

Taxonomic revision of the South American fish genus *Chalceus* Cuvier (Teleostei: Ostariophysi: Characiformes) with the description of three new species

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Received June 2002; accepted for publication July 2003

The Neotropical characid fishes of the genus *Chalceus* Cuvier, 1817, are reviewed. In total, five species are recognized (including three new species). *Chalceus epakros* sp. nov. is the most widespread geographically, occurring in many rivers of the Amazon basin, the Río Orinoco and in the Essequibo River drainage in Guyana. *Chalceus guaporensis* sp. nov. is restricted to the upper Rio Madeira, Rio Guaporé and Río Madre de Dios, of Brazil, Bolivia and Peru, respectively. *Chalceus spilogyros* sp. nov. occurs only in the Rio Trombetas, lower Rio Tapajós and lower Rio Madeira drainages. *Chalceus macrolepidotus* Cuvier occurs in the Rio Negro drainage, middle and lower Río Orinoco basin and in the rivers of the Atlantic slopes of the Guianas, and *Chalceus erythrurus* Cope in the Rio Amazonas and Rio Solimões to Río Ucayali drainage in Peru. *Chalceus ararapeera* Cuvier & Valenciennes and *Creagrutus pellegrini* Puyo are considered synonyms of *C. macrolepidotus*, and *Pellegrinina heterolepis* Fowler is placed into the synonymy of *C. erythrurus*. Characters pertaining to the monophyly of *Chalceus* are discussed and a key to species is presented. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 103–135.

ADDITIONAL KEYWORDS: Characidae – freshwater fishes – Neotropical region – systematics.

INTRODUCTION

Fishes of the characid genus *Chalceus* include species that are relatively common in rivers of the Amazon and Orinoco basins, and in the Atlantic drainages of the Guianas. They reach up to 30 cm in length and are readily recognized by their bright silvery body, red fins and large scales, attributes that contribute to their relative popularity in the aquarium trade. Little is known about the biology of *Chalceus* species in their natural habitats. They usually occur in the middle of the water column in areas varying from flooded forests to region of riverine rapids, and they feed on invertebrates, small fishes and vegetable matter (Schomburgk, 1841; Goulding, Carvalho & Ferreira, 1988: 217; Planquette, Keith & Le Bail, 1996: 230).

Chalceus was proposed by Cuvier (1817: 454) to include a new species, *C. macrolepidotus* from Brazil. A second species, *C. ararapeera*, was described by

Cuvier & Valenciennes (1850) from the Essequibo River in Guyana. During the period between the descriptions of the two species, various additional species were assigned to *Chalceus* by Cuvier (1819), Spix & Agassiz (1829), Müller & Troschel (1845) and Cuvier & Valenciennes (1850). However, all have subsequently been reassigned to *Brycon* Müller & Troschel or *Triportheus* Cope. Günther (1864: 333) was the first author to restrict *Chalceus* to *C. macrolepidotus* and *C. ararapeera*, and to suggest that the latter species be considered a junior synonym of the former.

The remaining three nominal species currently assigned to *Chalceus* have been historically proposed as members of different genera with some confusion concerning their identity. Cope (1870) described the new genus and species, *Plethodectes erythrurus*, but subsequently transferred the species to *Chalceus* (Cope, 1872: 262). Fowler (1906: 441) nonetheless retained *C. erythrurus* in *Plethodectes* and in addition described a new genus and species, *Pellegrinina heterolepis*, based on one specimen presumably from West Africa, later shown to be from South America and to

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represent a *Chalceus* species (Géry, 1977: 18). Puyo (1943: 143) proposed *Creagrutus pellegrini* based on two specimens from the Maroni river basin in French Guiana. This species was later cited as a *Chalceus* species (Myers, 1960: 211; Géry, 1977: 654; Vari & Harold, 2001: 43).

Géry (1977: 342) recognized only two *Chalceus* species – *C. macrolepidotus* and *C. erythrurus* – as valid, an action followed by all subsequent authors prior to this study. The two nominal forms were distinguished on the basis of colour pattern, primarily on the presence of a humeral blotch in *C. erythrurus* which is absent in *C. macrolepidotus*, along with differences in the life coloration of the fins. Examination of material from throughout the geographical distribution of the genus revealed that both *Chalceus* species currently recognized are more widely distributed than previously reported and that there are three additional undescribed species in the genus.

The objectives of the present paper are as follows: (1) redescribe *C. macrolepidotus* and *C. erythrurus*; (2) describe the three new *Chalceus* species; (3) provide an estimate of the geographical distributions of all recognized species and (4) discuss the monophyly of *Chalceus*.

MATERIAL AND METHODS

The taxonomic revision of *Chalceus* was based on the analysis of meristic and morphometric characters taken from specimens deposited in various institutions. Counts and measurements were made on the left side of specimens except when the structure being measured or counted was recognizably abnormal or damaged, in which case corresponding data were taken from the right side. Measurements were taken with calipers and data recorded to tenths of a millimetre for lengths under 150 mm and to a millimetre for longer measurements. All measurements were taken point to point. Vertebral counts and pterygiophore insertion relative to neural and haemal spines were obtained from cleared and stained specimens. Counts and measurements follow Fink & Weitzman (1974) except for body depth (measured at the dorsal-fin origin), number of scales below the lateral line (counted from the pelvic-fin insertion) and the last two branched dorsal-fin rays (counted as a single one; in *Chalceus* species, those two rays are associated with a single pterygiophore). Vertebrae incorporated into the Weberian apparatus were counted as four elements and the fused PU1 + U1 was counted as one. Counts are presented in the species descriptions with the value of the holotype, when available, given first, followed (in parentheses) by range, mean and total number of specimens in which counts were made. Measurements are presented in tables. Subunits of

the head are given as proportions of head length (HL). Head length and measurements of body subunits are given as proportions of standard length (SL). Numbers in parentheses following a particular vertebral count are the number of specimens with that count.

Although we summarize the statistical procedures used herein, see Weitzman & Malabarba (1999: 2–4) for more complete comments about their use. In running simple *t*-tests our samples failed to pass the normality test. Thus our comparisons of counts were made using the Mann–Whitney rank sum test. We utilize Tukey box plots to present visual comparisons of the count distribution of two species (*C. epakros* and *C. guaporensis* spp. nov.). In these plots the mean is represented by a thick vertical bar, the median by a thin vertical line that is often the same as one of the vertical lateral borders of the boxes. Therefore, the numerical value of the median is given in the legend. The 25th and 75th percentiles are represented by the lateral borders of the boxes and indicate the respective values at which 25% of the samples fall below and 25% fall above the lateral borders of the boxes. Error bars represent the 10th and 90th percentile points and circles represent the 5th and 95th percentiles. When the minimum and maximum, respectively, are different from these, each is represented by an asterisk.

Live body coloration is described based on photographs of freshly collected specimens and on specimens maintained in aquaria. In each 'Material Examined' section, lots are grouped by country and within each country, by state or department, followed by institutional abbreviation, catalogue number, number of specimens in the lot, number of cleared and stained (C & S) specimens when present, their range of standard lengths and specific locality data. An asterisk after a catalogue number refers to a lot containing specimens having a characteristic wide and dark longitudinal band, discussed in detail in 'Comments on the colour pattern of *Chalceus* species' and 'Colour in alcohol' in the species descriptions. Institutional abbreviations follow Leviton *et al.* (1985) and Leviton & Gibbs (1988).

MONOPHYLY OF *CHALCEUS*

Characters discussed below pertaining to the question of the monophyly of *Chalceus* were derived from a cladistic analysis carried out by Zanata (2000) that focused primarily on the systematics of the characid genus *Brycon*. The analysis was based on 144 morphological characters and 58 characiform taxa and included one *Chalceus* species (*C. macrolepidotus*). In that analysis *Chalceus* is hypothesized as more closely related to African characids and representatives of the Neotropical families Hemiodontidae and Crenuchidae, followed by a clade formed by several representatives

of the Neotropical Characidae. The most basal taxa included in that analysis was *Xenocharax*, proposed as the sister-group of all other characiforms (Fink & Fink, 1981: 306).

Characters that supported the monophyletic condition of *Chalceus* in that analysis were, in the present study, checked in all recognized *Chalceus* species. Some of the characters proposed by Zanata (2000) as derived for *Chalceus* species are also present in groups previously hypothesized as being closely related to *Chalceus* (e.g. *Brycon* and the African characids (= alestids)) and their eventual utility as synapomorphies for *Chalceus* depends on a more detailed phylogenetic analysis focused on the relationships of these taxa. We chose to include those characters in the discussion below since they constitute additional distinguishing characters for *Chalceus*.

Supramaxilla (Fig. 1)

All *Chalceus* species possess a supramaxilla situated along the posterodorsal margin of the maxilla. Among characiforms the presence of this ossification has also been reported for *Agoniates ladigesi* (Géry, 1963: 278, fig. 7; = *A. anchovia* Eigenmann; Zarske & Géry, 1997: 180) and the Chilodontidae (Roberts, 1969: 416; Vari, 1983: 10, fig. 1). The presence of a supramaxilla in *Agoniates* has not been confirmed (Castro, 1984: 80). The maxilla of *Agoniates* possesses a median stria that extends along the entire length of the ossification and which separates that bone into dorsal and ventral portions. This structure may have been erroneously interpreted by Géry (1963) as a joint between two separate bony elements.

The phylogenetic relationships of the Chilodontidae lie with the Neotropical characiform families Anostomidae, Prochilodontidae and Curimatidae (Vari, 1983) all of which lack a supramaxilla. The common possession of a supramaxilla in the Chilodontidae and

Chalceus is consequently considered to represent convergence and is hypothesized to be a synapomorphy for *Chalceus* species.

Series of premaxillary teeth (Fig. 2)

Chalceus species are characterized by the presence of three series of cuspidate teeth on the premaxilla. This feature is also present in *Chilobrycon*, *Brycon* and *Triporthus* among characiforms, and has been interpreted as evidence of relationship among the latter two genera and *Chalceus* by various authors (Regan, 1911; Howes, 1982; Lucena, 1993). However, the arrangement of teeth in the premaxillary series differs among all these genera, raising questions about the homology of the feature.

Chalceus species possess well-defined elongate outer and inner premaxillary teeth series with 6–13 and 5–10 teeth, respectively. A third series is formed by two more widely spaced teeth of intermediate size situated between the outer and inner tooth series.

The premaxillary dentition in *Brycon* and *Chilobrycon* is characterized by an outer series with many cuspidate teeth and an inner series of two large teeth. One or two additional series of teeth are situated between the outer and inner series anteriorly and become aligned posteriorly with the inner series (e.g. see illustrations in Howes, 1982). In *Triporthus* there is variation in the arrangement of teeth on the premaxilla with two or three series present, in a pattern more similar to that of *Brycon*.

The arrangement of premaxillary teeth in *Chalceus* is thus a unique pattern among characiforms and is hypothesized to be synapomorphic.

Internal series of dentary teeth

All *Chalceus* species possess an internal series of dentary teeth formed by a large symphyseal conical tooth

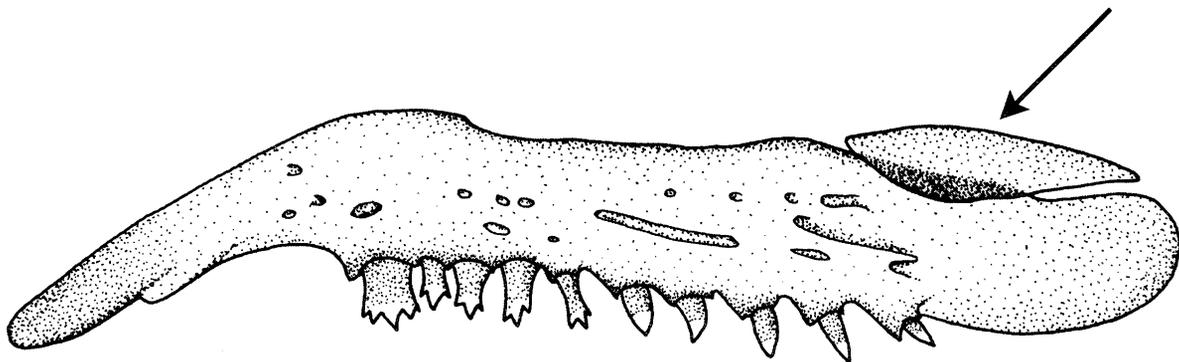


Figure 1. Maxilla and supramaxilla (arrowed) of *Chalceus erythrurus*, MZUSP 20385, 104.6 mm SL, lateral view, anterior to left.

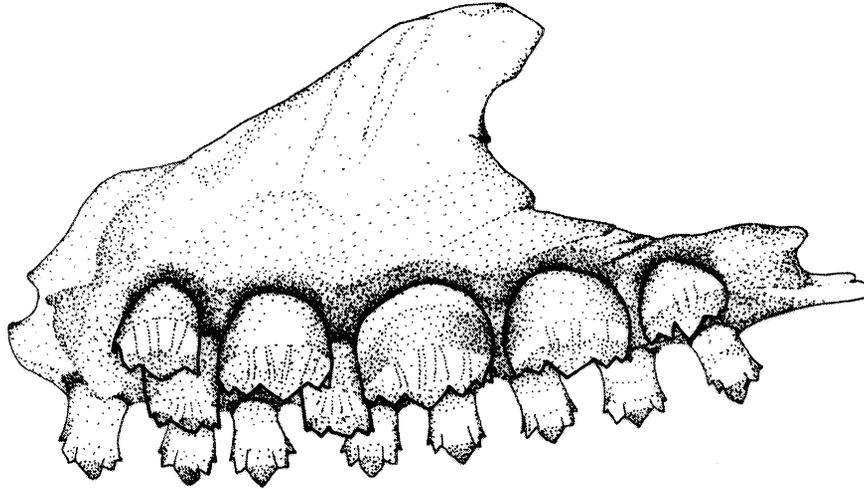


Figure 2. Premaxilla of *Chalceus erythrurus*, MZUSP 20385, 104.6 mm SL, right side, medial view, anterior to left.

(sometimes tricuspid in large specimens) followed by a gap and a series of smaller conical teeth situated along the dorsal margin of the replacement tooth trenches. The size of the gap varies among *Chalceus* species and is almost absent in *C. macrolepidotus* in which the series of small conical teeth is almost continuous with the symphyseal tooth.

Internal series of dentary teeth similar to those of *Chalceus* occur in *Brycon* and *Chilobrycon deuterodon* (Zanata, 2000). According to this study, the phylogenetic relationships of *Chalceus* apparently do not lie with either of those genera and the arrangement of the internal dentary teeth of *Chalceus* is thus hypothesized to be a synapomorphy for the species of the genus, with the condition in *Brycon* and *Chilobrycon* representing convergence.

Anterolateral process of the mesethmoid (Fig. 3)

In *Chalceus* spp. the anterolateral process of the mesethmoid (lateral ethmoid wing *sensu* Weitzman, 1962: 19) is greatly reduced, thereby providing a small region for the support of the posterior region of the premaxilla. In the majority of characiforms, including genera proposed as closely related to *Chalceus* (Zanata, 2000), such a mesethmoid process is well developed, serving as an anchoring site for the premaxilla. In evaluating the form of the lateral wing of the mesethmoid in other outgroup characiforms we confronted some problems with the coding of this character. In *Hemiodus*, *Hepsetus* and *Xenocharax*, the overall forms of the mesethmoid differ significantly from those present in *Chalceus*, thereby rendering an evaluation of the homology of the components of the mesethmoid between these various taxa problematic. In the present study the condition of this character in

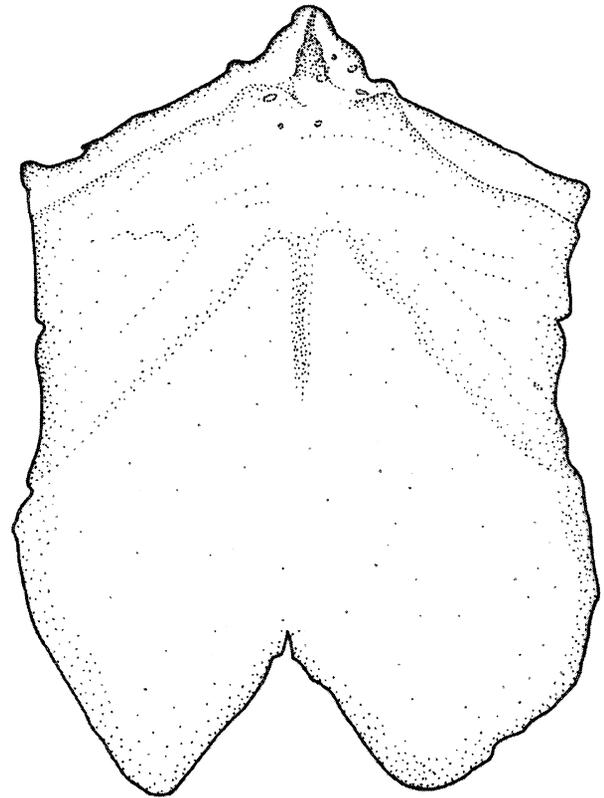


Figure 3. Mesethmoid of *Chalceus spilogyros* sp. nov., paratype, MZUSP 76069, 122.7 mm SL, dorsal view, anterior at top.

Xenocharax was treated as absent and in *Hemiodus* and *Hepsetus* as unknown. A reduced anterolateral process of the mesethmoid in *Chalceus* is herein hypothesized as autapomorphic for the genus.

Size of body scales

In all *Chalceus* spp. the scales situated dorsal to the lateral line are about twice the size of those situated ventral to it. In the majority of characiforms, including genera proposed as closely related to *Chalceus* (Zanata, 2000), the scales either decrease gradually in size dorsally to ventrally or those below the lateral line are only slightly smaller than those above it. A condition of the scales similar to that of *Chalceus* occurs only in the African characid *Arnoldichthys spilopterus* (Paugy, 1990: 232) among Characiforms. As discussed above, determining whether this feature is either synapomorphic for *Chalceus* with an independent acquisition in *Arnoldichthys* or homologous between the two genera necessitates resolution of the relationships of the African characids, which has yet to be determined.

Size of lateral-line scales

The scales along the lateral-line series of all *Chalceus* species are alternatively large or small in the region from the posterior margin of the opercle to the anterior portion of the caudal peduncle, and then are approximately equal in size. In the majority of characiforms, including genera proposed as closely related to *Chalceus* (Zanata, 2000), the scales along the lateral-line series are all of similar size or gradually decrease in size posteriorly. Only *Arnoldichthys spilopterus* has an arrangement of lateral line scales similar to that of *Chalceus*. Determining whether this feature is either synapomorphic for the species of *Chalceus* with an independent acquisition in *Arnoldichthys*, or indicates

phylogenetic affinity between the two genera, depends, as already mentioned, on the resolution of the phylogenetic relationships of the African characids and is beyond the scope of this study.

TAXONOMIC REVISION

CHALCEUS CUVIER, 1817

Chalceus Cuvier, 1817: 454 (type species *Chalceus macrolepidotus* Cuvier, 1817: 454, by monotypy).

Plethodectes Cope, 1870: 563 (type species *Plethodectes erythrurus* Cope, 1870: 563, by monotypy).

Pellegrinina Fowler, 1906: 442 (type species *Pellegrinina heterolepis* Fowler, 1906: 442, by original designation and monotypy).

