of such a dark pigmentation along the lateral line in outgroups to *Steindachnerina* within the Curimatidae, the possession of such dark midlateral pigmentation at some point during development is hypothesized to be derived. Within the overall most parsimonious hypothesis of relationships within *Steindachnerina* the species with distinct dark markings along the lateral line do not, however, constitute a monophyletic group. Such pigmentation is rather assumed to have undergone secondary reduction within the lineage. Under that scheme the lateral-line pigmentation is hypothesized to be a synapomorphy for the clade consisting of *S. amazonica*, *S. atratoensis*, *S. biornata*, *S. brevipinna*, *S. dobula*, *S. elegans*, *S. fasciata*, *S. gracilis*, *S. guentheri*, *S. hypostoma*, *S. insculpta*, *S.*

notonota, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa* (SYNAPOMORPHY 25). The absence of a distinct dark stripe along the lateral line (*S. pupula* and *S. dobula*), or a faint version of such pigmentation (*S. quasimodoi*, *S. planiventris*, *S. hypostoma*, and *S. gracilis*) is, in turn, hypothesized to be a derived secondary reduction for those six species (SYNAPOMORPHY 37) relative to the more highly developed form of that pigmentation in the sequential outgroups to that assemblage. The absence of the pigmentation in nearly all examined specimens of *S. dobula* and *S. pupula* is, in turn, hypothesized to be a further derived secondary reduction of the pigmentation (SYNAPOMORPHY 38).

Three species of *Steindachnerina* (*argentea*, *conspersa*, and *bimaculata*) have a discrete, small spot of dark pigmentation on the basal portions of the middle rays of the caudal fin. Such a pattern of pigmentation does not occur elsewhere in the genus or proximate outgroups and is thus hypothesized to be derived. The phylogenetic distribution of the feature is, however, not congruent with the overall most parsimonious hypothesis of intrageneric relationships. *Steindachnerina conspersa* and *S. bimaculata* share numerous derived features with *S. leucisca* and *S. binotata*, which lack that pigmentation pattern. *Steindachnerina bimaculata*, in turn, shares a derived detail of body pigmentation with *S. leucisca* and *S. binotata*. In light of those features it is most parsimonious to hypothesize that the possession of the small spot of dark pigmentation on the basal portions of the middle rays of the caudal-fin rays is a synapomorphy for the lineage formed by the five species of *Steindachnerina* (*argentea*, *conspersa*, *bimaculata*, *leucisca*, and *binotata*) (SYNAPOMORPHY 6) and was secondarily lost in the clade consisting of *S. leucisca* and *S. binotata* (SYNAPOMORPHY 15). Alternative hypotheses to explain the distribution of the feature require additional assumptions about character shifts.

Another pigmentation pattern of note relative to hypotheses of intrageneric relationships in *Steindachnerina* involves the presence of a variably sized spot of dark pigmentation on at least the basal portions of the middle rays of the dorsal fin. That pattern occurs in the majority of species of *Steindachnerina* (*amazonica*, *argentea*, *atratoensis*, *bimaculata*, *brevipinna*, *conspersa*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *notonota*, *planiventris*, *pupula*, and *quasimodoi*). The remaining species of *Steindachnerina* (*biornata*, *binotata*, *dobula*, *hypostoma*, *insculpta*, *leucisca*, and *runa*) lack such pigmentation at all observed ontogenetic stages. Discrete spots of pigmentation on the middle rays of the dorsal fin are relatively rare within the Curimatidae, occurring outside of *Steindachnerina* only in some species of *Cyphocharax*, in which they are typically positioned somewhat differently. On the basis of such a restricted distribution of the feature within the family, the possession of such pigmentation must be considered derived within the Curimatidae. The species with a dark spot on the basal portion of the dorsal fin do not, however, form a monophyletic group within the overall most parsimonious

hypothesis of relationships within *Steindachnerina*. Under that scheme of relationships two equally parsimonious hypotheses exist to explain the distribution of the spot of dark pigmentation on the dorsal fin. These two alternatives have in common three assumptions concerning the distribution of the lack of the dorsal-fin spot at subgeneric phylogenetic levels. Under both of these scenarios the absence of the spot in *S. hypostoma* is an autapomorphic secondary loss (SYNAPOMORPHY 49). Similarly, both schemes agree in having the lack of the pigmentation on the fin of *S. runa* and *S. insculpta* as a derived loss of the feature for the clade consisting of these species (SYNAPOMORPHY 36), with the same assumption applying both to the unmarked fin in the lineage formed by *S. leucisca* and *S. binotata* (SYNAPOMORPHY 16), and the autapomorphic absence of pigmentation on the dorsal fin in *S. dobula* (SYNAPOMORPHY 39). The two hypotheses differ, however, in their assumptions at higher phylogenetic levels. Under one of the alternatives the spot was present in the ancestor of *Steindachnerina*, thus representing a synapomorphy for the genus, and was subsequently lost four times in the lineages and species noted above, and additionally it is assumed to have been secondarily lost in *S. biornata*. That evolutionary scheme makes six assumptions involving one gain and five independent losses. The alternative hypothesis assumes the four losses noted above along with the independent gain of the pigmentation in the ancestor of the lineage consisting of *S. argentea*, *S. bimaculata*, *S. conspersa*, *S. binotata*, and *S. leucisca*, and in the ancestor to the lineage formed by *S. amazonica*, *S. atratoensis*, *S. brevipinna*, *S. dobula*, *S. elegans*, *S. fasciata*, *S. gracilis*, *S. guentheri*, *S. hypostoma*, *S. insculpta*, *S. leucisca*, *S. notonota*, *S. planiventris*, *S. quasimodoi*, and *S. runa*. This alternative also makes six assumptions, namely two independent gains associated with four separate subsequent losses. No evidence exists to choose between these two equally parsimonious sets of assumptions, and neither higher-level phylogenetic hypothesis would change the final topology of the resulting cladogram. As a consequence, only the assumptions common to the two alternative hypotheses are used as synapomorphies in the analysis and included in the "Synapomorphy List and Phylogenetic Reconstruction" (synapomorphies 16, 36, 39, 48). The incongruent components of the two scenarios, although not incorporated in the phylogenetic analysis, are briefly noted at the appropriate points in that discussion.

Derived features of the pigmentation patterns are autapomorphic for three species of *Steindachnerina*. *Steindachnerina atratoensis* and *S. fasciata* are each characterized by a series of longitudinal stripes along the body. On first analysis these might be taken to represent a shared derived feature indicative of a sister-group relationship between the two species. Closer analysis shows that the main stripe extending along the lateral line in the two species is evidently equivalent although differing in the degree of development. That stripe in these species is, however, homologous with the stripe present in a large number of species in the family. Thus, although its

possession is derived, it represents a synapomorphy at a considerably higher level of inclusiveness than *S. atratoensis* and *S. fasciata*. The remaining body stripes in *S. atratoensis* and *S. fasciata*, in contrast, are not homologous. Whereas the secondary stripes in *S. atratoensis* are centered along the region of overlap of neighboring scales rows, the longitudinal patterns of spots on the body in *S. fasciata* are situated along the center of each scale row (compare Figures 36, 37 with 39, 40). The patterns of secondary longitudinal markings in the two species are thus hypothesized to be nonhomologous, but given their unique nature within the Curimatidae, are considered autapomorphies for *S. atratoensis* (SYNAPOMORPHY 28) and *S. fasciata* (SYNAPOMORPHY 33) respectively. *Steindachnerina atratoensis* is also characterized by the broad band of dark pigmentation that extends from the tip of the snout across the eye to the rear of the opercle (Figures 36, 37). That feature is unique to the species within the family and is considered an additional autapomorphy for *S. atratoensis* (SYNAPOMORPHY 29).

The final autapomorphic feature of the pigmentation discovered within *Steindachnerina* during this study involves *S. conspersa*. In that species the region of the body proximate to the origin of the dorsal fin typically has much lighter pigmentation than the remainder of the body. This feature, unique to the species within the family, is considered an autapomorphy for the taxon (SYNAPOMORPHY 13).

POSITION OF ANUS

Several morphometric and meristic features also show phylogenetically useful variation within *Steindachnerina*. The first of these involves the position of the anus relative to the origin of the anal fin. In the Prochilodontidae, the sister group to the Curimatidae, curimatid genera outside of *Steindachnerina*, and in most species of *Steindachnerina* the anus is located only a short distance anterior of the origin of the first anal-fin ray. The anal opening and base of the first anal-fin ray are consequently separated by only 1 to 3 series of scales. Six species of *Steindachnerina* have a much larger relative distance between the anus and the anterior ray of the anal fin. This increased space is, in turn, reflected in the greater number of series of transverse scale rows that reach the ventral midline in the area between the anus and origin of the anal fin. The species of *Steindachnerina* with an increased space between those structures and the number of scales along the midventral line in those taxa are as follows: *S. leucisca* (7–8), *S. binotata* (9–11), *S. planiventris* (5–6), *S. quasimodoi* (5–6), *S. gracilis* (6–7), and *S. hypostoma* (6–7).

The number of scales along the ventral midline between the anus and anal fin is a function both of the available space in that gap, and of the relative size of the scales in that area. Indeed, there is no significant difference in the proportional distance between the anus and anal-fin in *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma*, which have 5 to 7 scales in that

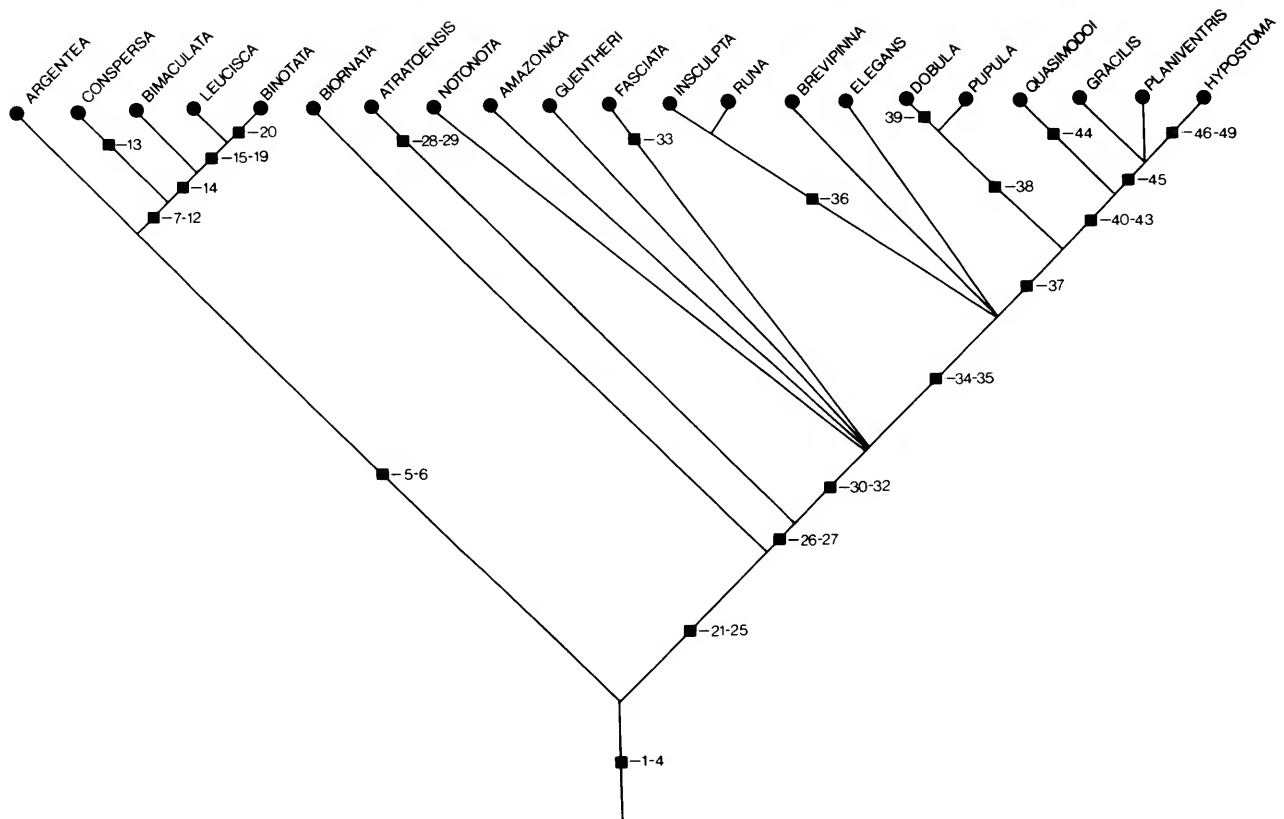


FIGURE 11.—Cladogram of the most parsimonious hypothesis of relationships for the species of the genus *Steindachnerina*. The numbered synapomorphies and autapomorphies of the figure correspond to those of the text (see "Character Description and Analysis" and "Synapomorphy List and Phylogenetic Reconstruction").

area and *S. leucisca* and *S. binotata*, which have 7 to 11 scales in the same region. The higher number of scales in the two latter species correlates with and reflects the proportionally smaller scales found in those species. Thus, it would be inappropriate to use both the greater anus to origin of the anal fin distance, and the higher number of scales in that region in *S. leucisca* and *S. binotata* as independent derived features.

Although the increased distance between the anus and the origin of the anal fin, and the associated higher number of transverse series of scales reaching the ventral midline in that region of the body are considered derived for *S. planiventris*, *S. quasimodoi*, *S. gracilis*, *S. hypostoma*, *S. leucisca*, and *S. binotata*, the distribution of that character is incongruent with the arrived at intrageneric phylogeny (see Figure 11). Within that hypothesis of relationships *S. leucisca* and *S. binotata* are hypothesized to be sister species, with that clade separated by a series of dichotomies from the lineage formed by *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma*. The increased space between the anus and the origin of the anal fin

is thus hypothesized to be homoplastic between those groups of species within the final phylogeny. The attributes are nonetheless synapomorphies for two less universal clades, first that consisting of *S. leucisca* and *S. binotata* (SYNAPOMORPHY 17), and a second lineage formed by *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma* (SYNAPOMORPHY 42).

VERTEBRAE

As can be seen in Table 1 those species of *Steindachnerina* with an increased distance between the anus and anal fin also have absolutely or modally greater numbers of vertebrae than their congeners. The number of vertebrae in those species is also increased relative to the counts in most species of curimatids outside of *Steindachnerina* and the number of vertebrae in those species is thus hypothesized to represent a derived condition. The distribution of an increased number of vertebrae within *Steindachnerina* is incongruent with the overall most parsimonious phylogeny, evidently having arisen

TABLE 1.—Number of specimens of the species of *Steindachnerina* with cited number of vertebrae. Vertebrae incorporated in fused $PU_1 + U_1$ counted as a single element and vertebrae in the Weberian apparatus counted as four elements. Species with posterior margin of anus and origin of first anal-fin ray separated by five or more scales indicated by asterisks. Species arranged in order of presentation on Figure 11.

Species	Vertebrae									
	30	31	32	33	34	35	36	37	38	
<i>argentea</i>	7	68	1							
<i>conspersa</i>				18	27					
<i>bimaculata</i>				10	47	32				
<i>leucisca</i> *								33	53	2
<i>binotata</i> *							1	14	1	
<i>biornata</i>				29	1					
<i>atratoensis</i>				5	23	2				
<i>notonota</i>		22	40							
<i>amazonica</i>		1	7	2						
<i>guentheri</i>		9	34	45	3					
<i>fasciata</i>			4	20	1					
<i>insculpta</i>				28						
<i>runa</i>				3	15					
<i>brevipinna</i>		28	30	30						
<i>elegans</i>			6	33						
<i>dobula</i>			5	74	30					
<i>pupula</i>			8	33						
<i>quasimodoi</i> *						11	36			
<i>gracilis</i> *					8	5				
<i>planiventris</i> *					19	109	7			
<i>hypostoma</i> *						8	86	2		

independently in the ancestor of the species-pair *S. leucisca* and *S. binotata*, and in the ancestor of the lineage consisting of *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma*.

Whereas the number of vertebrae in *S. leucisca* and *S. binotata* does not overlap the counts in the sister group to that pair, *S. bimaculata* and *S. conspersa*, the number of vertebrae in the clade consisting of *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma* slightly overlaps the counts in proximate sister species to that lineage. This difference in the degree of discreteness of the increased number of vertebrae leads me to treat that feature somewhat differently in the two groups. The discrete increased vertebral counts in *S. leucisca* and *S. binotata* are used as a synapomorphy for that species-pair (SYNAPOMORPHY 18). Alternatively, although the increased number of vertebrae in *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma* would admittedly provide additional evidence for the monophyly of that assemblage I prefer, given the partial overlap of those values with counts in proximate outgroups, to conservatively not utilize that feature as a synapomorphy for the lineage formed by those four species. The congruence between increased vertebral number and a greater anus to anal-fin distance raises the question of whether the additional vertebrae in *S. leucisca*, *S. binotata*, *S. planiventris*, *S. quasimodoi*, *S. gracilis*, and *S. hypostoma* were

added to the vertebral column in such a way as to shift the posterior portion of the body, including the anal fin, posteriorly relative to the anus. If it were found that those changes are tied together phylogenetically across the Curimatidae, it would raise the question of the appropriateness of using both the increased number of vertebrae and the greater space between the anus and anal fin as independent synapomorphies. Given the problems with homologizing most individual vertebrae within curimatids across species and genera, it is not possible to determine the exact location of the "new" vertebrae in those six species with any certainty. Similarly, there is no test internal to the phylogeny of *Steindachnerina* that would allow us to resolve this question. Reference to other lineages in the Curimatidae shows, however, that in the genera *Potamorhina* (Vari, 1983:8) and *Pseudocurimata* (Vari, 1989d) of the Curimatidae there occur pronounced intrageneric increases of vertebrae in the absence of an associated increase in the distance between the anus and anal-fin origin within those taxa. It thus appears that the two features are independent within curimatids as a whole. Given the independence of the features in those curimatid lineages and in the absence of any evidence that these attributes are, in contrast, two manifestations of some more encompassing derived modification, the increased vertebral number and greater anus to anal-fin space in the two groupings of species within *Steindachnerina* are tentatively hypothesized to represent separate synapomorphies.

SQUAMATION

In the course of the discussion on the number of scales between the anus and the first anal-fin ray, passing reference was made to the relatively small size of the scales in *Steindachnerina leucisca* and *S. binotata*. The relative size of the scales in these species is best judged in terms of the number of scales in the series along the lateral line from the supracleithrum to the hypural joint. *Steindachnerina leucisca* has 53 to 62 scales in that series and *S. binotata* has 67 to 72. Those counts are higher than in all other species of the genus with one exception, *S. gracilis*, which has 50 to 54 scales in the series. The sequential sister taxa to the species pair formed by *S. leucisca* and *S. binotata* have lower lateral-line scale counts (*S. bimaculata*, 43–49; *S. conspersa*, 38–43; and *S. argentea*, 32–36). Furthermore, the lineage formed by *S. leucisca* and *S. binotata* is quite distant phyletically from *S. gracilis*. In light of those factors the increased number of scales along the lateral line in *S. leucisca* and *S. binotata* is considered a synapomorphy for the species pair (SYNAPOMORPHY 19), with the particularly high count in *S. binotata* hypothesized as an autapomorphy for that species (SYNAPOMORPHY 20). The high number of lateral-line scales in other lineages of the Curimatidae (e.g., *Cyphocharax abramoides* (Kner) and the species of *Potamorhina*; see Vari, 1984a) are hypothesized to be homoplastic within the most parsimonious hypothesis of

intrafamilial phylogeny (Vari, 1989a), and the hypothesis of intrageneric relationships for *Steindachnerina* advanced herein.

BODY FORM

Fernández-Yépez (1948) utilized various aspects of body form, particularly the presence or absence of distinct longitudinal keels and ridges on various parts of the body as the foundation of his generic and suprageneric classification of curimatids. Vari (1989a:63, 64) notes that those external features have evidently undergone a high degree of homoplastic evolution within the Curimatidae when evaluated in the context of an hypothesis of intrafamilial phylogeny based on multiple internal and external characters. Those modifications of the form of the body are, nonetheless, useful in defining some clades within genera. Although the members of *Steindachnerina* differ from each other in overall body form, only one small clade within the genus possesses a discrete modification in the form of one of the surfaces of the body. *Steindachnerina quasimodoi*, *S. gracilis*, *S. planiventris*, and *S. hypostoma* have the prepelvic region of the body distinctly flattened transversely, with an increased number of longitudinal scale series across this region of the body. The flattening of the prepelvic region in these species differs from that in various species of *Curimata* (Vari, 1989b) and *Psectrogaster* (Vari, 1989c) in not having the scales of this portion of the body greatly enlarged compared to the condition of the scales in most curimatids. The scales of the flattened prepelvic region of these species of *Steindachnerina* also differ from the conditions in subunits of *Curimata* and *Psectrogaster* in the absence of the distinct, nearly right angle, flexures of the enlarged scales along the lateral margin of the flattened area, with the flexure conforming to the underlying sharp angles in the body wall. The species of *Curimata* and *Psectrogaster* with flattened prepelvic regions also have numerous features that unite them with congeners characterized by transversely rounded prepelvic regions of the body.

In summary, given the unique nature of the flattened prepelvic region in *S. quasimodoi*, *S. gracilis*, *S. planiventris*, and *S. hypostoma* within *Steindachnerina*, that feature is hypothesized to be a synapomorphy for the lineage consisting of those four species (SYNAPOMORPHY 43), having arisen in a somewhat different form in several other lineages within the Curimatidae.

Synapomorphy List and Phylogenetic Reconstruction

The preceding section details the series of shared derived features common to all members of *Steindachnerina* or subunits of the genus of differing levels of inclusiveness. Vari (1989a) analyzes the relationships of *Steindachnerina* within the Curimatidae. The reader is referred to that publication for further details on, and analysis of, the phyletically more encompassing derived characters pertinent to the question of

the higher-level relationships of *Steindachnerina* within the Curimatidae. Vari (1983) discusses a number of derived features pertinent to the question of the relationship of the Curimatidae to proximate outgroups.

In the following discussion and enumeration the shared derived features congruent with an hypothesis of the monophyly of *Steindachnerina* will be listed first. Further details on some of these character complexes and more in-depth discussions on their polarization are found in Vari (1989a). This is followed by a listing of less universal synapomorphies common to intrageneric clades of *Steindachnerina* together with an enumeration of the known autapomorphies for the species. The synapomorphies and autapomorphies are numbered sequentially in the following text, with the numbering in that section and the immediately preceding "Character Description and Analysis" corresponding to that in Figure 11.

To supplement the brief descriptions of the characters in the following enumeration, consult the table of contents for the location of more complete discussions of the characters, their phylogenetic distribution, and associated polarity assumptions in "Character Description and Analysis." Subsequent to the reconstruction of the most parsimonious hypothesis of phylogenetic relationships within *Steindachnerina* there is a discussion of the known homoplastic characters found in the genus.

The most parsimonious hypothesis incorporating the previously described synapomorphies, including homoplasies and reversals, is presented in Figure 11. The parsimony of this hypothesis was confirmed by use of David L. Swofford's (1985) numeric computer algorithm PAUP (Phylogenetic Analysis Using Parsimony), Version 2.4. The character matrix for the analysis and brief descriptions of the characters are presented in the Appendix, together with further details on the methods used in the analysis.

MONOPHYLY OF *Steindachnerina*

Vari (1989a) lists four features as synapomorphic for the species of *Steindachnerina*. These features are:

1. The expansion of the cartilaginous portion of the first infrapharyngobranchial (PB₁).
2. The ventral and dorsal ridges on the lateral surface of the second infrapharyngobranchial (PB₂) that bracket the anteromedial portion of the third infrapharyngobranchial (PB₃).
3. The attachment of the ligament between the second and third hypobranchials (H₂ and H₃) to a distinct anterior process on the anterolateral surface of the ventral process of the third hypobranchial.
4. The pronounced lateral expansion of the anterior portion of the basihyal and associated basihyal tooth-plate.

As noted under "Pigmentation" there exist two equally parsimonious hypotheses to explain the distribution of the spot of dark pigmentation on the basal portions of the middle rays of

the dorsal fin within *Steindachnerina*. Under one of these hypotheses the possession of pigmentation on the fin would represent an additional synapomorphy for *Steindachnerina*, with a secondary loss of the feature several times within the genus.

INTRAGENERIC RELATIONSHIPS WITHIN *STEINDACHNERINA*

The genus *Steindachnerina*, defined by synapomorphies 1 to 4, consists, in turn, of two major subclades, one consisting of five species and the other of sixteen species.

The first of these, the five species clade consisting of *Steindachnerina argentea*, *S. conspersa*, *S. bimaculata*, *S. leucisca*, and *S. binotata*, is defined on the basis of two derived features.

5. The fringe-like processes along the margin of the anterior posteromedian flap of the buccopharyngeal complex.
6. The presence of a small spot of dark pigmentation near the base of the middle rays of the caudal fin. As noted under "Pigmentation" this character is hypothesized to have been secondarily lost in the sister-species *S. leucisca* and *S. binotata* (see Synapomorphy 16).

Two equally parsimonious hypotheses explain the phylogenetic distribution of the dark spot of pigmentation on the basal portions of the middle rays of the dorsal fin within *Steindachnerina*. One of those hypotheses assumes the apomorphic gain of the spot at this level within the phylogeny. If correct, that scenario would result in an additional synapomorphy for the clade consisting of these five species, albeit with a secondary loss at a less inclusive level (see discussion under "Pigmentation").

The lineage characterized by synapomorphy 5 contains two subclades, *Steindachnerina argentea* and the assemblage consisting of *S. conspersa*, *S. bimaculata*, *S. leucisca*, and *S. binotata*.

No autapomorphies for *Steindachnerina argentea*, a species widely distributed through the Río Orinoco basin, were discovered during this study.

The lineage formed by *S. conspersa*, *S. bimaculata*, *S. leucisca*, and *S. binotata* is characterized by the following derived features:

7. The subdivision of the anterior tip of the anterior extension of the ventral process of the third hypobranchial (H_3).
8. The expansion of the third infraorbital (IO_3) posteriorly with a resultant elongation of its margin along the orbit.
9. The reduction of the fourth infraorbital (IO_4) to a small triangular element.
10. The reduction of the plate-like anterior and posterior processes on the tubular ossification surrounding the laterosensory canal segment in the fifth infraorbital (IO_5).
11. The dark, round, or transversely wider, mid-dorsal spot immediately anterior to the origin of the dorsal fin.

12. The longitudinally elongate mid-dorsal spot located slightly posterior of the tip of the supraoccipital spine.

Characters 7 to 12 define two less-inclusive clades, one consisting solely of *Steindachnerina conspersa* and the second of *S. bimaculata*, *S. leucisca*, and *S. binotata*.

Steindachnerina conspersa, an endemic of the La Plata basin, is characterized by a single known derived condition involving body pigmentation.

13. The much more lightly pigmented region of the body surrounding the origin of the dorsal fin.

The clade formed by *S. bimaculata*, *S. leucisca*, and *S. binotata* is distinguished by a single synapomorphy.

14. The one or more longitudinal series of small dark spots on the dorsolateral surface of the body.

Within that clade are two sublineages, *S. bimaculata*, on the one hand, and species-pair *S. leucisca* and *S. binotata* on the other.

Steindachnerina bimaculata, a species distributed through both the Amazon and Orinoco basins, has no known autapomorphies.

The species-pair *S. leucisca* and *S. binotata* shares the following five derived features.

15. The secondary loss of the spot of pigmentation at the base of the middle rays of the caudal fin (see Synapomorphy 6).
16. The secondary loss of the small spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin (see also Synapomorphies 36, 39, 49).
17. The increased longitudinal gap between the anus and the point of origin of the first anal-fin ray.
18. The increased number of vertebrae.
19. The high number of scales along the lateral line from the supracleithrum to the hypural joint.

Steindachnerina leucisca, widely distributed through the Amazon basin, is not known to demonstrate any autapomorphic features, whereas *S. binotata*, an endemic of the upper Río Madeira system, is characterized by the following single autapomorphy.

20. The very high number of scales in the series along the lateral line from the supracleithrum to the hypural joint (see also Synapomorphy 19).

The sister lineage to that consisting of *Steindachnerina argentea*, *S. conspersa*, *S. bimaculata*, *S. leucisca*, and *S. binotata* contains sixteen species (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*). Those species share a series of derived characters.

21. The expansion of the folds of the buccopharyngeal complex on the roof of the oral cavity into thickened flaps

and/or lobulate bodies.

22. The well-developed posterior lobulate bodies of the buccopharyngeal complex.
23. The well-developed lobulate processes of the buccopharyngeal complex situated on the anteromedial portion of the first and second gill-arches.
24. The pronounced development of the dorsal and ventral processes on the medial surface of the second infrapharyngobranchial.
25. The pattern of dark pigmentation extending along the lateral-line scales during at least some point in development. This feature is hypothesized to have undergone secondary reduction within this clade (see Synapomorphy 37).

Characters 21 to 25 unite two clades, one consisting of *S. biornata* and the other of the remaining 15 species.

Steindachnerina biornata, a species limited to southeastern Brazil and proximate regions, is not known to have any autapomorphic features.

The lineage consisting of *S. amazonica*, *S. atratoensis*, *S. brevipinna*, *S. dobula*, *S. elegans*, *S. fasciata*, *S. gracilis*, *S. guentheri*, *S. hypostoma*, *S. insculpta*, *S. notonota*, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa* is characterized by one derived feature of the buccopharyngeal complex and one derived feature of the branchial arches.

26. The presence of one or more series of lobulate bodies on the three fleshy flaps forming the portion of the buccopharyngeal complex on the roof of the oral cavity.
27. The widened form of the fifth upper pharyngeal toothplate and the reduction or near elimination of the longitudinal twisting of the ossification (see also Synapomorphy 46).

As noted under "Pigmentation" there exist two equally parsimonious hypotheses as explanations for the phyletic distribution of the spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin among the majority of species of *Steindachnerina*. Under one of these hypotheses the feature is hypothesized to have been acquired at this point in the phylogeny, with secondary losses within the clade. If correct, that hypothesis would represent another synapomorphy at this level within the cladogram.

The lineage characterized by synapomorphies 26 and 27 is formed of two monophyletic subgroups, *S. atratoensis* and the clade containing *S. amazonica*, *S. brevipinna*, *S. dobula*, *S. elegans*, *S. fasciata*, *S. gracilis*, *S. guentheri*, *S. hypostoma*, *S. insculpta*, *S. notonota*, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa*.

Steindachnerina atratoensis, whose known distribution is limited to the Río Atrato system of Colombia, is distinguished by two unique aspects of its pigmentation.

28. The series of secondary longitudinal dark stripes on the lateral and dorsolateral surfaces of the body centered

along the horizontal lines where adjoining longitudinal rows of scales overlap.

29. The stripe of dark pigmentation extending from the snout to the posterior border of the opercle.

The lineage composed of *S. amazonica*, *S. brevipinna*, *S. dobula*, *S. elegans*, *S. fasciata*, *S. gracilis*, *S. guentheri*, *S. hypostoma*, *S. insculpta*, *S. notonota*, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa* is defined by the following synapomorphies:

30. The multiple lobulate fleshy bodies on the portion of the buccopharyngeal complex occupying the roof of the oral cavity.
31. The increased convolution of the dorsal portion of, and presence of a ridge along the posteromedial margin of the mesopterygoid.
32. The vertical thickening of the posterior portion of the mesopterygoid.

At this point in the phylogeny there exists a polytomy that has not been resolved with the evidence from the examined features. The five components of the polytomy are first, *S. amazonica*; second, *S. fasciata*; third, *S. guentheri*; fourth, *S. notonota*; and fifth, the lineage composed of *S. brevipinna*, *S. dobula*, *S. elegans*, *S. gracilis*, *S. hypostoma*, *S. insculpta*, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa*. These will be discussed sequentially, with the order of presentation not indicative of any hypothesis of relationships.

Neither *S. amazonica*, an endemic of the Rio Tocantins system, *S. guentheri*, distributed through the Orinoco and western portions of the Rio Amazonas system, nor *S. notonota*, limited to northeastern Brazil, have any known autapomorphies.

Steindachnerina fasciata, with a known distribution limited to the southern tributaries of the Rio Madeira system, is distinguished by the following unique feature of its pigmentation.

33. The multiple longitudinal series of dark spots aligned along the center of the longitudinal scale rows on the lateral and dorsolateral surfaces of the body.

The lineage consisting of *Steindachnerina brevipinna*, *S. dobula*, *S. elegans*, *S. gracilis*, *S. hypostoma*, *S. insculpta*, *S. planiventris*, *S. pupula*, *S. quasimodoi*, and *S. runa* is defined on the basis of two derived features of the metapterygoid.

34. The vertical expansion of the anterior portion of the metapterygoid.
35. The medial convexity of the central portion of the metapterygoid.

Those two derived characters unit a group of species whose phylogenetic relationships have only been partially resolved on the basis of examined characters into a polytomy consisting of four components. These are first, *S. brevipinna*; second, *S. elegans*; third, a clade consisting of *S. insculpta* and *S. runa*;

and fourth, a lineage formed by *S. dobula*, *S. gracilis*, *S. hypostoma*, *S. planiventris*, *S. pupula*, and *S. quasimodoi*.

Neither *S. brevipinna* of the Río de La Plata basin, nor *S. elegans* distributed through the rivers of the states of Bahia and Minas Gerais in Brazil, are characterized by any known autapomorphic features. The lineage consisting of *S. insculpta* and *S. runa* is tentatively united on the basis of a single derived reversal.

36. The secondary loss of the spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin (see also Synapomorphies 16, 39, 49).

The lineage consisting of *S. dobula*, *S. gracilis*, *S. hypostoma*, *S. planiventris*, *S. pupula*, and *S. quasimodoi* is united by a single derived feature.

37. The secondary reduction in the degree of development of the stripe of dark pigmentation along the lateral line (see also Synapomorphy 25).

Synapomorphy 37 unites two monophyletic sublineages, one consisting of *S. dobula* and *S. pupula*, and the other of the clade formed by *S. gracilis*, *S. hypostoma*, *S. planiventris*, and *S. quasimodoi*. The species-pair *S. dobula* and *S. pupula* is characterized by one apomorphic reversal.

38. The elimination of the dark pigmentation along the lateral line (see also Synapomorphies 25, 37).

No autapomorphic characters for *S. pupula*, an endemic of the Río Orinoco system, were discovered during the study. The following autapomorphy for *S. dobula*, a species limited to the western portions of the Amazon basin, has been identified.

39. The secondary loss of the spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin (see also Synapomorphies 16, 36, 49).

The sister clade to the species-pair *S. dobula* and *S. pupula* consists of four species, *S. planiventris*, *S. gracilis*, *S. hypostoma*, and *S. quasimodoi*. These form a distinctive group of species characterized by a series of four derived features.

40. The posterior expansion of the median section of the mesethmoid into the area primitively occupied by the anterior region of the cranial fontanel.
41. The expansion of the medial margins of the frontals resulting in a reduction in the extent of the anterior portion of the median cranial fontanel (see also Synapomorphies 45, 48).
42. The increased gap between the anus and the origin of the first anal-fin ray.
43. The flattened prepelvic region of the body.

The pronounced, although not absolute, increase in the number of vertebrae in *Steindachnerina planiventris*, *S. gracilis*, *S. hypostoma*, and *S. quasimodoi* may be an additional synapomorphy for the group (see discussion under "Vertebrae").

The group of four species sharing features 40 to 43 consists

of two subunits, the species *Steindachnerina quasimodoi* and a trichotomy formed by *S. planiventris*, *S. gracilis*, and *S. hypostoma*.

Steindachnerina quasimodoi, a species of the Brazilian-Peruvian border region, has one known autapomorphy.

44. The triangular flange extending anteriorly from the uncinat process on the first epibranchial (E_1).

Steindachnerina planiventris, *S. gracilis*, and *S. hypostoma* share one derived feature.

45. The extensive contact medially of the anterior portions of the frontals with the resultant longitudinal shortening of the dorsomedian cranial fontanel (see also Synapomorphies 41, 48).

No autapomorphies for *Steindachnerina planiventris*, a species widespread in the Amazon basin, and *S. gracilis*, an endemic of the Rio Tocantins system, were discovered during this study.

Steindachnerina hypostoma, a broadly distributed Amazonian species, is characterized by four known autapomorphies.

46. The expansion of the fifth upper pharyngeal tooth-plate (UP_5) into a very wide plate-like structure demonstrating little longitudinal twisting.
47. The fusion of the ventral processes of the second hypobranchial (H_2) along the ventral midline below the ventral aorta.
48. The very extensive medial area of contact of the frontals, with a pronounced reduction in the longitudinal extent of the cranial fontanel anterior to the epiphyseal bar (see also Synapomorphies 41, 45).
49. The secondary loss the small spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin (see also Synapomorphies 16, 36, 39).

Convergent Characters

Among the shared derived characters noted in the phylogenetic analysis of *Steindachnerina* are various synapomorphies for the members of the genus or for lineages within that clade that are homoplastic when evaluated at more inclusive taxonomic levels. For purposes of discussion we can subdivide such features into the two admittedly arbitrary groupings utilized by Vari (1989a:59–61), external homoplasies, that is those that occur homoplastically in both *Steindachnerina* and outgroups to the genus, and internal homoplasies, those occurring in two subunits of the genus.

Relatively few external homoplasies have been identified in this study. One of these involves a feature common to the species of *Steindachnerina* and the Prochilodontidae, whereas the others involve varying species of *Steindachnerina* and *Psectrogaster* or *Curimata*.

The anterior widening of the basihyal and associated basihyal tooth-plate characteristic of *Steindachnerina* (Synapo-

morphology 4) is paralleled by an indistinguishable modification of those elements in all members of the Prochilodontidae. These alterations are hypothesized to be homoplastic synapomorphies for *Steindachnerina* on the one hand and the Prochilodontidae on the other within the context of the overall most parsimonious hypothesis of generic-level phylogenetic relationships within the Curimatidae (Vari, 1989a).

Identified homoplastic characters common to *Steindachnerina*, or one of its component clades, and a curimatid outgroup involve either *Psectrogaster*, or more commonly *Curimata*. As noted by Vari (1989a:25), the medially directly flange on the dorsomedial surface of the second infrapharyngobranchial in the species of *Steindachnerina* (Synapomorphy 2) cannot be discriminated from the similarly situated process common to all members of *Psectrogaster*. When we evaluate the dorsal process on the second infrapharyngobranchial within the context of the most parsimonious hypothesis of relationships within the Curimatidae as derived from multiple characters of a variety of body systems, it is by far most parsimonious to hypothesize that the feature arose independently in *Steindachnerina* on the one hand and *Psectrogaster* on the other.

Four homoplasies involve *Steindachnerina* and *Curimata* or subunits of those taxa. The first of these involves the elaborate forms of the anterior portion of the buccopharyngeal complex that occur in 16 species of *Steindachnerina* (*amazonica*, *atratoensis*, *biornata*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (Synapomorphy 21) and all members of *Curimata*. Although the details of the expansions of the buccopharyngeal complexes in the two genera differ, the expansion and elaboration of the three simple folds primitive for a higher-level clade within the Curimatidae is appropriately considered a derived feature common to the two cited lineages. The second convergence between the two genera involves the distinct process on the anterior extension of the ventral process of the third hypobranchial characteristic of all the species of *Steindachnerina* (Synapomorphy 1), which is paralleled by a somewhat differently situated process on that ossification in a subclade of *Curimata* consisting of *C. roseni* and *C. inornata*. The third of the evident homoplasies is the posterior thickening of the mesopterygoid in 14 species of *Steindachnerina* (*amazonica*, *brevipinna*, *dobula*, *elegans*, *fasciata*, *gracilis*, *guentheri*, *hypostoma*, *insculpta*, *notonota*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (Synapomorphy 32) and in three species of *Curimata* (*mivartii*, *cerasina*, and *aspera*). The fourth and final of this set of homoplasies involves the vertical expansion of the anterior portion of the metapterygoid in ten species of *Steindachnerina* (*brevipinna*, *dobula*, *elegans*, *gracilis*, *hypostoma*, *insculpta*, *planiventris*, *pupula*, *quasimodoi*, and *runa*) (Synapomorphy 34) and all species of *Curimata*.

On first consideration this set of four convergences between species of *Steindachnerina* and *Curimata* seems indicative of a close phylogenetic relationship between those two taxa. Closer examination reveals that the characters involve different, sometimes mutually exclusive, degrees of phylogenetic inclu-

siveness. Thus the evidence even when evaluated in the absence of other data provides, at best, equivocal support for an hypothesis of a close relationship between *Steindachnerina* and *Curimata*. When we go beyond that internal evidence to examine the higher-level relationships of those two genera within a phylogenetic hypothesis based on data from a number of different body systems, the most parsimonious phylogenetic scheme (Vari, 1989a) indicates that the four characters represent homoplasies at the levels of or within *Steindachnerina* and *Curimata*.

Other homoplasies involve features that are hypothesized to have arisen independently within different lineages of *Steindachnerina*. These internal homoplasies are as follows.

The increased distance between the anus and origin of the first anal-fin ray, together with an associated increase in the number of series of scales in that region in the clade consisting of *S. binotata* and *S. leucisca* (Synapomorphy 17), on the one hand, and the lineage formed by *S. gracilis*, *S. hypostoma*, *S. planiventris*, and *S. quasimodoi* on the other (Synapomorphy 42).

The increased number of vertebrae in the species-pair *S. binotata* and *S. leucisca* (Synapomorphy 18), which is paralleled by a similar, although not as discrete, increase in the number of vertebrae in *S. gracilis*, *S. hypostoma*, *S. planiventris*, and *S. quasimodoi* (not utilized as a synapomorphy in the phylogenetic analysis, see "Character Description and Analysis").

The independent loss of the dark spot of pigmentation on the basal portions of the middle rays of the dorsal fin in *S. hypostoma* (Synapomorphy 49) and *S. dobula* (Synapomorphy 39), the clade consisting of *S. leucisca* and *S. binotata* (Synapomorphy 16), and in the lineage formed by *S. insculpta* and *S. runa* (Synapomorphy 36).

Looking at the various homoplasies internal to *Steindachnerina* we find only one repeated pattern in the phylogenetic distribution of these features. That involves the species-pair *S. binotata* and *S. leucisca*, and the lineage formed by *S. hypostoma*, *S. quasimodoi*, *S. planiventris*, and *S. gracilis*. The hypothesis that these two characters define a monophyletic lineage within *Steindachnerina* is markedly outweighed by the numerous other derived characters whose phyletic distributions supports the overall most parsimonious hypothesis of relationships presented in Figure 11.

Genus *Steindachnerina* Fowler, 1906

TABLE 2

- Steindachnerina* Fowler, 1906:298 [type-species: *Curimatus trachystetus* Cope, 1878 (= *Curimatus bimaculatus* Steindachner, 1876), by original designation].
- Curimatorbis* Fernández-Yépez, 1948:42 [type-species: *Curimatus atratoensis* Eigenmann, 1912, by original designation].
- Cruentina* Fernández-Yépez, 1948:52 [type-species: *Curimata hypostoma hastata* Allen (in Eigenmann and Allen), 1942 (= *Curimatus dobula* Günther, 1868a), by original designation].

Rivasella Fernández-Yépez, 1948:56 [type-species *Curimata melaniris* Fowler, 1940 (= *Curimatus bimaculatus* Steindachner, 1876), by original designation].

DIAGNOSIS.—*Steindachnerina* is distinguished within the Curimatidae by modifications of the first and second infra-pharyngobranchials (PB₁ and PB₂), of the ventral process of the third hypobranchial (H₃), and of the basihyal and associated basihyal tooth-plate (BH and BHTP). The presence of a spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin may represent an additional synapomorphy for the genus (see "Character Description and Analysis" and Synapomorphies 1 to 4 of "Phylogenetic Reconstruction" for further details).

Maximum known standard lengths of species range from 55.5 to 151.2 mm. Dorsal-fin rays ii,8 to ii,10 (ii,8 and ii,10 rare), or iii,9; anal-fin rays ii,7 to ii,8, or iii,7; pectoral-fin rays 12 to 17; pelvic-fin rays usually i,8, sometimes i,9; adipose fin always present, moderately developed. Pored lateral-line scales from supracleithrum to hypural joint range from 29 to 72; sensory canals in lateral-line scales straight. Number of scales in transverse series from origin of dorsal fin to lateral line 5¹/₂ to 13; number of scales in transverse series from origin of anal fin to lateral line 4¹/₂ to 10. Total vertebrae 31 to 38.

DISTRIBUTION.—*Steindachnerina* has a broad distribution through most of lowland South America, with the greatest intrageneric species diversity occurring to the east and south of the Andes in rivers from the Río Orinoco basin through to drainages slightly to the south of Buenos Aires, Argentina. One species of *Steindachnerina* common in the Río Orinoco also occurs in two of the rivers draining the northern coastal versant of Venezuela, and the western drainages of the island of Trinidad. A single species of *Steindachnerina* is known from the Río Atrato basin of western Colombia. The genus is absent from other river systems of the western and northern versants of the Andes, most notably the Río Magdalena and the rivers of the Lago Maracaibo basin.

Although *Steindachnerina* has a broad distribution to the east of the Andes it is unknown from many of the major tributaries of the mainstream Amazon (e.g., Río Tapajós and most of the Río Xingu); however, that absence is likely a consequence of the poor samples of fishes available from those river basins. The genus also appears to be absent or nearly so in the acidic, relatively better-collected black-waters of the Río Negro system of the Amazon basin. Goulding et al. (1988) do not report the genus among the large series of curimatids they studied from that system. I have only discovered two lots of one species of *Steindachnerina* (*planiventris*) among the extensive series of curimatids originating in the Río Negro that I examined. At least one of those, in turn, came from the mouth of the Río Branco, a clearwater tributary of the Río Negro.

The absence of *Steindachnerina* from the blackwater portions of the Río Negro basin, or its occurrence only in the lower reaches of the river or proximate to confluences with

TABLE 2.—Nominal species, subspecies, and varieties of curimatids assigned herein to the genus *Steindachnerina* and the recognized equivalent species of *Steindachnerina* according to the results of this study. Nominal species are cited as in original description and are arranged alphabetically by specific, subspecific, or varietal epithet.

Nominal species	<i>Steindachnerina</i>
<i>Curimatus elegans</i> var. <i>amazonica</i> Steindachner, 1911	<i>amazonica</i>
<i>Curimatus argenteus</i> Gill, 1858	<i>argentea</i>
<i>Curimatus atratoënsis</i> Eigenmann, 1912b	<i>atratoënsis</i>
<i>Curimatus elegans bahiensis</i> Eigenmann and Eigenmann, 1889	<i>elegans</i>
<i>Curimatus bimaculatus</i> Steindachner, 1876	<i>bimaculata</i>
<i>Curimatus binotatus</i> Pearson, 1924	<i>binotata</i>
<i>Curimata biornata</i> Braga and Azpelicueta, 1987	<i>biornata</i>
<i>Curimatus leuciscus bolivae</i> Eigenmann and Ogle, 1907	<i>leucisca</i>
<i>Curimatus gilberti brevipinnis</i> Eigenmann and Eigenmann, 1889	<i>brevipinna</i>
<i>Curimatus conspersus</i> Holmberg, 1891	<i>conspersa</i>
<i>Curimatus dobula</i> Günther, 1868	<i>dobula</i>
<i>Curimatus elegans</i> Steindachner, 1874	<i>elegans</i>
<i>Curimatus fasciata</i> Vari and Géry, 1985	<i>fasciata</i>
<i>Steindachnerina gracilis</i> Vari and Vari, 1989	<i>gracilis</i>
<i>Curimatus güntneri</i> Eigenmann and Eigenmann, 1889	<i>güntneri</i>
<i>Curimata hypostoma hastata</i> Allen (in Eigenmann and Allen), 1942	<i>dobula</i>
<i>Curimatus hypostoma</i> Boulenger, 1887	<i>hypostoma</i>
<i>Cruentina insculpta</i> Fernández-Yépez, 1948	<i>insculpta</i>
<i>Curimatus issororoënsis</i> Eigenmann, 1912a	<i>güntneri</i>
<i>Curimatus leuciscus</i> Günther, 1868	<i>leucisca</i>
<i>Curimatus melaniris</i> Fowler, 1940	<i>bimaculata</i>
<i>Curimatus metae</i> Eigenmann, 1922	<i>güntneri</i>
<i>Curimatus morawhannae</i> Eigenmann, 1912a	<i>güntneri</i>
<i>Curimatus nasus</i> Steindachner, 1882	<i>dobula</i>
<i>Curimata niceforoi</i> Fowler, 1943a	<i>dobula</i>
<i>Curimatus nigrotaenia</i> Boulenger, 1902	<i>brevipinna</i>
<i>Curimatus nitens</i> Holmberg, 1891	<i>brevipinna</i>
<i>Curimatus notonotus</i> Miranda-Ribeiro, 1937	<i>notonota</i>
<i>Allenina pectinata</i> Fernández-Yépez, 1948	<i>leucisca</i>
<i>Steindachnerina planiventris</i> Vari and Vari, 1989	<i>planiventris</i>
<i>Prochilodus pterostigma</i> Fowler, 1913	<i>bimaculata</i>
<i>Steindachnerina pupula</i> , new species	<i>pupula</i>
<i>Steindachnerina quasimodoi</i> Vari and Vari, 1989	<i>quasimodoi</i>
<i>Curimatus robustula</i> Allen (in Eigenmann and Allen), 1942	<i>güntneri</i>
<i>Steindachnerina runa</i> , new species	<i>runa</i>
<i>Curimatus semiornatus</i> Steindachner, 1914	<i>bimaculata</i>
<i>Curimatus bimaculatus sialis</i> Eigenmann and Eigenmann, 1889	<i>bimaculata</i>
<i>Prochilodus stigmaturus</i> Fowler, 1911	<i>dobula</i>
<i>Curimata stigmata</i> Vari, 1987	<i>biornata</i>
<i>Curimatus trachystetus</i> Cope, 1878	<i>bimaculata</i>

clearwater tributaries parallels the findings of Goulding et al. (1988:100) who note a series of fish taxa of various orders that are absent from such acidic blackwater systems. Among these

absent taxa is *Psectrogaster*, another genus of curimatids. Goulding et al. propose that the hydrochemistry of blackwaters is inimical to some taxa, thus accounting for the absence of various species and genera in the Rio Negro system. We cannot presently determine whether that hypothesis is valid with respect to *Steindachnerina*, or whether some alternative factor accounts for the absence of the members of the genus in acidic blackwaters (e.g., the absence of adequate populations of the food items utilized by the members of the genus).

Three other distinct gaps exist in the known geographic distribution of *Steindachnerina* to the east of the Andes. All three involve moderately well-collected river basins of the eastern margins of the continent and probably represent the actual absence of the members of the genus in those systems rather than reflecting the poor samples available of the ichthyofaunas in those basins. *Steindachnerina* is unknown from the drainages of the narrow coastal versant of Brazil ranging from central Rio Grande do Sul to southern Bahia. Similarly, no samples of *Steindachnerina* are known from the series of coastal rivers immediately north of the mouth of the Rio Amazonas in the state of Amapá, Brazil. Finally, the genus is unknown from the rivers along the coastal slopes of the Guianas from northwestern Guyana to central Surinam including the relatively well-sampled Essequibo and Corantijn river systems.

REMARKS.—As defined by Vari (1989a) and in this study, *Steindachnerina* has three junior synonyms. All three were proposed by Fernández-Yépez (1948) under his dramatically subdivided classification of the family Curimatidae (his subfamily Curimatinae). The type species of *Steindachnerina*, *Curimatus trachystetus*, is herein placed as a synonym of *Curimatus* (= *Steindachnerina*) *bimaculatus*. The latter species is, in turn, considered the senior synonym of *Curimata melaniris*, the type species of *Rivasella*. Thus, *Rivasella* is not

considered to be available for use within the *Steindachnerina* clade. Two other nominal genera, *Curimatorbis* and *Cruxentina*, with type-species sharing the synapomorphies of the lineage do, however, remain available. Reference to the topology of the most parsimonious hypothesis of intrageneric relationships (Figure 11) shows that the continued recognition of *Curimatorbis* and *Cruxentina*, with type-species *atratoensis* and *dobula* respectively, presents a number of problems. In order to recognize those genera, one could conservatively limit *Steindachnerina* to the species phylogenetically proximate to *bimaculata* (*argentea*, *conspersa*, *leucisca*, and *binotata*). The location of *atratoensis* and *dobula* within the phylogeny is such that the recognition of *Curimatorbis* for *atratoensis* would at a minimum require a new genus for *biornata*. *Cruxentina*, in turn, could be expanded to include the remaining species of the tree, but under such a scheme it would form a genus that contains two-thirds of the species of the lineage. If a more even balance in the number of species in the different genera were judged desirable that result could be achieved by further subdividing that clade generically. That course of action would necessitate the description of a number of new genera so that all recognized taxa be monophyletic or in the case of polytomies possibly monophyletic. Selection among these alternatives is arbitrary. In the interest of simplicity and in order to avoid the addition of new genera to the multitude already available within the Curimatidae, only a single genus, *Steindachnerina*, is recognized in this study for the 21 species of the clade.

Curimata hypostoma hastata Allen (in Eigenmann and Allen, 1942), the type species of *Cruxentina* Fernández-Yépez was assigned to *Steindachnerina* in tables 2 and 3 of Vari (1989a:7-9). *Cruxentina* was, however, incorrectly listed under *Cyphocharax* rather than *Steindachnerina* in the generic synonymy in Table 1 of that paper (Vari, 1989a:6).

