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Systematics of the Neotropical Characiform Genus Pseudocurimata Fernández-Yépez (Pisces: Ostariophysi)

Richard P. Vari



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ABSTRACT

Vari, Richard P. Systematics of the Neotropical Characiform Genus *Pseudocurimata* Fernández-Yépez (Pisces: Ostariophysi). *Smithsonian Contributions to Zoology*, number 490, 28 pages, 18 figures, 1 table, 1989.—The genus *Pseudocurimata* Fernández-Yépez (1948) is redefined as a monophyletic subunit of the characiform family Curimatidae. Shared derived features in the position of the first proximal radial pterygiophore of the dorsal fin relative to the neural spines of the anterior vertebrae, the form of the anterior and medial articular surfaces of the second hypobranchial, and the pronounced reduction or complete loss of the second set of uroneurals define *Pseudocurimata* as a monophyletic lineage. Derived conditions of the second hypobranchial, fourth ceratobranchial, second set of uroneurals, position of the first proximal pterygiophore of the dorsal fin, number of vertebrae, and pigmentation characterize monophyletic clades within the genus or are autapomorphic for species. *Pseudocurimata* is unique among the genera recognized by Vari (1989) in being endemic to the rivers of the western versant of the Andes.

Six species are recognized in *Pseudocurimata: P. troschelii* (Günther, 1859), which inhabits the rivers draining into the Gulf of Guayaquil in southwestern Ecuador, and the Río Zarumilla and Río Tumbes of northwestern Peru; *P. boulengeri* (Eigenmann in Eigenmann and Ogle, 1907), which occurs in the rivers in southwestern Ecuador draining into the northern portions of the Gulf of Guayaquil; *P. lineopunctata* (Boulenger, 1911) of the Río San Juan, Río Dagua, and upper Río Atrato in western Colombia, and the coastal rivers of northern Ecuador; *P. patiae* (Eigenmann in Eigenmann, Henn, and Wilson, 1914) known only from the Río Patia in southwestern Colombia; *P. peruana* (Eigenmann, 1920a) of the Río Chira and Río Piura in northwestern Peru; and *P. boehlkei*, a new species from the Río Esmeraldas basin and possibly the Río Santiago system of northwestern Ecuador.

Curimatus brevipes Eigenmann and Ogle (1907) described on the basis of a specimen originating from an uncertain, possibly Peruvian, locality, and Curimatus aureus Pellegrin (1908) described from specimens collected in the Río Guayas basin of Ecuador, are both placed as synonyms of Pseudocurimata troschelii. Citations of the occurrence of Curimatus patiae in the coastal rivers of northwestern Peru and those of Curimatus peruanus from the Amazon drainages of Ecuador were misidentifications.

The historical zoogeography of the species of *Pseudocurimata* is discussed. The hypothesis of intrageneric phylogenetic relationships is congruent with a scheme of sequential north to south vicariance events along the western versant of the Andes in northwestern South America. The majority of the species in the genus have discrete allopatric distributions, with some degree of secondary, post-vicariance, dispersal evident in the rivers draining into the northern portions of the Gulf of Guayaquil in the southwest of Ecuador, and possibly in the Río Santiago system of northwestern Ecuador.

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Contents

	Page
Introduction	. 1
Methods and Materials	. 2
Abbreviations	_
Acknowledgments	
Character Description and Analysis	
Gill Arches	
Supraneurals and Proximal Radial Pterygiophores of Dorsal Fin	
Vertebrae	
Uroneurals	-
Pigmentation	-
Synapomorphy List and Phylogenetic Reconstruction	
Convergent Characters	
Comparisons with Previous Classifications	
Pseudocurimata Fernández-Yépez, 1948	
Key to the Species of <i>Pseudocurimata</i> Fernández-Yépez	
Pseudocurimata lineopunctata (Boulenger)	
Pseudocurimata patiae (Eigenmann)	
Pseudocurimata peruana (Eigenmann)	
Pseudocurimata boulengeri (Eigenmann)	
Pseudocurimata troschelii (Günther)	
Pseudocurimata boehlkei, new species	
Phylogenetic Biogeography	
Literature Cited	-
Index	. 28
چن از	

iii

Systematics of the Neotropical Characiform Genus Pseudocurimata Fernández-Yépez (Pisces: Ostariophysi)

Richard P. Vari

Introduction

The genus Pseudocurimata Fernández-Yépez as defined by Vari (1989) inhabits the Río Atrato of southwestern Colombia, which drains north to the Caribbean Sea, and a series of rivers emptying into the Pacific Ocean from southwestern Colombia, through western Ecuador, to northwestern Peru. Pseudocurimata, in the sense of that study, includes the majority of curimatid species resident in the river systems to the west of the Andean Cordilleras and is the only generic-level clade of the Curimatidae endemic to the rivers of the western slopes of the Andes. The restricted geographic distribution of the genus in northwestern South America is, in turn, reflected in the limited ranges of the species of Pseudocurimata, which are in some cases endemic to one or two small river systems. Such generic and specific level endemism in *Pseudocurimata* is noteworthy both in comparison to the more extensive ranges typical of most components of the South American ichthyofauna and relative to the much broader geographic distributions of all other curimatid genera (e.g., Curimatopsis (Vari, 1982a,b), Potamorhina (Vari, 1984a), Curimata (Vari, in press a), and Psectrogaster (Vari, in press b).

Vari (1989) redefined *Pseudocurimata* on the basis of the common possession of several derived features, and assigned seven nominal species of curimatids to the genus. The first of these was *Anodus troschelii* proposed by Günther (1859) based on specimens from the "Western Andes of Ecuador." That species was followed chronologically by *Curimatus boulengeri* Eigenmann (in Eigenmann and Ogle, 1907) from the Río Vinces of Ecuador, *C. brevipes* Eigenmann and Ogle (1907)

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from an unspecified location possibly in Peru, *C. aureus* Pellegrin (1908) based on specimens from the "Rio Guayas" of Ecuador, *C. lineopunctatus* Boulenger (1911) of the Río Tamana in Colombia, *C. patiae* Eigenmann (in Eigenmann, Henn, and Wilson, 1914) originating in the Río Patia of Colombia, and finally *C. peruanus* Eigenmann (1920a) from the Río Chira of northern Peru.

The nominal species of Pseudocurimata have been reported in checklists (e.g., Fowler, 1945; Ovchynnyk, 1968; Ortega and Vari, 1986), faunal studies (e.g., Böhlke, 1958; Chirichigno, 1963; Orcés, 1967), and monographic studies (e.g., Eigenmann, 1922). Nonetheless, the distinguishing features and actual distribution of all members of the genus, and indeed of all curimatids of the entire western versant of the Andes. remained poorly understood. This situation is the outgrowth of a number of factors. Most significant of these is the inadequate sampling of the fish fauna in all the rivers along the western slope of the Andes. The lack of detail in the original descriptions of all nominal forms presents addition problems in resolving questions of species validity and distribution. These problems and others, general within the Curimatidae, are well exemplified in Pseudocurimata, in which neither the recognizable species nor their exact distributions have been well understood. Indeed, reference to the species distribution maps in this paper indicates that although our knowledge of the distribution of the species of Pseudocurimata recognized as valid has improved to a degree in recent years, we can still only describe the geographic ranges of many forms in general terms.

The supraspecific taxonomy of the species united in *Pseudocurimata* in this paper has been the subject of alternative, often drastically different, schemes. Günther (1859:418) placed his species (*troschelii*) in *Anodus* Spix (in Spix and Agassiz, 1829), a genus that is not available in the Curimatidae (Roberts, 1974; Vari, 1983, 1989). He soon thereafter (Günther, 1864) shifted the species to *Curimatus*

(= Curimata Bosc). The other previously proposed species united herein in *Pseudocurimata* were originally described in Curimatus, Curimatus was used by nearly all authors prior to 1948 to encompass the vast majority of the then-known species of curimatids. That generic-level taxonomic stability was dramatically challenged with Fernández-Yépez's (1948:15) partitioning of the members of the Curimatidae (his Curimatinae) among twenty-seven genera. Fernández-Yépez proposed and diagnosed Pseudocurimata to encompass ten nominal species distributed through much of the geographic range of the Curimatidae on both sides of the Andean Cordilleras. Böhlke (1958:108) noted that the purported distinguishing features for Pseudocurimata failed, however, to separate the members of the genus from Curimatorbis, also described by Fernández-Yépez (1948). As a consequence Böhlke placed Pseudocurimata as a synonym of Curimatorbis. Böhlke's more inclusive concept of Curimatorbis was utilized by Orcés (1967) and Ovchynnyk (1968), but not by Chirichigno (1963), Géry (1972), and Fowler (1975). Those authors rather used Pseudocurimata or Curimata for some of the species in Pseudocurimata of this study.

Leaving aside momentarily the question of generic recognizability raised by Böhlke, we nonetheless confront the problem that Pseudocurimata as defined by Fernández-Yépez is not monophyletic. Only four of the species of Pseudocurimata of Fernández-Yépez (lineopunctata, troschelii, boulengeri, and brevipes) share the derived features hypothesized by Vari (1989) as diagnostic for the genus. The data of Vari indicate that these four species are furthermore united in a monophyletic lineage with three other nominal species assigned by Fernández-Yépez to Curimatorbis (peruana and patiae) or retained incerti sedis in Curimata (aureus). Fernández-Yépez incorporated six other nominal species in his broadly inclusive Pseudocurimata. Those species, excluded from the genus in this study, neither share the synapomorphies characteristic of the species assigned to Pseudocurimata by Vari (1989) and in this study, nor do they form a monophyletic group. Rather Pseudocurimata elegans (Steindachner, 1874), P. elegans bahiensis (Eigenmann and Eigenmann, 1889), P. morawhannae (Eigenmann, 1912a), and P. guentheri (Eigenmann and Eigenmann, 1889) of the classification proposed by Fernández-Yépez possess a number of derived features characteristic of Steindachnerina Fowler, and were consequently assigned by Vari (1989) to that genus. Pseudocurimata ocellata (Eigenmann and Eigenmann, 1889) of Fernández-Yépez shares synapomorphies in diverse body systems with the species of Curimata (Vari, 1989). Finally Pseudocurimata gilberti (Quoy and Gaimard, 1824) is transferred by Vari (1989) to the questionably monophyletic genus Cyphocharax Fowler. Thus it is evident that Pseudocurimata as defined by Fernández-Yépez was neither readily recognizable phenetically nor natural phyletically.

The uncertainties about species identity and distribution noted above, along with a lack of information on the intrageneric evolutionary history of the clade, demonstrate the need for a revisionary and phylogenetic reanalysis of Pseudocurimata. The present study has three major aims: first, to determine the recognizable species in the group and their distinguishing features; second, to analyze the morphological variation within *Pseudocurimata*, and propose a hypothesis of the phylogenetic relationships within the genus; and third, to delimit the known geographic distributions of the recognizable forms, and put forward a hypothesis on the historical biogeography of the genus. This paper is part of a series that deals with aspects of the phylogeny, taxonomy, and historical biogeography of curimatid characiforms (Vari, 1982a,b, 1983, 1984a,b, 1987, 1988; in press a,b; Vari and Castro, 1988; Vari and Géry, 1985; Vari and Nijssen, 1986; Vari and Vari, 1989). Vari (1989) advanced a hypothesis of generic- and suprageneric-level phylogenetic relationships within the Curimatidae. That study and the hypothesis of the relationship of the Curimatidae to its proximate sister groups, the Prochilodontidae, Anostomidae, and Chilodontidae, put forward by Vari (1983) provide the phyletic framework for the outgroup analyses and polarity determinations of those features that demonstrate discrete variability within Pseudocurimata. The hypothesis of the evolutionary relationships within Pseudocurimata is derived following the methodology outlined in previous phylogenetic studies of the Curimatidae, its components, and proximate relatives of the family (Vari, 1982a, 1983, 1984a, 1989, in press a,b).

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. Counts of total vertebrae were taken from radiographs and cleared and stained specimens, with the fused PU₁+U₁ considered a single bone, and the vertebrae incorporated into the Weberian complex counted as four elements. The numbers in parentheses that follow a particular vertebral count are the numbers of radiographed specimens with that count. In the species descriptions, 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). In the counts of median and pelvic fins, the unbranched fin-rays are indicated by lower case roman numerals and branched fin-rays are indicated by arabic numerals. The observed range in each species for the values of each count and measurement is presented first, followed by the value of the holotype or lectotype for a particular count or measurement, when available, in brackets. In the case of *Pseudocurimata troschelii*, which has two junior synonyms, the data in parentheses are the values for the lectotype of P. troschelii. Morphometric and meristic data for the type series of all nominal species considered conspecific with P. troschelii are presented in Table 1.

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 presented 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 first country (capitalized), then state, province, department or district as appropriate (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 Pseudocurimata boehlkei. The common names presented are those found in the literature, although such terminology is not necessarily standardized across the entire range of the species. Osteological preparations were cleared and counterstained for cartilage and bone using a modification of the technique outlined by Taylor and Van Dyke (1985).

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 (collections now at FMNH)
FMNH	Field Museum of Natural History, Chicago
IU	former Indiana University collections, now dis-
	persed to various repositories.
KU	University of Kansas, Museum of Natural History,
	Lawrence
MCZ	Museum of Comparative Zoology, Cambridge
MEPN	Museo de Biología de la Escuela Politécnica
	Nacional, Quito, Ecuador
MNHN	Muséum National d'Histoire Naturelle, Paris
NMNH	National Museum of Natural History, Smithsonian

NMW Naturhistorisches Museum, Vienna
NRM Swedish Museum of Natural History, Stockholm
UMMZ University of Michigan, Museum of Zoology, Ann
Arbor

Institution, Washington, D.C.

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USNM former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

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Character Description and Analysis

The synapomorphies defining *Pseudocurimata* as a monophyletic component of the Curimatidae and diagnosing monophyletic subunits of the genus are detailed in the immediately following sections. These shared derived features are listed and numbered sequentially on Figure 4. The numbering of the synapomorphies in the following descriptions and analyses corresponds to that in Figure 4 and the "Phylogenetic Reconstruction." In some instances, features that are phylogenetically informative relative to the monophyly of *Pseudocurimata* or clades within the genus were discussed in detail in previous publications centering on questions of intrafamilial or intrageneric relationships of curimatids. The reader is referred to the cited papers for further information on those features, the morphology of homologs in examined outgroups, and underlying hypotheses of polarity.