Diagnosis: *Chalceus* is phylogenetically diagnosed on the basis of the following synapomorphies (but see comments in previous section):

- (1) Presence of supramaxilla;
 - (2) Three series of teeth on premaxilla;
 - (3) Internal series of dentary teeth formed by a large symphyseal conical tooth followed by a gap and a series of smaller conical teeth;
 - (4) Reduced anterolateral process of mesethmoid;
 - (5) Scales situated dorsal to lateral line much larger than those ventral to it;
 - (6) Relative size of scales along lateral line other than on caudal peduncle alternatively large and small.
- In addition, the combination of the following characters is useful to distinguish the species of *Chalceus* among characiforms: bright silvery body, red fins and short anal fin.

KEY TO THE SPECIES OF *CHALCEUS*

- (1) Absence of distinct spots or conspicuous stripes of dark pigmentation on body (except for wide and inconspicuous longitudinal band formed by chromatophores located superficially in the skin in some specimens during reproductive period) (See 'Comments on the colour pattern of *Chalceus* species') (Figs 4, 5) *C. macrolepidotus*
- (1') Presence of dark pigmentation forming humeral spots or stripes 2
- (2) Humeral spot absent or poorly defined, round to vertically elongate and located deep under scales; presence of narrow longitudinal dark stripe from posterodorsal margin of opercle to caudal peduncle; snout relatively acute; median fontanel between frontals and parietals absent 4
- (2') Presence of conspicuous humeral spot, round in shape and located superficially beneath scales; lateral surface of body usually with reticulate pattern; snout rounded; median fontanel present between frontals and parietals 3
- (3) Humeral spot with notch on its posterodorsal margin; reticulate pattern of body coloration more evident along series of scales posterior to humeral blotch; pelvic and anal fins dark; caudal-fin lobes robust and rounded (Fig. 10) *C. erythrurus*
- (3') Humeral spot without notch on its posterodorsal margin; reticulate pattern of body coloration uniformly distributed over lateral and dorsal portions of body; pelvic and anal fins hyaline; caudal-fin lobes elongate and slender (Figs 15, 16) *C. spilogyros*
- (4) Number of branched pelvic-fin rays 7 (Figs 22, 23) *C. guaporensis*
- (4') Number of branched pelvic-fin rays 8 (Figs 18, 19) *C. epakros*

CHALCEUS MACROLEPIDOTUS CUVIER, 1817
(FIGS 4–9; TABLE 1)

Chalceus macrolepidotus Cuvier, 1817: 454, pl. I, fig. 1 [original description, type locality: Brazil]. Schomburgk, 1841: 216, pl. XIV [description, Guyana: Essequibo River, Camuti mountain]. Cuvier & Valenciennes, 1850: 240 [description based on same specimen of Cuvier, 1817]. Günther, 1864: [in part: British Guiana (= Guyana), Essequibo River; not the specimen cited for Brazil: Rio Cupai (= Cupari); *Chalceus ararapeera* Cuvier & Valenciennes placed as synonym]. Cope, 1872: 262 [species listed, Brazil: Rio Solimões]. Eigenmann & Eigenmann, 1891: 55 [literature compilation, in part: British Guiana (= Guyana), not including the citation of species for the Rio Cupai (= Cupari) (Brazil) and (Río) Ambyiacu (= Ampiyacu) (Peru)]. Regan, 1905: 190 [Rio Negro,

based on drawings made by A. R. Wallace]. Eigenmann, 1910: 439 [in part: not including the synonymy of *Pellegrinina heterolepis*]. Eigenmann: 1912: 372 [British Guiana (= Guyana)]. Regan, 1912: 388 [in part: British Guiana (= Guyana: Essequibo River; Surinam; not including the synonymy of *Pellegrinina heterolepis* Fowler]. Cockerel, 1914: 107, pl. 27, fig. 5 [scale morphology]. Eigenmann & Allen, 1942: 277 [literature compilation in part, not including the citation of species for The Río Ambyiacu (= Ampiyacu) (Peru)]; not including the listed specimens; not including the synonymy of *Chalceus macrolepidotus iquitensis* and *Pellegrinina heterolepis*]. Bertin, 1948: 9 [type specimen at MNHN, Paris]. Puyo, 1949: 129 [French Guiana]. Fowler, 1950: 364 [literature compilation, in part, not including the synonymy of *Pellegrinina heterolepis* and *Chalceus macrolepidotus iquitensis* Nakashima; common



Figure 4. *Chalceus macrolepidotus*, ANSP 176678, 200.3 mm SL, Guyana, Siparuni River at Tumbledown Rapids, 4°48'39"N, 58°51'11"W.



Figure 5. *Chalceus macrolepidotus*, MZUSP 66482, 91.6 mm SL, Brazil, Amazonas, Rio Tiquié, about 1 h downriver from the Indian community of Cunuri, below Cachoeira do Tucano.



Figure 6. *Chalceus macrolepidotus*, juvenile, AMNH 214938, 37.3 mm SL, Guyana, Bartica, junction Mazaruni-Cuyuni and Essequibo rivers.



Figure 7. *Chalceus macrolepidotus*, holotype, MNHN 2634, 144.6 mm SL, Brazil.

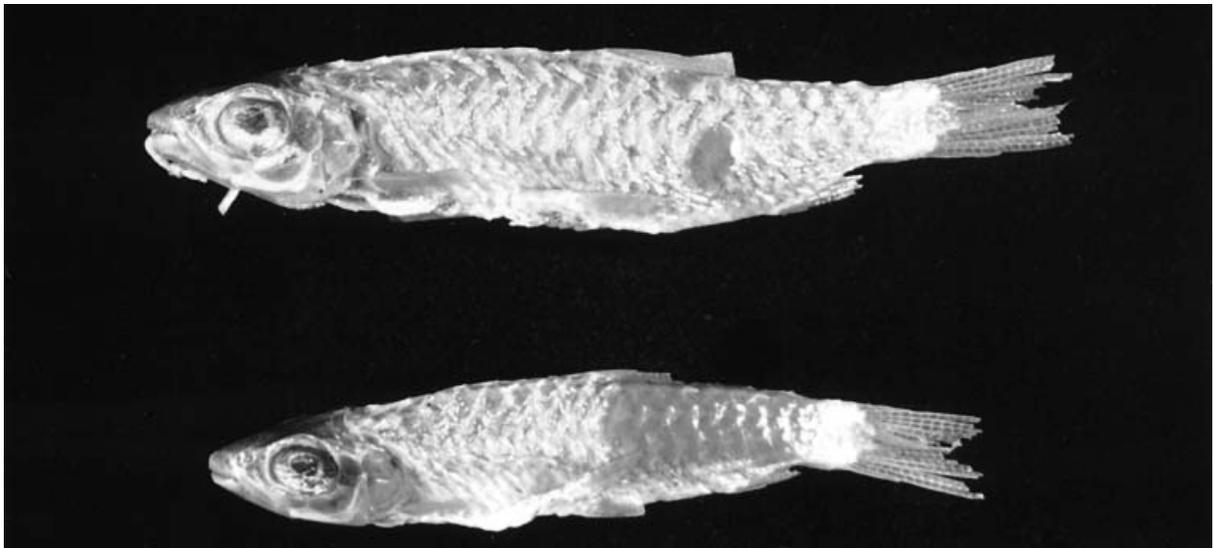


Figure 8. *Chalceus macrolepidotus*, syntypes of *Chalceus ararapeera*, MNHN A9830, 66.9–80.2 mm SL, Guyana, Essequibo River.

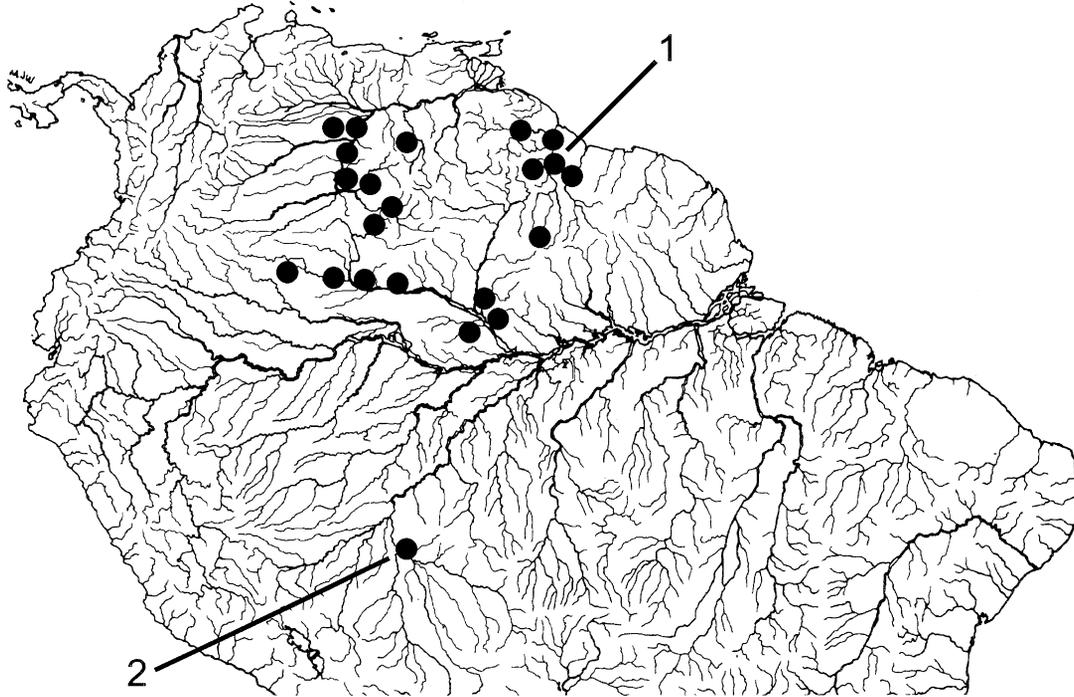


Figure 9. Map of northern portion of South America showing geographical distribution of *Chalceus macrolepidotus* (type locality inexact, Brazil; 1 = type locality of *C. ararapeera*, Essequibo River, Guyana; 2 = geographically disjunct population tentatively identified as *C. macrolepidotus*). Some symbols represent more than one locality or lot of specimens.

name: Saragui, São Pedro]. Boeseman, 1952: 189 [Surinam (specimen not examined, identification inferred by geographical distribution), local name: morokò]. Mago Leccia, 1971: 10 [Rio Casiquiare (specimen not examined, identification on geographical distribution)]. Heyer, 1975: 343 [aquarium; photograph of live specimens]. Cala, 1977: 7 [Colombia, Rio Orinoco basin, Río Inirida and Río Vichada; (specimens not examined); common name Arari, Raborrojo]. Géry, 1977: 342 [diagnosis]. Azuma, 1979: 58–62 [aquarium, spawning and photographs of live specimen and fry]. Lauder, 1981: 162 [functional morphology: feeding mechanism]. Géry & Planquette, 1982: 73 [French Guiana (specimen not examined, identification inferred by geographical distribution)]. Géry, Planquette & Le Bail, 1991: 43 [French Guiana: Fleuve Oyapock and Fleuve Approuague (specimen not examined, identification inferred by geographical distribution)]. Planquette, Keith & Le Bail, 1996: 230 [French Guiana: Fleuve Maroni, local common names, photograph of live specimen]. Taphorn *et al.*, 1997: 70 [list of species of Venezuela].

Brycon macrolepidotus Müller & Troschel, 1845 [diagnosis; incorrect placement in the genus *Brycon*].

Chalceus ararapeera Cuvier & Valenciennes, 1850: 244 [original description, type locality Essequibo

River, Guyana; common name: Arara-pira, Parshama (= poisson perroquet)]. Bertin, 1948: 9 [syntypes at MNHN, Paris].

Creagrutus pellegrini Puyo, 1943: 143, fig. 2 [original description, type locality French Guiana: upper Fleuve Itany, upper Fleuve Maroni system]. Puyo, 1949: 128, fig. 66 [description; based on Puyo, 1943]. Myers, 1960: 211 [placement of species in genus *Chalceus*]. Géry, 1977: 654 [referred species to *Chalceus macrolepidotus*]. Vari & Harold, 2001: 2, 43 [discussion of taxonomic status, placement of species in genus *Chalceus*].

Diagnosis

Chalceus macrolepidotus can be readily distinguished from all other *Chalceus* species by the absence of any distinct spots of pigmentation or stripes (Figs 4–6) (except for some sexually mature specimens, see next section: ‘Comments on the colour pattern of *Chalceus* species’, henceforth abbreviated to ‘Comments . . .’). It differs from *C. erythrurus* and *C. spilogyros* by the lack of a humeral spot and from *C. epakros* and *C. guaporensis* by the lack of a longitudinal band along the body sides located deep under the skin. In life *C. macrolepidotus* can be distinguished from *C. epakros* by the lack of red pigmentation on the central portions of scales on the

Table 1. Morphometrics of *Chalceus macrolepidotus*. Data of syntypes of *Chalceus ararapeera* Cuvier & Valenciennes – MNHN A9830 – not included due to poor condition of specimens. All dimensions in mm

Character	Holotype	<i>n</i>	Range	Mean
Standard length (mm)	244.6	97	31.1–227.8	
Body depth	23.7	96	21.2–29.6	26.1
Snout to dorsal-fin origin	55.2	95	52.9–61.4	57.5
Snout to pectoral-fin origin	25.5	96	23.7–35.4	28.5
Snout to pelvic-fin origin	51.1	96	49.3–59.5	54.8
Snout to anal-fin origin	79.7	95	76.9–85.4	80.7
Caudal-peduncle length	–	74	11.3–15.8	13.1
Caudal-peduncle depth	9.7	97	9.2–12.1	10.5
Dorsal-fin length	18.8	93	18.7–27.3	23.2
Anal-fin base	8.9	69	7.9–11.2	9.4
Anal-fin length	13.9	90	13.7–19.9	16.4
Pectoral-fin length	18.2	94	16.4–23.5	20.0
Pelvic-fin length	15.4	95	15.4–20.4	18.2
Head length	24.5	97	22.6–36.3	28.4
Snout length	32.5	96	28.4–37.7	33.4
Orbital diameter	26.2	94	22.6–41.9	30.2
Interorbital width	46.7	93	27.9–50.8	39.4
Upper jaw length	36.8	95	36.4–50.0	42.1

longitudinal series above the lateral line and from *C. erythrurus* by having the pelvic and anal fins tinged with red or hyaline (vs. yellow; compare photographs in Géry, 1977: 329 and 332). *Chalceus macrolepidotus* may be further distinguished from *C. erythrurus*, *C. spilogyros* and *C. guaporensis* in having the first small inner dentary row tooth originating very close to the symphyseal tooth and forming a nearly continuous series (vs. having first small tooth of inner dentary row located well behind the fourth or fifth tooth of the outer row with a distinct gap between the symphyseal tooth and first small conical tooth). *Chalceus macrolepidotus* can be further distinguished from *C. epakros* and *C. guaporensis* by the presence of a fontanel between the contralateral frontal and parietal bones in all but the larger specimens (vs. fontanel absent in all specimens of *C. epakros* and *C. guaporensis*).

Description

Morphometric data presented in Table 1. Maximum size 228.0 mm SL. Body robust, relatively elongate, greatest body depth slightly anterior to dorsal-fin origin. Dorsal profile of head distinctly convex anteriorly along snout region, nearly straight to posterodorsally inclined from anterior end of snout to tip of supraoccipital spine. Dorsal profile of head in large specimens (over 200 mm SL) slightly convex and continuous with dorsal body profile. Anterior margin of snout somewhat acute in dorsal view. Interorbital

distance wide, proportionally wider relative to SL in large specimens. Dorsal body profile convex from tip of supraoccipital spine to dorsal-fin origin, posterodorsally inclined along dorsal-fin base, straight to relatively convex to adipose fin and concave along dorsal profile of caudal peduncle to origin of procurvent caudal-fin rays. Overall dorsal profile of head and body of juveniles up to 50 mm SL nearly straight to slightly convex. Ventral profile of head distinctly convex in region of lower jaw, resembling a chin. Ventral body profile gently convex from the posterior limit of isthmus to anal-fin origin. Body profile along anal-fin base posterodorsally inclined, slightly concave along ventral margin of caudal peduncle. Head robust in large specimens (over 180 mm SL). Smaller specimens with relatively longer heads and more acute snout. Dorsal surface of head with distinct medial fontanel restricted to small region anterior to epiphyseal bar between contralateral frontals and completely separating parietals. Fontanel wide in small specimens and progressively narrower in larger individuals. Fontanel completely closed in 200 mm SL specimen. Mouth terminal, large, upper jaw slightly longer than lower jaw, tip of premaxillary teeth extending below margin of upper lip giving saw-like appearance to margin of premaxilla even in closed mouth. Maxilla extending approximately to vertical through anterior margin of orbit. Supramaxilla present.

Dorsal-fin rays ii,10 (ii,10, *n* = 92). Dorsal-fin origin posterior to vertical through insertion of innermost

pelvic-fin rays. First basal dorsal-fin pterygiophore inserting behind neural spine of 14th vertebra ($n = 1$). Distal margin of dorsal fin nearly straight to convex. Adipose fin present. Anal-fin rays iii,9 (iii,9; iii,8 in one specimen, $n = 87$). First basal anal-fin pterygiophore inserting behind haemal spine of 26th vertebra ($n = 1$). Distal margin of anal fin straight to emarginate with anterior branched rays approximately 3 times length of ultimate ray. Pectoral-fin rays i,15 (range 14–18, mean 16, $n = 88$), pointed distally, with unbranched- and first branched rays longest. Tip of pectoral fin not reaching pelvic-fin insertion. Pelvic-fin rays i,8 (i,8; i,7 in 3 specimens, $n = 92$); fin pointed distally. Caudal fin forked, with lobes slender, especially in specimens up to 120 mm SL, lower fin lobe slightly more developed than upper lobe.

Premaxillary teeth in three rows. Outer row 9 (range 7–10; 11 in one specimen, mean 8.5, $n = 92$) tricuspid or pentacuspoid in large specimens; smaller specimens with tricuspid or conical teeth, with medial cusp larger. Tooth close to premaxillary symphysis slightly larger than others in series. Remaining teeth of similar size except for slightly smaller one or two lateralmost teeth. Cusps slightly curved with concave portion facing mouth cavity. Inner row 6 (range 6–8; 5 in one specimen, 9 in two, mean 6.4, $n = 92$) with largest, symphyseal tooth usually asymmetric with one cusp on the medial side and two on the lateral side of tooth. Remaining teeth penta- or heptacuspoid in large specimens, all teeth tricuspid in small specimens, with second tooth from symphysis larger and teeth gradually diminishing in size laterally. Cusps slightly curved, with concave portion opposite of mouth cavity. Intermediate row 2 (2; 1 in three specimens, $n = 91$) pentacuspoid (rarely tricuspid) teeth more spaced than teeth of other rows and of intermediate size. Cusps straight.

Maxillary teeth 12 (range 8–13, with single specimens each having 7, 14, 16 and 17 teeth, mean 10.9, $n = 90$); smaller specimens usually with higher tooth counts. First teeth pentacuspoid followed by tricuspid and conical teeth distally. Maxillary dentition not extending along entire margin of ossification in large specimens. Small specimens with maxillary teeth conical and extending along entire margin of ossification. Dentary teeth in two rows. Outer row 8 (range 8–13, 14 in one specimen, 16 in 2, mean 10.9, $n = 90$). Teeth large and pentacuspoid anteriorly, sometimes heptacuspoid in large specimens or tricuspid in small specimens, gradually diminishing in size and number of cusps posteriorly. Posteriormost teeth conical. Cusps slightly curved with concave portion facing mouth cavity. Inner row consists of large conical symphyseal tooth (tricuspid in few larger specimens) followed by series of approximately 30 minute conical teeth. First tooth origi-

nates very close to symphyseal tooth, forming an almost continuous series.