Key to the Species of *Steindachnerina* Fowler

1. Roof of oral cavity immediately posterior of upper jaw with three thin, weakly developed longitudinal folds [Figure 1], folds not readily obvious, median fold more developed; no well-developed fleshy flaps or lobulate fleshy processes on roof of oral cavity 2
- Roof of oral cavity immediately posterior of upper jaw with three very fleshy flaps and/or one or many series of lobulate fleshy processes [Figure 2]; fleshy flaps and lobulate processes more highly developed in larger specimens 6
2. Scales along lateral line from supracleithrum to hypural joint 53 to 70; no small discrete spot of dark pigmentation at base of middle rays of caudal fin; 36 to 38 vertebrae 3
- Scales along lateral line from supracleithrum to hypural joint 31 to 49; small discrete spot of dark pigmentation at base of middle rays of caudal fin; 30 to 35 vertebrae 4

3. Scales along lateral line from supracleithrum to hypural joint 53 to 62; 9 to 11 scales in transverse series from lateral line to origin of dorsal fin; $6\frac{1}{2}$ to 8 scales in transverse series from lateral line to origin of anal fin *S. leucisca*
(Amazon basin)
Scales along lateral line from supracleithrum to hypural joint 67 to 72; $11\frac{1}{2}$ to 13 scales in transverse series from lateral line to origin of dorsal fin; $8\frac{1}{2}$ to 10 scales in a transverse series from lateral line to origin of anal fin *S. binotata*
(upper Rio Madeira system)
4. Scales along lateral line from supracleithrum to hypural joint 38 to 49; $7\frac{1}{2}$ to 9 scales in a transverse series from lateral line to origin of dorsal fin; 33 to 35 vertebrae 5
Scales along lateral line from supracleithrum to hypural joint 32 to 36; $5\frac{1}{2}$ to 6 scales in transverse series from lateral line to origin of dorsal fin; 30 to 32 vertebrae *S. argentea*
(rivers of western Trinidad, Río Orinoco basin, and rivers of northern Venezuelan coastal versant)
5. Scales along lateral line from supracleithrum to hypural joint 38 to 43; no series of small spots on lateral and dorsolateral surfaces of body; region ventral of origin of dorsal fin typically less pigmented than surrounding areas *S. conspersa*
(Río Paraguay and lower Río Paraná systems)
Scales along lateral line from supracleithrum to hypural joint 43 to 49; larger specimens typically with series of small dark spots on lateral and dorsolateral surfaces of body; region ventral of origin of dorsal fin not less pigmented than surrounding areas *S. bimaculata*
(Amazon and Río Orinoco basins)
6. Roof of oral cavity in adults with three very fleshy flaps in region posterior of upper jaw; no distinct lobulate processes associated with flaps *S. biornata*
(southeastern Brazil, Uruguay, and northern Argentina)
Roof of oral cavity in adults with one or more series of well-developed lobulate fleshy processes on or covering three fleshy flaps [Figure 2]; if only one series of lobulate processes present anteriorly, species has broad, dark band extending from snout to base of middle rays of caudal fin; with that primary band in specimens over 40 mm SL paralleled by narrower stripes along body 7
7. Prepelvic region of body distinctly flattened; 5 to 7 scales between posterior border of anus and origin of anal fin; 5 or 6 scales in transverse series across flattened region immediately anterior of origin of pelvic fin 8
Prepelvic region of body not flattened or only obtusely flattened, 1 to 3 scales between posterior border of anus and origin of anal fin; 3 or 4 scales in transverse series across obtusely rounded prepelvic region immediately in front of insertion of pelvic fin 11
8. Dorsal fin plain, without spot of dark pigmentation on basal portion of middle rays; snout length 0.28–0.31 of HL; scales along lateral line to hypural joint 46 to 50 *S. hypostoma*
(central and western portions of Amazon basin)
Dorsal fin with spot of dark pigmentation on basal portion of middle rays, spot faint in some individuals; snout length 0.31–0.34 of HL; scales along lateral line to hypural joint 40 to 46 or 50 to 54 9
9. Scales along lateral line to hypural joint 50 to 54 *S. gracilis*
(Rio Tocantins basin)
Scales along lateral line to hypural joint 40 to 46 10
10. Greatest body depth in specimens over 50 mm SL 0.30–0.34 of SL, body with distinctly humped dorsal profile [Figures 32, 33]; frontals separated by slight gap anteriorly [Figure 10A] *S. quasimodoi*
(western portions of Amazon basin)

- Greatest body depth in specimens over 50 mm SL 0.27–0.30 of SL, dorsal profile of body without distinct hump [Figure 34]; frontals in contact anteriorly (Figure 10B) *S. planiventris*
 (central and western portions of Amazon basin)
11. Body of adults with multiple longitudinal dark stripes 12
 Body without multiple longitudinal dark stripes at any time during development, sometimes with single dark stripe developed to varying degrees along lateral line 13
12. Body with prominent wide dark midlateral stripe at all sizes, midlateral stripe of adults flanked dorsally and ventrally by narrower continuous dark stripes; large spot of dark pigmentation present on dorsal fin in specimens of all sizes; only one series of lobulate processes present on fleshy flaps of roof of oral cavity
 *S. atratoensis*
 (Río Atrato system of Colombia)
- Midlateral stripe on body narrow, continuous posteriorly but stuttering anteriorly, other stripes on body noncontinuous, consisting of individual spots of pigmentation on each scale; spot of dark pigmentation present on dorsal fin in smaller specimens, diffuse in larger individuals; multiple series of lobulate fleshy processes on roof of oral cavity *S. fasciata*
 (upper Rio Madeira system)
13. Dorsal fin without distinct dark patch of pigmentation on basal portions of middle rays at any age 14
 Dorsal fin with dark patch of pigmentation on basal portions of middle rays; pigmentation sometimes less obvious in either larger or smaller individuals of a particular species 16
14. No dark stripe along midlateral surface of body *S. dobula*
 (western portions of Amazon basin from Colombia to Bolivia)
- Distinct dark midlateral stripe along at least posterior half of body 15
15. Dark midlateral stripe extending from rear of opercle posteriorly onto middle rays of caudal fin, stripe of nearly uniform width, particularly on posterior two-thirds of body; greatest depth of body 0.29–0.34 of SL *S. insculpta*
 (upper portions of Rio Paraná and Río Paraguay basins)
- Dark midlateral stripe beginning under dorsal fin, gradually widening posteriorly to form lanceolate spot on caudal peduncle, spot widest posteriorly; greatest depth of body 0.34–0.38 of SL *S. runa*
 (Fleuve Oyapock (Río Oiapoque) of French Guiana and Brazil, Fleuve Maroni (Morawijne River) of French Guiana and Surinam, and Surinam River in Surinam)
16. Scales along lateral line to hypural joint 42 to 46; 7¹/₂ to 9 scales in transverse series from lateral line to origin of dorsal fin; no dark midlateral line on body
 *S. pupula*
 (Río Orinoco basin)
- Scales along lateral line to hypural joint 29 to 41; 5¹/₂ to 6¹/₂ scales in transverse series from lateral line to origin of dorsal fin; dark midlateral stripe present on at least posterior half of body 17
17. Dark midlateral stripe on body in adults limited to posterior half of body . . . 18
 Dark midlateral stripe on body in adults extending from supracleithrum at least to base of caudal fin 20
18. Scales along lateral line to hypural joint 36 to 41; gape width 0.23–0.26 of HL
 *S. amazonica*
 (upper Rio Tocantins)
- Scales along lateral line to hypural joint 29 to 36; gape width 0.26–0.33 of HL 19

19. Dark midlateral stripe on posterior half of body expanded in large specimens into distinct lozenge-shaped mark on caudal peduncle, sometimes very faint
 *S. guentheri*
 (rivers of northwestern Guyana, Río Orinoco basin, and western portions of Amazon basin from Colombia to northwestern Bolivia)
 Dark midlateral stripe on posterior half of body forming a stripe that is only slightly expanded, if at all, on caudal peduncle *S. notonota*
 (rivers of northeastern Brazil)
20. Midlateral stripe on body narrow and somewhat irregular anteriorly, widening posteriorly, extending to base of caudal fin rays, larger specimens with distinct vertical expansion of stripe on caudal peduncle, stripe often extending onto middle caudal-fin rays *S. elegans*
 (coastal rivers of states of Minas Gerais and Bahia in Brazil)
 Midlateral stripe on body of nearly continuous width, typically terminating posteriorly before base of middle rays of caudal fin; stripe not expanded vertically on caudal peduncle; stripe not present on middle rays of caudal fin
 *S. brevipinna*
 (Río Paraguay, lower Río Paraná, and lower Río Uruguay systems)

Steindachnerina leucisca (Günther, 1868)

FIGURES 12, 13, 14, TABLE 3

- Curimatus leuciscus* Günther, 1868a:239 [type locality: Peru: Río Huallaga].—1868b:479 [Peru: Río Huallaga].—Eigenmann and Eigenmann, 1889:426 [Brazil: Obidos (= Obidos)].—1891:47 [reference].—Pellegrin, 1909:148 [Brazil: Tonantins].—Eigenmann, 1910:422 [reference].—Starks, 1913:13 [Río Madeira].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus bimaculatus sialis*.—Eigenmann and Eigenmann, 1889:422 [part of syntype series; Brazil, Manacapuru].
- Curimatus leuciscus bolivae* Eigenmann and Ogle, 1907:4 [type locality: Bolivia: (Río Mamoré)].—Eigenmann, 1910:422 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata leucisca*.—Eigenmann and Allen, 1942:294 [Peru: Gosulimacocha, Río Morona, Río Huallaga, Yurimaguas, Río Paranaupura, Río Ucayali, Orellana, Lago Cashiboya, Lago Sanango].—Fowler, 1945:118 [reference].—Ortega and Vari, 1986:11 [Peru, Amazon basin; common name].
- Allenina pectinata* Fernández-Yépez, 1948:40, fig. 19 [type locality: Brazil, Maracapuru (= Manacapuru); author incorrectly indicated as Eigenmann].—Fowler, 1975:365 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Cruentina leucisca*.—Fernández-Yépez, 1948:53 [assignment to *Cruentina*].
- Cruentina leucisca bolivae*.—Fernández-Yépez, 1948:53 [assignment to *Cruentina*].—Fowler, 1975:368 [reference].
- Curimata leucisca leucisca*.—Fowler, 1950:286 [literature compilation].
- Curimata leucisca bolivae*.—Fowler, 1950:286 [literature compilation].
- Curimata leuciscus boliviae*.—Terassas-Urquidi, 1970:31 [reference].
- Cruentina leucisca leuciscus*.—Fowler, 1975:368 [reference].

DIAGNOSIS.—The presence of three weakly developed longitudinal folds on the roof of the oral cavity rather than three well-developed fleshy flaps and/or one or more series of lobulate fleshy processes in that region discriminates *Steindachnerina leucisca* from other members of the genus with the exception of *S. binolata*, *S. argentea*, *S. conspersa*, and *S. bimaculata*. The 53 to 62 scales in the lateral line from the supracleithrum to the hypural joint separates *S. leucisca* from *S. binolata*, which has 67 to 70 along the lateral line, and from *S.*

argentea, *S. conspersa*, and *S. bimaculata*, which have 53 or fewer scales in that series.

DESCRIPTION.—Body elongate, somewhat compressed, more so in specimens over 100 mm SL. Dorsal profile of head straight or very slightly convex. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin; slightly convex or straight, posteroventrally slanted at base of dorsal fin; gently convex or straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with distinct median keel anterior to dorsal fin, keel more obvious proximate to fin; surface of body smoothly rounded transversely posterior to fin. Ventral profile of body nearly straight from tip of lower jaw to vertical through insertion of pectoral fin, slightly convex from that point to insertion of pelvic fin, straight from there to anal-fin insertion, and then slightly sigmoid to caudal peduncle. Prepelvic region obtusely flattened, with indistinct lateral keels. Indistinct median keel posterior to pelvic-fin insertion. Anus distinctly anterior of insertion of first anal fin-ray, with 7 or 8 series of scales in intervening space.

Greatest depth of body 0.28–0.32 [0.30]; snout tip to origin of dorsal fin 0.44–0.48 [0.47]; snout tip to origin of anal fin 0.81–0.86 [0.83]; snout tip to insertion of pelvic fin 0.48–0.53 [0.50]; snout tip to anus 0.71–0.75 [0.71]; origin of dorsal fin to hypural joint 0.57–0.62 [0.59]. Profile of dorsal fin acute, less so with increasing age; anteriormost rays approximately three times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.18–0.22, extends about three-quarters of distance to vertical line through insertion of pelvic fin. Pelvic-fin border pointed, length of pelvic fin 0.22–0.26 [0.23], reaches two-thirds of distance to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed. Anal fin distinctly emarginate, anteriormost branched rays 2.5–3.0 times length of ultimate ray; reaching nearly to insertion of ventral rays of caudal fin when anal fin is depressed. Caudal peduncle depth

0.11–0.12 [0.11].

Head profile distinctly pointed, head length 0.25–0.28 [0.26]; upper jaw longer, mouth subterminal; anterior portion of buccopharyngeal complex on roof of oral cavity consisting of three weakly developed fleshy folds without fleshy lobulate bodies; snout length 0.27–0.31 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.34 [0.30]; adipose eyelid present, with broad, vertically ovoid opening over center of eye; length of postorbital portion of head 0.39–0.45 [0.44]; gape width 0.28–0.33 [0.30]; interorbital width 0.41–0.46 [0.42].

Pored lateral-line scales to hypural joint 53 to 62 [56]; all scales of lateral line pored, canals in scales of lateral line straight; 4 to 7 series of scales extend beyond hypural joint onto caudal-fin base; 9 to 11 [11] scales in transverse series from origin of dorsal fin to lateral line; $6\frac{1}{2}$ to 8 [7] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (iii,9 rare, first unbranched ray very small) [ii,9]; anal-fin rays ii,7 or iii,7 (iii,7 rare, first unbranched ray very small) [ii,7]; pectoral-fin rays 13 to 17

[15]; pelvic-fin rays i,8 or i,9 [i,9].

Total vertebrae 36 (33), 37 (53), 38 (2).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery or silvery golden; darker on dorsal portions of head and body. Ground coloration of specimens fixed in formalin and lacking guanine on scales yellowish tan to brown, darker on dorsal portions of head and body. Obscure, deep-lying, midlateral stripe extends from supracleithrum to caudal peduncle. Most specimens of less than 50 mm SL with single series of three to six small, dark, irregular spots forming a wavy pattern above midlateral band. Each spot about one-half size of pupil. Number of spots increasing in larger specimens (Figure 12); 11 or 12 present in largest specimens examined. Second longitudinal series of spots located dorsal of primary set present in larger specimens. Two or three spots in dorsal series in specimens of approximately 100 mm SL, seven or eight in specimens of 150 mm SL. Neither midlateral band nor spots readily apparent in specimens retaining guanine on scales; spots very faint in some individuals (Figure 13). Distinct dark spot along dorsal midline immediately anterior of origin of dorsal fin (Figure 13). Spot

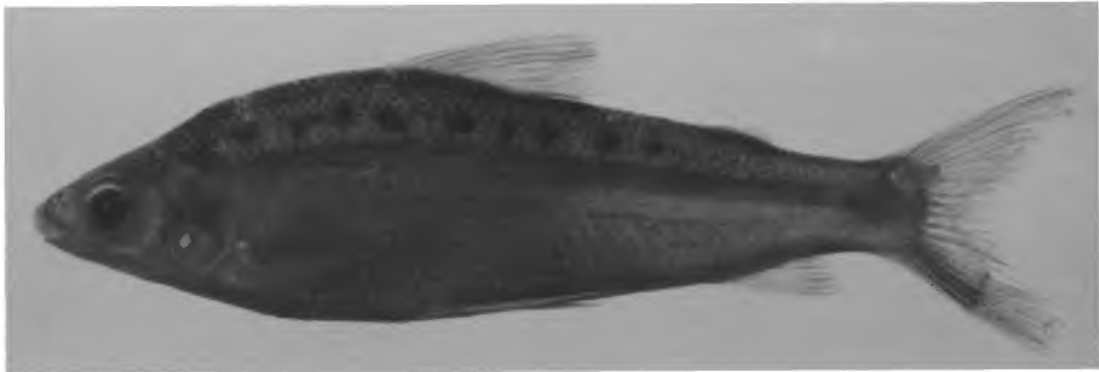


FIGURE 12.—*Steindachnerina leucisca*, USNM 261520, 107.7 mm SL; Peru, Ucayali, Río Ucayali at Masisea.

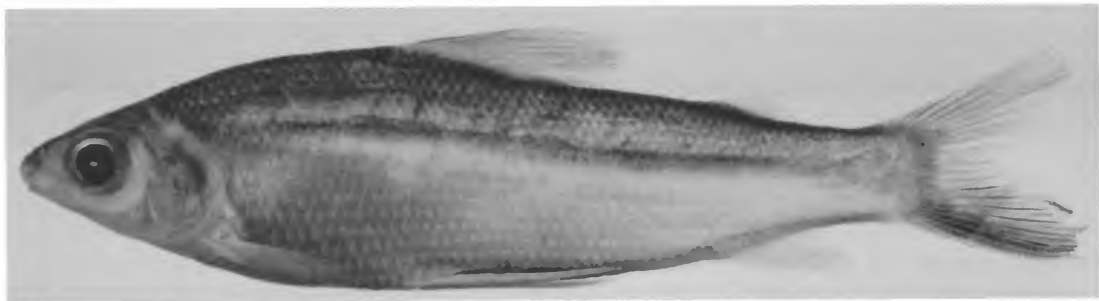


FIGURE 13.—*Steindachnerina leucisca*, USNM 261500, 87.7 mm SL; Peru, Ucayali, Río Ucayali at Masisea.

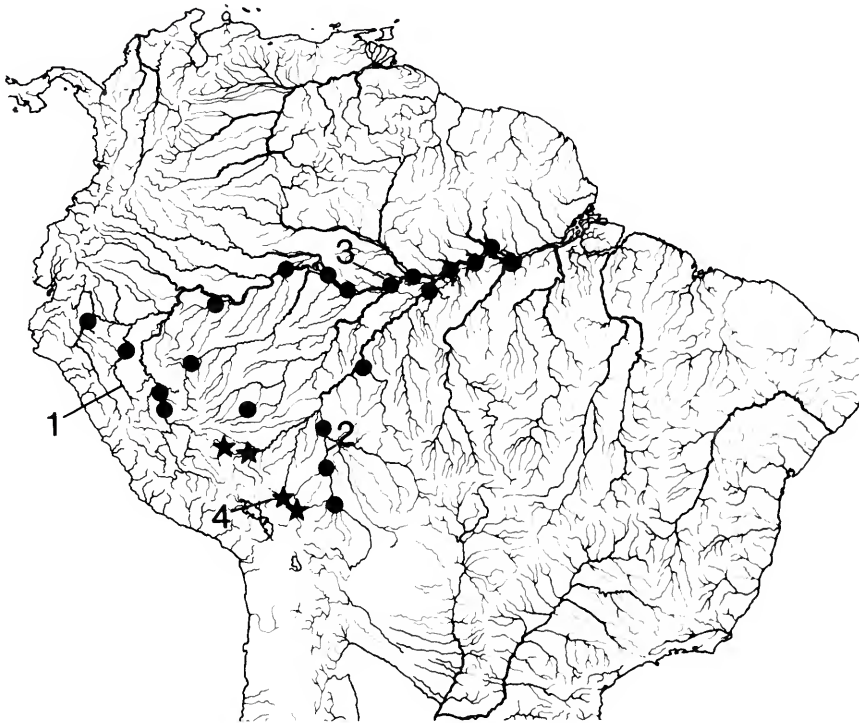


FIGURE 14.—Map of northern and central sections of South America showing geographic distribution of *Steindachnerina leucisca* (dots; 1 = Río Huallaga, approximate type locality of *Curimatus leuciscus*, 2 = Río Mamoré, approximate type locality of *Curimatus leuciscus bolivae*, 3 = type locality of *Allenina pectinata*) and *Steindachnerina binotata* (stars; 4 = type locality) (some symbols represent more than one collecting locality and/or lot of specimens).

developed to greater extent transversely in smaller specimens, more rounded in largest individuals examined. Longitudinally elongate, dark, mid-dorsal spot immediately posterior of tip of supraoccipital spine; spot less obvious but still apparent in larger individuals. Dorsal midline between dorsal fin and caudal peduncle with dark streak. Caudal-fin rays outlined by series of small chromatophores. Lower lobe of caudal fin ranges from slightly dusky to very dark. Anterior and distal portions of dorsal fin dusky. Other fins hyaline.

DISTRIBUTION.—Middle, western, and southwestern portions of Rio Amazonas basin (Figure 14).

REMARKS.—Günther described *Curimatus leuciscus* on the basis of two specimens originating in the Río Huallaga. The larger of the specimens (BMNH 1867.6.13:53, 112.0 mm SL) is designated as the lectotype. The second syntype (BMNH 1867.6.13:54) becomes a paralectotype. The titles of the two papers involving *C. leuciscus* published by Günther (1868a, 1868b) imply that the specimens originated in Brazil. The entire Río Huallaga system lies, however, within the boundaries of Peru.

In 1907 Eigenmann and Ogle described a subspecies of

Steindachnerina leucisca as *Curimatus leuciscus bolivae* based on a single specimen (USNM 44832) with a stated collection locality of Bolivia. Data in the USNM register indicate that the specimen was collected at an unspecified site in the Río Mamoré basin in that country. Eigenmann and Ogle (1907:4) distinguished their nominal subspecies from the "typical species in having 57 scales in the lateral line instead of 60 to 64" and certain details of pigmentation. The number of lateral-line scales, along with all examined meristic and morphometric features of the holotype of *Curimatus leuciscus bolivae*, fall within the range for *S. leucisca* (Table 3). The purported differences in pigmentation, in turn, represent individual variants in that feature comparable to those that occur repeatedly within samples of the species from diverse localities throughout its range. Consequently, no basis can be found for the continued recognition of *Curimatus leuciscus bolivae* as a separate subspecies.

Eigenmann and Eigenmann (1889b:422) described a subspecies, *Curimatus bimaculatus sialis*, from a series of specimens collected by the Thayer expedition at Manacapuru, Brazil, in the central Amazon. Those authors noted, however, that there

TABLE 3.—Morphometrics and meristics of (A) lectotype of *Curimatus leuciscus* (BMNH 1867.6.13:53), (B) paralectotype of *Curimatus leuciscus* (BMNH 1867.6.13:54), (C) holotype of *Curimatus leuciscus bolivae* (USNM 44832), (D) holotype of *Allenina pectinata* (CAS 57149, formerly IU 4317), and (E) all specimens of *Steindachnerina leucisca* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 14 are proportions of head length. Question marks indicate values that could only be estimated as a consequence of the condition of the cited specimen. Dashes indicate values that could not be taken due to condition of specimen.

Character	A	B	C	D	E
MORPHOMETRICS					
Standard Length	112.0	102.2	91.5	125.1	68.7–151.2
1. Greatest body depth	0.30	0.29	0.30	0.30	0.28–0.32
2. Snout to dorsal-fin origin	0.47	0.45	0.47	0.46	0.44–0.48
3. Snout to anal-fin origin	0.83	0.84	0.83	0.83	0.81–0.86
4. Snout to pelvic-fin origin	0.50	0.50	0.50	0.48	0.48–0.53
5. Snout to anus	0.71	0.72	0.72	0.72	0.71–0.75
6. Origin of rayed dorsal fin to hypural joint	0.59	0.57	0.58	0.58	0.57–0.62
7. Pectoral-fin length	–	–	–	–	0.18–0.22
8. Pelvic-fin length	0.23	–	0.25	–	0.22–0.26
9. Caudal peduncle depth	0.11	0.12	0.12	0.12	0.11–0.12
10. Head length	0.26	0.26	0.26	0.25	0.25–0.28
11. Snout length	0.30	0.31	0.30	0.29	0.27–0.31
12. Orbital diameter	0.30	0.31	0.30	0.29	0.28–0.34
13. Postorbital length	0.44	0.43	0.45	0.43	0.39–0.45
14. Interorbital width	0.42	0.42	0.43	0.44	0.41–0.46
MERISTICS					
Lateral-line scales	56	58	53?	55?	53–62
Scale rows between dorsal-fin origin and lateral line	11	11	–	–	9–11
Scale rows between anal-fin origin and lateral line	7	7	8	8	6 ^{1/2} –8
Branched dorsal-fin rays	9	9	–	9	9
Branched anal-fin rays	7	7	7	7	7
Total pectoral-fin rays	15	13	–	–	13–17
Branched pelvic-fin rays	9	9	8	9	8–9
Vertebrae	38	37	36	37	36–38

was pronounced variability in a number of features within the type series of the subspecies. Reanalysis has shown that the syntypes include two species, *Steindachnerina bimaculata* (USNM 120401, MCZ 20206) and *S. leucisca* (MCZ 86348, out of MCZ 20206), accounting for the variability noted in the series by Eigenmann and Eigenmann.

Fernández-Yépez (1948:40) described a new species, *Allenina pectinata*, on the basis of a specimen collected by the Thayer expedition at Manacapuru, Brazil. Surprisingly, he cited Eigenmann posthumously as the author of the name. Eigenmann had evidently separated the holotype (CAS 57149, formerly IU 4317) from a series of Thayer Expedition specimens of *Steindachnerina leucisca* he examined in the Museum of Comparative Zoology (MCZ 27416). The specimen was subsequently taken by Eigenmann to Indiana University, and later transferred to the California Academy of

Sciences along with the bulk of the Indiana University fish collection. Although Eigenmann provisionally assigned the manuscript name *Curimata pectinata* to the specimen, he neither published the description, nor is there any indication that he dealt subsequently with the question of the validity of the then undescribed form. Thus, although Eigenmann first raised the question of the possible distinctiveness of the species, he is not the author of the species. Authorship of the species belongs to Fernández-Yépez. Examination of the holotype of *Allenina pectinata* has not revealed any differences between that individual and the series of specimens with which it was originally catalogued (MCZ 27416). Neither have any differences been discovered to discriminate that nominal species from *Steindachnerina leucisca* (Table 3). *Allenina pectinata* is thus placed as a synonym of *Steindachnerina leucisca*.

MATERIAL EXAMINED.—211 specimens (69, 68.7–151.2).

BRAZIL. *Pará*: Santarém, CAS 41730, 1, (120.2). Óbidos, MCZ 20350, 1; MCZ 20329, 1; MCZ 20335, 4. *Amazonas*: Rio Solimões, Ilha da Marchantaria, USNM 229189, 1; USNM 229188, 2; USNM 229175, 3; GC, 2 (103.0–120.8); USNM 229186, 1 (84.0). Parantins, mouth of Lago José Açu, MZUSP 7634, 5 (72.5–102.3). Vicinity of Manaus, MZUSP 19289, 6 (3, 115.2–138.0). Mouth of Rio Negro, NMW 67038, 12. Lago Janaucá, MZUSP 21698, 2. Manacapuru, CAS 57149, 1 (125.0, holotype of *Allenina pectinata*; formerly IU 4317); MCZ 20211, 1; MCZ 27426, 9 (86.3–142.6); MCZ 86348, 6 (paralectotypes of *Curimatus bimaculatus sialis*; formerly MCZ 20206). Ilha Xibeco, above mouth of Rio Jutai, MZUSP 21018, 16 (6, 76.8–111.5). Rio Madeira, 25 km below Nova Olinda, MZUSP 6951, 5 (3, 88.7–96.2). Paraná de Urucará, Município de Urucará, MZUSP 7508, 4 (2, 93.2–93.7). Rio Solimões near Ilha Baruruá, above mouth of Rio Jutai, MZUSP 20990, 2 (69.7–87.6). Fonte Boa, mouth of Rio Juruá, MZUSP 27396, 2. Rio Solimões, Jacaré near Fonte Boa, MZUSP 20955, 3. Rio Solimões, Fonte Boa, MZUSP 21031, 1. Junction of Rio Iaco and Rio Purus, AMNH uncat., 3; AMNH uncat., 3; AMNH 12565, 3 (103.8–109.5); MCZ 33515, 3; USNM 94655, 4 (99.5–113.0). Hyavary (= Rio Javari), MCZ 20236, 1. Tefé, lower Rio Japurá, Costa Japão, MZUSP 27368, 6 (2, 68.7–87.3). Ilha Sorubim, Rio Solimões above Coarí, MZUSP 20925, 6. *Acre*: Rio Juruá, município de Cruziero do Sul, ZUEC 414, 1 (133.8). *Rondônia*: Calama, USNM 242133, 2 (112.7–114.3). Rio Mamoré, Guajará Mirim, INPA-Polo 94, 5.

PERU. Río Huallaga, BMNH 1867.6.13:53, 1 (112.0, lectotype of *Curimatus leuciscus*); BMNH 1867.6.13:54, 1 (102.2, paralectotype of *Curimatus leuciscus*). *Amazonas*: Río Marañon, LACM 41738-20, 2 (147.3–151.2). *Loreto*: Río Huallaga, Yurimaguas, IU 15826, 1 (98.3). *Ucayali*: Río Ucayali at Bahuanisho, AMNH 35683, 1 (105.3). Río Ucayali at Pucallpa, USNM 261407, 2 (70.3–97.3); USNM 261405, 1 (80.9); USNM 261410, 2 (91.5–94.5); USNM 261455, 1; USNM 261485, 3. Río Ucayali at Masisa, USNM 261500, 1 (85.2); USNM 261520, 10 (5, 76.1–104.2); USNM 243238, 3 (76.0–109.8); USNM 261504, 1; AMNH uncat., 1; MZUSP 25958, 5. Río Ucayali at Utuquinia, USNM 289221, 2; USNM 289222, 1.

BOLIVIA. Río Mamoré, USNM 44832, 1 (91.5, holotype of *Curimatus leuciscus boliviae*). *Beni*: Río Mamoré, 8 km N of Exaltacion, AMNH uncat., 6 (1, 93.0). Río Mamoré, 2.3 km W of San Javier, AMNH uncat., 3. Río Mamoré, 15 km S of Limoquije, AMNH uncat., 12. Mouth of Río Ibarré, AMNH uncat., 18. Río Mamoré, at Isla Nicolas Suarez, UMMZ 205116, 4.

Steindachnerina binotata (Pearson, 1924)

FIGURES 14, 15

Curimatus binotatus Pearson, 1924:28, pl. 19, fig. 1 [type locality: Bolivia: Rurrenbaque].—1937:109 [Río Beni drainage system].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

Curimata binotata.—Fowler, 1940b:98 [reference].—1950:279, fig. 377 [literature compilation].—Terrasas-Urquidí, 1970:30 [reference].

Cruzentina binotata.—Fernández-Yépez, 1948:53 [assignment to *Cruzentina*].—Fowler, 1975:367 [reference].

DIAGNOSIS.—The presence of three longitudinal, weakly developed folds on the roof of the oral cavity rather than three fleshy flaps and/or one or more series of lobulate fleshy processes in that region discriminates *Steindachnerina binotata* from its congeners with the exception of *S. leucisca*, *S. argentea*, *S. conspersa*, and *S. bimaculata*. The presence of 67 to 70 scales along the lateral line from the supracleithrum to the hypural joint separates *S. binotata* from all those taxa that have 62 or fewer scales in that series.

DESCRIPTION.—Body elongate, somewhat compressed, more so in smaller specimens. Dorsal profile of head straight or very slightly convex. Dorsal profile of body straight or very slightly convex from rear of head to origin of dorsal fin; straight or slightly convex, posteroventrally slanted at base of dorsal fin, slightly concave to slightly convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with distinct median keel anterior to dorsal fin, keel most pronounced posteriorly; body smoothly rounded transversely posterior to fin. Ventral profile of body straight from tip of lower jaw to vertical through origin of pectoral fin, gently convex from that point to origin of anal fin, then sigmoid to caudal peduncle. Prepelvic region broadly but obtusely flattened, with obtuse lateral keels. Postpelvic region rounded. Anus distinctly anterior of origin of first anal fin-ray, with 9 to 11 scales in intervening space.

Greatest depth of body 0.25–0.31 [0.31]; snout tip to origin of dorsal fin 0.44–0.48 [0.45]; snout tip to origin of anal fin 0.82–0.85 [0.84]; snout tip to origin of pelvic fin 0.47–0.50 [0.48]; snout tip to anus 0.70–0.73 [0.71]; origin of dorsal fin to hypural joint 0.57–0.61 [0.60]. Dorsal-fin profile acute, less so with increasing age; anteriormost rays approximately three times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.16–0.25 [0.17], extends about three-quarters distance to vertical line through origin of pelvic fin in smaller specimens, slightly over one-half distance in larger individuals. Pelvic-fin profile acute, length of pelvic fin 0.20–0.24 [0.23], reaches one-half to two-thirds distance to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed. Border of anal fin emarginate, anteriormost branched rays about three times length of ultimate ray. Caudal peduncle depth 0.10–0.11 [0.11].

Head distinctly pointed in profile, head length 0.23–0.26 [0.23]; upper jaw longer, mouth inferior; anterior portion of buccopharyngeal complex consisting of three weakly developed fleshy folds without fleshy lobulate bodies; snout length 0.28–0.32 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.32 [0.29]; adipose eyelid present, with broad, vertically ovoid opening over center of eye; length of postorbital portion of head 0.39–0.45 [0.42];



FIGURE 15.—*Steindachnerina binotata*, USNM 279335, 131.7 mm SL; Bolivia, La Paz, San Miguel de Huachi, Río Bopi.

gape width 0.27–0.33 [0.33]; interorbital width 0.41–0.43 [0.43].

Pored lateral-line scales to hypural joint 67 to 72 [67]; all scales of lateral line pored, canals in scales straight; 5 to 7 series of scales extend beyond hypural joint onto caudal-fin base; $11\frac{1}{2}$ to 13 [$12\frac{1}{2}$] scales in transverse series from origin of rayed dorsal fin to lateral line; $8\frac{1}{2}$ to 10 [$8\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Rayed dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 15 to 17 [16]; pelvic-fin rays i,9 [i,9].

Total vertebrae 36 (1), 37 (14), 38 (1).

COLOR IN ALCOHOL.—Holotype retains guanine on scales; overall coloration silvery, darker on dorsal portions of head and body. Other specimens fixed in formalin, with reduced guanine on scales; overall coloration tan to light brown, darker on dorsal portions of head and body. Distinct, narrow, deep-lying, dark band of pigmentation along midlateral surface of body from supracleithrum to caudal peduncle; band expands into broad field of slightly dusky pigmentation on peduncle. Midlateral stripe and dark pigmentation on peduncle masked by guanine on scales in some specimens. Distinct, very dark spot along dorsal midline immediately anterior of dorsal fin; spot approximately circular, somewhat more transversely elongate in smaller individuals. Anteroposteriorly elongate spot of dark pigmentation along dorsal midline immediately posterior of tip of supraoccipital spine; somewhat less apparent in larger individuals. Mid-dorsal line from rear of dorsal fin to caudal peduncle very dark. Few variably sized, dark spots approximately size of pupil scattered on lateral and dorsolateral portions of body (Figure 15). Rays of caudal fin outlined by series of small chromatophores; lower lobe of caudal fin dusky. Other fins hyaline.

DISTRIBUTION.—Upper Río Madeira system in Bolivia and

Peru (Figure 14).

COMPARISONS.—The distribution of *Steindachnerina binotata* is known to overlap that of three congeners, *S. bimaculata*, *S. dobula*, and *S. guentheri*. The overall body form, high lateral-line scale and vertebral counts, and various details of the pigmentation pattern in *S. binotata* readily discriminate that species from each of the cited taxa.

MATERIAL EXAMINED.—31 specimens (17, 89.6–133.0).

BOLIVIA. *Beni*: Rurrenbaque, CAS-IU 17285, 1 (133.0, holotype of *Curimatus binotatus*). *La Paz*: San Miguel de Huachi (Río Boopi), USNM 279335, 1 (131.7).

PERU. *Madre de Dios*: Río Tambopata, Puerto Maldonado, USNM 301960, 1 (89.6; cleared and counterstained for cartilage and bone). Parque Nacional Manú, streams flowing into Río Manú, vicinity of Pakitzta, USNM 295339, 28 (14, 92.5–123.5).

Steindachnerina argentea (Gill, 1858)

FIGURES 16–20

Curimatus argenteus Gill, 1858:422 [type locality: Western portion of Trinidad].—Günther, 1864:289 [based on Gill, 1858].—Lütken, 1874b:255 [Trinidad].—Eigenmann and Eigenmann, 1889:421 [reference].—1891:47 [reference].—Regan, 1906:385, pl. 11, fig. 5 [Trinidad: Caroni River system. Dominica?, see "Remarks" under this species concerning this record].—Eigenmann, 1910:421 [reference].—Fowler, 1915:530 [Trinidad].—Pearse, 1920:20, figs. 3, 4 [diet; Venezuela: Lago Valencia].—Eigenmann, 1920a:9 [Venezuela: Lago Valencia system, Río Bue at Maracay; Río Tuy system, Río Tiquirito at El Concejo].—1922:230 [Colombia: Barrigon, Villavicencio; Venezuela: El Concejo at Río Tiquirito near Caracas, Río Bue at Maracay].—Mago-Leccia, 1967:254 [Venezuela: Llanos of Río Orinoco basin].—1970:75 [Venezuela].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

Curimatus argentea.—Fowler, 1931:407 [Venezuela: Guarico].—1943b:65, fig. 1 [Trinidad; Dominica, based on Regan, 1906, see "Remarks" under this species concerning this record].—Schultz, 1944:250 [reference].—Fowler, 1946:2 [Trinidad: Tumpuna River].—Price, 1955:10 [Trinidad: Caroni, Caparo, and northern Oropouche systems; not seen].—Luengo, 1963:324

[Venezuela, Carabobo, Lago Valencia basin].—Boeseman, 1960:86, 87 [Trinidad, east of Port of Spain; common names].

Curimatorbis argenteus.—Fernández-Yépez, 1948:42 [assignment to *Curimatorbis*].—Fowler, 1975:370 [reference].

Curimata spec.—Price, 1955:5, 8, pl. 3 [northern Trinidad; not seen].

DIAGNOSIS.—The presence of three longitudinal weakly developed folds on the roof of the oral cavity rather than very fleshy flaps and/or one or more series of lobulate fleshy processes in that region discriminates *Steindachnerina argentea* from other members of the genus with the exception of *S. leucisca*, *S. binotata*, *S. conspersa*, and *S. bimaculata*. The presence of 32 to 36 scales along the lateral line from the supracleithrum to the hypural joint separates *S. argentea* from all those taxa that have 38 or more scales in that series.

DESCRIPTION.—Body moderately elongate, slightly compressed, less so in ripe females. Dorsal profile of head convex anteriorly, straight from vertical line through nostrils to rear of head. Dorsal profile of body convex from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, straight to slightly convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded immediately posterior to head, with indistinct median keel in region anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened, with irregular median series of scales. Obtuse median keel posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body one scale dorsal of ventral midline.

Greatest depth of body 0.35–0.42 [0.41]; snout tip to origin of dorsal fin 0.47–0.53 [0.52]; snout tip to origin of anal fin 0.82–0.88 [0.84]; snout tip to origin of pelvic fin 0.51–0.59 [0.52]; snout tip to anus 0.76–0.84 [0.77]; origin of dorsal fin to hypural joint 0.55–0.60 [0.59]. Dorsal-fin profile obtusely pointed, anteriormost rays two and one-half to two and three-quarters times length of ultimate ray. Pectoral-fin profile

acute; length of pectoral fin 0.18–0.22 [0.19], extends at least three-quarters distance to vertical line through origin of pelvic fin, reaching that line in some specimens. Pelvic-fin profile acute, length of pelvic fin 0.20–0.24 [0.21], reaches almost to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed. Border of anal fin emarginate, anteriormost branched rays three to three and one-half times length of ultimate ray. Caudal peduncle depth 0.14–0.16 [0.15].

Head distinctly pointed, head length 0.27–0.34 [0.30]; upper jaw slightly longer, mouth barely subterminal; portion of buccopharyngeal complex on roof of oral cavity consisting of three weakly developed folds without any associated fleshy lobulate bodies; snout length 0.26–0.32 [0.27]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.26–0.34 [0.26]; adipose eyelid present, more developed anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.42–0.48 [0.47]; gape width 0.26–0.32 [0.26]; interorbital width 0.44–0.48.

Pored lateral-line scales to hypural joint 32 to 36 [34]; all scales of lateral line pored, canals in lateral-line scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; 5½ or 6 [5½] scales in transverse series from origin of dorsal fin to lateral line; 4½ or 5 [5] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or ii,10, or iii,9 (ii,10 rare; when three unbranched rays present, first very short) [ii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 12 to 15 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 30 (7), 31 (68), 32 (1).

COLOR IN LIFE.—(The following life coloration description is based on information provided by Dr. Robin Bruce from specimens originating in the Arouca River, Trinidad, and from specimens collected by the author in the central portions of the Llanos of the Río Orinoco basin). Overall coloration silver,

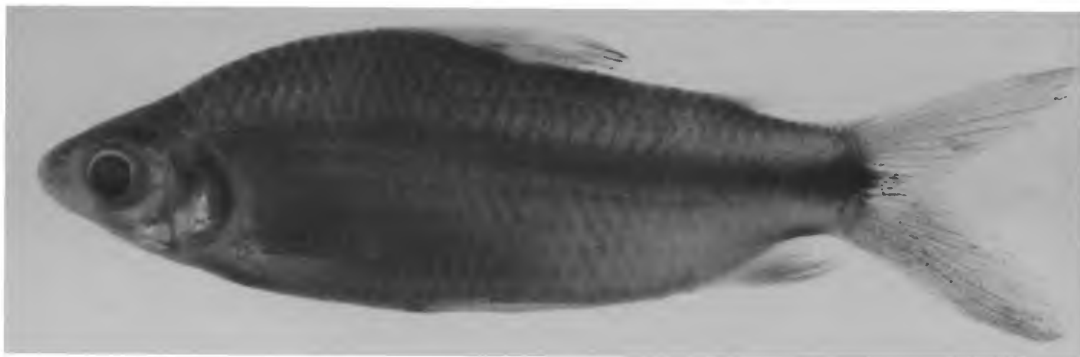


FIGURE 16.—*Steindachnerina argentea*, USNM 285663, 72.4 mm SL; Trinidad, Northern Trinidad, Arouca River.



FIGURE 17.—*Steindachnerina argentea*, MAC 69214, 57.4 mm SL; Venezuela, Codegas, Río Portuguesa system.



FIGURE 18.—*Steindachnerina argentea*, USNM 235417, 58.9 mm SL; Venezuela, Territorio Federal Delta Amacuro, Isla Tortola.

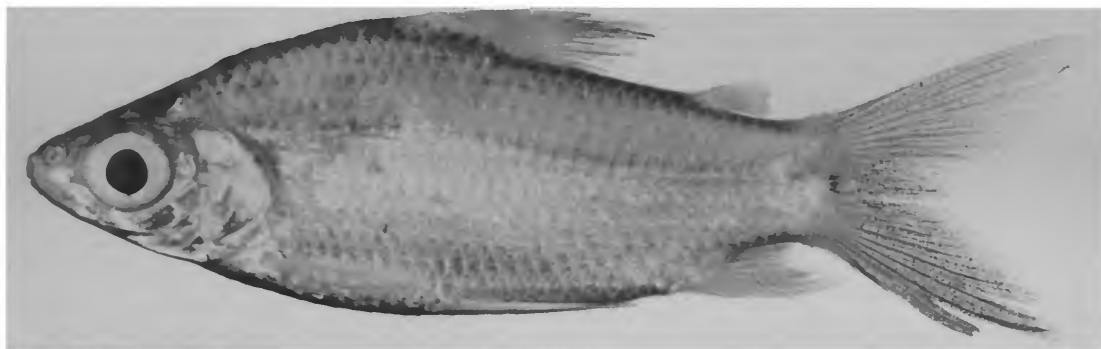


FIGURE 19.—*Steindachnerina argentea*, USNM 258186, 33.1 mm SL; Venezuela, Apure, Modulos de Mantecal.

darker on dorsal portions of head and body, with purplish iridescence, shading ventrally to white. Caudal peduncle with horizontally elongate black spot extending anteriorly to varying degrees. Dorsal fin yellowish brown with conspicuous dark spot basally on middle rays. Adipose fin yellowish. Anal fin yellowish, more so distally. Pectoral fin with slight yellowish cast. Anterior five pelvic-fin rays yellowish; remaining rays pale. Iris silver.

COLOR IN ALCOHOL.—Specimens retaining guanine on scales silvery overall, darker on dorsal portions of head and body. Overall coloration of specimens lacking guanine on scales yellowish tan, darker dorsally. Variably present mid-lateral patch of dark pigmentation on rear of caudal peduncle (Figures 16–19). When patch is present, it is continuous posteriorly with very dark spot on basal portions of middle caudal-fin rays (Figures 16, 17). Basal spot present in all specimens; developed to greater extent and darker in some populations, particularly those on Trinidad (Figure 16). Basal spot on middle caudal fin-rays sometimes continued posteriorly as faint horizontal band in specimens with particularly dark overall pigmentation (Figure 16). Spot of dark pigmentation on basal portions of middle dorsal-fin rays and fin membrane. Caudal fin dusky, lower lobe more so in some individuals. Dorsal and anal fins dusky, other fins hyaline.

DISTRIBUTION.—Rivers of the western portion of the island of Trinidad, the Río Orinoco basin of central Venezuela and eastern Colombia, and some of the coastal rivers draining into the Caribbean Sea along the north coast of Venezuela (Figure 20; see also “Remarks” below with respect to reported occurrence of the species on the island of Dominica).

COMMON NAMES.—Trinidad: silverfish, stout sardine, hump-backed sardine (Boeseman, 1960:87).

GEOGRAPHIC VARIATION.—Material of *Steindachnerina argentea* from Trinidad, the type region, tends to have a larger and relatively darker mid-lateral spot on the caudal peduncle, with a smaller particularly dark spot at the base of the middle caudal-fin rays (Figure 16). Many individuals of *S. argentea* in continental populations from the Río Orinoco basin, although retaining the smaller prominent spot at the base of the caudal-fin rays, have the larger patch of dark pigmentation on the caudal peduncle faint or absent. Nonetheless, those mainland populations include varying percentages of specimens that also have darker mid-lateral caudal peduncle spots whose intensity approximates those in Trinidadian samples of the species. It is not possible at this time to determine whether these geographic differences in the degree of development of pigmentation on the caudal peduncle within *S. argenteus* are a consequence of local water conditions, other ecological factors, or genetic variation across the species range. The Trinidad and mainland populations otherwise agree in examined morphometrics and meristics and consequently are considered conspecific.

COMPARISONS.—The range of *Steindachnerina* overlaps, at least to some degree, that of three congeners, *S. bimaculata*, *S. dobula*, and *S. guentheri*. The poorly developed fleshy folds on the roof of the oral cavity of *Steindachnerina argentea* readily discriminate that species from *S. dobula* and *S. guentheri* in which that portion of the buccopharyngeal complex is developed into a compact mass of fleshy lobulate processes. *Steindachnerina argentea* and *S. bimaculata*, in turn, differ in a number of meristic and morphometric features (see “Key” and “Diagnosis” under this species).

REMARKS.—Gill’s original description of *Curimatus argenteus* (1858:422) was based on a series of unspecified size.

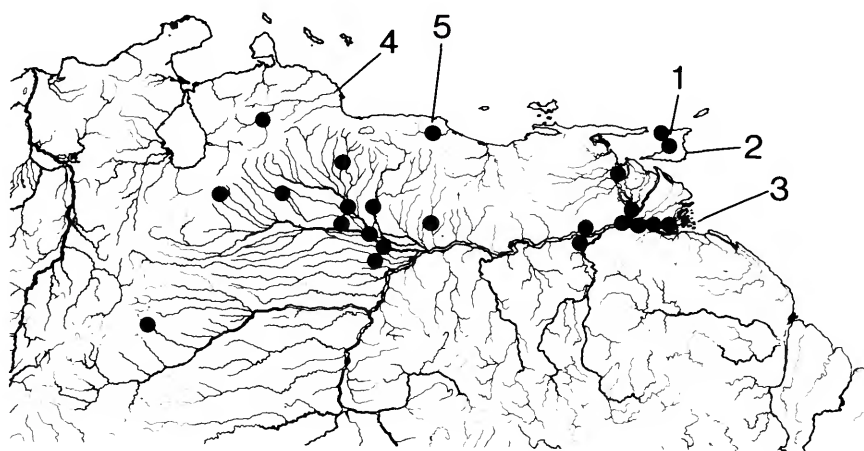


FIGURE 20.—Map of northern South America and Trinidad showing geographic distribution of *Steindachnerina argentea* (1 = western Trinidad, approximate type locality of *Curimatus argenteus*; 2 = Trinidad; 3 = mouth of Río Orinoco; 4 = Río Tocuyo; 5 = Río Tuy) (some symbols represent more than one collecting locality and/or lot of specimens).

Three syntypes, presently in poor condition, were deposited by Gill in the USNM fish collection. The largest of these specimens, which is also in the best condition (USNM 1114, 67.3 mm SL), is designated as the lectotype. The two remaining syntypes (USNM 293745) become paralectotypes.

Regan (1906:385) reported *Curimatus* (= *Steindachnerina*) *argenteus* from the island of Dominica in the Lesser Antilles, a location that is a considerable distance from the known populations of the species in both mainland South America and Trinidad. That locality seems unlikely in light of the known distribution of other groups of South American freshwater fishes. Nonetheless, an examination of the specimens that served as the basis for Regan's report (BMNH 1866.1.22:94-95) has confirmed that they are *Steindachnerina argentea*. Information in the catalogue of the British Museum (Natural History) indicates that the material was purchased from a "Mr. Cutter." Mr. Cutter also provided the BMNH with a number of different species of fishes from Trinidad in the same transaction. Among these was a series of *S. argentea* from an unspecified locality on Trinidad (BMNH 1866.1.22:49-52). Furthermore, the specimens of *argentea* from Trinidad were catalogued into the BMNH collections on the same day as the specimens purportedly from Dominica. Given the geographic complexity of the original purchase and the presence of *S. argentea* from Trinidad in that material, it is possible that the specimens catalogued as collected in Dominica actually originated in Trinidad and were erroneously ascribed to Dominica at some point during processing.

A series of relatively small, discrete river basins drain portions of the coastal versant of northern Venezuela in the region between the Golfo de Venezuela and the Golfo de Cariaco. These systems are separated from the tributaries of the Río Orinoco that lie to the south by variously elevated regions that are continuous to the west with the Cordillera de Merida of the northeastern portion of the Andean mountain chain. The ichthyofauna of those coastal rivers is poorly known, with the only paper apparently dealing with the fish fauna of one of the rivers being that of Eigenmann (1920a). In that paper he reports *Curimatus argenteus* from the Río Tiquirito, a tributary of the Río Tuy that is separated from tributaries of the Orinoco by relatively low rises. That record was subsequently repeated by Eigenmann (1922:230) and Luengo (1963:324). Although I have been unsuccessful in my attempts to locate the specimens that served as the basis for the original record (IU 15110), limited collections of fishes from the Río Tuy basin deposited at MBUCV have confirmed the presence of *Steindachnerina argentea* in that river system (Figure 20, locality 5). Material in the same depository has shown that the species is also unexpectedly present in the Río Tocuyo that lies to west of the Río Tuy system (Figure 20, locality 4), and which is isolated from the Río Orinoco basin to the south by relatively high hills. Further sampling is necessary to determine whether *S. argentea* occurs in the other isolated coastal river basins between the Río Tuy and Río Tocuyo.

MATERIAL EXAMINED.—758 specimens (106, 23.4–93.4). DOMINICA. No specific locality, BMNH 1866.1.22:94-95, 2 (questionable locality, see "Remarks" above).

TRINIDAD. No specific locality, AMNH 13697, 1 (58.1); BMNH 1936.1.32:2, 1 (97.0); BMNH 1906.6.23:40-42, 3 (2, 72.3–81.3); BMNH 1866.1.22:49-52, 4. "Western Portion," USNM 1114, 1 (67.3, lectotype of *Curimatus argenteus*); USNM 293745, 2 (51.5–61.5, paralectotypes of *Curimatus argenteus*). Piarco, USNM 191644, 22 (7, 23.4–61.1). Arouca River, BMNH 1985.3.14:128-132, 5. Arouca River, just north of Churchill to Roosevelt Highway, USNM 285663, 27 (12, 59.7–71.4). Guanapo River, USNM 163863, 2 (66.5–68.0). Tunapana River, BMNH 1985.3.14:127, 1.