Gill Arches

SECOND HYPOBRANCHIAL (H₂).—The genera Curimata, Psectrogaster Eigenmann and Eigenmann, Steindachnerina, Curimatella Eigenmann and Eigenmann, and Cyphocharax, the proximate outgroups to Pseudocurimata (Vari, 1989), have a continuous cartilage of approximately constant thickness along the anterior and medial margins of the ossified portion of the second hypobranchial. That articular cartilage and the associ-

ated proximate ossified portions of H2 are significantly modified in Pseudocurimata. In all species of the genus both the ossified and cartilaginous portions of the second hypobranchial proximate to the anterolateral margin of the third basibranchial (BB3) are expanded vertically. As a consequence the articular surface (PMAP) between the second hypobranchial and the third basibranchial is vertically more extensive (Figures 1, 2) than in proximate outgroups. Associated with the vertical expansion of the articular surface on the second hypobranchial is the subdivision of the continuous articular cartilage along the anterior and medial margins of the element that is characteristic of sister groups to Pseudocurimata. All species of Pseudocurimata have two cartilage bodies along those margins of the second hypobranchial instead of a continuous cartilage. These cartilaginous articular surfaces are separated by an ossified region at the anteromedial angle of the bone (Figures 1, 2). The anterior cartilage mass extends along the anterior and anteromedial portion of the second hypobranchial, meeting its counterpart of the other side at the midsagittal plane (Figure 2). The longitudinally elongate medial articular cartilage on H2 contacts the lateral surface of the unpaired median cartilage body that extends along the anterior border of the ossified portion of the third basibranchial (BB₂).

The vertical expansion of the portion of the articular surface of the second hypobranchial proximate to the anterior cartilage of the third basibranchial and the subdivision of the originally continuous cartilage along the anterior and medial surfaces of the element into two discrete articular cartilages are hypothesized to jointly constitute a synapomorphy for the species of *Pseudocurimata* (SYNAPOMORPHY 1).

As discussed by Vari (1989), the presence of two separate cartilages along the anterior and medial margins of the second hypobranchial is not, however, limited to Pseudocurimata within the Curimatidae. Two distinct cartilage bodies along those borders of the ossification also occur in the curimatid genera Curimatopsis Steindachner and Potamorhina Cope. The cartilages in those two genera differ from the those in Pseudocurimata both in relative position and overall morphology. Furthermore neither the second hypobranchials in Curimatopsis nor those in Potamorhina demonstrate the vertical expansion characteristic of that element in Pseudocurimata. These structural differences raise the possibility of the non-homology of the conditions of the H₂ cartilages among those taxa. Such a hypothesis is furthermore congruent with the most parsimonious hypothesis of intrafamilial relationships (Vari, 1989). The presence of two cartilages along the anterior and medial margins of the second hypobranchial in Curimatorsis and Potamorhina on the one hand and Pseudocurimata on the other is consequently hypothesized to be homoplastic (see Vari, 1989, for further details on these features in the Curimatidae).

The ventral surface of the second hypobranchial also demonstrates a series of modifications that characterize monophyletic subunits of *Pseudocurimata*. All curimatids, with the exception of some species of *Pseudocurimata*, have a

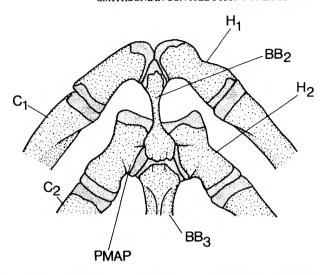


FIGURE 1.—Pseudocurimata peruana, USNM 285667, anterior section of ventral portion of gill arches, dorsal view (dense patterned stippling represents cartilage). (BB = basibranchial (2 and 3); C = ceratobranchial (1 and 2); H = hypobranchial (1 and 2); and PMAP = posteromedial articular process of second hypobranchial.)

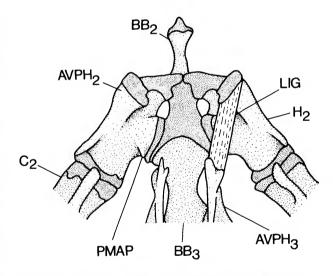


FIGURE 2.—Second hypobranchial and proximate elements of anterior section of ventral portions of gill arches, *Pseudocurimata peruana*, USNM 285667; ventral view (dense patterned stippling represents cartilage). Elements of first gill-arch not shown; ligament between anteroventral processes of second and third hypobranchials depicted only on one side. (AVPH = anteroventral process of hypobranchials (2 and 3); BB = basibranchials (2 and 3); C₂ = ceratobranchial 2; H₂ = hypobranchial 2; LIG = ligament between anteroventral processes of hypobranchials 2 and 3; PMAP = posteromedial articular process of second hypobranchial.)

relatively flat ventral surface of the second hypobranchial, characterized by a moderate development of ridges and bony sculpturing. This hypothesized plesiomorphous condition of the element, limited to *P. lineopunctata* within *Pseudocuri*

mata, is apomorphously modified at two levels in the genus. Five of the species in the genus (patiae, boehlkei, boulengeri, troschelii, and peruana) have a distinct ventral ridge on the anterolateral portion of the second hypobranchial (AVPH₂), Figure 2). The anterior portion of this ridge on the second hypobranchial is notably transversely expanded and serves as the area of attachment for the ligament (LIG) extending between the second hypobranchial and an anteriorly developed ventral process of the third hypobranchial (AVPH₃). The ventral process on the second hypobranchial is moderately developed in P. patiae, P. boulengeri, and P. boehlkei, and very prominent in P. troschelii and P. peruana (Figure 2). The increased degree of development of the anteroventral process of the second hypobranchial is derived at two levels of universality in Pseudocurimata. A moderately- to welldeveloped process on the second hypobranchial is synapomorphic for all species of Pseudocurimata other than P. lineopunctata (SYNAPOMORPHY 5). The highly developed, further derived, form of the process in P. troschelii and P. peruana is, in turn, a synapomorphy for that species pair (SYNAPOMORPHY 8).

FOURTH CERATOBRANCHIAL (C₄).—Vari (1983:13, 1989) noted that the Curimatidae and Prochilodontidae have in common a distinct process arising from the medial margin of the ventral surface of the fourth ceratobranchial. This apomorphous elaboration of C₄ serves as the area of attachment for various connective tissue bands associated with, and presumably involved in the support of, the ventral aorta and its branches. In Pseudocurimata lineopunctata there is an additional ventral bony process located somewhat lateral to the spur of the fourth ceratobranchial common to the Curimatidae and Prochilodontidae. This pair of processes straddles the efferent artery extending along the ventral surface of the fourth ceratobranchial. The presence of a second process on the ventral surface of the fourth ceratobranchial is unique to P. lineopunctata among examined curimatids and hypothesized autapomorphic for the species (SYNAPOMORPHY 4).

Supraneurals and Proximal Radial Pterygiophores of Dorsal Fin

Supraneurals are a series of midsagittal transversely flattened ossifications positioned dorsal of the vertebral column in the region between the rear of the neurocranium and the anteriormost subadjacent radial pterygiophore of the dorsal fin. The ventral sections of these elements and the proximal radial pterygiophores of the dorsal fin interdigitate with the dorsal portions of the neural spines of the proximate vertebrae. The vast majority of curimatids, including all proximate sister groups to *Pseudocurimata*, have two supraneurals located anterior of the neural spine on the first vertebrae posterior to the Weberian complex (the fifth vertebra). In some individuals, these two supraneurals are represented by a single plate having the overall outer profile of the two discrete supraneurals. Further posteriorly along the supraneural series, the third to

fifth supraneurals and the distal portions of the second to fourth neural spines interdigitate sequentially. The ventral portion of the first proximal radial pterygiophore of the dorsal fin interdigitates, in turn, between the distal portions of the fourth and fifth neural spines (see also Vari, 1989, fig. 43a for an illustration of the described arrangement of those elements common to most members of the Curimatidae).

All species of *Pseudocurimata* have patterns of association of the supraneurals, first proximal pterygiophore, and neural spines that differ from the generalized condition just described. The first proximal radial pterygiophore in *P. lineopunctata* and *P. patiae* inserts between the fifth and sixth neural spines (Figure 3A). A similar condition occurs in three-quarters of the examined specimens of *P. boehlkei*, with the other individuals of the species having the insertion of the element lying between sixth and seventh neural spines. The remaining species of *Pseudocurimata* (boulengeri, troschelii, peruana) have a more posterior insertion of the first pterygiophore between the sixth and seventh neural spines (Figure 3B).

Vari (1989) hypothesized on the basis of outgroup information that a posterior position of the interdigitation of the first proximal pterygiophore is derived within the Curimatidae. Pseudocurimata demonstrates shifts that are derived at two levels of universality. A shift posteriorly of the site of interdigitation of the first proximal pterygiophore one or more interneural spaces relative to the condition in other curimatids is synapomorphous for all species of Pseudocurimata (SYNA-POMORPHY 2). The posterior shift of the interdigitation two intraneural spaces, in turn, is hypothesized to be a synapomorphy for P. boulengeri, P. troschelii, and P. peruana (SYNAPO-MORPHY 6). The condition in P. boehlkei in which the majority of specimens have the site of insertion shifted posteriorly one interneural space, and one-quarter of the examined individuals have a more derived, further posterior insertion, is equivocal in terms of phylogenetically useful information. As a species, P. boehlkei presents an admixture of a more generalized condition and a further derived state. On the one hand one can hypothesize that the situations in P. boehlkei represents an intermediate condition in which the derived state is not fixed in all member of the species. This, nonetheless, does not address the appropriateness of using as a synapomorphy for the species a non-sexually dimorphic feature not manifest in all members of that taxon. As an alternative, it is possible to use a more conservative hypothesis in which the condition in P. boehlkei is considered equivalent to the more generalized condition found in P. lineopunctata and P. patiae. This does not make assumptions about the utility of the equivocal feature as a synapomorphy for P. boehlkei and the clade consisting of P. boulengeri, P. troschelii, and P. peruana, and is the procedure followed herein.

As noted by Vari (1989) a comparable posterior shift in the position of the insertion of the first proximal radial pterygiophore of the dorsal fin also occurs in one other species in the Curimatidae, *Curimata ocellata* Eigenmann and Eigenmann (1889) (with *Curimatus semitaeniatus* Steindachner (1917) as

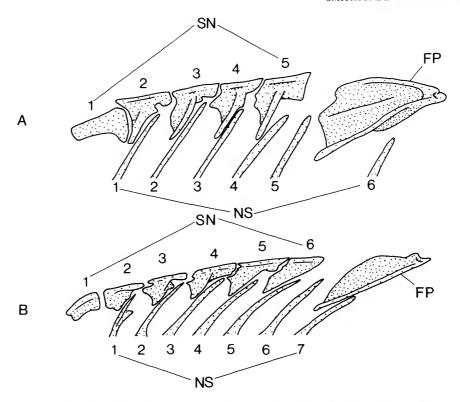


FIGURE 3.—Supraneurals, neural spines of proximate vertebrae, and first proximal radial pterygiophore of dorsal fin: A, Pseudocurimata lineopunctata, MCZ 54029; B, P. peruana, USNM 285667; left side, lateral view, anterior to left. (FP = first proximal radial pterygiophore of dorsal fin; NS = distal portions of neural spines of six or seven vertebrae posterior of Weberian complex; and SN = supraneurals.)

a junior synonym; Vari, in press a). On the basis of the overall most parsimonious phylogeny within the Curimatidae (Vari, 1989) and within *Curimata* (Vari, in press a), the common occurrence of that posterior position of the interdigitation of the first proximal pterygiophore in the species of *Pseudocurimata* on the one hand and *Curimata ocellata* on the other is hypothesized homoplastic.

Vertebrae

The number of vertebrae in the species of *Pseudocurimata* fall into two distinct groupings. *Pseudocurimata patiae* has 31 or 32 vertebrae, *P. boehlkei* has 33 or 34, and the number of those elements in *P. lineopunctata* ranges from 31 to 33. The remaining members of the genus have higher numbers of these elements, with *P. boulengeri* having 36 or 37 vertebrae, *P. peruana* having 35 or 36, and *P. troschelii* having 35 to 37. The lower number of vertebrae found in *P. patiae*, *P. boehlkei*, and *P. lineopunctata* is typical of the vast majority of curimatids including the species of *Psectrogaster* and *Curimata*, which are the proximate sister groups to the multichotomy in the Curimatidae that includes *Pseudocurimata* (Vari, 1989). Similarly, the members of the other lineages in the unresolved

multichotomy that includes *Pseudocurimata*, the genera *Curimatella*, *Cyphocharax*, and *Steindachnerina*, typically have low vertebral counts. A lower number of vertebrae is thus considered plesiomorphous within *Pseudocurimata*, and the presence of 35 to 37 vertebrae in *P. troschelii*, *P. peruana*, and *P. boulengeri* is considered a synapomorphy for those species (SYNAPOMORPHY 7).

Uroneurals

Vari (1982a:4-5) hypothesized that a reduction to one set of uroneurals from the two sets typical for characiforms was a synapomorphy for the species of the curimatid genus *Curimatopsis*. Subsequent analysis has shown that a greatly reduced or completely absent set of second uroneurals also occurs within the Curimatidae in all species of *Pseudocurimata*, albeit with intraspecific variation in the presence of those ossifications in one species. Three of the six examined cleared and stained specimens of *P. boulengeri* lack a second set of uroneurals, whereas in the remaining three individuals those elements are represented by very small ossifications. A set of second uroneurals of greatly reduced size occurs in the examined cleared and stained specimens of *P. lineopunctatus*, *P. patiae*,

and P. boehlkei. No indication of a second set of uroneurals was found in P. troschelii or P. peruana.

