

The Catfish Genus *Tetranematichthys* (Auchenipteridae)

RICHARD P. VARI AND CARL J. FERRARIS, JR.

The neotropical auchenipterid catfish genus *Tetranematichthys* is reviewed. *Tetranematichthys* was previously thought to be monotypic with its single species, *T. quadrifilis*, reported to have a broad range encompassing major portions of the Amazon basin and southern tributaries of the Río Orinoco. *Tetranematichthys quadrifilis* was rather found to be endemic to the Rio Guaporé in the southwestern portions of the Amazon basin and a new species of the genus is described from material originating in the upper Rio Negro system in Brazil and Venezuela and the upper Río Orinoco basin in southern Venezuela. The new species is also apparently widespread within the Amazon basin and the southern and north-central portions of the Río Orinoco system. The species of *Tetranematichthys* have distinctive modifications of the mandibular barbel and associated systems, which are proposed as synapomorphic for the species of the genus and that potentially function as a fishing lure.

TETRANEMATICHTHYS was proposed by Bleeker (1858) to include a species of auchenipterid catfish described by Kner (1857) as *Ageneiosus quadrifilis* on the basis of a single specimen collected in the Rio Guaporé system in the southwestern portion of the Amazon basin. Subsequent authors identified all samples of *Tetranematichthys* that originated at diverse localities within the Rio Tocantins and Amazon basins and the southern portions of the Río Orinoco system as *T. quadrifilis*. Our analysis reveals that *T. quadrifilis* is, rather, endemic to the Rio Guaporé of the upper Rio Madeira system. The reports of *Tetranematichthys* from other regions of the Amazon basin and southern and north-central portions of the Río Orinoco system all apparently represent a second congeneric species that we describe herein. We detail synapomorphic modifications of the mandibular barbel and associated musculature that may allow the barbel to serve as a fishing lure in the species of *Tetranematichthys*.

MATERIALS AND METHODS

Unpaired fin-ray counts were taken primarily from radiographs. Such data were supplemented by counts from non-radiographed specimens in some instances. The two posterior-most dorsal and anal-fin rays articulating on the last pterygiophore of each fin were counted as separate rays. Caudal-fin ray counts report the principal-fin rays (i.e., branched rays and the first unbranched ray of the dorsal and ventral lobes). Paired fin rays were counted under a stereomicroscope and included all elements. Vertebral counts obtained from radiographs and cleared-and-stained specimens are presented in terms of precaudal, caudal, and total vertebrae. The

terminal centrum was counted as a single element, and the Weberian complex was considered to include five centra. Values for the holotype are indicated in brackets.

Measurements were taken point-to-point, with the limits of most distances self-evident from the descriptors and the following measurements delimited as follows: the body width was measured across the bony cleithra immediately anterior to the insertions of the pectoral-fin spines; the head length was measured as a straight line distance from the tip of the snout to the posterior-most point on the fleshy operculum; the horizontal diameter of the orbit equals the distance bounded by the infraorbital bones across the middle of the eye; the length of the dorsal-fin spine was measured from the tip of the bony spine to the junction point between the first spine (spinelet) and the second spine, excluding the terminal fleshy or flexible portions of the spine; and the length of the anal-fin base was measured from the anal-fin origin to the insertion of the last anal-fin ray. Institutional abbreviations follow Leviton et al. (1985) with the following abbreviations used in the text: HL, head length; SL, standard length; and TL, total length.

In light of the pronounced overall similarity of the two species of *Tetranematichthys*, we describe the new species, *T. wallacei*, in detail but restrict the redescription of *T. quadrifilis* to those features that differ between the congeners. All features not discussed in the description of *T. quadrifilis* are comparable in that species to the conditions present in *T. wallacei*.

Tetranematichthys Bleeker, 1858

Tetranematichthys Bleeker, 1858:357 [type-species: *Ageneiosus quadrifilis* Kner, 1857. Type by monotypy].

Diagnosis.—The species of *Tetranematichthys* share the three proposed synapomorphies for the species of the subfamily Auchenipterinae: mature males with the urogenital pore located at the distal tip of the anterior margin of the anal fin and females with urogenital opening enlarged, a lateral-line canal that is forked on the basal portion of the caudal fin, a lateral-line canal that is sinusoidal along length of body, and sexual dimorphism in the degree of development and form of the dorsal-fin spine (see de Pinna, 1998, fig. 15). *Tetranematichthys* is readily distinguishable from all other members of the Auchenipterinae by its possession of only a single pair of mandibular (mental) barbels. Other members of the Auchenipterinae retain either two pairs of mandibular barbels (all other genera in the subfamily except *Ageneiosus*) or entirely lack mandibular barbels (*Ageneiosus*). A reduction to a single mandibular barbel also occurs within the Auchenipteridae in *Gelanoglanis* of the subfamily Centromochlinae (Böhlke, 1980, fig. 1). *Tetranematichthys* differs from *Gelanoglanis* in the degree of development of the maxillary barbel (barely extending beyond the fleshy posterior margin of the opercle vs. distinctly beyond that point, respectively; see Böhlke, 1980, fig. 1; Soares-Porto et al., 1999, fig. 1), in the overall form of the head and body, and in the alternate states for the synapomorphies for the Auchenipterinae and Centromochlinae (see de Pinna, 1998, fig. 15). We propose the following as synapomorphies for the species of *Tetranematichthys*: the presence of multiple fleshy, digitiform elaborations on the distal portions of the mandibular barbel, the anterior alignment of the mandibular barbel with the distal elaborations consequently extending forward to the region anterior of the mouth, and the presence of a discrete, well-developed portion of the protractor hyoidei muscle attaching to the anterior surface of the base of the mandibular barbel (see discussion below under *Mandibular barbel and associated musculature*).

Remarks.—Alternative hypotheses as to the phylogenetic relationships of *Tetranematichthys* were detailed in de Pinna (1998) with the salient points of that discussion reiterated herein. *Tetranematichthys* was originally aligned with *Ageneiosus* by Bleeker (1863), whereas most authors of the late nineteenth through mid-twentieth century (e.g., Eigenmann and Eigenmann, 1890; Gosline, 1945) placed *Tetranematichthys* in the Auchenipteridae (or Auchenipterinae) and assigned *Ageneiosus* to a separate family or subfamily. In a departure from the latter practice, Miranda-Ribeiro (1911) proposed an

alignment of *Tetranematichthys* with the Ageneiosidae, a return to the concept advanced by Bleeker (1863), but one that did not enter into general use. A separate Ageneiosidae consisting of *Ageneiosus* and *Tetranematichthys* was subsequently recognized by Britski (1972) based on his analysis of various anatomical systems. In his phylogenetic analysis of the Auchenipteridae and allied taxa, Ferraris (1988) hypothesized that *Ageneiosus* and *Tetranematichthys* jointly formed a natural unit on the basis of a set of synapomorphies (see enumeration of characters in de Pinna [1998, fig. 15]). The clade formed by those two genera proved, however, to be deeply nested in what traditionally constituted the Auchenipteridae making it inappropriate to recognize the Ageneiosidae as a separate family. Walsh (1990), in his analysis of the Ageneiosidae (*sensu* Miranda-Ribeiro, 1911; Britski, 1972), similarly proposed that *Tetranematichthys* was the sister group to the species of *Ageneiosus*; however, contrary to Ferraris (1988), Walsh retained the Ageneiosidae as separate from the Auchenipteridae. More recently de Pinna (1998) summarized the series of synapomorphies in support of the hypothesis advanced by Ferraris (1988) that *Ageneiosus* and *Tetranematichthys*, the Ageneiosidae of Walsh (1990), constituted a clade embedded within a broader Auchenipteridae. Under that tree topology the continued recognition of a separate Ageneiosidae was untenable in the absence of the proposal of additional family-level names, and as suggested by Ferraris (1988) and de Pinna (1998), we recognize *Tetranematichthys* as a member of the Auchenipteridae.