VENEZUELA. *Monagas*: Río Guarapiche, USNM 163158, 2 (57.1–57.5). Río Caripe, near Carapito, MBUCV V-12402, 1. Río Orinoco, Barrancas, Laguna El Guatero, USNM 235430, 8 (41.3–50.0). Isla Tapatapa, Los Castillos, USNM 235434, 2 (55.4–56.0); USNM 235415, 2 (46.5–49.2). Río Orinoco, Isla Cocos, opposite Los Castillos, USNM 235427, 13. Isla Chivera, near Barrancas, USNM 235429, 3. *Territorio Federal Delta Amacuro*: Río Orinoco (08°29'N, 61°18'W), USNM 235419, 7 (6, 41.3–51.0). Isla Tortola, USNM 235417, 1 (58.9); USNM 233827, 75. Caño Paloma, USNM 235416, 3 (2, 40.9–55.3). Caño Fiscal, USNM 235425, 6 (40.8–54.2). Caño Araguaito, USNM 233802, 75 (6, 42.5–54.2); USNM 235422, 1; USNM 235428, 3. Caño Araguaio, USNM 235432, 2. *Bolívar*: Río Aro, USNM 235418, 2. Río Orocopiche, USNM 235420, 1; USNM 235421, 5; USNM 235423, 12; USNM 235424, 27; USNM 235426, 1; USNM 235425, 5. Río Marhuanta, 12 km S of Ciudad Bolívar, MBUCV V-1598, 1. Río Arojenel, where crossed by highway from Ciudad Bolívar to Maripa, MBUCV V-11590, 1. *Guarico*: Fundo Pequario Masagual (08°34'N, 67°35'W), USNM 260145, 6 (5, 45.2–53.2). Tributary of Río Guarico, 3 km S of Calabozo, ANSP 138840, 13 (1, 73.5). Río Portuguesa, near Camaguan, MBUCV V-9128, 17; MBUCV V-9366, 1; MBUCV V-7163, 1. Caño Falcon, near Camaguan, MBUCV V-8841, 2; MBUCV V-8843, 2. Esteros de Camaguan, MBUCV V-11810, 1; MBUCV V-11818, 1. Río Manapire, Santa Rita, MBUCV V-5749, 1. Río Cuirá, Río Tuy system, MBUCV V-3728, 23. *Codejas*: Km 63 along road from El Pao to El Baul, GC, 2 (50.7–60.6). Quebrada La Sulforosa, Río Tinaco system, at San Luis between San Carlos and Tinaco, MBUCV V-9886, 1. Río Portuguesa system, MBUCV V-uncat., 6 (formerly MAC 69214). *Apure*: Vicinity of San Fernando de Apure, USNM 220580, 2 (53.3–53.9). Río Apure, 5 km W of San Fernando de Apure, USNM 258019, 18 (5, 43.9–66.7). Río Apure Viejo, San Fernando de Apure, MBUCV V-8250, 2. San Fernando de Apure, USNM 258021, 100. Caño near Río Apurito, where crossed by road from San Fernando de Apure to Cunaviche, USNM 260158, 22 (5, 44.3–53.8). Modulos de Mantecal, MBUCV V-9263, 3; MBUCV V-9216, 15; USNM 258186, 65. Río Cunaviche, USNM 258085, 4. *Portuguesa*: Caño Maraca, at bridge on road from Guanare to Guanarito, MCZ 54345, 3

(44.7–65.2). Río Las Marias, near Guanare, MBUCV V-7417, 2 (57.3–59.3). *Barinas*: Río Másparro, between Bozonito and Barrancas, USNM 220581, 3 (29.7–36.7). *Lara*: Río Curarigo, Río Tocuyo basin, near Curarigo, MBUCV V-10858, 1 (93.4). Río Camoruro, Río Tocuyo basin, MBUCV uncat., 2 (formerly MAC 68137).

COLOMBIA. Río Guachiria basin, Pore, GC, 2 (42.3–44.5). *Meta*: Río Meta basin, Caño Chichimene, 2 km E of Quebraditas, NRM SIL/1987514.3138, 10. Mouth of Caño Quenane into Río Negro, NRM 1988623.3144, 1. Río Meta system, Río Negro where crossed by Villavicencio to Puerto Lopez Road, La Balsa, NRM SIL/1988026.3133, 11. Río Meta basin, oxbow lake connected to Río Negro, 500 m S of La Balsa, NRM SIL/1988021.3190, 51. Río Negro, 2 km S of Rincon de Pompeya, NRM SIL/1987527.3143, 2. Caño draining into Río Negro, approx. 5 km S of Rincon de Pompeya, NRM SIL/1987521.3136, 28. Caño draining into Río Negro, approx. 6 km S of Rincon de Pompeya, NRM SIL/1987514.3142, 4.

Steindachnerina conspersa (Holmberg, 1891)

FIGURES 21–23, TABLE 4

- Curimatus conspersus* Holmberg, 1891:185 [type locality: Argentina: Formosa, Río Paraguay].—Eigenmann, 1910:421 [reference].—Bertoni, 1914:9 [Paraguay, ? based on Holmberg, 1891].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus bimaculatus*.—Boulenger, 1900:2 [Mato Grosso].—Eigenmann and Kennedy, 1903:511 [Paraguay: Estancia La Amónia, Arroyo Tremintina, Asunción].—Eigenmann, McAtee and Ward, 1907:124 [Paraguay: Corumbá].—Eigenmann and Ogle, 1907:3 [Paraguay].—Eigenmann, 1910:421 [reference in part; Paraguay basin citations].—Bertoni, 1914:9 [? based on Eigenmann, McAtee, and Ward, 1907].
- Curimata conspersa*.—Pearson, 1937:109 [Río Paraguay basin, based on Holmberg, 1891].—Bertoni, 1939:54 [Paraguay, ? based on Holmberg, 1891].—Fowler, 1950:281 [literature compilation].—Ringuélet and Aramburu, 1961:36 [Argentina, based on Holmberg, 1891].—Fowler, 1975:368 [reference].—Ringuélet, 1975:72 [Río Paraguay, based on Holmberg, 1891].—[not Géry et al., 1987:427].
- Curimata bimaculatus*.—Pearson, 1937:109 [in part, Paraguay basin citations].
- Curimata bimaculata*.—Bertoni, 1939:54 [Paraguay, based on Eigenmann and Kennedy, 1903].—Géry et al., 1987:424, fig. 40 [Paraguay, Río Paraguay and Río Paraná systems; Brazil, Río Cuiabá].
- Cruentina bimaculata*.—Fernández-Yépez, 1948:53 [in part, Alto Río Paraná citations].
- Curimata bimaculata bimaculata*.—Fowler, 1950:278 [references in part, Río de La Plata basin citations; not Amazon basin references].—Ringuélet and Aramburu, 1961:36 [Argentina].—Lopez et al., 1987:19 [Argentina].
- Pseudocurimata bimaculata*.—Aramburu, Aramburu, and Ringuélet, 1962:227 [Argentina].—Ringuélet, 1975:61 [in part, Río de La Plata system references; not Amazon basin citations].—Bonetto et al., 1978:17 [Argentina: Río Riachulo basin, Lagunas Totoras and Gonzalez].—Pignalberi de Hassan and Cordiviola de Yuan, 1985:21 [Argentina: middle Río Paraná, Corrientes and Santa Fe areas].—Cordiviola de Yuan and Pignalberi de Hassan, 1985:215 [Argentina: lower Río Paraná, Diamante and San Pedro areas].
- Pseudocurimata bimaculata bimaculata*.—Ringuélet, Aramburu, and Aramburu, 1967:198 [Argentina].—Bonetto et al., 1978:57 [Argentina: Río Riachulo basin, Laguna La Brava].—Azpelicueta, 1980:85 [osteological observations].
- Rivasella conspersa*.—Ringuélet, Aramburu, and Aramburu, 1967:202 [Argen-

tina, based on Holmberg, 1891].—Lopez et al., 1987:20 [possible assignment to *Rivasella*; Argentina].

Steindachnerina conspersa, Venere and Galetti, 1989:19, 21, fig. 1 [Brazil: Mato Grosso do Sul, Corumbá, Río Paraguai; karyotype information].

DIAGNOSIS.—The presence of three weakly developed longitudinal folds on the roof of the oral cavity rather than three very fleshy flaps and/or one or more series of lobulate fleshy processes in that region discriminates *Steindachnerina conspersa* from its congeners with the exception of *S. binotata*, *S. leucisca*, *S. argentea*, and *S. bimaculata*. The 38 to 43 scales along the lateral line from the supracleithrum to the hypural joint separate *S. conspersa* from *S. bimaculata*, *S. binotata*, and *S. leucisca*, which have 43 or more scales along the lateral line, and from *S. argentea*, which has 36 or fewer scales in that series. *Steindachnerina conspersa* is most similar to its allopatric congener *S. bimaculata* of the Amazon and Orinoco basins. In addition to differing in the number of scales in a series along the lateral line, the species differ in details of pigmentation. *Steindachnerina bimaculata* typically has a series of small dark spots on the dorsal and dorsolateral surfaces of the body, with the pigmentation around the base of the dorsal fin of the same overall intensity as in proximate portions of the body. Specimens of *S. conspersa*, in contrast, lack the small dark spots on the body and typically have the region proximate to the base of the dorsal fin much lighter than neighboring regions of the body.

DESCRIPTION.—Body moderately elongate, somewhat compressed, less so in large specimens. Dorsal profile of head straight or very slightly concave. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin, somewhat more convex with increasing size; straight and posteroventrally slanted at base of dorsal fin, straight or very slightly convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with discrete median keel anterior to dorsal fin, keel more distinct posteriorly; surface of body smoothly rounded transversely posterior to fin. Ventral profile of body straight from tip of lower jaw to vertical line through origin of pectoral fin, gently curved from that point to origin of anal fin, sigmoid from origin of anal fin to caudal peduncle. Prepelvic region obtusely flattened, with rounded lateral keels; keels more distinct proximate to origin of pelvic fin. Obtuse median keel posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body, about two scales dorsal of ventral midline.

Greatest depth of body 0.35–0.41; snout tip to origin of dorsal fin 0.46–0.52; snout tip to origin of anal fin 0.80–0.87; snout tip to origin of pelvic fin 0.51–0.55; snout tip to anus 0.75–0.81; origin of dorsal fin to hypural joint 0.58–0.61. Border of dorsal fin pointed, less so with increasing age; anteriormost rays approximately three times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.18–0.23, extends about three-quarters of distance to origin of pelvic fin. Pelvic-fin profile acute, length of pelvic fin 0.24–0.28, reaches about three-quarters of distance to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed, unscaled. Border of

anal fin distinctly emarginate, anteriormost branched rays over three times length of ultimate ray; tips of depressed anterior rays contacting lower lobe of caudal fin. Caudal peduncle depth 0.14–0.15.

Head distinctly pointed in profile, head length 0.27–0.32; upper jaw slightly longer; mouth subterminal; portion of buccopharyngeal complex on roof of oral cavity consisting of three weakly developed folds without fleshy lobulate bodies; snout length 0.28–0.33; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.30–0.36; adipose eyelid present, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.38–0.44; gape width 0.30–0.35; interorbital width 0.44–0.49.

Pored lateral-line scales to hypural joint 38 to 43; all scales of lateral line pored, canals in scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $7\frac{1}{2}$ to

$8\frac{1}{2}$ scales in transverse series from origin of dorsal fin to lateral line; $5\frac{1}{2}$ to $6\frac{1}{2}$ scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very small); anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very small); pectoral-fin rays 13 to 16; pelvic-fin rays i,8 or i,9.

Total vertebrae 33 (18), 34 (27).

COLOR IN ALCOHOL.—Specimens retaining guanine on scales silvery, darker on dorsal portions of head and body. Overall ground coloration of specimens fixed in formalin and lacking guanine on scales yellowish tan to brown, darker on dorsal portions of head and body. Dorsal portion of body proximate to base of dorsal fin typically slightly (Figure 21) to markedly (Figure 22) less pigmented than adjoining areas or body. Faint, narrow, deep-lying, dusky band extends along mid-lateral surface of body from supracleithrum to caudal



FIGURE 21.—*Steindachnerina conspersa*, MZUSP 21676, 104.2 mm SL; Brazil, Mato Grosso do Sul, Rio Miranda, Município de Corumbá.



FIGURE 22.—*Steindachnerina conspersa*, USNM 229442, 62.7 mm SL; Paraguay, Presidente Hayes, 194 km north of Asuncion of Trans-Chaco Highway.

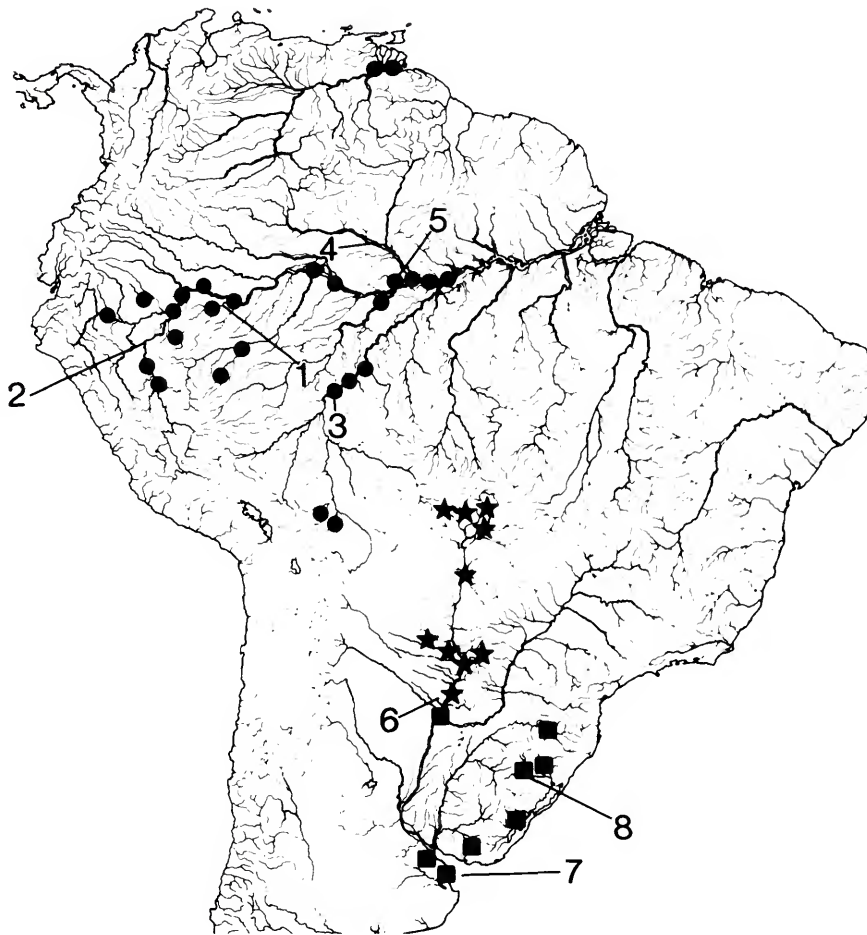


FIGURE 23.—Map of South America showing geographic distribution of *Steindachnerina bimaculata* (dots; 1 = Rio Javari, approximate type locality of *Curimatus bimaculatus*; 2 = Río Ucayali, approximate type locality of *Curimatus melaniris*; 3 = type locality of *Prochilodus pterostigma*, 4 = Rio Negro, approximate type locality of *Curimatus semiornatus*; 5 = type locality of *Curimatus bimaculatus sialis*; inexact type locality of *Curimatus trachystetus*, "Peruvian Amazon" not indicated), *Steindachnerina conspersa* (stars; 6 = type locality of *Curimatus conspersus*), and *Steindachnerina biornata* (squares; 7 = type locality of *Curimata biornata*; 8 = type locality of *Curimata stigmosa*) (some symbols represent more than one collecting locality and/or lot of specimens).

peduncle. Distinct, transversely elongate spot of dark pigmentation situated along dorsal midline immediately anterior of dorsal fin. Second, less distinct, longitudinally elongate mid-dorsal spot of pigmentation immediately posterior of tip of supraoccipital spine. Dorsal fin typically with spot of dark pigmentation near base of middle fin-rays and their membranes (Figure 21); spot more pronounced in smaller individuals; sometimes very faint (Figure 22). Anterior and distal portions of dorsal fin dusky. Distinct spot of dark pigmentation at base of middle rays of caudal fin. Lower lobe of caudal fin dusky. Ventral and distal portions of anal fin dusky.

DISTRIBUTION.—Río Paraguay and lower Río Paraná systems (Figure 23).

KARYOTYPE.—Venere and Galetti (1989:19) report that *Steindachnerina conspersa* has $2n = 54$ chromosome consisting exclusively of metacentric and submetacentric chromosomes.

REMARKS.—*Curimatus conspersus* was described by Holmberg (1891:185) from a single specimen collected in the Río Paraguay in northern Argentina. The original description of *Curimatus conspersus* by Holmberg fits or closely approximates the specimens identified as that species in this study

TABLE 4.—Morphometrics and meristics of (A) type series of *Curimatus conspersus* (based on information in original description of species (Holmberg, 1891:185 note that presented proportions are less precise than those for other cited specimens); and (B) all specimens of *Steindachnerina conspersa* from which counts and measurements were taken. Proportions are provided only for those measurements presented in original description of *Curimatus conspersus*. Standard length is expressed in mm; measurements 1 and 2 are proportions of standard length; 3 and 4 are proportions of head length.

Character	A	B
MORPHOMETRICS		
Standard Length	80.0	48.2–128.1
1. Greatest body depth	0.34	0.35–0.41
2. Head length	0.25	0.27–0.32
3. Snout length	0.25	0.28–0.33
4. Orbital diameter	0.35	0.30–0.36
MERISTICS		
Lateral-line scales	43–45*	38–43
Scale rows between dorsal-fin origin and lateral line	7	7 ¹ / ₂ –8 ¹ / ₂
Scale rows between anal-fin origin and lateral line	7†	5 ¹ / ₂ –6 ¹ / ₂
Branched dorsal-fin rays ‡	9	9
Branched anal-fin rays ‡	7†	7
Total pectoral-fin rays ‡	16	13–16
Branched pelvic-fin rays ‡	9	8–9

* Lateral-line scale counts given by Holmberg appear to also include scales on base of the caudal fin posterior of the hypural joint.

† Scales below the lateral line in original descriptions by Holmberg evidently refer to scales between lateral line and midventral scale row rather than between lateral line and origin of anal fin.

‡ Counts of total median and pelvic-fin rays in the original species description have been adjusted in the table to allow for unbranched fin-rays.

(Table 4) with the exception of one character. Holmberg reports a small spot present at the base of the anal fin in his species. No such pigmentation pattern on the anal fin has been found in any examined curimatid. It seems likely that the cited anal spot is rather an erroneous description of the small discrete spot at the base of the dorsal fin that is found in this species, but not commented on by Holmberg. Géry et al. (1987:427) similarly hypothesize that the reported spot of dark pigmentation on the anal fin is a “lapsus.” Unfortunately, attempts to locate the holotype of Holmberg’s species were unsuccessful (Dr. M. Azpelicueta, in litt.) making it impossible to confirm this supposition. Nonetheless, among the curimatids known from the Paraguay basin only the samples herein identified as *Steindachnerina conspersa* closely approximate Holmberg’s description with the exception of the noted questionable spot of pigmentation. Furthermore, no other name appears to be available for this species. Applying the name *conspersa* to this species is more conservative than the alternative of proposing a new species for the material, and is the procedure followed

herein.

Citations of *Curimatus conspersus* subsequent to Holmberg’s original description (see synonymy for this species) were made without reference to additional specimens. The identity of the species has been problematical and the form that is identified as *Steindachnerina conspersa* in this study having been repeatedly identified as *S. bimaculata*. *Steindachnerina bimaculata*, which is considered to be limited to the Río Orinoco and Rio Amazonas basins in this study, was first cited as an element of the ichthyofauna of the Río de La Plata system by Boulenger (1900:2) who identified it as *Curimatus bimaculatus*, a practice followed by numerous subsequent authors (see references in synonymy). The specimens that were the basis of the original Boulenger citation of *S. bimaculata* from the Rio Paraguay system (BMNH 1900.4.14:40–41) are not that species, but have instead proved to be individuals of *S. conspersa*. Similarly, subsequent citations of *Curimatus bimaculatus* in the Río de La Plata system by Eigenmann and Kennedy, 1903:511 and Eigenmann and Ogle (1907:3) were based on material of *S. conspersa* (AMNH 1297 and USNM 2107 respectively). Examination of an extensive series of curimatids originating in the Río de La Plata system has failed to reveal any specimens of *S. bimaculata* in that basin and it is presumed that all records of that species in the Paraná-Paraguay basin are based on misidentified individuals of *S. conspersa*.

Géry et al. (1987:427) identify a specimen from the Río Acaray, a tributary of the lower Río Paraná below the location of Sete Quedas rapids, as *Curimata conspersa*. The specimen appears rather to be a species of *Cyphocharax*. The identification by Géry et al. may be a consequence of their identification as *Curimata* (= *Steindachnerina*) *bimaculata* of the species herein considered *Steindachnerina conspersa*. As noted in the “Key” and “Diagnosis” for *S. conspersa* those species differ in a number of features.

MATERIAL EXAMINED.—132 specimens (53, 45.3–128.1).

BRAZIL. *Mato Grosso*: Fazenda Jofre, Rodovia Transpan-taneira, MZUSP 26915, 1. Santo Antônio de Leverger, MZUSP 21578, 1. Rio Pixaim, Município de Poconé, MZUSP 21589, 1. Município de Barão de Malgaço, MZUSP 21661, 1; MZUSP 21687, 1. Rio Cuiabá, Sangradouro Grande, Município de Barão de Melgaço, MZUSP 21599, 2 (53.9–66.5). Rio Jaurú, Porto Esperidião, MZUSP 28103, 6 (5, 99.5–103.2). *Mato Grosso do Sul*: Rio Miranda, Município de Corumbá, MZUSP 21676, 12 (6, 83.7–104.2). Rio Miranda, Salobra, MNRJ 8898, 2 (1, 100.1). Corumbá, MZUSP 21676, 12. Carandazininho (= Carandazininho), BMNH 1900.4.14:40–41, 2 (45.3–58.2).

PARAGUAY. No specific locality, USNM 2107, 2; USNM 55648, 2. Paraguayan Chaco, BMNH 1898.7.4:7, 1 (112.4). *Central*: Asuncion Bay, USNM 181639, 1 (118.0); USNM 181636, 22 (8, 77.4–102.4); USNM 181638, 8 (5, 66.0–92.3); USNM 181637, 9 (5, 76.5–128.1); USNM 220164, 1 (48.2); USNM 181644, 3 (71.3–102.8); USNM 181641, 1; BMNH 1935.6.4:319–322, 7. Río Paraguay at Asuncion, AMNH 1297,

2 (99.0–99.4). Vicinity of Asuncion, BMNH 1935.6.4:326–329, 10 (3, 79.0–83.7); BMNH 1935.6.4:319–322, 7. Hatipapunta, NMW 67032, 1. *Cordillera*: Lago Ypacarai, 17.6 km west of San Bernardino, USNM 232222, 1 (92.6). *Presidente Hayes*: Trans Chaco Highway, 194 km north of Asuncion, USNM 229442, 1 (62.7); USNM 232223, 2 (54.5–57.4). Trans Chaco Highway, 50 km north of Asuncion, USNM 232224, 4 (69.5–82.3).

ARGENTINA. Río Paraná, USNM 196671, 1.

URUGUAY. No specific locality, NMW 67033, 5.

Steindachnerina bimaculata (Steindachner, 1876)

FIGURES 23–25, TABLE 5

- Curimatus bimaculatus* Steindachner, 1876:76 [type locality: Brazil: Hyavary (= Rio Javari); ? mouth of Rio Negro].—Eigenmann and Eigenmann, 1889:422 [Brazil: Hyavary (= Rio Javari), Coary (= Coari), Villa Bella; not specimens from Ica (= Rio Içá)].—1891:47 [reference].—Pellegrin, 1909:148 [Brazil: Tonantins].—Eigenmann, 1910:421 [references in part, not Río Paraguay basin citations].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].—[not Boulenger, 1900:2; Eigenmann and Kennedy, 1903:511; Eigenmann and Ogle, 1907:3; Eigenmann, McAtee, and Ward, 1907:124; Bertoni, 1914:9].
- Curimatus trachystetus* Cope, 1878:684 [type locality: Peruvian Amazon].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus bimaculatus sialis* Eigenmann and Eigenmann, 1889:422 [type locality: Brazil: Manacapuru].—1891:47 [reference].—Eigenmann, 1910:421 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus bimaculatus trachystetus*.—Eigenmann and Eigenmann, 1889:422 [*Curimatus trachystetus* Cope, 1878, placed as a subspecies; Amazon basin, Serpa (= Itacoatiara, Brazil) to Peru].—1891:47 [reference].—Eigenmann, 1910:421 [reference].
- Curimata trachystetus*.—Fowler, 1906:299, fig. 5 [based on holotype of *Curimatus trachystetus*; designated as type species of subgenus *Steindachnerina* Fowler].—1942b:209 [reference].—1945:117 [reference].
- Prochilodus pterostigma* Fowler, 1913:520, fig. 3 [type locality: Brazil: Rio Madeira about 20 miles north of Porto Velho].—1940b:68 [as a probable synonym of *Curimata bimaculata*].—1941:164 [assigned to *Curimata*; hypothesized to be related to *Curimata elegans* Steindachner].—Géry, 1965:35 [assigned to *Curimata*].—1972b:32 [as a synonym of *Curimata bimaculata*].—Vari and Castro, 1988:779 [as a synonym of *Steindachnerina bimaculata*].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus semiornatus* Steindachner, 1914:262 [type locality: Brazil: Rio Negro].—1917:20, pl. 5, fig. 5 [Rio Negro].—Fernández-Yépez, 1948:73 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata bimaculatus*.—Pearson, 1937:109 [in part, Río Mamoré basin references].
- Curimata melaniris* Fowler, 1940a:253, fig. 54 [type locality: Peru: Río Ucayali, Boca Chica].—Eigenmann and Allen, 1942:299 [reference].—Fowler, 1942b:207 [reference].—1945:115 [reference].—1950:287, fig. 344 [literature compilation].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata pterostigma*.—Fowler, 1941:164 [removed from *Prochilodus*; related to *Curimata elegans*].—Fernández-Yépez, 1948:72 [as a possible species of *Pseudocurimata* Fernández-Yépez].—Fowler, 1950:290, fig. 348 [literature compilation].
- Curimata bimaculata*.—Eigenmann and Allen, 1942:292 [Peru: Río Morona, Yurimaguas].—Fowler, 1945:118 [reference].—Terasas-Urquidí, 1970:31 [reference].—[not Bertoni, 1939:54].
- Curimata trachysteta*.—Eigenmann and Allen, 1942:293 [reference].—Fowler, 1950:293, fig. 354 [literature compilation].
- Cruzeirina bimaculata*.—Fernández-Yépez, 1948:53 [assignment to *Cruzeirina*; not cited Alto Paraná references].
- Cruzeirina bimaculata sialis*.—Fernández-Yépez, 1948:53 [assignment to *Cruzeirina*].—Fowler, 1975:367 [reference].
- Rivasella melanira*.—Fernández-Yépez, 1948:56 [assignment to *Rivasella*].
- Steindachnerina trachystetha*.—Fernández-Yépez, 1948:58, fig. 30 [reference].—Fowler, 1975:375 [reference].
- Curimata bimaculata bimaculata*.—Fowler, 1950:278 [references in part, not Paraguay citations].—[not Ringuelet and Aramburu, 1961:36; Lopez et al., 1987:19].
- Curimata bimaculata sialis*.—Fowler, 1950:279 [literature compilation].
- Curimata semiornata*.—Fowler, 1950:292 [literature compilation].—1975:369 [reference].—Junk et al., 1983:406 [Rio Amazonas, Ilha de Marchantaria, Lago Camaleao].
- Pseudocurimata bimaculata*.—Ringuelet, 1975:61 [in part, Amazon basin citation].—[not Aramburu, Aramburu, and Ringuelet, 1962:227; Bonnetto et al., 1978:17; Pignalberi de Hassan and Cordiviola de Yuan, 1985:21; Cordiviola de Yuan and Pignalberi de Hassan, 1985:215].
- Cruzeirina bimaculatus bimaculatus*.—Fowler, 1975:367 [reference].
- Pseudocurimata pterostigma*.—Fowler, 1975:373 [reference].

DIAGNOSIS.—The presence of three weakly developed longitudinal folds on the roof of the oral cavity rather than three very fleshy flaps and/or one or more series of lobulate fleshy processes in that region discriminates *Steindachnerina bimaculata* from other members of the genus with the exception of *S. binotata*, *S. leucisca*, *S. argentea*, and *S. conspersa*. The 43 to 49 scales along the lateral line from the supracleithrum to the hypural joint separate *S. bimaculata* from *S. binotata* and *S. leucisca*, which have 53 or more lateral line scales, and from *S. argentea* and *S. conspersa*, which have 43 or fewer scales in that series. *Steindachnerina bimaculata* is most similar to its allopatric congener *S. conspersa*. In addition to differing in the number of scales in a series along the lateral line, the species differ in details of pigmentation. *Steindachnerina bimaculata* typically has a series of small dark spots on the dorsal and dorsolateral surfaces of the body, with the pigmentation around the base of the dorsal fin of the same overall intensity as in proximate portions of the body. Specimens of *S. conspersa*, in contrast, lack the small dark spots on the body and typically have the region proximate to the base of the dorsal fin much lighter than neighboring regions of the body.

DESCRIPTION.—Body moderately elongate, somewhat compressed, less so in larger specimens; specimens from Río Orinoco basin with somewhat shallower bodies. Dorsal profile of head straight or very slightly concave. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin, somewhat more convex in larger specimens; straight and posteroventrally slanted at base of dorsal fin; straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel from rear of head to anterior of dorsal fin, keel more obvious posteriorly; body surface smoothly rounded transversely posterior to fin. Ventral profile of body straight or gently curved from tip of lower jaw to vertical line through origin of pectoral fin, gently curved from that point to origin of anal fin, sigmoid from origin of anal fin to caudal peduncle. Prepelvic region obtusely

flattened, with rounded lateral keels; keels most distinct proximate to origin of pelvic fins. Obtuse median keel posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body about two scales dorsal of ventral midline.

Greatest depth of body 0.30–0.37 [0.36]; snout tip to origin of dorsal fin 0.45–0.51 [0.50]; snout tip to origin of anal fin 0.80–0.87 [0.82]; snout tip to origin of pelvic fin 0.49–0.55 [0.52]; snout tip to anus 0.75–0.83 [0.80]; origin of dorsal fin to hypural joint 0.56–0.62 [0.59]. Dorsal-fin profile acute, less so with increasing age; anteriormost rays 2.5–3.2 times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.18–0.22 [0.18], extends nearly to vertical line through origin of pelvic fin in smaller individuals, only three-quarters of that distance in largest specimens examined. Pelvic-fin profile

acute, length of pelvic fin 0.23–0.27 [0.26], reaches three-quarters distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Border of anal fin distinctly emarginate, anteriormost branched rays approximately three times length of ultimate ray. Caudal peduncle depth 0.12–0.13 [0.13].

Head distinctly pointed in profile, head length 0.25–0.30 [0.27]; upper jaw slightly longer, mouth subterminal; anterior portion of buccopharyngeal complex consisting of three weakly developed fleshy folds on roof of oral cavity, without fleshy lobulate bodies; snout length 0.27–0.32 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.30–0.36 [0.30]; adipose eyelid present, with vertically ovoid opening over center of eye; length of

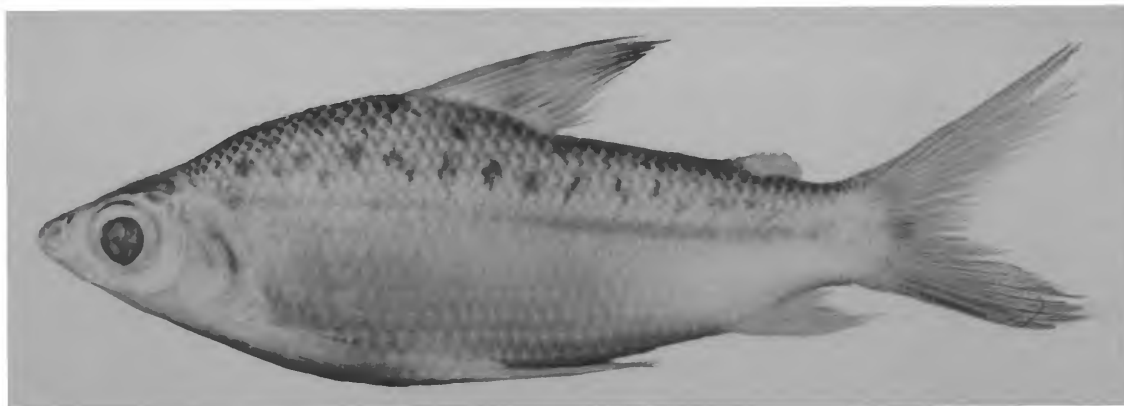


FIGURE 24.—*Steindachnerina bimaculata*, USNM 261450, 90.8 mm SL; Peru, Loreto, Río Amazonas, Santa Rosa, opposite Tabatinga, Brazil.



FIGURE 25.—*Steindachnerina bimaculata*, USNM 235463, 67.4 mm SL; Venezuela, Terretorio Federal Delta Amacuro, Lagoon off Río Orinoco, west of Caño Araguaito.

postorbital portion of head 0.38–0.44 [0.44]; gape width 0.29–0.35 [0.33]; interorbital width 0.41–0.46 [0.46].

Pored lateral-line scales to hypural joint 43 to 49 [45]; all scales of lateral line pored, canals in scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $7\frac{1}{2}$ to 9 [9] scales in transverse series from origin of dorsal fin to lateral line; $5\frac{1}{2}$ to 6 [6] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 14 to 16 [15]; pelvic-fin rays i,8 [i,8].

Total vertebrae 33 (10), 34 (47), 35 (32).

COLOR IN ALCOHOL.—Specimens retaining guanine on scales silvery, darker on dorsal portions of head and body. Overall ground coloration in specimens fixed in formalin and lacking guanine on scales light tan to brown, darker on dorsal portions of head and body. Distinct dusky, deep-lying, narrow band extends along mid-lateral surface of body from supracleithrum to caudal peduncle. Series of small spots of varying degrees of darkness on dorsal and dorsolateral portions of body in most individuals (Figure 24); spots less apparent in some Amazonian specimens and most population samples from Río Orinoco basin (Figure 25; see also comments under “Variation” below). Each spot one-third to one-half size of pupil. When dark spots present, a single longitudinal series apparent in specimens of approximately 40 mm SL; two incomplete series present in larger specimens. Discrete, very dark, saddle-shaped spot along dorsal midline immediately anterior of origin of dorsal fin. Spot more extensive transversely, straddles keel along dorsal midline. Second, somewhat longitudinally elongate, spot along dorsal midline one or two scales posterior of tip of supraoccipital spine. Dorsal fin with spot of dark pigmentation situated on basal portion of middle rays and their associated membranes. Spot most apparent and proportionally larger in specimens under 40 mm SL; becoming progressively more diffuse and less apparent in larger individuals. Anterior and distal margins of dorsal fin dusky in larger specimens. Small but distinct spot of dark pigmentation at base of middle rays of caudal fin; spot sometimes very faint or lacking in specimens under 30 mm SL and in most individuals from Río Orinoco basin (Figure 25), most prominent when present in larger individuals. Lower lobe of caudal fin dusky. Anal fin with series of small scattered chromatophores.

DISTRIBUTION.—Río Orinoco and Río Amazonas basins (Figure 23).

VARIATION.—There is a notable degree of variation in body form and dark pigmentation on the body and fins between samples of *Steindachnerina bimaculata* originating in the Río Amazonas basin and those from the Río Orinoco system. A less-pronounced degree of variation occurs in the intensity of the pigmentation within the Amazon basin populations. The significance of these differences is difficult to evaluate as a consequence of the limited available population samples from

the Río Orinoco system, and the large geographic gap in the distribution of the specimens herein considered *S. bimaculata* (Figure 23).

Individuals from the Río Orinoco system tend to have shallower bodies than comparably sized specimens from the Amazon basin. The degree of development of both the series of irregular spots located on the dorsolateral surface of the body, and of the patches of dark pigmentation at the base of the dorsal and caudal fins also varies between the two river basins. Specimens from the Río Amazonas system typically have one or more series of spots on the body and relatively obvious spots at the base of the fins (Figure 24). Available population samples from the Río Orinoco basin, in contrast, usually have fainter spots, with the body and fin spots in some individuals totally absent (Figure 25). Nonetheless, some individuals from the Amazon system also have weakly developed body and fin pigmentation approximating that found in Río Orinoco specimens. Unfortunately the sample of *Steindachnerina bimaculata* from the Río Orinoco system consists of juveniles making it impossible to determine at this time whether the spots on the body and fins in adults of *S. bimaculata* from that basin differ from the conditions typical of Amazonian populations of the species. Until such time as additional population samples from the Río Orinoco basin are available, it is premature to recognize these differences formally.

REMARKS.—Steindachner in his original description of *Curimatus bimaculatus* (1876:76) notes that his description was based on “numerous specimens ... now housed in the museum at Cambridge ... Several specimens from the Amazon River ... probably from the Río Negro are from Natterer’s collection at the Museum in Vienna” (my translation). The cited Natterer specimens could not be found during several searches of the NMW collections. Specimens identified as syntypes from Hyavary (= Río Javari along Brazilian-Peruvian border) were located in the collections of both MCZ and NMW. A 133.4 mm SL individual (MCZ 20232), which is in the best condition of the available specimens, is selected as the lectotype. The remaining specimens from that locality (MCZ 20235, NMW 67030/1) become paralectotypes. In addition, a series of specimens of *Steindachnerina bimaculata* collected by the Thayer expedition at “Hyavary,” identified as “*Anodus binotatus*,” and forming part of the same series as the identified syntypes were located in the NMW collection (NMW 62351, 62532, 62533, 62534, 62664). Steindachner never published that name, nor has it been used elsewhere in the family. It appears that these represent the remainder of the “numerous” syntypes cited by that author. Presumably Steindachner changed the name of the species in the interval between determining that it represented an undescribed species, and the completion of the final manuscript, a practice he followed in other instances (see also following discussion in this section with respect to *Curimatus semiornatus*).

Steindachnerina bimaculata has been the subject of considerable taxonomic confusion as reflected by the complexity of

TABLE 5.—Morphometrics and meristics of (A) lectotype of *Curimatus bimaculatus* (MCZ 20232), (B) holotype of *Curimatus trachystetus* (ANSP 21470), (C) lectotype of *Curimatus bimaculatus sialis* (USNM 120401), (D) holotype of *Prochilodus pterostigma* (ANSP 39187), (E) holotype of *Curimatus melaniris* (ANSP 68669), and (F) all specimens of *Steindachnerina bimaculata* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 14 are proportions of head length. Question marks indicate values that could only be estimated as a consequence of condition of cited specimen. Dashes indicate values that could not be taken due to condition of specimen.

Character	A	B	C	D	E	F
MORPHOMETRICS						
Standard Length	133.4	92.2	126.0	59.5	112.5	28.3–133.4
1. Greatest body depth	0.36	0.34	0.34	0.32	0.30	0.30–0.37
2. Snout to dorsal-fin origin	0.50	0.47	0.49	0.50	0.47	0.45–0.51
3. Snout to anal-fin origin	0.82	0.84	0.87	0.88	0.83	0.80–0.87
4. Snout to pelvic-fin origin	0.52	0.50	0.53	0.55	0.54	0.49–0.55
5. Snout to anus	0.80	0.76	0.81	0.83	0.75	0.75–0.83
6. Origin of rayed dorsal fin to hypural joint	0.59	0.59	0.60	0.62	0.58	0.56–0.62
7. Pectoral-fin length	0.18	0.21	–	–	–	0.18–0.22
8. Pelvic-fin length	0.26	0.24	–	–	0.26	0.23–0.27
9. Caudal peduncle depth	0.13	0.13	0.13	0.12	0.12	0.12–0.13
10. Head length	0.27	0.27	0.27	0.30	0.27	0.25–0.30
11. Snout length	0.31	0.30	0.28	0.31	0.32	0.27–0.32
12. Orbital diameter	0.30	0.34	0.30	0.35	0.30	0.30–0.36
13. Postorbital length	0.44	0.43	0.44	0.40	0.38	0.38–0.44
14. Interorbital width	0.46	0.44	0.44	0.44	–	0.41–0.46
MERISTICS						
Lateral-line scales	45	43	44	44?	–	43–49
Scale rows between dorsal-fin origin and lateral line	9	9	–	–	–	7½–9
Scale rows between anal-fin origin and lateral line	6	6	5½	6?	–	5½–6
Branched dorsal-fin rays	9	9	9	9	9	9
Branched anal-fin rays	7	7	7	7	7	7
Total pectoral-fin rays	15	15	14?	14?	14	14–16
Branched pelvic-fin rays	8	8	8	8	8	8

the species synonymy. *Curimatus trachystetus* was described by Cope (1878:648) based on a single specimen originating in the Peruvian Amazon. Examination of the holotype (ANSP 21470) has shown that it agrees with *Steindachnerina bimaculata* in all examined meristic and morphometric features (Table 5). Although not mentioned by Cope in his description of the species, the holotype of *Curimatus trachystetus* has the spot of dark pigmentation at the base of the middle rays of the caudal fin typical of *S. bimaculata*. Given this evidence *Curimatus trachystetus* is considered a synonym of *Steindachnerina bimaculata*.

Eigenmann and Eigenmann (1889) in their original description of *Curimatus bimaculatus sialis* noted that the syntypic series of their subspecies was characterized by an unusual degree of variability both in details of pigmentation and scale form. Examination has shown that the series is complex, consisting of both *Steindachnerina bimaculata* (USNM 120401, MCZ 20206) and *S. leucisca* (MCZ 86348, out of

MCZ 20206), accounting for the extreme variability noted by those authors. The complexity of the type series makes it advisable to designate a lectotype for *Curimatus bimaculatus sialis* in order to unequivocally associate the nominal subspecies name with a particular species. In so far as it was obviously the intent of the Eigenmanns to associate their subspecies with *Curimatus bimaculatus* Steindachner, and given that they recognized a separate *Curimatus leuciscus* in the same publication (1889:426) it seems appropriate to select one of the *Steindachnerina bimaculata* specimens as the lectotype. The syntype of *S. bimaculata sialis* in the best overall condition (USNM 120401, 126.0 mm SL), is designated as the lectotype. The other syntypes (MCZ 20206, MCZ 86348) thus become paralectotypes of the species.

All of the examined features of the specimens of *S. bimaculata* in the type series of *Curimatus bimaculatus sialis* fall within the degree of variation of the available samples of *Steindachnerina bimaculata* (Table 5). The subspecies *sialis* is

thus not recognized as a distinct taxon in this study, but rather placed into the synonymy of *S. bimaculata*.

Fowler in 1913 described a new species, *Prochilodus pterostigma*, from the upper Rio Madeira system within Brazil. In 1940b he noted that the species was a member of the Curimatidae rather than of the Prochilodontidae, and that it might be a synonym of *Curimata* (= *Steindachnerina*) *bimaculata*. Examination of the holotype (ANSP 39187) indicates that reidentification is correct (Table 5). *Prochilodus pterostigma* is thus considered a synonym of *Steindachnerina bimaculata*.

In 1914 Steindachner described a species, *Curimatus semiornatus*, based on specimens from the mouth of the Rio Negro. No specimens labelled as the types of *C. semiornatus* were located during repeated searches through the NMW holdings. Two series of specimens agreeing with the type series in size, collector, locality, and fitting the description of and published figure of *C. semiornatus* were, however, located in the holdings of that institution. These were registered as *Curimatella semimaculata* (NMW 67101, 67102.1-3 [latter now 67102.1 and 67102.2-3]). Steindachner never published a species under that name and it would appear that the specimens are the syntypes of *Curimatus semiornatus*. Reference to the original notes by Steindachner on the species in the Naturhistorisches Museum Wien shows that the file for *Curimatus semiornatus* contains data sheets labelled with both species names. Steindachner presumably changed the species name in the interval between deciding that the specimens represented a new form and completion of the final manuscript. A 84.2 mm SL syntype of *Curimatus semiornatus* (NMW 67102.1) is designated as the lectotype. The remaining syntypes (NMW 67101 and NMW 67102.2-3) become paralectotypes.

In his original description of *Curimata semiornata*, Steindachner did not compare his species to previously described species, nor did he comment on the reasons why he considered it to be new to science. The type specimens of *Curimata semiornata* have proved to fall in the range of *Steindachnerina bimaculata* in all examined meristic and morphometric features (Table 5), and agrees with that species in all other studied characters. No basis has been found for the continued recognition of *Curimata semiornata*, which is consequently placed in the synonymy of *Steindachnerina bimaculata*.

Fowler (1940a:253) described a new nominal form, *Curimata melaniris*, from a single specimen collected at "Boca Chica" in the Rio Ucayali system of Peru. Although commenting on its "black contrasted eyes and small black caudal spot" he did not compare it with any other nominal form of curimatid. It is not apparent what Fowler found remarkable about the eyes, and the specimen does not now appear unusual in that character. The caudal spot of *C. melaniris* is of a size and position typical for *Steindachnerina bimaculata*, as are the mid-dorsal spots anterior to the dorsal fin and posterior to the supraoccipital spine (the latter neither illustrated in the original

figure of the species nor commented upon by Fowler). *Curimata melaniris* is not distinguishable from *Steindachnerina bimaculata* in any examined morphometric or meristic features (Table 5) or details of pigmentation, and is placed as a synonym of the latter species. I have been unable to determine where the stated type locality for the species, Boca Chica, lies within the Rio Ucayali basin.

Steindachnerina bimaculata has been cited, in various genera, as a component of the ichthyofauna of the Rio Paraguay-Paraná system by authors commencing with Boulenger (1900:2) (see synonymy of *S. conspersa* for a listing). The examined specimens reported on by Boulenger and those of subsequent authors who have reported *Curimatus bimaculatus* from drainages south of the Amazon basin (Eigenmann and Kennedy, 1903:511; Eigenmann and Ogle, 1907:3) have all proved to be *Steindachnerina conspersa*, a very similar species. No specimens of *S. bimaculata* from south of Rio Amazonas basin have been located in the extensive series of examined curimatids that originated in the Rio de La Plata basin. It is thus assumed that all citations of *Steindachnerina bimaculata* in various genera from those southern drainages are based on misidentified specimens of *Steindachnerina conspersa*.

Eigenmann and Eigenmann (1889:422) cite *S. bimaculata* from a number of Amazonian localities including Ica (= Rio Içá), Brazil. The specimens that served, at least in part, as the basis for that record (USNM 120250, formerly MCZ 19571) are *S. planiventris*.

MATERIAL EXAMINED.—292 specimens (87, 28.3–133.4)

VENEZUELA. *Territorio Federal Delta Amacuro*: Rio Orinoco near Caño Araguaito, USNM 235463, 3 (2, 66.1–68.3). Isla Portuguesa Pequeña, USNM 235446, 1. *Monagas*: Caño Chivera, Isla Chivera, USNM 235445, 6. *Barrancas*, USNM 235472, 1 (70.7); USNM 235473, 1 (61.0). *Bolívar*: Isla Isabela, USNM 235450, 1. Rio Orocopiche, USNM 235469, 2. Rio Aro, USNM 235443, 34.

BRAZIL. *Pará*: Paraná Jacaré, Município de Faro, MZUSP 7821, 19 (54.5–89.1). *Amazonas*: Hyavary (= Rio Javari), MCZ 20232, 1 (133.4, lectotype of *Curimatus bimaculatus*); MCZ 20235, 3 (paralectotypes of *Curimatus bimaculatus*); NMW 67030 and 67031, 6 (79.4–118.0, paralectotypes of *Curimatus bimaculatus*); NMW 62531, 4 (probable paralectotypes of *Curimatus bimaculatus*); NMW 62532, 1 (probable paralectotype of *Curimatus bimaculatus*); NMW 62533, 1 (probable paralectotype of *Curimatus bimaculatus*); NMW 62534, 3 (probable paralectotypes of *Curimatus bimaculatus*); NMW 62664, 1 (probable paralectotype of *Curimatus bimaculatus*). Lake near Manaus, USNM 220349, 10 (50.0–91.6). Mouth of Rio Negro, NMW 67101, 3 (28.3–36.8, paralectotypes of *Curimatus semiornatus*); NMW 67102.1, 1 (84.2, lectotype of *Curimatus semiornatus*); NMW 67102.2-3, 2 (73.1–75.9, paralectotypes of *Curimatus semiornatus*). Ilha de Marchantaria, 2 (62.4–72.3); USNM 229194, 1 (75.8); USNM 229195, 5; USNM 229202, 8; GC, 3. Manacapuru, MCZ 20206, 1 (paralectotype of *Curimatus bimaculatus sialis*);

USNM 120401, 1 (126.0, lectotype of *Curimatus bimaculatus sialis*). Lago Beruri, Rio Purus, MZUSP 6370, 1 (65.3). Paraná de Uruará, Município de Uruará, MZUSP 7510, 3 (2, 89.2–125.4). Paraná do Mocambo, Parintins, MZUSP 7584, 2 (67.6–83.0). Lago José Açu, Parintins, MZUSP 7635, 3 (100.0–103.4). Fonte Boa, MZUSP 21030, 3 (55.5–100.6). Rio Tarauacá at Rio Juruá, USNM 94639, 5. Lago Castro, mouth of Rio Purus, MZUSP 6310, 3. Tefé, lower Rio Japurá, MZUSP 27394, 7. *Rondônia*: Calama, USNM 242134, 2 (103.4–120.7). Rio Madeira, approximately 20 miles north of Porto Velho, ANSP 39187, 1 (63.2, holotype of *Prochilodus pterostigma*). *Acre*: Rio Tarauacá, Tarauacá, Lago da Esperanca, USNM 267954, 6; MZUSP 29523, 14.

COLOMBIA. *Amazonas*: Leticia, ANSP 139798, 1 (84.3).

PERU. Peruvian Amazon, ANSP 21470, 1 (92.2, holotype of *Curimatus trachystetus*). Río Ucayali, Boca Chica, ANSP 68669, 1 (112.5, holotype of *Curimata melaniris*). *Amazonas*: Ayambis, LACM 36342-3, 2 (108.2–123.3). *Loreto*: Río Amazonas, Santa Rosa, opposite Tabatinga, Brazil, USNM 261450, 9 (62.4–90.8). Vicinity of Iquitos, BMNH 1977.3.10:167, 1 (70.8). Río Corrientes, Teniente Lopez, NRM SOK/1986312.5600, 47; NRM SOK/1986313.4716, 2. Río Tahuyo basin, Caño Huayti, NRM SOK/1986281.4547, 1. Lago Cashiboya, USNM 289294, 2 (64.4–76.3). Trueno Cocha, NRM SOK/1983354.3738, 5. Río Yavari near Petropolis, USNM 261442, 1 (100.3); USNM 261435, 1. Río Yavari system, Río Yaquerana, NRM SOK/1984307.4094, 13. Río Ampiyacu, USNM 175869, 1 (108.0); USNM 175846, 1 (110.0). Río Ampiyacu, vicinity of Pevas, USNM 289293, 3 (50.3–87.7). *Ucayali*: Río Ucayali, Utuquinia, USNM 261440, 6; USNM 289292, 4; USNM 289225, 2. Río Ucayali, Curicocha, USNM 299225, 2.

ECUADOR. Jatuncocha, BMNH 1920.4.81, 1.

BOLIVIA. Río Chapare, MZUSP 27822, 3. *Beni*: Río Mamoré, Lagoa Santa Rosa, USNM 278566, 5. Río Isiboro, USNM 278570, 5.

Steindachnerina biornata (Braga and Azpelicueta, 1987)

FIGURES 23, 26, 27

Curimata biornata Braga and Azpelicueta, 1987:466 [type-locality: Argentina, Buenos Aires, Rio de la Plata basin, Arroyo Juan Blanco].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

Curimata stigmata Vari, 1987:606 [type-locality: Brazil, Rio Grande do Sul, Rio Jacui, at bridge on road between Santa Maria and Veracruz].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

DIAGNOSIS.—The presence of three very fleshy flaps on the roof of the oral cavity rather than weakly developed folds or three fleshy flaps and one or more series of lobulate fleshy processes on the roof of the oral cavity discriminates *Steindachnerina biornata* from its congeners. The species is further distinguished from the other members of the genus by the combination of the absence of a wide, flattened, prepelvic

region of the body, presence of a single series of dark spots along the lateral line, absence of a distinct black spot on the basal portions of the middle rays of the dorsal fin, the wide region of dark pigmentation in the midlateral stripe on the caudal peduncle, and the possession of 31 to 34 scales in the lateral line to the hypural joint.

DESCRIPTION.—Body moderately deep, more so in larger specimens, somewhat compressed. Dorsal profile of head convex anteriorly, straight from region above nostrils to rear of head. Dorsal profile of body gently convex from rear of head to origin of dorsal fin; straight and slightly posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened proximate to pelvic-fin origin. Obtuse median keel located posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body one scale dorsal of ventral midline.

Greatest depth of body 0.35–0.40 [0.40]; snout tip to origin of dorsal fin 0.48–0.53 [0.49]; snout tip to origin of anal fin 0.80–0.84 [0.82]; snout tip to origin of pelvic fin 0.53–0.57 [0.56]; snout tip to anus 0.76–0.79 [0.78]; origin of dorsal fin to hypural joint 0.52–0.57 [0.55]. Dorsal-fin profile rounded; anteriormost rays three to three and one-half times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.17–0.21 [0.19], extends about two-thirds distance to vertical line through origin of pelvic fin. Pelvic-fin profile acute; length of pelvic fin 0.19–0.22 [0.22], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal-fin border emarginate, anteriormost branched rays about two and one-third to two and two-thirds times length of ultimate ray. Caudal peduncle depth 0.12–0.14 [0.12].

Head obtusely pointed in profile, head length 0.25–0.29 [0.26]; upper jaw slightly longer, mouth subterminal; portion of buccopharyngeal complex on roof of oral cavity consisting of three very fleshy flaps without associated lobulate bodies; snout length 0.29–0.33 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.30–0.36 [0.31]; adipose eyelid present, more developed anteriorly, with vertically ovoid opening over center of eye; length of postorbital portion of head 0.39–0.44 [0.39]; gape width 0.25–0.29 [0.28]; interorbital width 0.44–0.50 [0.44].