Under the overall most parsimonious hypothesis of generic relationships within the Curimatidae advanced by Vari (1989), the absence of a second set of uroneurals in the species of Curimatopsis and the reduction or loss of those elements in Pseudocurimata are considered to represent homoplastic reductions within the family. Thus the reductive trend in Pseudocurimata is hypothesized to be derived and is phylogenetically informative at two levels of universality. The loss of at least a portion (reduction) of the second set of uroneurals in all species of Pseudocurimata is considered to represent a synapomorphy for the genus (SYNAPOMORPHY 3). The loss of the remaining sections of the second set of uroneurals in all examined specimens of P. troschelii and P. peruana, in turn, is hypothesized to be a synapomorphy for the species pair (SYNAPOMORPHY 9). The variability in the presence of the ossifications in P. boulengeri might be hypothesized to be an intermediate condition between the reduced form of the bone in P. lineopunctata, P. patiae, and P. boehlkei and the complete loss of the elements in P. troschelii and P. peruana. Under such an assumption it would represent an additional synapomorphy for the clade consisting of P. boulengeri, P. troschelii, and P. peruana. Such a hypothesis, however, raises the question of the appropriateness of using as a synapomorphy for the species a non-sexually dimorphic feature not manifest in all members of that taxon. In light of the equivocal nature of such a transitional feature I prefer to adopt the more conservative practice of considering the condition in that species equivalent to the more generalized state in the genus, the presence of the ossifications.

Pigmentation

One autapomorphous pigmentation feature of *Pseudocurimata peruana* was noted during this study. That species has a discrete spot of dark pigmentation at the base of the middle rays of the caudal fin. Such a discrete spot, although unique to *P. peruana* in the genus, is approximated in a subunit of the curimatid genus *Psectrogaster*. The most parsimonious hypothesis of generic relationships within the Curimatidae (Vari, 1989) and of species relationships within *Psectrogaster* (Vari, in press b) indicate that the common occurrence of such a pigmentation pattern in subunits of *Psectrogaster* and *Pseudocurimata* is homoplastic. Thus the possession of the spot in *P. peruana* is considered autapomorphic (SYNAPOMORPHY 10).

Both *Pseudocurimata patiae* and *P. lineopunctata* have a discrete, dark, round or slightly horizontally elongate spot on the mid-lateral surface of the caudal peduncle. The two species also have in common multiple series of small, dark spots aligned in longitudinal patterns on the lateral and dorsolateral surfaces of the body. These pigmentation patterns are not apparent in adults of other species of *Pseudocurimata*, and would at first consideration appear to be derived conditions having a phyletic distribution incongruent with the proposed intrageneric cladogram. That hypothesis is, however, rendered less tenable when ontogenetic data on the development of adult

pigmentation patterns in other species of *Pseudocurimata* is considered.

An obscure round spot on the lateral surface of the caudal peduncle comparable to that in adults of P. lineopunctata and P. patiae occurs in smaller specimens of P. boulengeri, with a more elongate patch of chromatophores present in that region in larger specimens of that species. Juveniles of P. boehlkei similarly undergo an ontogenetic transition from a round mid-lateral dark spot on the caudal peduncle to a horizontally ovoid spot and finally to mid-lateral stripe (see Figures 15-17). The ontogenetic changes in P. boulengeri and P. boehlkei may parallel the phylogenetic polarity of the forms of dark pigmentation on the mid-lateral surface of the caudal peduncle within Pseudocurimata. If that is the case, then the dark round spot on the caudal peduncle in P. patiae and P. lineopunctata, although unique to them as adults, is primitive within Pseudocurimata. If that is the case, then the elongate mid-lateral patch of dark pigmentation in P. boehlkei, P. boulengeri, P. troschelii, and P. peruana may represent a synapomorphy for that assemblage of species.

Mid-lateral spots or stripes of dark pigmentation on the caudal peduncle have a restricted distribution within the Curimatidae. Thus the presence of those features in the species of Pseudocurimata is potentially an additional synapomorphy for *Pseudocurimata*. A rigorous evaluation of that hypothesis is not presently possible because Pseudocurimata is a portion of an unresolved multichotomy within the Curimatidae (Vari, 1989). Some, but not all, species of the other lineages in that incompletely dichotomized portion of the tree (Curimatella and Cyphocharax) have either dark spots or elongate patches of pigmentation mid-laterally on the caudal peduncle. Corroborated hypotheses of relationships among and within those genera are necessary before we can determine whether the dark pigmentation on the caudal peduncle in Pseudocurimata, Curimatella, and Cyphocharax is a primitive feature for all the genera or a derived condition with a homoplastic distribution among those taxa. It is thus premature to hypothesize on the level of inclusiveness at which it is appropriate to use this derived characteristic of the pigmentation.

The longitudinally aligned small dark spots on the body scales in juveniles and adults of P. patiae and P. lineopunctata are paralleled by comparable small patches of dense chromatophores on the lateral and dorsolateral surfaces of the body of juveniles of at least P. boehlkei. That species does not, however, manifest such pigmentation in larger specimens. Individuals of other species of Pseudocurimata of appropriate sizes to determine whether a comparable ontogenetic shift in body pigmentation occurs elsewhere in the genus are not available for study. The ontogenetic variability in the longitudinally aligned spots on the body of P. boehlkei nonetheless raises questions about the possible derived nature of the presence of such spots in adults of P. patiae and P. lineopunctata. Ontogenetically more inclusive series of all species of Pseudocurimata are necessary to resolve the questions of the distribution and phylogenetic polarity of this feature.

Synapomorphy List and Phylogenetic Reconstruction

The preceding section detailed the series of shared derived features common to members of Pseudocurimata or subunits of the genus. Vari (1989) analyzed the relationships of Pseudocurimata 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 Pseudocuri-In the following discussion the shared derived features congruent with a hypothesis of the monophyly of Pseudocurimata will be listed first. Further details on these character complexes and more in-depth discussions on their polarization are found in Vari (1989). The enumeration of the shared derived characters defining Pseudocurimata is followed by a listing of less universal synapomorphies common to intrageneric clades. The synapomorphies 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 4. Subsequent to the reconstruction of the most parsimonious hypothesis of phylogenetic relationships within Pseudocurimata there is a discussion of the known homoplastic characters in the genus.

Pseudocurimata does not have any known externally visible synapomorphies, although various subunits of the genus are phenetically distinctive. The genus is, however, characterized by three internal derived features. These synapomorphies are as follows:

- Expansion of the ossified and cartilaginous components of the portion of the second hypobranchial proximate to the third basibranchial. Associated with that expansion is the fission of the articular cartilage on the anterior and medial surfaces of the second hypobranchial (H₂) into two discrete cartilage bodies separated by an ossified notch (Figures 1, 2).
- Posterior shift of the region of interdigitation of the ventral portion of the first proximal radial pterygiophore of the dorsal fin to between the neural spines of the fifth and sixth, or sixth and seventh vertebrae posterior of the Weberian complex (Figure 3).
- Pronounced reduction to complete loss of the second set of uroneurals.

As noted under the discussion of "Pigmentation," the presence of a round spot or elongate stripe of dark pigmentation on the mid-lateral surface of the caudal peduncle may represent an additional synapomorphy for *Pseudocurimata*.

Pseudocurimata, characterized by synapomorphies 1 to 3, consists, in turn, of two less inclusive monophyletic lineages, one comprised by *P. lineopunctata*, and the second by the other five species of the genus.

Pseudocurimata lineopunctata has one known autapomorphous feature:

4. Possession of a ventrolateral bony process on the an-

teroventral surface of the fourth ceratobranchial (C_4) proximate to the afferent artery extending along the ventral surface of that element.

The lineage consisting of *Pseudocurimata patiae*, *P. boehlkei*, *P. boulengeri*, *P. troschelii*, and *P. peruana* is characterized by one known synapomorphy:

5. Moderately- to well-developed ridge on the anteroventral surface of the second hypobranchial (H₂) (Figure 2). That process serves as the point of attachment for the ligament joining the second hypobranchial with a comparable process of the third hypobranchial (H₃).

At this point in the phylogeny there exists a trichotomy that has not been resolved with evidence from the examined features. Those three clades are first, P. patiae, second, P. boehlkei, and third, the lineage consisting of P. boehlkei, P. boulengeri, P. troschelii, and P. peruana. These clades are discussed sequentially, with the order of presentation not indicative of any hypothesis of relationships.

No autapomorphous feature for *P. patiae* has been discovered during this study.

Pseudocurimata boehlkei is not known to have any autapomorphous features. If an elongate mid-lateral dark stripe on the caudal peduncle is indeed derived within Pseudocurimata as indicated by preliminary ontogenetic data (see "Pigmentation"), then the occurrence of that feature in P. boehlkei would be evidence that the species is the sister to the clade consisting of P. boulengeri, P. troscheli, and P. peruana, which also share that pattern. As noted under "Supraneurals and Proximal Radial Pterygiophores of Dorsal Fin," the variable shift posteriorly of the area of interdigitation of the first proximal radial pterygiophore one or two intraneural spaces in P. boehlkei could also be hypothesized to be a intermediate condition between the more generalized state and the derived condition in P. boulengeri, P. troscheli, and P. peruana in which the interdigitation is always located two intraneural spaces posteriorly. Under such a hypothesis the posterior shift of the site of interdigitation two intraneural spaces in at least some species would similarly indicate that P. boehlkei is the sister species to the lineage consisting of P. boulengeri, P. troscheli, and P. peruana.

Pseudocurimata boulengeri, P. troschelii, and P. peruana have in common the following synapomorphies:

- Posterior shift of the region of interdigitation of the ventral portion of the first proximal radial pterygiophore of the dorsal fin to between the neural spines of the sixth and seventh vertebrae posterior of the Weberian complex (Figure 3B).
- 7. Possession of 35 to 37 vertebrae.

The variably present second set of uroneurals in *P. boulengeri* may be another synapomorphy uniting that species to *P. troscheli* and *P. peruana* in which those elements are totally lacking (see discussion under "Uroneurals").

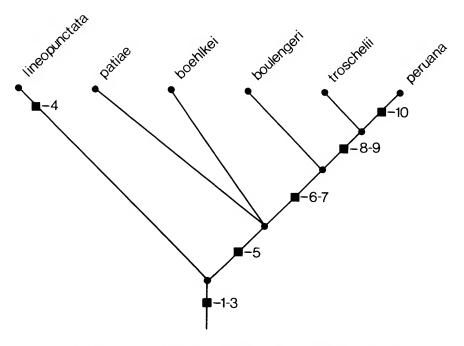


FIGURE 4.—Cladogram of the most parsimonious hypothesis of relationships for the species of the genus *Pseudocurimata*. The numbered synapomorphies of the figure correspond to those of the text (see "Phylogenetic Reconstruction").

The clade sharing synapomorphies 6 and 7 is subdivided into two lineages, with one formed by *Pseudocurimata boulengeri* and the other by the species pair *P. troschelii* and *P. peruana*.

No autapomorphies for *Pseudocurimata boulengeri* were found during this study.

Pseudocurimata troschelii and P. peruana, in contrast, have in common two synapomorphies.

- 8. Well-developed form of the ridge on the anteroventral surface of the second hypobranchial (H₂). That process serves as the point of attachment for the ligament extending to the comparable process on the third hypobranchial (H₂).
- 9. Complete loss of the second set of uroneurals.

Pseudocurimata peruana has one known autapomorphous feature.

 The small, discrete spot of dark pigmentation at the base of the middle rays of the caudal fin.

No autapomorphies for *P. troschelii* were discovered in the course of this study.

Convergent Characters

Among the shared derived characters noted in the phylogenetic analysis of *Pseudocurimata* are two synapomorphies for the members of the genus that appear homoplasticly elsewhere within the Curimatidae. The posterior shift of the

interdigitation of the ventral portion of the first proximal radial pterygiophore of the dorsal fin, common to all members of *Pseudocurimata*, is also found in *Curimata ocellata*. As noted by Vari (1989, in press a) it is most parsimonious to assume that the common occurrence of the posterior shift of that area of interdigitation in *Pseudocurimata* and *Curimata ocellata* is homoplastic.

The pronounced reduction or complete loss of the second set of uroneurals in *Pseudocurimata* is paralleled by the absence of those elements in all species of *Curimatopsis* (Vari, 1982a:4-5). Once again the most parsimonious hypothesis of intrafamilial relationships (Vari, 1989) indicates that the reductive trend occurred independently in the two lineages.

No homoplasies internal to *Pseudocurimata* were identified during the course of this study (but see also discussion under "Pigmentation").

Comparisons with Previous Classifications

Classifications of the Curimatidae prior to Fernández-Yépez (1948) (e.g., Eigenmann, 1910, 1922) united all the members of *Pseudocurimata* in the sense of this study in a practically all-encompassing *Curimata*. Under that definition, *Curimata* included all members of the family lacking the distinctive external features used to delimit the other, typically less speciose, genera then in general use (*Curimatopsis*, *Potamorhina*, *Curimatella*). In retrospect we can now see that *Curimata* served as a catch-all genus defined on the basis of shared primitive features. The groupings of species on the basis

of such features may or may not delimit a monophyletic unit, and there does not exist any a priori system for determining the naturalness of such taxa. Subsequent analysis has shown that the characters distinguishing *Curimata* under the classifications in use during most of the first half of this century did not delimit a monophyletic assemblage within the Curimatidae. These classifications also failed to indicate the phyletic associations of the species united herein in *Pseudocurimata*.

Various authors prior to 1948, most notably Fowler, proposed a limited number of additional genera and subgenera within the Curimatidae. These were rarely or only irregularly used by most researchers publishing on the family. A major shift in the taxonomy of the family involved the revamping of the classification of the family by Fernández-Yépez (1948). The introduction to the present paper alluded to the diverse permutations of supraspecific taxonomy involved in various concepts of *Pseudocurimata* as first advanced by Fernández-Yépez and subsequently modified by Böhlke (1958) and other researchers. Those authors noted the problems in determining in retrospect why Fernández-Yépez thought it necessary to segregate the species of his *Pseudocurimata* from those of his Curimatorbis. Reference to the generic diagnoses and "key" in Fernández-Yépez's publication (1948:16, 42, 45) reveals only one purported distinguishing feature, a difference in the relative length of the pectoral fins. Böhlke (1958:108-109) noted that this reported gap between Pseudocurimata and Curimatorbis was bridged within samples of a single species of Pseudocurimata. As a result Böhlke united the two genera as Curimatorbis. This taxonomic shift was followed by Orcés (1967) and Ovchynnyk (1968) but not by Chirichigno (1963) and Géry (1972) who rather used Curimata for the species of Pseudocurimata, or Fowler (1975) who continued to recognize Pseudocurimata. A re-examination of the single feature purportedly distinguishing Pseudocurimata from Curimatorbis has shown that it is ontogenetically and geographically variable, conclusions in agreement with those of Böhlke.