Scales cycloid, large overall, approximately twice as large above lateral line as below it. Circuli on exposed portion of scales not concentric with those of anterior portion; circuli on exposed portion of scales straight and extending to posterior margin of scale in small specimens; restricted to upper and lower portion of scale in specimens around 140 mm SL; disorganized and with labyrinthic pattern in specimens around 170 mm SL. Radii originating on centre of scale and radiating anteriorly and posteriorly on scale surface.

Lateral line low on body sides, complete, with alternating large and small perforated scales from posterior margin of opercle to vertical through base of last anal-fin ray; scales smaller and of similar size from that point to end of caudal peduncle. Canals in large specimens with 3–9 elevated branches, forming ridges on scale surface; ridges more evident on region of caudal peduncle. Number of branches decreases toward caudal peduncle with posterior scales unbranched. Small specimens (less than 140 mm) with branching pattern less developed. Lateral-line scales 38 (range 36–40, mean 38, $n = 90$). Scale rows between dorsal-fin origin and lateral line 3; between lateral line and pelvic-fin insertion 2. Scales around caudal peduncle 12. Vertebrae 39 ($n = 1$).

Colour in life. (Description based on photographs in Géry, 1977: 329 and Planquette *et al.*, 1996: 231). Overall coloration of head and body bright silver. No conspicuous humeral spot. Dorsal portion of eye yellow. One specimen (Géry, 1977: 329) with dorsal profiles of head and body darker. Somewhat indistinct longitudinal stripe extending from rear of orbit through opercle to vertical through adipose fin and patch of dark pigmentation present on middle portion of opercle. Caudal fin bright red, adipose yellowish, all other fins hyaline. Other specimens (Planquette *et al.*, 1996: 231) with dorsal portions of head and body darker. Margins of scales on dorsal portions of body with light concentration of chromatophores, forming fine reticulate pattern. All fins (except pectoral) bright red, more so on their proximal portions.

Colour in alcohol. All available specimens lacking guanine on body except for few that retain silvery pigmentation on infraorbital and opercular regions. Ground coloration of head and body in specimens ≥ 60 mm SL yellowish to tan (Figs 4, 5), becoming darker dorsal of horizontal line through dorsal margin of orbit. No longitudinal body stripe or humeral blotch. Dark chromatophores scattered over infraorbitals and opercular region. Scales on body with chromatophores slightly more concentrated along posterior margin, forming fine reticulate pattern more evident in recently collected specimens

(although less evident in large specimens). All fins hyaline. Some specimens with dark tips on dorsal- and caudal-fin rays.

Ground coloration of specimens ≤ 60 mm SL (Fig. 6) pale yellowish, somewhat darker dorsally, but difference between dorsal and ventral regions of body less pronounced than in larger specimens. Reticulate pattern of scales more conspicuous than in larger specimens. Pectoral and pelvic fins hyaline. Dorsal and adipose fins dusky. Lower and ventralmost rays of the upper caudal-fin lobes and anal fin dark.

Some specimens (MZUSP 58962 (1 of 2); MZUSP 43291; and ANSP 161220) with a dark and wide longitudinal band along the body sides (see 'Comments . . .').

Distribution

Rio Negro and its tributaries in Amazon basin, middle and upper Río Orinoco basin, Essequibo River drainage in Guyana, Corantijn River drainage in Suriname and perhaps Río Baures, a tributary of Río Guaporé, along Brazilian-Bolivian border ($12^{\circ}32'S$; $64^{\circ}19'W$) (for latter locality see 'Remarks') (Fig. 9).

Ecology

Puyo (1943: 130) and Planquette *et al.* (1996: 230) report *Chalceus macrolepidotus* from well oxygenated waters in regions of rapids; the latter authors mention that the species is uncommon in the lower portions of river drainages.

Remarks

All samples of *C. macrolepidotus* examined in the present study, with one exception, originated in the Rio Negro, Río Orinoco and in the Atlantic drainages of Guyana and Suriname. A single sample (UMMZ 204688) is from a southern locality, in the Río Baures, a tributary of the Río Guaporé, along the Bolivian-Brazilian border (indicated by 2 in Fig. 9). The series of 15 specimens from this locality have a cranial fontanel, lack any conspicuous body pigmentation such as a longitudinal stripe and/or a humeral blotch and cannot be distinguished from the population samples of *C. macrolepidotus* from the Rio Negro, Río Orinoco and the Guianas. Therefore, they were tentatively identified as *C. macrolepidotus*; this population sample occurs sympatrically with *C. guaporensis*, the only other *Chalceus* species that occurs in the Rio Guaporé drainage. This record represents a major range extension to the south for that species. A similar disjunct distribution pattern was reported by Vari & Harold (2001) for *Creagrutus maxillaris* (Myers).

The description of *Chalceus ararapeera* Cuvier & Valenciennes, 1850 was based on two specimens col-

lected by Robert Schomburgk in the Essequibo River in Guyana. These two syntypes (MNHN A9830) (Fig. 8) were examined in the present study and although in poor condition have a cranial fontanel and can be identified as *C. macrolepidotus* (Fig. 7). The only other species that occurs in Guyana is *C. epakros*, which lacks a cranial fontanel. *Chalceus ararapeera* is herein considered a junior synonym of *C. macrolepidotus* as first proposed by Günther (1864: 333). The type locality of *C. macrolepidotus* is indicated as originating in Brazil. The specimen on which Cuvier (1817) based the original description of the species was originally deposited in the 'Cabinet de Lisbonne' (Lisbon, Portugal). At the beginning of the 19th century, this and additional specimens from that collection were transferred to MNHN, Paris. They were originally collected by the Brazilian naturalist Alexandre Rodrigues Ferreira in the Brazilian Amazon (Vanzolini, 1996: 196–197).

The generic placement of *Creagrutus pellegrini* Puyo (1943: 143) was discussed by Vari & Harold (2001: 43) who suggested that it should be assigned to *Chalceus* and considered it to be a doubtful species, *C. pellegrini*, following Myers (1960: 211). We follow these authors in assigning the species to *Chalceus*. The question of the taxonomic status of *Chalceus pellegrini* (Puyo) is somewhat difficult to address in view of the apparent loss of type material of various species described by Puyo (Géry, 1959: 345) and the lack of information in Puyo's (1943: 143) description which would permit an unambiguous identification of the species. In addition, and as was also pointed out by Myers (1960: 211), Puyo (1949: 128–130) provided a description for *C. macrolepidotus* Cuvier following that of *Creagrutus pellegrini*, but surprisingly failed to recognize any relationship between the two nominal forms.

Puyo (1943: 143) described *C. pellegrini* on the basis of two specimens, one from the Fleuve Maroni and one from Fleuve Itany in French Guiana. Based solely on Puyo's description it is impossible to readily determine whether the specimens he examined represent *C. macrolepidotus* or *C. epakros*, the two *Chalceus* species known to occur in the Guianas. The currently known distribution of *C. macrolepidotus* and *C. epakros* in the Guianas helps to resolve this problem. Of the two species, only *C. macrolepidotus* has been reported in the Fleuve Maroni system (Planquette *et al.*, 1996: 230). In addition, *C. macrolepidotus* also occurs in the Corantijn River in Suriname and in the Essequibo River in Guyana. *Chalceus epakros* has a more restricted distribution in the Guianas, being recorded only from the middle Essequibo River. Therefore, we consider *Creagrutus pellegrini* to be a junior synonym of *Chalceus macrolepidotus* (see Géry, 1977: 654).

Material examined

Type material. MNHN 2634, 1, 244.6 mm SL, Brazil, holotype of *Chalceus macrolepidotus* Cuvier, 1817; MNHN A9830, 2, 66.9–80.2 mm SL; Guyana, Essequibo River, syntypes of *Chalceus ararapeera* Cuvier & Valenciennes, 1850.

Non-type material. BRAZIL: AMAZONAS: MZUSP 44570, 2, 100.9–141.0 mm SL; Rio Negro, São João, near Tapurucuara. MZUSP 20201, 3, 104.0–123.0 mm SL; Rio Negro, Rio Jauaperi, from mouth to 100 km upstream. MZUSP 43291(*), 7, 183.2–227.8 mm SL; Rio Negro, Cantagalo. – MZUSP 59046, 1, 197.4 mm SL; Rio Negro, lake in São João, near Tapurucuara. – MZUSP 58962(*), 2, 206.9–210.5 mm SL; Rio Negro, Cantagalo, floodplain lake. – MZUSP 62223, 2, 71.9–72.1 mm SL; lagoon in island of Rio Negro, Paricatuba. – MZUSP 63649, 3, 84.5–129.0 mm SL; Rio Uaupés. – MZUSP 66482, 2, 91.6–96.2 mm SL; Rio Tiquié, c. 1 h downriver from the Indian community of Cunuri, below Cachoeira do Tucano. – CAS 156171, 1, 49.9 mm SL; Rio Negro or Río Orinoco. – CAS 156172, 1, 86.1 mm SL; Rio Negro, Caranguejo, above São Gabriel. – CAS 156170, 1, 95.7 mm SL; CAS 156830, 3, 149.0–168.0 mm SL; Rio Negro, Bucuri. – INPA 16950, 6, 175.0–221.0 mm SL; Rio Jaú, Lago Ibama.

GUYANA: ANSP 176678, 1, 200.3 mm SL; Siparuni River, Tumbledown Rapids. FMNH 59467, 2, 166.7–198.0 mm SL; FMNH 7473, 1, 161.6 mm SL; AMNH 7082, 1, 178.0 mm SL; USNM 66156, 1, 161.0 mm SL; FMNH 53479, 5, 67.4–200.2 mm SL; FMNH 69807, 2, 75.3–188.3 mm SL; lower Potaro River, Tumatumari. – CAS 69079, 1, 65.1 mm SL; Essequibo River drainage, above the falls at Tumatumari Cataract. – CAS 121888, 1, 164.0 mm SL; Potaro River at Tumatumari Cataract. – AMNH 14331, 15, 82.4–105.4 mm SL; AMNH 214975, 6, 70.5–84.7 mm SL; AMNH 13399, 2, 35.5–57.5 mm SL; AMNH 14322, 1, 104.3 mm SL; Essequibo River, Rockstone. – AMNH 214938, 6, 35.8–43.4 mm SL; junction Mazaruni-Cuyuni and Essequibo Rivers, Bartica. – AMNH 43352, 9, 31.1–60.7 mm SL; BMNH 1936.4.4.5–6, 2, 41.4–44.9 mm SL; Essequibo, Bartica. – CAS 69081, 3, 160.0–190.0 mm SL; BMNH 64.1.21.46, 1, 134.2 mm SL; Essequibo River drainage. – CAS 69084, 2, 76.6–90.1 mm SL; Essequibo River drainage, Konawaruk pool, near the mouth of the Konawaruk River. – FMNH 53477, 3, 67.6–104.5 mm SL; Konawaruk. – FMNH 53478, 3, 74.2–83.4 mm SL; Gluck Island. – CAS 69086, 2, 83.3–84.7 mm SL; Essequibo River channels around Gluck Island, near Rockstone. – AMNH 216222, 1, 171.0 mm SL; headwaters between Mandi and Kuyuwini rivers, Essequibo River drainage. – AMNH 73020, 1, 54.2 mm SL; sandbar on north bank Cuyuni River, just upstream of Caowry Creek,

Essequibo. – AMNH 220375, 2, 56.9–76.5 mm SL; USNM 94124, 1, 135.2 mm SL; Essequibo River drainage, Kartabo. – AMNH 221068, 2, 22.0–27.5 mm SL; Akima Island. – BMNH 1972–10.17: 1438, 1, 68.1 mm SL; Amatuk Creek, Potaro River. – BMNH 1972–10.17: 1440, 2, 66.5–68.5 mm SL; Kanaima Creek, Potaro River. – AMNH 16792, 3, 77.6–88.1 mm SL; AMNH 14313, 4, 88.5–101.2 mm SL; unspecified localities in Guyana.

SURINAME: AMNH 16421, 1, 168.0 mm SL; BMNH 70.3.10.53, 1, 55.3 mm SL; unspecified locality in Suriname. – AMNH 54870, 5, 89.1–95.3 mm SL; Toeboeroe Creek. – AMNH 54810, 2, 67.2–90.5 mm SL; Dalbana Creek, 150 m upstream from junction with Kabelebo River. – USNM 226115, 46, 58.0–127.9 mm SL; Corantijn River at km 180, side channel of main river along Surinamese shore. – USNM 226114, 1, 198.0 mm SL; Corantijn River, Matapi Creek. – USNM 225373, 1, 76.4 mm SL; Corantijn River, about 2 km N of Matapi.

VENEZUELA: AMAZONAS: ANSP 161220(*), 1, 164.4 mm SL; Río Iguapo c. 1 h. above its mouth, Río Orinoco drainage. – ANSP 161221, 2, 131.7–138.0 mm SL; Río Ventuari c. 12 km from its confluence with Río Orinoco. – ANSP 161223, 2, 89.1–125.5 mm SL; Río Pamoni, lagoon c. 0.5 km from confluence of Río Casiquiare. FMNH 103882, 1, 84.8 mm SL; backwater and beach of Río Atabapo c. 40 ft above mouth. – FMNH 103883, 2, 79.1–98.9 mm SL; Río Atabapo (pools) c. 1.2 h. above San Fernando de Atabapo. – FMNH 103885, 1, 76.9 mm SL; Río Autana at Playa Cucurito. – FMNH 103884, 1, 164.9 mm SL; Caño Guasuripana at Guasuripana, tributary of Río Atabapo, c. 7 min from San Fernando de Atabapo. – FMNH 103886, 3, 77.3–91.8 mm SL; pool of Río Ventuari above mouth in Río Orinoco Laguna Pavon. – FMNH 103881, 2, 80.9–89.9 mm SL; Caño Tuparero c. 2.5 h above San Fernando de Atabapo in Río Orinoco. – MZUSP 62454, 1, 125.8 mm SL; lagoon on Río Pamoni, c. 0.5 km from mouth in Río Casiquiare. – CAS 154592, 1, 92.2 mm SL; Río Casiquiare. – MZUSP 62455, 2, 78.8–92.5 mm SL; Laguna Pavon in pond behind beach of Río Ventuari, c. 30 min. from mouth. APURE: ANSP 165684, 4, 74.2–170.4 mm SL; Caño Potrerito, 24 km S of Río Cinaruco on San Fernando de Apure, Puerto Paez Highway. – FMNH 69909, 1, 104.1 mm SL; FMNH 69910, 13; Río Cinaruco. – USNM 270135, Balneario Pozo Azul, c. 1 km E of Puerto Ayacucho to Solano road. BOLIVAR: MZUSP 62456, 2, 83.6–87.5 mm SL; Departamento Cedeño, mouth of caño tributary to Río Nichare. – FMNH 85686, 6, 122.6–125.8 mm SL (1 C & S); Río Orinoco drainage, 50 km toward Puerto Ayacucho from Puerto Nuevo.

The following sample is tentatively identified as *Chalceus macrolepidotus* (see 'Remarks', above):

BOLIVIA: UMMZ 204688, 15, 70.7–91.0 mm SL; El Beni: Río Baures at mouth on right bank, 6 km SW of Costa Marques, Brazil.

CHALCEUS ERYTHRURUS (COPE, 1870)
(FIGS 10–14, TABLE 2)

Plethodectes erythrurus Cope, 1870: 563 [original description, type locality Pebas, Peru]. Fowler, 1906: 441 [description, based on type specimen]. Eigenmann, 1910: 439 [Peru]. Eigenmann & Allen, 1942: 278 [Pebas, Peruvian Amazon; not Rio Cupai (= Rio Cupari)]. Fowler, 1950: 365 [literature compilation].

Plethodectes erythrinus: Eigenmann *et al.*, 1891: 51 [incorrect spelling of *P. erythrurus* Cope, 1870].

Chalceus erythrurus Cope, 1872: 262 [Ecuador (now Peru) Río Ambyiacu (= Ampiyacu)]. Eigenmann & Eigenmann, 1891: 55 [literature compilation]. Regan, 1912: 388 [in part: Upper Amazon (not including the

reported specimen from Rio Cupai (= Cupari)]. Géry, 1977: 332 [photograph of live specimen]. Ortega & Vari, 1986: 7 [list of species: Peru].

Chalceus macrolepidotus (not of Cuvier, 1817). Misidentification: Eigenmann & Allen, 1942 [listed specimens]. La Monte, 1935: 7 [Rio Juruá, Brazil].

Pellegrinina heterolepis Fowler, 1906: 442, fig. 39 [original description; type locality erroneously cited as from West Africa].

Chalceus macrolepidotus iquitensis Nakashima, 1941: fig. on p. 76 [original description, type locality, Peru, surroundings of Iquitos, common name, San Pedro].

Diagnosis

The presence of a conspicuous rounded humeral spot with a notch on its posterodorsal margin, the dark pel-



Figure 10. *Chalceus erythrurus*, AMNH 78064, 139.0 mm SL, Peru, Loreto, Río Yarapa, tributary of Río Ucayali, one of several sites along a 10-km stretch of river.



Figure 11. *Chalceus erythrurus*, male, INPA 16190, 149.3 mm SL, Brazil, Amazonas, Rio Amazonas, Ilha do Careiro, Igapó Terra Nova.

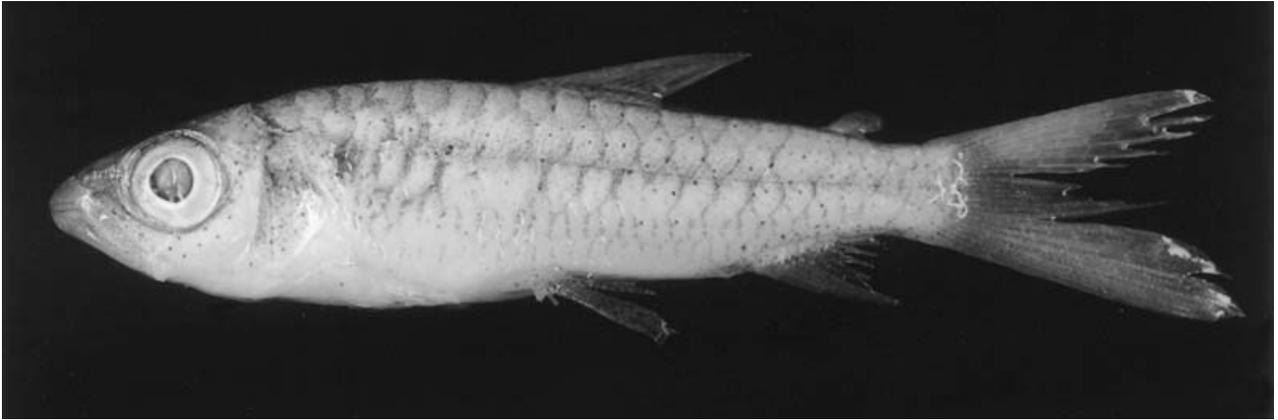


Figure 12. *Chalceus erythrurus*, juvenile, USNM 308820, 28.8 mm SL, Brazil, Amazonas, Manaus, Lago Janauari, small house in front of brickworks.