Tetranematichthys wallacei, new species

Figures 1A, 2–4; Table 1

Tetranematichthys quadrifilis (not of Kner, 1857), Miranda-Ribeiro, 1962:4 [Brazil: Amazonas, Rio Negro, Uipiranga; Amazonas, Rio Quixito, mouth of Javary (= Rio Javari)].—Miranda-Ribeiro, 1968:pl. 6 [lateral view of head and body, dorsal view of head, lateral view of anal fin of nuptial male].—Goulding et al., 1988:123 [Brazil, Rio Negro].—Royer et al., 1992 [Venezuela, Amazonas, Río Atabapo].—Franke, 1995:245, fig. 3 [Venezuela, Río Orinoco basin, Guarico, Caño El Toro].—Taphorn et al., 1997:82 [Venezuela].—Wallace, 2002:306, 499, fig. 122 [sources of Rio Negro].—Rodríguez-Olarte et al., 2003:199 [Venezuela, Río Orinoco basin, lower Río Caura].—Lasso et al., 2003:239 [Venezuela, Río Orinoco basin, Río Caura].—Ferraris, 2003:477 [in part; citations from Venezuela, Colombia, Río Orinoco, and those portions of

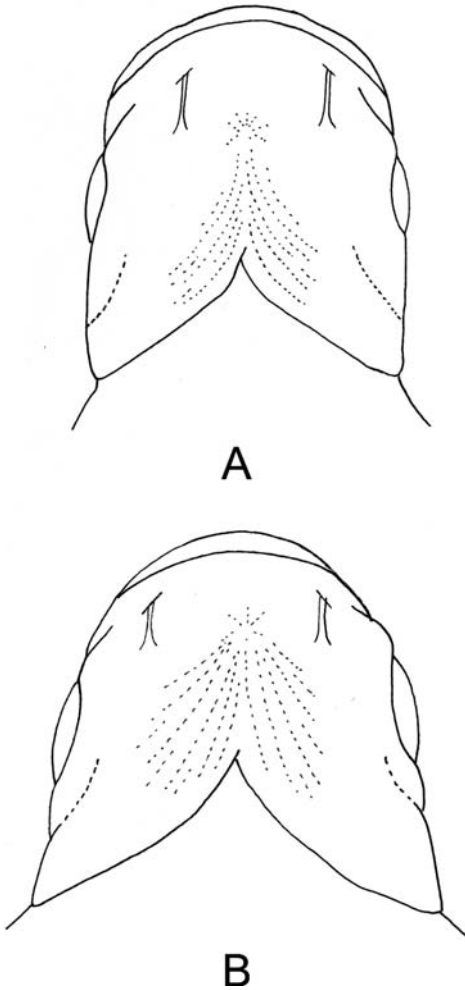


Fig. 1. Drawings of ventral surface of head and anterior portion of body of (A) *Tetranematichthys wallacei*, MZUSP 30590, 142 mm SL; and (B) *T. quadrifilis*, MZUSP 37517, 141 mm SL, showing the differing alignments of the postorbital portions of the head. Only basal portions of mandibular barbels illustrated.

Amazon basin outside of Rio Guaporé].—Lasso et al., 2004a:167 [Venezuela, Río Negro and Río Orinoco].—Lasso et al., 2004b:139 [Venezuela and Colombia: Ríos Apure, Atabapo, Capanaparo, Casiquiare, Caura, Cinaruco, Inirida, Meta, Orinoco, Ventuari].

Holotype.—MZUSP 31096, 1, 171 mm SL, nuptial male, Brazil, Amazonas, upper Rio Negro, São Pedro, mouth of Igarapé do Ibará, approximately $0^{\circ}15'S$, $66^{\circ}46'W$, 23 May 1979, M. Goulding.

Paratypes.—11 specimens, 120–206 mm SL. MZUSP 59048, 3, 173–206 mm SL, Brazil, Ama-

zonas, Município Santa Isabel do Rio Negro, lago in São João near Tapurucuara (= Santa Isabel do Rio Negro), approximately $0^{\circ}24'S$, $65^{\circ}02'W$, 8 Nov. 1972, Expedição Permanente à Amazônia. USNM 269994, 1, 145 mm SL, nuptial male, Venezuela, Amazonas, Departamento Río Negro, Caño Chola, where crossed by road between San Carlos de Río Negro and Solano, approximately $1^{\circ}58'N$, $67^{\circ}00'W$, 5 Dec. 1984, R. P. Vari, C. J. Ferraris, Jr., A. Machado-Allison, O. Castillo, and J. Fernandez. USNM 269995, 1, 120 mm SL, Venezuela, Amazonas, Departamento de Río Negro, small caño off Caño Urami, left bank tributary just upriver of Santa Lucía, $1^{\circ}17'N$, $66^{\circ}51'W$, 6 Dec. 1984, R. P. Vari, C. J. Ferraris, Jr., A. Machado-Allison, O. Castillo, and J. Fernandez. USNM 270008, 1, 188 mm SL, Venezuela, Amazonas, Departamento de Río Negro, Caño Loro, where crossed by road between San Carlos de Río Negro and Solano, $1^{\circ}59'N$, $66^{\circ}58'W$, 7 Dec. 1984, R. P. Vari, C. J. Ferraris, Jr., A. Machado-Allison, O. Castillo, and J. Fernandez. AMNH 74444, 2, 131–164 mm SL, nuptial males, Venezuela, Amazonas, Departamento de Río Negro, Río Mawarinuma, at Cerro de Neblina base camp, $0^{\circ}55'N$, $66^{\circ}10'W$, 6–13 Feb. 1984, C. J. Ferraris, Jr., G. J. Nelson, and R. Royero. ANSP 163022, 1, 123 mm SL, Venezuela, Amazonas, Departamento de Casiquiare, Caño Caripo (first right bank caño on Río Casiquiare approximately five minutes from confluence of Río Casiquiare and Río Orinoco), approximately 3 km from its mouth, $3^{\circ}06'N$, $65^{\circ}50'W$, 16 March 1987, B. Chernoff, J. Fernandez, and O. Castillo. MCNG 23086, 2, 132–138 mm SL, nuptial males, Venezuela, Amazonas, Departamento de Atures, Caño Cuchaken, 7 km from its confluence with Río Atabapo, $3^{\circ}31'N$, $67^{\circ}24'W$, 28 Oct. 1983, L. Nico and H. Bolivar.

Non-type material.—Brazil, Amazonas: MZUSP 30590, 1, 142 mm SL, Rio Negro; MZUSP 30591, 1, 121 mm SL, Rio Arirará, near its mouth, approximately $0^{\circ}20'S$, $63^{\circ}40'W$; MZUSP 84735, 1, 189 mm SL, Município Santa Isabel do Rio Negro, mouth of lago in São João near Tapurucurara (= Santa Isabel do Rio Negro), approximately $0^{\circ}24'S$, $65^{\circ}02'W$; INPA 9894, 1, 151 mm SL, Rio Jaú, Igarapé Miratuca, approximately $0^{\circ}30'S$, $64^{\circ}32'W$. Brazil, Pará: MZUSP 63633, 1, 67 mm SL, left bank of Rio Tapajós, Igarapé Jacaré, near Boim, approximately $2^{\circ}49'S$, $55^{\circ}10'W$; MZUSP 63637, 1, 125 mm SL, Município Baião, Igarapé do Limão, Rio Tocantins basin, approximately $4^{\circ}31'S$, $49^{\circ}36'W$; MZUSP 9354, 1, 163 mm SL, Igarapé Pacuí, at km 97 on highway from Belem to Brasília, $1^{\circ}36'S$, $47^{\circ}13'W$.