Pseudocurimata as defined by Vari (1989) is, however, distinguished from Steindachnerina, the senior synonym of Curimatorbis, in a number of derived features. Pseudocurimata is consequently resurrected from the synonymy of Curimatorbis (see Vari, 1989, for a more in-depth discussion).

Pseudocurimata Fernández-Yépez, 1948

Pseudocurimata Fernández-Yépez, 1948:45 [type species Curimatus lineopunctatus Boulenger, 1911, by original designation].

DIAGNOSIS.—Pseudocurimata is a group of curimatid species occurring along the western versant of the Andes. The genus is distinctive within the Curimatidae in three derived features: (a) the pattern of interdigitation of the ventral portions of the supraneurals and first proximal radial pterygiophore of the dorsal fin with the distal portions of the anterior neural spines, (b) the form of the medial articular surface and anterior and medial articular cartilages of the second hypobranchial, and (c) the pronounced reduction or complete loss of the second set of uroneurals (see "Phylogenetic Reconstruction").

Maximum known standard lengths of species 109 to 155 mm. Dorsal-fin rays ii,9 or 10, iii,9; anal-fin rays ii,7-8 or iii,7; pectoral-fin rays 12 to 16; pelvic-fin rays i,7-9; adipose fin always present. Pored lateral-line scales from supracleithrum to hypural joint range from 33 to 57; sensory canals in lateral-line scales straight. Number of scales in transverse series from origin of dorsal fin to lateral line 7 to 11; number of scales in transverse series from origin of anal fin to lateral line 5 to 9. Total vertebrae 31 to 37.

REMARKS.—This genus is unique in the Curimatidae in being endemic to the drainage systems to the west of the Andean Cordilleras. Although Pseudocurimata is not considered to have any junior synonyms in this study, Fernández-Yépez in his original description of the genus (1948:45) placed Cyphocharax Fowler (1906) (misspelled by Fernández-Yépez as Ciphocharax) as a synonym of Pseudocurimata. Fernández-Yépez (1948:45) implied that his unusual action was a consequence of his uncertainty as to the validity of Cyphocharax, which he felt was based on "characters without importance, which in reality cannot be clearly defined" (my translation). Fernández-Yépez did not examine specimens of the type species of Cyphocharax (Curimatus spilurus Günther, 1864) prior to questioning the usefulness of the characters used by Fowler to distinguish the genus. The phylogenetic hypothesis put forward by Vari (1989) indicates that Cyphocharax does not share the defining features of Pseudocurimata. The two genera as a result are recognized as distinct.

Böhlke (1958) recognized that the difference in relative pectoral-fin length used by Fernández-Yépez to distinguish *Pseudocurimata* from *Curimatorbis* was not valid, and united the two genera under the latter genus, which had page priority. Contrary to that practice I use *Pseudocurimata* for the species treated in this study. This action is taken because the type species of *Curimatorbis* (*Curimatus atratoensis* Eigenmann, 1912b) is more closely aligned phyletically to the species placed in *Steindachnerina* Fowler (1906) by Vari (1989) rather than to the taxa included in *Pseudocurimata*.

The hypothesis of relationships within Pseudocurimata could be translated into a classification using a variety of alternative schemes. Many involve the proposal of a formal name for all clades defined by shared derived characters. Such systems have the advantage of allowing the reader to derive the proposed phylogeny from the presented classification in the absence of a cladogram. Such systems can, however, be cumbersome in practice in almost invariably necessitating the proposal of additional taxa at diverse taxonomic levels. In Pseudocurimata the application of that system would require three new subgeneric but supraspecific names. In light of the limited advantages of a cumbersome system in this moderately speciose group, formal nomenclatural recognition is given only to Pseudocurimata and its contained species. The reader is referred to "Phylogenetic Reconstruction" and the proposed phylogeny (Figure 4) for details on the hypothesis of intrageneric relationships.

Key to the Species of Pseudocurimata Fernández-Yépez

1.	Discrete, dark, large, round spot on mid-lateral surface of caudal peduncle [Figures
	5-7, 9]; scales on lateral and dorsolateral surface of body with distinct dark spots,
	spots aligned into longitudinal series in specimens of all sizes
	Caudal peduncle with mid-lateral, distinctly horizontally elongate band [Figures 10,
	13, 16, 17] or obscure mid-lateral patch of dark pigmentation [Figure 12], but
	without dark, round spot except in smaller specimens; body scales without distinct
	spots aligned to form longitudinal series, or with spots faintly present only in small
	individuals
2.	Lateral line scales from supracleithrum to hypural joint 33 to 41 (Río San Juan, Río
_,	Dagua, upper Río Atrato, western Colombia; rivers of northern Esmeraldas
	Province, Ecuador)
	Lateral line scales from supracleithrum to hypural joint 42 to 47 (Río Patia basin,
	Colombia)
3.	Discrete small spot of dark pigmentation at base of middle caudal-fin rays [Figure
٥.	10]; spot separate from mid-lateral stripe on caudal peduncle (Río Chira and Río
	Tumbes, northwestern Peru and southeastern Ecuador
	Mid-lateral stripe of caudal peduncle terminating at hypural joint in adults, without
	discrete spot at base of middle rays of caudal fin; body stripe sometimes extending
	as diffuse band onto base of caudal-fin rays in juveniles, but not forming discrete
4	basal spot on fin
4.	Lateral line scales to hypural joint 50 to 57; 10 to 11 scales above lateral line to origin
	of dorsal fin; 8 or 9 scales below lateral line to origin of anal fin (rivers draining
	into northern portions of Gulf of Guayaquil, southwestern Ecuador)
	P. boulengeri
	Lateral line scales to hypural joint 39 to 47; 7 to 9 scales above lateral line to origin
_	of dorsal fin; 5 to 7 scales below lateral line to origin of anal fin 5
5.	Dark patch of pigmentation on mid-lateral surface of caudal peduncle in the form of
	horizontally moderately elongate triangle, wider posteriorly; 35 to 37 vertebrae;
	greatest body depth 0.33-0.37 of SL; lateral line scales to hypural joint 42 to 47;
	scales above lateral line to origin of dorsal fin 7 or 8 (rivers flowing into Gulf of
	Guayaquil, southwestern Ecuador, and Río Zarumilla and Río Tumbes,
	northwestern Peru)
	Dark patch of pigmentation on mid-lateral surface of caudal peduncle horizontally
	elongate, not distinctly wider posteriorly; 33 or 34 vertebrae; greatest body depth
	0.29-0.33 of SL; lateral line scales to hypural joint 39 to 42; scales above lateral
	line to origin of dorsal fin 81/2 or 9 (Río Esmeraldas and Río Santiago basins,
	northwestern Ecuador)

Pseudocurimata lineopunctata (Boulenger)

FIGURES 5-8

Curimatus lineopunctatus Boulenger, 1911:213 [type locality: Colombia: Choco, Río Tamana at Novita].—Regan, 1913:466 [Colombia: Tamana].— Eigenmann, 1920a:15 [Colombia: Río Atrato, Río San Juan, Río Dagua]; 1920b:11 [Colombia, Río Atrato, Río San Juan]; 1922:103, pl. 18: fig. 2 [Colombia: Río Dagua, Río San Juan, Río Atrato].—Vari, 1989, tables 2, 3 [phylogenetic relationships].

Curimata lineopunctata.—Fowler, 1944:227 [Colombia: Nuqui].

Pseudocurimata lineopunctata.—Fernández-Yépez, 1948:45, fig. 22 [designated as type species of Pseudocurimata Fernández-Yépez].—Vari, 1988:337, fig. 13 [historical biogeography].

Curimatorbis lineopunctata.—Orcés, 1967:138 [possible citation; Ecuador, Río Santiago system, Río Bogotá, Río Balzalito, Río Palabí; see "Remarks"].
Curimatorbis lineopunctatus.—Ovchynnyk, 1968:250 [Ecuador: Río Esmeraldas system, Río Santiago].

Pseudocurimata lineopunctatus.—Fowler, 1975:373 [reference].

DIAGNOSIS.—The possession of a pattern of distinct dark spots arranged in longitudinal series on the lateral and dorsal surfaces of the body, a discrete large, round or slightly horizontally elongate dark spot on the mid-lateral surface of the caudal peduncle, and 31 to 33 vertebrae distinguish *Pseudocurimata lineopunctata* from all other members of the genus other than *P. patiae* and smaller individuals of *P. boehlkei. Pseudocurimata lineopunctata* has 33 to 41 lateral line scales in contrast to the 42 to 47 scales in that series in *P. patiae.* Adults of *Pseudocurimata lineopunctata* and *P. boehlkei* are differentiated by a variety of features of body pigmentation (see Figures 5-7 versus 15-17, and "Key").

DESCRIPTION.—Body relatively robust, only slightly com-



FIGURE 5.—Pseudocurimata lineopunctata, USNM 287744, juvenile, 40.1 mm SL; Ecuador, Esmeraldas, Estero La Boveda, 4 km from Camerones (Atahualpa).



FIGURE 6.—Pseudocurimata lineopunctata, USNM 287744, 83.7 mm SL; Ecuador, Esmeraldas, Estero La Boveda, 4 km from Camerones (Atahualpa).



FIGURE 7.—Pseudocurimata lineopunctata, USNM 79193, 98.9 mm SL; Colombia, Chocó, Istmina.

pressed. Dorsal profile of head straight or more typically 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. Pre-pelvic region transversely rounded, somewhat obtusely flattened proximate to pelvic fins, without enlarged scales. Post-pelvic region with obtuse median keel posterior to pelvic fin insertion. Secondary obtuse keel on each side of post-pelvic portion of body about two scales dorsal of ventral midline.

Greatest body depth at origin of dorsal fin, depth 0.36–0.41 [0.36]; snout tip to origin of dorsal fin 0.48–0.52 [0.50]; snout tip to origin of anal fin 0.79–0.83 [0.79]; snout tip to insertion of pelvic fin 0.51–0.58 [0.51]; snout tip to anus 0.74–0.79 [0.74]; origin of dorsal fin to hypural joint 0.53–0.58 [0.56]. Margin of dorsal fin rounded; anteriormost rays approximately two-and-one-half times length of ultimate ray. Border of pectoral fin pointed; length of pectoral fin 0.18–0.23 [0.19], extends about two-thirds distance to vertical through insertion of pelvic fin. Pelvic fin pointed, length of pelvic fin 0.21–0.26 [0.22], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Border of anal fin emarginate, anteriormost branched anal-fin rays about three times length of ultimate ray. Caudal peduncle depth 0.14–0.15 [0.15].

Head distinctly pointed, head length 0.27-0.33 [0.27]; jaws equal, mouth terminal; snout length 0.26-0.32 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.31-0.33 [0.33]; adipose eyelid poorly developed, with broad ovoid opening over center of eye; length of postorbital portion of head 0.37-0.44 [0.43]; gape width 0.27-0.32 [0.28]; interorbital width 0.43-0.47 [0.44].

Pored lateral line scales from supracleithrum to hypural joint 33 to 41 [39]; all scales of lateral line pored, canals in scales straight; 3 to 6 series of scales extend beyond hypural joint onto caudal-fin base; 7 to $8^1/2$ [8] scales in transverse series from origin of dorsal fin to lateral line; $5^1/2$ to 7 [6] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or rarely iii,9 [ii,9]; anal-fin rays ii,7 or 8 or iii,7 [ii,7]; pectoral-fin rays 13 or 14 [13]; pelvic-fin rays i,8 or 9 (i,9 rare) [i,8].

Total vertebrae 31 (1), 32 (13), 33 (4).

COLOR IN ALCOHOL.—Specimens retaining guanine on scales silvery to silvery-golden, darker on dorsal portions of head and body. Specimens lacking guanine on scales with overall tan ground coloration. No pronounced pigmentation pattern on head. Scales of lateral surface of body with small central spots of dark pigmentation. Spots aligned in longitudinal series along scale rows. Longitudinal series of spots distinct along three longitudinal rows on scales dorsal to lateral line, along scales of lateral line, and on three longitudinal rows of

scales ventral of lateral line. Spots on dorsal portion of body blending into darker overall pigmentation. Larger specimens with incomplete series of spots on fourth longitudinal series of scales ventral of lateral line. Prominent rotund, mid-lateral patch of dark pigmentation on caudal peduncle. Patch more prominent in juveniles; extends four or five scales longitudinally and three or four scales vertically. Scattered small chromatophores on median fins. Paired fins hyaline.

DISTRIBUTION.—Río San Juan, Río Dagua, and upper portions of Río Atrato systems in Colombia; rivers of northern portion of Esmeraldas Province in Ecuador (Figure 8, see "Remarks").

REMARKS.—Boulenger's original description of *Curimatus* lineopunctatus (1911:213) was based on four specimens in the

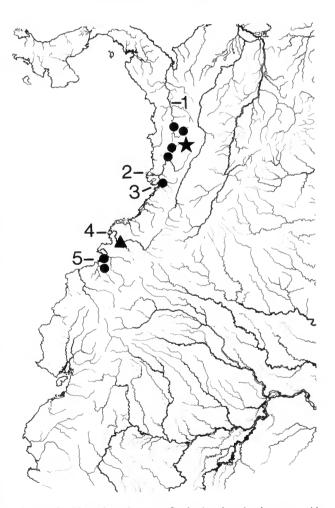


FIGURE 8.—Map of northwestern South America showing geographic distribution of *Pseudocurimata lineopunctata* (star = lectotype locality, filled circles = sites of other collections of the species) and *Pseudocurimata patiae* (triangle) (some symbols represent more than one collecting locality or lot of specimens). (Locations: 1 = Río Atrato; 2 = Río San Juan; 3 = Río Dagua; 4 = Río Patia; and 5 = rivers of northwestern Ecuador, see "Material Examined" under *Pseudocurimata lineopunctata*).

British Museum (Natural History). One of the syntypes, a 113.5 mm SL individual in the best overall condition, is designated as the lectotype (BMNH 1910.7.11:159). The other three syntypes (BMNH 1910.7.11:160–162) thus become paralectotypes.