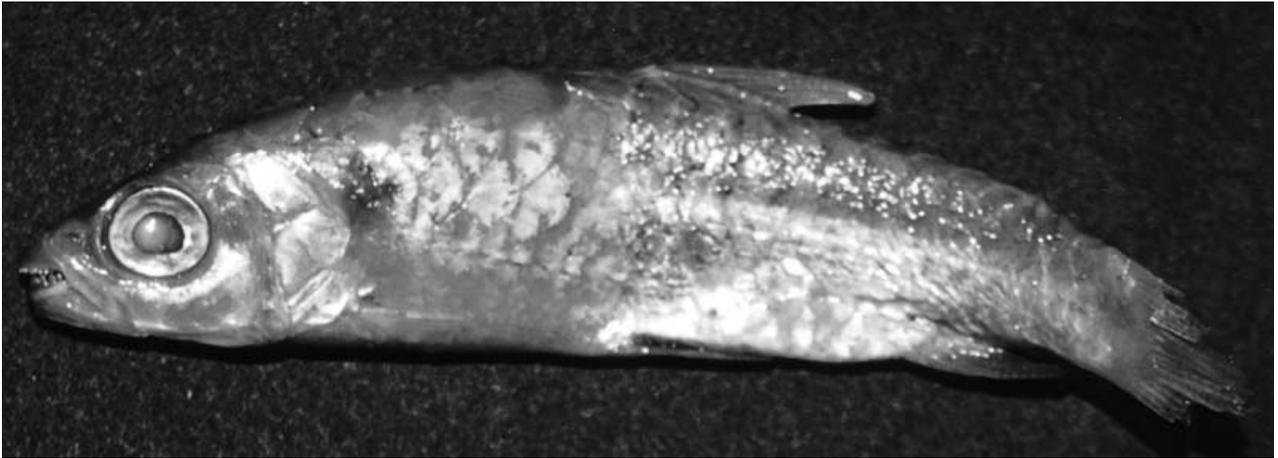


Figure 13. *Chalceus erythrurus*, holotype of *Pellegrinina heterolepis*, ANSP 8150, 95.8 mm SL (type locality inexact, South America, see text for details).

vic and anal fins and the presence of dark chromatophores on the posterior margin of the longitudinal series of scales posterior to the humeral spot distinguishes *C. erythrurus* (Fig. 10) from its congeners (in some sexually mature specimens, the humeral spot may be obliterated by a wide dark longitudinal band, see ‘Comments . . .’, below) (Fig. 11). Although *C. spilogyros* also has a rounded humeral spot, that spot is not notched and is relatively smaller than the spot in *C. erythrurus*. A humeral spot is present in *C. guaporensis* and sometimes in *C. epakros*, however, in these species it is usually rounded to vertically elongate and located deeper in the skin being consequently less conspicuous than the humeral spots of *C. erythrurus* and *C. spilogyros* in which the spot is located superficially on the skin (see ‘Comments . . .’, below). In addition, the caudal-fin lobes in *C. erythrurus* are robust and rounded compared to the

more elongate and slender lobes in all other *Chalceus* species.

Description

Morphometric data presented in Table 2 (some meristic data for holotype not recorded due to poor condition of specimen). Maximum size 213.5 mm SL. Body robust, relatively elongate, greatest body depth located slightly anterior to dorsal-fin origin. Dorsal profile of head straight from snout tip to end of supraoccipital spine in all specimens. Anterior profile of head distinctly rounded from dorsal view. Interorbital distance wide, proportionally wider relative to body size in larger specimens. Dorsal surface of head in interorbital region flat. Dorsal body profile straight to slightly convex from tip of supraoccipital spine to dorsal-fin origin. Dorsal body profile posteroventrally

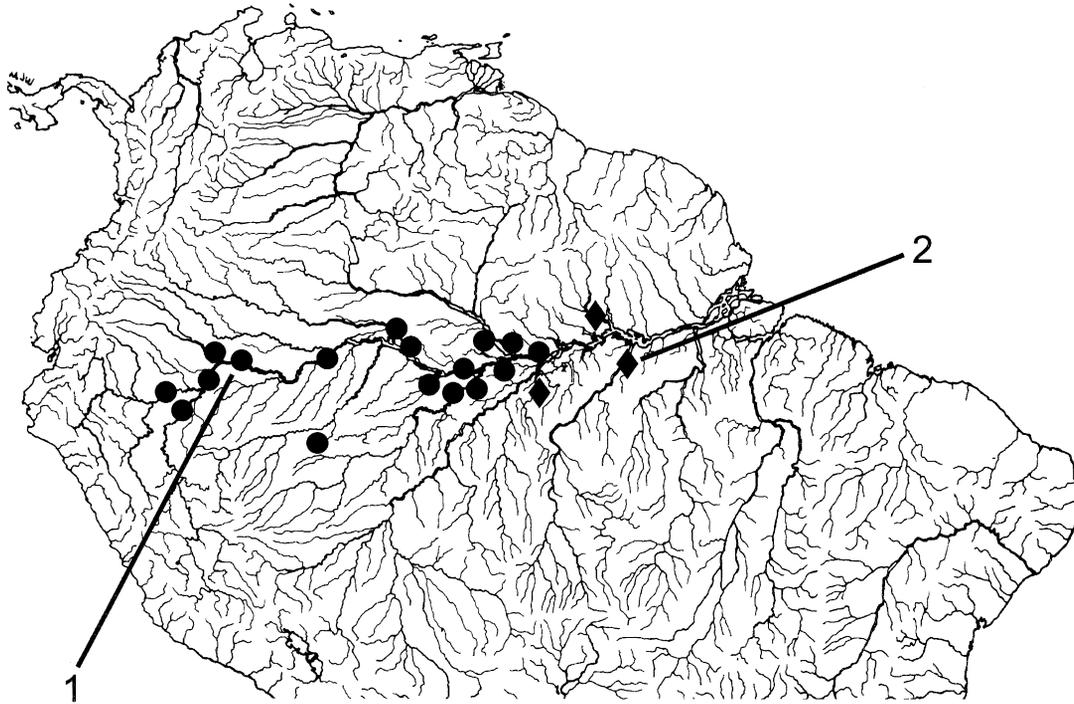


Figure 14. Map of northern portion of South America showing geographical distribution of *Chalceus erythrurus* (dots, 1 = type locality) and *C. spilogyros* sp. nov. (diamonds, 2 = type locality) (some symbols represent more than one locality or lot of specimens).

Table 2. Morphometrics of *Chalceus erythrurus* (holotype of *Plethodectes erythrurus* Cope – ANSP 8032 – not measured due to poor condition of specimen). Holotype is of *Pellegrinina heterolepis*. All dimensions in mm

Character	Holotype	<i>n</i>	Range	Mean
Standard length	95.8	108	28.7–213.5	
Body depth	24.1	108	22.8–28.7	25.8
Snout to dorsal-fin origin	56.1	108	53.2–58.2	55.3
Snout to pectoral-fin origin	29.7	108	24.4–33.3	27.9
Snout to pelvic-fin origin	53.9	106	50.5–59.5	53.7
Snout to anal-fin origin	83.1	108	79.4–87.1	82.9
Caudal-peduncle length	11.9	97	9.8–13.5	11.5
Caudal-peduncle depth	10.4	108	8.3–12.0	10.8
Dorsal-fin length	20.8	107	20.8–26.8	23.8
Anal-fin base	9.4	95	8.2–12.5	9.7
Anal-fin length	17.7	96	13.4–20.0	17.8
Pectoral-fin length	24.2	105	14.2–25.0	22.5
Pelvic-fin length	19.8	105	17.1–22.7	20.0
Head length	29.7	108	23.6–33.7	27.8
Snout length	32.6	108	27.6–35.4	31.9
Orbital diameter	31.2	96	20.6–34.7	26.8
Interorbital width	41.8	108	29.9–50.2	43.9
Upper jaw length	36.8	108	34.5–40.6	37.2

inclined along dorsal-fin base, straight to relatively convex to adipose fin and concave along dorsal profile of caudal peduncle to origin of procurrent caudal-fin rays. Overall dorsal body profile of juveniles up to

40 mm SL convex. Ventral profile of head strongly convex to pectoral-fin, slightly convex to somewhat straight to pelvic-fin insertion, convex to anal-fin origin. Body profile along anal-fin base posterodorsally



Figure 15. *Chalceus spilogyros* sp. nov., holotype, MZUSP 20314, 208.0 mm SL, Brazil, Pará, Igarapé Jacaré, right margin of Rio Tapajós, near Boim, 3°0'S; 55°15'W.

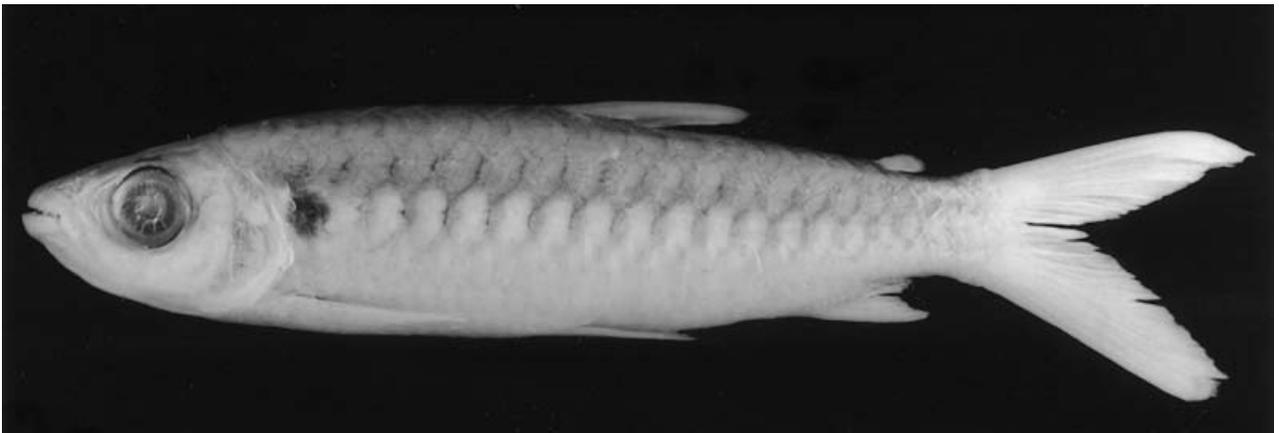


Figure 16. *Chalceus spilogyros* sp. nov., paratype, MZUSP 76069, 91.6 mm SL, Brazil, Pará, Igarapé Jacaré, right margin of Rio Tapajós, near Boim, 3°0'S; 55°15'W.



Figure 17. *Chalceus spilogyros* sp. nov., paratype, male, MZUSP 76069, 181.4 mm SL, Brazil, Pará, Igarapé Jacaré, right margin of Rio Tapajós, near Boim, 3°0'S; 55°15'W.

inclined and slightly concave along ventral margin of caudal peduncle. Head robust. Dorsal surface of head with distinct median fontanel restricted to small region anterior to the epiphyseal bar between frontals and completely separating parietals. Fontanel wide in small specimens and progressively narrower in larger individuals. Fontanel almost completely closed in a 213.5-mm SL specimen but with small space remaining between contralateral parietals. Mouth large, terminal, slightly superior, upper and lower jaw of equal length. Maxilla not reaching vertical through anterior margin of orbit. Supramaxilla present.

Dorsal-fin rays (ii,10; ii,11 in one specimen, $n = 102$). Dorsal-fin origin located posterior to vertical through insertion of innermost pelvic-fin rays. First basal dorsal-fin pterygiophore inserting behind neural spine of 12th vertebra 9 ($n = 1$). Distal margin of dorsal fin nearly straight to convex. Adipose fin present. Anal-fin rays (iii,9; iii,8 in one specimen, $n = 98$). First basal anal-fin pterygiophore inserting behind haemal spine of 25th vertebra ($n = 1$). Distal margin of anal fin straight to emarginate with anterior branched rays approximately 3 times length of ultimate ray. Pectoral-fin rays (range i,15–18, mean 16.5, $n = 104$). Pectoral-fin pointed distally, with unbranched- and first branched rays longest and not reaching pelvic-fin insertion. Pelvic-fin rays i,8 (i,8; i,7 in 3 specimens, i,9 in one specimen, $n = 102$); fin pointed distally. Caudal fin forked, with lobes robust and rounded, lower fin lobe slightly more developed than upper lobe.

Premaxillary teeth in three rows. Outer row 8 (range 6–9, 10 in one specimen, mean 7.6, $n = 104$) with teeth tricuspid or pentacuspoid in large specimens and smaller specimens with conical or tricuspid teeth, with medial cusp larger. Tooth close to premaxillary symphysis slightly larger than other teeth in series. Remaining teeth of similar size, but with one or two lateralmost teeth slightly smaller. Cusps slightly curved with concave portion facing mouth cavity. Inner row 5 (range 5–6, mean 5.1, $n = 104$) with largest, symphyseal tooth usually asymmetric with one cusp on medial margin and two on lateral margin of tooth. Remaining teeth penta- or heptacuspoid in large specimens, with second tooth from symphysis larger. Teeth tricuspid in small specimens, with teeth gradually diminishing in size laterally. Cusps slightly curved with concave portion opposite of mouth cavity. Intermediate row 2 (2, $n = 105$) pentacuspoid (rarely tricuspid) teeth more widely separated than those of other rows and of intermediate size. Cusps straight.

Maxillary teeth 9 (range 7–10, with one specimen each having 5, 11 and 12, mean 8.5, $n = 93$) with smaller specimens usually with higher numbers of teeth. First tooth pentacuspoid followed by tricuspid and conical teeth distally. Teeth not extending along

entire margin of ossification in large specimens. In small specimens teeth conical and extending along entire margin of ossification. Dentary teeth in two rows. Outer row 8 (range 7–11, 12, 13 and 16 in one specimen each, mean 9.4, $n = 105$). Teeth large and pentacuspoid anteriorly, sometimes heptacuspoid in large specimens, tricuspid in small specimens, gradually diminishing in size and number of cusps posteriorly. Posteriormost teeth conical. Cusps slightly curved with concave portion facing mouth cavity. Inner row consisting of large conical symphyseal tooth followed by series of minute conical teeth. First tooth originating behind fourth to fifth tooth of outer row with consequent gap between the symphyseal tooth and first minute conical tooth.

Scales cycloid, large overall and approximately twice as large above lateral line as below it. Circuli on exposed portion of scales not concentric with those of anterior portion. Circuli on exposed portion of scales straight and extending to posterior margin of scale in small specimens; disorganized and with labyrinthic pattern in specimens around 200 mm SL. Radii originating on centre of scale and radiating anteriorly and posteriorly on scale surface.

Lateral line low on body sides, complete, with alternating large and small perforated scales from posterior margin of opercle to vertical through base of last anal-fin ray; scales smaller and of similar size from that point to end of caudal peduncle. Canals in large specimens with 3–7 elevated branches (usually 3 or 4), forming ridges on scale surface; ridges more evident on region of the caudal peduncle. Number of branches decreases towards caudal peduncle, with canals of posterior scales unbranched. Small specimens (less than 140 mm) with branching pattern less developed. Lateral-line scales (range 36–39, 35 in two specimens, mean 37.2, $n = 97$). Scale rows between dorsal-fin origin and lateral line 3; between lateral line and pelvic-fin insertion 2. Scales around caudal peduncle 12. Vertebrae 37 ($n = 1$).

Colour in life. (Description based on photograph in Géry, 1977: 332, and personal observations of one specimen kept in aquarium). Overall coloration of head and body bright silver. Conspicuous humeral spot present on region of four first scales along longitudinal series just above lateral line. Overall shape of humeral spot rounded with notch on posterodorsal margin of spot. Dorsal portion of eye yellow. Dorsal profiles of head and body darker. Margins of scales on dorsal portions of body with strong concentration of dark chromatophores, forming well-defined reticulate pattern. Caudal fin bright red. Pelvic and anal fins distinctly yellow. Adipose and dorsal fins yellowish, both tinged with red. Pectoral fin hyaline.

Colour in alcohol. Few specimens that retain guanine on body and head have silvery ground

coloration. Most specimens only retain silvery pigmentation on infraorbital and opercular regions. Ground coloration of head and body in specimens ≥ 50 mm SL, lacking guanine on scales, yellowish to tan, darker dorsally. Conspicuous humeral spot on region of first four scales of longitudinal series just above lateral line. Overall shape of spot rounded with notch on its posterodorsal margin. Margins of scales on dorsal portions of body with strong concentration of dark chromatophores, forming well-defined reticulate pattern, that may be present over entire dorsal region of body, or restricted to dorsal portion of lateral-line scales and on longitudinal series just above it. Dark chromatophores scattered over infraorbitals and opercular region. Reticulate pattern less evident in large specimens and sometimes restricted to series of longitudinal diffuse dark patches. Pelvic and anal fins dark. Dorsal, adipose and caudal fins dusky. Some specimens with dark tips on caudal-fin rays. Some specimens (AMNH 58440, INPA 16190 (4 of 5), INPA 17226, INPA 18620; MZUSP 13533, MZUSP 20385 (4 of 9) and MZUSP 77595) have dark and wide longitudinal band along body (Fig. 11) (see 'Comments . . .', below).

Ground coloration of specimens ≤ 50 mm pale yellowish (Fig. 12). Reticulate pattern on scales more conspicuous than in larger specimens and extending to longitudinal series of scales below lateral line. Humeral spot small, rounded and somewhat elongated vertically. Dark narrow longitudinal line from dorsal margin of humeral spot to end of caudal peduncle. Pelvic, dorsal, anal, adipose and lower lobe of caudal fin dark. Pectoral fin hyaline.

Distribution

Rio Amazonas and Rio Solimões from Manaus to the Rio Ucayali drainage in Peru (Fig. 14). Localities distributed mainly along main channel of Rio Amazonas and Rio Solimões and mouths of their tributaries.

Remarks

Fowler (1906: 444) described *Pellegrinina heterolepis* on the basis of one specimen that he believed originated from West Africa; as a consequence, he made comparisons of that nominal form with the African alestid genera *Alestes*, *Brycinus* and *Brachyalestes* in the diagnosis of the species. Subsequently the locality was shown to be incorrect and the fish was identified as a *Chalceus* species from South America (Géry, 1977: 18). The holotype of *Pellegrinina heterolepis* (ANSP 8150) was examined in the present study (Fig. 13) and on the basis of the presence of a humeral spot with a notch along its posterodorsal margin it is readily identified as *Chalceus erythrurus*. Additional characters present on the specimen that also characterize *C. erythrurus* are the presence of a cranial fontanel,

the dark pelvic and anal fins and the first small inner dentary row tooth originating behind the fifth tooth of the anterior outer tooth row with a gap between the symphyseal tooth and minute first conical tooth. Based on these features, *Pellegrinina heterolepis* is herein considered to be a junior synonym of *Chalceus erythrurus*.

Nakashima (1941: 76) described *Chalceus macrolepidotus iquitensis* from the surroundings of Iquitos, in the Peruvian Amazon, but did not provide any explanation as to why he recognized the material as a new subspecies. No information about type specimens was provided and no types are known to be extant. Based on his description, especially regarding the colour pattern and the shape of the humeral spot in the illustrated specimen, the species is most probably *Chalceus erythrurus*. *Chalceus epakros* also occurs in the Peruvian Amazon, but the humeral spot is usually absent in this species and when present it is less conspicuous than that of *C. erythrurus* and is, furthermore, more vertically elongate. In addition, *C. epakros* does not exhibit the reticulate pattern on the scales described by Nakashima (1941) which is, however, present in *C. erythrurus*. *Chalceus macrolepidotus iquitensis* Nakashima is therefore considered to be a synonym of *C. erythrurus*.