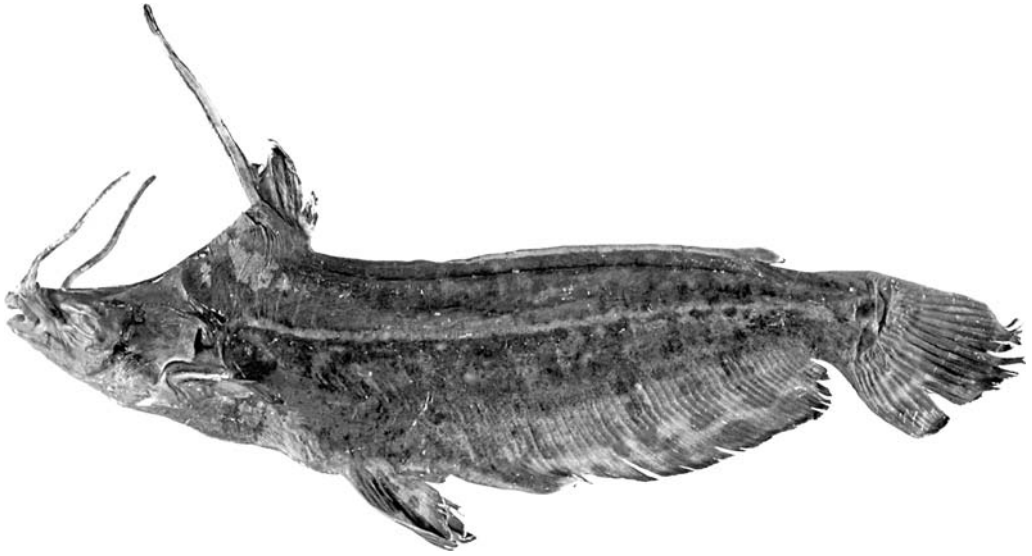


Fig. 2. *Tetranematichthys wallacei*, MZUSP 31096, 171 mm SL, holotype.

Colombia, Meta: ANSP 128688, 1, 111 mm SL, nuptial male, Caño El Viento, Finca El Viento, S of Matazul, 4°08'N, 72°39'W; ANSP 134591, 1, 145 mm SL, Rancho El Viento, small stream approximately 33.5 km NE of Puerto Lopez, 4°08'N, 72°39'W.

Peru, Loreto: ANSP 165030, 5, 46–68 mm SL, small stream approximately 70 km S of Iquitos near Genero Herrera, Río Ucayali basin, 5°00'S, 73°38'W.

Venezuela, Amazonas, Departamento de Casiquiare: MCNG 23369, 1, 69 mm SL, Caño Bocachica, N of airport of Mauca, 2°47'N, 67°40'W. Venezuela, Amazonas, Departamento de Atures: MCNG 23421, 2, 146–173 mm SL, smaller specimen nuptial male, cañito 2 km from Caño Cuchaken, approximately 13 km from its confluence with Río Atabapo, 3°31'N, 67°22'W. Venezuela, Amazonas, Departamento de Río Negro: MCNG 12396, 1, 188 mm SL, approximately 1 km above Caño Buridajow, 20 km from mouth of Río Pasimoni with Río Orinoco, 1°50'N, 66°35'W; MCNG 37742, 3, 148–154 mm SL, Río Siapa basin, 2°5'47"N, 66°10'78"W; MCNG 38170, 1, 148 mm SL, Caño Linda, between Puerto Ayacucho and Caicara, approximately 30 km N of Puerto Ayacucho; UF 120029, 1, 143 mm SL, nuptial male, Laguna de Candela, backwater area along right bank of Río Pasimoni, downstream of Río Yatua, 1°31'25.2"N, 66°33'31.2"W.

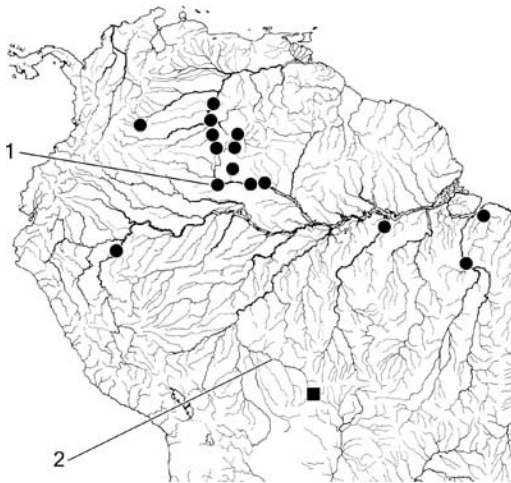


Fig. 3. Map of central and northern South America showing distribution of *Tetranematichthys wallacei* (dots, 1 = holotype locality) and *T. quadrifilis* (square, 2 = Río Guaporé, inexact type locality of *Ageneiosus quadrifilis*). Some symbols represent more than one lot and/or locality.

Diagnosis.—*Tetranematichthys wallacei* is distinguished from *T. quadrifilis* in the alignment of the lateral margins of the head in the region from the anterior margin of the orbit to the posterior limit of the opercle (running approximately in parallel from ventral view vs. diverging laterally, respectively; Fig. 1); in the body width at the pectoral-fin insertion as a proportion of the head width at the posterior margin of the orbit (0.99–1.10 vs. 1.17–1.25, respectively); in the distance from the tip of the snout to the anal-fin origin (0.29–0.32 of SL vs. 0.33–0.36 of SL, respectively); and in the position of the anterior

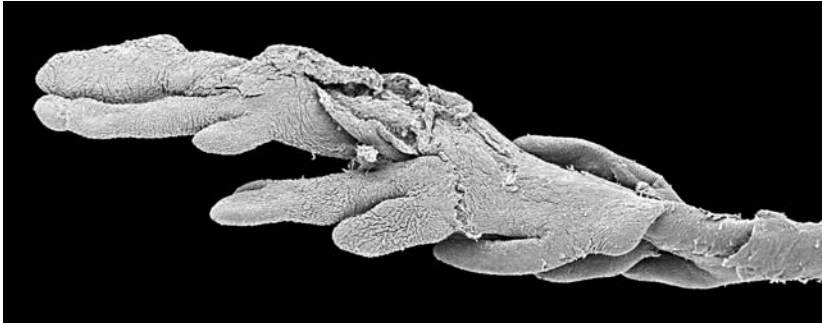


Fig. 4. SEM photograph of the distal portion of the mandibular barbel of *Tetranematichthys wallacei* showing the fleshy digitiform processes of that region.

termination of the gill opening (one orbital diameter posterior of the transverse plane running through the posterior margin of the orbit vs. positioned in the transverse plane running through the center of the orbit, respectively).

Description.—See Table 1 and below for morphometrics of *Tetranematichthys wallacei*. Body widest anteriorly; compressed posterior of pectoral-fin insertion, increasingly so posteriorly. Body depth at anal-fin origin greater than body width at cleithrum. Posterior portion of head and anterior portion of body proximate to dorsal-fin base higher than profile of portion of body posterior of dorsal-

fin base; disparity more pronounced in nuptial males than in females and non-nuptial males.

Lateral line complete, midlateral, and more obvious in smaller individuals. Lateral line canal with irregular, zig-zag pattern on anterior one-third to one-half of body, but with zig-zags less pronounced along remainder of its length. Canal forked at posterior margin of hypural plate, with posterodorsal and posteroventral branches extending short distances onto base of caudal fin. Precaudal vertebrae 15–17 [17]; caudal vertebrae 28–30 [30]; total vertebrae 45–47 [47] (14 specimens).

Head strongly depressed anteriorly; head depth at vertical through middle of orbit 0.52–

TABLE 1. MORPHOMETRIC DATA FOR HOLOTYPE AND PARATYPES ($N = 11$) OF *Tetranematichthys wallacei* AND MEASURED SPECIMENS OF *T. quadrifilis* ($N = 4$). Standard length expressed in mm. Values 1 to 13 are presented as proportions of standard length and 14 to 18 are proportions of head length. Distal portion of first dorsal-fin ray of holotype of *T. wallacei* damaged.