Pseudocurimata lineopunctata is the only member of the genus inhabiting both river systems draining into the Caribbean Sea and rivers running into the Pacific Ocean. The distribution of the species extends from the Río Atrato of Colombia south to various river systems in Esmeraldas Province of northern Ecuador, but with a major gap in the known distribution of the species in southwestern Colombia. With the exception of the Río Patia, the rivers of that region were not sampled by Eigenmann and his associates in their extensive collecting efforts along the western versant of the Andes (see Eigenmann. 1922, pl. XXXVII). Neither do I know of subsequent collecting efforts in those drainage systems. It is thus likely that the gap in the known distribution of P. lineopunctata in southwestern Colombia is a sampling artifact. Interestingly, P. patiae, a closely related species occurs in, and is endemic to, at least one of the intervening rivers in that region, the Río Patia of southwestern Colombia.

Orcés (1967:138) cited Curimatorbis (= Pseudocurimata) lineopunctata from the Río Santiago drainage basin. Although the species does occur in that drainage system (see "Material Examined") it questionable whether the material examined by Orcés was that species. The number of lateral line scales given by Orcés for his specimens (42 to 47) is greater than that in P. lineopunctata (33 to 41) and P. boehlkei (39 to 42), the only curimatids known from that portion of Ecuador. More significantly the anal-fin ray counts reported by Orcés (1967:138) for the specimens ("iv25 to iv27") lie outside the range of those counts for all members of the Curimatidae.

MATERIAL EXAMINED.—50 specimens (31, 33.4-113.5)

COLOMBIA. Choco. Río Tamana at Novita, BMNH 1910.7.11:159, 1 (113.5, lectotype of Curimatus lineopunctatus); BMNH 1910.7.11:160-162, 3 (75.0-100.8, paralectotypes of Curimatus lineopunctatus); NMW 68810, 2; NMW 68811, 2. Miqui, Río Jurabida, ANSP 136672, 1. Managru, Río Atrato basin, USNM 287595, 2 (44.5-105.1). Río Condoto, BMNH 1914.5.18:1-3, 4 (2, 84.0-99.9). Istmina, CAS 60761, 3 (84.2-107.9, formerly IU 12808); USNM 79193, 3 (92.5-107.9). Río Atrato basin, Boca de Raspadura, CAS

60760, 1 (82.0, formerly IU 13057). Río San Juan, Andagoya, BMNH 1915.10.1:1-3, 3 (1, 65.2). Río San Juan, Puerto Negria, USNM 287596, 4 (33.4-97.3).

ECUADOR. Esmeraldas. Ríos Cayapas, Hoja Blanca and San Miquel near village of San Miquel (Río Santiago basin), MCZ 54029, 10 (5, 40.0-84.5). Río Cachabí (Río Santiago basin), FMNH uncat., 2 (65.9-77.2). Estero La Boveda, 4 km from Camerones (Atahualpa) (0°52'N, 78°59'W) (Río Santiago system), USNM 287744, 9 (4,56.7-83.0).

Pseudocurimata patiae (Eigenmann)

FIGURES 8,9

Curimatus patiae Eigenmann in Eigenmann, Henn, and Wilson, 1914:12 [type locality: Colombia: Barbacoas].—Eigenmann, 1914:279 [Colombia: Barbacoas]; 1920a:15 [Colombia: Río Patia basin]; 1922:104, pl. 18: fig. 3 [Colombia: lower Río Patia basin].—Vari, 1989, tables 2, 3 [phylogenetic relationships; assignment to Pseudocurimata] [not Chirichigno, 1963:19; Ortega and Vari, 1986:11].

Curimatorbis patiae.—Fernández-Yépez, 1948:43 [assignment to Curimatorbis].—Fowler, 1975:370 [reference].

Pseudocurimata patiae.—Vari, 1988:337, fig. 13 [historical biogeography].

DIAGNOSIS.—The possession of a discrete, dark, round or slightly elongate dark spot on the mid-lateral surface of the caudal peduncle of all size specimens, distinguishes *Pseudocurimata patiae* from all congeners other that *P. lineopunctata*. The pattern of distinct dark spots on the body scales arranged in longitudinal series also separates *Pseudocurimata patiae* from congeners, with the exception of *P. lineopunctata* and smaller individuals of *P. boehlkei*. The 42 to 47 lateral line scales of *P. patiae* contrast with the 33 to 41 scales in that series in *P. lineopunctata*. Differences in meristics and adult pigmentation, in turn, distinguish *P. patiae* and *P. boehlkei* (see Figures 9, 15–17, and "Key").

DESCRIPTION.—Body moderately elongate, somewhat compressed, more so in larger specimens. Dorsal profile of head straight or more typically 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, 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

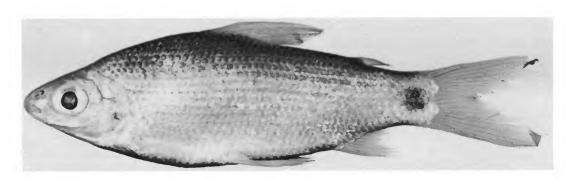


FIGURE 9.—Pseudocurimata patiae, paratype, CAS 60622 (formerly IU 13055), 110.8 mm SL; Colombia, Nariño, Barbacoas.

of lower jaw to caudal peduncle. Pre-pelvic region obtusely flattened, without enlarged scales. Obtuse median keel posterior to pelvic fin insertion.

Greatest body depth at origin of dorsal fin, depth 0.31–0.35 [0.32]; snout tip to origin of dorsal fin 0.49–0.54 [0.50]; snout tip to origin of anal fin 0.78–0.84 [0.84]; snout tip to insertion of pelvic fin 0.52–0.55 [0.54]; snout tip to anus 0.73–0.79 [0.79]; origin of dorsal fin to hypural joint 0.53–0.57 [0.55]. Margin of dorsal fin obtusely pointed; anteriormost rays about three times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.18–0.21 [0.18], extends about two-thirds distance to vertical through insertion of pelvic fin. Pelvic-fin margin pointed, length of pelvic fin 0.20–0.24 [0.20], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin-border slightly emarginate, anteriormost branched rays two-and-one-half times length of ultimate ray. Caudal peduncle depth 0.13–0.14 [0.13].

Head distinctly pointed, head length 0.26-0.28 [0.26]; upper jaw longer, mouth subterminal; snout length 0.27-0.31 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.30-0.32 [0.31]; adipose eyelid poorly developed, with broad ovoid opening over center of eye; length of postorbital portion of head 0.39-0.42 [0.39]; gape width 0.26-0.31 [0.31]; interorbital width 0.42-0.44 [0.44].

Pored lateral line scales from supracleithrum to hypural joint 42 to 47 [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; 8 or 9 [9] scales in transverse series from origin of dorsal fin to lateral line; 7 or 8 [7] 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 8 [ii,7]; pectoral-fin rays 12 to 14 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 32 (9), 33 (4).

COLOR IN ALCOHOL.—All examined specimens retaining guanine on scales, overall coloration silvery to silvery-golden, darker on dorsal portions of head and body. Pattern of dark spots arranged in longitudinal series along scale rows of lateral and dorsolateral surfaces of body faintly visible through guanine. Irregularly rotund patch of small dark chromatophores on mid-lateral surface of caudal peduncle. Patch of chromatophores on caudal peduncle extends three to five scales horizontally and about three scales vertically. Scattered small chromatophores on median fins. Paired fins hyaline.

DISTRIBUTION.—Río Patia basin, southwestern Colombia (Figure 8).

REMARKS.—No additional material of *Pseudocurimata* patiae appears to have been collected since the original type series was described by Eigenmann. This species was reported by Chirichigno (1963:19) from rivers of Tumbes Department in northwestern Peru, a considerable distance to the south of the known populations of *P. patia* in southwestern Colombia. That record was, in turn, cited by Ortega and Vari (1986:11). A specimen illustrated by Chirichigno has a horizontally more

elongate patch of dark pigmentation on the caudal peduncle than in *P. patiae*. Furthermore, the longitudinal series of small dark spots on the body found in *P. patiae* are not evident in the photograph. Nonetheless it is not possible to unequivocally identify the illustrated specimen, and checks of various repositories in Peru failed to locate the material that served as the basis of that record. Recent collecting efforts throughout the rivers of Tumbes Department by the author and Hernan Ortega of the Museo de Historia Natural in Lima revealed the presence of only a single species of curimatid, *Pseudocurimata troschelii*. As best as can be determined the specimen illustrated by Chirichigno agrees with specimens of *P. troschelii* from northwestern Peru and her report of *P. patiae* in that region is presumed to represent a misidentification of *P. troschelii*.

MATERIAL EXAMINED.—14 specimens (14, 26.5-124.5).

COLOMBIA. Narino. Río Telembi, Barbacoas, FMNH 56554, 1 (124.5, holotype of Curimatus patiae; formerly CM 5368). Barbacoas, CAS 60622, 8 (86.3-110.0, paratypes of Curimatus patiae; formerly IU 13055); USNM 287597, 3 (26.5-116.1). Stream emptying into Río Telembi above Barbacoas, IU 12987, 2 (94.3-108.5).

Pseudocurimata peruana (Eigenmann)

FIGURES 10, 11

Curimatus peruanus Eigenmann, 1920a:15 [Peru: Río Chira basin]; 1921:514 [Peru: Paita]; 1922:104, pl. 18: fig. 4 [type locality: Peru, Río Chira at Sullana].—Fowler, 1945:117 [reference].—Ringuelet, 1975:94 [Peru, Lambayeque, San Jose near Lambayeque].—Vari, 1989, tables 2, 3 [phylogenetic relationships; shift of species to Pseudocurimata] [not Saul, 1975:113].

Curimata peruana.—Fowler, 1950:290, fig. 347 [literature compilation].—
Ortega and Vari, 1986:11 [Peru; common name].

Curimatorbis peruanus.—Fernández-Yépez, 1948:43 [assignment to Curimatorbis].—Fowler, 1975:370 [reference].

Pseudocurimata peruana.—Vari, 1988:337, fig. 13 [historical biogeography].

DIAGNOSIS.—The discrete small spot of dark pigmentation at the base of the middle rays of the caudal fin distinguishes *Pseudocurimata peruana* from all other members of the genus. The possession of 35 to 37 vertebrae in *P. peruana* further distinguishes that species from *P. boulengeri*, *P. boehlkei*, and *P. patiae*, which have 34 or fewer vertebrae. Finally *P. peruana* differs from *P. lineopunctata* in a variety of pigmentation features (Figures 10, 11 versus 5 to 8).

DESCRIPTION.—Body moderately elongate, somewhat compressed, more so in larger specimens. Dorsal profile of head straight or more typically very slightly convex. Dorsal profile of body smoothly curved 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 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. Pre-pelvic region rounded, without enlarged scales. Obtuse median keel posterior to pelvic fin insertion.

Greatest body depth at origin of dorsal fin, depth 0.30-0.34 [0.30]; snout tip to origin of dorsal fin 0.48-0.52 [0.48]; snout



FIGURE 10.—Pseudocurimata peruana, USNM 285667, 104.9 mm SL; Peru, Piura, Tinajones.

tip to origin of anal fin 0.78-0.82 [0.81]; snout tip to insertion of pelvic fin 0.54-0.56 [0.54]; snout tip to anus 0.75-0.79 [0.77]; origin of dorsal fin to hypural joint 0.52-0.56 [0.55]. Dorsal fin obtusely pointed; anteriormost rays three to three-and-one-half times length of ultimate ray. Pectoral-fin margin obtusely pointed, short; length of pectoral fin 0.16-0.18 [0.16], extends approximately one-third distance to vertical through insertion of pelvic fin. Pelvic-fin margin pointed, length of pelvic fin 0.16-0.18 [0.16], reaches about one-half distance to origin of anal fin. Caudal fin forked. Adipose fin well developed. Anal fin slightly emarginate, anteriormost branched rays two to two-and-one-half times length of ultimate ray. Caudal peduncle depth 0.13-0.14 [0.13].

Head profile obtusely pointed, head length 0.23-0.27 [0.23]; upper jaw slightly longer than lower, mouth subterminal; snout length 0.28-0.32 [0.28]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.23-0.25 [0.23]; adipose eyelid poorly developed, with broad opening over center of eye; length of postorbital portion of head 0.46-0.49 [0.49]; gape width 0.25-0.31 [0.25]; interorbital width 0.42-0.46 [0.43].

Pored lateral line scales from supracleithrum to hypural joint 47 to 52 [52]; all scales of lateral line pored, canals in scales straight; 4 to 6 series of scales extend beyond hypural joint onto caudal-fin base; 9 to 11 [10] scales in transverse series from origin of dorsal fin to lateral line; 7 to 9 [9] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 [ii,9]; anal-fin rays ii,7 or iii,7 [ii,7]; pectoral-fin rays 14 to 16 [16]; pelvic-fin rays i,8 or 9 [i,8].

Total vertebrae 35 (7), 36 (1).

COLOR IN ALCOHOL.—Specimens retaining guanine on scales silvery-golden, darker on dorsal portions of head and body. Specimens lacking guanine on scales tan, with dorsal two-thirds of head and body peppered by small chromatophores. Distinct longitudinally elongate dark mid-lateral band on caudal peduncle. Band commencing three to five scales anterior of vertical line through insertion of adipose fin and extending

posteriorly one or two scales beyond hypural joint. Caudal peduncle band becoming progressively wider posteriorly, approximately three scales high at posterior terminus. Second vertically elongate spot of dark pigmentation overlapping margin of posteriormost mid-lateral scales and proximate portion of middle rays of caudal fin. Caudal spot distinct from mid-lateral stripe on caudal peduncle. All fins with scattered small dark chromatophores on membranes.

DISTRIBUTION.-Río Chira and Río Piura of northwestern Peru (Figure 11). The single lot of Pseudocurimata peruana from Tinajones on the Río Piura is only the second report of additional specimens of the species since its description, and the first reported occurrence in the Río Piura system. That river and the Río Chira, the type locality of the species, are now connected by an irrigation canal system. Thus it is no longer possible to determine whether the species was originally common to the two basins, or has migrated into the Río Piura system through the canal. Ringuelet (1975:94) reported on a specimen of Curimatus peruanus collected at San Jose, close to Lambayeque in the department of the same name in northwestern Peru. That record represents the most southerly record on the western versant of the Andes for the species or any curimatid and, if correct, increases the likelihood that the Río Piura was originally part of the natural range of Pseudocurimata peruana. Dr. Ramiro Barriga (MEPN) informs me (in litt.) that P. peruana occurs in the Río Maraca of the upper Río Chira basin in Ecuador.