Material examined

Type material. ANSP 8032, 1, 44.5 mm SL; Peru, Río Ambyiacu (= Ampiyacu) at Pebas; holotype of *Plethodectes erythrurus* Cope, 1870 (specimen in very poor condition). – ANSP 8150, 1, 95.8 mm SL; Probably West Africa (?) [locality data incorrect, specimen from South America, see Géry, 1977: 18]; holotype of *Pellegrinina heterolepis* Fowler, 1906.

Non-type material. BRAZIL: AMAZONAS: INPA 16928, 1, 195.0 mm SL; Rio Amazonas, Ilha do Careiro, Lago do Mingal. – INPA 16190(*) 5, 119.7–158.7 mm SL; INPA 16929, 1, 189.0 mm SL; Rio Amazonas, Ilha do Careiro, Terra Nova. – INPA 18619, 1, 92.1 mm SL; Mamirauá Lake system, Paraná Maiana station A, 2.5 km from Comunidade Boca do Mamirauá; INPA 18620(*), 3, 102.9–176.0 mm SL; Rio Solimões, Lago Capivara, Costa das Capivaras. – MZUSP 6881, 12, 95–166.7 mm SL; MZUSP 64203, 1, 106.8 mm SL; USNM 308376, 2, 38.3–39.1 mm SL; USNM 308820, 7, 28.7–37.9 mm SL; USNM 308371, 1, 1, 106.7 mm SL; USNM 308596, 1, 50.1 mm SL; Lago Januári, right margin of Rio Negro, Manaus. – INPA 16949, 3, 75.6–88.6 mm SL; Januári. – MZUSP 75610, 1, 89.4 mm SL; Lago Januári, near Canta Galo. – MZUSP 75611, 2, 86.9–85.4 mm SL; Lago Januári, near its mouth. – MZUSP 75612, 2, 79.6–88.1 mm SL;

Lago Janaurai, first brick factory. – MZUSP 6707, 35, 94.7–136.3 mm SL; Rio Negro, vicinity of Manaus. – MZUSP 6462, 3, 160.7–213.5 mm SL; Lago Jacaré, right margin of Rio Solimões, above Manacapuru. – MZUSP 20053, 1, 161.7 mm SL; Lago do Rei, Ilha Canini, in front of Santo Antonio do Içá. – MZUSP 27297, 2, 95.5–104.2 mm SL; Paranã do Lago Amanã, lower Rio Japurá. – MZUSP 27296, 6, 84.4–112.5 mm SL (1 C & S); Costa Japão, Ressaca do Japão, lower Rio Japurá. – MZUSP 27298, 4, 140.0–145.9 mm SL; Lago Mamirauá, mouth of Rio Japurá. MZUSP 13533(*), 1, 195.9 mm SL; Lago do Miguel, below Itacoatiara. – MZUSP 20385(*) 1, 109.6 mm SL; Lago Janauacá. – CAS 139277, 5, 158.0–166.0 mm SL; Rio Solimões, Lago Coari. – CAS 69083, 2, 174.3–187.7 mm SL; Manaus. – INPA 17226(*), 2, 157.0–190.0 mm SL; MZUSP 77595, 3, 158–178 mm SL; Rio Purus, Paranã do Lago Jacaré. – INPA 17235, 1, 186.0 mm SL; Rio Purus, Igarapé do Sacado. – INPA 17240, 1, 177.0 mm SL; Rio Purus, Beruri, at mouth of lake. – INPA 17257, 1, 84.0 mm SL; Rio Purus, Beruri, Paranã do Seixo. – INPA 17294, 1, 172.0 mm SL; Rio Purus, Beabá. – AMNH 12556, 1, 82.2 mm SL; vicinity of mouth of Rio Embira, tributary of Rio Tarauacá, Rio Juruá. – MZUSP 75614, 1, 118.8 mm SL; São José, Lago do Castanho, Janauacá. – USNM 229093, 1, 95.8 mm SL; Paranã do Lago Janauacá, entrance of Castanho. – USNM 308821, 3, 72.8–101.1 mm SL; Lago Murumuru, Lago Janauacá, near INPA stable. – USNM 308807, 2, 87.2–90.6 mm SL; MZUSP 75613, 6, 84.8–100.4 mm SL; Lago Murumuru, Lago Janauacá, at stable, near Manaus. – USNM 229083, 2, 86.4–98.2 mm SL; Lago Murumuru, at stable, near Manaus. – USNM 119947, 18, 92.6–126.0 mm SL; Rio Solimões, Codajás. – BMNH, 1929.11.18.3, 1, 189.6 mm SL; Manaus, Rio Amazonas. – BMNH, 1925.10.28.85–84, 5, 87.8–195.3 mm SL; Rio Solimões, Manacapuru.

PERU: LORETO: CAS 69082, 4, 147.7–172.0 mm SL; Rio Amazonas drainage, Iquitos. – CAS 69074, 6, 92.2–128.1 mm SL; Rio Amazonas drainage, Yarinacocha, lake connected to Rio Pacaya. – CAS 136871, 6, 66.3–87.7 mm SL; Caño Tuye, Pebas. – CAS 17272, 2, 86.8–141.5 mm SL; Caño Chanco, near Pebas. – MZUSP 78064, 1, 139.0 mm SL; Rio Yarapa, tributary of Rio Ucayali, tributary of Rio Amazonas, several sites along a 10-km stretch of river. – AMNH 218032, 1, 79.9 mm SL; Rio Itaya, near Iquitos. – USNM 167798, 4, 113.7–124.9 mm SL; Yarinacocha. – USNM 280437, 1, 99.5 mm SL; Rio Itaya, main river channel and lower portion of caños, 5–20 km upstream of Belen, Iquitos. – USNM 280441, 3, 74.4–81.7 mm SL; green water caño on leftbank of Rio Manite, about 8 km upriver of junction of Rio Manite and Rio Amazonas. – FMNH 70229, 3, 90.3–116.8 mm SL; Rio Maniti, Santa Cecilia 20. – FMNH 100438, 1,

105.4 mm SL; Río Airico, 5 km above mouth in Río Chambira.

AMNH 58440 (*), 1, 105.9 mm SL; South America, no locality data.

CHALCEUS SPILOGYROS SP. NOV.

(FIGS 14–17; TABLE 3)

Diagnosis

The presence of a dark rounded humeral spot readily distinguishes *C. spilogyros* (Figs 15–17) from *C. macrolepidotus* and *C. epakros*. *Chalceus spilogyros* shares with *C. erythrurus* the presence of a humeral spot formed by dark chromatophores located superficially on the skin. However, the spot of *C. spilogyros* is rounded and relatively small compared with the larger spot of *C. erythrurus*; in the latter, there is also a notch along its posterodorsal margin. In addition, the caudal-fin lobes in *C. spilogyros* are relatively elongate and slender compared to the robust and rounded lobes of *C. erythrurus*. A humeral spot is present in *C. guaporensis* and sometimes in *C. epakros*; however, in these species it is usually rounded to vertically elongate, located deeper in the skin and thus somewhat less conspicuous than that of *C. spilogyros*. In addition, *C. spilogyros* lacks the longitudinal dark stripe characteristic of *C. epakros* and *C. guaporensis*, although in some specimens a wide dark longitudinal band is present. However, it differs from the band of *C. epakros* and *C. guaporensis* in the pattern of distribution of the chromatophores on the skin (see ‘Comments . . .’, below).

Description

Morphometric data presented in Table 3. Maximum size 223.2 mm SL. Body robust, relatively elongate, greatest body depth located slightly anterior to dorsal-fin origin. Dorsal profile of head distinctly convex anteriorly in snout region, posterodorsally inclined to convex from anterior end of snout to tip of supraoccipital spine and continuous with dorsal body profile. Anterior profile of head somewhat acute from dorsal view. Interorbital distance wide, proportionally wider relative to body size in larger specimens. Dorsal body profile somewhat convex to straight from tip of supraoccipital spine to dorsal-fin origin. Dorsal body profile posteroventrally inclined along dorsal-fin base, straight to relatively convex to adipose fin and concave along dorsal profile of caudal peduncle to origin of procurent caudal-fin rays. Ventral profile of head distinctly convex along lower jaw. Ventral body profile gently convex from posterior limit of isthmus to anal-fin origin. Body profile posterodorsally inclined along anal-fin base, slightly concave along ventral margin of caudal peduncle. Head robust in specimens larger than 120 mm SL. Smaller specimens with relatively



Figure 18. *Chalceus epakros* sp. nov., holotype, MZUSP 33392, 132.6 mm SL, Brazil, Pará, Rio Tapajós, São Luís, above Itaituba, 4°25'S; 56°10'W.

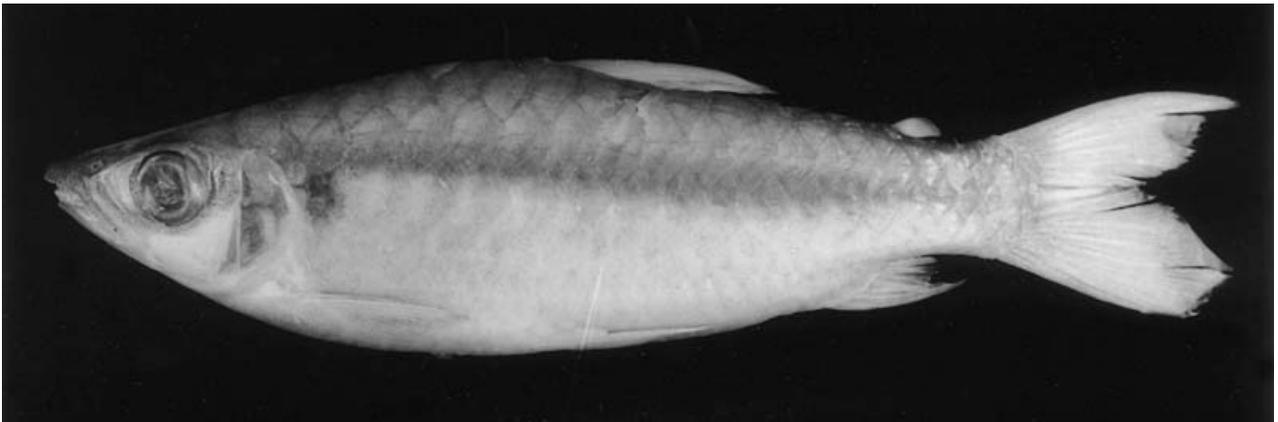


Figure 19. *Chalceus epakros* sp. nov., INPA 16926, 95.6 mm SL, Brazil, Pará, Rio do Côco, Caseara, Lago do Casé.

Table 3. Morphometrics of *Chalceus spilogyros* sp. nov. All dimensions in mm

Character	Holotype	<i>n</i>	Range	Mean
Standard length	208.0	88	77.7–223.2	
Body depth	24.5	88	23.4–28.7	25.2
Snout to dorsal-fin origin	51.7	88	50.6–59.4	54.3
Snout to pectoral-fin origin	24.0	88	23.4–29.8	26.1
Snout to pelvic-fin origin	52.1	88	49.0–55.3	52.8
Snout to anal-fin origin	77.9	88	77.5–83.2	80.2
Caudal-peduncle length	13.4	88	12.1–15.6	13.6
Caudal-peduncle depth	9.3	88	9.3–11.2	10.2
Dorsal-fin length	19.7	85	19.2–23.3	21.1
Anal-fin base	9.4	87	7.9–11.5	9.3
Anal-fin length	14.6	83	12.7–16.8	15.0
Pectoral-fin length	18.7	87	17.8–20.8	19.4
Pelvic-fin length	16.8	87	15.0–18.8	17.5
Head length	23.5	88	22.6–29.6	25.4
Snout length	32.8	88	30.5–35.9	33.4
Orbital diameter	27.5	86	22.8–33.7	28.3
Interorbital width	47.3	88	35.9–50.0	43.3
Upper jaw length	40.0	88	36.0–43.9	40.1

longer heads and more acute snout. Dorsal surface of head with distinct fontanel restricted to a small portion anterior to the epiphyseal bar between frontals and completely separating contralateral parietals. Fontanel wide in small specimens and progressively narrower in larger individuals. Small fontanel still present in largest examined specimen (223.2 mm SL). Mouth terminal, large, upper and lower jaw equally long. Maxilla extending approximately to vertical through anterior margin of orbit. Supramaxilla present.

Dorsal-fin rays ii,10 (ii,10; ii,9 in one specimen, ii,11 in three specimens, $n = 88$). Dorsal-fin origin located posterior to vertical through insertion of innermost pelvic-fin rays. First basal dorsal-fin pterygiophore inserting behind neural spine of 13th vertebra ($n = 1$). Distal margin of dorsal fin nearly straight to convex. Adipose fin present. Anal-fin rays iii,9 (iii,9; iii, 8 in one; iii,10 in two specimens, $n = 84$). First basal anal-fin pterygiophore inserting behind haemal spine of 26th vertebra ($n = 1$). Distal margin of anal fin straight to emarginate with anterior branched rays approximately 3 times length of ultimate ray. Pectoral-fin rays i,15 (range 13–17, 18 in two specimens, mean 16.1, $n = 88$), pointed distally, with unbranched- and first branched rays longest, but not reaching pelvic-fin insertion. Pelvic-fin rays i,8 (i,8 $n = 88$), fin pointed distally. Caudal fin forked, with lobes slender particularly in specimens up to 120 mm SL, lower fin lobe slightly more developed than upper lobe.

Premaxillary teeth in three rows. Outer row 8 (range 8–11, 7 in four specimens, mean 9.0, $n = 88$) either tricuspid or pentacuspoid, with medial cusp larger. Tooth close to premaxillary symphysis slightly larger than other teeth of series. Remaining teeth of similar size with one or two lateralmost teeth slightly smaller. Cusps slightly curved with concave portion facing mouth cavity. Inner row 7 (range 6–7, 5 in four specimens, mean 6.2, $n = 88$), with largest, symphyseal tooth usually asymmetric with one cusp on medial margin and two on lateral margin of tooth. Remaining teeth, penta- or heptacuspoid in large specimens, with second tooth from symphysis larger and remaining teeth gradually diminishing in size laterally. Cusps slightly curved with concave portion opposite of mouth cavity. Intermediate row, with 2 (2; 1 in one specimen, $n = 88$) pentacuspoid teeth more widely spaced than teeth of other rows and of intermediate size. Cusps straight.

Maxillary teeth 8 (range 7–11, 6 in two specimens, 12 in three specimens, mean 9.2, $n = 88$) with smaller specimens usually having more teeth. First teeth pentacuspoid, followed by tricuspid and conical teeth distally. Teeth not extending along entire margin of ossification in large specimens. In small specimens conical and extending almost along entire margin of ossi-

fication. Dentary teeth in two rows. Outer row 12 (range 9–14, 8 and 17 in one specimen each, mean 11.0, $n = 87$), with teeth large and pentacuspoid anteriorly, sometimes heptacuspoid in large specimens and tricuspid in small specimens. Teeth gradually diminishing in size and number of cusps posteriorly. Posteriormost teeth conical. Cusps slightly curved with concave portion facing mouth cavity. Inner dentary row with large, conical, symphyseal tooth (tricuspid in a few larger specimens) followed by series of minute conical teeth. First small tooth usually situated behind fourth tooth of anterior row with gap between symphyseal tooth and first small conical tooth of rest of series.

Scales cycloid, large overall and approximately twice as large above lateral line as below it. Circuli on exposed portion of scales not concentric with those of anterior portion. Circuli on exposed portion of scales straight and extending to posterior margin of scale in small specimens; disorganized and labyrinthic pattern in specimens around 200 mm SL. Radii originating on centre of scale and radiating anteriorly and posteriorly on scale surface.

Lateral line low on body sides, complete, with alternating large and small perforated scales from posterior margin of opercle to vertical through base of last anal-fin ray. Lateral-line scales smaller and of similar size from that point to end of caudal peduncle. Canals in large specimens with 3–6 (usually 3 or 4) elevated branches, forming ridges on scale surface. Ridges more evident on region of caudal peduncle. Number of branches decreases toward caudal peduncle with posterior scales unbranched. Smaller specimens (≤ 140 mm) with branching pattern less developed. Lateral-line scales 38 (range 36–39, 34 and 40 in one specimen each, mean 38.2, $n = 79$). Scale rows between dorsal-fin origin and lateral line 3; between lateral line and pelvic-fin insertion 2. Scales around caudal peduncle 12. Vertebrae 38 ($n = 1$).

Colour in alcohol. All available specimens lack guanine on body except for few individuals that retain silvery pigmentation on infraorbital and opercular regions. Ground coloration of head and body yellowish to tan, darker dorsally. Conspicuous, small, rounded humeral spot on region of three first scales of longitudinal series just above lateral line. Humeral spot formed by dark chromatophores located superficially on skin (see 'Comments . . .', below). Dark chromatophores scattered over infraorbitals and opercular region. Some specimens with dark blotch present on lower half of opercle. Scales of dorsal portion of body with chromatophores concentrated along posterior margin, more so in central portion and forming reticulate pattern, more conspicuous on two longitudinal series of scales above lateral line. Reticulate pattern more evident in specimens ≤ 150 mm SL (Fig. 16). All fins hyaline. Distal portion of longer caudal-fin rays

darkened. Some specimens (MZUSP 7053 (5 of 7), MZUSP 20314 (1 of 55) and MZUSP 54568 (1 of 5)) with dark, wide longitudinal band along body (Fig. 17) (see 'Comments . . .', below).

Distribution

Occurs only in Rio Trombetas, lower Rio Tapajós and Rio Canumã in the Rio Madeira drainage (Fig. 14).

Etymology

Spilogyros, from the Greek *spilos* meaning spot and *gyros*, meaning circle, round, in reference to the rounded humeral spot of the species.

Material examined

Type material. HOLOTYPE: MZUSP 20314, 1, 208.0 mm SL; Brazil, Pará, Igarapé Jacaré, right margin of Rio Tapajós, near Boim. (3°0'S; 55°15'W). Collector Expedição Permanente à Amazônia, 27/Oct/1970. PARATYPES: MZUSP 76069 42, 1C & S 86.2–214.0 mm SL; INPA 18589, 3, 100.3–201.0 mm SL; USNM 368278, 3, 107.1–196.0 mm SL; UMMZ 239930, 3, 106.8–183.0 mm SL; same data as holotype.

Non-type material. BRAZIL. AMAZONAS: MZUSP 7054, 10, 92.3–134.8 mm SL; MZUSP 7053(*), 7, 175.9–198.0 mm SL; Rio Canumã. PARÁ: MZUSP 15801–802, 2, 92.7–174.0 mm SL; MZUSP 15791–92, 2, 145.4–223.2 mm SL; Igarapé do Lago Farias, Rio Trombetas, Reserva Biológica Trombetas. – MZUSP

54566, 2, 205.1–206.0 mm SL; MZUSP 54568(*), 5, 149.4–195.7 mm SL; Lago Mussurá, left margin of Rio Trombetas, Porto Trombetas, Oriximiná. – MZUSP 54569, 2, 184.4–200.4 mm SL; MZUSP 54570, 1, 188.9 mm SL; Lago Batata, right margin of Rio Trombetas, Porto Trombetas, Oriximiná. – MZUSP 19698, 18, 77.7–148.6 mm SL; Lagoa Jacaré, Rio Trombetas. – INPA 16930, 2, 193.0–203.0 mm SL; Lago Cruz Alta, Rio Trombetas. – INPA 16943, 2, 165.0–210.0 mm SL; Lago Corusca, Igarapé do Braço, Rio Trombetas drainage. – INPA 16944, 4, 166.0–190.0 mm SL; Lago Jamari, Rio Trombetas drainage.