	<i>T. wallacei</i>		<i>T. quadrifilis</i>
	holotype	paratypes	
Standard length	171	120–206	114–140
1. Body depth at anal-fin origin	0.24	0.24–0.27	0.27–0.29
2. Body width at pectoral-fin insertion	0.20	0.20–0.25	0.24–0.27
3. Caudal-peduncle depth	0.10	0.09–0.12	0.10–0.11
4. Snout to dorsal-fin origin	0.32	0.29–0.32	0.33–0.36
5. Snout to anal-fin origin	0.53	0.53–0.56	0.54–0.59
6. Length of base of anal fin	0.42	0.37–0.44	0.35–0.45
7. Snout to pelvic-fin insertion	0.43	0.42–0.46	0.46–0.48
8. Length of first dorsal-fin ray	—	0.16–0.23	0.16–0.22
9. Length of first pelvic-fin ray	0.16	0.14–0.17	0.14–0.16
10. Length of pectoral-fin spine	0.15	0.14–0.18	0.15–0.17
11. Length of first pectoral-fin ray	0.16	0.16–0.18	0.16–0.17
12. Length of dorsal principal caudal-fin ray	0.18	0.17–0.20	0.19–0.20
13. Head length	0.26	0.25–0.31	0.30–0.33
14. Snout length	0.47	0.42–0.51	0.45–0.49
15. Horizontal diameter of orbit	0.12	0.14–0.20	0.12–0.15
16. Interorbital width	0.56	0.55–0.66	0.53–0.68
17. Head width at posterior margin of orbit	0.75	0.70–0.76	0.66–0.76
18. Body width at pectoral-fin insertion	0.79	0.71–0.78	0.78–0.88

0.65 of head width at posterior margin of orbit. Dorsal profile of head concave from posterior margin of lip approximately to middle of supraoccipital spine and straight or slightly convex from that point to dorsal-fin origin. Snout margin broadly rounded from dorsal view. Lateral margins of head in region from anterior margin of orbit to posterior limit of opercle running approximately in parallel from ventral view (Fig. 1A; see also Miranda-Ribeiro [1968, pl. 6]). Approximately parallel alignment of lateral profiles of head along that region reflected in proportion of body width at pectoral-fin insertion vs. head width at posterior margin of orbit (0.99–1.10). Interorbital width approximately equal to distance from anterior margin of orbit to posterior margin of opercle. Eye laterally positioned and visible in both dorsal and ventral views. Orbit round.

Maxillary barbel of juveniles, females, and non-nuptial males slender, thread-like, falling short of anterior margin of orbit and approximately equal in length to horizontal diameter of orbit. Barbel of nuptial males distinctly thickened and well ossified for entire, or nearly entire, length, but often terminating in fine, unossified, filamentous, distal extension. Ossified portion of adpressed maxillary barbel with distinct dorsomedial curvature. Maxillary barbel in nuptial males distinctly longer than that in juveniles, mature females, and non-nuptial males and extending posteriorly nearly to transverse plane through pectoral-spine insertion. Medial surface of ossified portion of maxillary barbel of males covered with series of epidermal ridges aligned perpendicular to long axis of barbel. Epidermal ridges sometimes extending onto dorsal surface of distal portion of barbel. Ridges easily abraded and often missing from part, or all, of medial and dorsal surfaces of barbel. Form of epidermal ridges comparable to those illustrated for *Auchenipterus nuchalis* by Ferraris and Vari (1999, fig. 1d), but with greater spacing between individual ridges.

Only one pair of mandibular barbels present. Barbels originating approximately one orbital diameter posterior of margin of lower lip and closer to rictus of mouth than to midsagittal plane. Apparently intact barbels in smallest examined specimens (46–50 mm SL) unelaborated and relatively short (1–1.5 times width of orbit). Intact mandibular barbel of larger specimens (69–206 mm SL) significantly longer than in smaller individuals and extending posteriorly to point located varying distances posterior of vertical through posterior margin of orbit. Distal portion of mandibular barbel in all but smallest examined specimens highly modified into series of short, digitiform, closely-clustered, fleshy processes.

Fleshy processes extend along approximately one-quarter of barbel in most individuals and along approximately one-third of barbel in some larger specimens. Fleshy processes arranged in variety of patterns ranging from flat, irregular sheet-like mass to three-dimensionally complex terminal tuft (Fig. 4). Mandibular barbel in larger preserved specimens usually anteriorly-directed rather than with posterior orientation typical of other catfishes. Approximately one-half to three-quarters of basal portion of anterior-directed mandibular barbel adpressed along ventral surface of anterior region of head, with remaining portion of unelaborated shaft of barbel along with distal, fleshy elaborations of barbel extending beyond margin of lower lip to region in front of mouth. Distally elaborated portion of barbel often extending to, or beyond, anterior margin of upper lip in partially open mouth (see also below under *Mandibular barbel and associated musculature*). Distal portion of barbel and associated fleshy processes absent in some specimens as consequence of damage.

Branchiostegal membrane broadly attached to isthmus. Gill opening very wide. Ventral margin of gill opening extending anteriorly to site one orbital diameter posterior of transverse plane running through posterior margin of orbit. Lateral surface of first gill arch with 12–16 [15] gill rakers.

Mouth terminal, but with upper jaw extending slightly beyond margin of lower jaw in closed mouth. Premaxillary teeth minute, distally pointed, posteriorly recurved, and arranged in broad band of approximately ten or more irregular series along most of dentigerous surface of bone. Premaxillary tooth band narrowing rapidly to one or two series of teeth in region proximate to symphysis. Dentary teeth of same form and of approximately same size as those on premaxilla. Dentary dentition arranged in band of up to ten series of teeth.

Length of dorsal-fin base approximately one-third length of first branched dorsal-fin ray of females and non-nuptial males, only about one-sixth of length of ray in nuptial males. Length of dorsal-fin spine approximately one-half of HL in juveniles, mature females, and non-nuptial adult males but distinctly lengthened and greater than HL in fully nuptial males. Dorsal-fin spine in juveniles and mature females straight and pungent, with anterior surface slightly rugose but lacking distinct serrae and with posterior margin smooth. Anterior surface of elongate dorsal-fin spine in fully nuptial males with single row of retrorse serrae extending along entire length of spine. Serrae aligned either along, or somewhat oblique to, midsagittal plane and progressively increasing in

size distally. Posterior margin of spine smooth. Dorsal fin with spinelet and spine followed by 6 [6] slender, branched rays. Adipose fin in form of fleshy flap with maximum length approximately equal to horizontal diameter of orbit.

Caudal fin obliquely truncate with dorsal-most branched ray longest. Principal caudal-fin rays typically i,7,9,i or i,7,8,i [i,7,8,i].

Anal-fin origin located distinctly posterior of middle of SL and slightly anterior of middle of TL. Anal-fin margin in juveniles and mature females slightly convex, with convexity more pronounced along anterior and posterior portions of fin. Anal-fin rays becoming progressively longer posteriorly other than for posterior-most rays that alternatively become progressively slightly shorter. Form of anal-fin margin in mature males comparable to that in mature females and juveniles other than for elongation of last unbranched and first branched rays supporting elongate, adhered urogenital tube of males (see Miranda-Ribeiro, 1968:pl. 6). Posterior-most anal-fin ray without membranous attachment to caudal peduncle. Anal-fin rays iv (rarely iii),35–43 [iv,41].

Distal margin of pelvic fin broadly convex with second branched ray longest. Tip of adpressed pelvic fin extending slightly past anal-fin origin. Pelvic-fin rays i,6 [i,6].

Pectoral-fin spine well developed. Anterior surface of spine rugose but lacking distinct serrae. Posterior surface of spine with single series of retrorse serrae extending along entire length. Anterior-most pectoral-fin rays longest. Distal margin of spread fin straight along anterior rays but convex along posterior rays. Branched pectoral-fin rays 9–11 [9].

Pigmentation pattern in alcohol.—Overall ground coloration of head and body tan in smaller specimens and brown to dark brown in specimens over 60 mm SL. Dorsal portion of head somewhat darker than both ventral and post-orbital regions. Horizontal band of dark pigmentation running from posterior rim of orbit to posterior margin of opercle. Band very obvious in more lightly pigmented specimens of less than 60 mm SL but nearly completely masked in individuals with overall very dark pigmentation. Pigmentation of portion of head posterior of orbit relatively darker in larger individuals. Band of horizontal pigmentation extending anteriorly from orbit onto snout slightly darker than stripe posterior of orbit. Degree of discernability of band on snout dependent on intensity of dark ground coloration in that region.

Maxillary and, particularly, mandibular barbels more lightly pigmented than remainder of head.

Distal elaborated region of mandibular barbel unpigmented in nearly all specimens. Some irregular lines of dark pigmentation within basal portion of tuft present in larger individuals with proportionally more extensive distal elaborations of mandibular barbel.