REMARKS.—Eigenmann used the name Curimatus peruanus in two publications (1920a, 1921) that predate the description of the species (1922). In the second of those papers (1921:514) he reported that the species occurs at Paita, Peru. That locality is a desert coastal town not proximate to any rivers and an unlikely locality for a curimatid. The gazetteer in Eigenmann (1922:271) indicates that the freshwater fishes reported from Paita were actually collected from the Río Chira and Río Piura.

Saul (1975:113) reported Curimatus peruanus from the Río Aguarico of the Amazon basin of Ecuador. This citation was followed by Ortega and Vari (1986:11). A re-examination of a large series of the specimens studied by that author has shown that they are Steindachnerina dobula (Günther) (KU 13483,

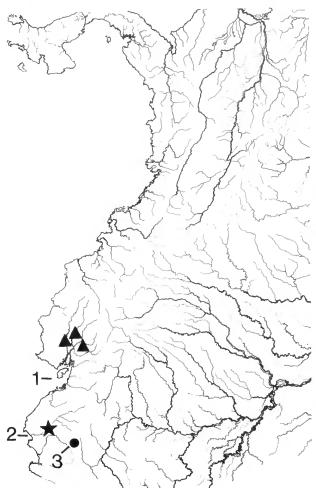


FIGURE 11.—Map of northwestern South America showing geographic distribution of *Pseudocurimata peruana* (star = holotype locality, filled circle = site of other collections of the species) and *Pseudocurimata boulengeri* (triangles) (some symbols represent more than one collecting locality or lot of specimens). See also discussion under *P. peruana* relative to the presence of the species in the upper Río Chira. (Locations: 1 = Gulf of Guayaquil; 2 = Río Chira; and 3 = Río Piura.)

13485, 13586, 13487, 13488, 13489, 13490, 13492, 13493). MATERIAL EXAMINED.—9 specimens (9, 79.3-127.3).

PERU. Piura. Río Chira at Sullana, CAS 41722, 1 (127.3, holotype of Curimatus peruanus; formerly IU 15162); CAS 41723, 1 (79.3, paratype of Curimatus peruanus; formerly IU 15162); FMNH 58673, 1 (116.2, paratype of Curimatus peruanus; formerly CM 7684). Tinajones, Río Piura basin, USNM 285667, 6 (85.6-104.9, one specimen cleared and counterstained for cartilage and bone.

Pseudocurimata boulengeri (Eigenmann)

FIGURES 11, 12

Curimatus guentheri Boulenger, 1898:4 [type locality: Ecuador: Río Vinces; name preoccupied in Curimatidae by Curimata güntheri Eigenmann and Eigenmann, 1889].

Curimatus boulengeri Eigenmann in Eigenmann and Ogle, 1907:3 [substitute for Curimatus guentheri Boulenger, preoccupied in Curimatidae by Curimata güntheri Eigenmann and Eigenmann].—Pellegrin, 1908:343 [substitute for Curimatus guentheri Boulenger, preoccupied in Curimatidae; action repeats that of Eigenmann in Eigenmann and Ogle, 1907].—Eigenmann, 1910:422 [reference]; 1920a:15 [Ecuador: Guayaquil basin]; 1921:514 [Ecuador: Guayas basin]; 1922:105, pl. 15: fig. 3 [Ecuador: Pacific slope rivers].—Vari, 1989, tables 2, 3 [phylogenetic relationships].

Pseudocurimata boulengeri.—Fernández-Yépez, 1948:46 [assignment to Pseudocurimata].—Vari, 1988:337, fig. 13 [historical biogeography]. Curimatorbis boulengeri.—Ovchynnyk, 1968:250 [Ecuador: Río Vinces, Río Daule, Río Barranca Alta, Río Guayas].

DIAGNOSIS.—The absence of small, discrete, dark spots aligned in longitudinal rows on the lateral and dorsolateral surfaces of the body in *Pseudocurimata boulengeri* distinguishes that species from *P. lineopunctata* and *P. patiae*, which have that pigmentation pattern. The 36 or 37 vertebrae of *P. boulengeri* separates it from *P. lineopunctata* and *P. patiae*, which have 31 to 33 vertebrae, and from *P. boehlkei*, which has 33 or 34 vertebrae. *Pseudocurimata boulengeri* lacks the discrete spot at the base of the middle caudal-fin rays characteristic of *P. peruana*, and has 50 to 57 scales along the lateral line to the hypural joint, contrary to the 42 to 47 that typify *P. troschelii*, and the 39 to 42 of *P. boehlkei*.

DESCRIPTION.—Body moderately elongate, somewhat compressed. Dorsal profile of head straight or sometimes very slightly concave in larger specimens. 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. Pre-pelvic region rounded, without enlarged scales. Discrete median keel posterior to pelvic fin insertion.

Greatest body depth at origin of dorsal fin, depth 0.31-0.33 [0.33]; snout tip to origin of dorsal fin 0.49-0.53 [0.52]; snout tip to origin of anal fin 0.75-0.79 [0.75]; snout tip to insertion of pelvic fin 0.49-0.55 [0.51]; snout tip to anus 0.72-0.76 [0.72]; origin of dorsal fin to hypural joint 0.51-0.57 [0.53]. Dorsal fin pointed, posterior border somewhat emarginate in larger specimens; anteriormost rays approximately three-andone-half times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.17-0.20 [0.20], extends nearly to vertical through insertion of pelvic fin in smaller specimens, somewhat shorter in larger specimens. Pelvic-fin margin pointed, length of pelvic fin 0.19-0.22 [0.22], reaches nearly to origin of anal fin in smaller specimens, somewhat shorter in larger specimens. Caudal fin forked. Adipose fin well developed. Anal-fin margin distinctly emarginate, anteriormost branched rays two to two-and-one-half times length of ultimate ray. Caudal peduncle depth 0.11-0.13 [0.12].

Head profile distinctly pointed, head length 0.29-0.34 [0.31]; upper jaw slightly longer than lower, mouth barely subterminal; snout length 0.24-0.29 [0.27]; nostrils very close,



FIGURE 12.—Pseudocurimata boulengeri, USNM 287891, 81.2 mm SL; Ecuador, Provincia Los Rios, Río Vinces at Vinces.

anterior circular, posterior crescent shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.26-0.32 [0.31]; adipose eyelid poorly developed, with broad, vertically ovoid opening over center of eye; length of postorbital portion of head 0.42-0.50 [0.44]; gape width 0.23-0.28 [0.28]; interorbital width 0.38-0.41 [0.38].

Pored lateral line scales from supracleithrum to hypural joint 50 to 57 [50]; all scales of lateral line pored, canals in scales straight; 3 to 7 series of scales extend beyond hypural joint onto caudal-fin base; 10 or 11 [11] scales in transverse series from origin of dorsal fin to lateral line; 8 or 9 [8] 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,8 [ii,8]; pectoral-fin rays 13 to 15 [13]; pelvic-fin rays i,7 or 8 [i,8].

Total vertebrae 36 (12), 37 (1).

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales silvery to silvery-golden, darker on dorsal portions of head and body. Specimens lacking guanine on scales tan, dorsal two-thirds of head and body peppered with small dark chromatophores. Obscure patch of dark pigmentation on mid-lateral surface of caudal peduncle; patch somewhat triangular with anterior point of triangle lying short distance posterior of vertical through posterior margin of adipose fin. Posterior terminus of spot four scales high. Patch of dark pigmentation on peduncle barely discernable in adults. Caudal-fin rays outlined by small dark chromatophores on membranes. Small dark chromatophores scattered on other fins.

DISTRIBUTION.—Rivers draining into the northern portion of the Gulf of Guayaquil, southwestern Ecuador (Figure 11).

REMARKS.—Boulenger (1898:4) originally named this species Curimatus guentheri, a name already used by Eigenmann and Eigenmann (1889:423) within the Curimatidae for a species from the Amazon basin. The Eigenmann and Eigenmann species was assigned by Vari (1989) to Steindachnerina. Eigenmann (in Eigenmann and Ogle, 1907:3) substituted Curimatus boulengeri for the preoccupied Boulenger name, an action almost simultaneously proposed by Pellegrin (1908:343).

Boulenger's original description was based on two specimens in the collection of the British Museum (Natural History). The larger syntype (BMNH 1898.11.40:50, 65.2 mm SL) is designated as the lectotype, and the second syntype (BMNH 1898.11.40:51, 63.2 mm SL) thus becomes the paralectotype.

MATERIAL EXAMINED.—68 specimens (48, 42.4–146.0)

ECUADOR. Los Ríos. Río Vinces, BMNH 1898.11.4:50, 1 (65.2, lectotype of Curimatus boulengeri); BMNH 1898.11.4:51, 1 (63.2, paralectotype of Curimatus boulengeri). Vinces, USNM 76952, 20 (81.2-95.9); AMNH 5355, 8 (4, 77.5-93.5); BMNH 1924.3.3:58-60, 3 (84.6-91.0); MCZ 48741, 2; USNM 287892, 5. Guayas. Río Daule, Colimes, MCZ 30931, 8; BMNH 1920.12.20:65-66, 2 (51.3-58.7); USNM 76951, 15 (42.4-112.3). Río Barranca Alta, FMNH 57711, 1 (146.0)

Pseudocurimata troschelii (Günther)

FIGURES 13, 14

Anodus troschelii Günther, 1859:418 [type locality: "Western Andes of Ecuador"].—Vari, 1989, tables 2, 3 [phylogenetic relationships].

Curimatus troschelii Günther, 1864:290 [based on type series].—Steindachner, 1880:101 [Ecuador: Guayaquil].—Eigenmann and Eigenmann, 1889:421 [reference].—Eigenmann, 1910:421 [reference]; 1920a:16 [Ecuador: Guayaquil basin]; 1921:514 [Ecuador: Guayas basin]; 1922:106, pl. 17: fig. 4 [rivers of western slopes of Ecuador].—Rendahl, 1937:5 [Ecuador, Río de Clementina, northwest of Babahoyo].

Curimatus troscheli.—Steindachner, 1902:142 [Ecuador: Río de Bodegas at Babahoyo].

Curimatus brevipes Eigenmann and Ogle, 1907:3, fig. 1 [type locality: Peru].—Eigenmann, 1910:422 [reference].—Fowler, 1945:119 [reference].

Curimatus aureus Pellegrin, 1908:342 [type locality: Ecuador: Río Guayas].— Eigenmann, 1910:422 [reference]; 1922:106 [placed as a synonym of Anodus troschelii Günther, 1859].—Fernández-Yépez, 1948:73 [reference].— Fowler, 1975:373 [as a synonym of Anodus troschelii Günther].

Curimata brevipes.—Eigenmann and Allen, 1942:299 [reference].—Fowler, 1950:279, fig. 338 [literature compilation].

Pseudocurimata troscheli.—Fernández-Yépez, 1948:46 [assignment to Pseudocurimata].—Fowler, 1975:373 [reference].—Vari, 1988:337, fig. 13 [historical biogeography].

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

Curimatorbis troscheli.—Böhlke, 1958:108, pl. 7: figs. 3-4 [Ecuador: Río Santa Rosa, Río Balao; Pseudocurimata placed as a synonym of Curimatorbis Fernández-Yépez].—Ovchynnyk, 1968:250 [Ecuador: Río Vinces, Río Clementina, Río Santa Rosa, Colimes, Río Barranca Alta, Río Chanchan, Río Guayas].

Curimatus patiae.—Chirichigno, 1963:19, fig. 19 [Peru: Departamento Tumbes; Río Tumbes, Río Zarumilla].—Ortega and Vari, 1986:11 [Peru; on Chirichigno, 1963].

Curimata aureus.—Ovchynnyk, 1968:250 [Ecuador: Río Guayas]. Curimata troscheli.—Géry, 1972:96 [Ecuador: Guayaquil].



FIGURE 13.—Pseudocurimata troschelii, USNM 280639, 109.8 mm SL; Peru, Tumbes, Provincia Tumbes, Río Tumbes, vicinity of Boca Tumbes irrigation dam.

DIAGNOSIS.—The absence of discrete dark spots aligned in longitudinal rows on the scales along the lateral and dorso-lateral surfaces of the body distinguishes *Pseudocurimata troschelii* from *P. lineopunctata* and *P. patiae*, which are characterized by that pigmentation pattern. The 35 to 37 vertebrae of *P. troschelii* further separate it from those two species, which have 31 to 33 vertebrae, and from *P. boehlkei*, which has 33 or 34 vertebrae. *Pseudocurimata troschelii* also lacks the discrete spot at the base of the middle caudal-fin rays characteristic of *P. peruana*, and has 39 to 47 scales along the lateral line to the hypural joint contrary to the 50 to 57 that typify *P. boulengeri*.

DESCRIPTION.—Body moderately elongate, somewhat compressed. Dorsal profile of head straight or very slightly concave in larger specimens. Dorsal profile of body distinctly convex from rear of head to origin of dorsal fin; straight and slightly 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. Pre-pelvic region rounded without enlarged scales. Obtuse median keel posterior to pelvic fin insertion.

Greatest body depth at or somewhat anterior of origin of dorsal fin, depth 0.33-0.36 [0.33]; snout tip to origin of dorsal fin 0.50-0.54 [0.51]; snout tip to origin of anal fin 0.78-0.83 [0.80]; snout tip to insertion of pelvic fin 0.51-0.56 [0.53]; snout tip to anus 0.75-0.80 [0.76]; origin of dorsal fin to hypural joint 0.51-0.55 [0.53]. Dorsal fin pointed, less so in larger specimens, anteriormost rays two-and-one-half to three times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.17-0.20 [0.19], extends approximately two-thirds distance to vertical through insertion of pelvic fin. Pelvic-fin margin pointed, length of pelvic fin 0.20-0.23 [0.21], reaches about two-thirds 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 0.12-0.14 [0.13].