CHALCEUS EPAKROS SP. NOV. (FIGS 18–20, TABLE 4)

Chalceus macrolepidotus (not of Cuvier, 1817), misidentification: de Mérona, Santos & Almeida, 2001: 387 [Brazil, Rio Tocantins at Tucuruí dam]. Ferreira, 1984: 356 [Brazil, Pará, Rio Curuá-Una].

Chalceus erythrurus (not of Cope, 1870), misidentification: Regan, 1912: 389 [Rio Cupari, Brazil].

Diagnosis

Chalceus epakros can be readily distinguished from all other *Chalceus* species with the exception of *C. guaporensis* by the lack of a median fontanel between the frontal and parietal bones, the presence of a longitudinal dark stripe from the posterodorsal margin of opercle to caudal peduncle and by the relatively longer and more acute snout (Figs 18, 19). It differs from *C. guaporensis* by having 8 branched pelvic-

Table 4. Morphometrics of *Chalceus epakros* sp. nov. All dimensions in mm

Character	Holotype	<i>n</i>	Range	Mean
Standard length	132.6	183	64.9–175.6	
Body depth	24.1	183	22.1–30.8	26.3
Snout to dorsal-fin origin	53.7	183	51.1–58.5	54.7
Snout to pectoral-fin origin	27.1	182	24.3–32.4	27.7
Snout to pelvic-fin origin	52.6	183	50.5–56.7	53.1
Snout to anal-fin origin	80.1	183	77.8–86.2	80.9
Caudal-peduncle length	14.3	183	10.9–15.8	13.6
Caudal-peduncle depth	10.9	183	9.9–12.2	10.9
Dorsal-fin length	24.3	181	20.8–26.5	23.8
Anal-fin base	8.9	165	7.2–10.4	8.7
Anal-fin length	17.3	177	13.1–20.4	17.2
Pectoral-fin length	18.9	183	16.2–21.8	19.1
Pelvic-fin length	17.6	180	15.6–20.6	18.1
Head length	27.0	183	24.5–31.2	27.7
Snout length	36.6	182	32.1–38.8	35.5
Orbital diameter	27.9	183	24.6–35.6	29.3
Interorbital width	40.8	183	32.9–46.7	40.8
Upper jaw length	43.9	183	39.7–49.2	44.5

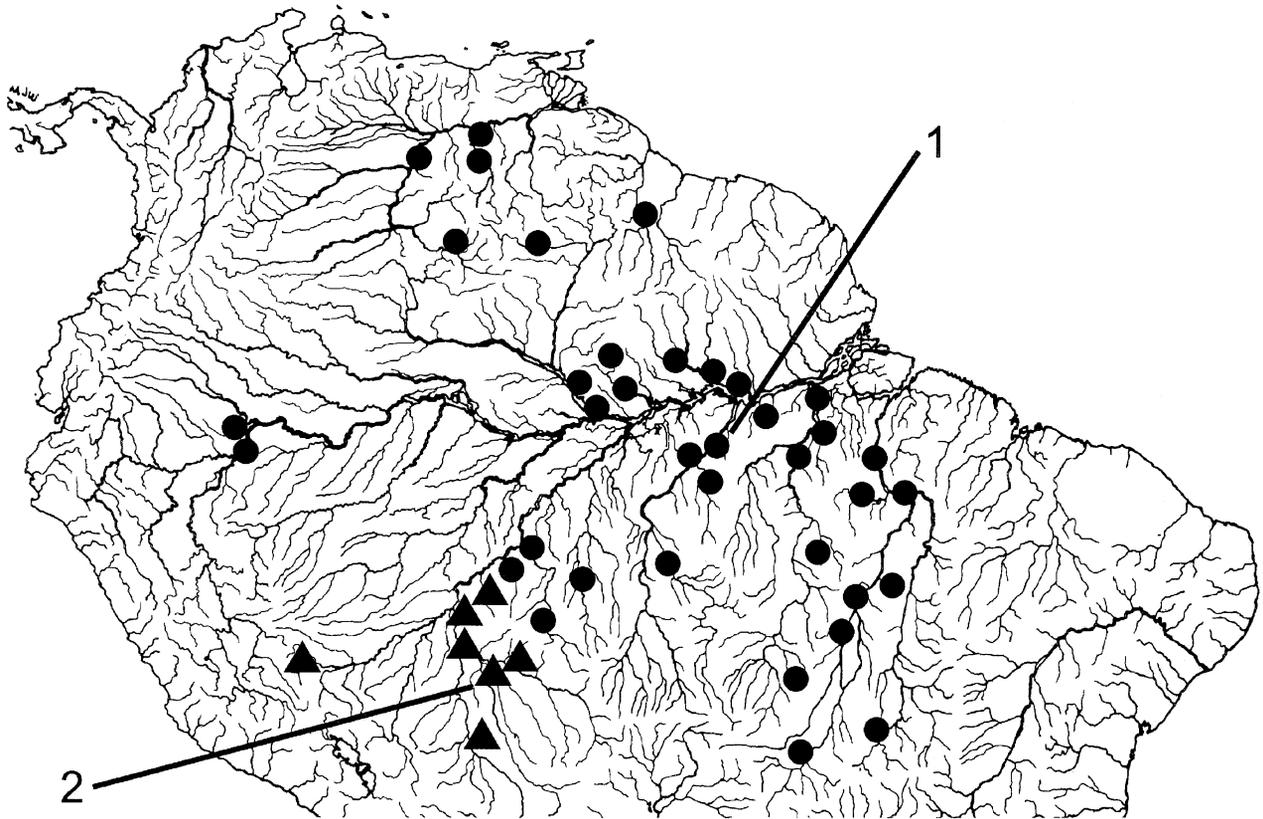


Figure 20. Map of northern portion of South America showing geographical distribution of *Chalceus epakros* (dots, 1 = type locality) and *C. guaporensis* spp. nov. (triangles, 2 = type locality). Some symbols represent more than one locality or lot of specimens.

fin rays (vs. 7 in the latter species, see 'Remarks' under *C. guaporensis*). Although there is broad overlap in the ranges, the number of lateral line scales in *C. epakros* tends to be lower than that in *C. guaporensis* (Table 6, Fig. 21). *C. epakros* may be further distinguished from *C. erythrurus*, *C. spilogyros* and *C. guaporensis* in having the first small tooth of the inner dentary row located very close to the symphyseal tooth, consequently forming an almost continuous series (vs. first small tooth of inner dentary row located behind fourth to fifth tooth of anterior row with a distinct gap between the symphyseal tooth and first small conical tooth). The central portions of the scales on the longitudinal series above the lateral line are tinged with red in live specimens of *C. epakros* (Géry, 1977: 329) (vs. red pigmentation absent in *C. erythrurus* and *C. macrolepidotus*); there is no information about live coloration of *C. guaporensis* and *C. spilogyros*). A humeral spot is sometimes present in *C. epakros* (Fig. 19), although in this species it is usually round to vertically elongate and located deeper in the skin and thus less conspicuous than those of *C. erythrurus* and

C. spilogyros in which it is located superficially on the skin (see 'Comments . . .', below).

Description

Morphometric data are presented in Table 4. Maximum size 175.6 mm SL. Body robust, somewhat compressed, relatively elongate, greatest body depth slightly anterior to dorsal-fin origin. Dorsal profile of head convex anteriorly on snout region, posterodorsally inclined from anterior end of snout to tip of supraoccipital spine. Anterior profile of head distinctly acute in dorsal view. Interorbital distance wide, proportionally wider relative to body size in larger specimens. Dorsal surface of head in interorbital region flat in specimens around 100 mm SL and smaller and slightly convex in larger specimens. Dorsal body profile convex from tip of supraoccipital spine to dorsal-fin origin. Dorsal body profile posteroventrally inclined along dorsal-fin base, straight to relatively convex to adipose fin and concave along dorsal profile of caudal peduncle to origin of procurrent caudal-fin rays. Ventral profile of

head somewhat convex from tip of lower jaw to vertical through posterior limit of isthmus in specimens up to 120 mm SL, straight and posteroventrally inclined in larger specimens. Ventral body profile convex from posterior limit of isthmus to anal-fin origin. Body profile along anal-fin base posterodorsally inclined, slightly concave along ventral margin of caudal peduncle. Smaller specimens have larger head lengths relative to SL. Median fontanel between frontals and parietals absent in all samples including smallest specimens. Mouth terminal, large; upper jaw slightly longer than lower jaw, tip of premaxillary teeth extending below margin of upper lip, giving saw-like appearance to margin of premaxilla even in closed mouth. Maxilla extending to vertical through anterior margin of orbit. Supramaxilla present.

Dorsal-fin rays ii, 10 (ii,10; ii,9 in one and ii,11 in two specimens, $n = 181$). Dorsal-fin origin located posterior to vertical through insertion of innermost pelvic-fin rays. First dorsal-fin pterygiophore inserting behind neural spine of 11th vertebra ($n = 2$). Distal margin of dorsal fin slightly straight to convex. Adipose fin present. Anal-fin rays iii,9 (iii,9; iii,8 in 22 specimens, iii,10 in one specimen, $n = 177$). First anal-fin pterygiophore inserting behind haemal spine of 23rd vertebra ($n = 2$). Distal margin of anal fin straight to emarginate with anterior branched rays approximately 3 times length of ultimate ray. Pectoral-fin rays i,16 (range 14–17, 12 in one and 13 in three specimens, respectively, mean 16.1, $n = 175$), pointed distally, with unbranched- and first branched rays longest, not reaching pelvic-fin insertion. Pelvic-fin rays i,8 (i,8; i,7 in 2 specimens, i,9 in 4; $n = 180$), pointed distally. Caudal fin forked, lower fin lobe slightly more developed.

Premaxillary teeth in three rows. Outer row 12 (range 9–13, 8 and 14 in one specimen each, mean 10.7, $n = 180$); tricuspid or pentacuspoid, with medial cusp larger and all teeth of similar size. Cusps slightly curved with concave portion facing mouth cavity. Inner row 8 (range 7–10, 6 in 3 specimens; mean 8.0, $n = 180$); largest, symphyseal tooth usually asymmetric with one cusp on medial margin and two on lateral margin of tooth. Remaining teeth penta- or heptacuspoid, with second tooth from symphysis larger and teeth gradually diminishing in size laterally. Cusps slightly curved with concave portion opposite of mouth cavity. Intermediate row 2 (2; 1 in five specimens, 3 in one specimen $n = 180$) pentacuspoid teeth, more widely separated than teeth of other rows and of intermediate size. Cusps straight.

Maxillary teeth 15 (range 9–16, 8 in 2 specimens, 17 in one, mean 12.6, $n = 177$). Anterior teeth tricuspid or conical posteriorly; teeth extending along almost entire margin of ossification. Dentary teeth in two

rows. Outer row 11 (range 10–18, 9 in one specimen, 19 in 2; mean 13.3, $n = 178$), large and pentacuspoid anteriorly, sometimes heptacuspoid, gradually diminishing in size and number of cusps posteriorly. Posteriormost teeth conical. Cusps slightly curved with concave portion facing mouth cavity. Inner row teeth consisting of large, conical, symphyseal tooth followed by series of minute conical teeth. First small tooth originating very close to symphyseal tooth and forming an almost continuous series.

Scales cycloid, large overall and approximately twice as large above lateral line as below it. Circuli on exposed portion of scales not concentric with those of anterior portion. Circuli on exposed portion of scales straight and extending to posterior margin of scale in small specimens; disorganized and labyrinthic pattern in specimens around 160 mm SL. Radii originating on centre of scale and radiating anteriorly and posteriorly on scale surface.

Lateral line low on body sides, complete, with alternating large and small perforated scales from posterior margin of opercle to vertical through base of last anal-fin ray; scales smaller and of similar size from that point to end of caudal peduncle. Canals in large specimens with 1–6 branches. Number of branches decreases toward caudal peduncle with posterior scales unbranched. Small specimens (≤ 150 mm) with branching pattern less developed. Lateral-line scales 35 (range 31–37, mean 34.3, $n = 169$). Scale rows between dorsal-fin origin and lateral line 3; between lateral line and pelvic-fin insertion 2. Scales around caudal peduncle 12. Vertebrae 34 ($n = 1$), 35 ($n = 1$).

Colour in life. Description based on photographs taken by various collectors, Géry (1977: 329) and personal observation of 3 specimens kept in aquarium. Overall coloration of head and body bright silver. No conspicuous humeral spot. Dorsal portion of eye yellow. Central portions of scales on longitudinal series just above lateral line tinged with red, coloration less evident posterior to vertical through anal-fin origin. All fins (except pectoral) bright red. Pectoral fin hyaline. Three specimens kept in tanks exhibited rapid changes in coloration with fins turning pale under stressful conditions.

Colour in alcohol. Few examined specimens retain guanine and have silvery reflections on body and head. Most only retain silvery pigmentation on infraorbital and opercular regions. Specimens lacking guanine on body yellowish to tan, darker dorsally. Longitudinal dark stripe extends from posterodorsal margin of opercle to caudal peduncle, but not reaching base of caudal-fin rays. Stripe formed of dark chromatophores located deep in skin (see 'Comments . . .', below); less evident in specimens retaining guanine on body. Small specimens with inconspicuous vertically elongate humeral spot extending over first three scales of lateral line (see

'Comments . . .', below). Scales above lateral line with chromatophores slightly more concentrated along posterior margin forming fine reticulate pattern. Humeral spot and reticulate pattern progressively less evident in larger specimens. All fins hyaline, some specimens with dorsal and anal fins with scattered chromatophores. Most specimens with dark tips on adipose fin and dorsal- and caudal-fin rays.

Distribution

The species is widespread throughout the central and lower portions of the Amazon basin including the Rio Madeira, Rio Xingu, Rio Tapajós, Rio Negro, Rio Branco, Rio Trombetas and Rio Tocantins-Araguaia basins (Fig. 20). It also occurs in the middle and upper Río Orinoco basin, the Essequibo River in Guyana and in the Río Nanay in Peru (see 'Remarks').

Etymology

Epakros, from the Greek for 'pointed at the end', referring to the snout of the species.

Remarks

The single specimen of *C. epakros* (ANSP 175371) from the Essequibo River represents an extension to the north-east relative to the other records of the species. A major extension to the west is represented by samples from the Río Nanay, in the Peruvian Amazon. These samples could not be distinguished from those originating in the more central and eastern portions of the Amazon basin and are consequently considered conspecific despite the gap in the known distribution of the species.

Material examined

Type material. HOLOTYPE: MZUSP 33392, 1, 132.6 mm SL; Brazil, Pará, Rio Tapajós, São Luís, above Itaituba (4°25'S; 56°10'W). Collector M. Goulding, 22/Oct/1983. PARATYPES: MZUSP 76070, 53, 1 C & S, 110.1–150.7 mm SL; INPA 18590, 3, 119.1–129.6 mm SL; USNM 368279, 3, 121.8–138.4 mm SL; UMMZ 239931, 3, 128.4–136.2 mm SL; same data as holotype.

Non-type material. BRAZIL: AMAZONAS: INPA 705, 2, 107.5–138.1 mm SL. – INPA 16931, 5, 129.6–148.4 mm SL; Rio Uatumã. – INPA 16965, 2, 124.1–131.7 mm SL; Rio Uatumã, mouth of Igarapé Catitu. – INPA 16960, 1, 162.0 mm SL; INPA 16963, 2, 128.0–145.5 mm SL; Igarapé da Arraia, Rio Uatumã. – INPA 16956, 1, 162.0 mm SL; Igarapé da Água Branca, Rio Pitinga. – INPA 18617, 7, 112.2–141.9 mm SL; Rio Pitinga, Cachoeira Travessão. – MZUSP 6706, 24, 93.7–156.0 mm SL; Rio Negro, surroundings of Manaus. – MZUSP 31341, 1, 103.9 mm SL; Rio Negro, Anavilhanas. PARÁ: INPA 16961, 2, 143.0 (from 1 spec.), Rio

Jari, Igarapé and margin of island in front of Porto Sabão. – INPA 16969, 9, 135.0–156 mm SL; Rio Jari, below Cachoeira de Santo Antônio. – INPA 4293, 2, 58.5–66.1 mm SL; Rio Xingu, Arroz Cru, Lagoa da Palmeira. – INPA 4181, 3, 70.7–72.8 mm SL; INPA 4133, 2, 117.1–132.9 mm SL; Rio Xingu, Ilha de Babaquara. – MZUSP 33394, 31, 125–175.6 mm SL; MZUSP 30758, 1, 81.6 mm SL; MZUSP 63651, 3, 127.0–146.1 mm SL; Rio Xingu, Belo Monte. – MZUSP 45884, 1, 125.3 mm SL; Rio Riozinho, Serra de Kukoinhokren. – MZUSP 36816, 1, 133.3 mm SL; Cachoeira do Espelho, Rio Xingu. – USNM 119949, 3, 98.1–178.8 mm SL; Rio Xingu, Porto de Moz. – INPA 6746, 3, 136.0–158.0 mm SL; Rio Jamaxim, tributary of Rio Tapajós, Ilha Terra Preta. – MZUSP 22095, 4, 86.4–95.3 mm SL; Rio Tapajós, Ilha da Barreirinha, near São Luís. – MZUSP 25431, 1, 88.4 mm SL; right margin of Rio Tapajós, in front of Pimental. – MZUSP 30750, 3, 127.0–133.0 mm SL; Rio Tapajós, between Itaituba and São Luís. – CAS 69080, 1, 88.5 mm SL; Rio Tapajós, Itaituba. – MZUSP 25503, 2, 102.9–108.5 mm SL, left margin of Rio Tapajós, between National Park headquarters and branch of Saita, km 67. – MZUSP 30754, 14, 1 C & S, 69.3–94.7 mm SL; Rio Tapajós, Pederneiras. – MZUSP 21992, 4, 114.4–128.5 mm SL; Rio Tapajós, São Luís, Poça de Pedra. – MZUSP 20276, 8, 103.8–115.6 mm SL; Rio Tapajós, inland lake in front of Monte Cristo. INPA 748, 1, 133.7 mm SL; Rio Curuá-Una. – INPA 16945, 1, 99.4 mm SL; INPA 16946, 2, 104.2–106.5 mm SL; INPA uncat., 10, 93.6–101.7 mm SL; Içangui, Rio Tocantins. – INPA 16947, 21, 79.1–103.8 mm SL; Rio Tocantins, below Tucuruí dam. – MZUSP 30751, 1, 133.2 mm SL; Rio Itacaiunas, Rio Tocantins, Caldeirão. – MZUSP 20364, 2, 71.5–77.2 mm SL; on marginal lagoons of Rio Tocantins, near Tucuruí. – MZUSP 20649, 2, 74.4–74.6 mm SL; Igarapé Muru, Rio Tocantins, below Tucuruí. – MZUSP 20324, 2, 71.9–77.0 mm SL; Igarapé Urubu, Rio Tocantins, near Posto Trocará. – MZUSP 20088, 2, 77.8–97.5 mm SL; Rio Trombetas, Oriximiná. – INPA 16968, 2, 135.2–137.1 mm SL; INPA 16959, 4, 105.2–116.4 mm SL; Rio Trombetas, below Cachoeira Porteira. INPA 16948, 5, 131.7–144.4 mm SL; Rio Trombetas, above Cachoeira Porteira. – CAS 69075, 1, 102.5 mm SL; Rio Amazonas, market at Santarém. – CAS 69077, 3, 108.0–115.3 mm SL; Rio Amazonas, Marabá. GOIÁS: MZUSP 54571, 1, 132.0 mm SL; Rio Tocantins, Minaçu, Porto do Garimpo, below Serra da Mesa dam. – MZUSP 54572, 2, 105.3–122.3 mm SL; Rio Tocantins, Porto do Garimpo, below Serra da Mesa dam. MATO GROSSO: MZUSP 64960, 3, 118.0–130.3 mm SL; Ribeirão Suaizinho near Fazenda Cascavel, tributary of Rio Suiá-Missu, Rio Xingu. – INPA 16970, 9, 87.6–99.0 mm SL; Rio do Côco, Caseara, Lago do Case. INPA 18602, 1, 89.5 mm SL, Rio do Côco; Caseara,

Cantão. – INPA uncat., 21, 84.5–99.8 mm SL; Rio Araguaia, Fazenda Santa Fé. – INPA 18604, 4, 91.3–104.3 mm SL; Lago Santa Fé, Rio Araguaia; Cantão State Park. – INPA 18603, 1, 98.4 mm SL; Lago Ariranhãs. – INPA 18605, 3, 87.6–88.2 mm SL; Porto Balsa, Rio Côco. – MZUSP 63650, 3, 117.4–125.7 mm SL; Rio Correntes, Rio Araguaia, Barra do Garça. – MZUSP 19631, 3, 73.9–108.8 mm SL; Rio Araguaia, Santa Terezinha. – MZUSP 3847, 1, 107.7 mm SL; Rio Araguaia. – MZUSP 64202, 5, 138.8–165.3 mm SL. – MZUSP 54445, 1, 109.1 mm SL; Rio Cristalino, Rio Araguaia. – MZUSP 62535, 4, 124.6–138.8 mm SL; Rio Teles Pires, Pesqueiro do Dentinho, município de Alta Floresta – USNM 31083, 5, 132.9–173.0 mm SL; Rio Batovi, small tributary and shallow lake drainage, Rio Xingu. *Rondônia*: INPA 16925, 3, 105.6–140.2 mm SL; Rio Jamari, c. 5 km above Samuel dam. – INPA 16967, 1, 79.9 mm SL; Rio Urupá, tributary of Rio Jiparaná (= Rio Machado). – INPA 16966, 2, 110.8–114.9 mm SL; Rio Urupá, tributary of Rio Machado, c. 10 km above Jiparaná; INPA 16957, 2, 158.0 mm SL; Lago Espanha, below Samuel dam. – INPA 16962, 2, 139.0–158.0 mm SL; Igarapé Japiim, c. 45 km above Samuel dam. – MZUSP 14032, 5, 129.6–167.3 mm SL; Lago do Paraíso, Rio Machado, Rio Madeira. – MZUSP 77270, 1, 89.3, Panelas, Rio Roosevelt, above falls. RORAIMA: MZUSP 30752, 1, 128.3 mm SL; Cachoeira do Bem-Querer, Rio Branco. – MZUSP 30749, 5, 108.1–144.6 mm SL; Rio Uraricoera, Maracá. – INPA 8113, 1, 74.7 mm SL; Igarapé number 1.