Body pigmentation dark overall, but with irregular regions of variably lighter coloration. Regions ventral and posteroventral of base of dorsal fin and along and proximate to remaining middorsal regions of body darker than adjoining areas. Remainder of body, including abdomen, brown, with pigmentation sometimes slightly less intense in specimens of all sizes. Lateral line overlain by distinct, narrow band of dark pigmentation, with that dark band margined dorsally by lighter, narrow, posteriorly-attenuating stripe in many specimens. Lateral surface of body in some specimens with irregular, apparently randomly positioned, dark marks situated both dorsal and ventral of lateral line.

Dorsal fin with spine slightly to distinctly darkly pigmented and rays uniformly dark. Basal portions of anal fin continuing darker pigmentation of adjoining region of body, with remainder of fin, particularly distal portions of rays, distinctly darker. Adipose fin dark. Caudal fin dark overall with some irregular, dark pigmentation on basal portions of all fin rays. Dark pigmentation on basal portion of caudal fin occasionally forming vertical bar and sequentially followed posteriorly in some specimens by slightly less intensely pigmented region and then by irregular, dark pigmentation varying from nearly uniform, through irregularly marmorated, to forming irregular, dark vertical bars. Distal-most portions of caudal-fin rays unpigmented, with light margin of fin more obvious along upper lobe of fin. Anal-fin coloration variable and correlated with intensity of dark pigmentation of adjoining ventral portions of body. Some specimens with ground coloration of anal fin tan with band of darker pigmentation along distal margin of fin. Width of dark, distal band ranges from thin stripe to covering nearly one-half of fin. Overall darker specimens with ground coloration of anal fin dark. Series of darker spots of variable shapes and positions distributed over anal fin, but with darker spots less obvious in overall darker individuals. Pectoral-fin spine variably dark. Pectoral-fin rays consistently very dark. Pelvic fin dark overall, but with distal margin unpigmented.

Pigmentation in life.—Overall coloration as in preserved specimens other than for slight reddish overcast on head, body, and fins. Reddish pigmentation more obvious over areas of head,

body, and fins with light ground coloration (see also Franke, 1995, fig. 3).

Sexual dimorphism.—*Tetranematichthys wallacei* has sexually dimorphic modifications of the maxillary barbel, the portions of the head and body proximate to the base of the dorsal fin, the form and proportional length of the dorsal-fin spine, and the form of the anterior-most anal-fin rays. There was no sexual dimorphism in the degree of development of the distal elaborations of the mandibular barbel. No transforming males of the species were examined during this study, but the two smallest available nuptial males of *T. wallacei* were 111 and 134 mm SL and the fully nuptial male illustrated by Wallace (2002, fig. 122) was approximately 124 mm SL.

Distribution.—Examined samples of *Tetranematichthys wallacei* originated at sites in the Rio Tocantins, various locations within the Amazon basin, and the southern and southwestern portions of the Río Orinoco basin (Fig. 3). *Tetranematichthys quadrifilis* has also been reported elsewhere within the Río Orinoco basin from the Río Caura, a southern tributary of the eastern portion of the Río Orinoco basin (Lasso et al., 2003:239; Rodríguez-Olarte et al., 2003:199), the Ríos Apure and Capanaparo in the western portions of the Río Orinoco basin (Lasso et al., 2004b:139), and a site in Guarico State of Venezuela north of the main channel of the Río Orinoco (Franke, 1995:245). Those reports and others citing *T. quadrifilis* from the Río Orinoco system (see synonymy) are considered herein to refer to *T. wallacei*, which is the only member of the genus known to occur in that river basin.

Biology.—The holotype (MZUSP 31096) originated in an acidic, slow-flowing, blackwater igarapé within the flooded rainforest (Goulding et al., 1988:121). Habitat information is lacking for most of the other examined specimens of *Tetranematichthys wallacei*; however, several of the paratype lots (USNM 269994, USNM 269995, USNM 27008) were captured in still rain forest backwaters or in shallow rain forest streams with sandy bottoms and barely perceptible water flow. All those sites were characterized by blackwaters and numerous submerged logs and branches. Individuals of *Tetranematichthys* collected in the lower Río Ucayali basin in northeastern Peru and the region of the Rio Japurá in Amazonas, Brazil, but not examined in this study, were similarly associated with submerged logs (F. Lima, pers. comm.). A local fisherman at the Rio Japurá reported that members of the genus were always

collected among submerged logs and branches (F. Lima, pers. comm.). These reports presumably refer to *T. wallacei*, which is the only member of the genus known from northeastern Peru and Rio Japurá region.

Mandibular barbel and associated musculature.—The mandibular barbel of *Tetranematichthys wallacei* demonstrates a number of striking unique modifications. Most obvious among these is the expansion and elaboration of the distal portion of that barbel in all but the smallest examined specimens into a series of fleshy, digitiform processes that together form an elaborate structure at the terminus of the barbel. The overall arrangement of these processes ranges from an overall flat, irregularly-margined, sheet-like structure to a three-dimensionally more elaborate tuft-like complex (Fig. 4). There was no indication of sexual dimorphism in the form or degree of development of these structures.

Histological examination reveals that this distal elaboration of the mandibular barbel of *T. wallacei* has a narrow central shaft that presumably consists of elastic-cell rich cartilage comparable to that present in many siluriforms (Benjamin, 1990; Fox, 1999). Surrounding this thin cartilaginous core are a series of digitiform processes formed of relatively loose series of cells without strong connective tissue fibers. This arrangement differs dramatically from the morphology of the mandibular barbels of other examined auchenipterids, which have a thin epithelium overlying the rigid central shaft. As a consequence of its cellular structure, the fleshy processes of the distal process of the mandibular barbel in *Tetranematichthys* are likely to be relatively floppy in life (J. Burns, pers. comm.). Although catfishes commonly have the epithelium of the barbels covered with taste buds along their entire length (Grover-Johnson and Farbman, 1976; Ovalle and Shinn, 1977; Michel and Caprio, 1991), neither the SEM scans nor the histological sections revealed any taste buds within the elaborated distal portion of the mandibular barbel in *Tetranematichthys wallacei* (pers. obs.; J. Burns, pers. comm.). Thus, it does not appear that the elaborate distal portions of the barbel serve a taste function. Those noted modifications of the distal portion of the mandibular barbel at both the gross anatomical and histological levels are absent in other members of the Auchenipteridae, and indeed across the Siluriformes. Although we were unable to histologically examine the distal elaborations of the mandibular barbel in *T. quadrifilis*, that species shares the same gross morphological specializations of that system that are present in

T. wallacei. This suite of modifications of the mandibular barbel is, thus, hypothesized to represent a series of synapomorphies for the species of *Tetranematichthys*.

Another unusual aspect of the mandibular barbel in the species of *Tetranematichthys* is its anterior orientation in many preserved specimens; an alignment most likely resulting from a muscular reflex in life and which is presumably reflective of its orientation in live specimens. This alignment contrasts with the typical posterior orientation of this barbel in other catfishes that retain mandibular barbels. Such unusual positioning of the barbel in the species of *Tetranematichthys* may be a function of the well-developed, discrete muscle mass extending anteromedially from its attachment at the base of the mandibular barbel towards the symphysis of the lower jaw. Given its position, this apparent protractor muscle is likely a component of the underlying protractor hyoidei (*sensu* Winterbottom, 1974; Adriaens and Verraes, 1997; the protractor tentaculi of Singh, 1967).

The species of *Ageneiosus*, the sister group to *Tetranematichthys* (Ferraris, 1988; de Pinna, 1998), lack mandibular barbels and are thereby uninformative as to the polarity of the possession of the muscle associated with the barbel in the species of the latter genus. Although retractor muscles attaching to the base of the mandibular barbels are present in *Trachelyopterus*, *Entomocorus*, and *Auchenipterus*, genera that lie proximate to the clade formed by *Ageneiosus* and *Tetranematichthys* within the Auchenipteridae (see de Pinna, 1998, fig. 15), those outgroup auchenipterids lack well-developed protractor muscles comparable to those characteristic of *Tetranematichthys*. The pronounced degree of development of the component of the protractor hyoidei at the base of the mandibular barbel and the associated anterior orientation of that barbel are, thus, considered derived and are hypothesized to be synapomorphies for the species of *Tetranematichthys*.