Pored lateral-line scales to hypural joint 31 to 34 [32]; all scales of lateral line pored, canals in scales of lateral line straight; 2 to 4 series of scales extend beyond hypural joint onto caudal-fin base; 5½ to 6 [5½] scales in transverse series from origin of dorsal fin to lateral line; 4½ [4½] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (iii,9 rare) [ii,9]; anal-fin rays ii,7

[ii,7]; pectoral-fin rays 13 to 15 [14]; pelvic-fin rays i,8 or i,9 [i,8].

Total vertebrae 33 (29), 34 (1).

COLOR IN ALCOHOL.—Overall ground coloration of specimens lacking guanine on scales tan to tannish brown, darker on dorsal portions of head and body. Obscure mid-dorsal band extends from rear of head to origin of dorsal fin, and between dorsal and adipose fins. Scales of dorsal portion of body with field of dark chromatophores on exposed surface; chromatophore field more extensive on scales on dorsal portions of body. Scales of lateral line with pores outlined by patches of dark pigmentation. Deep-lying dark band extends from vertical line through origin of dorsal fin posteriorly to somewhat beyond hypural joint; both deep-lying stripe and surface chromatophores forming dark, anteriorly pointed, slightly elongate spot on lateral surface of caudal peduncle. Field of small, dark chromatophores continuing posteriorly on lateral surface of tail

to base of middle caudal-fin rays. Median fins somewhat dusky; other fins hyaline.

DISTRIBUTION.—Atlantic coastal drainages of Rio Grande do Sul, Brazil; Uruguay; Rio Uruguai in Santa Catarina, Brazil; lower Río Paraná, lower Río Paraguay (Figure 23). Braga and Azpelicueta (1987, fig. 3) also report this species from short coastal rivers emptying into the Río de La Plata southeast of Buenos Aires.

COMPARISONS.—Only three other species of *Steindachnerina* (*conspersa*, *brevipinna*, and *insculpta*) are recognized in this study from within the general region of the known range of *S. biornata*. *Steindachnerina biornata* is readily distinguished from *S. brevipinna* and *S. insculpta* by its lack of numerous lobulate processes on the roof of the oral cavity, and by details of pigmentation (compare figures of the species). *Steindachnerina conspersa* is readily discriminated from *S. biornata* in various details of pigmentation (compare Figures 21 and 22



FIGURE 26.—*Steindachnerina biornata*, MZUSP 28252, 31.2 mm SL, juvenile; Brazil, Santa Catarina, Poças do Rio Uruguai, Divisa Rio Grande do Sul-Concordia.

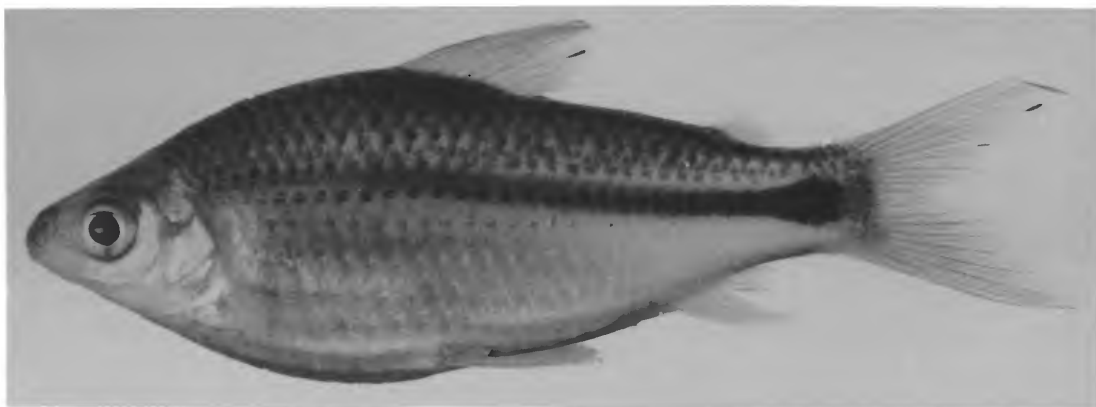


FIGURE 27.—*Steindachnerina biornata*, MZUSP 37133, 73.4 mm SL, holotype of *Curimata stigmosa*; Brazil, Rio Grande do Sul, Rio Jacuí, at bridge on road between Santa Maria and Vera Cruz.

with Figures 26 and 27) and in its lack of the three well-developed fleshy flaps on the roof of the oral cavity.

REMARKS.—This species was described nearly simultaneously by Braga and Azpelicueta (1987) and Vari (1987). The description of *Curimata biornata* Braga and Azpelicueta predates that of *Curimata stigmata* Vari by approximately two months and represents the senior synonym.

MATERIAL EXAMINED.—39 specimens (34, 31.2–73.4).

BRAZIL. *Rio Grande do Sul*: Rio Jacuí, at bridge on road between Santa Maria and Vera Cruz (~29°41'S, 53°19'W), MZUSP 37133, 1, (73.4; holotype of *Curimata stigmata*); USNM 285194, 12 (36.9–59.7, paratypes of *Curimata stigmata*, one specimen cleared and counterstained for cartilage and bone); MCP 9613, 4 (43.4–62.8, paratypes of *Curimata stigmata*); MZUSP 37134, 7 (34.7–43.4; paratypes of *Curimata stigmata*). Rio Forqueta, at Marquês de Souza, Município de Lajeado, USNM 285192, 1 (53.7; paratype of *Curimata stigmata*); MZUSP 21721, 1 (53.4; paratype of *Curimata stigmata*). Arroio Sarandi, along highway (Br 116) between Pelotas and Jaguarão, MZUSP 21728, 1 (43.0; paratype of *Curimata stigmata*). Arroio Chasqueiro, along highway (Br 116) between Pelotas and Jaguarão, USNM 285190, 2 (43.5–56.5; paratypes of *Curimata stigmata*). *Santa Catarina*: Pools along Rio Uruguai, near Concórdia, MZUSP 285242, 2 (2, 71.5–72.3). Posasdo Rio Uruguai, Divisa Rio Grande do Sul, Concórdia, MZUSP 28252, 1 (31.2).

URUGUAY. *Florida*: Arroio Chamizo, USNM 285192, 2 (64.2–70.4).

ARGENTINA. *Entre Ríos*: SU 31599, 2. Río Paraguay, USNM 295341, 1. *Buenos Aires*: no specific location, USNM 176008, 1. Río de La Plata, San Pedro, USNM 295354, 1.

Steindachnerina hypostoma (Boulenger, 1887)

FIGURES 28–30

Curimatus hypostoma Boulenger, 1887a:172 [type locality: Ucayali River].—Vari, 1989a, tables 2, 3 [phylogenetic relationships].

Curimatus hypostomus.—Eigenmann and Eigenmann, 1889:426 [reference].—Eigenmann and Eigenmann, 1891:47 [reference].—Eigenmann, 1910:422 [reference].

Curimata hypostoma.—Fowler, 1942b:208 [reference].—Eigenmann and Allen, 1942:296 [Peru: Río Huallaga, Yurimaguas; Río Morona; Río Paranapura, Yurimaguas (in part)].—Fowler, 1945:116 [reference].—Géry, 1977:235 [reference].—Ortega and Vari, 1986:11 [Peru, Amazon basin; common name].

Curimata hypostoma hypostoma.—Fowler, 1950:285 [literature compilation].

Steindachnerina hypostomus.—Fernández-Yépez, 1948:58 [assignment to *Steindachnerina*].

Steindachnerina hypostoma.—Fowler, 1975:375 [reference].—Vari and Vari, 1989:470, figs. 2, 3 [redescription, Amazonian Peru, Brazilian Amazon upstream of Manaus].

DIAGNOSIS.—The 6 or 7 scales between the anus and the anal fin, the 5 or 6 scale rows across the distinctly transversely flattened prepelvic region of the body, and the reduced dorsomedian cranial fontanel distinguishes *Steindachnerina hypostoma* from its congeners with the exception of *S. gracilis*,

S. planiventris, and *S. quasimodoi*. The absence of a discrete patch of dark pigmentation on the basal portion of the middle rays of the dorsal fin distinguishes *S. hypostoma* from those species, all of which have such pigmentation developed to some degree. The 46 to 50 lateral-line scales of *S. hypostoma* further differentiate the species from *S. gracilis*, which has 50 to 54 scales in that series and from *S. quasimodoi* and *S. planiventris*, which have 40 to 46. Differences in other meristic and morphometric features also discriminate *S. hypostoma* from *S. gracilis*, *S. planiventris*, and *S. quasimodoi* to varying degrees.

DESCRIPTION.—Body elongate, relatively wide transversely, particularly in ripe females. Dorsal profile of head straight or very slightly convex. Dorsal profile of body smoothly curved, slightly convex from rear of head to origin of dorsal fin; straighter and slightly posteroventrally slanted at base of dorsal fin, straight or very gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with distinct median keel anterior to dorsal fin, keel more pronounced proximate to fin; surface of body smoothly rounded transversely posterior to fin. Ventral profile of body very gently curved from tip of lower jaw to caudal peduncle. Prepelvic region wide, distinctly flattened, with 5 series of scales in a transverse series across flattened surface. Pelvic fins distinctly separated medially. Postpelvic region somewhat flattened proximate to pelvic fin, gradually becoming transversely rounded posteriorly. Anus distinctly anterior of origin of first anal-fin ray, with 6 or 7 scales in intervening space.

Greatest depth of body 0.24–0.27 [0.25]; snout tip to origin of dorsal fin 0.44–0.48 [0.45]; snout tip to origin of anal fin 0.80–0.85 [0.82]; snout tip to origin of pelvic fin 0.48–0.53 [0.48]; snout tip to anus 0.70–0.75 [0.72]; origin of dorsal fin to hypural joint 0.56–0.60 [0.59]. Dorsal-fin profile acute; anteriormost rays 2.8–3.5 times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.17–0.20 [0.18], extends slightly over three-quarters of distance to vertical line through origin of pelvic fin. Pelvic-fin profile obtusely acute, length of pelvic fin 0.19–0.22 [0.20], reaches about three-fifths of distance to origin of anal fin. Caudal fin distinctly forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays approximately two and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.12 [0.11].

Head distinctly pointed in profile, more so in larger specimens, head length 0.24–0.28 [0.27]; upper jaw distinctly longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.28–0.31 [0.28]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.34 [0.29]; adipose eyelid present, poorly developed, with a rotund opening over center of eye; length of postorbital portion of head 0.39–0.45 [0.43]; gape width 0.28–0.34; interorbital width 0.38–0.42 [0.39].

Pored lateral-line scales to hypural joint 46 to 50 [49]; all scales of lateral line pored, canals in scales of lateral line straight; 4 to 6 series of scales extend beyond hypural joint onto caudal-fin base; $8\frac{1}{2}$ to $9\frac{1}{2}$ [$8\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $6\frac{1}{2}$ to $7\frac{1}{2}$ [7] scales in transverse series from the lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (iii,9 rare; when three unbranched rays present, first very short) [ii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 14 to 16 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 35 (8), 36 (86), 37 (2).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery to silvery golden, darker on dorsal portions of head and body. Specimens fixed in formalin and lacking guanine on scales with overall ground coloration tan to light brown, darker on dorsal portions of head and body. Pores of lateral-line scales outlined by dark pigmentation in some specimens. Lateral-line pigmentation more intense, when present, in smaller individuals, sometimes forming a distinct

midlateral stripe (Figure 28). Deeper-lying, dusky, midlateral band extends from supracleithrum to caudal peduncle; typically more obvious in smaller individuals; masked in specimens retaining guanine on scales. Caudal-fin rays outlined by series of small chromatophores, lower lobe of caudal fin dusky. Anterior margin of dorsal fin sometimes dusky, but without spot of dark pigmentation at base of middle rays; other fins hyaline.

DISTRIBUTION.—Amazon basin upstream of Manaus, Brazil (Figure 30).

COMMON NAME.—Chio-chio (Ortega and Vari, 1986:11, Peru).

REMARKS.—Allen (in Eigenmann and Allen, 1942:297) described a subspecies *Curimata hypostoma hastata* on the basis of a single specimen originating at Puerto Bermudez, on the Río Pichis, Peru. A re-examination of the holotype (CAS 19881, formerly IU 17859) reveals that it is a specimen of *Steindachnerina dobula*. In the same publication Eigenmann and Allen (1942:296) identified a series of specimens from the

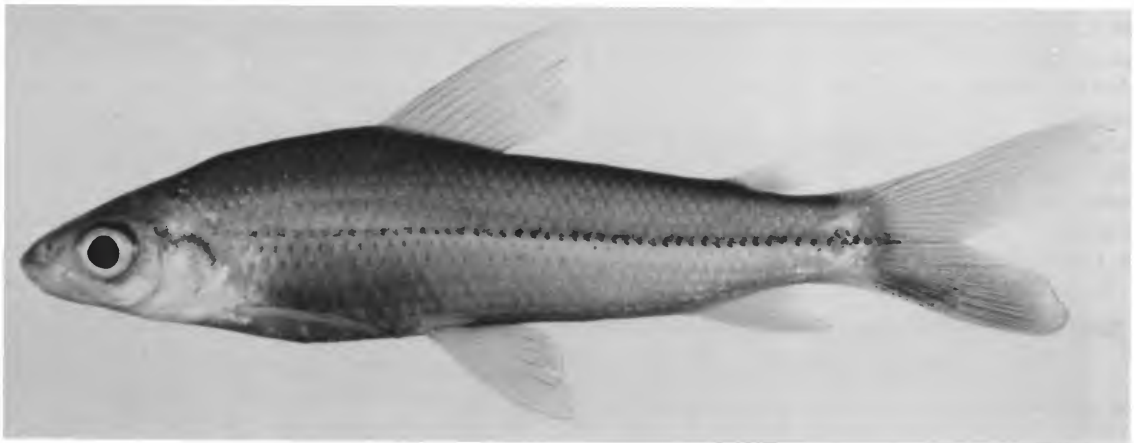


FIGURE 28.—*Steindachnerina hypostoma*, USNM 278579, 48.9 mm SL, juvenile; Bolivia, Pando, Río Madre de Dios, Laguna San Luis.

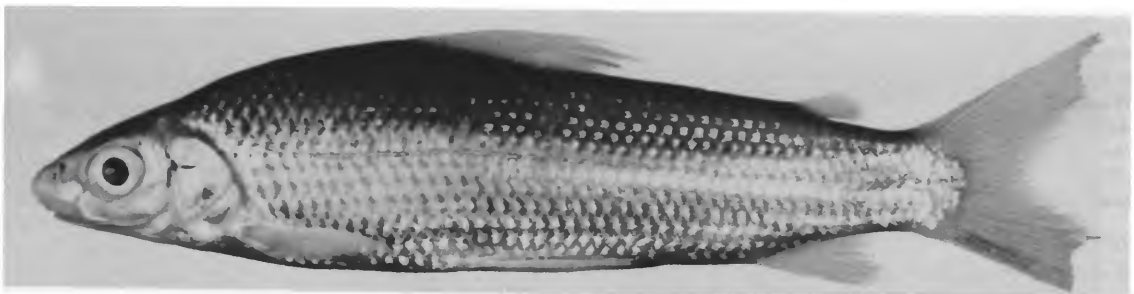


FIGURE 29.—*Steindachnerina hypostoma*, USNM 229190, 94.1 mm SL; Brazil, Amazonas, Rio Solimões, Ilha Marchantaria.

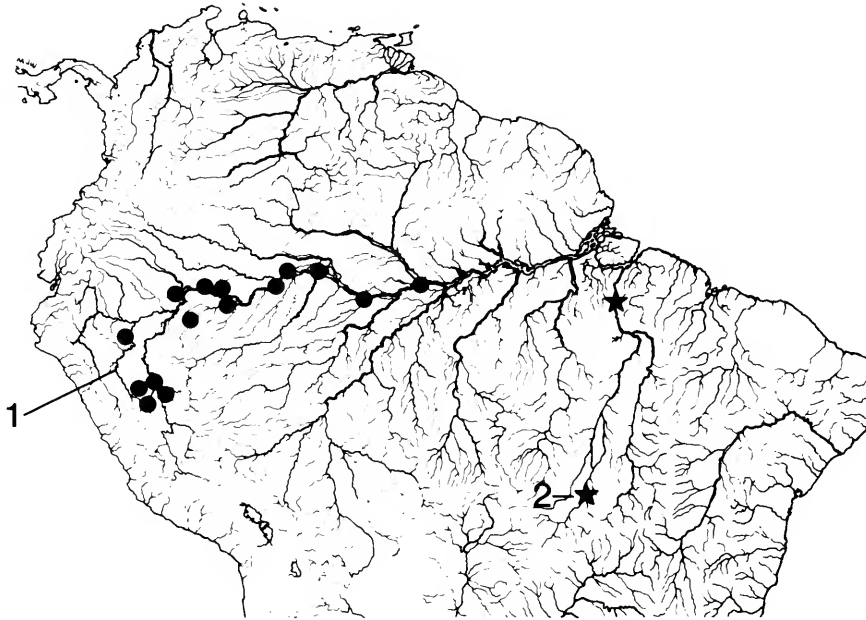


FIGURE 30.—Map of northern South America showing geographic distribution of *Steindachnerina hypostoma* (dots; 1 = Río Ucayali, approximate type locality of *Curimatus hypostoma*) and *Steindachnerina gracilis* (stars; 2 = type locality) (some symbols represent more than one lot of specimens and/or collecting locality).

Peruvian Amazon as *Curimatus hypostoma*. At least some of that material (IU 17858 from Río Paranapura at Yurimaguas) has proved to be a mixture of *S. hypostoma* and *S. dobula*.

MATERIAL EXAMINED.—299 specimens (71, 48.9–98.3).

PERU. Ucayali River, BMNH 1881.5.13:105, 1 (87.5, lectotype of *Curimatus hypostoma*); BMNH 1881.5.13:106–108, 3 (85.5–90.0, paralectotype of *Curimatus hypostoma*). Loreto: Shansho Caño, USNM 175867, 1. Beirut, near mouth of Río Ambiyacu, USNM 261452, 2 (76.3–77.8). Río Yavari, near Petropolis, USNM 261438, 1 (78.3). Río Amazonas, Ramon Castilla, USNM 261512, 1 (79.6). Río Yavari system, Río Galvez near mouth, NRM SOK/1984314.4058, 3. Río Huallaga, Yurimaguas, USNM 293094, 1 (98.3); USNM 167802, 5 (83.0–91.3); CAS 63192, 3 (83.8–92.0; formerly IU 15825; specimens intermingled with IU 15829 from Río Morona). Río Paranapura, Yurimaguas, CAS 63191, 2 (84.0–86.8, formerly IU 17858, in part); Huanuco: Río Pachitea, Tournavista, USNM 293092, 1. Ucayali: Río Ucayali, Pucallpa, USNM 261513, 5 (80.1–91.2); USNM 261489, 5 (65.8–96.5); USNM 261465, 6 (3, 55.3–59.8); USNM 261477, 5 (3, 70.4–83.4); AMNH 35686, 1 (70.0); USNM 261493, 6; USNM 261496, 2; USNM 261488, 6; USNM 293087, 1. Río Neshuyo where crossed by Pucallpa-Huanuco Road, USNM 261401, 1. Río Ucayali, Masisea, USNM 243237, 3 (60.4–63.4); USNM 293090, 5; USNM 293095, 10. Río Ucayali, Nuevo San Juan near Masisea, USNM 293089, 3. Río Ucayali, Utuquinia, USNM 293091, 1.

BRAZIL. Amazonas: Ilha da Marchantaria, USNM 293096, 1 (89.0); Géry, 3 (86.3–92.0); USNM 229190, 1 (94.1); USNM 229187, 1; USNM 229185, 2. Rio Solimões, Fonte Boa, MZUSP 20947, 6 (77.5–92.8); MZUSP 20957, 2 (81.5–84.9). Rio Juruá, BMNH 1897.12.1:88–100, 8 (4, 55.1–60.7). Ilha Xibeco, Rio Solimões above mouth of Rio Jutai, MZUSP 21018, 1 (91.4); MZUSP 21017, 6 (3, 79.3–83.7). Rio Solimões, Ilha Sorubim above Coari, MZUSP 20926, 175 (6, 68.5–84.5). Santo Antonio do Içá, mouth of Rio Içá, MZUSP 21000, 4 (75.0–82.8).

BOLIVIA. Pando: Río Madre de Dios, Laguna San Luis, USNM 278579, 5 (1, 48.9).

Steindachnerina gracilis Vari and Vari, 1989

FIGURES 30, 31

Steindachnerina gracilis Vari and Vari, 1989:474, fig. 5 [type-locality: Brazil, Goiás, Rio Araguaia, Aruanã].

DIAGNOSIS.—The 5 to 7 scales between the anus and the anal fin, the 5 or 6 scale rows across the distinctly transversely flattened prepelvic region of the body, and the reduced dorsomedian cranial fontanel distinguishes *S. gracilis* from all other species of *Steindachnerina* with the exception of *S. hypostoma*, *S. planiventris*, and *S. quasimodoi*. The 50 to 54 scales in the lateral line to the hypural joint and 10 or 10½ scales above the lateral line to the origin of the dorsal fin



FIGURE 31.—*Steindachnerina gracilis*, MZUSP 4847, 63.5 mm SL, holotype; Brazil, Goiás, Rio Araguaia, Aruanã.

distinguish *S. gracilis* from *S. planiventris* and *S. quasimodoi*, which have 40 to 46 lateral-line scales and $7\frac{1}{2}$ to $8\frac{1}{2}$ and $7\frac{1}{2}$ to $9\frac{1}{2}$ scales above the lateral line respectively, and from *S. hypostoma*, which has 46 to 50 lateral-line scales and $8\frac{1}{2}$ to $9\frac{1}{2}$ scales above the lateral line. *Steindachnerina gracilis*, which has a spot of dark pigmentation at the base of the middle rays of the dorsal fin, is readily separable from *S. hypostoma*, which lacks such pigmentation. A variety of meristic features also distinguish *S. gracilis* from *S. hypostoma*, *S. planiventris*, and *S. quasimodoi*.

DESCRIPTION.—Body elongate, moderately wide transversely. Dorsal profile of head straight or very slightly concave. Dorsal profile of body straight or very slightly convex from rear of head to origin of dorsal fin; straight and very slightly posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with distinct median keel anterior to dorsal fin, keel more pronounced proximate to dorsal fin; body surface smoothly rounded transversely posterior to fin. Ventral body profile very slightly convex from tip of lower jaw to caudal peduncle. Prepelvic region wide, distinctly flattened transversely, with obtuse lateral keels, five or six series of scales extend transversely across flattened region. Pelvic fins distinctly separated medially. Postpelvic region somewhat flattened proximate to pelvic fin, gradually becoming transversely rounded posteriorly. Anus distinctly anterior of origin of first anal-fin ray, with 6 or 7 series of scales in intervening space.

Greatest depth of body 0.25–0.27 [0.26]; snout tip to origin of dorsal fin 0.46–0.49 [0.46]; snout tip to origin of anal fin 0.84–0.86 [0.83]; snout tip to origin of pelvic fin 0.53–0.55 [0.53]; snout tip to anus 0.73–0.75 [0.73]; origin of dorsal fin to hypural joint 0.54–0.58 [0.56]. Dorsal-fin profile obtusely acute, anteriormost rays slightly less than three times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.17–0.21 [0.19], extends about three-quarters distance to vertical line through origin of pelvic fin. Pelvic fin obtusely acute, length of pelvic fin 0.19–0.21 [0.20], reaches about

three-fifths distance to origin of anal fin. Caudal fin distinctly forked. Adipose dorsal fin well developed. Border of anal fin emarginate, anteriormost branched rays about two and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.12 [0.11].

Head distinctly pointed in profile, head length 0.27–0.29 [0.27]; upper jaw distinctly longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.31–0.34 [0.32]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.32–0.35 [0.32]; adipose eyelid poorly developed, with a rotund opening over center of eye; length of postorbital portion of head 0.39–0.42 [0.39]; gape width 0.32–0.35 [0.33]; interorbital width 0.39–0.42 [0.41].

Pored lateral-line scales to hypural joint 50 to 54 [53]; all scales of lateral line pored, canals in scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; 10 to $10\frac{1}{2}$ [$10\frac{1}{2}$] scales in a transverse series from origin of dorsal fin to lateral line; $6\frac{1}{2}$ to $7\frac{1}{2}$ [$7\frac{1}{2}$] scales in a transverse series from the lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 15 to 17 [16]; pelvic fin rays i,8 [i,8].

Total vertebrae 35 (8), 36 (5).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery golden, darker on dorsal portions of head and body. Overall coloration of specimens fixed in formalin and lacking guanine on scales tan to light brown, darker on dorsal portions of head and body. Pores in scales of lateral line outlined by patches of dark pigmentation, individual spots forming irregular midlateral stripe. Deeper-lying dusky stripe extending from supracleithrum to caudal peduncle, stripe masked in individuals retaining guanine on scales. Anterior margin and distal portions of dorsal fin dusky. Distinct dusky spot on basal portion of middle rays of dorsal

fin, spot faint in some individuals. Rays of caudal fin outlined by series of small chromatophores; lower lobe of caudal fin dusky. Other fins hyaline.

DISTRIBUTION.—Rio Tocantins system (Figure 30).

MATERIAL EXAMINED.—17 specimens (17, 56.7–73.4).

BRAZIL. Goiás: Rio Araguaia, Aruan, MZUSP 4847, 1 (63.5, holotype of *Steindachnerina gracilis*); MZUSP 38591, 2 (56.7–63.5, paratypes of *Steindachnerina gracilis*); USNM 293035, 1 (67.2, paratype of *Steindachnerina gracilis*); USNM 191632, 1 (–73.4, paratype of *Steindachnerina gracilis*). Pará: Rio Tocantins, lagoons along margin of river near Tucuruí (–3°42'S, 49°27'W), MZUSP 38592, 6 (61.5–64.9, paratypes of *Steindachnerina gracilis*); USNM 293034, 6 (57.4–65.4, paratypes of *Steindachnerina gracilis*, 2 specimens cleared and counterstained for cartilage and bone).

Steindachnerina quasimodoi Vari and Vari, 1989

FIGURES 32–34

Steindachnerina quasimodoi Vari and Vari, 1989:476, figs. 6, 7 [type-locality: Peru, Loreto, Río Javari, near Petropolis].

DIAGNOSIS.—The 5 to 7 scales between the anus and the anal fin, the 5 scale rows across the distinctly transversely flattened prepelvic region of the body, and the reduced dorsomedian cranial fontanel distinguishes *Steindachnerina quasimodoi* from its congeners with the exception of *S. gracilis*, *S. planiventris*, and *S. hypostoma*. The 40 to 46 lateral-line scales to the hypural joint distinguish *S. quasimodoi* from *S. gracilis*, which has 50 to 54 scales in that series, and *S. hypostoma*, which has 46 to 50. The presence of a discrete spot of dark pigmentation in the basal portions of the middle rays of the dorsal fin further separates *S. quasimodoi* from *S. hypostoma*, which lacks such pigmentation. Other differences in meristic and morphometric features further differentiate *S. quasimodoi* from *S. hypostoma* and *S. gracilis*. Specimens of *S. quasimodoi* of greater than 50 mm SL are distinguished from comparably sized individuals of *S. planiventris* in their greater body depth (0.30–0.34 of SL versus 0.27–0.30), by differences in the degree of convexity of the dorsal surface of the body (compare Figures 32 and 33 with 35), length of the pelvic fins (0.23–0.26 of SL versus 0.19–0.23), and degree of contact of frontals anterior to cranial fontanel (Figure 10).



FIGURE 32.—*Steindachnerina quasimodoi*, USNM 293041, 88.9 mm SL, holotype; Peru, Loreto, Río Javari, near Petropolis.



FIGURE 33.—*Steindachnerina quasimodoi*, USNM 293040, 53.7 mm SL, paratype; Brazil, Rio Javari, opposite Colonia Angamos, Peru.

DESCRIPTION.—Body elongate, deeper bodied in larger specimens, somewhat compressed. Dorsal profile of head slightly convex anterior to vertical line through nostrils, straight from that line to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin, angle more pronounced with increasing size; straight and slightly posteroventrally slanted at base of dorsal fin in juveniles, adults with angle more pronounced, straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body very gently curved from tip of lower jaw to origin of anal fin, sigmoid from that point to caudal peduncle. Prepelvic region broadly flattened, with about 5 irregular series of scales across flattened ventral surface. Scale series of prepelvic region flanked on each side by series of scales slightly bent to conform to shape to lateral angles of body. Obtuse median keel posterior to pelvic fin origin. Secondary obtuse keel on each side of postpelvic portion of body two scales dorsal of ventral midline. Anus distinctly anterior of origin of first anal fin-ray, with 5 or 6 scales in intervening space.

Greatest depth of body 0.27–0.34 (0.30–0.34 in specimens above 50 mm SL) [0.33]; snout tip to origin of dorsal fin 0.47–0.50 [0.49]; snout tip to origin of anal fin 0.84–0.86 [0.86]; snout tip to origin of pelvic fin 0.50–0.54 [0.50]; snout

tip to anus 0.75–0.78 [0.76]; origin of dorsal fin to hypural joint 0.54–0.59 [0.59]. Dorsal-fin profile acute, less so with increasing age; anteriormost rays about three to three and one-half times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.19–0.21 [0.21], extends posteriorly to a point about two scales anterior of vertical through origin of pelvic fin. Pelvic-fin profile acute, length of pelvic fin 0.23–0.26 [0.26], reaches two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays about three to three and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.13 [0.13].

Head distinctly pointed, head length 0.27–0.33 [0.28]; upper jaw much longer, mouth inferior; anterior portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.31–0.34 [0.33]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.31–0.37 [0.32]; adipose eyelid present, more developed in larger specimens, particularly anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.36–0.40 [0.36]; gape width 0.30–0.35 [0.33]; interorbital width 0.36–0.43 [0.42].

Pored lateral-line scales to hypural joint 40 to 46 [44]; all scales of lateral line pored, canals in scales of lateral line

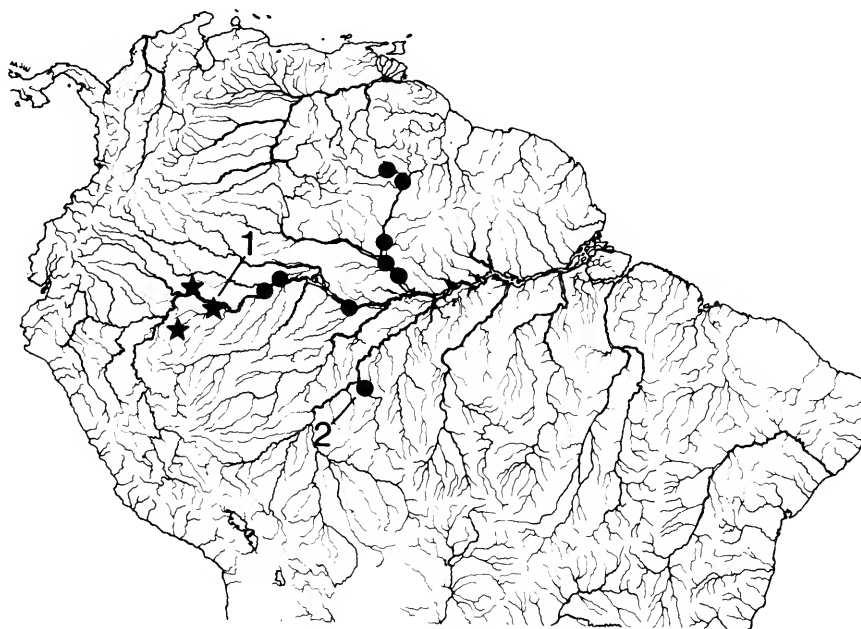


FIGURE 34.—Map of northern South America showing geographic distribution of *Steindachnerina quasimodoi* (stars; 1 = type locality) and *Steindachnerina planiventris* (dots; 2 = type locality) (some symbols represent more than one lot of specimens and/or collecting locality).

straight; 4 to 6 series of scales extend beyond hypural joint onto caudal-fin base; $7\frac{1}{2}$ to $9\frac{1}{2}$ [$8\frac{1}{2}$] scales in a transverse series from origin of dorsal fin to lateral line; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$6\frac{1}{2}$] scales in a transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 15 to 17 [16]; pelvic-fin rays i,8 or rarely i,7; [i,8].

Total vertebrae 35 (11), 36 (20).

COLOR IN LIFE.—(The following description is based on a color transparency of a specimen captured in the Rio Javari by S.O. Kullander). Overall coloration bright silver, somewhat darker on dorsal portions of head and body. Iris silver. Fins yellowish with light margins. Dorsal fin with a small dark patch on basal portion of middle rays.

COLOR IN ALCOHOL.—Ground coloration of specimens lacking guanine on scales tan, darker on dorsal portion of body. Dorsal portion of head dusky. Margins of scales on lateral and dorsal portions of body outlined by series of small chromatophores in juveniles. Pigmentation field expanded in larger specimens to cover exposed surface of scales, particularly dorsally. Mid-dorsal line somewhat darker, particularly immediately anterior of dorsal fin. Pores in lateral-line scales outlined dorsally and ventrally by chromatophores. Dorsal fin with diffuse patch of dark pigmentation on basal portion of membranes between third and fifth ray. Dorsal and caudal fins dusky. Adipose dorsal-fin margin dusky. Anal fin hyaline or with scattered chromatophores. Paired fins hyaline.

DISTRIBUTION.—Río Yavari (= Rio Javari) system of Peru and Brazil, and proximate portions of Peruvian Amazon (Figure 34).

MATERIAL EXAMINED.—41 specimens (41, 33.3–122.6).

PERU. Loreto: Río Yavari, near Petropolis, USNM 293041, 1 (88.9, holotype of *Steindachnerina quasimodoi*); USNM 293042, 7 (49.7–122.6, paratypes of *Steindachnerina quasimodoi*); two specimens cleared and counterstained for cartilage and bone); MHN-USM 1698, 4 (50.7–100.6, paratypes of *Steindachnerina quasimodoi*); MZUSP 38593, 2 (58.4–59.6, paratypes of *Steindachnerina quasimodoi*). Río Ampiyacu, near the mouth, USNM 175868, 1 (48.4). Pevas (Pevas), CAS-SU 36888, 1 (81.7).

BRAZIL. Amazonas: Rio Javari system, immediately downstream of confluence of Rio Jaquirana and Rio Gálvez, NRM SOK/1984312.4093, 9 (33.3–121.8, paratypes of *Steindachnerina quasimodoi*); MZUSP 38594, 3 (50.1–53.6, paratypes of *Steindachnerina quasimodoi*). Rio Javari system, opposite Colonia Angamos, Peru, NRM SOK/1984317.4091, 7 (40.0–69.2, paratypes of *Steindachnerina quasimodoi*); MHN-USM 1699, 3 (49.8–57.0, paratypes of *Steindachnerina quasimodoi*); USNM 293040, 3 (34.3–61.5, paratypes of *Steindachnerina quasimodoi*).

Steindachnerina planiventris Vari and Vari, 1989

FIGURES 34, 35

Curimatus bimaculatus.—Eigenmann and Eigenmann, 1889:422 [in part, specimens from Içá, Brazil].

Steindachnerina planiventris Vari and Vari, 1989:479, fig. 11 [type-locality: Brazil, Rondonia, Rio Machado, near mouth].

DIAGNOSIS.—The 6 or 7 scales between the anus and the anal fin, the 5 or 6 scale rows across the distinctly transversely flattened pre-pelvic region of the body, and the reduced dorsomedian cranial fontanel distinguish *Steindachnerina planiventris* from its congeners with the exception of *S. gracilis*, *S. quasimodoi*, and *S. hypostoma*. The 40 to 46 scales along the lateral line to the hypural joint distinguish *S. planiventris* from *S. gracilis*, which has 50 to 54 scales in that series, and from *S. hypostoma*, which has 46 to 50 scales. The presence of a discrete spot of dark pigmentation in the basal portions of the middle rays of the dorsal fin further separates *S. planiventris* from *S. hypostoma*, which lacks such pigmentation. Other differences in meristic and morphometric features further differentiate *S. planiventris* from *S. hypostoma* and *S. gracilis*. Specimens of *S. planiventris* of greater than 50 mm SL are distinguished from comparably sized individuals of *S. quasimodoi* in their greater body depth (0.27–0.30 of SL versus 0.30–0.34), differences in the degree of convexity of the dorsal surface of the body (compare Figures 32 and 33 with 35), pelvic-fin length (0.19–0.23 of SL versus 0.23–0.26), and degree of contact of the frontals anterior of the cranial fontanel (Figure 10).

DESCRIPTION.—Body elongate, slightly compressed. Dorsal profile of head distinctly convex anteriorly to vertical through nostrils, slightly convex or straight from that point to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin; straight and slightly posteroventrally slanted at base of dorsal fin, straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with distinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region distinctly flattened, with 5 longitudinal series of scales on ventral flattened surface. Ventral scale series flanked on each side by a series of scales slightly bent to conform to shape to lateral angles of body. Barely discernable median keel posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body about two scales dorsal of ventral midline. Anus distinctly anterior of origin of first anal-fin ray, with 5 or 6 scales in intervening space.

Greatest depth of body 0.27–0.30 [0.29]; snout tip to origin of dorsal fin 0.46–0.50 [0.49]; snout tip to origin of anal fin 0.83–0.87 [0.87]; snout tip to origin of pelvic fin 0.52–0.56 [0.54]; snout tip to anus 0.72–0.76 [0.75]; origin of dorsal fin to hypural joint 0.54–0.59 [0.57]. Dorsal fin pointed, less so with increasing age; anteriormost rays three to three and



FIGURE 35.—*Steindachnerina planiventris*, MZUSP 38557, 65.7 mm SL, holotype; Brazil, Rio Machado, near mouth.

one-half times length of ultimate ray. Pectoral fin pointed; length of pectoral fin 0.18–0.23 [0.20], extends about three-quarters distance to vertical line through origin of pelvic fin. Pelvic fin pointed, length of pelvic fin 0.19–0.23 [0.21], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed. Anal fin barely emarginate, anteriormost branched rays three to three and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.12 [0.12].

Head distinctly pointed in profile, head length 0.26–0.31 [0.30]; upper jaw distinctly longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.33–0.36 [0.33]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.29–0.33 [0.30]; adipose eyelid present, moderately developed, more so anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.36–0.41 [0.38]; gape width 0.28–0.34 [0.32]; interorbital width 0.38–0.44 [0.40].

Pored lateral-line scales to hypural joint 40 to 46 [41]; all scales of lateral line pored, canals in lateral-line scales straight; 4 to 6 series of scales extend beyond hypural joint onto caudal-fin base; $6\frac{1}{2}$ to $8\frac{1}{2}$ [$7\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 15 to 17 [15]; pelvic-fin rays i,8 [i,8].

Total vertebrae 34 (19), 35 (109), 36 (7).

COLOR IN ALCOHOL.—Specimens retaining guanine on scales golden, somewhat purplish dorsally. Ground pigmentation in specimens lacking guanine on scales tan to light brown, darker on dorsal portions of head and body. Scales on lateral and dorsal surfaces of body with margins outlined by series of small, dark chromatophores; chromatophore series most developed dorsally, increasingly less so ventrally. Dorsal fin with

patch of dark chromatophores on basal portion of membranes between third and fifth rays. Median fins, particularly lower lobe of caudal fin in some individuals, dusky. Paired fins hyaline.

DISTRIBUTION.—Rio Madeira and Rio Negro basins, main channel and tributaries of middle Rio Solimões (Figure 34).

REMARKS.—In their revision of the then-known species of curimatids, Eigenmann and Eigenmann (1889:422) listed extensive series of specimens of *Curimatus bimaculatus* Steindachner (= *Steindachnerina bimaculata*) from various localities in the central and western portions of the Amazon basin. At least some of the specimens from “Ica” (the Rio Içá of the western portion of Amazonas State in Brazil) are *Steindachnerina planiventris* (USNM 120250).

MATERIAL EXAMINED.—163 specimens (119, 46.2–87.0).

BRAZIL. *Rondonia*: Rio Machado, near mouth, MZUSP 38587, 1 (65.7, holotype of *Steindachnerina planiventris*); MZUSP 38588, 17 (55.5–74.1, paratypes of *Steindachnerina planiventris*); USNM 267986, 18 (56.3–78.8, paratypes of *Steindachnerina planiventris*). Rio Machado, Jauari, River Channel Beach, USNM 267989, 18 (46.2–67.8, paratypes of *Steindachnerina planiventris*), MZUSP 38590, 18 (53.5–65.2, paratypes of *Steindachnerina planiventris*). Rio Machado, Santo Antônio, USNM 267987, 6 (56.5–65.1, paratypes of *Steindachnerina planiventris*), MZUSP 38589, 5 (59.0–67.9, paratypes of *Steindachnerina planiventris*). Rio Machado, Cururu, USNM 267988, 8. *Roraima*: Rio Branco, 20 km below Boiaçu, MZUSP 21164, 4 (49.3–53.7). Rio Branco, Serra Grande, NMW 68885, 6 (53.1–87.0). *Amazonas*: Rio Negro, just below mouth of Rio Branco, USNM 293097, 22 (11, 52.5–80.6). Rio Negro, Anavilhanas, Município de Ayrão, USNM 293098, 7. Rio Solimões, Ilha Sorubim, above Coarí, MZUSP uncat., 10 (62.3–71.3). Rio Solimões, Coarí, USNM 293099, 12. Rio Solimões, near Ilha Baruruá, above mouth of Rio Jutáí, MZUSP 20987, 3 (2, 63.2–71.7). Rio Solimões, Ilha Xibeco, above mouth of Rio Jutáí, MZUSP uncat., 1 (73.8). Ica (= Rio Içá), USNM 120250, 5 (formerly MCZ 19571).

BOLIVIA. *Beni*: Río Mamoré, Puerto Siles, AMNH uncat., 2 (65.7-73.5).

Steindachnerina atratoensis (Eigenmann, 1912)

FIGURES 36-38

Curimatus atratoënsis Eigenmann, 1912b:19 [type-locality: Colombia: Quibdo].—1920a:15 [Colombia: Río Atrato basin].—1920c:11 [Río Atrato basin].—1922:102 [Río Atrato basin].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

Curimatorbis atratoensis.—Fernández-Yépez, 1948:42, fig. 20 [designation as type-species of *Curimatorbis* Fernández-Yépez].—Fowler, 1975:370 [reference].

Steindachnerina atratoensis.—Vari, 1988:324, 335, 343 [phylogenetic biogeography].

DIAGNOSIS.—The distinctive pigmentation pattern in adults of a dark, wide, midlateral stripe on the body with parallel narrower dark stripes on the dorsal and lateral surface of the body is unique to *Steindachnerina atratoensis* within the

genus. The only congener with multiple body stripes is *S. fasciata*, an amazonian species in which the pigmentation pattern differs in a number of details (compare Figures 36 and 37 with 40). The species are also distinguishable in the presence of a single series of lobulate bodies on the portion of buccopharyngeal complex on the roof of the oral cavity in *S. atratoensis* contrary to numerous such structures in that region in *S. fasciata*.

DESCRIPTION.—Body moderately elongate, slightly compressed. Dorsal profile of head typically straight, sometimes slightly convex. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region transversely rounded, without enlarged scales.

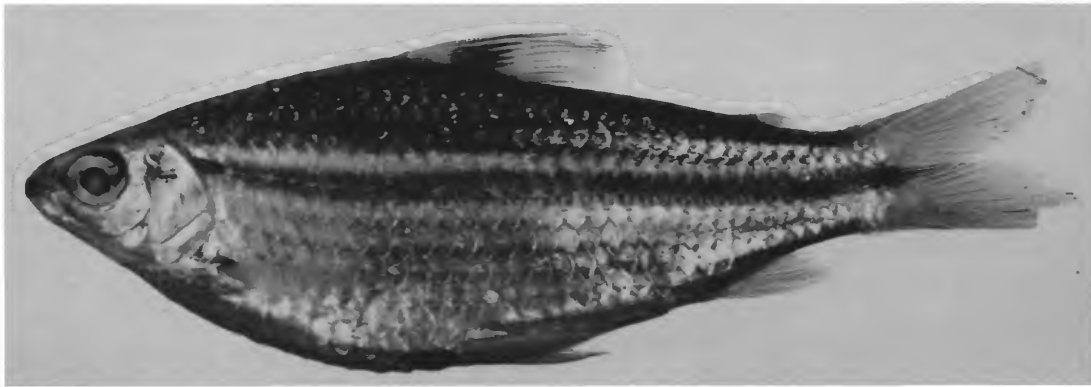


FIGURE 36.—*Steindachnerina atratoensis*, FMNH 56024 (formerly CM 4814a), 78.9 mm SL, holotype; Colombia, Choco, Quibdo.



FIGURE 37.—*Steindachnerina atratoensis*, USNM 220199, 51.8 mm SL; Colombia, Choco, Río Pavarando, tributary of Río Salaqui.

Obtuse median keel posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body about two scales dorsal of ventral midline.

Greatest depth of body 0.31–0.36 [0.36]; snout tip to origin of dorsal fin 0.45–0.52 [0.47]; snout tip to origin of anal fin 0.77–0.84 [0.82]; snout tip to origin of pelvic fin 0.53–0.56 [0.54]; snout tip to anus 0.73–0.78 [0.78]; origin of dorsal fin to hypural joint 0.57–0.61 [0.58]. Dorsal-fin margin obtusely acute, anteriormost rays about three times length of ultimate ray. Pectoral-fin margin acute, length of pectoral fin 0.17–0.22 [0.18], extends two-thirds to three-quarters distance to vertical line through origin of pelvic fin. Pelvic-fin profile acute, length of pelvic fin 0.19–0.24 [0.19], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal-fin border emarginate, anteriormost branched rays about two and one-half times length of ultimate ray. Caudal peduncle depth 0.12–0.14 [0.14].

Head distinctly pointed in profile, head length 0.24–0.31 [0.25]; upper jaw longer, mouth subterminal; anterior portion of buccopharyngeal complex consisting of three weakly developed fleshy folds with a single series of fleshy lobulate bodies anteriorly; snout length 0.28–0.32 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.34 [0.29]; adipose eyelid poorly developed, with broad ovoid opening over center of eye; length of postorbital portion of head 0.38–0.45 [0.41]; gape width 0.26–0.31 [0.26]; interorbital width 0.40–0.44 [0.44].

Pored lateral-line scales to hypural joint 34 to 38 [36]; all scales of lateral line pored, canals in scales straight; 2 to 4 series of scales extend beyond hypural joint onto caudal-fin base; 5 or 6 [6] scales in transverse series from origin of dorsal fin to lateral line; 4 or 5 [5] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,8 or ii,9, or iii,8 (when three unbranched rays present, first very short) [ii,9]; anal-fin rays ii,7 [ii,7]; pectoral-fin rays 13 to 15 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 32 (5), 33 (23), 34 (2).

COLOR IN ALCOHOL.—Ground coloration of specimens retaining guanine on scales silvery or silvery golden, darker on dorsal surfaces of head and body. Ground coloration of specimens lacking guanine on scales tan to brown.

Smaller specimens of approximately 15 to 30 mm SL with horizontal stripe of dark pigmentation commencing at tip of snout and continuing onto anterior margin of orbit. Stripe continues from anterior margin of orbit, across orbit, and along midlateral surface of body to base of caudal-fin rays. Body stripe continuous posteriorly with stripe of dark pigmentation on middle rays of caudal fin. Stripe on body increasingly obvious in specimens of 25 to 30 mm SL. Dorsal surface of body darker in specimens over 20 mm SL, more so in individuals over approximately 30 mm SL; dusky dorsal region of body with discrete ventral margin; separated from dark midlateral stripe by distinct, horizontal, lightly pigmented region. Distinct spot of dark pigmentation on dorsal fin in

specimens of 15 to 30 mm SL, but somewhat less heavily pigmented in smaller examined specimens.

Larger specimens with distinct horizontal band of dark pigmentation extending from tip of snout and upper lip to anterior margin of orbit. Second band of dark pigmentation continues from rear of orbit across opercle; postorbital stripe aligned with midlateral body stripe. Body in adults with series of lateral longitudinal stripes. Stripe extending along lateral line most prominent and heavily pigmented; extending posteriorly onto middle rays of caudal fin; stripe one scale wide. One or two faint, narrower, subsidiary longitudinal stripes ventral of lateral line and one or two dorsal of lateral line. Subsidiary stripes aligned along junctions between vertical scale rows. Stripes ventral of lateral line falling short of ventral margin of caudal peduncle posteriorly. Stripes dorsal of lateral line merging posteriorly into overall darker pigmentation of dorsal surface of body. Stripes dorsal of lateral line not distinct in some specimens 30 to 40 mm SL. Body stripes masked to varying degrees in those specimens retaining guanine on scales.

Dorsal fin in adults with vertical patch of dark pigmentation extending from middle of anterior border of fin to base of third to fifth dorsal-fin rays. Scattered chromatophores on remainder of fin. Middle rays of caudal fin with horizontal band of dark pigmentation continuous with stripe along lateral line. Remainder of caudal fin and other median and paired fins with scattered small chromatophores.

DISTRIBUTION.—Río Atrato drainage basin of Colombia (Figure 38).

REMARKS.—*Steindachnerina atratoensis* is the only mem-

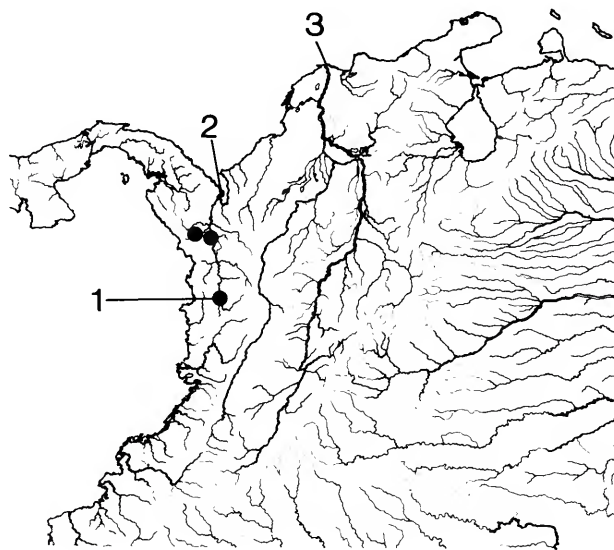


FIGURE 38.—Map of northwestern South America showing geographic distribution of *Steindachnerina atratoensis* (1 = type locality of *Curimatus atratoensis*; 2 = mouth of Río Atrato; 3 = mouth of Río Magdalena) (some symbols represent more than one collecting locality and/or lot of specimens).

ber of the genus known to occur to the west of the main cordilleras of the Andes. The distribution of the species is further noteworthy because *Steindachnerina* is unknown in the Río Magdalena, a major drainage basin that lies between the Río Atrato and the range of the rest of the genus to the east of the Andes. This disjunct distribution may be a consequence of extinction of *Steindachnerina* populations within the Río Magdalena system, comparable to that noted for *Colossoma*, a genus of large characid characiforms, by Lundberg et al. (1986:208) (see also "Phylogenetic Biogeography").

MATERIAL EXAMINED.—118 specimens (47, 36.0–83.0).

COLOMBIA. *Choco*: Quibdó, FMNH 56024, 1 (78.9, holotype of *Curimatus atratoënsis*; formerly CM 4814a); CAS 44218, 10 (68.0–80.3, paratypes of *Curimatus atratoënsis*; formerly IU 12676, in part); USNM 79192, 3 (69.5–76.5; paratypes of *Curimatus atratoënsis*; formerly IU 12676, in part); AMNH 5273, 8 (5, 38.3–66.6); CAS-SU 22742, 2 (66.8–83.0); BMNH 1924.3.3:55–57, 3 (49.4–83.0); MCZ 30933, 12; BMNH 1920.12.20:71–72, 2. Río Truando, CAS 65360, 19 (4, 42.5–61.5; formerly IU 13050, in part); USNM 76950, 18 (8, 36.0–66.9; formerly IU 13050, in part); USNM

291691, 3 (37.2–63.8). Río Salado near Teresita, USNM 220204, 3 (44.7–50.0). Río Pavarando, tributary of Río Salaquí, USNM 220199, 5 (50.3–57.2). Río Atrato system, Napipí, Cienega Napipí, NRM SOK/1989043.5801, 6. *Antioquia*: Río Atrato system, Buchadó, Caño Ponelaolla and mouth of Río Guaguandó, 1 km upstream of village of Buchadó, NRM SOK/1989046.5803, 23.

Steindachnerina fasciata (Vari and Géry, 1985)

FIGURES 39–41

Curimata fasciata Vari and Géry, 1985:1030 [type locality: Brazil, Rondônia, Rio Romari near Nova União].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

DIAGNOSIS.—The multiple longitudinal stripes of the lateral surfaces of the body distinguish *Steindachnerina fasciata* from its congeners with the exception of *S. atratoensis*. The longitudinal body stripes in *S. fasciata* differ from those in *S. atratoensis* in relative position, form, and number (compare Figures 36 and 37 with 39 and 40). The species are also readily

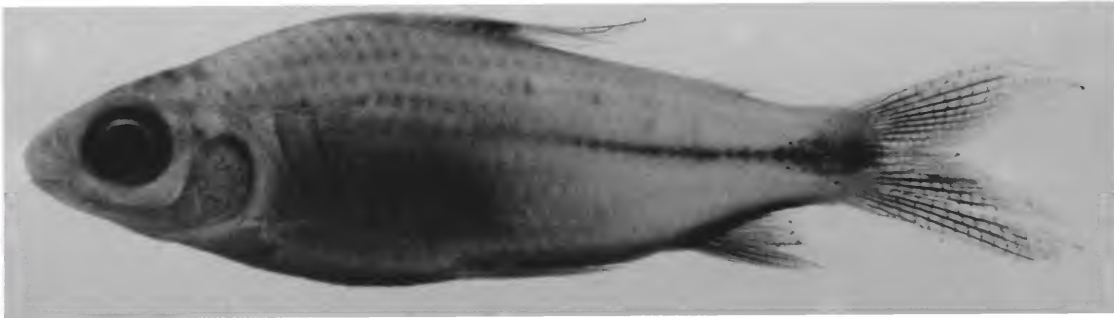


FIGURE 39.—*Steindachnerina fasciata*, USNM 295126, 35.6 mm SL, juvenile; Brazil, Rondonia, Rio Machado system, 20 km upstream of Ji-Paraná.