Head distinctly pointed, head length 0.27–0.32 [0.28]; upper jaw longer, mouth subterminal; snout length 0.27–0.31 [0.31]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.26–0.31 [0.27]; adipose eyelid present, with vertically ovoid opening over center of eye; length of postorbital portion of head 0.42–0.48 [0.46]; gape width 0.24–0.30 [0.28]; interorbital width 0.40–0.43 [0.41].

Pored lateral line scales from supracleithrum to hypural joint 42 to 47 [43]; 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 to 8 [7] scales in transverse series from origin of dorsal fin to lateral line; 5 to 7 [6] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or 10, or iii,9 (ii,10 and iii,9 rare) [ii,9]; anal-fin rays ii,7, or iii,7 (iii,7 rare) [ii,7]; pectoral-fin rays 13 to 15 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 35 (10), 36 (19), 37 (13).

LIFE COLORATION.—(Based on a series of specimens collected in the Río Tumbes system of northwestern Peru, August 1986). Overall coloration bright silver, darker on dorsal portions of head and body. Mid-lateral band on caudal peduncle largely masked by guanine on scales, more apparent posteriorly. Lateral surface of head at level of orbit light yellow, similar pigmentation present on ventral surface of lower jaw, and across branchiostegal membranes. Adipose fin distinctly yellow. Dorsal and anal fins with faint yellow coloration. Caudal-fin rays yellow basally.

COLOR IN ALCOHOL.—Overall coloration of specimens retaining guanine on scales golden to golden-tan, darker on dorsal portions of head and body. No pronounced pigmentation pattern on head. Specimens up to 30 mm SL with an indefinite mid-lateral round patch of dark chromatophores on posterior portion of caudal peduncle. Pigmented area on caudal peduncle becoming more intense and horizontally elongate with age, forming an elongate dark spot in specimens of 50 to 90 mm SL. Caudal peduncle spot more diffuse in larger specimens. Surface chromatophores underlain by a deeper-lying, longitudinally elongate area of dark pigmentation. Fins with scattered small,

TABLE 1.—Morphometrics and meristics of (A) lectotype of *Pseudocurintata troschelii*, BMNH 1860.6.16:173, (B) paralectotypes of *P. troschelii*, BMNH 1860.6.16:174-178 and BMNH 1860.6.16:199-200, (C) lectotype of *Curimatus aureus*, MNHN 9774, (D) paralectotypes of *C. aureus*, MNHN 1988-798, (E) holotype of *Curimatus brevipes*, USNM 35333, and (F) all specimens of *Pseudocurimata troschelii* 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.

Measurements and Counts	A	В	С	D	E	F	
	Morphometrics						
Standard length	102.8	70.4-91.2	122.5	123.5-128.2	120.9	51.4-155.3	
1. Greatest body depth	0.33	0.33-0.35	0.35	0.33-0.36	0.34	0.33-0.36	
2. Snout to dorsal-fin origin	0.51	0.51-0.54	0.51	0.50-0.52	0.53	0.50-0.54	
3. Snout to anal-fin origin	0.80	0.80-0.83	0.80	0.78	0.80	0.78-0.83	
4. Snout to pelvic-fin origin	0.53	0.52-0.55	0.50	0.53	0.53	0.51-0.56	
5. Snout to anus	0.76	0.75-0.79	0.76	0.75-0.76	0.78	0.75-0.80	
6. Origin of dorsal fin to hypural joint	0.53	0.51-0.57	0.57	0.57	0.56	0.51-0.55	
7. Pectoral fin length	0.19	0.18-0.20	0.18	0.19-0.20	_	0.17-0.20	
8. Pelvic fin length	0.21	0.20-0.22	0.21	0.20-0.21	_	0.20-0.23	
9. Caudal peduncle depth	0.13	0.12-0.14	0.13	0.13-0.14	0.14	0.12-0.14	
10. Head length	0.28	0.30-0.32	0.27	0.27	0.31	0.27-0.32	
11. Snout length	0.31	0.28-0.31	0.28	0.30-0.31	0.28	0.27-0.31	
12. Orbital diameter	0.27	0.26-0.29	0.26	0.28-0.29	0.27	0.26-0.31	
13. Postorbital length	0.46	0.44-0.47	0.47	0.47-0.48	0.48	0.42-0.48	
14. Interorbital length	0.41	0.40-0.42	0.41	0.41	0.41	0.40-0.43	
	MERISTICS						
Lateral line scales	43	41-44	46	43-45	40?	42-47	
Scale rows between dorsal-fin origin and lateral line	7	7-8	7	7	8?	7-8	
Scale rows between anal-fin origin and lateral line	6	6	6	6-7	6?	5-7	
Branched dorsal-fin rays	9	9	9	9	9	9-10	
Branched anal-fin rays	7	7	7	7	7	7	
Total pectoral-fin rays	14	13-15	15	14	-	13-15	
Branched pelvic-fin rays	8	8	8	8	8	8	
Vertebrae	36	35-36	36	35-37	35	35-37	

dark chromatophores on membranes.

DISTRIBUTION.—Rivers draining into Gulf of Guayaquil, southwestern Ecuador, and Río Zarumilla and Río Tumbes in northern Peru (Figure 14).

REMARKS.—Günther's original description of *Anodus troscheli* (1859:418) was based on eight specimens. A 102.8 mm SL syntype that is in the best overall condition (BMNH 1860.6.16:173) is designated as the lectotype. The remaining syntypes (BMNH 1860.6.16:174-178, BMNH 1860.6.16: 199-200) thus become paralectotypes.

Several nominal *Pseudocurimata* species were described from within the range of *P. troschelii*. Pellegrin (1908:342) described *Curimatus aureus* based on specimens from the Río Guayas of Ecuador. Eigenmann (1922:106) placed *C. aureus* as a synonym of *Anodus troschelii* Günther. An examination of the syntype series of those two species (Table 1) has not revealed differences between those nominal forms. The two species are thus considered conspecific. In his description of *Curimatus aureus* Pellegrin commented on some unspecified similarities between that species and two nominal Amazonian

forms, Curimatus trachystetus Cope and C. leucostictus Eigenmann and Eigenmann. Contrary to Pellegrin's suggestion, the phyletic relationships of Curimatus trachystetus and C. leucostictus lie with the genera Steindachnerina and Curimatella respectively, rather than with Pseudocurimata (Vari, 1989).

Pellegrin's description of *Curimatus aureus* was based on three specimens. The smallest of these, MNHN 9774, a 122.5 mm SL individual, is designated as the lectotype. The other two syntypes (MNHN 1988-798, 123.5-128.2 mm SL) thus become paralectotypes.

Eigenmann and Ogle (1907:3) described Curimatus brevipes from a single specimen (USNM 35333) with an imprecise locality of "Peru?" collected by Orton during his travels in western South America. Gill (1870:92) noted that the Orton material was collected during "an expedition to the Andes of Ecquador and Peru." Re-examination of the holotype of C. brevipes has failed to demonstrate any differences between that specimen and Anodus troschelii of Günther (Table 1). The species are thus considered conspecific. The known distribu-

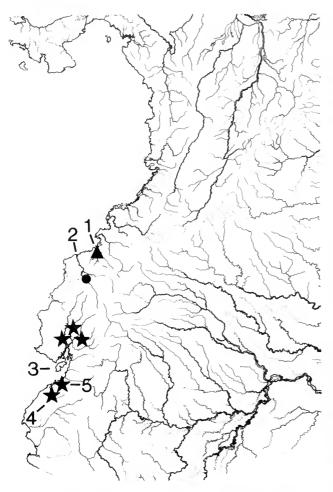


FIGURE 14.—Map of northwestern South America showing geographic distribution of *Pseudocurimata troschelii* (stars) and *Pseudocurimata boehlkei* (filled circle = holotype locality, triangle = sites of collection of other specimens) (some symbols represent more than one collecting locality or lot of specimens). See also discussion under *P. boehlkei* relative to collections of that species from the Río Santiago. (Locations: 1 = Río Santiago; 2 = Río Esmeraldas; 3 = Gulf of Guayaquii; 4 = Río Tumbes; and 5 = Río Zarumilla.)

tion of *Pseudocurimata troschelii* extends through the Pacific slope rivers of southwestern Ecuador and northwestern Peru and the original imprecise locality data of "Peru" may be correct.

MATERIAL EXAMINED.—227 specimens (38, 51.4-155.3)

ECUADOR. "Western Andes of Ecuador," BMNH 1860.6.16:173,1 (102.8, lectotype of Anodus troschelii); BMNH 1860.6.16:174-178 and BMNH 1860.6.16:199-200, 7 (70.4-91.2, paralectotypes of Anodus troschelii). Río Guayas, MNHN 9774, 1 (122.5, lectotype of Curimatus aureus), MNHN 1988-798, 2 (123.5-128.2, paralectotypes of Curimatus aureus). Los Ríos. Vinces, BMNH 1920.12.20:73-74, 2 (91.8-94.5); CAS 60758, 6 (89.3-116.9, formerly IU 13535); USNM 76953, 6 (77.6-107.5). Río Vinces, BMNH 1898.11.4:47-49, 3; NMW 68762, 1. Bababoyo, NRM 10360, 4 (142.8-155.3). Río Palenque at Centro Cientifico, FMNH 93104, 41; FMNH 92671,

132. Guayaquil. Guayaquil. NMW 68763, 1; NMW 68764, 2. Guayas. Colimes, BMNH 1924.3.3:61-63, 3 (70.7-92.5); AMNH 5368, 3 (44.6-100.1); UMMZ 160221, 3.

PERU. No specific locality, USNM 35333, 1 (120.9, holotype of Curimatus brevipes); NMW 67044, 4. Tumbes. Provincia Zarumilla, middle Río Zarumilla at Pozo Lajas, USNM 280642, 2 (1, 98.1). Provincia Tumbes, Río Tumbes, north of town of Francos, USNM 280644, 1. Provincia Tumbes, Río Tumbes, south of Garbanzal, USNM 280643, 1. Provincia Tumbes, Río Tumbes, Río Playa, USNM 280640, 2. Provincia Tumbes, Río Tumbes, vicinity of Boca Tumbes irrigation dam, USNM 280639, 11 (7, 92.1-119.8).

Pseudocurimata boehlkei, new species

FIGURES 14-17

Curimatorbis sp., Böhlke, 1958:109, pl. 7: fig. 5 [Ecuador, Esmeraldas, Río Quinindé, Río Santiago].

DIAGNOSIS.—The presence of an elongate stripe rather than a discrete, dark round spot on the mid-lateral surface of the caudal peduncle in combination with 33 or 34 vertebrae distinguishes *Pseudocurimata boehlkei* from all congenerics, which either have a dark, round or horizontally ovoid mid-lateral spot (*lineopunctata* and *patiae*) or 35 or more vertebrae (*boulengeri*, *troschelii*, *peruana*).

DESCRIPTION.—Body moderately elongate, more so in specimens over approximately 80 mm SL, somewhat compressed. Dorsal profile of head straight or very slightly convex. Dorsal profile of body smoothly curved from rear of head to nape, nearly straight from that point to origin of dorsal fin; straight and posteroventrally slanted at base of dorsal fin. nearly straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body anterior to dorsal fin with an indistinct median keel or transversely rounded; smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle, degree of ventral curvature not as pronounced as that of dorsal profile of body. Pre-pelvic region obtusely rounded transversely, with irregular series of scales approximately same size as those of lateral surface of body. Weakly developed median keel posterior to pelvic-fin insertion. Secondary obtuse keel on each side of post-pelvic portion of body about one-and-one-half scales dorsal of ventral midline.

Greatest body depth at or slightly anterior of origin of dorsal fin, depth 0.29-0.33 [0.30]; snout tip to origin of dorsal fin 0.50-0.53 [0.51]; snout tip to origin of anal fin 0.81-0.82 [0.81]; snout tip to insertion of pelvic fin 0.54-0.56 [0.54]; snout tip to anus 0.76-0.79 [0.77]; origin of dorsal fin to hypural joint 0.50-0.54 [0.54]. Distal margin of dorsal fin rounded, no notable difference in form of fin ontogenetically; anterior most rays approximately three times length of ultimate ray. Pectoral-fin margin obtusely pointed; length of pectoral fin 0.18-0.20 [0.18], extends two-thirds of distance to vertical through insertion of pelvic fin in smaller individuals, about one-half distance in largest specimens examined. Pelvic-fin margin obtusely pointed, length of pelvic fin 0.18-0.21 [0.18], reaches to within two scales of origin of anal fin in young adults, distinctly shorter in larger specimens. Caudal fin forked;



FIGURE 15.—Pseudocurimata boehlkei, new species, USNM 291690, juvenile, paratype, 33.9 mm SL; Ecuador, Esmeraldas, Esteros La Bocana del Cupa.



FIGURE 16.—Pseudocurimata boehlkei, new species, USNM 291690, paratype, 94.8 mm SL; Ecuador, Esmeraldas, Esteros La Bocana del Cupa.



FIGURE 17.—Pseudocurimata boehlkei, new species, USNM 287745, holotype, 109.1 mm SL; Ecuador, Esmeraldas, Esteros La Bocana del Cupa.

lobe margins somewhat rounded. Adipose fin well developed. Anal fin emarginate, anteriormost branched rays two to two-and-one-half times length of ultimate ray. Caudal peduncle depth 0.12-0.12 [0.13].

Head profile obtusely pointed, head length 0.28-0.33 [0.28]; upper jaw longer, mouth subterminal; snout length 0.28-0.33 [0.33]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.25-0.28 [0.26]; adipose eyelid present, moderately developed, with a large, ovoid opening over eye; length of postorbital portion of head 0.43-0.47 [0.45]; gape width 0.24-0.30 [0.30]; interorbital width 0.40-0.44 [0.43].

Pored lateral line scales from supracleithrum to hypural joint 39 to 42 [41]; all scales of lateral line pored, canals in scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal-fin base; $8^{1}/2$ or 9 [9] scales in transverse series from origin of dorsal fin to lateral line; $5^{1}/2$ to 7 [$6^{1}/2$] scales in transverse series from the lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 [ii,9]; anal-fin rays ii,7 or iii,7 [iii,7]; pectoral-fin rays 13 or 14 [14]; pelvic-fin rays i,7,i [i,7,i].