The portion of the protractor hyoidei attaching to the base of the mandibular barbel apparently functions to move the barbel far anteriorly such that the distal digitiform elaboration of the barbel lies anterior to the open mouth. Presumably this muscle similarly facilitates movements of the entire barbel which when transmitted along the shaft-like portion of the barbel would result in pronounced motions of the floppy, distal elaboration. Such motions of the elaborate distal portions of the mandibular barbel in the region anterior to the mouth in the species of *Tetranematichthys* may function as a fishing lure in a manner comparable to the

escae that are present in various ceratioids. Confirmation of this hypothesis in the case of *Tetranematichthys* would require the observations of live specimens of the genus in nature.

The use of barbels as a lure to assist in capturing prey has been observed in one other group of catfishes. Species of the Asian catfish family Chacidae have been observed to lure prey items by wiggling their small maxillary barbels (Ferraris, 1991:109). The barbels in the Chacidae are both non-homologous with the modified mandibular barbels of *Tetranematichthys* and, furthermore, lack the terminal elaborations of the mandibular barbel that are characteristic of the members of the latter genus.

Remarks.—During his collecting expedition in the Rio Negro and tributary Rio Uaupés basins (1850 to 1852), Wallace collected and sketched a specimen that was most likely *Tetranematichthys wallacei*. His pencil sketch of the specimen (Wallace, 2002:fig. 122) clearly illustrated the elongate dorsal-fin spine, the ossified, curved maxillary barbels, the elongation of the anterior rays of the anal fin, and the overall form of the head and body characteristic of nuptial males of *Tetranematichthys* (note: the orientation of the fish in the illustration is such that the mandibular barbels are not apparent). Given that *T. wallacei* is the only species of the genus known to occur in the Rio Negro and Rio Uaupés basins, we identify Wallace's specimen as that species.

The specimen that served as the basis of the drawing was lost, along with the remainder of Wallace's collection, as a consequence of a shipboard fire during his return voyage to England. Wallace eventually deposited his fish drawings in the British Museum (Natural History), and Regan (1905) commented on many of the species depicted in the Wallace sketches but not that of *T. wallacei*. It is likely that this species was one of the forms depicted by Wallace that Regan characterized "as yet undescribed" and explicitly excluded from his discussion. The annotation "*Ageneiosus* n.s." (= ? new species; Wallace, 2002) on the figure may have been an entry by Wallace. If that was the case, it utilized the concept of *Ageneiosus* in use at the time of the collection of the species (1850 to 1852) that encompassed species now assigned to both that genus and *Tetranematichthys*.

Tetranematichthys quadrifilis was reported to range across major portions of the Orinoco and Amazon River basins (see synonymy); however, the single examined sample of *T. quadrifilis* originated in the Rio Guaporé of the upper Rio Madeira system in the southwestern portions of the Amazon basin. The Rio Guaporé is similarly



Fig. 5. *Tetranematichthys quadrifilis*, MZUSP 37517, 141 mm SL, Brazil, Matto Grosso, Rio Guaporé basin.

the type-locality for the species. Specimens of *Tetranematichthys* examined during this study that originated in the Río Orinoco system and from locations across the Amazon basin, with the exception of the Rio Guaporé, all proved to be *T. wallacei*. We therefore consider all citations of *T. quadrifilis* from outside the Rio Guaporé system to represent misidentified specimens of the similar *T. wallacei* (see synonymy under that species). Given that *T. wallacei* occurs in areas that are centers for the collection and export of fishes for the aquarium trade (e.g., Manaus, Brazil; Iquitos, Peru) it is likely that many of the illustrated specimens identified as *T. quadrifilis* in popular articles dealing with aquarium fishes are instead misidentified samples of *T. wallacei*.

Miranda-Ribeiro (1968) provided a lateral view of a fully nuptial male that he identified as *Tetranematichthys quadrifilis* and supplemented that illustration with a dorsal view of the head. This specimen has the approximately parallel margins of the postorbital portion of the head that are characteristic of *T. wallacei*. Furthermore, that sample (MNRJ 3580) originated at Uipiranga, a location within the Rio Negro basin that falls within the range of *T. wallacei* but which is distant from the restricted known distribution of *T. quadrifilis* in the southwestern portions of the Amazon basin.

Etymology.—The species name, *wallacei*, is in honor of the English naturalist Alfred Russel Wallace who collected and first illustrated this species in his expedition to the Rio Negro and Rio Uaupés region during 1850 to 1852, albeit with a 15-decade hiatus until the drawing was recently published (Wallace, 2002, fig. 122).

***Tetranematichthys quadrifilis* (Kner, 1857)**

Figures 1B, 3, 5; Table 1

Ageneiosus quadrifilis Kner, 1857:442, pl. 9, fig. 29 [type locality: Rio Guaporé].—Eschmeyer, 1998:1414 [holotype depository].

Tetranematichthys quadrifilis, Bleeker, 1858:357 [shift of species to *Tetranematichthys*].—Bleeker, 1863:108 [as species of *Tetranematichthys*].—Günther, 1864:193 [based on Kner, 1857].—Eigenmann and Eigenmann, 1888:151 [name in listing of neotropical catfishes].—Eigenmann and Eigenmann, 1890:298 [description based on Kner, 1857].—Eigenmann and Eigenmann, 1891:108 [in listing of neotropical fishes].—Eigenmann, 1910:397 [in listing of neotropical catfishes].—Miranda-Ribeiro, 1911:399, fig. 144 [based on Kner, 1857].—Gosline, 1945:15 [in listing of neotropical catfishes].—Fowler, 1951:471, fig. 498 [literature summary; figure based on Kner, 1857, fig. 29].—Britski, 1972:103 [assignment of *Tetranematichthys* to the Ageneiosidae].—Mees, 1974:12 [distinguishing features relative to other auchenipterids].—Burgess, 1989:286 [as member of Ageneiosidae].—Ferraris, 2003:477 [in part; cited occurrence in Rio Guaporé].

Setranematichthys quadrifilis, Miranda-Ribeiro, 1911:478 [genus name misspelled; listing of prior literature citations].

Material examined.—Brazil, Matto Grosso, Rio Guaporé basin, Município Vila Bela de la Santíssima Trindade, Vila Bela de la Santíssima Trindade, 15°30'S, 59°20'W, MZUSP 37517, 5 (110–141; 2 specimens, 110–114 mm SL, transforming males; 1 specimen cleared-and-stained for bone and cartilage).

Diagnosis.—*Tetranematichthys quadrifilis* is distinguished from *T. wallacei* in the alignment of the lateral margins of head in the region from the anterior margin of the orbit to the posterior limit of the opercle (diverging laterally vs. running approximately in parallel from ventral view respectively; Fig. 1), in the body width at the pectoral-fin insertion as a proportion of the head width at the posterior margin of the orbit (1.17–1.25 vs. 0.99–1.10, respectively), in the distance from the tip of the snout to the anal-fin origin

(0.33–0.36 of SL vs. 0.29–0.32 of SL, respectively), and in the location of the anterior termination of the gill opening (in transverse plane running through the center of the orbit vs. positioned one orbital diameter posterior of the transverse plane running through the posterior margin of the orbit, respectively).

Description.—See Table 1 and below for morphometrics of *Tetranematichthys quadrifilis*. Overall morphology of head, body, fins, and barbels including highly modified mandibular barbel of *T. quadrifilis* comparable to conditions of those systems in *T. wallacei* (see previous account) other for features noted in the following sections.

Lateral margins of head in region from anterior margin of orbit to posterior limit of opercle diverging laterally from ventral view (Fig. 1B); divergence of profile in this region of head reflected in proportion of body width at pectoral-fin insertion vs. head width at posterior margin of orbit (1.17–1.25). Head depth at vertical through middle of orbit 0.49–0.59 of head width at posterior margin of orbit. Gill opening extending anteriorly to point along transverse plane running through orbit. Precaudal vertebrae 15–16; caudal vertebrae 28–29; total vertebrae 44–45 (5 specimens). Lateral surface of first gill arch with 12–14 gill rakers.