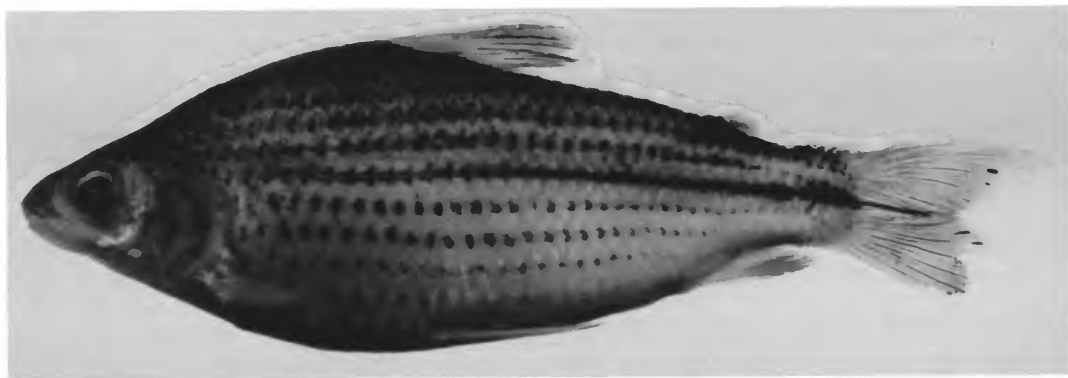


FIGURE 40.—*Steindachnerina fasciata*, MNRJ 11208, 89.6 mm SL, holotype; Brazil, Territorio de Rondonia, Rio Romari (or São Domingo), near Nova União, Município de Ouro Preto de Oeste.

distinguished by the numerous lobulate processes on the portion of the buccopharyngeal complex on the roof of the oral cavity in *S. fasciata* in contrast to the three fleshy flaps on the roof with a single series of lobulate processes in *S. atratoensis*.

DESCRIPTION.—Body moderately elongate, deeper in ripe females; compressed. Dorsal profile of head convex above snout, straight or very slightly concave above orbit. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of head nearly straight; ventral profile of body straight or gently concave to origin of pelvic fin, gently curved from that point to caudal peduncle. Prepelvic region indistinctly flattened anteriorly; somewhat more flattened posteriorly proximate to pelvic-fin origin with median series of three or four somewhat enlarged scales immediately anterior to pelvic-fin origin. Indistinct median keel posterior to pelvic-fin origin. Secondary obtuse keel on each side of postpelvic portion of body about two scales dorsal of ventral midline.

Greatest depth of body 0.36–0.42 [0.39]; snout tip to origin of dorsal fin 0.47–0.52 [0.50]; snout tip to origin of anal fin 0.84–0.89 [0.86]; snout tip to origin of pelvic fin 0.53–0.58 [0.55]; snout tip to anus 0.79–0.84 [0.82]; origin of dorsal fin to hypural joint 0.54–0.59 [0.56]. Dorsal-fin margin obtusely acute; anteriormost rays 2.3–2.6 times length of ultimate ray. Pectoral-fin margin acute; length of pectoral fin 0.19–0.22 [0.20], extends approximately two-thirds distance to origin of pelvic fin. Pelvic-fin margin acute; length of pelvic fin 0.23–0.25 [0.24], reaches three-quarters of distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Border of anal fin emarginate, anteriormost branched rays approximately two and one-half times length of ultimate ray. Caudal peduncle depth 0.13–0.14 [0.13].

Head obtusely pointed in profile, head length 0.28–0.30 [0.28]; upper jaw longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.29–0.32 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.31 [0.30]; adipose eyelid moderately developed, with vertically ovoid opening over center of eye; length of postorbital portion of head 0.40–0.44 [0.43]; gape width 0.28–0.32 [0.31]; interorbital width 0.39–0.45 [0.43].

Pored lateral-line scales to hypural joint 32 to 37 [34]; all scales of lateral line pored, canals in scales of lateral line straight; 4 or 5 series of scales extend beyond hypural joint onto caudal-fin base; $5\frac{1}{2}$ or $6\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [$4\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays

present, first very short) [ii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very small) [iii,7]; pectoral-fin rays 14 to 16 [15]; pelvic-fin rays i,8 [i,8].

Total vertebrae 32 (4), 33 (20), 34 (1).

COLOR IN LIFE.—(The following is based on a photograph taken by Dr. Geraldo Mendes dos Santos of a recently captured 93.0 mm SL specimen collected in the Território de Rondônia; INPA Polo 135.) Overall body and head coloration yellow, darker dorsally with ventral surface of body silvery. Horizontal series of dark spots apparent along dorsal and lateral series of scales on body. Lateral-line scale series with distinct dark line extending from under dorsal fin to base of middle rays of caudal fin; stripe becoming progressively wider posteriorly. Median and paired fins yellow. Dorsal fin with spot of dark pigmentation on basal portions of middle rays.

COLOR IN ALCOHOL.—Specimens lacking guanine on scales with overall ground coloration tan or light brown, darker on dorsal portions of head and body; lighter overall in smaller specimens. Head with field of dark chromatophores dorsally. Distinct spots of pigmentation centered at junction of scales along middle of dorsal and lateral rows of body scales. Individual dark spots along scale rows form irregular, longitudinal stripes of differing degrees of intensity. Longitudinal stripe of third scale row ventral of lateral line with poorly developed pigmentation anteriorly and posteriorly, particularly in smaller specimens. Width of pigmentation patches along first and second scale rows ventral of lateral line diminishing in size posteriorly. Dark spots along lateral-line scales more developed, outlining lateral-line canals on posterior portion of body in smaller individuals, extending further anteriorly in specimens of increasing size. Spots forming a distinct midlateral pattern in largest specimens in which spots are contiguous on posterior half of body. Spots of scale series dorsal of lateral line well developed, forming irregular horizontal stripes that merge into overall darker coloration of dorsal portion of body. Horizontally elongate, diffuse patch of dark pigmentation on midlateral surface of caudal peduncle in smaller specimens (Figure 39). Spot pronounced in specimens under 40 mm SL, becoming more diffuse in specimens of 30 to 50 mm SL, and barely apparent in specimens over 70 mm SL. Basal portion of median rays of caudal fin with distinctly dusky to black band of pigmentation continuous with dark stripe along lateral line. Adipose dorsal and pelvic fins dusky. Dorsal fin with distinct rotund spot on basal portion of middle rays in smaller specimens. Spot more diffuse and barely apparent in larger specimens.

DISTRIBUTION.—Tributaries of the southeastern portion of the Rio Madeira system (Figure 41).

REMARKS.—Vari and Géry (1985) provisionally described *fasciata* in *Curimata*, recognizing, however, that ongoing studies of the phylogenetic relationships within the Curimatidae by the senior author would probably result in a change in the generic classification of the species. Vari (1989a) notes a number of shared derived features that indicate that the species

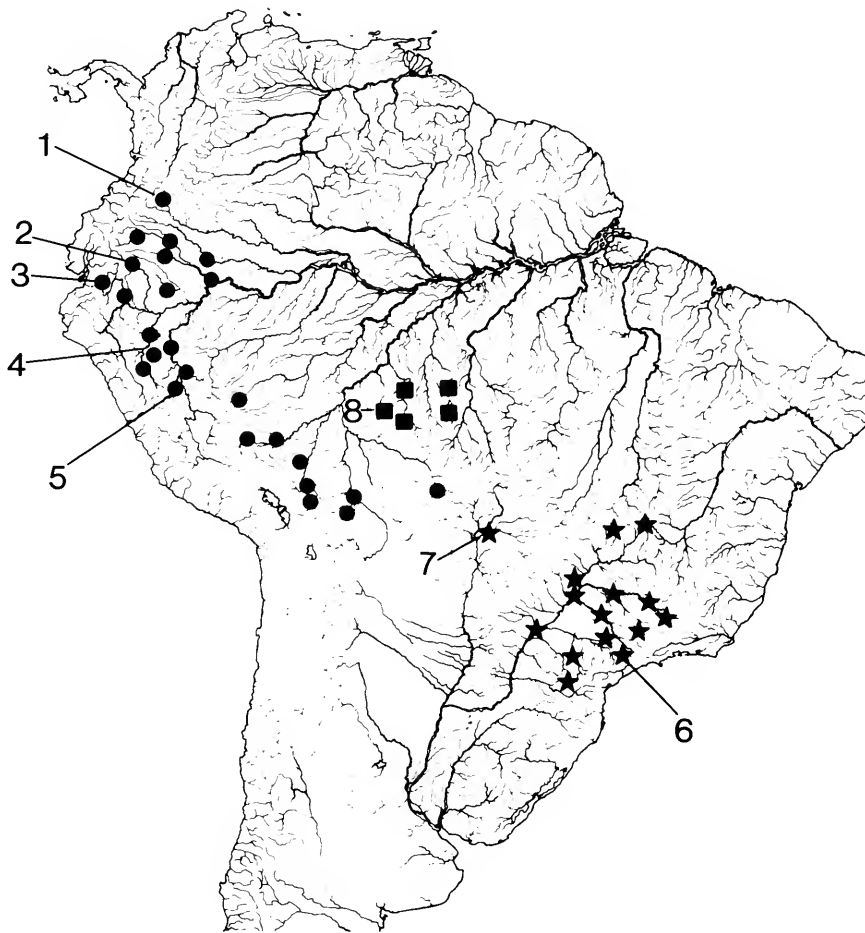


FIGURE 41.—Map of South America showing geographic distribution of *Steindachnerina dobula* (dots; 1 = type locality of *Curimata niceforoi*; 2 = type locality of *Curimatus nasus*; 3 = putative type locality of *Prochilodus stigmaturus*, see “Remarks” under *Steindachnerina dobula*); 4 = Río Huallaga, approximate type locality of *Curimatus dobula*; 5 = type locality of *Curimata hypostoma hastata*, *Steindachnerina insculpta* (stars; 6 = approximate type locality; 7 = possibly introduced populations in the upper Rio Paraguay basin, see “Remarks” under *Steindachnerina insculpta*), and *Steindachnerina fasciata* (squares; 8 = type locality of *Curimata fasciata*) (some symbols represent more than one collecting locality and/or lot of specimens).

is a member of the clade recognized as *Steindachnerina* both in that publication and herein.

Steindachnerina fasciata is remarkably similar externally to another curimatid, *Cyphocharax pantostictos* Vari and Barriga (1990), of the western portions of the Amazon basin in eastern Ecuador and northern Peru. Despite these similarities in body form and pigmentation, *C. pantostictos* lacks the derived features diagnosing *Steindachnerina* and the clades within the genus that include *S. fasciata*. The two species are not known to be sympatric and it does not appear that mimicry is involved in these striking similarities.

MATERIAL EXAMINED.—32 specimens (32, 34.2–96.0).

BRAZIL. *Território de Rondônia*: Rio Romarí (or São Domingo) near Nova União, Município d’Ouro Preto do Oeste, MNRJ 11208, 1 (89.6, holotype of *Curimata fasciata*); USNM 270377, 4 (72.3–92.3, paratypes of *Curimata fasciata*; 1 specimen cleared and counterstained for cartilage and bone); MNRJ 11271, 4 (74.3–90.4, paratypes of *Curimata fasciata*). Jiparaná, Rio Urupá, tributary of Rio Jiparaná, USNM 273306, 3 (34.2–46.5). Rio Machado system, 20 km upstream of Jiparaná, USNM 295126, 1 (35.6). *Mato Grosso*: Rio Aripuanã, above cachoeira de Dardanelos (–10°19’42”S, 59°12’30”W), USNM 270375, 2 (90.1–96.0, paratypes of *Curimata fasciata*); INPA, 3 (64.0–86.8, paratypes of *Curi-*

mata fasciata). Rio Aripuanã, approximately 10 km above cachoeira de Dardanelos, Cidade de Humboldt, USNM 270376, 2 (78.0–83.3, paratypes of *Curimata fasciata*); INPA, 2 (77.8–79.1, paratypes of *Curimata fasciata*); BMNH 1985.2.5:1-2, 2 (79.4–80.1, paratypes of *Curimata fasciata*); MZUSP 28724, 2 (86.1–87.1, paratypes of *Curimata fasciata*). Rio Aripuanã, above cachoeira das Andorinhas, MHNG 2226.24, 6 (55.3–83.9; paratypes of *Curimata fasciata*).

Steindachnerina dobula (Günther, 1868)

FIGURES 41–46

- Curimatus dobula* Günther, 1868a:243 [type-locality: Río Huallaga].—1868b:479 [Río Huallaga].—Boulenger, 1887b:279 [Ecuador, Canelos].—Eigenmann and Eigenmann, 1889:423 [reference].—1891:47 [reference].—Boulenger, 1898:426 [Brazil, Rio Jurua].—Pellegrin, 1909:148 [Brazil, Tefé (= Tefé)].—Eigenmann, 1910:421 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus nasus* Steindachner, 1882:80, pl. 5, fig. 2 [type-locality: Ecuador, Canelos].—Eigenmann and Eigenmann, 1889:421 [reference].—1891:47 [reference].—Eigenmann, 1910:421 [reference].—Pearson, 1924:27 [Bolivia: Huachi, Rurrenbaque, Iximias, Peña Colorado, Río Bopi, Río Iniqui].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].—[not Eigenmann and Kennedy, 1903:510; Bertoni, 1914:9].
- Prochilodus stigmaturus* Fowler, 1911:494, fig. 1 [type-locality: "Affluent of Chimbo River near Bucay, Province of Guayas, Ecuador"; see "Remarks"].—Eigenmann, 1920b:16 [Ecuador, Guayaquil (= Guayas) basin; based on Fowler, 1911].—1922:116 [Ecuador, based on Fowler, 1911].—Mago-Leccia, 1972:47 [comments on possible relationships of species].—Fowler, 1975:360 [reference].—Vari and Castro, 1988:777, fig. 1 [transfer from Prochilodontidae to Curimatidae; assignment to *Steindachnerina*].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata nasus*.—Pearson, 1937:109 [in part, Bolivia, Río Beni; not Río Paraguay system citation].—Fowler, 1940b:98 [reference].—[not Bertoni, 1939:54].
- Curimata nasa*.—Eigenmann and Allen, 1942:292 [reference].—Fowler, 1950:288 [literature compilation].—Terrasas-Urquidí, 1970:31 [reference, Bolivia].—Géry, 1972a:99 [Ecuador: Río Conambo, tributary to Río Tigre].—[not Ringuélet, 1975:72; Géry et al., 1987:425].
- Curimata dobula*.—Eigenmann and Allen, 1942:293 [reference].—Fowler, 1942b:208 [reference].—1945:117 [reference].—1950:281 [literature compilation].
- Curimata hypostoma*.—Eigenmann and Allen, 1942:296 [in part, some specimens from Peru: Río Parapapura, Yurimaguas; Río Huallaga, Yurimaguas].
- Curimata hypostoma hastata* Allen [in Eigenmann and Allen], 1942:297 [type-locality; Peru: Río Pichis, Puerto Bermudez].—Fowler, 1945:116 [reference].—1950:285 [literature compilation].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata niceforoi* Fowler, 1943a:224, figs. 1–3 [type-locality: Colombia, Florencia, Río Ortegusa basin].—1950:288, fig. 346 [literature compilation].—1975:369 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Cruxentina hastata*.—Fernández-Yépez, 1948:52, fig. 26 [designation as type species of *Cruxentina*].—Fowler, 1950:368 [reference].
- Cruxentina nasa*, Fernández-Yépez, 1948:52 [reference].—Böhlke, 1958:107, pl. 7, fig. 2 [Ecuador: Río Vilano].—Ovchynnyk, 1968:250 [Ecuador].—Fowler, 1975:368 [reference].
- Cruxentina dobula*.—Fernández-Yépez, 1948:53 [reference].—Ovchynnyk, 1968:250 [Ecuador].—Fowler, 1975:367 [reference].
- Ichthyoelephas stigmaturus*.—Ovchynnyk, 1968:251 [Ecuador, transfer from *Prochilodus* to *Ichthyoelephas*].
- Curimatus cf. peruanus*.—Saul, 1975:113 [Ecuador, Santa Cecilia, Río Aguatico; stomach contents].
- Steindachnerina nasa*.—Stewart et al., 1987:24 [eastern Ecuador, Río Napo drainage basin].
- Steindachnerina stigmaturus*.—Vari and Castro, 1988:779 [transfer from Prochilodontidae to Curimatidae; assignment to *Steindachnerina*].

DIAGNOSIS.—The numerous lobulate fleshy processes on the roof of the mouth, absence of a wide, flattened, prepelvic region of the body, of a distinct spot of dark pigmentation on the basal portion of the middle rays of the dorsal fin, or of a dark midlateral stripe on the body distinguishes *Steindachnerina dobula* from its congeners.

DESCRIPTION.—Body moderately elongate, somewhat compressed. Dorsal profile of head somewhat convex anteriorly, straight or very slightly convex from vertical line through anterior nostril to anterior portion of supraoccipital. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle in smaller specimens, degree of curvature more pronounced in larger individuals, particularly ripe females. Prepelvic region obtusely flattened, with median series of scales posteriorly. Postpelvic region rounded.

Greatest depth of body found in largest specimens, depth 0.29–0.34 [0.30]; snout tip to origin of dorsal fin 0.45–0.49 [0.46]; snout tip to origin of anal fin 0.80–0.86 [0.84]; snout tip to origin of pelvic fin 0.50–0.56 [0.51]; snout tip to anus 0.74–0.78 [0.76]; origin of dorsal fin to hypural joint 0.55–0.60 [0.56]. Margin of dorsal fin straight or slightly convex posteriorly; anteriormost rays two and one-half to three times length of ultimate ray. Pectoral-fin profile obtusely acute; length of pectoral fin 0.17–0.21 [0.17], extends about one-half distance to vertical line through origin of pelvic fin. Pelvic-fin profile acute; length of pelvic fin 0.19–0.24 [0.20], reaches about one-half distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin distinctly emarginate, anteriormost branched rays approximately three times length of ultimate ray. Caudal peduncle depth 0.11–0.13 [0.12].

Head obtusely pointed in profile, head length 0.26–0.31 [0.28]; mouth distinctly inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.27–0.33 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture partially closed by thin flap of skin separating nares; orbital diameter 0.27–0.32 [0.31]; adipose eyelid present, more developed anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.40–0.46 [0.43]; gape width 0.27–0.32 [0.21]; interorbital width 0.38–0.43 [0.38].

Pored lateral-line scales to hypural joint 39 to 46 [41]; all scales of lateral line pored, canals in scales straight; 4 to 7 series

of scales extend beyond hypural joint onto caudal-fin base; $6\frac{1}{2}$ to $7\frac{1}{2}$ [$6\frac{1}{2}$] scales in transverse series from origin of rayed dorsal fin to lateral line; 5 to $6\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or ii,8, or iii,7 (ii,8 rare, when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 13 to 16; pelvic-fin rays i,7 or i,8 (i,7 rare) [i,8].

Total vertebrae 33 (5), 34 (74), 35 (30).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery, darker and somewhat grayish or purplish on dorsal portions of head and body (Figures 42 to 46). Specimens lacking guanine on scales tan to brown, darker dorsally. Caudal peduncle with variably developed dusky to dark, midlateral spot; ranging in degree of development from diffuse patch limited to peduncle (Figures

44, 45) to a prominent patch extending further anteriorly and to varying degrees posteriorly onto middle rays of caudal fin (Figures 42, 43). Some specimens with intense elongate spot on caudal peduncle that extends to posterior of middle caudal-fin rays. Lower lobe of caudal fin often dusky. Dorsal fin with faint, diffuse, posteriorly slanting band of dark pigmentation in a few individuals.

VARIATION.—As noted under "Color in Alcohol" there is a pronounced degree of variation in the intensity of pigmentation on the midlateral surface of the caudal peduncle in *Steindachnerina dobula*. Pigmentation in that region ranges from a faint, slightly elongate spot limited to the posterior portion of the caudal peduncle to a very intense dark streak extending across the caudal peduncle and the middle rays of the caudal fin (compare Figures 42 to 45). The degree of development of the pigmentation demonstrates a continuum both in population samples from a single region and in specimens across the



FIGURE 42.—*Steindachnerina dobula*, USNM 229203, 105.6 mm SL; Peru, Huanuco, Río Yamushimas, Río Pachitea system.



FIGURE 43.—*Steindachnerina dobula*, USNM 261517, 71.5 mm SL; Peru, Ucayali, Río Ucayali, Masisea.



FIGURE 44.—*Steindachnerina dobula*, MZUSP 27820, 78.5 mm SL; Bolivia, Cochabamba, Río Chapare, between Todos Santos and mouth.



FIGURE 45.—*Steindachnerina dobula*, NRM SOK/1986313.5294, 83.0 mm SL; Peru, Loreto, Río Corrientes, Teniente Lopez.

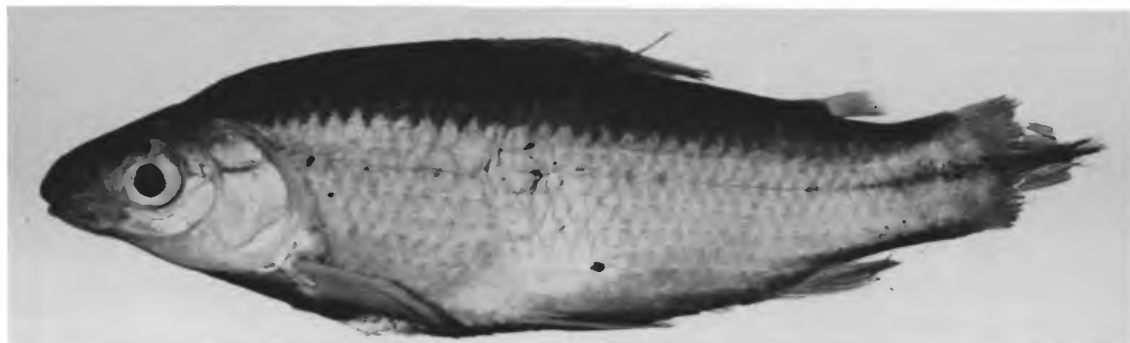


FIGURE 46.—*Steindachnerina dobula*, ANSP 39104, 104.8 mm SL, holotype of *Prochilodus stigmaturus*; Ecuador, Guayas, Río Chimbo, near Bucay (see also "Remarks" under *Steindachnerina dobula*).

geographic range of the species, thus making it an unsuitable feature to subdivide what is herein considered *Steindachnerina dobula* into two or more species. It is not clear whether the variation is a consequence of different water types, intrapopulation genetic variation, or some other factor.

DISTRIBUTION.—Western portions of the Amazon basin in Colombia, Ecuador, Bolivia, Peru, and Brazil (Figure 41; see also comments on reported type-locality of *Prochilodus stigmaturus* under “Remarks” below).

LIFE HISTORY.—Saul (1975:113) reports that in the region of Santa Cecilia, Ecuador, *Steindachnerina dobula* (cited in that study as *Curimatus cf. peruanus*) typically occurs in moderately flowing waters adjoining sandbars, and that stomachs of examined specimens contained “bottom detritus.”

REMARKS.—As noted above under “Variation,” the degree of development of pigmentation on the midlateral surface of the caudal peduncle and the relative body depth of *Steindachnerina dobula* vary significantly both within population samples of the species and across the species range. Such variation, coupled with the limited detail in the brief original description of *Curimatus dobula* by Günther (1868a:243), may account for the subsequent redescription of the species as *Curimatus nasus* by Steindachner (1882:80), *Curimata niceforoi* by Fowler (1943a:224), incorrectly in the family Prochilodontidae as *Prochilodus stigmaturus* by Fowler (1911:495), and as a subspecies, *Curimata hypostoma hastata* by Allen (in Eigenmann and Allen, 1942:293).

Günther’s original description of *Curimatus dobula* (1868a:243) was based on three specimens, all of which are in very poor condition at this time. The syntype in the best overall condition (BMNH 1867.6.13:55, 76.3 mm SL) is designated as the lectotype. The two remaining syntypes (BMNH 1867.6.13:56-57) thus become paralectotypes. Both the lectotype and paralectotypes have become quite dark, but traces of midlateral pigmentation on the caudal peduncle still exist on the lectotype.

Steindachnerina dobula and *Curimatus nasus*, which was subsequently described by Steindachner (1882:80), both originated in the upper portions of the Río Marañón system of the western Amazon. In his brief original description of *Curimatus nasus*, Steindachner neither compares his species to the other then described nominal species of curimatids, nor indicates the features of the form that he believed distinguished it within the family. The syntypes of *Curimatus nasus* do not differ from *Steindachnerina dobula* in any of the examined features (Table 6) and the species are herein considered conspecific.

Steindachner based his description of *Curimatus nasus* on a type-series of unspecified size originating at Canelos, Ecuador. Five specimens identified as syntypes were located in the holdings of the Naturhistorisches Museum Wien. A 86.4 mm SL specimen is selected as the lectotype (NMW 68900.1). The remaining syntypes (NMW 68899.1-2, NMW 68900.2-3) become paralectotypes.

Allen (in Eigenmann and Allen, 1942:297) assigned his subspecies *hastata* to *Curimatus hypostoma*. In his original description he notes a number of differences in body form and pigmentation differentiating his subspecies from the material that Eigenmann and Allen (1942:296) identified as typical *hypostoma*. The specimens considered by those authors to be *Curimata hypostoma* are a mixture of *Steindachnerina hypostoma* and *S. dobula* (e.g., CAS 63191, formerly IU 17858 from Yurimaguas, Río Paranapura). Perhaps as a consequence of this confusion as to the true identity of *S. hypostoma*, Allen incorrectly aligned *hastata* with *hypostoma*, a species that differs in numerous details of body form and pigmentation. The holotype of *Curimata hypostoma hastata* (CAS 19881, formerly IU 17859) agrees in all examined features with material considered herein to represent *Steindachnerina dobula* (Table 6), and the subspecies is considered synonymous with *S. dobula*.

Fowler (1943a:224) described *Curimata niceforoi* from a single specimen collected at Florencia, Colombia, in the Río Ortegusa basin by Brother Niceforo Maria. The holotype (ANSP 70490) is now in poor condition and appears to have a shallower greatest body depth than the drawing in the original species description (Fowler, 1943a, fig. 3). Comparisons of the holotype of *Curimata niceforoi* with other material considered to represent *Steindachnerina dobula* (Table 6) has not revealed any differences between the nominal forms and the species are considered conspecific. The holotype of *Curimata niceforoi* along with a second specimen collected by Niceforo Maria in the same location, evidently at the same time, represent the most northerly records for *S. dobula*.

Fowler (1911:495) described *Prochilodus stigmaturus* from the Río Chimbo drainage that drains into the Gulf of Guayaquil in southeastern Ecuador. The species was subsequently referred to by various authors on the basis of its original description (e.g., Eigenmann, 1922:116) and transferred without comment by Ovchynnyk (1968:251) to the prochilodontid genus *Ichthyoelephas* Posada-Arango. No other reports of the species based on additional specimens appear to exist. Vari and Castro (1988:778) demonstrate that the species is not a prochilodontid, but is rather a curimatid. In that same publication (1988:779) they assigned it to *Steindachnerina*. Comparisons of the holotype of *Prochilodus stigmaturus* (ANSP 39104), which is somewhat damaged (Figure 46), with other species of *Steindachnerina* has shown that the species agrees with *S. dobula* in examined features (Table 6) and is evidently conspecific with that species.

The hypothesis that *Prochilodus stigmaturus* is conspecific with *Steindachnerina dobula* does raise questions about the purported site of origin of the species. *Steindachnerina* is unknown from any of the Pacific drainages of southwestern Colombia, Ecuador, and northwestern Peru that are inhabited by other curimatid species. The only curimatids known to occur in those river systems are *Pseudocurimata boulengeri* (Eigenmann) and *P. troschelii* (Günther), members of a clade of the

TABLE 6.—Morphometrics and meristics of (A) holotype of *Curimata dobula* (BMNH 1867.6.13:55), (B) lectotype of *Curimatus nasus* (NMW 68900.1), (C) holotype of *Curimata hypostoma hastata* (CAS 19881, formerly IU 17859), (D) holotype of *Curimata niceforoi* (ANSP 70490), (E) holotype of *Prochilodus stigmaturus* (ANSP 39104), and (F) all specimens of *Steindachnerina dobula* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 14 are proportions of head length. Holotype of *Curimata niceforoi* is twisted, precluding accurate measurement of standard length or estimates of body proportions based on that measurement. Dashes indicate values that could not be taken due to condition of specimen.

Character	A	B	C	D	E	F
MORPHOMETRICS						
Standard Length	76.3	86.4	111.5	~72.0	104.8	55.0-163.0
1. Greatest body depth	0.30	0.28	0.30	-	0.30	0.29-0.34
2. Snout to dorsal-fin origin	0.46	0.48	0.47	-	0.49	0.45-0.49
3. Snout to anal-fin origin	0.84	0.79	0.82	-	0.80	0.80-0.86
4. Snout to pelvic-fin origin	0.51	0.53	0.51	-	0.53	0.50-0.56
5. Snout to anus	0.76	0.74	0.73	-	0.76	0.74-0.78
6. Origin of rayed dorsal fin to hypural joint	0.56	0.56	0.56	-	0.55	0.55-0.60
7. Pectoral-fin length	0.17	-	0.18	-	0.18	0.17-0.21
8. Pelvic-fin length	0.20	0.19	0.20	-	0.19	0.19-0.24
9. Caudal peduncle depth	0.12	0.11	0.11	-	0.13	0.11-0.13
10. Head length	0.28	0.27	0.27	-	0.28	0.26-0.31
11. Snout length	0.30	0.31	0.32	0.33	0.32	0.27-0.33
12. Orbital diameter	0.31	0.31	0.28	0.32	0.27	0.27-0.32
13. Postorbital length	0.43	0.40	0.45	0.41	0.43	0.40-0.46
14. Interorbital width	0.38	0.38	0.40	0.39	0.42	0.38-0.43
MERISTICS						
Lateral-line scales	41	40	44	40	40?	39-46
Scale rows between dorsal-fin origin and lateral line	6½	6½	7½	6½	7½	6½-7½
Scale rows between anal-fin origin and lateral line	5½	5	6	5	5½	5-6½
Branched dorsal-fin rays	9	9	9	9	9	9
Branched anal-fin rays	7	7	7	7	7	7-8
Total pectoral-fin rays	-	14	15	15	15	13-16
Branched pelvic-fin rays	8	8	8	8	8	7-8
Vertebrae	34	34	34	34	33	33-35

Curimatidae restricted to the western versant of the Andes (Vari, 1989d).

The fish fauna of the rivers of the southwestern portion of Ecuador has been moderately well sampled although no large collections from the Río Chimbo are available. Nonetheless, the combination of the apparent conspecificity of *Prochilodus stigmaturus* with *Steindachnerina dobula* and the lack of any other specimens of *Steindachnerina* from the western rivers of Ecuador raises the possibility that the holotype of *Prochilodus stigmaturus* came from the Amazonian portions of Ecuador and was inadvertently mixed up with material from the Río Chimbo system.

Eigenmann and Kennedy (1903:510) followed by Bertoni (1914:9, 1939:54), Pearson (1937:109), Ringuelet (1975:72), and Géry et al. (1987:424) reported *Curimatus nasus* from the Paraguay basin. No material of *Steindachnerina dobula*, the

senior synonym of *Curimatus nasus*, has been located among the examined curimatid specimens from the La Plata system. The original Eigenmann and Kennedy record is assumed to represent a misidentification of another *Steindachnerina* species, perhaps *S. brevipinna*.

MATERIAL EXAMINED.—307 specimens (97, 55.0-163.0).

COLOMBIA. *Caqueta*: Florencia, Río Ortegusa basin, ANSP 70490, 1 (~72.0, holotype of *Curimata niceforoi*); USNM 100775, 1 (68.6).

PERU. Río Huallaga, BMNH 1867.6.13.55, 1 (76.3, lectotype of *Curimatus dobula*); BMNH 1867.6.13:56-57, 2 (80.2-83.5, paralectotypes of *Curimatus dobula*). *Loreto*: Río Putomayo system, downstream of El Estrecho, NRM SOK/1986296.5416, 1. Río Napo system, upstream of Mazán, NRM uncat., 74. Río Corrientes, Teniente Lopez, NRM SOK/1986313.5294, 3 (1, 83.0); NRM SOK/1986313.5368, 9. Río

Paranapura, Yurimaguas, CAS 63191, 4 (formerly IU 17858, in part); USNM 300040, 1. Río Huallaga, Yurimaguas, CAS 65351, 3 (formerly IU 15827); USNM 298397, 2. *Amazonas*: Río Santiago, La Poza, LACM 39898-5, 2 (78.6–85.1). Río Marañón, LACM 41738-21, 11. *Ucayali*: Río Ucayali, Masisea, USNM 261517, 34 (10, 68.2–89.3); USNM 298455, 3. USNM 261494, 1 (70.0). Nuevo San Juan near Masisea, USNM 261443, 7. Río Ucayali, Pucallpa, USNM 261487, 1 (74.0); USNM 261415, 1 (105.2); USNM 298378, 5 (86.8–107.8). Río Ucayali, 10 km upstream of Pucallpa, USNM 280452, 1. Río Ucayali, Utuquinia, USNM 300052, 2. Río Neshuya near Pucallpa to Huanuco road, AMNH uncat., 1; USNM 261486, 3. IVITA station, 60 km from Pucallpa along road from Pucallpa to Huanuco, USNM 261473, 1. Bosque Nacional von Humboldt, 86 km from Pucallpa, GC, 1 (81.0). *Huanuco*: Río Pichis, Puerto Bermudez, CAS 19881, 1 (111.5, holotype of *Curimata hypostoma hastata*, formerly IU 17859). Río Pachitea system, USNM 229203, 2 (99.9–105.6). Río Pachitea, Tournavista, USNM 261417, 1 (108.4); USNM 261453, 1; USNM 261476, 5. Quebrada Ayamira, tributary of Río Pachitea, BMNH 1969.11.18.1, 1 (112.3). *Madre de Dios*: Parque Nacional Manú, Pakitza, USNM 295173, 10. Río Tambopata, Puerto Maldonado, USNM 300062, 9 (4, 55.0–74.0).

BOLIVIA. *Beni*: Río Mamoré, ~15 km S of Limoquije, AMNH uncat., 3 (55.9–75.6). *La Paz*: Iximias, USNM 300048, 2 (59.9–84.3, formerly IU 17133, in part); UMMZ 66479, 4 (65.0–88.2, formerly IU 17133, in part). Lower Río Bopi, UMMZ 66500, 3 (84.5–92.0, formerly IU 17135, in part); USNM 298348, 2 (77.3–84.2, formerly IU 17135, in part). Huachi, USNM 298410, 3 (82.8–88.8, formerly IU 17130, in part); UMMZ 66509, 6 (5, 75.8–106.3, formerly IU 17130, in part). Rurrenabaque, UMMZ 66512, 8 (5, 64.8–74.5, formerly IU 17132). San Miguel de Huachi, Río Bopi, USNM 278576, 1. *Cochabamba*: Villa Tunari, USNM 278573, 3. Villa Tunari, Río Chapare, MZUSP 27810, 5. Río Chapare, USNM 278574, 5. Río Chapare, between Todos Santos and mouth, MZUSP 27820, 4 (57.6–98.4).

ECUADOR. *Napo Pastaza*: Río Aguarico, at Santa Cecilia, KU 13483, 2 (1, 163.0); KU 13488, 21 (10, 75.8–96.5). Río Vilano, at Río Vilano, USNM 164050, 4 (84.7–100.4). Río Napo, Coca, USNM 300049, 2 (64.7–65.1). Río Payamino, USNM 300047, 5 (58.0–76.5). Canelos, NMW 68900.1, 1 (86.4, lectotype of *Curimatus nasus*); NMW 68900.2-3, 2 (1, 80.5, paralectotype of *Curimatus nasus*); NMW 68899.1-2, 2 (85.9–91.1, paralectotypes of *Curimatus nasus*). *Guayas*: “Affluent of Chimbo River near Bucay,” ANSP 39104, 1 (104.8, holotype of *Prochilodus stigmaturus*; see “Remarks” with respect to questions concerning cited locality).

BRAZIL. *Mato Grosso*: Município de Pontes e Lacerda, Río Branco, tributary of Río Guaporé, above bridge on BR 364 between Cuiabá and Porto Velho, MZUSP 37421, 8 (3, 121.2–143.3). *Acre*: Río Tarauacá, Tarauacá, USNM 267990, 4.

Steindachnerina insculpta (Fernández-Yépez, 1948)

FIGURES 41, 47–49

- Curimatus elegans*.—Campos, 1945:46 [Brazil: Río Mogi-Guaçu].—Britski, 1972:83 [Brazil: São Paulo, Río Paraná basin].—Foresti et al., 1974:249 [karyotypes].—Nomura, 1977:727 [Brazil: Río Mogi-Guaçu; meristics].—Nomura and Taveira, 1979:331 [life history].
- Cruxentina insculpta* Fernández-Yépez, 1948:53, figs. 27, 28 [type-locality: Brazil: São Paulo, Río Tatuhy (= Tatu); authorship cited as Amaral Campos].—Britski, 1969:200, 203 [correction of originally cited authorship, depository and collector; meristics and morphometrics].—Fowler, 1975:368 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata elegans*.—Gomes and Monteiro, 1955:88, 103, 129 [São Paulo, Pirassununga, occurrence in flowing and still waters].—Oliveira et al., 1988:594 [in part, Brazil: São Paulo, Río Mogi-Guaçu and Botucatu; not Minas Gerais, Três Marias; chromosome counts].
- Pseudocurimata elegans elegans*.—de Godoy, 1975:585, fig. 132A, 133 [Brazil: São Paulo, Río Mogi Guassu (= Guaçu); life history data; meristics and morphometrics; not cited occurrence in drainage basins other than upper Río Paraná].
- Curimata nasa*.—Géry et al., 1987:425, fig. 41 [Paraguay: Río Paraguay and Río Paraná].
- Steindachnerina insculpta*.—Venere and Galeffi, 1989:18, 19, fig. 19 [Brazil: upper Río Paraná basin, Río Mogi-Guaçu and Río Passa-Cinco; karyotype information].

DIAGNOSIS.—The multiple lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened prepelvic region of the body, lack of a dark spot on the basal portions of the dorsal fin, possession of 36 to 46 lateral-line scales to the hypural joint, and the presence of a dark midlateral stripe along the length of the body discriminate *Steindachnerina insculpta* from its congeners.

DESCRIPTION.—Body relatively elongate, somewhat compressed. Dorsal profile of head very slightly convex anteriorly, straight from above orbit to rear of head. Dorsal profile of body straight or very slightly convex from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened, with median series of scales proximate to pelvic-fin origin, median series less regularly arranged anteriorly. Barely discernible median keel posterior to pelvic-fin origin.

Greatest depth of body 0.29–0.34 [0.33]; snout tip to origin of dorsal fin 0.45–0.50 [0.48]; snout tip to origin of anal fin 0.80–0.85 [0.83]; snout tip to origin of pelvic fin 0.52–0.55 [0.55]; snout tip to anus 0.73–0.78 [0.76]; origin of dorsal fin to hypural joint 0.55–0.59 [0.58]. Dorsal-fin margin rounded; anteriormost rays three to three and one-half times length of ultimate ray. Pectoral-fin margin acute; length of pectoral fin 0.17–0.21 [0.20], extends one-half to two-thirds distance to origin of pelvic fin in smaller adults, barely beyond that point in largest specimens examined. Pelvic-fin margin acute; length of pelvic fin 0.18–0.22 [0.19], reaches about one-half distance

to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays two and one-half to three times length of ultimate ray. Caudal peduncle depth 0.11–0.13 [0.12].

Head pointed in profile, head length 0.27–0.31 [0.28]; upper jaw distinctly longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.29–0.33 [0.32]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.25–0.29 [0.28]; adipose eyelid present, more developed anteriorly, with broad, vertically ovoid opening over center of eye; length of postorbital portion of head 0.42–0.47 [0.46]; gape width 0.25–0.30 [0.26]; interorbital width 0.38–0.42 [0.41].

Pored lateral-line scales to hypural joint 37 to 42 [38]; all scales of lateral line pored, canals in scales of lateral line straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $6\frac{1}{2}$ to $7\frac{1}{2}$ [$6\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [5] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 [ii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 12 to 15 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 33 (28), 36 (1, see "Remarks" below).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery to silvery golden, darker on dorsal portions of head and body. Ground coloration of specimens lacking guanine on scales tan to yellow, darker dorsally. Head dusky dorsally, with irregular patch of dark pigmentation extending from rear of orbit across opercle; degree of intensity of dark pigmentation and extent of patch variable among individuals. Irregular, dark, longitudinal stripe extending along lateral line from supracleithrum to base of middle caudal-fin rays. Stripe slightly wider posteriorly, continuous posteriorly with dusky stripe on middle caudal-fin rays. Stripe in adults continuous, about one scale wide (Figures 47, 48); not as well developed in juveniles, consisting of discrete spots surrounding pores of lateral line (Figure 49). Caudal-fin stripe more prominent on anterior portion of rays. Anterior margin and distal portions of dorsal fin typically dusky in adults. Ventral lobe and dorsal rays of dorsal lobe of caudal fin dusky. All caudal-fin rays outlined by small chromatophores on membranes. Adipose fin dusky distally. Dorsal fin with dusky anterior region in many specimens, without any discrete dark spot on middle rays. Other fins hyaline.

DISTRIBUTION.—Upper Rio Paraná basin above Sete Quedas and Rio Paraguay system (Figure 41; see also "Remarks" with respect to records from Río Paraguay system).

KARYOTYPE.—Foresti et al. (1974:249; as *Curimatus elegans*) followed by Oliveira, et al. (1988:594; as *Curimata elegans*) report that this species has $2n = 54$ chromosomes, with

a fundamental number of 108. No evidence of chromosomal heteromorphism was found. Venere and Galetti (1989:19) confirm the karyotype count and discuss it within a broader phylogenetic framework.

ECOLOGY AND LIFE HISTORY.—Gomes and Monteiro (1955) note that this species is common at Pirassununga along the Rio Mogi-Guaçu, and occurs in large numbers in both still and slow running waters. de Godoy (1975:590) cites this species as a member of the "piracema," the mass fish migration through the rapids at the Cachoeira de Emas in the Rio Mogi Guassu. The species is found in the area throughout the year, but is most common during the period from September to February. Both sexes begin ripening in September and spawning takes place between the end of November and the middle of January. According to de Godoy (1975:591) the species eats zooplankton for the first 30 to 50 days after hatching. At the end of that period the larval dentition is lost, the intestinal system lengthens, and the species switches to a diet of algae and organic detritus. Nomura and Taviera (1979) found at least 23 different genera of algae in the stomachs of adults of the species. Those authors also provide additional life history data for the species.

REMARKS.—Fernández-Yépez (1948:53) described this species (in *Cruxentina*) on the basis of the holotype and a single paratype from the Rio Tatuhy (= Tatuí), in the upper portions of the Rio Paraná basin. That author cites Antonia de Amaral Campos as both the collector of the type-series, and as the researcher who first recognized the species as being undescribed. Fernández-Yépez consequently felt that it was appropriate to credit Amaral Campos with the authorship of the species. Britski (1969:201, 203) demonstrates that the types were collected rather by J. Lima and that the identification of the material was done by H.W. Clark of the California Academy of Sciences. Clark did not, however, publish his conclusion that the specimens represented a then undescribed species. Regardless of who may have originally determined that the specimens represented an undescribed form, the actual author of the species is Fernández-Yépez.

Both the holotype and the paratype of *Cruxentina insculpta* had the same original number (MZUSP 1376), which Fernández-Yépez (1948:53) mistakenly reports as a CAS register number. That author states that the holotype was 101 mm (? SL) and the paratype 111 mm. The one specimen now in the CAS collection (CAS 20312) is 95.3 mm SL and the second individual now deposited at MZUSP (MZUSP 1376) is 105.6 mm SL. It would appear that the smaller individual, now at CAS, is the holotype of the species. The erroneous length information in the original description of the species led to the assumption that the holotype was deposited in the MZUSP collection (Britski, 1969).

Following the original description of *Steindachnerina insculpta* the species is referred to under that name by only two authors, Britski (1969) who corrects various details of the

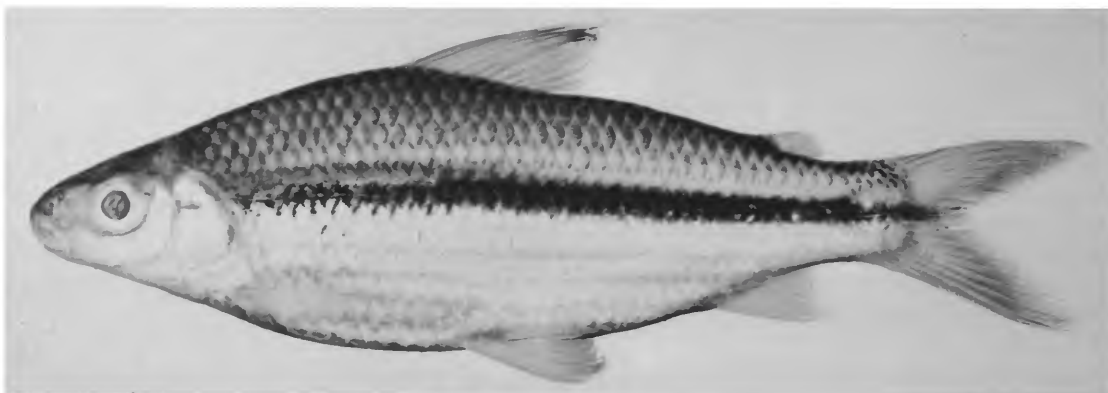


FIGURE 47.—*Steindachnerina insculpta*, USNM 295273, 83.0 mm SL; Brazil, Distrito Federal, Ribeirão Santana, at road crossing 30 km S of Barragem de Paranoá, Rio São Bartolomeu system.



FIGURE 48.—*Steindachnerina insculpta*, MNRJ 11206, 81.3 mm SL; Brazil, Mato Grosso, Rio Acorizal, at bridge from Acorizal to Baús.



FIGURE 49.—*Steindachnerina insculpta*, USNM 295271, 38.5 mm SL; Brazil, São Paulo, Rio Magi-Guaçu, Emas.

original species description and Fowler (1975) who simply lists the species in an enumeration of the species in the Curimatidae. The general lack of recognition of *S. insculpta* was probably in large part a consequence of the difficulty in recognizing the species based on the original description. Most authors identify the population samples of *Steindachnerina* in the upper Rio Paraná system as *Curimatus elegans* Steindachner (see synonymy under this species).

Nomura (1977), was evidently unaware of Fernández-Yépez's nominal species, *Cruxentina insculpta*. He instead identifies his material from the Rio Mogi Guaçu (= Guassu) of the upper Rio Paraná basin as *Curimatus elegans*. The differences in diverse meristic features between the samples from the Rio Paraná system and material from the coastal rivers to the northeast led him to propose that the upper Rio Paraná populations be recognized as a separate subspecies. The populations in the upper Rio Paraná system differ from *Curimatus elegans* Steindachner in numerous details, both those noted by Nomura and others, and are considered herein to represent a separate species, *S. insculpta*.

Nomura (1977, table 8) indicates that the population samples he identifies as *Curimatus elegans* (actually = *Steindachnerina insculpta*) in the Rio Mogi-Guaçu had 28 to 31 vertebrae with most individuals having 29 elements. Nearly all radiographed specimens of *Steindachnerina insculpta* examined in this study have 33 vertebrae including the four elements incorporated into the Weberian apparatus (but see also last paragraph of "Remarks" below). It appears that Nomura does not include the vertebrae of the Weberian complex in his counts. The addition of those four vertebrae to the values given by Nomura would result in agreement between the most common count cited by that author and the results of this study.

The vast majority of the specimens of *Steindachnerina insculpta* examined during this study originated in the upper Rio Paraná system. A much smaller series of individuals evidently conspecific with that species (Figure 48) have been collected within the last decade in a relatively discrete region of the Rio Paraguai basin in Mato Grosso state, Brazil (MZUSP 4383, 4449, 21512, 21656, 21662; MNRJ 11206, 11207, 11210, 11213, 11214). The species has not, however, been found in examined collections made in other portions of the Rio Paraguay system, nor in older collections from various localities in Mato Grosso state. Géry et al. (1987:425) also report what appears to be a sample of this species (identified by them as *Curimata nasa*) from the same general area. A disjunct species distribution between the upper Rio Paraná and the upper Rio Paraguay is unknown in any other member of the Curimatidae. That factor and the absence of samples of *Steindachnerina insculpta* in older collections from the Rio Paraguay system raises the possibility that the occurrence of the species in the upper Rio Paraguay system is the consequence of a relatively recent introduction.

A single specimen apparently of *Steindachnerina insculpta*

(MNRJ 11210) from the Rio Corumbá in the upper Rio Paraná system of Goiás state, Brazil, differs from the other radiographed individuals of the species in having 36 rather than 33 vertebrae. The specimen does not, however, differ from other specimens of *S. insculpta* in any other examined character. Additional collections from the upper Rio Paraná system are necessary before it is possible to decide if this difference represents a single aberrant individual or perhaps an undescribed species.

MATERIAL EXAMINED.—886 specimens (64, 39.2–105.6).

BRAZIL. Rio Paraná, no specific locality, BMNH 1902.2.10:31, 1. *Goiás*: Goiânia, USNM 268046, 1 (79.5). Rio Corumbá, MNRJ 11210, 1 (94.8). *Distrito Federal*: Córrego Pipiripau, near Planaltina, MZUSP 21530, 4. Lagoa Paranoá, Brasília, MZUSP 21719, 1. Ribirão Santana, at road crossing 30 km S of Barragem de Paranoá (Rio São Bartolomeu system, 15°55'S, 47°46'W), USNM 295273, 11 (1, 83.0). *São Paulo*: Rio Tatuhy (= Tatuí), CAS 20312, 1 (95.3, holotype of *Cruxentina insculpta*; see also "Remarks" under this species); MZUSP 1376, 1 (105.6, paratype of *Cruxentina insculpta*). Município de Alfredo de Castilho, Córrego do Moinho, USNM 295275, 5 (76.3–104.0); MZUSP 20381, 98. Represa de Volta Grande, Miguelópolis, USNM 295272, 5 (4, 66.7–78.4); MZUSP 21515, 26. Rio Mogi-Guaçu, Emas, USNM 295271, 22 (5, 51.8–87.8); MNRJ 5669, 5 (3, 74.4–81.7); MZUSP 20750, 74 (10, 80.9–90.4); BMNH 1946.12.23:97-111, 11 (67.9–79.5); MZUSP 20741, 1; MZUSP 20791, 1; MZUSP 20700, 15; MZUSP 20744, 2; MZUSP 20704, 33; MZUSP 20739, 19. Rio Mogi-Guaçu, Cachoeira de Emas, MZUSP 20672, 36; MZUSP 20691, 17. Rio Mogi-Guaçu, Pirassununga (= Piraçununga), USNM 295274, 9; MZUSP 20711, 10. Piracicaba, CAS 41729, 4 (66.0–91.9); NMW 67002, 3; NMW 68914, 2. Rio Corumbataí, Corumbataí, MZUSP 20768, 1; MZUSP 20755, 64; MZUSP 20758, 37. Borborema, Rio Tietê, MZUSP 21317, 10 (88.7–101.4); USNM 295266, 2. Rio Grande, Marimondo, MZUSP 21525, 1. Rio Jaguarí, Pedreira, MZUSP 21603, 2. Rio Pardo, Usina de Limoeiro, MZUSP 20865, 1. Botucatu, MZUSP 21471, 1. *Minas Gerais*: Rio Grande, Represa de Furnas, Município de Alfenas, MZUSP 21505, 2. Rio Grande, Boa Esperança, MZUSP 21502, 1. Rio Miranda, Salobra, MNRJ 8900, 4 (2, 89.0–90.1). Represa de Jaguará, USNM 295267, 2. *Mato Grosso*: Rio Paraná, Jupiá, MZUSP 20853, 18; MZUSP 20683, 15; MZUSP 20714, 84. Rio Scuriú, Três Lagoas, MZUSP 20824, 1; MZUSP 20894, 1. Ilha Solteira, MZUSP 21429, 106. Rio Cuiabá, Santo Antônio do Leverger, MZUSP 4383, 3; MZUSP 4449, 1 (39.2). Rio Acorizal, at bridge along road from Acorizal to Baús, MNRJ 11206, 3 (59.8–85.7). Ribeirão Baús, Município Acorizal, MNRJ 11207, 1 (102.0). Ribeirão Tugará, along road from Acorizal to Cuiabá, MNRJ 11214, 1. Município de Barão de Melgaço, MZUSP 21662, 2. *Paraná*: Rio Paraná, Guáira, above Sete Quedas, MZUSP 21620, 103.

Steindachnerina runa, new species

FIGURES 50-53

DIAGNOSIS.—The numerous lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened prepelvic region of the body, absence of a distinct dark spot on the basal portion of the middle rays of the dorsal fin, and the limitation of the midlateral stripe on the body to the posterior half of the body discriminate *Steindachnerina runa* from its congeners.