COLOMBIA: AMNH 38183, 1, 118.9 mm SL, C&S; Amazon Basin.

GUYANA: ANSP 175371, 1, 89.3 mm SL; Essequibo River, sandbars 1.0–1.5 h upstream from Maipuri campsite.

PERU: LORETO: USNM 280438, 2, 67.3–77.1 mm SL; Rio Nanay, c. 20 km upstream of mouth in the main channel. – USNM 280440, 1, 64.9 mm SL; Rio Nanay, north-east of Iquitos. – USNM 240442, 1, 76.6 mm SL; Rio Nanay at Nanay beach, West of Iquitos. – ANSP 167068, 1, 69.8 mm SL; Rio Nanay, right bank, 0.5 mi below Santa Clara. – ANSP 167067, 2, 71.8–76.6 mm SL; Rio Nanay, creek tributary of Rio Nanay (above confluence) c. 0.25 mi below Santa Clara. – ANSP 136900, 5, 73.0–86.3 mm SL; ANSP 136901, 5, 70.8–86.3 mm SL; Vicinity of Iquitos, Moronacocha outlet, right bank of Rio Nanay, c. 9 min above Rio Amazonas.

VENEZUELA: AMAZONAS: ANSP 161222, 1, 121.3 mm SL; Rio Orinoco at playa across from mouth of Rio Iguapo. – ANSP 161224, 1, 130.3 mm SL; Caño of Rio Casiquiare, playa c. 1.5 h. from confluence of Rio Casiquiare and Rio Orinoco. – ANSP 159781, 1, 79.7 mm SL; Rio Orinoco at El Burro. – ANSP 161219, 1, 130.1 mm SL; Rio Orinoco, caño separating island and playa just downstream from Quiratare. BOLIVAR:

ANSP 135641, 2, 71.8–89.1 mm SL; Caño Chuapo, c. 20 min downstream from Jabillae on Rio Caura. – ANSP 139554, 5, 88.9–99.0 mm SL; isolated backwater of Rio Nichare, c. 10 min from Rio Nichare/Rio Caura junction. – ANSP 159779, 1, 94.0 mm SL; Rio Orinoco, vicinity of Puerto Las Majadas, Rio Orinoco/Rio Caura confluence. – ANSP 159780, 2, 92.1–101.3 mm SL; Rio Caura at Puerto das Majadas. – ANSP 139559, 1, 119.5 mm SL; sand bar along Rio Mato.

CHALCEUS GUAPORENSIS SP. NOV.

(FIGS 21–23; TABLE 5)

Chalceus erythrurus (not of Cope, 1870) – misidentification: Chang, 1998: 22 [Peru, Rio Madre de Dios basin, Rio Malinowski; (specimen not examined, identification inferred by geographical distribution)]. Ortega, 1996: 464 [Peru, Rio Manu system].

Chalceus sp. Lauzanne & Loubens, 1985: 108 [Bolivia, Rio Mamoré basin (specimen not examined, identification inferred by geographical distribution)].

Diagnosis

Chalceus guaporensis can be readily distinguished from all other *Chalceus* species except *C. epakros* by the lack of a median fontanel between the frontal and parietal bones, by the relatively longer and more acute snout and by the presence of a longitudinal dark stripe from the posterodorsal margin of opercle to caudal peduncle formed by chromatophores located deep in the skin (see 'Comments . . .', below) (Figs 22, 23). *Chalceus guaporensis* differs from *C. epakros* in having 7

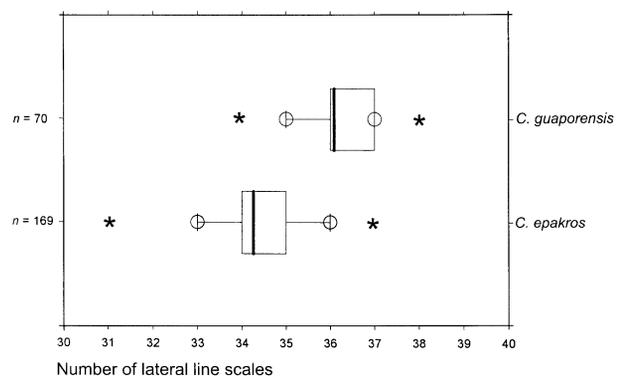


Figure 21. *Chalceus guaporensis* and *C. epakros* spp. nov. Tukey box plots of the number of lateral line scales. Visual comparison shows that these scale counts are obviously different in the two species. Although overlapping, the counts are significantly different when subject to Mann–Whitney rank-sum tests ($t = 13158.5$, $P < 0.001$; median: *C. guaporensis* = 36, *C. epakros* = 34).



Figure 22. *Chalceus guaporensis* sp. nov., holotype, UMMZ 239851, 112 mm SL, Bolívia, Beni, Rio Itenez at mouth of Rio Baurés, 6 km SW Costa Marques (Brazil), 12°31'S; 64°19'W.



Figure 23. *Chalceus guaporensis* sp. nov., paratype, UMMZ 204783, 80.5 mm SL, Bolívia, Rio Baurés, 400 m above mouth on left bank, 6 km SW Costa Marques (Brazil), 12°34'6'S; 64°19'W.

branched pelvic-fin rays (vs. 8 in the latter species, see 'Remarks'). It may be further distinguished from *C. epakros* and *C. macrolepidotus* in having the first small tooth of the inner dentary row located behind the fourth or fifth tooth of the anterior row with a distinct gap between the symphyseal tooth and first small conical tooth (vs. first small tooth of inner dentary row located very close to the symphyseal tooth and forming an almost continuous series). *Chalceus guaporensis* also has a somewhat rounded, conspicuous humeral spot extending over the first four scales of the lateral line and located deep in the skin (see 'Comments . . .', below). A humeral spot located deep in the skin is sometimes present in *C. epakros*, although when present in the latter species it is usually more vertically elongate than the spot of *C. guaporensis*. Although there is broad overlap in the ranges, the number of lateral line scales in *C. guaporensis* tends to be higher than those in *C. epakros* (Table 6, Fig. 21).

Description

Morphometric data presented in Table 5. Maximum size 140.4 mm SL. Body robust, somewhat compressed, relatively elongate, greatest body depth located slightly anterior to dorsal-fin origin. Dorsal profile of head convex anteriorly at snout region, posterodorsally inclined from anterior end of snout to tip of supraoccipital spine. Anterior profile of head distinctly acute in dorsal view. Interorbital distance wide, proportionally wider relative to SL in larger specimens. Dorsal surface of head in interorbital region flat. Dorsal body profile convex from tip of supraoccipital spine to dorsal-fin origin. Dorsal body profile posteroventrally inclined along dorsal-fin base, then straight to relatively convex to adipose fin and concave along dorsal profile of caudal peduncle to origin of procurent caudal-fin rays. Ventral profile of head somewhat convex from tip of lower jaw to vertical through posterior limit of isthmus. Ventral body pro-

Table 5. Morphometrics of *Chalceus guaporensis* sp. nov. All dimensions in mm

Character	Holotype	<i>n</i>	Range	Mean
Standard length	112.0	74	60.2–140.4	
Body depth	24.6	74	22.7–26.9	24.6
Snout to dorsal-fin origin	54.5	74	52.2–58.0	55.1
Snout to pectoral-fin origin	27.6	74	25.6–31.0	28.4
Snout to pelvic-fin origin	51.3	74	50.2–55.5	52.6
Snout to anal-fin origin	81.0	74	78.1–84.3	81.0
Caudal-peduncle length	13.2	63	11.1–14.9	13.2
Caudal-peduncle depth	10.9	74	9.4–11.5	10.6
Dorsal-fin length	22.9	71	22.2–26.7	24.4
Anal-fin base	9.4	63	7.3–10.3	9.1
Anal-fin length	16.7	70	14.9–20.0	17.9
Pectoral-fin length	16.9	74	17.8–21.3	19.2
Pelvic-fin length	18.2	74	16.2–20.3	18.2
Head length	28.0	74	25.8–31.8	28.6
Snout length	37.6	73	32.6–40.1	36.3
Orbital diameter	29.3	74	25.1–37.4	32.2
Interorbital width	40.8	74	32.8–45.3	38.2
Upper jaw length	45.5	74	40.9–49.1	46.2

Table 6. Number of specimens of *Chalceus epakros* and *C. guaporensis* spp. nov. with cited number of lateral line scales

	No. lateral line scales								Total
	31	32	33	34	35	36	37	38	
<i>C. epakros</i>	3	4	32	62	44	23	1	–	169
<i>C. guaporensis</i>	–	–	–	1	13	36	19	1	70

file convex from that point to anal-fin origin. Body profile along anal-fin base posterodorsally inclined, slightly concave along ventral margin of caudal peduncle. Smaller specimens with relatively longer heads. Median fontanel absent between frontals and parietals even in smallest examined specimens. Mouth terminal, large, upper jaw slightly longer than lower jaw, tip of premaxillary teeth extends below margin of upper lip giving a saw-like appearance to margin of premaxilla even in closed mouth. Maxilla extending to vertical through anterior margin of orbit. Supramaxilla present.

Dorsal-fin rays ii,10 (ii,10; ii,9 in one and ii,11 in two specimens, $n = 70$). Dorsal-fin origin situated posterior to vertical through insertion of innermost pelvic-fin rays. First basal dorsal-fin pterygiophore inserting behind neural spine of 11th vertebra ($n = 3$). Distal margin of dorsal fin slightly straight to convex. Adipose fin present. Anal-fin rays iii,9 (iii,9; iii,8 in 2 specimens, $n = 70$). First basal anal-fin pterygiophore inserting behind haemal spine of 24th vertebra ($n = 4$). Distal margin of anal fin straight to emargin-

ate with anterior branched rays approximately 3 times length of ultimate ray. Pectoral-fin rays i,14 (range 14–16, 17 in one specimen, mean 16.1, $n = 70$), pointed distally, with unbranched- and first branched rays longest, but not reaching pelvic-fin insertion. Pelvic-fin i, 7 (i,7, $n = 70$); fin pointed distally. Caudal fin forked, lower fin lobe slightly more developed than upper lobe.

Premaxillary teeth in three rows. Outer row 9 (range 9–12, mean 10.8, $n = 68$); teeth tricuspid, sometimes pentacuspoid, with medial cusp larger and teeth of similar size. Cusps slightly curved with concave portion facing mouth cavity. Inner row 8 (range 7–10, 11 in 1 specimen; mean 8.5, $n = 70$) largest, symphyseal tooth usually asymmetric with one cusp on medial margin and two cusps on lateral margin of tooth. Remaining teeth pentacuspoid, or more lateral teeth tricuspid, with second tooth from symphysis larger and teeth gradually diminishing in size laterally. Cusps slightly curved, with concave portion opposite of mouth cavity. Intermediate row 2 (2; 1 in one specimen, $n = 70$) pentacuspoid or tricuspid teeth, more

widely separated than teeth of other rows and of intermediate size. Cusps straight.

Maxillary teeth 11 (range 9–16, 17 in one specimen, mean 12.5, $n = 70$). Anterior teeth tricuspid with remaining teeth conical. Teeth extending along almost entire margin of ossification. Dentary teeth in two rows. Outer row 14 (range 11–16, 18 in one specimen; mean 13.1, $n = 70$), with teeth large and pentacuspoid anteriorly, sometimes heptacuspoid, gradually diminishing in size and number of cusps posteriorly. Posterior-most teeth conical. Cusps slightly curved with concave portion facing mouth cavity. Inner row consists of large conical symphyseal tooth followed by series of minute conical teeth. First tooth usually positioned behind fourth or fifth tooth of anterior row with distinct gap between that tooth and symphyseal tooth.

Scales cycloid, large overall and approximately twice as large above lateral line as below it. Circuli on exposed portion of scales not concentric with those of anterior portion. Circuli on exposed portion of scales straight and extending to posterior margin of scale in examined specimens. Radii originating on centre of scale and radiating anteriorly and posteriorly on scale surface.

Lateral line low on body sides, complete, with alternating large and small perforated scales from posterior margin of opercle to vertical through last anal-fin ray; scales smaller and of similar size from that point to end of caudal peduncle. Canals in large specimens with 1–5 branches. Number of branches decreases toward caudal peduncle, with posterior scales unbranched. Small specimens with branching pattern less developed. Lateral-line scales 36 (range 35–37, 1 specimen with 34, 1 with 38; mean 36.1, $n = 69$). Scale rows between dorsal-fin origin and lateral line 3. Scale rows between lateral line and pelvic-fin insertion 2. Scales around caudal peduncle 12. Vertebrae 35 ($n = 3$).

Colour in alcohol. Specimens only retain silvery pigmentation on infraorbital and opercular regions. Body tan, darker dorsally. Longitudinal dark stripe formed by dark chromatophores located deep in the skin (see 'Comments . . .', below). Stripe extends from postero-dorsal margin of opercle to caudal peduncle, but not reaching base of caudal-fin rays. Somewhat rounded, conspicuous humeral spot extending over first four scales of lateral line and located more deeply in skin (see 'Comments . . .', below). Dorsal portion of humeral spot overlapping longitudinal stripe. Scales above lateral line with chromatophores slightly more concentrated along posterior margin and forming fine reticulate pattern. Some specimens also have chromatophores scattered on lateral-line scales and one longitudinal series above it. All fins hyaline, with dorsal, anal and adipose with dark chromatophores scattered. Tips of caudal-fin rays and ventral margin of first principal ray of lower caudal-fin lobe dark.

Distribution

The Rio Guaporé and Río Mamoré drainages, Río Madre de Dios and Río Jaci-Paraná in the upper Rio Madeira (see 'Remarks') (Fig. 20).

Etymology

Named after the Rio Guaporé.

Remarks

The main trait that distinguishes *C. guaporensis* from *C. epakros* is the number of branched pelvic-fin rays (7 vs. 8, respectively). Among specimens of *C. guaporensis* examined in this study (Table 7, $n = 71$) all have 7. Additional specimens from Río Madre de Dios basin (MUSM 3756, $n = 1$; 3907, $n = 1$; 16850, $n = 1$; and 8033, $n = 5$), all have 7 except for one specimen (MUSM 8033) with 8 (H. Ortega, pers. comm.). The latter specimen is considered atypical and herein tentatively identified as *C. guaporensis*.

Most of the *C. epakros* specimens ($n = 174$) have 8 rays (Table 7). Of the six remaining specimens, two have 7 (INPA 16968, 1 of 2, 137.1 mm SL, from the Rio Trombetas and INPA 16925, 1 of 3, 105 mm SL from the upper Rio Madeira); both belong to lots in which the other specimens have 8 and their number of lateral-line scales (34 and 36, respectively), falls within the range of variation for the two species (Table 6). The specimens from the Rio Trombetas all possess 8; that basin is, furthermore, distant from the distribution range of *C. guaporensis*. The specimen with 7 rays from the Rio Trombetas appears atypical and is herein assigned to *C. epakros*. The specimen from the upper Rio Madeira is somewhat more problematic because it comes from a location adjacent to the northern limit of the distribution range of *C. guaporensis*, raising the question as to whether *C. epakros* and *C. guaporensis* perhaps occur in sympatry along the edges of their distribution range, or whether the specimen is atypical. It was collected in the Rio Jamari, a tributary of the upper Rio Madeira below the waterfall region (a series of 19 waterfalls occurs along a 353-km river stretch between the cities of Porto Velho in the upper Rio Madeira and Guajará-Mirim in the Rio Mamoré; Goulding, 1979: 33–34). Within the Rio Madeira basin, *C. epakros*

Table 7. Number of specimens of *Chalceus epakros* and *C. guaporensis* spp. nov. with cited number of branched pelvic-fin rays

	No. branched pelvic-fin rays			Total
	7	8	9	
<i>C. epakros</i>	2	174	4	180
<i>C. guaporensis</i>	71	–	–	71

appears to occur only in regions downstream of the waterfalls, while all specimens of *C. guaporensis* from the region of the upper Rio Madeira were collected upstream. Until additional information on these two species becomes available, we have tentatively assigned the specimen to *C. epakros*.

Material examined

Type material. HOLOTYPE: UMMZ 239851, 1, 112.0 mm SL. BOLIVIA: BENI: Río Itenez at mouth of Río Baures, 6 km SW of Costa Marques; 12°31'S, 64°19'W. Collector R. M. Bailey & R. Ramos, 30/Sep/1964. PARATYPES: BOLIVIA: BENI: UMMZ 204719, 4, 1 DS, 75.0–128.4 mm SL; MZUSP 76071, 3, 78.1–84.7 mm SL; same data as holotype. – UMMZ 204209, 19, 2 C & S 62.2–86.2 mm SL; MZUSP 76072, 4 62.3–81.4 mm SL; Río Itenez, opposite Costa Marques, 12°29'30"S, 64°15'30"W. – UMMZ 204783 9, 2 DS, 75.3–109.9 mm SL; Río Baures, 400 m above mouth on left bank, 6 km SW of Costa Marques; PERU: MADRE DE DIOS: USNM 319294, 7, 1 C & S, 122.3–133.4 mm SL; Manu National Park, Pakitza, Picaflor Stream, Cana Brava Trail # 19.