Dorsal-fin with spinelet, spine, and six slender, branched rays. Principal caudal-fin rays i,7,8,i. Anal-fin rays iii, or iv,35–36. Pelvic-fin rays i,6. Pectoral fin with well-developed spine and 9–10 branched rays.

No fully nuptial males of species examined and degree of externally apparent sexual dimorphism in dorsal-fin spine, anterior rays of anal fin, and profile of body proximate to base of dorsal fin unknown.

Pigmentation in alcohol.—As for *Tetranematichthys wallacei* except for consistent presence in all specimens of distinct, vertical, dark bar extending across entire extent of caudal fin slightly posterior of bases of fin rays.

Sexual dimorphism.—The two examined smallest specimens (110–114 mm SL) of *Tetranematichthys quadrifilis* are males in the process of transformation as evidenced by the partial elongation of the dorsal-fin spine, the elongation of the maxillary barbel distinctly beyond the posterior margin of the eye, and the distinct thickening of the basal portion of that barbel. Based on these features, we assume that males of *T. quadrifilis* transform into the nuptial condition at the approximately the same body sizes as do those of *T. wallacei* in which the smallest examined

nuptial male was 111 mm SL. Other genera of the Auchenipteridae with such sexually dimorphic features typically have these modifications common to all members of the genus when present in one species. Thus, it is likely that *T. quadrifilis* demonstrates the same degree of sexual dimorphism of the dorsal-fin spine, anterior rays of the anal fin, and profile of the body at the base of the dorsal fin as occurs in *T. wallacei*.

Distribution.—*Tetranematichthys quadrifilis* is only known from the holotype (NMW 43343; Eschmeyer, 1998:1414) and the five specimens examined in this study (MZUSP 37517). Both samples originated in the Rio Guaporé of the upper Rio Madeira basin in the southwestern portions of the Amazon basin (Fig. 3).

Biology.—The single examined lot of *Tetranematichthys quadrifilis* lacks associated habitat data, but those specimens, along with the holotype, originated in the Rio Guaporé basin in the Rio Madeira basin. Although the Rio Madeira is one of the two muddiest of the large tributaries of the Amazon River, the Rio Guaporé itself is a clear water system draining a portion of the Brazilian Shield (Goulding et al., 2003). The chemistry of such a clear water river is more comparable to that of the black water streams inhabited by *T. wallacei* than it is to the muddy white waters of the main stream Rio Madeira.

Remarks.—*Tetranematichthys quadrifilis* was reported from scattered localities in the Rio Amazonas and Río Orinoco basins subsequent to its description by Kner (1857) based on a single, relatively small specimen that originated in the Rio Guaporé. The results of our analysis indicate that *T. quadrifilis* is, rather, only known to inhabit the Rio Guaporé in the upper Rio Madeira basin. Reports of that species from other portions of South America are consequently considered to refer to *T. wallacei* (see synonymies of both species and Remarks under *T. wallacei*).

KEY TO THE SPECIES OF *Tetranematichthys*

- 1a. Lateral margins of head in region from anterior margin of orbit to posterior limit of opercle approximately parallel from ventral view (Fig. 1A) with parallel alignment reflected in proportion of body width at pectoral-fin insertion vs. head width at posterior margin of orbit (0.99–1.10); distance from tip of snout to dorsal-fin origin 0.29–0.32 of SL; gill opening extending anteriorly to point

- one orbital diameter posterior of transverse plane running through posterior margin of orbit (Rio Tocantins, Rio Orinoco, and various portions of Amazon basin with exception of Rio Guaporé system)
- *Tetranematichtys wallacei*, new species
- 1b. Lateral margins of head in region from anterior margin of orbit to posterior limit of opercle diverging laterally from ventral view (Fig. 1B) with divergence reflected in proportion of body width at pectoral-fin insertion vs. head width at posterior margin of orbit (1.17–1.25); distance from tip of snout to dorsal-fin origin 0.33–0.36 of SL; gill opening extending anteriorly to point along transverse plane running through orbit (Rio Guaporé basin) *Tetranematichtys quadrifilis*

ACKNOWLEDGMENTS

Research associated with this study was supported by the Neotropical Lowland Research Program of the National Museum of Natural History, Smithsonian Institution, the All Catfish Species Inventory (NSF DEB-0315963), and the Herbert R. and Evelyn Axelrod Chair in Systematic Ichthyology in the Division of Fishes of the National Museum of Natural History, Smithsonian Institution. We thank M. Stiassny, B. Brown, J. Lundberg, M. Sabaj, J. Armbruster, D. Taphorn, M. de Pinna, J. de Figueiredo, O. Oyakawa, F. Lima, L. Page, and R. Robins who arranged for the loan and exchange of specimens, provided diverse forms of information, hospitality during visits, and myriad other types of assistance that facilitated this study. The photographs of fishes in this paper were prepared by S. Raredon and C. Moreira. The photo of the distal elaboration of the mandibular barbel was provided by S. Whitaker (SEM-Lab, USNM). J. Burns graciously prepared and interpreted histological sections of the fleshy, distal elaboration of the mandibular barbel of *Tetranematichtys wallacei* and other auchenipterids. This paper benefitted from the comments and suggestions of T. Munroe and B. Sidlauskas.

LITERATURE CITED

- ADRIAENS, D., AND W. VERRAES. 1997. Ontogeny of the hyoid musculature in the African catfish, *Clarias gariepinus* (Burchell, 1822) (Siluroidei: Clariidae). Zool. J. Linn. Soc. 121:105–128.
- BENJAMIN, M. 1990. The cranial cartilage of teleosts and their classification. J. Anat. 169:153–172.
- BLEEKER, P. 1858. De visschen van den Indischen Archipel. Beschreven en toegelicht. Siluri. Acta. Soc. Sci. Indo-Neerl. 4:i–xii + 1–370.
- . 1863. Systema Silurorum revisum. Nederl. Tijdsch. Dierk. 1:77–122.
- BÖHLKE, J. E. 1980. *Gelanoglanis stroudi*: a new catfish from the Rio Meta system in Colombia (Siluriformes, Doradidae, Auchenipterinae). Proc. Acad. Nat. Sci. Phila. 132:150–155.
- BRITSKI, H. A. 1972. Sistemática e evolução dos Auchenipteridae e Ageneiosidae (Teleostei, Siluriformes). Unpubl. Ph.D. diss., Universidade de São Paulo, São Paulo, Brazil.
- BURGESS, W. E. 1989. An Atlas of Freshwater and Marine Catfishes. A Preliminary Survey of the Siluriformes. T.F.H. Publications, Neptune City, New Jersey.
- EIGENMANN, C. H. 1910. Catalogue of the fresh-water fishes of tropical and south temperate America, p. 375–511. In: Reports of the Princeton University expeditions to Patagonia 1896–1899, Zoology, vol. 3.
- , AND R. S. EIGENMANN. 1888. Preliminary notes on South American Nematognathi, I. Proc. Calif. Acad. Sci. ser. 2, 1:119–172.
- , AND ———. 1890. A revision of the South American Nematognathi or cat-fishes. Occ. Pap. Calif. Acad. Sci. no. 1:1–508 + errata and map.
- , AND ———. 1891. A catalogue of the fresh-water fishes of South America. Proc. U.S. Natl. Mus. 14:1–81.
- ESCHMEYER, W. N. (ed.). 1998. Catalog of Fishes. Calif. Acad. Sci., San Francisco.
- FERRARIS, C. J., JR. 1988. The Auchenipteridae: putative monophyly and systematics, with a classification of the neotropical doradoid catfishes (Ostariophysi, Siluriformes). Unpubl. Ph.D. diss., City University of New York, New York.
- . 1991. Catfish in the Aquarium. An Introduction to Catfish Keeping and the Diversity of Catfish Forms and Behavior. Tetra Press Publications, Morris Plains, New Jersey.
- . 2003. Family Auchenipteridae (driftwood catfishes), p.470–486. In: Check List of the Freshwater Fishes of South and Central America. R. E. Reis, S. O. Kullander, and C. J. Ferraris, Jr. (eds.). Edipucrs, Porto Alegre, Brazil.
- , AND R. P. VARI. 1999. The South American catfish genus *Auchenipterus* Valenciennes, 1840 (Ostariophysi: Siluriformes: Auchenipteridae): monophyly and relationships, with a revisionary study. Zool. J. Linn. Soc. 126:387–450.
- FOX, H. 1999. Barbels and barbel-like tentacular structures in sub-mammalian vertebrates: a review. Hydrobiologia 403:153–193.
- FOWLER, H. W. 1951. Os peixes de água doce do Brasil. Arq. Zool. Estado São Paulo 6:405–624.
- FRANKE, H.-J. 1995. Erster nachweis für Venezuela: *Tetranematichtys quadrifilis*. DATZ. Aquarien Terrarien 48:245–247.
- GOSLINE, W. A. 1945. Catálogo dos nematognatos de água-doce da América do Sul e Central. Bol. Mus. Nac. Rio de Janeiro, nova série, Zool. no. 33:1–138.
- GOULDING, M., R. BARTHEM, AND E. FERREIRA. 2003. The Smithsonian Atlas of the Amazon. Smithsonian Books, Washington, D.C.