DESCRIPTION.—Body moderately elongate, moderately compressed. Dorsal profile of head slightly convex from tip of snout to vertical through posterior nostril, straight or slightly convex from that point to rear of head. Dorsal profile of body smoothly curved and slightly convex from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal body surface with an indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle, more so in gravid females. Prepelvic region somewhat flattened, but without distinct lateral keels; median series of scales present to varying degrees anterior to insertion of pelvic fins. Postpelvic region irregularly rounded transversely.

Greatest depth of body 0.34–0.38 [0.38], gravid females relatively deeper; snout tip to origin of dorsal fin 0.49–0.52 [0.50]; snout tip to origin of anal fin 0.83–0.88 [0.83]; snout tip to insertion of pelvic fin 0.52–0.56 [0.53]; snout tip to anus 0.78–0.84 [0.78]; origin of rayed dorsal fin to hypural joint 0.55–0.59 [0.58]. Dorsal fin distinctly pointed with anterior-most rays elongate and posterior margin distinctly emarginate, anteriormost rays five and one-half to six and one half times length of ultimate ray. Pectoral fin obtusely pointed; length of pectoral fin 0.20–0.23 [0.21], extends nearly to vertical line through insertion of pelvic fin in smaller specimens, falling somewhat short of that point in larger individuals. Pelvic fin pointed, length of pelvic fin 0.22–0.27 [0.23], reaches nearly to anus in smaller specimens, falls somewhat short of that point in larger specimens. Caudal fin forked. Adipose fin well developed. Anal fin distinctly emarginate, anteriormost branched rays about three times length of ultimate ray. Caudal peduncle depth 0.12–0.14 [0.13].

Head obtusely pointed in profile, head length 0.28–0.32 [0.28]; mouth distinctly inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.30–0.34 [0.33]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture partially closed by thin flap of skin separating nares; orbital diameter 0.29–0.33 [0.33]; adipose eyelid present, poorly developed posterior to eye, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.38–0.42 [0.42]; gape width 0.28–0.33 [0.33]; interorbital width 0.38–0.42 [0.40].

Pored lateral-line scales to hypural joint 36 to 40 [38]; all

scales of lateral line pored, canals in scales straight; 4 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$6\frac{1}{2}$] scales in transverse series from origin of rayed dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 14 to 17 [16]; pelvic-fin rays i,8 [i,8].

Total vertebrae 32 (3), 33 (15).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining some guanine on scales silvery golden to golden, darker with a purplish sheen on dorsal portions of head and body (Figure 50). Specimens lacking guanine on scales yellowish tan, with scattered dark chromatophores on dorsal portion of body (Figure 51). Head distinctly darker dorsally. Specimens of about 40 mm SL with faint but distinct midlateral band of dark pigmentation extending along posterior portion of lateral line and onto middle rays of caudal fin (Figure 52). Midlateral stripe becoming more prominent in larger specimens (Figures 50, 51), about one scale wide posteriorly, narrower anteriorly; stripe somewhat masked in specimens retaining guanine on scales. Narrow anterior portion in larger specimens begins approximately at vertical line through insertion of anterior portion dorsal-fin ray. Stripe becoming distinctly wider about four scales anterior of vertical line through anterior of insertion of adipose fin. Wider portion of stripe extends onto caudal-fin base and is continuous with dark band on middle rays of dorsal fin. Dorsal fin with elongate anterior rays darker, fin lacking discrete dark spot near base of middle fin-rays characteristic of many *Steindachnerina* species. Anal fin hyaline. Caudal fin hyaline other than for dark band on middle rays. Paired fins hyaline.

ETYMOLOGY.—The trivial name, *runa*, from the Latin for javelin, refers to the javelin-shaped darkly pigmented area on the midlateral surface of the caudal peduncle.

DISTRIBUTION.—The Fleuve Oyapock (Rio Oyapoque) system of French Guiana and Brazil, the Fleuve Maroni (Morawijne River) of French Guiana and Surinam, and the Surinam River in Surinam (Figure 53). The species also presumably occurs in the intervening smaller coastal rivers in French Guiana. Examination of the extensive series of curimatids collected by Dr. Michael Goulding of the Museu Goeldi in various rivers of the state of Amapa, Brazil, to the south of the Rio Oyapoque has not revealed any specimens of *Steindachnerina runa*, or indeed any member of the genus. Thus, it seems likely that the species and genus are absent in the coastal rivers between the Rio Oyapoque (Oyapock River) and lower Rio Amazonas. Numerous collecting efforts in Surinam by various researchers in the rivers lying to the west of the known range of *S. runa*, including extensive sampling of the fish fauna of the Corantijn River by the author, failed to reveal the presence of that species or any member of *Steindachnerina* in that region.

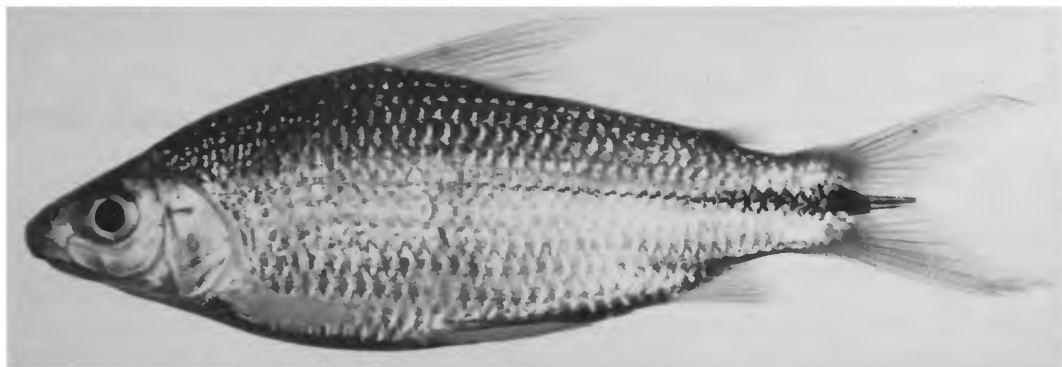


FIGURE 50.—*Steindachnerina runa*, new species, ZMA 120.501, 91.5 mm SL, holotype; Surinam, Brokopondo District, Morawijne or Gran Creek, 63 km S of Afobaka.



FIGURE 51.—*Steindachnerina runa*, new species, ZMA 119.708, 65.6 mm SL; French Guiana, Crique Alikene, left bank tributary to Fleuve Camopi, Fleuve Oyapock basin.



FIGURE 52.—*Steindachnerina runa*, new species, ZMA 119.426, 46.8 mm SL, paratype; Surinam, Brokopondo District, Morawijne or Gran Creek, 65 km S of Afobaka.

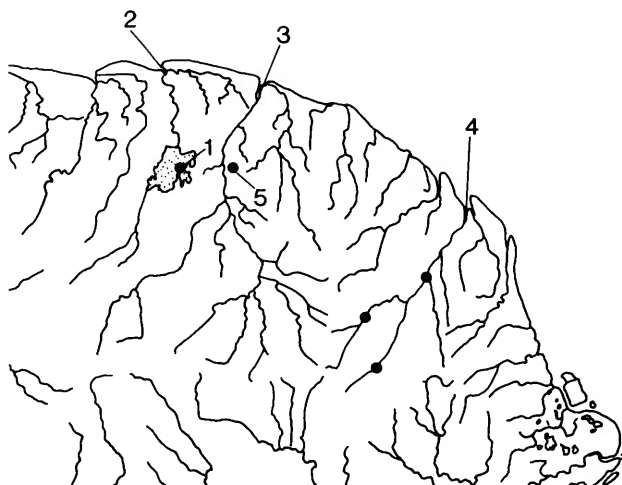


FIGURE 53.—Map of northeastern South America showing geographic distribution of *Steindachnerina runa* (1 = Gran or Morawijne Creek, type locality (now inundated by van Blumenstein (= Brokopondo) reservoir); 2 = mouth of Surinam River; 3 = mouth of Marowijne River or Fleuve Maroni; 4 = mouth of Rio Oiapoque or Fleuve Oyapock; 5 = Crique Kamaloea or Crique Saloea, paratype locality) (some symbols represent more than one lot of specimens).

HABITAT.—The type locality, Marowijne Creek, had running water approximately 150 cm deep over a sand and leaf bottom. The paratypes from French Guiana were collected in Crique Kamaloea, a 4 to 8 m wide tributary of the Fleuve Maroni (Morawijne River), approximately 30 to 200 cm deep, in running water over a sand and gravel bottom.

REMARKS.—Steindachner (1910) described *Curimatus surinamensis* from the upper Surinam River, the same basin as the type locality of *Steindachnerina runa*. The type series of *Curimatus surinamensis* has not been located despite repeated searches of the collections of the Naturhistorisches Museum over a ten year period. Nonetheless, the information in the original description of *C. surinamensis*, in particular the details of pigmentation and cited lateral-line scale counts, make it apparent that the species is very different from *Steindachnerina runa*. The available information indicates that *Curimatus surinamensis* is a member of *Cyphocharax*, being similar to or perhaps conspecific with *C. spilura* (Günther).

MATERIAL EXAMINED.—66 type specimens (66, 38.3–93.8).

HOLOTYPE.—SURINAM. *Brokopondo*: Morawijne or Gran Creek, 63 km S of Afobaka, collected by H. Nijssen, 20 Oct 1966, ZMA 120.501, 91.5 mm.

PARATYPES.—SURINAM. *Brokopondo*: Taken with holotype, ZMA 119.426, 40 (38.3–90.3); USNM 300000, 10 (57.6–92.7); ZMA 119.427, 1 (88.7).

FRENCH GUIANA. Crique Kamaloea or Saloea, right bank

tributary of the Fleuve Maroni (Marowijne River), about 9 KM SE of mouth of Gran Creek in Surinam, ZMA 119.428, 14 (57.4–93.8).

The following non-type specimens were also examined.

FRENCH GUIANA. Creek above Trois Sauts (02°15'N, 52°53'W), upper course of Fleuve Oyapock, ZMA 107.787, 2. Crique Pakoti, near Trois Sauts (02°15'N, 52°53'W), 1. Crique Alikene, left bank tributary to Fleuve Camopi, Fleuve Oyapock system, ZMA 119.708, 3 (60.5–75.3). Saut Maripa, Fleuve Oyapock (03°48'N, 51°54'W), ZMA 107.699, 4.

BRAZIL. Rio Oiapoque, Brazilian shore of river midway between St. Georges and Petit François on the French Guiana shore of river, USNM 298301, 1.

Steindachnerina pupula, new species

FIGURES 54–57

DIAGNOSIS.—The lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened prepelvic region of the body, lack of a dark midlateral stripe on the body, presence of a dark spot on the basal portions of the middle rays of the dorsal fin, and the possession of 42 to 46 lateral-line scales to the hypural joint and $7\frac{1}{2}$ to 9 scales above the lateral line to the origin of the dorsal fin, in combination, discriminate *Steindachnerina pupula* from its congeners.

DESCRIPTION.—Body moderately elongate, somewhat compressed, less so in ripe females. Dorsal profile of head convex anteriorly, straight or very slightly convex from vertical line through anterior nostril to rear of head. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin; straight or slightly convex and posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with obtuse median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle; curvature less pronounced in smaller specimens. Prepelvic region obtusely flattened, with scales irregularly arranged. Postpelvic region transversely rounded.

Greatest depth of body 0.29–0.36 [0.33]; snout tip to origin of dorsal fin 0.46–0.51 [0.48]; snout tip to origin of anal fin 0.82–0.86 [0.83]; snout tip to insertion of pelvic fin 0.51–0.55 [0.52]; snout tip to anus 0.75–0.80 [0.75]; origin of dorsal fin to hypural joint 0.55–0.59 [0.57]. Dorsal-fin margin straight or slightly convex; anteriormost rays approximately three times length of ultimate ray. Pectoral fin obtusely pointed; length of pectoral fin 0.16–0.22 [0.19], extends about three-quarters distance to vertical through insertion of pelvic fin. Pelvic fin pointed, length of pelvic fin 0.19–0.24 [0.21], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin distinctly emarginate, anteriormost branched rays about two and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.13 [0.12].



FIGURE 54.—*Steindachnerina pupula*, new species, MBUCV V-19300, 77.1 mm SL, holotype; Venezuela, Guarico, small caño on north shore of Río Orinoco, draining into Río Orinoco, 1 km upstream of mouth of Río Zuata.

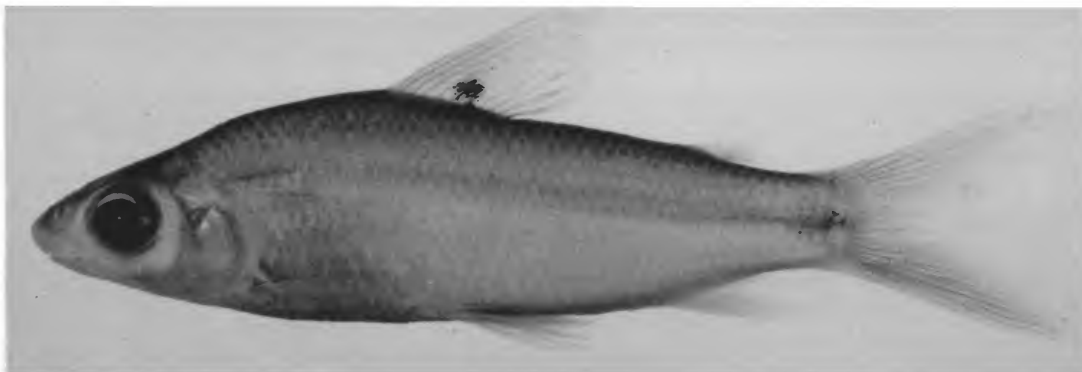


FIGURE 55.—*Steindachnerina pupula*, new species, USNM 258081, 52.2 mm SL, paratype; Venezuela, Guarico, Fundo Pecuario Masaguaral, Río Coracol.



FIGURE 56.—*Steindachnerina pupula*, new species, USNM 258008, 99.3 mm SL, paratype; Venezuela, Guarico, Fundo Pecuario Masaguaral, Laguna Los Guacimos.

Head obtusely pointed in profile, head length 0.28–0.31 [0.29]; mouth distinctly inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.29–0.34 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture partially closed by thin flap of skin separating nares; orbital diameter 0.29–0.34 [0.31]; adipose eyelid present, particularly well developed anteriorly, with broad, vertically ovoid opening over center of eye; length of postorbital portion of head 0.38–0.43 [0.38]; gape width 0.28–0.34 [0.32]; interorbital width 0.38–0.44 [0.41].

Pored lateral-line scales to hypural joint 42 to 46 [44]; all scales of lateral line pored, canals in scales straight; 4 to 6 series of scales extend beyond hypural joint onto caudal-fin base; $7\frac{1}{2}$ to 9 [$8\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; 6 or $6\frac{1}{2}$ [$6\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 14 to 16 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 33 (8), 34 (33).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales, silvery, darker on dorsal portions of head and body. Overall coloration of specimens lacking guanine on scales tan to tan-brown, darker on dorsal portions of head and body. Scales situated dorsal of lateral line with diffuse patches of small, dark chromatophores, pigmentation more dense proximate to dorsal midline. Specimens collected in whitewaters with dark pigmentation on body and dorsal fin less pronounced. Deep-lying band of dusky pigmentation extends from rear of supracleithrum to rear of caudal peduncle. Some

specimens with diffuse horizontally elongate patch of faint, dark pigmentation on midlateral surface of caudal peduncle (Figures 54, 55).

Dorsal fin typically with discrete patch of dark pigmentation on basal portion of middle rays of dorsal fin (Figures 54, 55), spot most frequently quite dark, but sometimes faint as in specimens known to be collected in whitewaters (Figure 56). Dorsal fin dusky anteriorly and distally. Lower lobe of caudal fin dusky, remainder of fin with scattered dark chromatophores. Anal and paired fins hyaline.

DISTRIBUTION.—Río Orinoco basin in both Venezuela and Colombia (Figure 57).

ETYMOLOGY.—The specific name, *pupula*, from the Latin for pupil of the eye, refers to the dark, pupil-like spot at the base of the dorsal fin that is characteristic for the species.

COMPARISONS.—*Steindachnerina pupula* is most similar to and most likely to be confused with *S. dobula*, a species occurring along the Amazonian Andean piedmont in Colombia, Peru, and Bolivia. *Steindachnerina pupula* is distinguished from *S. dobula* by the presence of $7\frac{1}{2}$ to 9, most frequently 8 or $8\frac{1}{2}$ scales in transverse series from origin of dorsal fin to lateral line, contrary to $6\frac{1}{2}$ to $7\frac{1}{2}$ scales in that series in *S. dobula*; by the presence of a very dark spot on the basal portions of the middle dorsal-fin rays, contrary to the lack of any pigmentation or rarely some very faint dorsal-fin pigmentation in *S. dobula*; and by the lack of pigmentation on the midlateral surface of the caudal peduncle in *S. pupula*, contrary to the faint to intense pigmentation in that region in *S. dobula*.

Three other species of *Steindachnerina* occur within the known range of *S. pupula*. Two of these, *S. bimaculata* and *S. argentea*, lack the lobulate fleshy processes on the roof the oral cavity found in *S. pupula*. *Steindachnerina pupula* is readily

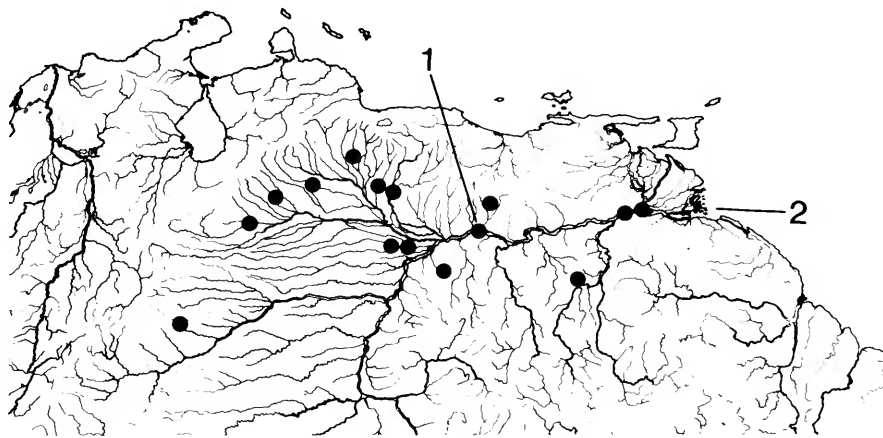


FIGURE 57.—Map of Río Orinoco basin and proximate areas showing geographic distribution of *Steindachnerina pupula* (1 = holotype locality; 2 = mouth of Río Orinoco) (some symbols represent more than one locality and/or lot of specimens).

distinguished from the third congener in the basin, *S. guentheri*, by overall body form, pigmentation, and various meristic features.

TYPE MATERIAL.—17 specimens (17, 48.3–99.3).

HOLOTYPE.—VENEZUELA. *Guarico*: Small caño on north shore of Río Orinoco, draining into Río Orinoco approximately 1 km upstream of mouth of Río Zuata, MBUCV V-19300, 1 (77.1).

PARATYPES.—VENEZUELA. *Guarico*: collected with holotype, USNM 302170, 1 (60.7). Laguna Los Guácimos, Fundo Pecuario Masaguaral (~08°34'N, 67°35'W), R.P. Vari et al., 19 Jan 1983, USNM 258008, 2 (97.8–99.3). Fundo Pecuario Masaguaral, Río Coracol, where crossed by bridge (~08°34'N, 67°30'W), R.P. Vari et al., 19 Jan 1983, USNM 258081, 3 (52.2–56.0). Caño near "El Estacion Campo El Salado, Universidad Simon Rodriguez," approximately 65 km S of Santa Maria de Ipire, F. Mago-Leccia et al., MBUCV V-19301, 4 (85.3–97.7). Río Portuguesa, near confluence with Río Apure, H. Mendoza et al., 9 May 1975, MBUCV V-8942, 1 (63.7). *Portuguesa*: Lagoon on right bank of Río Portuguesa, above Nueva Florida (~08°57'N, 69°01'W), L. Aguana, et al., MBUCV V-19302, 1 (79.7). *Bolivar*: La Paragua (06°50'N, 63°20'W), F. Mago-Leccia, 5–8 Oct 1966, MBUCV V-13489, 2 (50.7–54.4). *Territorio Federal Delta Amacuro*: Lagoon on north side of Río Orinoco, opposite Isla Tres Caños, west of Caño Araguaíto (08°40'30"N, 61°58'30"W), E. Marsh et al., 13 Nov 1979, USNM 235462, 2 (48.3–53.5).

The following 65 nontype specimens were also examined.

VENEZUELA. *Apure*: Caño Los Zorros and beaches, near Boquerones. MBUCV V-633, 1 (63.0). Río Apure, in front of its junction with Río Portuguesa, San Fernando de Apure, MBUCV V-9343, 1 (66.2). Mouth of Río Apurito, San Fernando de Apure, MBUCV V-9063, 6 (65.9–99.8). Río Apure, west of San Fernando de Apure, USNM 258218, 1 (62.4). Río Cunaviche, at Cunaviche (~07°24'N, 67°27'W), USNM 257556, 3. *Codegas*: Río Tinaco, below bridge on road from Tinaco to Pao, Río Portuguesa system, MAC 68530, 3 (now deposited at MBUCV). *Bolivar*: Lagoon on south side of Isla Isabella, USNM 235449, 2 (50.9–51.2). Mouth of Río Paraguazu, Río Cuchivero-Chivapuri system, MBUCV V-60104, 2 (72.0–73.4, formerly MAC 69104). *Barinas*: Río Las Palmas, USNM 194177, 3 (1, 68.1); MBUCV V-19304, 1. Río Michay, Río Suripa system, MAC 68095, 1 (now deposited at MBUCV). *Guarico*: Río Tizando, at bridge along highway from Tinaco to Don Caminto, MBUCV V-7105, 1 (100.1). Río Tinaco, below bridge along road from Tinaco to Pao, MBUCV V-19035, 3.

COLOMBIA. *Meta*: Río Meta system, ox-bow lake connected with Río Negro, approximately 500 m S of La Balsa, NRM SIL/1988021.3187, 2. Río Meta system, Río Negro where crossed by road from Villavicencio to Puerto Lopez at La Balsa, NRM SIL/1988021.3131, 3; NRM SIL/1988026.3132, 32.

Steindachnerina amazonica (Steindachner, 1911)

FIGURES 58–60

Curimatus elegans var. *amazonica* Steindachner, 1911:330 [type-locality: Brazil: Rio Tocantins].—Vari, 1989a, tables 2,3 [assignment to *Steindachnerina*].

Curimatus elegans amazonicus.—Fernández-Yépez, 1948:73 [reference].

Curimata elegans amazonica.—Fowler, 1950:282 [literature compilation].

Pseudocurimata elegans amazonicus.—Fowler, 1975:372 [reference].

DIAGNOSIS.—The multiple series of lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened, prepelvic region of the body, presence of a dark spot on the basal portions of the middle rays of the dorsal fin, presence of a dark midlateral stripe on the body, and the possession of 36 to 41 lateral-line scales to the hypural joint, in combination, discriminate *Steindachnerina amazonica* from its congeners.

DESCRIPTION.—Body moderately elongate, somewhat compressed. Dorsal profile of head convex anteriorly, straight from vertical line through posterior nostril posteriorly to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened transversely proximate to pelvic-fin origin. Postpelvic region irregularly rounded.

Greatest depth of body 0.32–0.35 [0.32]; snout tip to origin of dorsal fin 0.47–0.53 [0.47]; snout tip to origin of anal fin 0.83–0.88 [0.84]; snout tip to insertion of pelvic fin 0.52–0.58 [0.52]; snout tip to anus 0.78–0.83 [0.78]; origin of dorsal fin to hypural joint 0.53–0.58 [0.56]. Dorsal-fin margin emarginate, more so in larger individuals in which anterior rays are somewhat lengthened; anteriormost rays two to two and three-quarters times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.18–0.23 [0.18], extends about two-thirds distance to vertical line through insertion of pelvic fin. Pelvic-fin margin pointed, length of pelvic fin 0.19–0.22 [0.22], reaches two-thirds to three-quarters distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays about two and one-half times length of ultimate ray. Caudal peduncle depth 0.12–0.14 [0.12].

Head obliquely pointed in profile, head length 0.26–0.30 [0.28]; upper jaw distinctly longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.29–0.31 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.33 [0.28]; adipose eyelid present, more developed anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion

of head 0.42–0.46 [0.45]; gape width 0.23–0.26 [0.26]; interorbital width 0.38–0.44 [0.38].

Pored lateral-line scales to hypural joint 36 to 41 [40]; all scales of lateral line pored, canals in lateral-line scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$6\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or ii,10, or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 13 or 14 [13]; pelvic-fin rays i,8 [i,8].

Total vertebrae 31 (1), 32 (7), 33 (2) [33].

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery, darker on dorsal portions of head and body. An indistinct dark band extends along lateral line; band more prominent and wider posteriorly (Figure 58). Ground coloration of specimens lacking guanine on scales tan,

darker dorsally (Figure 59). Dorsal midline with narrow stripe of dark pigmentation extending from rear of head to dorsal fin, and from rear of dorsal fin to adipose fin. Lateral line with series of spots of dark pigmentation along scales; spots merge posteriorly into midlateral longitudinal stripe; stripe wider posteriorly. Stripe terminates on caudal peduncle in smaller individuals, extends onto basal portion of middle rays of caudal fin in some larger specimens. Dorsal fin with patch of dark pigmentation on basal portion of membranes between branched rays three and five. Patch most intense in smaller individuals (Figure 59), less apparent in larger specimens examined (Figure 58). Difference possibly a consequence of differing lengths of time various specimens have been in preservative, but paralleling ontogenetic shift found in other species of *Steindachnerina*. Remainder of dorsal fin together with anal and caudal fins ranging from hyaline to dusky in various specimens. Some larger specimens with stripe of dark pigmentation on middle rays of caudal fin, stripe more

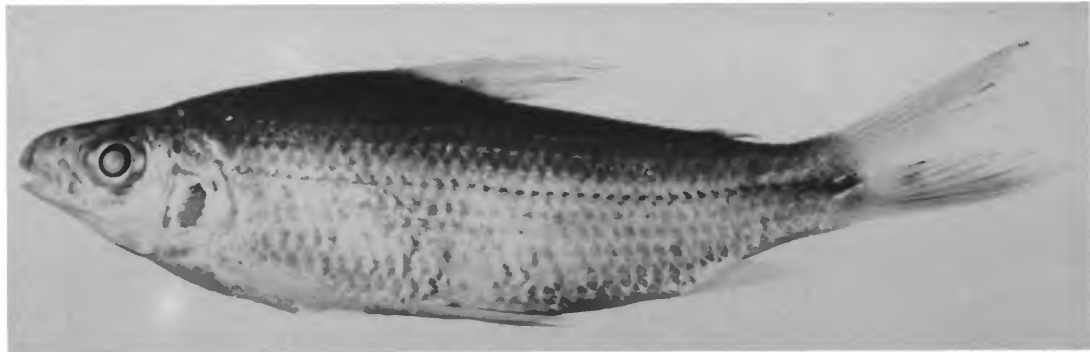


FIGURE 58.—*Steindachnerina amazonica*, NMW 66988, 98.9 mm SL, lectotype of *Curimatus elegans* var. *amazonica*; Brazil, Rio Tocantins.



FIGURE 59.—*Steindachnerina amazonica*, MNRJ 11209, 48.3 mm SL, juvenile; Brazil, Goiás, Rio Cangalha, tributary of Rio Paraná of Rio Tocantins system, Município de Formosa.

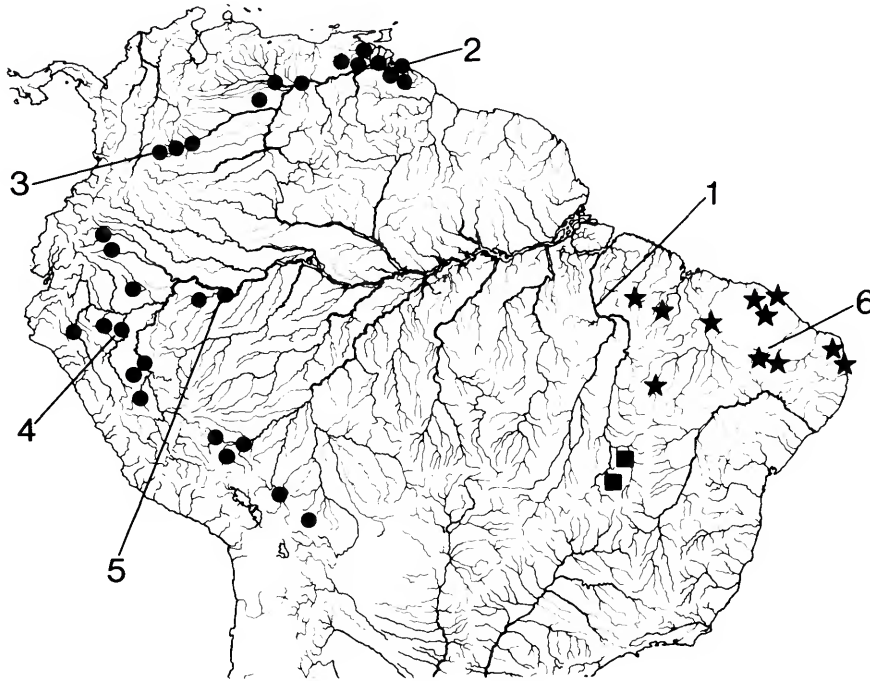


FIGURE 60.—Map of South America showing geographic distribution of *Steindachnerina amazonica* (squares; 1 = Rio Tocantins, approximate type locality of *Curimatus elegans* var. *amazonica*), *Steindachnerina guentheri* (dots; 2 = type localities of *Curimatus morawhannae* and *Curimatus issororoënsis*; 3 = type locality of *Curimatus metae*; 4 = type locality of *Curimatus robustula*; 5 = type locality of *Curimatus güntheri*), and *Steindachnerina notonota* (stars; 6 = type locality of *Curimatus notonotus*) (some symbols represent more than one collecting locality and/or lot of specimens).

prominent anteriorly. Paired fins hyaline.

DISTRIBUTION.—Rio Tocantins basin of eastern Brazil (Figure 60).

COMPARISONS.—*Steindachnerina amazonica* is the only member of the genus known from the Rio Tocantins basin. The southern tributaries of that system approximate the northern portions of upper Rio Paraná that has an endemic *Steindachnerina* species, *S. insculpta*, in its fauna. The upper reaches of the eastern tributaries of the Tocantins, in turn, lie close to the known range of *S. notonota*. *Steindachnerina amazonica* differs from both of those species in the possession of a distinct spot of dark pigmentation on the basal portions of the middle rays of the dorsal fin, whereas such pigmentation is absent in the other two forms.

REMARKS.—Steindachner's original description of *Curimatus elegans* var. *amazonica* was based on three specimens captured by Dr. Lisboa at an unstated locality in the Rio Tocantins. Only two of the syntypes (NMW 66988, 66992) were located during repeated searches of the collections of the Naturhistorisches Museum Wien. The larger syntype, which is also in the best overall condition (NMW 66988, 98.9 mm SL),

is designated as the lectotype (Figure 58). The other syntype (NMW 66992) becomes a paralectotype.

Steindachner considered *Curimatus elegans* var. *amazonica* as a variety of *Curimatus* (= *Steindachnerina*) *elegans*, which he had previously (1874) described from the Rio Jequitinhonha basin of coastal of eastern Brazil. He distinguished his variety from typical *Curimatus elegans* on the basis of various features of squamation, but did not discuss the reasoning behind retaining it as a variety rather than recognizing it as a different species. *Steindachnerina amazonica* differs from *S. elegans* in various meristic characters and morphometric features and is herein recognized as a distinct species.

MATERIAL EXAMINED.—12 specimens (12, 48.3–98.9).

BRAZIL. Rio Tocantins, NMW 66988, 1 (98.9, lectotype of *Curimatus elegans* var. *amazonica*); NMW 66992, 1 (92.9, paralectotype of *Curimatus elegans* var. *amazonica*). Goiás: Rio Cangalha, tributary to Rio Paraná, Município de Formosa (15°24'52"S, 47°17'23"W), MNRJ 11209, 1 (48.3). Salobro "Brook" into upper Rio Maranhão near Agua Doce, CAS 41728, 5 (60.8–72.3). Rio Paina, upper Rio Maranhão system, USNM 298161, 4 (61.0–74.3).

Steindachnerina guentheri
(Eigenmann and Eigenmann, 1889)

FIGURES 60–66, TABLE 7

- Curimatus guentheri* Eigenmann and Eigenmann, 1889:423 [type-locality: Brazil, Tabatinga].—1891:47 [reference].—Eigenmann, 1910:421 [reference].—[not Ulrey, 1895:259, see “Remarks”].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus morawhannae* Eigenmann, 1912a:266, pl. 34, fig. 3 [type-locality: British Guiana (= Guyana), Morawhanna].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus issororoënsis* Eigenmann, 1912a:266, pl. 34, fig. 4 [type-locality: British Guiana (= Guyana), Issororo Rubber Plantation].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus metae* Eigenmann, 1922:230, pl. 17, fig. 1 [type-locality: Colombia, Villavicencio, Quebrada Cramalote].—1922b:168 [based on Eigenmann, 1922a].—Myers, 1932:137 [Colombia, upper Río Meta basin, Río Upia, Guaicaramo].—Fernández-Yépez, 1948:73 [as a possible species of *Pseudocurimata*].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimatus elegans nitens*.—Pearson, 1924:28 [Bolivia, Huachi].
- Curimata guentheri*.—Fowler, 1940b:67 [Bolivia, Todos Santos].
- Curimata robustula* Allen (in Eigenmann and Allen), 1942:298 [type-locality: Peru, Yurimaguas].—Fowler, 1945:116 [based on Allen, 1942].—1950:290 [literature compilation].—Géry, 1972a:100 [Río Napo].—Lüling, 1981:72 [Peru, Pucallpa].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
- Curimata guentheri*.—Fowler, 1943c:2 [Bolivia, Todos Santos].—1950:285 [literature compilation].
- Curimata metae*.—Fowler, 1943:223 [Colombia: Villavicencio].—Géry, 1964:66, fig. 17 [Peru, Iquitos region].
- Pseudocurimata morawhannae*.—Fernández-Yépez, 1948:46 [assignment to *Pseudocurimata*].—Fowler, 1975:373 [reference].
- Pseudocurimata guentheri*.—Fernández-Yépez, 1948:46 [reference].
- Cruxentina issororoënsis*.—Fernández-Yépez, 1948:53 [assignment to *Cruxentina*].—Fowler, 1975:368 [reference].
- Rivasella robustula*.—Fernández-Yépez, 1948:56, fig. 29 [assignment to *Rivasella*].—Böhlke, 1958:106, pl. 7, fig. 1 [Ecuador, Río Villano].—Ovchynnyk, 1968:251 [Ecuador].—Géry, 1972a:99 [Ecuador, Río Napo, near Puerto Napo].—Fowler, 1975:374 [reference].
- Pseudocurimata guentheri*.—Fowler, 1975:372 [reference].
- Pseudocurimata metae*.—Fowler, 1975:373 [reference].

Steindachnerina robustula.—Stewart, et al., 1987:24 [eastern Ecuador, Río Napo drainage system].

DIAGNOSIS.—The numerous lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened, prepelvic region of the body, presence of a dark spot of pigmentation on the basal portion of the middle rays of the dorsal fin, possession of 30 to 36 scales along the lateral line to the hypural joint, and the presence of a dark midlateral stripe on the posterior half of body expanded in adults into a lozenge-shaped patch, in combination, discriminate *Steindachnerina guentheri* from its congeners (see also “Comparisons” below).

DESCRIPTION.—Body moderately elongate, somewhat compressed. Dorsal profile of head convex anteriorly, straight or very slightly convex from vertical line through anterior nostril to rear of head. Dorsal profile of body smoothly curved from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle, more convex in larger specimens, particularly ripe females. Prepelvic region obtusely flattened posteriorly, with irregular median series posteriorly. Postpelvic region irregularly rounded transversely.

Greatest depth of body 0.32–0.40 [0.36]; snout tip to origin of dorsal fin 0.47–0.53 [0.50]; snout tip to origin of anal fin 0.81–0.89 [0.86]; snout tip to insertion of pelvic fin 0.50–0.57 [0.53]; snout tip to anus 0.75–0.83 [0.81]; origin of rayed dorsal fin to hypural joint 0.54–0.60 [0.56]. Posterior margin of dorsal fin straight or slightly emarginate; anteriormost rays two and one-half to three and one-half times length of ultimate ray. Pectoral fin obtusely pointed; length of pectoral fin 0.18–0.25, extends nearly to vertical line through insertion of pelvic fin. Pelvic fin pointed, length of pelvic fin 0.22–0.28 [0.25],



FIGURE 61.—*Steindachnerina guentheri*, MCZ 20245, 57.1 mm SL, holotype of *Curimatus guentheri*; Brazil, Amazonas, Tabatinga.

reaches about three-quarters distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays about three times length of ultimate ray. Caudal peduncle depth 0.13–0.15 [0.13].

Head obtusely pointed in profile, head length 0.26–0.33 [0.29]; upper jaw slightly longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.26–0.31 [0.30]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed somewhat by thin flap of skin separating nares; orbital diameter 0.25–0.32 [0.31]; adipose eyelid present, but not highly developed, with vertically ovoid opening over center of eye; length of postorbital portion of head 0.39–0.47 [0.43]; gape width 0.26–0.32 [0.27]; interorbital width 0.40–0.46 [0.41].

Pored lateral-line scales to hypural joint 30 to 36 [34]; all scales of lateral line pored, canals in scales of lateral line

straight; 2 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$5\frac{1}{2}$?] scales in transverse series from origin of rayed dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [5 ?] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [ii,9]; anal-fin rays ii,7 or ii,8, or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 13 to 15 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 31 (9), 32 (34), 33 (45), 34 (3).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery, somewhat purplish on dorsal portions of head and body. Specimens lacking guanine on scales yellowish, with progressively more-developed fields of dark chromatophores on scale rows of dorsal portion of body. Dorsal portions of head and regions of body adjacent to mid-dorsal line darkest. Pattern of pigmentation on midlateral surface of posterior portion of body variably developed; ranging from irregular horizontal stripe in some specimens

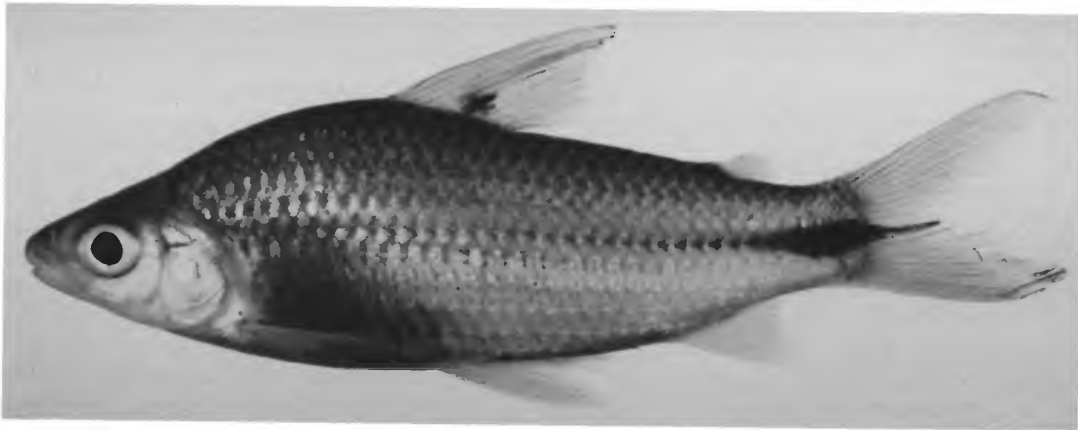


FIGURE 62.—*Steindachnerina guentheri*, USNM 298034, 77.4 mm SL; Peru, Ucayali, Pucallpa, Río Neshuya 60 km W of Pucallpa along Pucallpa to Huanuco highway.

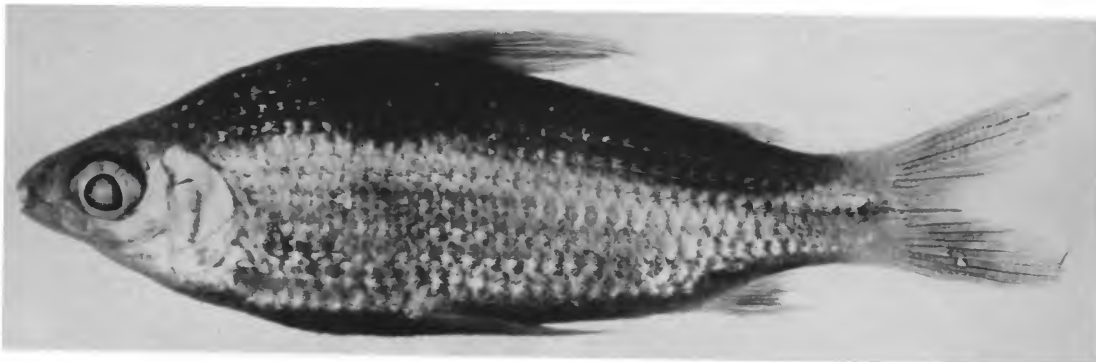


FIGURE 63.—*Steindachnerina guentheri*, FMNH 53650 (formerly CM 2122), 61.9 mm SL, holotype of *Curimatus morawhannae*; Guyana, Essequibo, Morawhanna.

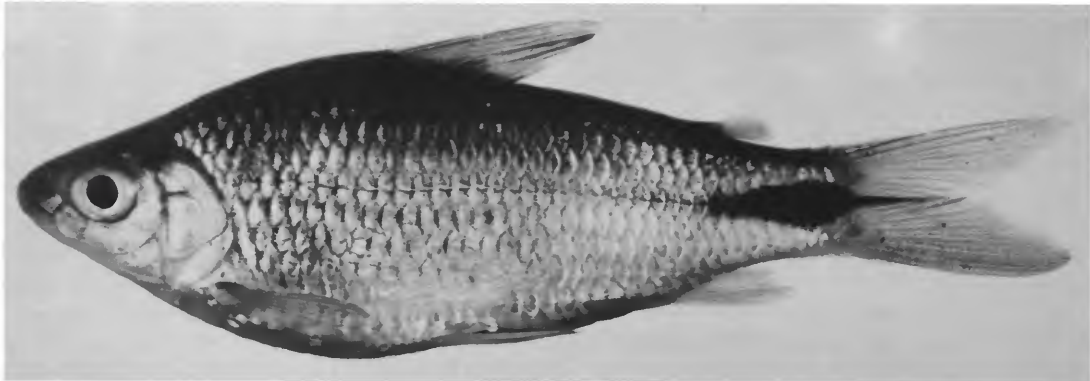


FIGURE 64.—*Steindachnerina guentheri*, USNM 298035, 71.8 mm SL; Peru, Huanuco, Río Pachitea basin, Río Yamushimas.

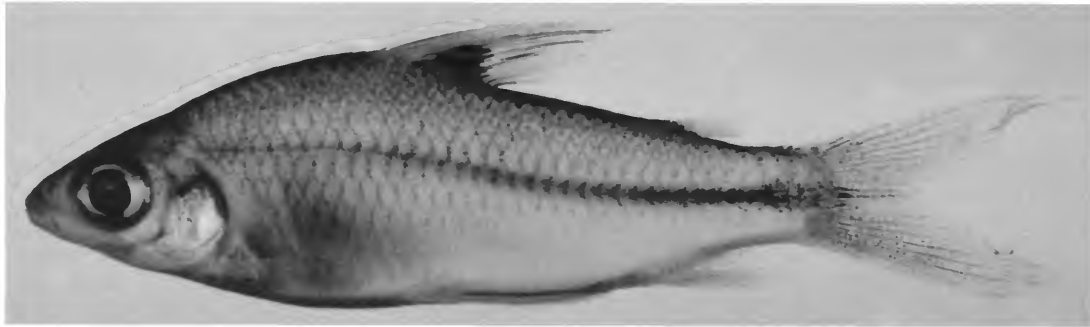


FIGURE 65.—*Steindachnerina guentheri*, NRM SOK/1984305.4043, 37.9 mm SL; Peru, Loreto, Río Yavari system, Colonia Angamos.

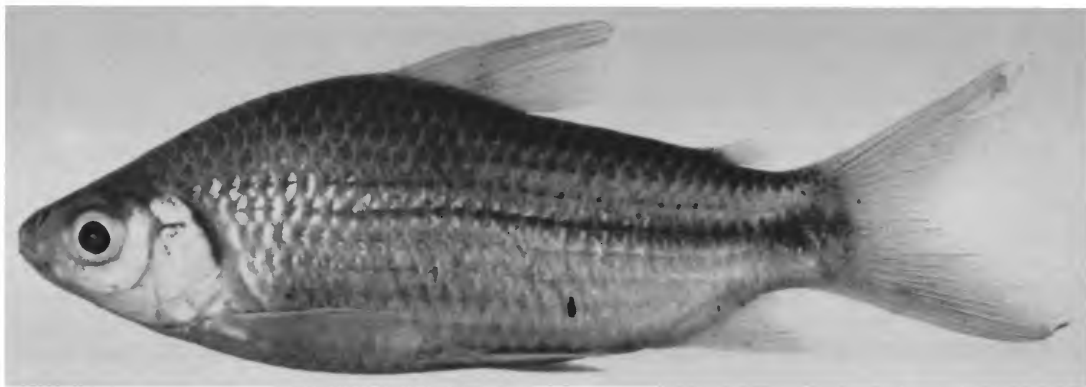


FIGURE 66.—*Steindachnerina guentheri*, USNM 263978, 89.4 mm SL; Peru, Madre de Dios, Río Tambopata system.

(e.g., Figures 63, 66), through diffuse spot (e.g., Figure 65), to very dark, wide, lanceolate patch in some individuals (e.g.,

Figures 62, 64). Degree of development and intensity of pigmentation variable ontogenetically, geographically, and

within populations (see also "Variation" below). Pigmentation most intense overall in individuals along western rim of Amazon basin. Within any population midlateral pigmentation typically most highly developed in larger individuals, although not invariably. Dark pigmentation of caudal peduncle extending somewhat onto base of caudal fin and middle caudal-fin rays; sometimes continuing anteriorly as thin line along lateral line to below dorsal fin, more so in individuals with darker overall coloration.

Dorsal fin with patch of dark pigmentation on basal portions of middle fin-rays. Spot more discrete and relatively darker in smaller specimens of any population (Figure 65); less obvious in larger specimens, particularly those from eastern limits of species range. Remainder of dorsal fin, caudal and anal fins hyaline to dusky, dark pigmentation on fins more developed in specimens with overall darker coloration. Pectoral and pelvic fins ranging from hyaline to slightly dusky; intensity of fin duskiness again correlated with that of overall pigmentation.

VARIATION.—*Steindachnerina guentheri* demonstrates a notable degree of ontogenetic and geographic intraspecific variation in the intensity of the dark pigmentation on the midlateral surface of the caudal peduncle, and of the dark spot situated on the basal portions of the middle rays of the dorsal fin. Within populations the spot of dark pigmentation on the dorsal fin is often notably darker in smaller individuals. Specimens of the species from the eastern portions of the Río Orinoco system, the delta of that river system, and the associated drainages of northwestern Guyana (the type localities of *C. morawhannae* (Figure 63) and *C. issororoënsis*) tend to have less intensely developed midlateral caudal peduncle pigmentation that often takes the form of an irregular midlateral stripe. Nonetheless, at least some of the specimens from Guyana and eastern Venezuela have obvious to well-developed, relatively wide, posterior midlateral bands. Furthermore, a continuum exists in the intensity and width of the band in the more extensive series of specimens from the central portions of the Río Orinoco system. The more highly developed forms of the pigmentation in those Venezuelan samples is, in turn, comparable to that most common in Colombian, Peruvian, and Bolivian populations of *S. guentheri*, which usually have dark, broad midlateral patches on the caudal peduncle (Figures 62, 64). As a consequence, the variation in these details of pigmentation does not serve to subdivide *S. guentheri* of this study into more than one species.

COMPARISONS.—*Steindachnerina guentheri* is most similar to and most likely to be confused with *S. notonota* endemic to the rivers of northeastern Brazil, all of which lie a considerable distance to the south of the known distribution of *S. guentheri* (see also comments on latter topic under "Distribution" below). The two species differ in various details of pigmentation. Most notable of these is the expansion of the midlateral stripe on the caudal peduncle into a prominent lozenge-shaped patch in *S. guentheri*. The midlateral stripe in that region in *S. notonota* is not well developed or only very faint at its maximum degree of

development. The species also differ in body form.

DISTRIBUTION.—Rivers of northwestern tip of Guyana, Río Orinoco basin, foothill rivers of western portion of Amazon basin in Colombia, Brazil, Ecuador, Peru, and northern Bolivia (Figure 60). The limited ichthyological collecting that has been carried out to the south of the known range of *Steindachnerina guentheri* in Bolivia makes it difficult to determine even the general limits of the distribution of the species in that section of the continent. We can be somewhat more certain of the limits of the range of the species in northeastern South America. Although the freshwater fish fauna of Guyana has not been exhaustively collected, the relatively inclusive collecting efforts in the other river systems of Guyana, most notably the Essequibo system, have not revealed specimens of *Steindachnerina guentheri*, or indeed of any member of the genus. The known distribution of *S. guentheri* in Guyana is limited to a few small rivers whose mouths are associated with the delta of the Río Orinoco. These drainages are, in contrast, quite separate from the major independent river systems in Guyana lying further to the south.

REMARKS.—*Steindachnerina guentheri* has been repeatedly described from diverse areas within its known range. That situation perhaps came about due to the previously limited available population samples of the species, a problem compounded by a marked degree of variation in the development of the dark pigmentation on the basal portions of the dorsal fin and on the midlateral surface of the caudal peduncle. Recognition of the species was also complicated by the incomplete description of the pigmentation in the original species description. Eigenmann and Eigenmann (1889:423) note that the holotype, the only specimen available to them, had "a conspicuous dark brown spot at base of middle dorsal rays." That spot of pigmentation is still obvious, although faded in the holotype. The holotype also retains traces of a distinct, albeit very faded, patch of dark pigmentation on the midlateral surface of the caudal peduncle (Figure 61). No comment was made on that pigmentation by the Eigenmanns, a situation that complicated subsequent attempts at recognition of the species.

Subsequent to the original description of *Steindachnerina guentheri* there were only two reports of the species based on additional specimens. Ulrey (1895:259) reports *Curimatus güntneri* from "Braret, two specimen; Brazil, one specimen." The specimens were part of a collection made by C.F. Hartt in Brazil. Ulrey (1895:258) notes "The name Braret occurs on many labels; so far I have not been able to determine whether it is a locality or the name of a collector." I have been similarly unable to resolve this question. The portions of the Hartt collection with specific collection localities all originated in the eastern portions of the Amazon basin, distant from the known range for *Steindachnerina guentheri*. Thus, it appears likely that the Ulrey record represents a misidentification. Fowler's record (1940b:67) and its subsequent reiteration (1943c:2), in contrast, are based on specimens of *S. guentheri* (ANSP 68911-14).

Eigenmann (1912a:266) described two nominal forms, *Curimatus morawhannae* and *C. issororoënsis*, from the northwestern portion of British Guiana (= Guyana). In the brief description of *Curimatus morawhannae* he suggests that it is "very similar to *C. microcephalus*." He also notes that *C. morawhannae* is characterized by "numerous conspicuous flaps, lobes and papillae" on the roof of the mouth. Such elaborations are also present in *C. issororoënsis*. The described structures, an elaborate form of the anterior portion of the buccopharyngeal complex, characterize a subunit of *Steindachnerina* but are lacking in *Curimatus microcephalus* Eigenmann and Eigenmann with which Eigenmann compared *C. morawhannae*. *Curimatus microcephalus* was assigned by Vari (1989a) to *Cyphocharax*, a genus with a simpler type of buccopharyngeal complex. The only feature cited by Eigenmann (1912a:263, 266) to discriminate *Curimatus morawhannae* from *C. issororoënsis* was the presence in the former species of a dark spot on the dorsal fin (Figure 63). A very faint dorsal-fin spot is, however, present in the holotype of *C. issororoënsis* (FMNH 53647) and that pigmentation is much more obvious in the two paratypes of the species (FMNH 53661, formerly CM 2123; CAS 60625, formerly IU 12301). The purported difference in the pigmentation of the dorsal fin between the nominal forms cited by Eigenmann thus fails to separate the nominal species. A comparison of those two nominal forms with *Steindachnerina guentheri* fails to reveal any differences between the species in examined meristics, morphometrics, or other features (Table 7) and *Curimatus morawhannae* and *C. issororoënsis* are placed into the synonymy of *Steindachnerina guentheri*.

The paratype series of *Curimatus morawhannae* is complex. The majority of the examined specimens are *Steindachnerina guentheri*, but three specimen from Morawhanna (FMNH 53649, in part, formerly CM 2121) are equivalent to the specimens from Guyana that Eigenmann (1912a) identified as *Curimatus microcephalus*. There is also a problem with the reported number of paratypes of *Curimatus morawhannae*. Eigenmann (1912a:266) designated three specimens collected at Mora Passage as "cotypes" (= paratypes). Four specimens from that locality identified as paratypes have been located in various repositories (USNM 66142, 2 specimens; BMNH 1917.11.2:7, 1 specimen; CAS 44222, formerly IU 12302, 1 specimen). I have been unable to determine the source of the discrepancy in the number of specimens.