Total vertebrae 33 (4), 34 (5)

COLOR IN ALCOHOL.—All examined specimens lacking guanine on scales, overall coloration grayish brown, darker on lateral and dorsal surfaces of body, opercle, snout, and dorsal

portions of head. Smallest individual examined (33 mm SL) with distinct mid-lateral body stripe on body extending from supracleithrum to basal portions of middle rays of caudal fin. Stripe on body most intense posterior of vertical through origin of dorsal fin, with very dark patch of chromatophores on mid-lateral surface of caudal peduncle and base of middle rays of caudal fin. Anterior portions of mid-lateral strip becoming increasingly less obvious in larger specimens.

Individuals of approximately 80 mm SL with anterior portion of mid-lateral stripe no longer evident. Portion of stripe lying between vertical through origin of dorsal fin and vertical through rear of adipose fin very faint, not as marked as in smaller individuals. Distinct, elongate, dark mid-lateral stripe on caudal peduncle. Dark band of pigmentation no longer extending posteriorly onto base of middle rays of caudal fin.

Largest individuals examined with diffuse dark stripe on caudal peduncle, stripe not as discrete as in smaller specimens. These specimens with traces of faint mid-lateral band anterior to vertical through adipose fin, but pigmentation is less apparent than in smaller individuals. Pectoral and pelvic fins hyaline in all individuals. Anal fin with scattered dark chromatophores distally in some specimens of various sizes. Caudal, dorsal, and adipose fins dusky to various degrees.

DISTRIBUTION.—Río Esmeraldas and Río Santiago basins of northwestern Ecuador (Figure 14; see also "Remarks").

ETYMOLOGY.—The species is named after the late Dr. James E. Böhlke, who first recognized it as undescribed, and who made many contributions to our knowledge of the South American freshwater fish fauna.

REMARKS.—In his publication dealing with a series of collections from various Ecuadorian localities, Böhlke (1958:109) reported on specimens of the Curimatidae originating in the Pacific slope rivers of northern Ecuador. In his discussion of a series of specimens that he identified as "Curimatorbis species," Böhlke (1958:109) noted: "These small specimens seem to represent an undescribed form, allied to C. troscheli on the one hand and C. lineopunctata on the other." As a consequence of the taxonomic confusion in the Curimatidae he postponed further action until additional material became available. A re-examination of a portion of the series examined by Böhlke (ANSP 75962, 75963) shows that the specimens are Pseudocurimata boehlkei, confirming that author's hypothesis about the undescribed nature of the species, and their phylogenetic associations. Dr. Ramiro Barriga (MEPN) (in litt.) notes, however, that he has been unable to confirm the locality information for the material from the Río Santiago system reported on by Böhlke, and that the specimens may have originated in the Río Esmeraldas system. Extensive collecting efforts in the Río Santiago basin by Dr. Barriga have furthermore failed to confirm the presence P. boehlkei in the Santiago system. His collections have shown that the species is, however, widely distributed through the Esmeraldas basin.

MATERIAL EXAMINED.—10 specimens (10, 33.9-109.1).

HOLOTYPE. ECUADOR. Esmeraldas. Esteros La Bocana del Cupa 100 m below Puerto Cupa, Río Esmeraldas basin (~0°26'N, 79°26'W), R. Barriga,

Cerón and J. Caicedo, 11 Mar 1985, USNM 287745, (109.1).

PARATYPES. ECUADOR. *Esmeraldas*. Same collection data as holotype, 9 specimens: USNM 291690, 6 (6, 33.9-98.6, one specimen cleared and counterstained for cartilage and bone); MEPN 4289, 3 (3, 72.8-74.5).

The following specimens of *Pseudocurimata boehlkei* were examined, but are not part of the type series (see also "Remarks" with respect to collection data of these specimens).

ECUADOR. Esmeraldas. Río Quinindé, near its mouth, Río Esmeraldas basin, ANSP 75962, 1 (52.3). Lower Río Santiago near Borbón (-1°05'N, 78°59'W), ANSP 75963, 1 (72.7).

Phylogenetic Biogeography

The rivers of the western versant of the Andean cordilleras of South America flow through a region with a complex geomorphological history and topography. Those factors in combination would, in theory, have resulted in numerous vicariance events within the affected freshwater ichthyofauna, and made that fauna fruitful for phylogenetic biogeographic studies. The contribution of the complex geological history and topography of the western versant of the Andes to possible species diversity among within the aquatic fauna is, however, progressively attenuated towards the south as a consequence of the increasingly xeric conditions that commence in Ecuador and which rapidly become pronounced in northern Peru. The reduced rainfall in the southern portions of that region restricts fishes to those rivers feed by year-round Andean runoff. The consequent limited river flows are reflected in the decreased species diversity of the ichthyofauna of those drainage basins, a pattern that is obvious in the Curimatidae.

Although the fish fauna of the western versant is not as speciose as that found on the Atlantic slopes of the Andes, it is diverse enough to permit the advancement of multiple independent cladograms of the aquatic fauna of the region. Unfortunately the lack of detailed revisionary studies for most of that fauna means that we cannot yet advance definitive estimates about the degree of endemism in the different basins, nor have a sense of the predominant biogeographic patterns in the area. The Curimatidae, however, demonstrates a significant degree of species-level endemism in relatively discrete geographic areas along the western versant of the Andes and the hypothesis of intrageneric relationships presented in the "Phylogenetic Reconstruction" for *Pseudocurimata* does reveal an interesting correlations with these areas of endemism.

Vari (1988) designated six regions of endemism in the ichthyofauna of trans-Andean South America based on the distribution patterns of curimatids. The majority of these regions were defined from data on the range of the species of *Pseudocurimata*. Two of these areas, Lago Maracaibo and its tributaries, and the Río Magdalena basin, do not have any *Pseudocurimata* species in their ichthyofaunas and will not be dealt with further in this account. The four remaining regions proposed by Vari are the Ríos Atrato, San Juan, and Dagua, which together form one area, the Río Patia forming the second region, the rivers draining into the Gulf of Guayaquil and the Río Zarumilla and Río Tumbes, which together constitute a

third area, and finally the Río Chira and Río Piura, which are the fourth area. All four regions have endemic species of *Pseudocurimata*.

Additional data and specimens that have become available since Vari (1988) have allowed a refinement of concepts of species distributions proposed in that study and resulted in further evidence supporting the hypothesis of intrageneric phylogenetic relationships originally proposed in that paper. Those studies have also revealed a sixth recognizable form, *Pseudocurimata boehlkei*, described in this paper from the Río Esmeraldas, which may identify an additional region of endemism (but see "Remarks" under that species with respect to its reported occurrence in the Río Santiago system).

Superimposing the hypothesized phylogeny of *Pseudocurimata* on a map of northwestern South America showing the distribution of the members of the genus (Figure 18), we note a general linear correlation between the branching pattern of the cladogram and the geographic distribution of the taxa. Such a pattern may reflect a series of speciation events associated with a sequence of north to south vicariance events affecting the freshwater fish fauna of the region. This, in turn, may represent a historical pattern for the aquatic biota of the region.

The evident pattern of Figure 18 must be qualified due to two factors. *Pseudocurimata lineopunctata* has a disjunct distribution in Colombia and Ecuador (regions connected by dotted line of Figure 18), with a considerable gap in the middle of the known range of the species. As noted previously this gap is undoubtedly a function of the limited degree to which the rivers of southwestern Colombia have been collected, but makes it difficult to evaluate the significance of the intervening region of endemism represented by *P. patiae. Pseudocurimata patiae*

(Figure 18, B) and P. boehlkei (C), together with the clade consisting of P. boulengeri (D), P. troschelii (E), and P. peruana (F) constitute an unresolved trichotomy. Thus the sequence of presentation of the first two species on the cladogram is arbitrary. A reversal of the sequence of patiae and boehlkei would obviously result in a less congruent pattern between distribution and phylogeny. The presented sequence of taxa was chosen, however, because preliminary ontogenetic data on the pigmentation patterns of the mid-lateral portion of the caudal peduncle, and somewhat equivocal information from the position of the interdigitation of the first proximal pterygiophore of the dorsal fin (see "Phylogenetic Reconstruction") indicate that P. boehlkei (C), may be the sister taxon to the clade consisting of P. boulengeri (D), P. troschelii (E), and P. peruana (F). Further revisionary and phylogenetic studies of other taxa in the aquatic fauna of the region will be necessary to determine whether the areas of endemism and the pattern of biotic relationships in Pseudocurimata are general for the biota.

Secondary dispersal appears to have taken at least one and perhaps two times within *Pseudocurimata*. *Pseudocurimata* lineopunctata from the Río Santiago is possibly sympatric with *P. boehlkei* in that drainage system. As noted under the species account for *P. boehlkei*, questions have been raised, however, about the records of that species in the Río Santiago system. No such questions exist about the sympatry of *P. boulengeri* (D, horizontal lines) and *P. troschelii* (E, vertical lines) in the rivers draining into the northern portions of the Gulf of Guayaquil. This sympatry under an allopatric speciation model, the most likely model for the members of the Curimatidae (see Vari, 1988), indicates large scale secondary dispersal of one or both species in those river systems.

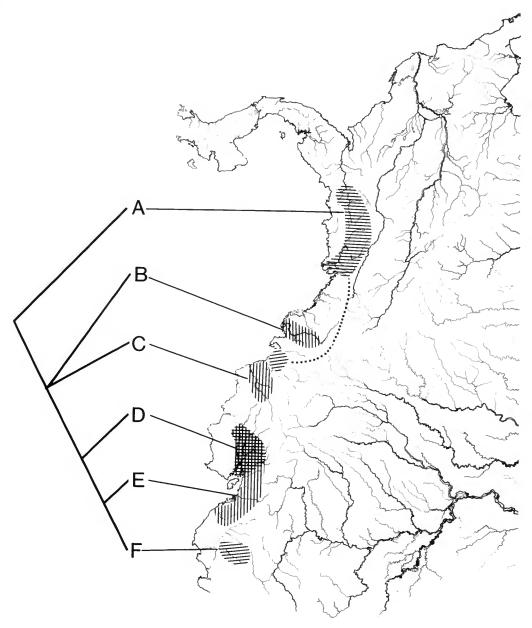


FIGURE 18.—Scheme of phylogenetic relationships in *Pseudocurimata* superimposed on a map of northwestern South America showing approximate limits of areas of distribution of the members of the genus. Species: A = P. lineopunctata; B = P. patiae; C = P. boehlkei; D = P. boulengeri; E = P. troschelii; and E = P. peruana. Disjunct regions of known distribution of *P. lineopunctata* in southwestern Colombia and northwestern Ecuador joined by dotted line. Distribution of *Pseudocurimata boulengeri* (D) in rivers draining into Gulf of Guayaquil indicated by horizontal lines. Range of *P. troschelii* (E), indicated by vertical lines, overlaps that of *P. boulengeri*.

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Index

(Synonyms and page numbers of principal accounts in italics)

```
gilberti, Cyphocharax, 2
Anodus troschelii, 1, 18, 20
                                                                                   guentheri, Curimatus, 17
atratoensis, Curimatus, 10
                                                                                   guentheri, Steindachnerina, 18
aureus, Curimata, 18
  Curimatus, 1, 18, 20
                                                                                   lineopunctata, Curimata, 11
                                                                                      Curimatorbis, 11, 14
boehlkei, Pseudocurimata, 4, 6-8, 11, 21-23, 24
                                                                                      Pseudocurimata, 4, 6-8, 11-14, 24
boulengeri, Curimatus, 1, 17
                                                                                   lineopunctatus, Curimatus, 1, 11, 13, 14
  Curimatorbis, 17
                                                                                      Curimatorbis, 11
  Pseudocurimata, 4, 6-9, 11, 17-18, 24
                                                                                      Pseudocurimata, 11
brevipes, Curimata, 18
  Curimatus, 1, 18, 20
                                                                                   morawhannae, Steindachnerina, 2
  Pseudocurimata, 18
                                                                                   ocellata, Curimata, 5, 6, 9
Ciphocharax, 10
                                                                                   patiae, Curimatus, 1, 14, 15
Curimata aureus, 18
                                                                                      Curimatorbis, 14
   brevipes, 18
                                                                                      Pseudocurimata, 4, 6-8, 11, 13, 14-15, 24
   lineopunctata, 11
                                                                                   peruana, Curimata, 15
   ocellata, 5, 6, 9
                                                                                      Pseudocurimata, 4, 6-9, 11, 15-17, 24
   peruana, 15
                                                                                   peruanus, Curimatus, 1, 15
   troscheli, 18
                                                                                      Curimatorbis, 15
Curimatorbis boulengeri, 17
                                                                                    Pseudocurimata, 10
   lineopunctata, 11, 14
                                                                                      boehlkei, 4, 6-8, 21-23, 24
   lineopunctatus, 11
                                                                                      boulengeri, 4, 6-9, 11, 17-18, 24
   patiae, 14
                                                                                      brevipes, 18
   peruanus, 15
                                                                                      lineopunctata, 4, 6-8, 11-14, 24
   species, 21, 23
                                                                                      lineopunctatus, 11
   troscheli, 18
                                                                                      patiae, 4, 6-8, 13, 14-15, 24
Curimatus atratoensis, 10
                                                                                      peruana, 4, 6-9, 15-17, 24
   aureus, 1, 18, 20
                                                                                      troscheli, 18
   boulengeri, 1, 17
                                                                                      troschelii, 2, 4, 6-9, 11, 18-21, 24
   guentheri, 17
   brevipes, 1, 18, 20
                                                                                    spilurus, Curimatus, 10
   leucostictus, 20
                                                                                    Steindachnerina elegans, 2
   lineopunctatus, 1, 11, 13, 14
                                                                                      elegans bahiensis, 2
   patiae, 1, 14, 15, 18
                                                                                      guentheri, 18
   peruanus, 1, 15
                                                                                      morawhannae, 2
   trachystetus, 20
   troscheli, 18
                                                                                    troscheli, Curimata, 18
   troschelii, 18
                                                                                      Curimatus, 18
Cyphocharax, 10
                                                                                       Curimatorbis, 18
   gilberti, 2
                                                                                       Pseudocurimata, 18
                                                                                    troschelii, Anodus, 1, 18, 20
                                                                                       Curimatus, 18
elegans, Steindachnerina, 2
                                                                                      Pseudocurimata, 2, 4, 6-9, 11, 18-21, 24
elegans bahiensis, Steindachnerina, 2
```

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