Non-type material. BOLIVIA: BENI: UMMZ 205201, 3, 70.9–84.9 mm SL; slough of Río Itenez, 10 km SE of Costa Marques (Brazil). – UMMZ 204272 (2 of 4) 101.8–121.1 mm SL; Río Itenez at mouth of dry run, 2 km SE of Costa Marques (Brazil). – UMMZ 204447, 3, 73.2–78.1 mm SL; Río Itenez, along sand bar about 9 km SE of Costa Marques (Brazil). – UMMZ 204949, 1, 82.5 mm SL; playa pond of Río Itenez, 9 km SE Costa Marques (Brazil). – UMMZ 204588, 1, 67.8 mm SL; Río Itenez, 5 km SW of Costa Marques, 1.5–2 km above mouth of Río Baures. – UMMZ 204848 (1 of 3 specimens examined) 140.4 mm SL; Río Baures, 2 km above mouth. – UMMZ 233932, 1, 66.6 Río Baures at mouth, on right bank, 6 km SW of Costa Marques, Brazil. – FMNH 57585, 2, 95.0–97.6 mm SL; Villa Bella. – MNHN 1989–1426, 2, 124.2–126.3 mm SL. San Luis, Madre de Dios – AMNH 40169, 1, 102.9 mm SL; Río Mamoré at Cachuela, below Guayaramerin. – AMNH 40059, 21, 61.7–124.2 mm SL; Río Baures, 500 m above mouth. SANTA CRUZ: AMNH 77533, 1, 83.6 mm SL; Río Mamoré, c. 2 km north of Boca Chapare.

BRAZIL: RONDÔNIA: FMNH 14988–14989, 2, 79.1–100.8 mm SL; FMNH 57584, 13, 77.3–126.9 mm SL; Río Guaporensis, Maciel. – INPA 16927 1, 94.0 mm SL; Río Jaci-Paraná, c. 3 km from town of Jaci-Paraná.

COMMENTS ON THE COLOUR PATTERN OF *CHALCEUS* SPECIES

Variations in the pigmentation pattern of the longitudinal dark band and of the humeral spot distinguish

various species in *Chalceus*. The band characteristic of *C. epakros* and *C. guaporensis* is relatively narrow, covering approximately the ventral half of the scales along the second longitudinal row of scales above the lateral line. Anteriorly, it reaches the posterodorsal margin of the opercle (Figs 18, 19, 22, 23). In these species it is formed by chromatophores located deep in the skin and not directly associated with the scales.

A band of differing appearance (Figs 11, 17) is sometimes present in specimens of *C. macrolepidotus* (MZUSP 43291; MZUSP 58962, 1 of 2; and ANSP 161220), *C. spilogyros* (MZUSP 76069, 1 of 55; MZUSP 7053, 5 of 7; and MZUSP 54568, 1 of 5) and *C. erythrurus* (AMNH 59440, INPA 16190, 4 of 5; INPA 17226, MZUSP 13533, MZUSP 20385, 4 of 9 and MZUSP 77595). When present, the band in these species is wider than that of *C. epakros* and *C. guaporensis* and covers approximately 1.5 longitudinal rows of scales above the lateral line. It also reaches further anteriorly, covering the opercle and subopercle. The pigmentation is formed by a more superficial concentration of chromatophores located in the skin covering the internal surface of each scale. Due to the more superficial location of the chromatophores, the band is more conspicuous and looks darker than that of *C. epakros* and *C. guaporensis*. In addition, it can be removed with the scales. In the specimens of *C. erythrurus*, the band is very dark and extends anteriorly onto the first two infraorbitals. While it covers the humeral spot, the latter, with its characteristic posterodorsal notch, is still visible underneath.

The presence of a dark and wide band in some specimens of *C. macrolepidotus*, *C. spilogyros* and *C. erythrurus* seems to be related to reproduction. Azuma (1979) reported the appearance of a dark longitudinal bar on the male during the spawning season of a pair of *C. macrolepidotus* kept in aquarium. Among specimens with the band that we examined ($n = 26$), 19 were males and 7 were females (4 and 3; 6 and 1; and 9 and 3, males and females of *C. macrolepidotus*; *C. spilogyros*; and *C. erythrurus*, respectively) and all had well developed gonads indicating that the presence of the band is probably associated with sexual maturity rather than with sexual dimorphism, as suggested by the observations of Azuma (1979). However, some of these specimens belong to lots that included mature females lacking the dark band (e.g. *C. macrolepidotus* MZUSP 58962; *C. spilogyros* MZUSP 7053; MZUSP 54568). Additional information from live specimens is needed before a clear understanding of the timing and conditions of the appearance of the band during the life cycle of *Chalceus* species is understood. We have not observed any specimens of *C. epakros* or *C. guaporensis* with a band characteristic of some of the individuals of *C. macrolepidotus*, *C. spilogyros* and *C. erythrurus*.

The humeral spot present in *C. erythrurus*, *C. spilogyros*, *C. guaporensis* and in many specimens of *C. epakros* shows differences in shape (as described in the various 'Diagnosis' and 'Colour in alcohol' sections) and variation in the pattern of distribution of the chromatophores. As with the band, the spot in *C. epakros* and *C. guaporensis* is formed only by chromatophores located deep under the scales of the humeral region. *Chalceus erythrurus* and *C. spilogyros* also have a deeply located dark spot in the humeral region, but they also have a second more superficial one formed by chromatophores located in the skin immediately underneath the scales. The superficial spot obscures the deeper one; the latter is exposed when the superficial pigmentation is removed. As a consequence of the presence of the superficial chromatophores, the spots in *C. erythrurus* and *C. spilogyros* are darker and more conspicuous than those in *C. epakros* and *C. guaporensis*.

ACKNOWLEDGEMENTS

We thank the following individuals for the loan of specimens, hospitality during visits and other assistance: M. L. J. Stiassny, M. Carvalho, B. Brown, D. R. Batista and X. Freilich (AMNH); J. G. Lundberg and M. Sabaj (ANSP); D. Siebert and A. Gill (BMNH); T. Iwamoto and D. Catania (CAS); J. Sarmiento (Colección Boliviana de Fauna, La Paz); B. Chernoff and M. A. Rogers (FMNH); L. Rapp Py-Daniel, J. Zuanon, G. M. dos Santos and Maria A. S. Brazil (Lana) (INPA); J. C. Hureau, G. Duhamel and P. Pruvost (MNH); H. Ortega (MUSM); R. P. Vari and S. L. Jewett (USNM); W. L. Fink and D. W. Nelson (UMMZ). Photographs were taken by J. C. Nolasco. E. L. B. Juste drew Figures 1–3. M. T. U. Rodrigues (IB-USP) and G. M. dos Santos (INPA) provided colour pictures of freshly collected specimens that served as the basis of some of the life coloration descriptions. The distribution maps are based on a map of South America prepared by M. Weitzman. Part of this study was developed at the Fish Division of MZUSP and we are grateful to O. Oyakawa, J. L. de Figueiredo, N. A. Menezes, H. A. Britski and M. de Pinna for providing workspace and access to facilities. For discussions on many aspects related to this study and/or for reviewing previous versions of this manuscript we thank R. P. Vari, S. H. Weitzman, N. A. Menezes, F. C. T. Lima, J. Zuanon and L. Rapp Py-Daniel. Part of the research associated with this project was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 01/02290–9).

REFERENCES

Azuma H. 1979. Spawning the pink-tailed *Chalceus*. *Tropical Fish Hobbyist* **27**: 58–62.

- Bertin L. 1948.** *Catalogue des Types de Poissons du Muséum National d'Histoire Naturelle. 3e partie. Ostariophysaires (Characiniiformes, Gymnotiformes)*. Paris: Imprimerie National.
- Boeseman M. 1952.** A preliminary list of Surinam fishes not included in Eigenmann's enumeration of 1912. *Zoologische Mededeelingen* **31**: 179–200.
- Cala P. 1977.** Los peces de la Orinoquia Colombiana. *Lozania* **24**: 1–21.
- Castro RMC. 1984.** Osteologia e relações filogenéticas de *Engraulisoma taeniatum* Castro 1981 (Ostariophysi, Characiformes, Characidae). Unpublished MSc Dissertation, Universidade de São Paulo.
- Chang F. 1998.** Fishes of the Tambopata-Candamo reserved zone, southeastern Peru. *Revista Peruana de Biología* **5**: 15–26.
- Cockerel TDA. 1914.** The scales of the South American characinid fishes. *Annals of the Carnegie Museum* **9**: 92–113, plates 23–28.
- Cope ED. 1870.** Contribution to the ichthyology of the Marañon. *Proceedings of the American Philosophical Society* **11**: 559–570.
- Cope ED. 1872.** On the fishes of the Ambyiacu River. *Proceedings of the Academy of Natural Sciences of Philadelphia* **23**: 250–294.
- Cuvier G. 1817.** Sur les poissons du sous-genre Mylètes. *Mémoires du Muséum d'Histoire Naturelle, Paris* **4**: 444–456, plates 21–22.
- Cuvier G. 1819.** Sur les poissons du sous-genre *Hydrocyn*, sur deux nouvelles espèces de *Chalceus*, sue les trois nouvelles espèces de des *Serrasalmes*, et sur l'*Argentina glossodonta* de Forskahl, qui est l'*Albula gonorhynchus* de Bloch. *Mémoires du Muséum d'Histoire Naturelle, Paris* **5**: 351–379.
- Cuvier G, Valenciennes A. 1850.** *Histoire Naturelle des poissons*, 22. Paris.
- Eigenmann CH. 1910.** Catalogue of the fresh-water fishes of tropical and south temperate America. *Reports of the Princeton University Expedition to Patagonia 1896–1899* **3**: 375–511.
- Eigenmann CH. 1912.** The freshwater fishes of British Guiana, including a study of the ecological grouping of species and the relation of the fauna of the plateau to that of the lowlands. *Memoirs of the Carnegie Museum* **5**: 1–578.
- Eigenmann CH, Allen WR. 1942.** *Fishes of western South America*. Lexington: University of Kentucky.
- Eigenmann CH, Eigenmann RS. 1891.** A catalogue of the fresh-water fishes of South America. *Proceedings of the United States National Museum* **14**: 1–81.
- Ferreira EFG. 1984.** A ictiofauna da represa hidrelétrica de Curuá-Una, Santarém, Pará. I – Lista e distribuição das espécies. *Amazoniana* **8**: 351–363.
- Fink SV, Fink WL. 1981.** Interrelationships of the Ostariophysan fishes (Teleostei). *Zoological Journal of the Linnean Society* **72**: 297–353.
- Fink WL, Weitzman SH. 1974.** The so called cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions to Zoology* **172**: 1–46.

- Fowler HW. 1906.** Further knowledge of some heterogonathous fishes. Part II. *Proceedings of the Academy of Natural Sciences of Philadelphia* **3**: 431–483.
- Fowler HW. 1950.** Os peixes de água doce do Brasil (2ª entrega). *Arquivos de Zoologia do Estado de São Paulo* **6**: 205–404.
- Géry J. 1959.** Contributions à l'étude de poissons characoides (Ostariophysi) (II). *Roeboexodon* gen. n. de Guyane, redescription de *R. guyanensis* (Puyo, 1948) et relations probables avec formes voisines. *Bulletin du Muséum National d'Histoire Naturelle, Série 2* **31**: 345–352.
- Géry J. 1963.** Essai sur les affinités phylogénétiques des Agoniates et l'origine des Characidae, à propos de la description d'une forme nouvelle de l'Amazone péruvienne: *Agoniates ladigesi* *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **60**: 265–284.
- Géry J. 1977.** *Characoids of the World*. Neptune City, NJ: TFH Publications.
- Géry J, Planquette P. 1982.** Additions à la Faune Characoïde (Poissons Ostariophysaires) de la Guyane. *Revue Française de Aquariologie Herpetologie* **9**: 65–76.
- Géry J, Planquette P, Le Bail PY. 1991.** Faune Characoïde (Poissons Ostariophysaires) de L'Oyapock, L'Approuague et la rivière de Kaw (Guyane Française). *Cybiurn* **15** (Suppl.): 1–69.
- Goulding M. 1979.** *Ecologia da pesca no Rio Madeira*. Manaus: INPA.
- Goulding M, Carvalho ML, Ferreira EFG. 1988.** *Rio Negro, rich life in poor water*. The Hague: SPB.
- Günther A. 1864.** *Catalogue of the fishes in the British Museum*, 5. London: British Museum (Natural History).
- Heyer HC. 1975.** Pflanzenräuber *Chalceus macrolepidotus*. *Aquarium Aqua Terra* **9**: 342–343.
- Howes GJ. 1982.** Review of the genus *Brycon* (Teleostei: Characoidei). *Bulletin of the British Museum (Natural History), Zoology* **43**: 1–47.
- La Monte FR. 1935.** Fishes from the Rio Juruá and Rio Purus, Brazilian Amazonas. *American Museum Novitates* **784**: 1–8.
- Lauder GV. 1981.** Intraspecific functional repertoires in the feeding mechanism of the Characid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia* **1981**: 154–168.
- Lauzanne L, Loubens G. 1985.** *Peces del Rio Mamoré*. Paris: Éditions de l'ORSTOM.
- Leviton AE, Gibbs RH Jr. 1988.** Standards in herpetology and ichthyology: standard symbolic codes for institutional resource collections in herpetology and ichthyology. Suppl. 1: additions and corrections. *Copeia* **1988**: 280–282.
- Leviton AE, Gibbs RH Jr, Heal E, Dawson CE. 1985.** Standards in herpetology and ichthyology, part I: standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* **1985**: 802–832.
- Lucena CAS. 1993.** Estudo filogenético da família Characidae com uma discussão dos grupos naturais propostos (Teleostei, Ostariophysi, Characiformes). Unpublished Doctoral Dissertation, Universidade de São Paulo.
- Mago-Leccia F. 1971.** La ictiofauna del Casiquiare. *Revista Defensa de la Naturaleza, Caracas* **1**: 5–10.
- de Mérona B, Santos GM, Almeida RG. 2001.** Short term effects of Tucuruí dam (Amazônia, Brazil) on the trophic organization of fish communities. *Environmental Biology of Fishes* **60**: 375–392.
- Müller J, Troschel FH. 1845.** *Horae Ichthyologicae Beschreibung und Abbildung Neuer Fische; die Familie Characinen*. Berlin: Verlag von Veit.
- Myers GS. 1960.** The South American characid genera *Exodon*, *Gnathoplax* and *Roeboexodon* with notes on the ecology and taxonomy of characid fishes. *Stanford Ichthyological Bulletin* **7**: 206–211.
- Nakashima S. 1941.** Algunos peces del Oriente peruano. *Boletín del Museo de Historia Natural 'Javier Prado'* **16**: 61–78.
- Ortega H. 1996.** Ictiofauna del Parque Nacional Manu, Peru. In: Wilson DE, Sandoval A, eds. *Manu, the biodiversity of Southeastern Peru*. Washington DC: Smithsonian Institution Press, 453–482.
- Ortega H, Vari RP. 1986.** Annotated checklist of the freshwater fishes of Peru. *Smithsonian Contributions to Zoology* **437**: 1–25.
- Paugy D. 1990.** Characidae. In: Lévêque C, Paugy D, Teugels GG, eds. *Faune des Poissons d'Eaux Douces et Saumâtres d'Afriques de l'Ouest*. Tervuren: Éditions de l'ORSTOM, 195–236.
- Planquette P, Keith P, Le Bail PY. 1996.** *Atlas des poissons d'eau douce de Guyane, 1. Collection du Patrimoine Naturel*, 22. Paris: Institut d'Ecologie et de Gestion de la Biodiversité du Muséum National d'Histoire Naturelle. Institut National de la Recherche Agronomique, Conseil Supérieur de la Pêche.
- Puyo J. 1943.** Nouveaux poissons d'eau douce de la Guyane française. *Bulletin de la Société d'Histoire Naturelle de Toulouse* **78**: 141–149.
- Puyo J. 1949.** *Poissons de la Guyane Française*. Paris: Librairie Larose.
- Regan CT. 1905.** On drawings of fishes of the Rio Negro. *Proceedings of the Zoological Society of London* **1**: 189–190.
- Regan CT. 1911.** The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidea. *Annals and Magazine of Natural History* **8**: 13–32.
- Regan CT. 1912.** A revision of the South-American characid fishes of the genera *Chalceus*, *Pyrrhulina*, *Copeina* and *Pogonocharax*. *Annals and Magazine of Natural History* **8**: 387–395.
- Roberts TR. 1969.** Osteology and relationships of characid fishes, particularly the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenolucius* and *Acestorhynchus*. *Proceedings of the California Academy of Sciences* **36**: 391–500.
- Schomburgk RH. 1841.** The fishes of Guiana. In: Jardine W, ed. *The Naturalist's Library: Ichthyology*, 3. Edinburgh.
- Spix JB, Agassiz L. 1829.** *Selecta genera et species piscium quos in itinere per Brasiliam annis MDCCCXXVII–MDCCCXXVIII jussu et auspiciis Maximiliani Josephi I. Bavarie regis augustissimi peracto collegit et pingendos curavit Dr. J. B. de Spix [. . .] J. B. Spix and L. Agassiz*. Munich: C. Wolf.
- Taphorn D, Royero R, Machado-Allison A, Mago-Leccia F. 1997.** Lista actualizada de los peces de agua dulce de Venezuela. In: La Marca E, ed. *Vertebrados actuales y fósiles de*

- Venezuela. *Serie Catálogo Zoológico de Venezuela*, Vol. I. Venezuela: Museo de Ciência y Tecnología de Mérida.
- Vanzolini PE. 1996.** A contribuição zoológica dos primeiros naturalistas viajantes no Brasil. *Revista USP* **30**: 190–238.
- Vari RP. 1983.** Phylogenetic relationships of the families Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae (Pisces: Characiformes). *Smithsonian Contributions to Zoology* **378**: 1–60.
- Vari RP, Harold AS. 2001.** Phylogenetic study of the Neotropical fish genera *Creagrutus* Günther and *Piabina* Reinhardt (Teleostei: Ostariophysi: Characiformes) with a revision of the cis-Andean species. *Smithsonian Contributions to Zoology* **613**: 1–239.
- Weitzman SH. 1962.** The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* **8**: 1–77.
- Weitzman SH, Malabarba LR. 1999.** Systematics of *Spintherobolus* (Teleostei: Characidae: Cheirodontinae) from eastern Brazil. *Ichthyological Exploration of Freshwaters* **10**: 1–43.
- Zanata AM. 2000.** Estudo das relações filogenéticas do gênero *Brycon* Muller & Troschel, 1844 (Characidae, Characiformes). Unpublished Doctoral Thesis, Universidade de São Paulo.
- Zarske A, Géry J. 1997.** Rediscovery of *Agoniates halecinus* Müller & Troschel, 1845, with a supplementary description of *Agoniates anchovia* Eigenmann, 1914 and a definition of the genus (Teleostei: Ostariophysi: Characiformes: Characidae). *Zoologische Abhandlungen Staatliches Museum Für Tierkunde in Dresden* **49**: 173–184.