Eigenmann (1922:230) described *Curimatus metae* from a series of specimens collected in the Río Meta system of the western portion of the Llanos in Colombia. In his brief original description, he compared his species with *Curimatus* (= *Steindachnerina*) *argenteus*, another species widely distributed through the Río Orinoco basin, but did not discriminate his new form from other species of curimatids. *Curimatus metae* agrees with *Steindachnerina guentheri* in examined meristics, morphometrics, and pigmentation features

(Table 7) along with other examined characters. The species, therefore, are considered conspecific. As discussed under "Variation" the pigmentation patch on the midlateral surface of the caudal peduncle shows a notable degree of variation in intensity within *Steindachnerina guentheri*. That pigmentation is particularly intense in the type series of *C. metae*, contrary to the situation in the type-specimens of *C. morawhannae* and *C. issororoënsis*. These differences may have lead Eigenmann to consider *C. metae* as a new species.

In his description of *Curimata robustula*, Allen (in Eigenmann and Allen, 1942:298) compared his species to *C. elegans*, another member of *Steindachnerina* that is, however, limited to the Atlantic coastal drainages of Brazil. The type series of *Curimata robustula* is not distinguishable from *Steindachnerina guentheri* in examined features (Table 7) and the species are herein considered conspecific. Allen did not designate a holotype for *Curimata robustula*, rather simply listing eight specimens (IU 15830) within the original description of the species. A 64.7 mm SL specimen (CAS 63052) is designated as the lectotype and the other seven syntypes (CAS 63053) become paralectotypes.

Pearson (1924:28) reports *Curimatus elegans nitens* (= *Curimatus nitens*) from Huachi, Bolivia, in the upper Rio Beni system. *Curimatus nitens*, herein considered a synonym of *Steindachnerina brevipinna*, is only known from the Río de La Plata system. Examination of a portion of the specimens cited by Pearson (UMMZ 66511, USNM 298160, both out of IU 17137) indicates they are individuals of *S. guentheri*.

MATERIAL EXAMINED.—355 specimens (142, 29.5–111.3).

GUYANA. *Essequibo*: Issororo Rubber Plantation, FMNH 53647, 1 (74.0, holotype of *Curimatus issororoënsis*, formerly CM 2119); FMNH 53651, 1 (69.1, paratype of *Curimatus issororoënsis*, formerly CM 2120); CAS 60625, 1 (73.5, paratype of *Curimatus issororoënsis*, formerly IU 12301). Morawhanna, FMNH 53650, 1 (61.9, holotype of *Curimatus morawhannae*, formerly CM 2122); FMNH 53649, 10 (30.3–61.7, paratypes of *Curimatus morawhannae*, formerly CM 2121 in part, see "Remarks"); SU-CAS 21901, 2 (32.5–35.9, paratypes of *Curimatus morawhannae*, formerly IU 12303); BMNH 1911.10.31:479, 1 (42.6, paratype of *Curimatus morawhannae*, formerly IU 12303). Mora Passage, USNM 66142, 2 (paratypes of *Curimatus morawhannae*); CAS 44222, 1 (32.1, paratype of *Curimatus morawhannae*, formerly IU 12302); BMNH 1917.11.2:7, 1 (43.9, paratype of *Curimatus morawhannae*). Middle Barama River, USNM 298094, 2 (1, 62.3). Watapoa, BMNH 1972.7.27:397-398, 2 (58.3–62.5). Aruau River, AMNH 14552, 2.

VENEZUELA. *Territorio Federal Delta Amacuro*: Small caño at mouth of Caño Fiscal (–08°32'N, 61°02'W), USNM 235494, 25 (15, 40.8–55.4). Caño Paloma system (–08°28'N, 61°25'36"W), USNM 235504, 32 (10, 30.6–40.7). Caño Aragua system (–08°38'N, 61°43'W), USNM 235512, 9. "Delta del Orinoco," MBUCV uncat., 4 (37.3–53.4; formerly MAC 67360). *Monagas*: Río Caripe, Chorreras near Caripito,

TABLE 7.—Morphometrics and meristics of (A) holotype of *Curimatus güntheri* (MCZ 20245), (B) holotype of *Curimatus morawhannae* (FMNH 53650, formerly CM 2122), (C) holotype of *Curimatus issororoënsis* (FMNH 53647, formerly CM 2119), (D) holotype of *Curimatus metae* (FMNH 55143, formerly CM 3844), (E) lectotype of *Curimata robustula* (CAS 63052, formerly IU 15830, in part), and (F) all specimens of *Steindachnerina guentheri* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 14 are proportions of head length. Question marks indicate values that could only be estimated as a consequence of condition of cited specimen. Dashes indicate values that could not be taken due to condition of specimen.

Character	A	B	C	D	E	F
MORPHOMETRICS						
Standard Length	57.1	61.9	74.0	93.3	64.5	30.3–111.3
1. Greatest body depth	0.36	0.37	0.38	0.35	0.35	0.32–0.40
2. Snout to dorsal-fin origin	0.50	0.48	0.49	0.47	0.49	0.47–0.53
3. Snout to anal-fin origin	0.86	0.82	0.85	0.82	0.82	0.81–0.89
4. Snout to pelvic-fin origin	0.53	0.53	0.52	0.51	0.51	0.50–0.57
5. Snout to anus	0.81	0.79	0.80	0.76	0.80	0.75–0.83
6. Origin of rayed dorsal fin to hypural joint	0.56	0.58	0.59	0.57	0.60	0.54–0.60
7. Pectoral-fin length	–	0.19	0.20	0.19	–	0.18–0.25
8. Pelvic-fin length	0.25	0.26	0.25	–	0.24	0.22–0.28
9. Caudal peduncle depth	0.13	0.14	0.14	0.13	0.13	0.13–0.15
10. Head length	0.29	0.29	0.27	0.26	0.28	0.26–0.33
11. Snout length	0.30	0.29	0.30	0.31	0.28	0.26–0.31
12. Orbital diameter	0.31	0.33	0.32	0.26	0.32	0.25–0.32
13. Postorbital length	0.43	0.41	0.42	0.45	0.45	0.39–0.47
14. Interorbital width	0.41	0.41	0.44	0.41	0.41	0.40–0.46
MERISTICS						
Lateral-line scales	34	33	32	34	33	30–36
Scale rows between dorsal-fin origin and lateral line	5 ^{1/2} ?	5 ^{1/2}	5 ^{1/2}	6	6	5 ^{1/2} –6 ^{1/2}
Scale rows between anal-fin origin and lateral line	5?	5	4 ^{1/2}	5	5	4 ^{1/2} –5 ^{1/2}
Branched dorsal-fin rays	9	9	9	9	9	9
Branched anal-fin rays	7	7	7	7	8	7–8
Total pectoral-fin rays	14	13	15	13	14	13–15
Branched pelvic-fin rays	8	8	8	8	8	8

MBUCV V-12402, 1 (68.3). Río Orinoco, Barrancas, Laguna El Guatero, USNM 235490, 13. Río Morichal Largo, El Silencio, below bridge from Maturin to Tremblador, MBUCV V-15259, 15. Río Morichal Largo, El Salto, MBUCV V-15260, 2. *Anzoátequi*: Río Urupia, Río Tigre basin, near San Tomé, USNM 298033, 6 (60.3–81.7). *Bolívar*: Laguna on south side of Isla Isabella (~08°18'43"N, 65°56'52"W), USNM 235478, 6. *Apure*: Caño León, 14 km S of El Piñal (San Camilo), MBUCV uncat., 11 (3, 80.0–87.9, formerly MAC 23-15). San Fernando de Apure, USNM 258091, 12.

COLOMBIA. *Meta*: Villavicencio, Quebrada Cramalote, FMNH 55143, 1 (93.3, holotype of *Curimatus metae*, formerly CM 3844); CAS 60585, 2 (50.9–89.8, paratypes of *Curimatus metae*, formerly IU 15023). Barrigón, USNM 83632, 9 (55.5–77.6, formerly IU 15022, in part); CAS 60586, 3 (81.5–111.3, formerly IU 15022, in part); USNM 298031, 6 (52.3–88.8, formerly IU 15022, in part). Río Ocoa, approxi-

mately 15 km E of Villavicencio, NRM SIL/1988014.3141, 14. Caño Union, tributary to Río Ocoa, where crossed by Villavicencio to Acacias Road, NRM SIL/1988013.319, 3. Laguna Santa Clara, Río Ocoa system, 5 km S of Villavicencio, NRM SIL/1988026.3134, 4. Río Upia, Guaricaramo, USNM 94284, 1 (82.0).

ECUADOR. *Napo*: Río Payamino at Puerto Coca, USNM 298157, 1 (49.0). *Pastaza*: Río Villano, Villano, USNM 164051, 2 (62.2–85.6).

PERU. *Loreto*: Yurimaguas, CAS 63052, 1 (64.7, lectotype of *Curimata robustula*, formerly IU 15830, in part); CAS 63053, 7 (49.0–67.4, paralectotypes of *Curimata robustula*, formerly IU 15830, in part). Río Ucayali system, Quebrada Carahuayate, km 20 along road from Jenaro Herrera to Colonia Angamos, NRM SOK/ 1983347.3733, 1 (80.7). Río Yavari system, Colonia Angamos, NRM SOK/1984305.4043, 1 (37.9). Río Corrientes system. Teniente Lopez, NRM SOK/

1986312.4689, 45. *Amazonas*: Río Kayamasa, 41 km upstream from Caterpiza, LACM 41856-3, 2 (1, 89.5). *Ucayali*: Quebrada Pecheria, IVITA station, 60 km from Pucallpa along Pucallpa to Huanuco road, USNM 261475, 1 (88.0). IVITA station, AMNH 35684, 1 (73.0); AMNH uncat, 1. Río Neshuyo, km 60 on Pucallpa to Huanuco Road, USNM 261409, 3 (63.1–78.6); USNM 298034, 3 (1, 77.4); USNM 298038, 4; USNM 298300, 5. Río Ucayali basin, stream on Pucallpa to Tournavista road, GC, 2 (1, 54.5). *Huanuco*: Quebrada Ayamira, Río Pachitea system, BMNH 1969.11.18:1, 1 (63.2); USNM 220347, 1 (29.5); USNM 204599, 1 (64.4). Río Pachitea system, pool 1 km upstream of Tournavista, NRM SOK/3460, 3 (2, 57.4–64.7). Río Yamushimas, Río Pachitea system, USNM 298035, 4 (48.4–78.4). *Cajamarca*: Río Marañón basin, tributary to Río Tabaconas, 52 km N of Jaen, ROM uncat., 2; ROM uncat., 5. *San Martín*: Moyabamba, Río Yuracyacu system, USNM 298156, 2; USNM 298036, 6. *Madre de Dios*: Río Tambopata system, Quebrada San Roque at km 11 on Puerto Maldonado to Cuzco road, NRM SOK/1983325.3736, 1 (75.7). Stream entering Río Tambopata 500 m downstream of Inn on Tambopata Reserve (–12°49'35"S, 69°17'30"W), USNM 263977, 5 (4, 65.0–86.9). Stream in Reserva Natural de Tambopata (–12°50'30"S, 69°17'30"W), USNM 263978, 4 (3, 80.5–89.7). Parque Nacional Manú, Pakitza, USNM 295254, 2. Río Madre de Dios, 10 km downstream of junction of Río Tambopata and Río Madre de Dios, USNM 263979, 4.

BRAZIL. *Amazonas*: Tabatinga, MCZ 20245, 1 (57.1, holotype of *Curimatus güntheri*).

BOLIVIA. *La Paz*: Huachi, junction of Río Bopi and Río Cochabamba, UMMZ 66511, 11 (48.5–73.4, formerly IU 17137, in part); USNM 298160, 4 (64.0–72.5, formerly IU 17137, in part). *Cochabamba*: Río Chapare, between Todos Santos and mouth, MZUSP 278221, 4 (2, 45.4–47.3). Río Chapare, above Todos Santos, GC, 1 (66.1). Río Chapare, Todos Santos, ANSP 68911-14, 5. Streams in region of Todos Santos, GC, 1 (51.3). Río Chapare, GC, 1 (75.7).

Steindachnerina notonota (Miranda-Ribeiro, 1937)

FIGURES 67–69, TABLE 8

Curimatus elegans.—Eigenmann and Eigenmann, 1889:421 [in part, Brazil, Rio Ipajica at Pernambuco].—Starks, 1913:14 [Brazil: Rio Grande do Norte, Lake Extremoz (= Lago Estremoz), Lake Papary (= Lagoa Papari), Ceara (= Ceará) Mirim].—Azevedo, 1938:51, 55 [feeding, reproductive biology].—Azevedo et al., 1938:481 [Brazil: Ceará, Fortaleza; common name, life history, anatomy, reproductive biology, development, sound production].—Azevedo and Vieira, 1939:3 [life history].

Curimatus notonotus Miranda-Ribeiro, 1937:55 [type-locality: Brazil, Ceará, Rio Granjeiro].—Miranda-Ribeiro, 1955:396 [lectotype designation].—Fernández-Yépez, 1948:73 [citation].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

Curimata elegans.—Fowler, 1941:164, figs. 75, 76 [Brazil: Ceará, Rio Jaguaribe, Russas and Oros; Rio Grande do Norte, Lago Papary (= Papari)].

Curimata elegans elegans.—Fowler, 1950:282, fig. 342 [references in part,

citations from Brazil: Pernambuco, Russas, Orós, Lago Papari]. *Pseudocurimata elegans elegans*.—de Godoy, 1987:168 [in part, Brazil, Pernambuco; not other cited localities].

DIAGNOSIS.—The numerous lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened, preopercular region of the body, presence of a dark spot of pigmentation on the basal portion of the middle rays of the dorsal fin, possession of 29 to 33 scales in the lateral line to the hypural joint, and the presence of a dark midlateral stripe typically of a uniform width on the posterior half of body in adults, in combination, discriminate *Steindachnerina notonota* from its congeners (see also "Comparisons" under *S. güntheri*).

DESCRIPTION.—Body moderately elongate in juveniles, deeper bodied in larger specimens, somewhat compressed in smaller individuals; more rotund in specimens over 40 mm SL. Dorsal profile of head convex anteriorly, straight or very slightly concave in region between vertical line through posterior nostril and rear of head. Dorsal profile of body smoothly convex from rear of head to origin of dorsal fin; straight or slightly convex, posteroventrally slanted at base of dorsal fin, straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel anterior to dorsal fin in juveniles, transversely rounded in larger specimens, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Preopercular region obtusely flattened, more so proximate to pelvic-fin insertion. Postopercular region irregularly rounded.

Greatest depth of body 0.35–0.41 [0.37]; snout tip to origin of dorsal fin 0.47–0.53 [0.51]; snout tip to origin of anal fin 0.82–0.88 [0.86]; snout tip to insertion of pelvic fin 0.53–0.58 [0.55]; snout tip to anus 0.78–0.84 [0.80]; origin of rayed dorsal fin to hypural joint 0.53–0.59 [0.57]. Dorsal-fin profile obtusely acute, dorsal margin nearly straight anteriorly, convex posteriorly; anteriormost rays two and three-quarters to three and one-quarter times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.20–0.25 [0.20], extends about two-thirds distance to vertical line through insertion of pelvic fin. Pelvic-fin profile acute; length of pelvic fin 0.22–0.27 [0.24], reaches three-quarters of distance to origin of anal fin in smaller individuals, slightly over one-half distance in larger specimens. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays twice length of ultimate ray. Caudal peduncle depth 0.14–0.15 (very rarely 0.13) [0.15].

Head obtusely pointed in profile, head length 0.27–0.33 [0.30]; jaws equal, mouth terminal; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.26–0.32 [0.28]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.35 [0.31]; adipose eyelid present, most developed anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.40–0.47

[0.45]; gape width 0.26–0.33 [0.30]; interorbital width 0.40–0.46 [0.41].

Pored lateral-line scales to hypural joint 29 to 33 [32]; all scales of lateral line pored, canals in scales of lateral line straight; 2 to 4 series of scales extend beyond hypural joint onto caudal-fin base; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [$4\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,8 or ii,9, or iii,9 (ii,8 very rare; when three unbranched rays present, first very short) [ii,9]; anal-fin rays ii,7 or iii,7 [ii,7]; pectoral-fin rays 13 to 16 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 31 (22), 32 (40).

COLOR IN ALCOHOL.—Overall color of specimens retaining

guanine on scales silvery to silvery purplish, darker on dorsal portions of head and body. Irregular, dark, midlateral line on body extends from region under dorsal fin posteriorly onto caudal peduncle. Line more obvious posteriorly; masked to varying degrees in different specimens by guanine on scales. Ground coloration in specimens lacking guanine on scales yellowish. Midlateral dark line more pronounced, having form of irregular spotting along lateral line on anterior half of body, spots larger in region under dorsal fin, gradually increasing in size and coalescing or nearly coalescing into irregular dark line along caudal peduncle (Figures 67, 68, 69). Dark pigmentation on caudal peduncle forming obscure horizontally elongate spot in larger specimens in some populations. Caudal peduncle pigmentation barely extending onto base of caudal fin. Dorsal



FIGURE 67.—*Steindachnerina notonota*, MNRJ 2611, 65.3 mm SL, lectotype of *Curimatus notonotus*; Brazil, Ceará, Rio Granjeiro.



FIGURE 68.—*Steindachnerina notonota*, MZUSP 5073, 70.2 mm SL; Brazil, Maranhão, Rio Corda, Barra do Corda.

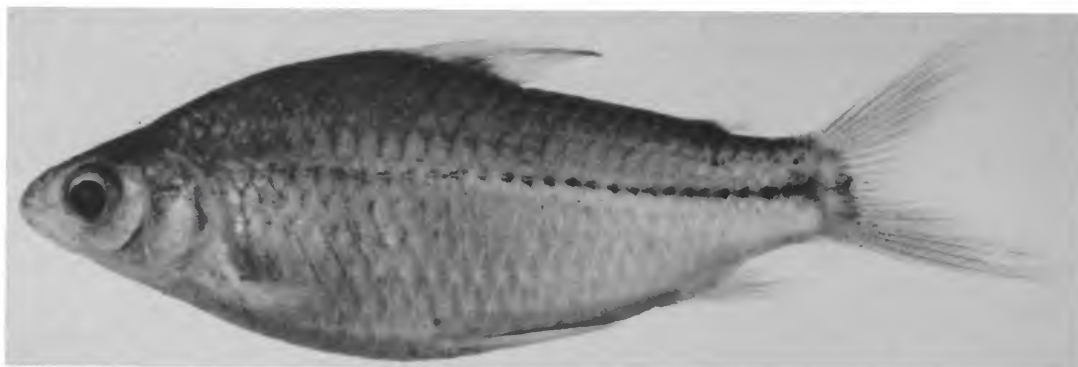


FIGURE 69.—*Steindachnerina notonota*, USNM 302059, 73.1 mm SL; Brazil, Ceará, Rio Jaguaribe.

fin with patch of dark pigmentation on base of middle rays. Pigmentation diffuse in smaller specimens, typically forming distinct dark spot in larger individuals (Figures 67, 69); but very faint in some individuals (Figure 68). Remainder of dorsal fin dusky. Caudal fin dusky to varying degrees, more so lower lobe. Anal and paired fins hyaline.

DISTRIBUTION.—Coastal rivers of northeastern Brazil (Figure 60). The exact limits of the distribution of *Steindachnerina notonota* are uncertain due to the limited available population samples of the species and the lack of comprehensive ichthyological collections within the general area of its known range. Material from the northern portions of the species range in the Brazilian state of Pará is practically nonexistent. Dr. Michael Goulding of the Museo Goeldi has collected extensive series of curimatids in the state of Amapá to the north of the lower reaches of the Rio Amazonas. No material of *S. notonota* occurs either among those specimens or in other collections from that region. It appears that the lower reaches of the Amazon may represent the northern limit of the distribution of the species. No comparable extensive collections exist from the region immediately to the south of the known distribution of *S. notonota*, and it is likely that the actual range of the species extends further south than presently known.

COMPARISONS.—The most similar species to *Steindachnerina notonota* is *S. guentheri*, a species with a range distinctly to the north and west of the known distribution of *S. notonota*. As noted in the "Key" and the "Comparisons" section under *S. guentheri*, the two species can be distinguished on the basis of details of body pigmentation. The distributions of *Steindachnerina amazonica* of the upper Rio Tocantins and *S. elegans* of the coastal rivers of the São Francisco system and the coastal rivers of Minas Gerais and Bahia most closely approach the known range of *S. notonota*. Those species are readily distinguished from *S. notonota* by a variety of meristic and morphometric features, along with details of pigmentation.

COMMON NAME.—Fortaleza, Rio Jaguaribe: piabussú; Pa-

raíba: saburú (Azevedo et al., 1938).

LIFE HISTORY AND ECOLOGY.—Azevedo et al. (1938) and Azevedo (1939) report that *Steindachnerina notonota* (identified by them as *Curimatus elegans*) feeds on organic components in the substrate detritus. Spawning migrations occur in large schools, with spawning taking place in shallow water among vegetation. Early larvae have an adhesive gland, small jaw, and pharyngeal teeth, and feed on plankton. The adhesive gland and all teeth are lost at the time that the larvae switch to their adult detritivorous diets. The authors also provide details of artificially induced spawning in the species and additional information on development of various body systems.

REMARKS.—Authors commencing with Eigenmann and Eigenmann (1889) have typically identified the specimens of *Steindachnerina* from the drainage systems in the region of Brazil from Rio Grande do Norte to Ceará as *Curimatus elegans*, a species described by Steindachner from the Rio Jequitinhonha in the state of Minas Gerais. Miranda-Ribeiro (1937:55) described *Curimatus notonotus* from Ceará in a very brief description without any accompanying figure. Perhaps as a consequence of the limited information available in the original description the species name was not applied to the *Steindachnerina* populations of northeastern Brazil by any of the subsequent authors dealing with that ichthyofauna and its components (e.g., Fowler, 1941:164; 1950:282). Those researchers continued to identify the *Steindachnerina* material from that region as *Curimatus elegans* or a subspecies of that form. Although *S. notonota* and *S. elegans* are very similar, discrete differences discriminate those nominal species (see "Key"). The species also differ to varying degrees in the counts of lateral-line scales to the hypural joint and in vertebral counts (Table 8). Consequently, *Steindachnerina notonota* is recognized as distinct in this study.

A. de Miranda-Ribeiro (1937:55) described *Curimatus notonotus* on the basis of three specimens. P. Miranda-Ribeiro

TABLE 8.—Number of lateral line scales from the supracleithrum to the hypural joint, and number of vertebrae in *Steindachnerina elegans* and *S. notonota*.

Species	Lateral-line scales							Vertebrae				
	29	30	31	32	33	34	35	36	37	31	32	33
<i>elegans</i>					10	18	18	19	6		6	23
<i>notonota</i>	6	27	20	18	19					22	40	

later (1955:396) designated one of the "cotypes" that he identified as "A" as the lectotype. The syntypes no longer have any associated alphabetical identification and it is not possible to determine which specimen Miranda-Ribeiro designated as the lectotype. In order to resolve the issue the largest syntype (65.3 mm SL), which is also in the best overall condition, is designated as the lectotype (MNRJ 2611) and the two other specimens in the lot thus become paralectotypes (MNRJ 11561-11562).

MATERIAL EXAMINED.—129 specimens (73, 39.2–97.9).

BRAZIL. *Rio Grande do Norte*: Ceará Mirim, AMNH 3804, 26 (9, 58.8–69.9). Vicinity of Natal, USNM 297905, 3. Lago Papari, ANSP 69453-56, 4. Ceará: no specific locality, MZUSP 21431, 4. Crato, Rio Granjeiro, MNRJ 2611, 1 (65.3, lectotype of *Curimatus notonotus*); MNRJ 11561-11562, 2 (59.9–64.7, paralectotypes of *Curimatus notonotus*; out of MNRJ 2611). Rio Cocó, AMNH uncat., 4 (3, 64.3–68.2). Rio Acaraú, reservoir, USNM 297907, 3 (2, 50.0–70.4). Rio Salgado, USNM 181971, 4 (83.4–89.4). Rio Jaguaribe, USNM 302059, 10 (6, 55.2–70.3). Rio Jaguaribe, Rusas, ANSP 69458-60, 3. Rio Jaguaribe, Orós, ANSP 69457, 1. Açude Pentecostes, USNM 220203, 3 (2, 79.2–97.9). *Piauí*: Pools along Rio Parnaíba downstream of Santa Filomena, USNM 297907, 7 (5, 42.0–53.4). Santa Filomena, upper Rio Parnaíba, USNM 297906, 7 (5, 56.2–77.4); USNM 297908, 2 (62.8–66.8). Santa Filomena, NMW 68790, 6 (1, 49.0); NMW 66999, 6 (2, 62.6–64.5). Rio Medonho, tributary to Rio Parnaíba near Santa Filomena, NMW 68908, 2 (81.4–96.2). Teresina (= Teresina), NMW 67004, 2 (63.5–83.2). Rio Parnaíba, Teresina, MZUSP 5094, 1; USNM 297908, 2. *Maranhão*: Rio Grajaú, Grajaú, MZUSP 5061, 17 (39.2–58.6). Barra do Corda, Rio Corda, MZUSP 5073, 8 (55.0–72.0). *Pará*: Rio Gurupi basin, along highway from Belém to Brasília, MZUSP 4961, 1.

Steindachnerina elegans (Steindachner, 1874)

FIGURES 70–73, TABLES 8, 9

Curimatus elegans Steindachner, 1874:529 [type-locality: Brazil, Minas Gerais, Rio Arassuahy (= Araçuaí), tributary to Rio Jequitinhonha].—Eigenmann and Eigenmann, 1889:421 [in part, Rio Arassuahy (= Araçuaí); Bahia; not Rio Ipajica at Pernambuco].—1891:17 [reference].—Eigenmann,

1910:421 [in part, "Coastwise streams of southeastern Brazil;" not Paraguay citation].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].—[not Boulenger, 1900:2; Starks 1913:14; Azevedo, 1938:51, 55; Azevedo et al., 1938:481; Azevedo and Vieira, 1939:3; Campos, 1945:460; Foresti et al., 1974:249; Nomura, 1977:727; Nomura and Tavera, 1979:331].

Curimatus albula.—Lütken, 1874a:127 [in part, one syntype, Brazil, Rio das Velhas].

Curimatus elegans bahiensis Eigenmann and Eigenmann, 1889:421 [type-locality: Brazil, Bahia].—1891:47 [reference].—Eigenmann, 1910:421 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].

Pseudocurimata elegans.—Fernández-Yépez, 1948:45 [reference].

Pseudocurimata elegans bahiensis.—Fernández-Yépez, 1948:46 [assignment to *Pseudocurimata*].—Fowler, 1975:372 [reference].

Curimata elegans bahiensis.—Fowler, 1950:282 [literature compilation].—Travassos, 1960:8 [compilation; Brazil, Bahia].—Fowler, 1975:282 [literature compilation].

Curimata elegans elegans.—Fowler 1950:282 [literature compilation; Brazil, Bahia references; not citations of Brazil: Ceará and São Paulo; not citations from Rio Paraguay basin; not fig. 342].—Travassos, 1960:8 [compilation, eastern Brazil].—[not Bertoni, 1939:54].

Curimata notonota.—Fowler, 1950:288 [literature compilation].

Curimata elegans.—Lowe-McConnell, 1975:233 [sound production].—Oliveira et al., 1988:594 [in part, Brazil: Minas Gerais, Três Marias; not São Paulo: Botucatu and Rio Mogi-Guaçu; karyotype].—[not Pearson, 1937:109; Fowler, 1941:164, figs. 75, 76; Gomes and Monteiro, 1955:88, 111].

Pseudocurimata elegans elegans.—Fowler 1975:372 [reference].—de Godoy, 1987:168 [in part, Bahia, not other cited localities].—[not de Godoy, 1975:585, figs. 132, 133].

Steindachnerina elegans.—Venere and Galetti, 1989:18, 19, fig. 1 [Brazil: Rio São Francisco, Três Marias; karyotype information].

DIAGNOSIS.—The numerous lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened, prepelvic region of the body, presence of a spot of dark pigmentation on the basal portion of the middle rays of the dorsal fin, possession of 33 to 37 scales along the lateral line to the hypural joint, and the presence of a dark midlateral stripe along the body, in combination, discriminate *Steindachnerina elegans* from its congeners (see also "Comparisons" below).

DESCRIPTION.—Body moderately elongate, more so in larger specimens, somewhat compressed in juveniles, more rotund in specimens over 60 mm SL. Dorsal profile of head slightly convex anteriorly, straight or very slightly convex from vertical line through posterior nostril to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin; straight and very slightly posteroventrally slanted at base of dorsal fin, nearly straight from base of last dorsal-fin ray to

caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region irregularly rounded transversely, somewhat flattened medially, more so proximate to insertion of pelvic fin. Postpelvic portion of body irregularly rounded transversely.

Greatest depth of body 0.29–0.35 [0.30]; snout tip to origin of dorsal fin 0.45–0.50 [0.47]; snout tip to origin of anal fin 0.82–0.88 [0.85]; snout tip to insertion of pelvic fin 0.53–0.58 [0.53]; snout tip to anus 0.76–0.80 [0.77]; origin of rayed dorsal fin to hypural joint 0.53–0.58 [0.54]. Dorsal-fin profile obtusely acute; posterior margin nearly straight; anteriormost rays three and one-half to three and three-quarters times length of ultimate ray. Pectoral-fin profile acute; length of pectoral fin 0.18–0.23, extends about three-quarters distance to vertical line through insertion of pelvic fin in juveniles, about two-thirds of that distance in larger specimens. Pelvic-fin profile acute; length of pelvic fin 0.20–0.25 [0.20], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays two and three-quarters to three and one-quarter times length of ultimate ray. Caudal peduncle depth 0.12–0.13 (very rarely 0.14) [0.13].

Head obtusely pointed in profile, head length 0.26–0.30 [0.28]; upper jaw longer, mouth distinctly inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.28–0.34 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture partially closed by thin flap of skin separating nares; orbital diameter 0.28–0.34 [0.31]; adipose eyelid present, particularly well developed anteriorly, with vertically ovoid opening over center of eye; length of postorbital portion of head 0.38–0.43 [0.43]; gape width 0.26–0.33 [0.26]; interorbital width 0.39–0.44 [0.40].

Pored lateral-line scales to hypural joint 33 to 37 [34?]; all scales of lateral line pored, canals in scales of lateral line straight; 3 to 4 series of scales extend beyond hypural joint onto caudal fin base; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from origin of rayed dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ [$5\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or ii,8, or iii,7 (ii,8 very rare, when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 13 to 16 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 32 (6), 33 (23).

COLOR IN LIFE.—(Based on slides taken by S.L. Jewett, July 1988 of a series of specimens (USNM 297902) from the Rio Jequitinhonha system.) Overall coloration of head and body bright silver, distinctly darker on dorsal portion of head and predorsal region of body. Fins yellowish, with lower lobe of caudal fin dusky. Irregular, dark, midlateral line obvious along

side of body, line extending along middle rays of caudal fin. Dark pigmentation otherwise as in preserved specimens.

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery, darker dorsally on head and body. Dark, midlateral, narrow stripe extending posteriorly to base of caudal fin. Stripe extends less far anteriorly in smaller specimens. Dark line masked to varying degrees by guanine on scales. Overall coloration of specimens lacking guanine on scales yellowish. Dorsal portion of body slightly dusky, more so proximate to dorsal midline. Dorsal surface of head very dusky. Dark narrow stripe along midlateral surface; commencing under dorsal fin in smaller specimens (Figure 70), more obvious and extending progressively more anteriorly in older specimens (Figure 71), reaching to posterior margin of supracleithrum in larger individuals (Figure 72). Line along side of body somewhat irregular and narrowest anteriorly, widest on caudal peduncle, continuous posteriorly with dark stripe along middle rays of caudal fin. Dorsal fin with discrete rotund dark spot on basal portions of middle rays; spot proportionally larger in smaller individuals (Figure 70 versus Figures 71, 72); rest of fin dusky. Adipose fin dusky in larger individuals. Lower lobe of caudal fin dusky, middle rays of caudal fin with very dark stripe. Anal and paired fins hyaline.

COMPARISONS.—The most similar species to *Steindachnerina elegans* and the one most likely to be confused with that form is *S. brevipinna* whose distribution in the Río Paraguay system and other portions of the Río de La Plata system is quite separate from that of *S. elegans*. The two species can be discriminated on the basis of the form and degree of development of the midlateral stripe, which gradually increases posteriorly in width in *S. elegans* contrary to its more constant width in *S. brevipinna*. The stripe also differs in the degree to which it extends posteriorly in the two species (see "Key"). *Steindachnerina insculpta*, an endemic to the upper Rio Paraná system, has a distribution that probably approximates that of *S. elegans* in the region where the upper reaches of the Rio São Francisco and Rio Paraná approach each other. The species are, however, readily distinguishable in pigmentation and in the number of scales along the lateral line to the hypural joint.

DISTRIBUTION.—Eastern Brazil in the Rio Pardo and Rio Jequitinhonha in Bahia and Minas Gerais, Rio São Francisco basin, and coastal rivers of the state of Bahia in Brazil (Figure 73).

COMMON NAME.—Rio São Francisco: biruba (Azevedo et al., 1938).

KARYOTYPE.—Oliveira et al. (1988:594) report that samples of the species (cited by those authors as *Curimata elegans*) from the Três Marias reservoir on the Rio São Francisco have $2n = 54$ chromosomes. Citations in that publication of *Curimata elegans* from Botucatu and the Rio Mogi-Guaçu, both in the Rio Paraná basin, are presumed to refer to *Steindachnerina insculpta*. Venere and Galetti (1989:19) confirm the previously reported chromosome counts and discuss them within a broader phylogenetic framework.

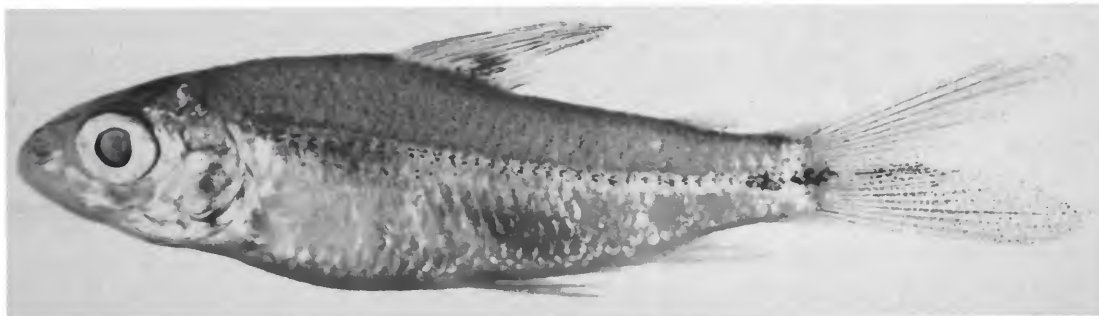


FIGURE 70.—*Steindachnerina elegans*, USNM 297904, 23.4 mm SL; Brazil, Minas Gerais, Rio Jequitinhonha, at km 205 on road between Salto da Divisa and Jacinto.



FIGURE 71.—*Steindachnerina elegans*, USNM 297904, 62.8 mm SL; Brazil, Minas Gerais, Rio Jequitinhonha, at km 205 on road between Salto da Divisa and Jacinto.



FIGURE 72.—*Steindachnerina elegans*, USNM 297903, 108.8 mm SL; Brazil, Minas Gerais, Rio Pardo system, approximately 20 km S of Itapetinga.

REMARKS.—The original description of *Curimatus elegans* Steindachner (1874:529) was based on a syntype series of unspecified size collected by the Thayer Expedition in the Rio Jequitinhonha basin. Steindachner examined the Thayer collection at MCZ and removed a portion of the material to the

Naturhistorisches Museum in Vienna. It is not apparent from the original description of *C. elegans* whether the type series was restricted to the specimens available to Steindachner in Vienna, or if it included other material he examined during his visit to MCZ. Three specimens identified as syntypes were

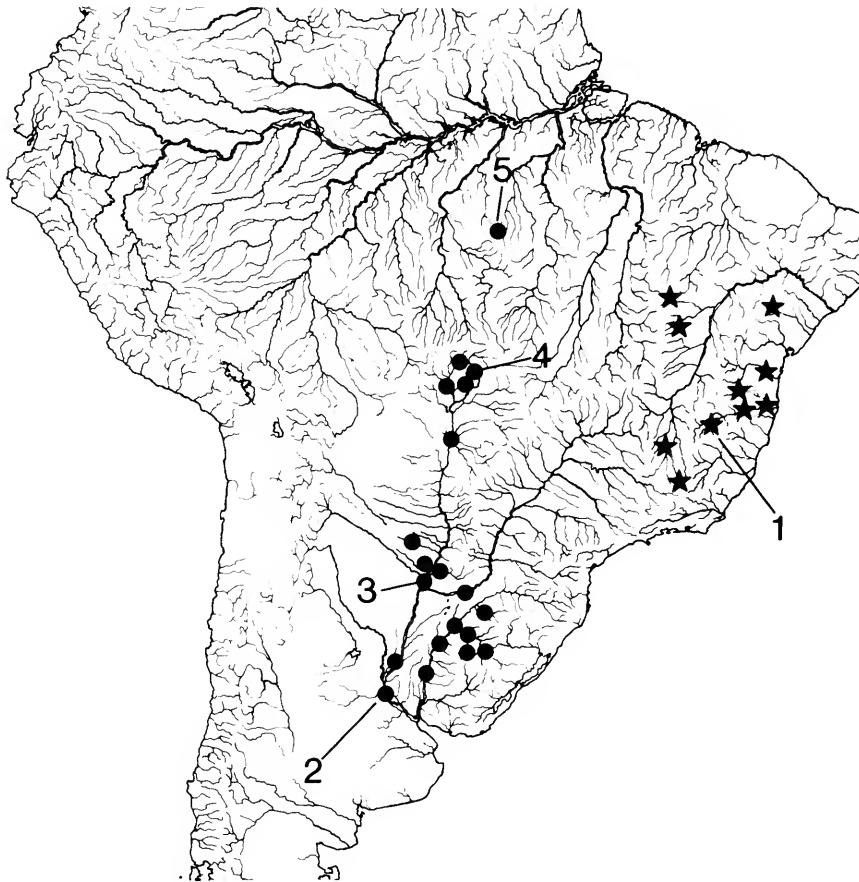


FIGURE 73.—Map of central and southern portions of South America showing geographic distribution of *Steindachnerina elegans* (stars; 1 = type locality of *Curimatus elegans*; inexact type locality of *Curimatus elegans bahiensis*, "Bahia," not indicated, but is likely in the vicinity of the city of Salvador) and *Steindachnerina brevipinna* (dots; 2 = type locality of *Curimatus gilberti brevipinnis*; 3 = type locality of *Curimatus nitens*; 4 = type locality of *Curimatus nigrotaenia*; 5 = possible extralimital sample of *S. brevipinna*, see "Remarks" under that species) (some symbols represent more than one collecting locality and/or lot of specimens).

located in the holdings of the Naturhistorisches Museum. The largest of these is designated as the lectotype (NMW 67001.1). The remaining NMW syntypes (NMW 67001.2-3) become paralectotypes. A series of specimens in the Museum of Comparative Zoology from the type locality that were apparently available to Steindachner presumably represent additional syntypes of *Curimatus elegans* (MCZ 20285). These are herein considered paralectotypes of the species.

Lütken (1874a:127) described *Curimatus albulus* on the basis of a series of specimens collected in the Rio das Velhas basin of the upper Rio São Francisco system. An examination of the syntype series of the species has shown that it is complex, consisting primarily of specimens of a species of *Cyphocharax*, but with a single syntype being *Steindachnerina elegans*

(ZMUC 56). The overall original description makes it apparent that Lütken's description was based on the *Cyphocharax* species rather than on *Steindachnerina elegans*. A lectotype for *Curimatus albulus* will be designated in a future revision of *Cyphocharax*.

Eigenmann and Eigenmann (1889:42) described a subspecies, *Curimatus elegans bahiensis*, on the basis of 44 specimens collected at an unspecified site in the Brazilian state of Bahia by the Thayer Expedition. On the basis of the itinerary of that expedition, it is likely that the material originated somewhere in the vicinity of the Bahian city of Salvador. The subspecies was distinguished from *Curimatus elegans* on the basis of differences in body depth and the number of scales along the lateral line. A comparison of the type series of the two

nominal forms and other material herein considered *Steindachnerina elegans* has not revealed any differences within those population samples (Table 9). Furthermore, only one species of *Steindachnerina* has been found among the examined curimatid specimens collected in the state of Bahia. Consequently, *Curimatus elegans bahiensis* is considered a synonym of *Steindachnerina elegans*. Eigenmann and Eigenmann (1889) cite 44 syntypic specimens for their subspecies. A 86.3 mm syntype (MCZ 20325) is designated the lectotype and the remaining syntypes (MCZ 20324, MCZ 20325; USNM 120251) become paralectotypes.

Literature references to *Steindachnerina elegans*, in various genera, typically cite a much more encompassing geographic range than that recognized in this paper. Many authors also proposed various subspecies within *elegans*. As noted in the preceding paragraph, *Curimatus elegans bahiensis* Eigenmann and Eigenmann (1889) is herein considered a synonym of *Steindachnerina elegans*. Eigenmann and Kennedy (1903) described another subspecies *Curimatus elegans paraguayensis* from the Río Paraguay system. Eigenmann et al. (1907:124) and subsequent authors considered this subspecies to be

equivalent to *Curimatus nitens* (Holmberg, 1891), which they recognized as a subspecies *Curimatus elegans nitens*. As discussed in "Remarks" under *Steindachnerina brevipinna*, and as noted by Vari (1989a, tables 2, 3), *Curimatus elegans paraguayensis* is correctly assigned to *Curimatella* Eigenmann and Eigenmann, and is not closely related to *Steindachnerina elegans*. Eigenmann et al. (1907:124) similarly include *Curimatus nitens* Holmberg (1891) of the Río de La Plata basin as a subspecies of *Curimatus elegans* without any discussion of the basis for their action. *Curimatus nitens* differs from *Steindachnerina elegans* in a number of features and is placed as a synonym of *S. brevipinna* in this study.

Pearson's report of *Curimata elegans nitens* from the Amazonian drainages of northeastern Bolivia was based on specimens of *Steindachnerina guentheri* (see "Remarks" under that species). The report of *Curimatus elegans* from the Paraguay system by Boulenger (1900:2) was based on a specimen (BMNH 1900.4.14:35) that, though in poor condition, would appear to be *Steindachnerina brevipinna*.

Steindachnerina elegans has been cited by a number of authors as an element of the ichthyofauna of the upper Río

TABLE 9.—Morphometrics and meristics of (A) lectotype of *Curimatus elegans* (NMW 67001.1), (B) lectotype of *Curimatus elegans bahiensis* (MCZ 20325), and (C) all specimens of *Steindachnerina elegans* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 14 are proportions of head length. Dashes indicate values that could not be taken due to condition of specimen.

Character	A	B	C
MORPHOMETRICS			
Standard Length	79.0	86.3	37.2–106.3
1. Greatest body depth	0.30	0.34	0.29–0.35
2. Snout to dorsal-fin origin	0.47	0.48	0.45–0.50
3. Snout to anal-fin origin	0.85	0.83	0.82–0.88
4. Snout to pelvic-fin origin	0.53	0.53	0.53–0.58
5. Snout to anus	0.77	0.76	0.76–0.80
6. Origin of rayed dorsal fin to hypural joint	0.54	0.57	0.53–0.58
7. Pectoral-fin length	–	–	0.18–0.23
8. Pelvic-fin length	0.20	–	0.20–0.25
9. Caudal peduncle depth	0.13	0.13	0.12–0.14
10. Head length	0.28	0.28	0.26–0.30
11. Snout length	0.31	0.28	0.28–0.34
12. Orbital diameter	0.31	0.30	0.28–0.34
13. Postorbital length	0.43	0.43	0.38–0.43
14. Interorbital width	0.40	0.42	0.39–0.44
MERISTICS			
Lateral-line scales	34?	34	33–37
Scale rows between dorsal-fin origin and lateral line	5½	5½	5½–6½
Scale rows between anal-fin origin and lateral line	5½	4½	4½–5½
Branched dorsal-fin rays	9	9	9
Branched anal-fin rays	7	7	7–8
Total pectoral-fin rays	14	–	13–16
Branched pelvic-fin rays	8	8	8

Paraná (see synonymy under *S. insculpta*). *Steindachnerina insculpta* is the only member of the genus known from that drainage system and all records of *elegans* from that basin are evidently misidentifications of *S. insculpta*.

Authors commencing with Eigenmann and Eigenmann (1889:421) have cited *Curimatus elegans* from the coastal rivers of northeastern Brazil in the states of Pernambuco, Ceará, and Rio Grande do Norte (see synonymy under *Steindachnerina notonota*). Further analysis has shown that *S. notonota* is the only member of *Steindachnerina* known from that region and all records of *S. elegans* in northeastern Brazil evidently represent records of *S. notonota*.

MATERIAL EXAMINED.—357 specimens (78, 37.2–106.3).

BRAZIL. Rio São Francisco, USNM 297898, 12 (5, 48.8–72.8). *Minas Gerais*: Represa Três Marias, Rio São Francisco, MZUSP 20819, 4 (2, 63.5–86.3); MZUSP 20853, 10 (5, 40.4–92.0); MZUSP 21451, 23 (5, 72.4–99.4); MZUSP 20819, 4 (3, 64.8–85.9); MZUSP 21716, 5 (4, 71.2–88.9); USNM 297901, 7 (3, 79.2–85.4). Corrego do Jacque, near Lapinha, W of Lagoa Santa, USNM 220579, 1 (37.2); MZUSP 21673, 2 (1, 44.4). Rio Arassuaí (= Araçuaí), Rio Jequitinhonha system, NMW 67001.1, 1 (79.0, lectotype of *Curimatus elegans*); NMW 67001.2-3, 2 (67.7–68.3, paralectotypes of *Curimatus elegans*); MCZ 20285, 4 (paralectotypes of *Curimatus elegans*). Rio Jequitinhonha, at km 205 on road between Salto da Divisa and Jacinto, USNM 297904, 31 (10, 43.3–60.2); MZUSP 40116, 32. Rio Jequitinhonha, Itaobim, MZUSP 5137, 2 (1, 63.8). *Bahia*: No specific locality, MCZ 20325, 1 (86.3, lectotype of *Curimatus elegans bahiensis*); MCZ 89837, 6 (49.7–73.9, paralectotypes of *Curimatus elegans bahiensis*; out of MCZ 20325); USNM 120251, 5 (38.5–43.0, paralectotypes of *Curimatus elegans bahiensis*); MCZ 20324, 31 (paralectotypes of *Curimatus elegans bahiensis*). Rio Pardo, ~20 km S of Itapetinga, USNM 297903, 10 (9, 79.2–106.3); MZUSP 40118, 10. Rio Jequitinhonha, Fazenda Canadá, 4 km from Salto da Daviza, USNM 297902, 3 (56.7–63.3). Rio da Catinga do Moura, MZUSP 21730, 2 (49.8–54.5). Santa Rita, NMW 68794, 17 (4, 48.5–50.5). Lagoon near mouth of Rio Preto, NMW 66998, 3 (1, 48.1). Rio Preto, vicinity of Santa Rita, USNM 297899, 5 (2, 51.4–60.1). Rio Desidério, São Desidério, near Barreiras, USNM 297900, 2 (81.7–87.9). Rio do Braço system, 2 km from town of Rio do Braço, USNM 297909, 61; MZUSP uncat., 61.

Steindachnerina brevipinna
(Eigenmann and Eigenmann, 1889)

FIGURES 73–77, TABLE 10

Curimatus gilberti brevipinnis Eigenmann and Eigenmann, 1889:424 [type-locality: Argentina: Rosario, La Plata].—1891:47 [reference].—Berg, 1897:279 [Argentina: San Pedro, Río Paraná; San Martín, Buenos Aires].—Eigenmann, 1910:421 [reference].—Pozzi, 1945:271 [Argentina: Río de La Plata, Río Paraná, Río Uruguay, Río Paraguay].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].—[not Eigenmann and Norris, 1900:355].

Curimatus nitens Holmberg, 1891:184 [type-locality: Argentina, Río Paraguay].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
Curimatus elegans.—Boulenger, 1900:2 [Brazil: Corumbá].
Curimatus spilurus.—Boulenger, 1900:2 [Brazil: Matto (= Mato) Grosso, Carandasinho].—Bertoni, 1914:9 [Paraguay, evidently based on Boulenger, 1900].
Curimatus nigrotaenia Boulenger, 1902:285 [type-locality: Mato Grosso, Rio Coxipo].—Eigenmann, 1910:421 [reference].—Vari, 1989a, tables 2, 3 [assignment to *Steindachnerina*].
Curimatus elegans nitens.—Eigenmann et al., 1907:124 [Paraguay: Asuncion, Sapucaí].—Eigenmann, 1910:421 [reference].—Steindachner, 1911:331 [Curimatus elegans paraguayensis Eigenmann and Kennedy incorrectly placed as a synonym of *Curimatus nitens*].—Bertoni, 1914:9 [Paraguay].—Pearson, 1937:109 [Paraguay].—Fowler, 1940b:98 [reference].—Pozzi, 1945:271 [Argentina, Río Paraguay].—Fowler, 1950:282 [literature compilation; not upper Rio Amazonas or Bolivia references].—Ringuélet and Aramburu, 1961:36 [Argentina].—[not Pearson, 1924:28].
Curimatus elegans elegans.—Bertoni, 1914:9 [Paraguay].
Curimatus Gilberti brevipinnis.—Marelli, 1923:556 [Argentina: Río Paraná, Río de La Plata, Isla de Martín García].
Curimatus spilurus.—Pearson, 1937:109 [in part, Río Paraguay basin, evidently based on Boulenger (1900) citation of *Curimatus spilurus*].
Curimatus gilberti brevipinnis.—Bertoni, 1939:54 [Paraguay: Asuncion].—Ringuélet and Aramburu, 1961:36 [Argentina].
Curimatus elegans elegans.—Bertoni, 1939:54 [Paraguay].
Curimatus spilurus.—Bertoni, 1939:54 [Paraguay; evidently based on Boulenger (1900) citation of *Curimatus spilurus*].—Ringuélet, 1975:72 [Argentina, Río Paraguay system, based on Bertoni, 1939].
Curimatus elegans paraguayensis.—Pozzi, 1945:257 [Argentina, Río Paraguay?].—[not Eigenmann et al., 1907:124; Eigenmann, 1910:421; Steindachner, 1911:331].
Cruxentina brevipinna.—Fernández-Yépez, 1948:52 [reference].—Ringuélet et al., 1967:191 [Argentina: Río Paraná, Río de La Plata, Río Paraguay].—Ringuélet, 1975:61 [Argentina: Río Paraná, Río de La Plata, Río Paraguay; not Rio Amazonas citation].—Lopez et al., 1987:19 [Argentina].
Cruxentina nitens.—Fernández-Yépez, 1948:53 [reference].—Fowler, 1975:368 [reference].
Curimatus nigrotaenia.—Fernández-Yépez, 1948:73 [reference].—Fowler, 1950:288 [literature compilation].—Fowler, 1975:369 [reference].—Ringuélet, 1975:72 [Argentina, Río Paraguay system].
Curimatus gilberti brevipinnis.—Fowler, 1950:284 [literature compilation].
Pseudocurimatus nitens.—Ringuélet et al., 1967:200 [Argentina].—Azpelicueta, 1980:85 [osteology].—Azpelicueta and Braga, 1980:165 [Argentina].—Lopez et al., 1984:76 [Argentina: Río Uruguay].—Miquelarena, 1984:619, fig. 51 [caudal skeleton].
Cruxentina brevipinnis.—Fowler, 1975:367 [reference].
Pseudocurimatus elegans nitens.—Fowler, 1975:372 [reference].—Ringuélet, 1975:61 and 72 [Río Paraná, Río Paraguay; not Rio Amazonas citation].
Pseudocurimatus elegans.—Ringuélet, 1975:72 [Río Paraguay system].
Curimatus nitens.—Lopez et al., 1987:19 [Argentina].

DIAGNOSIS.—The lobulate fleshy processes on the roof of the oral cavity, absence of a wide, flattened, prepelvic region of the body, presence of a dark spot of pigmentation on the basal portions of the middle rays of the dorsal fin, possession of 33 to 37 scales in the lateral line to the hypural joint, and the presence of a dark midlateral stripe of nearly continuous width along the body, in combination, discriminate *Steindachnerina elegans* from its congeners (see also “Comparisons” below).

DESCRIPTION.—Body moderately elongate, somewhat compressed, more so in larger specimens. Dorsal profile of head straight or very slightly concave. Dorsal profile of body

smoothly curved from rear of head to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin, typically straight, but sometimes gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with indistinct median keel anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Prepelvic region obtusely flattened, with median series of scales proximate to pelvic-fin origin. Obtuse median keel posterior to pelvic-fin insertion. Obtuse secondary keel on each side of postventral portion of body one scale dorsal of ventral midline.

Greatest depth of body 0.31–0.38 [0.32]; snout tip to origin of dorsal fin 0.47–0.52 [0.49]; snout tip to origin of anal fin 0.81–0.87 [0.86]; snout tip to insertion of pelvic fin 0.49–0.57 [0.54]; snout tip to anus 0.77–0.84 [0.80]; origin of dorsal fin to hypural joint 0.54–0.61 [0.56]. Dorsal-fin profile acute; anteriormost rays two and one-half to three times length of ultimate ray. Pectoral-fin margin acute; length of pectoral fin 0.17–0.22 [0.20], extends two-thirds to three-quarters distance to vertical line through insertion of pelvic fin. Pelvic-fin profile acute; length of pelvic fin 0.20–0.25 [0.24], reaches about one-half distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays two to two and one-half times length of ultimate ray. Caudal peduncle depth 0.12–0.15 [0.13].

Head obtusely pointed in profile, head length 0.27–0.32 [0.27]; upper jaw much longer, mouth inferior; portion of buccopharyngeal complex on roof of oral cavity in adults consisting of multiple lobulate fleshy bodies; snout length 0.27–0.34 [0.28]; nostrils very close, anterior circular, posterior crescent-shaped, with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.35 [0.32]; adipose eyelid present, more developed anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.38–0.45 [0.42]; gape width 0.26–0.33 [0.29]; interorbital width 0.39–0.45 [0.42].

Pored lateral-line scales to hypural joint 33 to 37 [holotype

only partially scaled, approximately 35]; all scales of lateral line pored, canals in scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $5\frac{1}{2}$ to $6\frac{1}{2}$ ($6\frac{1}{2}$ rare) [$5\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $4\frac{1}{2}$ to $5\frac{1}{2}$ ($5\frac{1}{2}$ rare) [$4\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,8 or ii,9, or iii,9 (ii,8 and iii,9 rare; when three unbranched rays present, first short) [ii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first short) [ii,7]; pectoral-fin rays 12 to 14 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 31 (28), 32 (30), 33 (30).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery, darker with somewhat olive cast on dorsal surface of head and body; dark pigmentation bordering pores of lateral-line scales masked to a degree by guanine on scales. Specimens lacking guanine on scales yellowish, darker dorsally. Dark pigmentation along lateral line much more obvious, forming dark horizontal band from posterior margin of supracleithrum to caudal peduncle, continuing on rear of caudal peduncle and middle rays of caudal fin as dusky band. Midlateral band faint in those populations characterized by limited overall development of dark pigmentation (Figure 76), sometimes present only as patches of slightly darkly pigmented chromatophores on lateral-line scales. Dorsal fin with posteroventrally sloping patch of dusky pigmentation on basal portions of fin membranes between second and fifth dorsal-fin rays; pigmentation sometimes very faint in some populations (Figure 77). Spot always more obvious in juveniles (Figure 75) than adults from a locality regardless of typical intensity of overall pigmentation in population. Adipose and caudal fins dusky overall in specimens from darker populations; hyaline in other populations. Other fins hyaline.

DISTRIBUTION.—Río Paraguay, lower Río Paraná and lower Río Uruguay (Figure 73).

COMPARISONS.—*Steindachnerina brevipinna* is most similar to and most likely to be confused with *S. elegans* of the coastal rivers of Minas Gerais and Bahia. As noted under



FIGURE 74.—*Steindachnerina brevipinna*, MCZ 789, 107.0 mm SL, holotype of *Curimatus gilberti brevipinnis*; Argentina, Santa Fe, Rosario.



FIGURE 75.—*Steindachnerina brevipinna*, USNM 295269, 36.3 mm SL; Brazil, Rio Grande do Sul, Rio Gaupa, along road from Uruguiana to Quarai.

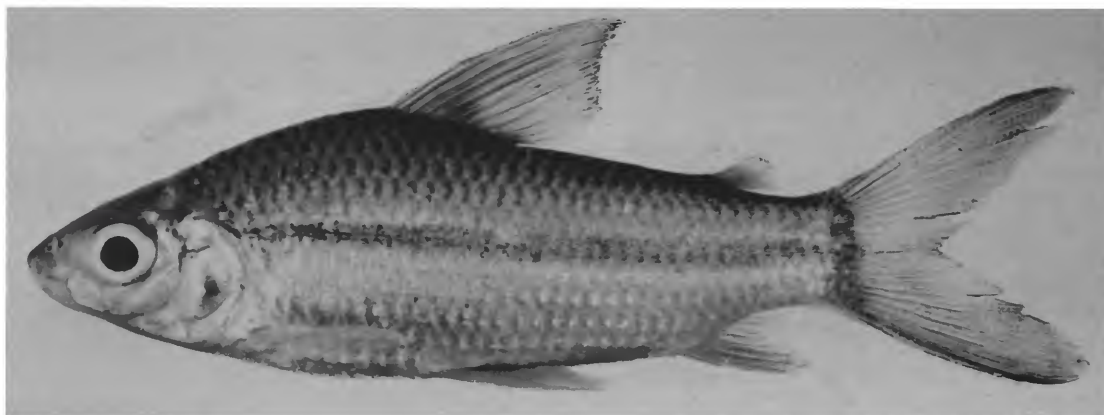


FIGURE 76.—*Steindachnerina brevipinna*, USNM 243240, 67.4 mm SL; Brazil, Mato Grosso, Rio Paraguai, Porto de Cáceres.



FIGURE 77.—*Steindachnerina brevipinna*, USNM 295327, 72.8 mm SL; Brazil, Mato Grosso, Município Poconé, along Rodovia Transpantaneira.

"Comparisons" for *S. elegans* and in the "Key," the species can be discriminated in various details of pigmentation. The known distribution of *S. brevipinna* overlaps that of two congeners, *S. biornata* and *S. conspersa*. *Steindachnerina brevipinna* and *S. biornata* can be readily distinguished by differences in the pigmentation on the caudal peduncle and overall body form. The numerous lobulate processes on the roof of the mouth in *S. brevipinna*, in turn, distinguish it from *S. conspersa*, which lacks those structures.

The northern portions of the range of *S. brevipinna* possibly approach the range of the poorly known Rio Tocantins endemic *S. amazonica*. The two species differ in the degree of development of the midlateral stripe on the body, number of scales along the lateral line to the hypural joint, and relative gape width.

REMARKS.—Eigenmann and Eigenmann (1889:424) described *Curimatus gilberti brevipinnis* from a single specimen (MCZ 789) collected at "Rosario (La Plata)" on the lower Río Paraná. Their five line description of the species provided little information on the holotype, nor did they discuss their rationale for aligning their "new variety" with *Curimatus gilberti* Quoy and Gaimard, a species assigned to *Cyphocharax* by Vari (1989a). Eigenmann and Eigenmann's concept of *C. gilberti* was, furthermore, problematical in that it included specimens of at least two species, *C. gilberti* and *C. voga* (Hensel). Examination of the holotype of *Curimatus gilberti brevipinnis* has shown that it differs markedly from *C. gilberti* and *C. voga* in numerous morphometric and meristic characters, and in details of the pigmentation. In addition, the holotype of *Curimatus gilberti brevipinnis* exhibits a number of the externally apparent, derived features characteristic of subclades of *Steindachnerina*. The most notable of these involve the form and position of the mouth, the possession of a mass of lobulate fleshy bodies on the portion of the buccopharyngeal complex situated on the roof of the oral cavity, and the pattern of dark pigmentation on the body and fins. Both *C. gilberti* and *C. voga*, in contrast, lack the distinctive derived features characteristic of *Steindachnerina*, and the derived characters that align *Curimatus gilberti brevipinnis* with subunits of *Steindachnerina*. In light of these factors the placement of *brevipinnis* as a subspecies of *Cyphocharax gilberti* is judged inappropriate, and *brevipinnis* is assigned to *Steindachnerina*.

Eigenmann and Eigenmann's original description stated that their one specimen of *Curimatus gilberti brevipinnis* was "silvery, with purple and greenish reflections. Lateral scales with a frosted appearance." Although the holotype (MCZ 789) now largely lacks dark pigmentation, there are remnants of dark chromatophores along the scales of the lateral-line series, and some dark pigmentation on the basal portions of the middle rays of the dorsal fin. The holotype is very rigid and preserved in a deformed position. The specimen, nonetheless, agrees in overall body form, meristics, morphometrics, and other morphological details with other *Steindachnerina* specimens from the type region that have a well-developed midlateral

band of dark pigmentation on the body and a dark spot on the basal portion of the middle rays of the dorsal fin. The somewhat shallower body in the holotype relative to other evidently conspecific specimens may be a consequence of its twisted form.

The brief original description of *Steindachnerina brevipinna* and its incorrect association with *Cyphocharax gilberti* made it impossible for subsequent authors to recognize the taxon. This may have contributed to the redescription of the species under other names by Holmberg (1891) and Boulenger (1902). Holmberg (1891:184) described *Curimatus nitens* based on an original series of unstated size. The syntypes are not known to be extant (Dr. M. Azpelicueta, in litt.), but it is nonetheless apparent from the information in the original description that the Holmberg species is equivalent to *Curimatus gilberti brevipinnis* of Eigenmann and Eigenmann (Table 10). The species are consequently herein considered conspecific.

Boulenger's description of *Curimatus nigrotaenia* (1902:285) was based on "several" specimens from the Rio Coxipo in the Mato Grosso of Brazil. He noted that the species has a black band along the lateral line, but failed to describe the prominent dark spot on the basal portion of the middle rays of the dorsal fin that is present in the relatively small sized (33.7–39.5 mm SL) syntypes. The information on scale counts in the original description is also significantly at variance with the actual counts for the syntypes. Whereas Boulenger described his specimens as having 43 or 44 lateral-line scales, the syntypes of *Curimatus nigrotaenia* have only 33 to 35 scales in that series. Although Boulenger cites $7\frac{1}{2}$ to $8\frac{1}{2}$ scales above the lateral line and 6 below it, examination of the specimens has shown that they have $5\frac{1}{2}$ scales above the lateral line to the dorsal-fin origin and $4\frac{1}{2}$ below the lateral line to the anal-fin origin. At this time it is impossible to determine whether the original published data contained typographical errors or if Boulenger's counts were incorrect. Boulenger compared his *Curimatus nigrotaenia* with *C. elegans* Steindachner, a distinct, nonsympatric species herein assigned to *Steindachnerina*, but did not contrast it with either *Curimatus nitens* or *Curimatus gilberti brevipinnis*, which had previously been described from the Río de La Plata basin. The syntypes of *Curimatus nigrotaenia* do not differ in any detail in examined meristic and morphometric values (Table 10) or any other examined features from *Steindachnerina brevipinna*. Thus, it appears that *Curimatus nigrotaenia* was based on juveniles of *S. brevipinna* and is consequently placed as a synonym of the latter species.

The largest specimen in the syntype series of *Curimatus nigrotaenia* (BMNH 1902.2.10:30, 39.5 mm SL), is designated as the lectotype. The four other syntypes (BMNH 1902.2.23:3–6) become paralectotypes.

Eigenmann et al. (1907:124) followed by Eigenmann (1910:421), Steindachner (1911:331), and subsequent authors considered *Curimatus elegans paraguayensis* Eigenmann and

TABLE 10.—Morphometrics and meristics of (A) holotype of *Curimatus gilberti brevipinna* (MCZ 789), (B) lectotype of *Curimatus nigrotaenia* (BMNH 1902.2.10:30), (C) type series of *Curimatus nitens* (based on information in original species description (Holmberg, 1891:184; note that presented measurements for that type series are less precise than for other specimens cited in table)), and (D) all specimens of *Steindachnerina brevipinna* from which counts and measurements were taken. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 14 are proportions of head length. Dashes indicate values that were not provided in the original description of the species.

Character	A	B	C	D
MORPHOMETRICS				
Standard Length	107.0	39.5	—	28.1–108.6
1. Greatest body depth	0.32	0.35	0.33	0.31–0.38
2. Snout to dorsal-fin origin	0.49	0.47	—	0.47–0.52
3. Snout to anal-fin origin	0.86	0.84	—	0.81–0.87
4. Snout to pelvic-fin origin	0.54	0.55	—	0.49–0.57
5. Snout to anus	0.80	0.80	—	0.77–0.84
6. Origin of rayed dorsal fin to hypural joint	0.56	0.56	—	0.54–0.61
7. Pectoral-fin length	0.20	0.18	—	0.17–0.22
8. Pelvic-fin length	0.24	0.23	—	0.20–0.25
9. Caudal peduncle depth	0.13	0.13	—	0.12–0.15
10. Head length	0.27	0.30	0.25*	0.27–0.32
11. Snout length	0.28	0.28	0.25	0.27–0.34
12. Orbital diameter	0.32	0.34	0.31	0.28–0.35
13. Postorbital length	0.42	0.38	—	0.38–0.45
14. Interorbital width	0.42	0.40	—	0.39–0.45
MERISTICS				
Lateral-line scales	35	34	38–41†	33–37
Scale rows between dorsal-fin origin and lateral line	5½	5½	5	5½–6½
Scale rows between anal-fin origin and lateral line	4½	4½	6‡	4½–5½
Branched dorsal-fin rays	9	9	9§	8–9
Branched anal-fin rays	7	7	7§	7
Total pectoral-fin rays	14	14	13	12–14
Branched pelvic-fin rays	8	8	8§	8

* Value given in original description of species indicates that head goes four times in body length; however, text states that head goes “almost four times” in body (my translation), thus indicating a higher proportional measurement.

† Lateral-line scale counts given by Holmberg appear to include pored scales on base of caudal fin posterior of hypural joint.

‡ Count of scales below lateral line in original description of species evidently refers to scales between lateral line and midventral line rather than between lateral line and origin of anal fin.

§ Counts of total median and pelvic-fin rays in original description of species have been adjusted in this table to allow for most common numbers of unbranched rays in each fin.

Kennedy (1903:510) to be equivalent with *C. nitens* (Holmberg, 1891), which they recognized as a subspecies of *Curimatus elegans nitens*. *Curimatus nitens* is, in turn, herein considered a synonym of *Steindachnerina brevipinna*. Analysis of the type series of *C. e. paraguayensis* has shown, however, that it is complex. The holotype of *C. e. paraguayensis* (CAS 60583, formerly IU 9928) is an individual of the *Curimatella dorsalis* complex and the paratype (CAS 60584, formerly IU 9954) a specimen of *Steindachnerina brevipinna*.

Thus, *Curimatus elegans paraguayensis* Eigenmann and Kennedy is neither a possible synonym of *Curimatus nitens*, nor even available in *Steindachnerina*.

Eigenmann and Norris (1900:355) cited *Curimata gilberti brevipinnis* from Piracicaba in the upper Río Paraná system of São Paulo state; a record evidently based on *Steindachnerina inculpta*, the only member of the genus found in that portion of the river basin. Pearson (1924:28) cited *Curimatus elegans nitens* from Huachi and Rurrenbaque in the Amazon basin of

Bolivia. All of the examined specimens that served as the basis for those citations are *Steindachnerina guentheri* (UMMZ 66511, USNM 298160, both out of IU 17137), and subsequent citations of *C. e. nitens* from the Amazon basin following Pearson's record (Fowler, 1950:282; Ringuelet, 1975:61) are all apparently based on that misidentification.

Boulenger (1900:2) reported *Curimatus spilurus* Günther from the vicinity of Corumbá, Mato Grosso, Brazil, in the Río Paraguay basin. The specimen that served as the basis for that record (BMNH 1900.4.14:35; actual locality Carandazinho) is in poor condition, but appears to be a specimen of *Steindachnerina brevipinna*. Records of *Curimatus spilurus* from the Paraguay basin by Bertoni (1914:9; 1939:54, as *Curimatus spilura*), Pearson (1937:109, as *Curimatus spilurus*), and apparently Ringuelet (1975:72, as *Curimata spilura*) are seemingly based on the Boulenger record rather than additional specimens, and all those citations are assumed herein to refer to *Steindachnerina brevipinna*.

A single lot of relatively small *Steindachnerina* specimens from the Serra do Cachimbo, in the upper Río Curua of the Río Xingu basin (USNM 267957) is either equivalent to *S. brevipinna* or represents a very similar undescribed species. Unfortunately the size and condition of the specimens prevents a more definitive identification. If this lot is indeed *S. brevipinna* it represents the first record of that species from the Amazon basin. On the basis of the ranges of other members of the genus and other curimatids, it is more likely, however, that the specimens represent an undescribed species. The specimens differ in pigmentation and meristics from *S. amazonica* of the Río Tocantins system to the east and are dramatically different in the pattern of body pigmentation from *S. fasciata* of the Río Guaporé system considerably to the west. The Río Curua specimens are the only records of a species of *Steindachnerina* in the portion of the Amazon basin to the far south of the main river channel in the region between the Tocantins and upper Madeira systems.

MATERIAL EXAMINED.—142 specimens (70, 28.1–108.6).

ARGENTINA. *Santa Fe*: Rosario, MCZ 789, 1 (107.0, holotype of *Curimatus gilberti brevipinnis*). Laguna Setubal, USNM 295325, 4 (56.1–77.3). *Corrientes*: Posadas, Río Paraná, BMNH 1902.2.10.31, 1 (63.4). *Entre Ríos*: Río Uruguay at Concordia, USNM 295326, 1 (85.0).

PARAGUAY. Río Tebicuary, USNM 229441, 1 (74.9). *Central*: San Bernardino, USNM 181647, 7 (58.0–81.3). Asuncion, Río Paraguay, CAS, 1 (77.4, paratype of *Curimatus elegans paraguayensis*; formerly IU 9954). Asuncion Bay, Río Paraguay, USNM 181538, 1 (39.2); USNM 181640, 1 (52.9). Asuncion, AMNH 1461, 1 (67.7). Lago Ypacarai, vicinity of Aregua, USNM 229438, 1 (66.5). Lago Ypacarai, USNM 229439, 1 (86.2); USNM 232221, 1 (77.0). *Cordillera*: 17.6 km W of San Bernardino, USNM 232220, 1 (67.5). *Presidente Hayes*: 84 km NE of Río Mantelindo, at km 216.5 on Trans-Chaco Highway, USNM 232216, 1. Río Paraguay, Villa Hayes, FMNH 70507, 2.

BRAZIL. *Mato Grosso*: Río Coxipó, BMNH 1902.2.10:30, 1 (39.5, lectotype of *Curimatus nigrotaenia*); BMNH 1989.2.23:3–6, 4 (33.7–38.8, paralectotypes of *Curimatus nigrotaenia*). Carandazinho, BMNH 1900.4.14:36–39, 4 (28.1–38.7). Município Poconé, Rodovia Transpantaneira, USNM 295327, 2 (72.8–73.2, formerly ZUEC 507 and 509). Lagoa along Rodovia Transpantaneira, 10 km from Poconé, MZUSP 28463, 3 (1, 60.1). Río Paraguai, Porto de Cáceres, USNM 243240, 9 (50.8–67.4). Río Coxipo da Ponte, Coxipó da Ponte, Município de Cuiabá, MZUSP 21512, 16. Santo Antônio de Leverger, MZUSP 4447, 1 (44.4). Río Cuiabá, Município de Santo Antônio de Leverger, MZUSP 21656, 6. Río Jaurú at Porto Esperidião, MZUSP 28089, 1 (56.4). *Mato Grosso do Sul*: Município de Corumbá, MZUSP 21680, 1 (68.2); MZUSP 21679, 5. *Rio Grande do Sul*: Río Santa Maria at bridge on Br 293, between Dom Pedrito and Livramento, MCP 9620, 20 (8, 72.6–108.6). Río Ibicuí, bridge between São Rafael and Cacequí, USNM 295264, 10 (35.5–80.3). Arroio do Salsa, tributary to Río Ibicuí, on road from Livramento to Rosario do Sul, Município de Rosario do Sul, USNM 295270, 2. Tributary to Río Ibicuí da Faxina, along road from Livramento to Rosário, Município de Livramento, USNM 295263, 2; MCP 12106, 2. Itaquí, Río Ibicuí, near mouth, USNM 295268, 9; MCP 12013, 7. Río Gaupa, along road from Uruguiana to Quaraí, USNM 295269, 2 (1, 36.3); MCP 12029, 2. Município de Santo Angelo, tributary to Río Uruguai, USNM 295265, 2; MCP 12014, 2. Santa das Águas Frias, off Río Uruguai, USNM 287002, 2 (70.2–76.2).

URUGUAY. No specific locality, NMW 67034, 1.

The following lot is tentatively identified as *Steindachnerina* cf. *brevipinna* (see last paragraph of "Remarks").

BRAZIL. *Pará*: Waterfall pool in Río Curuá, Serra do Cachimbo, near Cuiabá to Santarem Highway (upper Río Xingu drainage basin), USNM 267957, 12.

Phylogenetic Biogeography

A diverse set of attributes make the Curimatidae, at least in theory, an ideal group for studies of the phylogenetic biogeography of the South American lowland fish fauna. Despite the fact that the ichthyofaunas of nearly all Neotropical river systems are inadequately collected and are at best somewhat superficially analyzed, the available evidence suggests that the Curimatidae has a near cosmopolitan distribution in the river systems of tropical and subtropical South America inhabited by various members of the Ostariophysi. The only substantiated exception to that generalization is the absence of the family in the series of short rivers draining the Pacific versant of the Andean cordilleras in central and southern Peru, and in central Chile.

Above and beyond its broad range, the family is, furthermore, relatively speciose, is characterized by a notable degree

of variation in diverse body systems useful for resolving both supra and intrageneric phylogenetic relationships, and shows a high degree of sympatry between all the major intrafamilial clades. These attributes of the Curimatidae hold promise that a phylogenetic analysis of the family will result in multiple geographically overlapping area cladograms. Those, in turn, could reveal common patterns of historical relationships between areas of endemism. Furthermore, although curimatids inhabit some relatively fast-flowing streams, members of the family have not been collected in torrential waters, nor are they known from the mid to high altitude drainages along the slopes of the Andes. Thus, curimatids should be more reflective of the major hydrographic vicariance events that may have taken place on the continent than would fishes adapted to the higher velocity water flows typical of headwater streams along watershed boundaries.

Vari (1988) provided an overview of then available information on phylogenetic relationships within the Curimatidae and noted that under an allopatric speciation model curimatids must have undergone repeated, very large-scale dispersal as indicated by the high degree of secondary sympatry at phylogenetic levels ranging from the familial to the specific. Subsequent publications on *Curimata* (Vari, 1989b) and *Psectrogaster* (Vari, 1989c) have confirmed that such secondary dispersal is widespread in the components of those genera that occur in the Atlantic versants of South America. *Pseudocurimata*, a less speciose trans-Andean endemic genus of curimatids that inhabits a highly dissected geomorphological region, in contrast, shows a much lower degree of interspecific and intercladal sympatry (Vari, 1989d).

The phylogenetic biogeography of *Steindachnerina*, whose distribution totally overlaps that of *Psectrogaster* and *Curimata*, has a degree of secondary dispersal comparable to that found in those genera; additional evidence congruent with an hypothesis that post-speciation dispersal has been a major factor in the evolution of the fish fauna to the east of the Andes. Furthermore, *Steindachnerina* exhibits several interesting patterns when species distributions are evaluated within a phylogenetic context.

Figure 78 presents an area cladogram for *Steindachnerina* in which the species names have been replaced by the general range for each form. The internal nodes of the cladogram are lettered for cross-reference in the following discussion. On examination we can see that the two components of Node A identified as Nodes B and F have a high level of sympatry, albeit with several interesting differences. The distribution of the species in clade B is totally enclosed within that of clade F with three minor exceptions, all involving *Steindachnerina argentea*, a species limited to the northern portions of the geographical range of the genus. That species, widespread in the Río Orinoco basin, also inhabits two small rivers on the northern slopes of the Venezuelan coastal ranges and is widespread on the western portions of the island of Trinidad. None of those three areas is known to be inhabited by any other

species of curimatid. The presence of *S. argentea* on Trinidad indicates a past dispersal across what is presently the Gulf of Paria. One possible mechanism for that dispersal event involves a dispersion across a reduced or absent marine barrier in that area during a period of lowered sea levels associated with a period of glaciation in temperate regions of the world. An alternative scenario is the dispersal of the species across the Gulf of Paria during the flood season of the Río Orinoco when the large influx of freshwater into the Gulf reduces or eliminates the barrier posed by the saline waters during other periods of the year. Under that mechanism the dispersal event must have occurred after the late Miocene shift of the mouth of the Río Orinoco to the Atlantic proximate to Trinidad. Prior to that time the Orinoco drained into the Caribbean further to the west in the region of the present Lago Maracaibo (Rod, 1981).

With the exception of the Trinidad localities and the two small northern coastal rivers noted above, the species of Node B are limited to the three largest river systems of South America, the Orinoco, the Amazon, and the La Plata. That lineage of five species demonstrates sequential vicariance events between the Río de La Plata system and the Río Orinoco and Río Amazonas basins to the north (Node C) followed by subsequent speciation event between the two species at Node E, which have allopatric distributions within the central portion of the Amazon basin and the upper Río Madeira respectively.

The species of Node F encompass the total geographic range of *Steindachnerina* with the exception of the peripheral distributions of *S. argentea* on western Trinidad and in two small rivers of the northern versant of Venezuela. Once again there is large-scale sympatry within that clade at basal phyletic levels (Nodes F and H); however, such sympatry is less pronounced within less inclusive clades (Nodes I to N). Several exceptions to those generalizations are particularly noteworthy. Perhaps the most interesting of these involves the dichotomy at Node G, which can serve as a benchmark to establish a minimum age for at least some of the speciation events within the genus. We can see at Node G that *Steindachnerina atratoensis*, an endemic of the Río Atrato system to the west of the Andean cordilleras, is hypothesized to be the sister group to a lineage of 14 species (Node H) distributed through nearly the total range of the genus to the east of the Andes. Comparable sister group relationships across various portions of the Andean Cordilleras within the Curimatidae have been previously reported for *Potamorhina* (Vari, 1984a; 1988:342, 343, fig. 11), *Curimata* (Vari, 1988:343, fig. 12; 1989b), and also occur in *Cyphocharax* (Vari, 1988:343). It is simplest to hypothesize that this repeated pattern of phylogenetic relationships across the Andes is correlated with the Miocene uplift of various portions of that mountain chain. That assumption is more parsimonious than alternative hypotheses invoking repeated independent dispersal events across major barriers (see Vari, 1988:344). Furthermore, the single hypothesis is particularly reasonable in this instance given the ecological parameters of curimatids discussed above that make them ill-adapted to

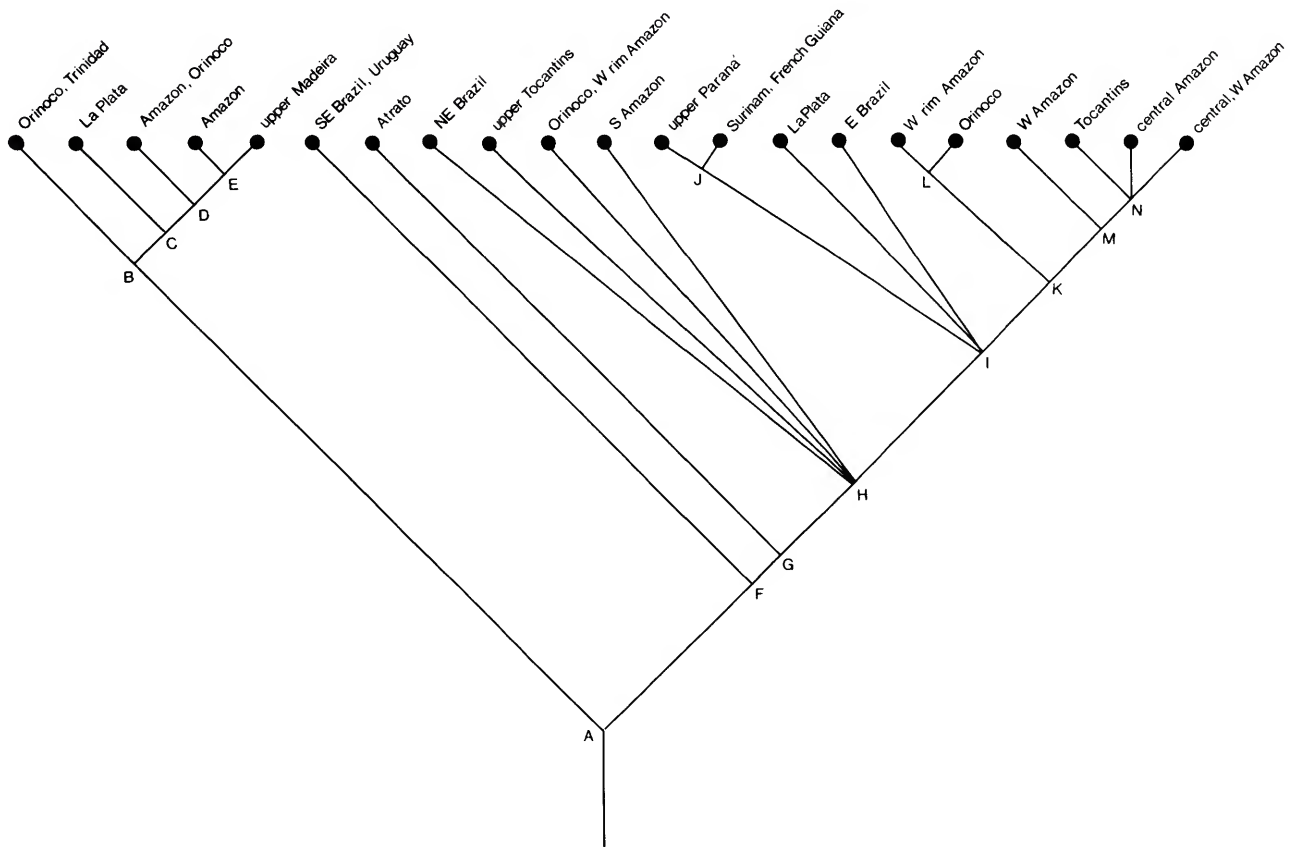


FIGURE 78.—Area cladogram of the species of *Steindachnerina* with species names replaced by general distribution of each species; topology of tree identical to that of Figure 11. Nodes lettered for cross-reference to text. See distribution maps for each species for exact known distributions.

dispersal through cold, high-altitude barriers. Thus, as noted by Vari (1988:343, 344), all of the major and much of the minor cladogenesis within the family is hypothesized to predate the formation of the Amazon basin.

The question of the contribution of the formation of the Amazon basin to the species diversity of the present-day South American fish fauna has been the subject of some contention (see Weitzman and Weitzman, 1982; Vari, 1988). The location of *S. atratoensis* within the phylogeny indicates that cladogenesis between the ancestors of the species at nodes A and F predated the vicariance event at node G, which presumably took place at the latest in the late Miocene. It is not possible at the present time to correlate the speciation events of nodes B through E with any specific vicariance events, although as noted above, the common occurrence of *Steindachnerina argentea* of node B on Trinidad may be the result of a post-Miocene dispersal event. Difficulties in correlating the speciation events within Node H with specific geomorphologi-

cal events apparently makes that portion of the tree similarly uninformative with respect to the question of speciation rates within the Amazon basin. Indeed, at first consideration, the occurrence of a large percentage of the species within Node H to the east of the Andes would appear to be congruent with an hypothesis that much of the cladogenesis within the genus postdates and perhaps was a result of the formation of the Amazon basin as a consequence of the Miocene uplift of the Andes. The large number of unresolved sister-group relationships at Nodes H, I, and N, and in particular the lack of benchmark vicariance events that can be confidently correlated with branching points within the Node H clade makes it impossible to critically test that hypothesis. An examination of the distribution of the species within Node H together with the available phylogenetic information in the clade does, however, provide some insight into the question.

Most of the species of Node H have distributions lying largely outside of the Amazon basin (*brevipinna*, *elegans*,

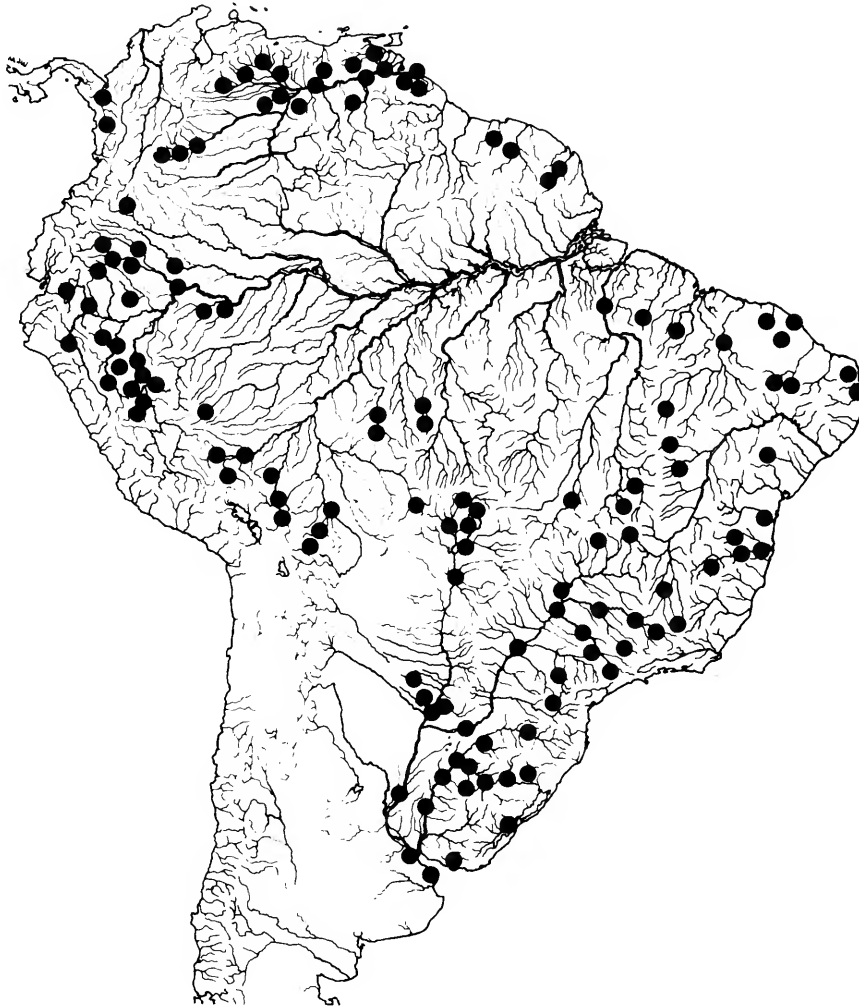


FIGURE 79.—Distribution of *Steindachnerina atratoensis*, *S. notonota*, *S. amazonica*, *S. guentheri*, *S. fasciata*, *S. insculpta*, *S. dobula*, *S. runa*, *S. elegans*, *S. brevipinna*, and *S. pupula* (Nodes G through L of Figure 78) showing absence of the species from the central portions of the Amazon basin.

insculpta, *notonota*, *pupula*, *runa*), or peripheral to the central Amazon (*amazonica*, *dobula*, *fasciata*, *guentheri*) (Figure 79). The only exceptions to that generalization are the four species of the terminal dichotomy and trichotomy (Nodes K and L), which appear to have undergone speciation with subsequent secondary dispersal within the central portions of the Amazon basin and the adjoining Rio Tocantins systems of eastern Brazil (Figure 80). The distribution patterns of the two groups of taxa overlap somewhat in the western portions of the Amazon basin and in the Rio Tocantins system, but are otherwise complementary. Indeed, if we leave aside the Tocantins system, which is actually peripheral to the main Amazon, the degree of overlap between the two assemblages of species is further reduced.

Admittedly no absolute timing of the speciation and dispersal events within the Node H portion of the phylogenetic tree is presently possible. Regardless of that limitation we can see that even in the Node F species of *Steindachnerina* where the sister-group relationship across the Andes occupies a relatively basal location within the cladogram, speciation within the central Amazon basin (Node M) apparently has contributed only a small degree to the overall number of intracladal speciation events.

A final feature of note with respect to the distribution of the species in *Steindachnerina* involves the distinct gap between the range of *S. atratoensis* to the west of the Andes, on the one hand, and the distribution of the remainder of the genus in the

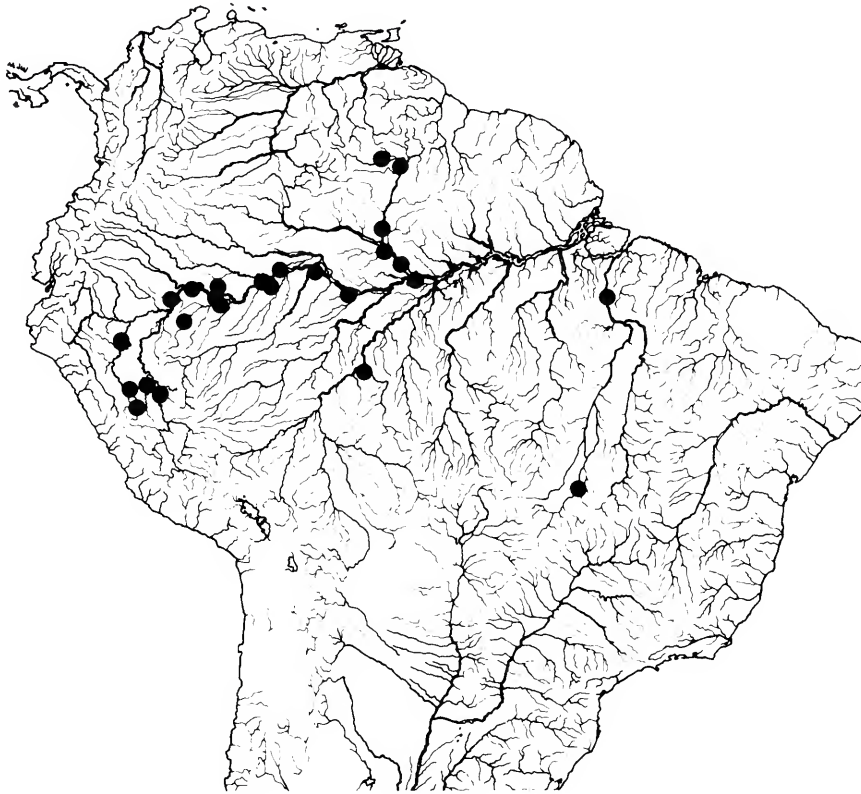


FIGURE 80.—Distribution of *Steindachnerina quasimodoi*, *S. gracilis*, *S. planiventris*, and *S. hypostoma* (Nodes M and N of Figure 78) showing occurrence of the species in the Rio Tocantins and central portions of the Amazon basin.

Atlantic drainages of the continent, on the other. As can be seen in Figure 38 the Río Atrato system is separated from the western cordilleras of the Andes by the Río Magdalena system. There is, in turn, an additional gap in the distribution of *Steindachnerina* across both the western slopes and intercordilleran valleys of the Andes and along the eastern piedmont of that mountain chain (Figure 79). Although curimatids are apparently poorly adapted for cold, high-gradient streams and rivers typical of the Andean highlands, the absence of any *Steindachnerina* species in the Río Magdalena basin, much of which is in the lowlands, and whose fish fauna has been reasonably well sampled, is unexpected.

The present distribution of *Steindachnerina* indicates that at some point prior to the uplift of the Andes the range of the ancestral species of Node G extended from some portion of what are now the Atlantic drainages of the continent across the area now occupied by the Magdalena basin to some portion of what is now the Río Atrato system. That ancestral species of Node G presumably underwent subsequent vicariance with a resultant separation of populations in areas now to either side of

the Andes. The lack of a species of *Steindachnerina* within the Río Magdalena system, an area of necessity within the range of the genus at some point, indicates that there has been secondary extinction within *Steindachnerina* in that drainage system. That extinction may have involved either populations of some ancestral species or populations of a descendant species of presently undeterminable phyletic affinities.

Lundberg et al. (1986) documented that extinction since the uplift of the Andean Cordilleras has taken place in at least some of the larger elements of the fish fauna of the Río Magdalena. A similar extinction phenomena also occurred in the fish fauna of those drainages to the east of the Andes located to the north of the Merida Andes (Lundberg et al., 1988). In the case of the Río Magdalena basin, Lundberg et al. (1986) hypothesized that such extinction, if common, might account for the present relatively depauperate nature of the ichthyofauna in that drainage basin. Such a hypothesis of large-scale extinction within the fish fauna of the Magdalena basin is congruent with indirect evidence arrived at from the phylogenetic and distributional data within *Steindachnerina*.

Appendix

Character Matrix for *Steindachnerina*

The following matrix presents the data for 29 discretely variable polarized features discussed in detail in the "Character Description and Analysis" that were used for the PAUP analysis (see "Synapomorphy List and Phylogenetic Reconstruction"). The characters are also briefly described in the "Character Summary" below. Synapomorphy numbers equivalent to those of Figure 11, the "Character Description and Analysis" and the "Synapomorphy List and Phylogenetic Reconstruction" follow each of the brief character summaries. This permits ready cross reference to the detailed discussions of the characters, their phylogenetic distribution, and polarities. No features uniquely autapomorphic for any species of the genus are included in the matrix. Such features are, however, discussed in the text and listed in the synapomorphy listing.

The outgroup was coded as "0" in all attributes for purposes of the analysis.

In order to use "Branch-and-Bound," the most powerful option in version 2.4 of PAUP, and simultaneously reduce the number of equivalent trees output by the program, all species that do not differ from each other or differ only in unique autapomorphies were combined into single encompassing units for purposes of the analysis (*notonota* + *amazonica* + *guentheri* + *fasciata*; *insculpta* + *runa*; *leucisca* + *binotata*; *elegans* + *brevipinna*; *gracilis* + *planiventris*). This procedure, which neither effects the actual topology of the final tree nor changes the consistency indices, resulted in three trees of 44 steps with consistency indices of 0.733. These trees only differed in the sequence of presentation of clades at one polytomy and thus represent the same phylogenetic topology that is presented in Figure 11.

Character matrix for species of *Steindachnerina*; 0 = primitive condition, 1-3 = derived conditions. See "Character Summary" for details of characters.

Species	Character																																	
	1	5	10	15	20	25																												
<i>amazonica</i>	3	1	0	1	1	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0		
<i>argentea</i>	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	
<i>atratoensis</i>	2	1	0	1	1	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	
<i>bimaculata</i>	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	
<i>binotata</i>	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	0	
<i>biornata</i>	1	1	0	1	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
<i>brevipinna</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	
<i>conspersa</i>	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	0	0	
<i>dobula</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>elegans</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	
<i>fasciata</i>	3	1	0	1	1	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	
<i>gracilis</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	1	2	0	0	0	1	0	1	0	1	1	1	0	1	0	1	
<i>guentheri</i>	3	1	0	1	1	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	
<i>hypostoma</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	1	2	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1
<i>insculpta</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>leucisca</i>	0	0	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0
<i>notonota</i>	3	1	0	1	1	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0
<i>planiventris</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	1	2	0	0	0	1	0	1	0	1	1	1	0	1	0	1	
<i>pupula</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>quasimodoi</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	1	1	0	0	0	1	0	1	0	1	1	1	0	1	0	1	
<i>runa</i>	3	1	0	1	1	2	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0

Character Summary

1. Portion of buccopharyngeal complex on roof of oral cavity: 0, three thin flaps; 1, thickened flaps, with or without lobulate bodies (Synapomorphy 21); 2, one or more series of lobulate bodies (Synapomorphy 26); 3, multiple series of lobulate bodies (Synapomorphy 30).
2. Posterior lobulate bodies of buccopharyngeal complex: 0, moderately developed; 1, well developed (Synapomorphy 22).
3. Anterior posteromedian flaps of buccopharyngeal complex: 0, simple; 1, fringed (Synapomorphy 5).
4. Lobulate processes of buccopharyngeal complex on anteroventral surface of first and second gill-arches: 0, absent or poorly developed; 1, well developed (Synapomorphy 23).
5. First infrapharyngobranchial (PB₁): 0, cartilaginous portion smaller than ossified; 1, cartilaginous portion much larger than ossified (Synapomorphy 1).
6. Second infrapharyngobranchial (PB₂): 0, no depression or dorsal and ventral flanges on medial surface; 1, moderately to well-developed depression and flanges (Synapomorphy 2); 2, well-developed depression and flanges (Synapomorphy 24).
7. Fifth upper pharyngeal tooth-plate: 0, narrow; 1, moderate to wide (Synapomorphy 27); 2, very wide (Synapomorphy 46).
8. Process on third hypobranchial (H₃) for attachment of ligament between second and third hypobranchials: 0, absent or poorly developed; 1, well developed (Synapomorphy 3).
9. Anterior extension of ventral process of third hypobranchial (H₃): 0, tip pointed; 1, tip subdivided (Synapomorphy 7).
10. Basihyal and basihyal tooth-plate: 0, narrow, elongate; 1, expanded anteriorly (Synapomorphy 4).
11. Mesopterygoid: 0, simple, not convoluted; 1, convoluted (Synapomorphy 31).
12. Mesopterygoid: 0, posterior portion narrow vertically; 1, posterior portion thickened vertically (Synapomorphy 32).
13. Metapterygoid: 0, vertically narrow anteriorly; 1, vertically thickened anteriorly (Synapomorphy 34).
14. Metapterygoid: 0, longitudinally straight; 1, longitudinally concave medially (Synapomorphy 35).
15. Third infraorbital (IO₃): 0, moderately elongate; 1, lengthened (Synapomorphy 8).
16. Fourth infraorbital (IO₄): 0, moderately developed, somewhat square; 1, reduced, more triangular (Synapomorphy 9).
17. Fifth infraorbital (IO₅): 0, definite anterior and posterior flanges on laterosensory canal segment; 1, flanges reduced (Synapomorphy 10).
18. Mesethmoid: 0, notched posteriorly; 1, expanded posteriorly (Synapomorphy 40).
19. Frontals: 0, well separated anteriorly; 1, slightly separated or in contact anteriorly (Synapomorphy 41); 2, in contact anteriorly (Synapomorphy 45).
20. Dark spot along dorsal midline immediately anterior of origin of dorsal fin: 0, absent; 1, present (Synapomorphy 11).
21. Dark spot along dorsal midline slightly posterior of tip of supraoccipital spine: 0, absent; 1, present (Synapomorphy 12).
22. Series of longitudinal spots along dorsal and dorsolateral surfaces of body: 0, absent; 1, present (Synapomorphy 14).
23. Dark pigmentation along lateral line: 0, absent; 1, slightly developed; 2, well developed (see discussion of Synapomorphies 25, 37, 38).
24. Dark spot of pigmentation at base of middle rays of caudal fin: 0, absent; 1, present (see discussion of Synapomorphies 6, 15).
25. Dark spot of pigmentation on basal portions of dorsal fin: 0, absent; 1, present (see discussion of Synapomorphies 16, 36, 39, 49).
26. Position of anus: 0, close to first anal-fin ray; 1, well separated from first anal-fin ray (Synapomorphies 17, 42).
27. Vertebrae: 0, number not increased; 1, number increased (Synapomorphy 18).
28. Number of scales along lateral line: 0, number not increased; 1, number increased (Synapomorphy 19).
29. Form of prepelvic region of body: 0, rounded or somewhat obtusely flattened; 1, distinctly flattened (Synapomorphy 43).

RESUMO

O gênero *Steindachnerina* Fowler (1906) é redefinido como uma unidade monofilética da família Curimatidae, ordem Characiformes. A posse em comum de caracteres derivados (sinapomorfias) no primeiro e segundo infra-faringobranquiais, terceiro hipobranquial, na forma do basi-hial e da placa dentígera do basi-hial, assim como, possivelmente, na pigmentação da nadadeira dorsal, diagnosticam o gênero. Sinapomorfias nos vários componentes dos arcos branquiais, complexo buco-faríngeo, série infra-orbital, arco palatino, neurocrânio, assim como a forma da região corporal pré-pélvica, detalhes de pigmentação, e caracteres merísticos definem subunidades monofiléticas para *Steindachnerina* ou são autapomórficos para as espécies do gênero.

Steindachnerina possui três sinônimos juniores, descritos por Fernández-Yépez (1948): *Curimatorbis*, *Cruxentina*, e *Rivasella*. São aqui reconhecidas 21 espécies no gênero *Steindachnerina*: *S. amazonica* (Steindachner, 1911), da bacia superior do rio Tocantins no leste do Brasil; *S. argentea* (Gill, 1858), encontrada nas partes ocidentais da ilha de Trinidad, partes média e baixa do sistema do rio Orinoco e em dois rios costeiros do norte da Venezuela; *S. atratoensis* (Eigenmann, 1912b), da bacia do rio Atrato, na Colômbia, a única espécie do gênero ocorrendo a oeste da Cordilheira Principal dos Andes; *S. bimaculata* (Steindachner, 1876), amplamente distribuída nos sistemas dos rios Amazonas e Orinoco; *S. binotata* (Pearson, 1924), limitada à parte superior da bacia do rio Madeira na Bolívia e Peru; *S. biornata* (Braga e Azpelicueta, 1987), do sistema do rio La Plata e dos rios costeiros do Uruguai e sudeste do Brasil; *S. brevipinna* (Eigenmann and Eigenmann, 1889), dos rios Uruguai, Paraguai, e parte inferior da bacia do rio Paraná e, possivelmente, da porção superior da bacia do rio Xingu; *S. conspersa* (Holmberg, 1891), habitando o rio Paraguai e baixo rio Paraná; *S. dobula* (Günther, 1868a), das partes ocidentais da bacia amazônica; *S. elegans* (Steindachner, 1874), dos rios costeiros da Bahia e partes setentrionais do estado de Minas Gerais, no Brasil; *S. fasciata* (Vari and Géry, 1985), endêmica das seções orientais da bacia do rio Madeira, no Brasil; *S. gracilis* Vari and Vari (1989), limitada ao sistema do rio Tocantins na porção oriental do Brasil; *S. guentheri* (Eigenmann and Eigenmann, 1889), ocorrendo em um arco começando na extremidade nordeste da Guiana, passando pela bacia do rio Orinoco e sopés da vertente ocidental dos Andes e terminando no noroeste da Bolívia; *S. hypostoma* (Boulenger, 1887a), amplamente distribuída nas porções central e oeste da bacia Amazônica; *S. insculpta* (Fernández-Yépez, 1948), endêmica da bacia do rio Paraná superior; *S. leucisca* (Günther, 1868), amplamente distribuída pela bacia Amazônica; *S. notonota* (Miranda-Ribeiro, 1937), das drenagens costeiras do nordeste do Brasil; *S. planiventris* Vari and Vari (1989), amplamente distribuída pela bacia Amazônica; *S. pupula*, uma espécie nova, endêmica da bacia do rio Orinoco; *S. quasimodoi* Vari and Vari (1989), do sistema do rio Yavarí (Javari), ao longo da fronteira entre o Brasil e o Peru; e *S. runa*, uma espécie nova, dos sistemas fluviais dos rios Suriname, Morawijne, e Oiapoque (Oiapock), no Suriname, Guiana Francesa, e Brasil, respectivamente. Uma chave para as espécies de *Steindachnerina* é fornecida.

Dezenove espécies e subespécies são colocadas em sinonímia neste estudo. *Curimatus leisciscus boliviae*, descrito por Eigenmann e Ogle (1907) da Bolívia, e *Allenina pectinata* Fernández-Yépez (1948), baseada em um espécime de Manacapuru, na Amazônia Central, são colocados na sinonímia de *Steindachnerina leucisca*. *Curimatus trachystetus* Cope (1878), baseado em um espécime da Amazônia Peruana, *C. bimaculatus sialis* descrito por Eigenmann and Eigenmann (1889) de uma série de exemplares originários de Manacapuru, Brasil, *Prochilodus pterostigma* Fowler (1913), com o holótipo da bacia do rio Madeira, *Curimatus semiornatus* Steindachner (1914), baseado em espécimes do rio Negro, no Brasil, e *Curimata melaniris* Fowler (1940), do rio Ucayali no Peru, são todas colocadas na sinonímia de *Steindachnerina bimaculata*. *Curimata stigmata* Vari (1987), descrita logo após *Curimata biornata* Braga e Azpelicueta (1987), é um sinônimo da última. *Curimatus nitens* Holmberg (1981), descrito do rio Paraguai na Argentina, e *Curimatus nigrotaenia* Boulenger (1902), com localidade-típica na parte superior da bacia do rio La Plata, são todos colocados na sinonímia de *Steindachnerina brevipinna*. *Curimatus nasus* Steindachner (1882), descritos de Canelos, no Equador, *Curimatus hypostoma hastata* Allen [in Eigenmann e Allen, 1942] baseada em um espécime do rio Pichis no Peru, *Curimata niceforei* Fowler (1943a), com a localidade-típica em Florencia, na Colômbia, e *Prochilodus stigmatarius* Fowler (1911), com uma localidade-típica questionável na vertente oriental dos Andes Equatorianos, são todas consideradas sinônimos de *Steindachnerina dobula*. *Steindachnerina guentheri* possui quatro sinônimos juniores: *Curimatus morawhannae* Eigenmann (1912a), *Curimatus issororoensis* Eigenmann (1912a), ambos descritos da região noroeste da Guiana, *Curimatus metae* Eigenmann (1922), baseado em espécimes de Villavicencio da bacia do rio Orinoco na Colômbia, e *Curimata robustula*

Allen (em Eigenmann e Allen, 1942), descrita a partir de material coletado em Yurimaguas, na Amazônia Peruana. *Curimatus elegans bahiensis* Eigenmann e Eigenmann (1889), descrito de uma série de exemplares coletados em local não especificado no estado da Bahia, no Brasil, é colocado na sinonímia de *Steindachnerina elegans*.

O estudo da biogeografia filogenética de *Steindachnerina* indica que dispersão secundária ocorreu várias vezes durante a evolução do gênero. De acordo com a hipótese formulada neste trabalho, os eventos de especiação mais antigos antecedem o levantamento dos Andes no final do Mioceno. Uma porção principal da especiação dentro do gênero ou antecedeu a formação da bacia Amazônica ou então ocorreu completamente fora do sistema do rio Amazonas ou, pelo menos, foi na periferia das porções centrais da bacia citada. A ocorrência prévia de uma espécie *Steindachnerina* na bacia do rio Magdalena na Colômbia e sua extinção subsequente no citado sistema fluvial, são previstas com base em dados filogenéticos e de distribuição.

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