- , M. L. CARVALHO, AND E. G. FERREIRA. 1988. Rio Negro, Rich Life in Poor Water. Amazonian diversity and foodchain ecology as seen through fish communities. SPB Academic Publishing, The Hague.
- GROVER-JOHNSON, N., AND A. I. FARBMAN. 1976. Fine structure of taste buds in the barbel of the catfish, *Ictalurus punctatus*. *Cell Tissue Res.* 169:395–403.
- GÜNTHER, A. 1864. Catalogue of the fishes in the British Museum, vol. 5. Catalogue of the Physostomi, containing the families Siluridae, Characiniidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiidae in the collection of the British Museum. Trustees, London.
- KNER, R. 1857. Ichthyologische Beiträge. II. Abtheilung. Sitzungsber. Akad. Wiss. Wien 26:373–448.
- LIASSO, C. A., D. LEW, D. TAPHORN, C. DONASCIMENTO, O. LIASSO-ALCALÁ, F. PROVEZANO, AND A. MACHADO-ALLISON. 2004a. Biodiversidad ictológica continental de Venezuela. Parte I. Lista de especies y distribución por cuencas. *Mem. Fund. La Salle Cien. Nat.* 159–160 (for 2003):105–195.
- , A. MACHADO-ALLISON, D. TAPHORN, D. RODRÍGUEZ-OLARTE, C. R. VISPO, B. CHERNOFF, F. PROVENZANO, P. LIASSO-ALCALÁ, A. CERVÓ, K. NAKAMURA, N. GONZÁLEZ, J. MERI, C. SILVERA, A. BONILLA, H. LÓPEZ-ROJAS, AND D. MACHADO-ARANDA. 2003. The fishes of the Caura River basin, Orinoco drainage, Venezuela: annotated checklist. *Scientia Guianae* 12:223–245.
- , J. I. MOJICA, J. S. USMA, J. A. MALDONADO-O, C. DONASCIMENTO, D. C. TAPHORN, F. PROVENZANO, O. M. LIASSO-ALCALÁ, G. GALVIS, L. VÁSQUEZ, M. LUGO, A. MACHADO-ALLISON, R. ROYERO, C. SUÁREZ, AND A. ORTEGA-LARA. 2004b. Peces de la cuenca del río Orinoco. Parte I: lista de especies y distribución subcuencas. *Biota Colombiana* 5:95–158.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- MEES, G. F. 1974. The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi). *Zool. Verhand. (Leiden)* no. 132:1–256, pls. 1–15.
- MICHEL, W., AND J. CAPRIO. 1991. Responses of single facial taste fibers in the sea catfish, *Arius felis*, to amino acids. *J. Neurophysiol.* 66:247–260.
- MIRANDA-RIBEIRO, A. 1911. Fauna brasiliense. Peixes. Tomo IV (A) [Eleutherobranchios Aspirophoros]. *Arq. Mus. Nac. Rio de Janeiro* 16:1–504, pls. 22–54.
- MIRANDA-RIBEIRO, P. 1962. Catálogo dos peixes do Museu Nacional. XI. Ageneiosidae A. de Mir. Rib., 1911, Cetopsidae A. de Mir. Rib., 1911, Auchenipteridae A. de Mir. Rib., 1911, Lophotidae Günther, 1861, Hypophthalmidae Cope, 1871, Rachicentridae Gill, 1895, Trachycoristidae A. de Mir. Rib., 1911, Uranoscopidae Gill, 1861. *Public. Avul. Mus. Nac. (Rio de Janeiro)* no. 45:1–12.
- . 1968. Apontamentos ictológicos III. *Bol. Mus. Nac. Rio de Janeiro, nova série, Zool.* no. 263:1–14.
- OVALLE, W. K., AND S. L. SHINN. 1977. Surface morphology of taste buds in catfish barbels. *Cell Tissue Res.* 178:375–384.
- DE PINNA, M. C. C. 1998. Phylogenetic relationships of neotropical Siluriformes (Teleostei: Ostariophysi); historical overview and synthesis of hypotheses, p. 279–330. *In: Phylogeny and Classification of Neotropical Fishes.* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena, and C. A. S. Lucena (eds.). Edipures, Porto Alegre, Brazil.
- REGAN, C. T. 1905. On drawings of fishes of the Rio Negro. *Proc. Zool. Soc. London* 1905:189–190.
- RODRÍGUEZ-OLARTE, D., D. C. TAPHORN, B. C. LIASSO, AND C. R. VISPO. 2003. Fishes of the lower Caura River, Orinoco basin, Venezuela. *Scientia Guianae* 12:181–122.
- ROYERO, R., A. MACHADO-ALLISON, C. CHERNOFF, AND D. MACHADO-ARANDA. 1992. Peces del Río Atabapo, Territorio Federal Amazonas, Venezuela. *Acta Biol. Venez.* 14:41–55.
- SINGH, B. R. 1967. Movements of barbels in siluroid fishes. *Zool. Anz.* 178:402–412.
- SOARES-PORTO, L. M., S. J. WALSH, L. G. NICO, AND J. MAIA NETO. 1999. A new species of *Gelanoglanis* from the Orinoco and Amazon river basins, with comments on miniaturization within the genus (Siluriformes: Auchenipteridae: Centromochlinae). *Ichthyol. Explor. Freshwaters* 10:63–72.
- TAPHORN, D., R. ROYERO, A. MACHADO-ALLISON, AND F. MAGO-LECCIA. 1997. Lista actualizada de los peces de agua dulce de Venezuela, p. 55–100. *In: Vertebrados Actuales y Fósiles de Venezuela. Serie Catálogo Zoológico de Venezuela.* E. La Marca (ed.). Museo de Ciencia y Tecnología de Merida, Venezuela.
- WALLACE, A. R. 2002. Peixes do Rio Negro [Fishes of the Rio Negro]. Organization, introductory text, and translation by Mónica de Toledo-Piza Ragazzo. Editoria de Universidade de São Paulo, São Paulo, Brazil.
- WALSH, S. J. 1990. A systematic revision of the Neotropical catfish family Ageneiosidae (Teleostei: Ostariophysi: Siluriformes). Unpubl. Ph.D. diss., University of Florida, Gainesville, Florida.
- WINTERBOTTOM, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Phila.* 125:225–317.
- (RPV) DIVISION OF FISHES, SMITHSONIAN INSTITUTION, P.O. BOX 37012, NATIONAL MUSEUM OF NATURAL HISTORY, WG-14, MRC-159, WASHINGTON, D.C. 20013-7012; AND (CJF) RESEARCH ASSOCIATE, DIVISION OF FISHES, SMITHSONIAN INSTITUTION, P.O. BOX 37012, NATIONAL MUSEUM OF NATURAL HISTORY, WG-14, MRC-159, WASHINGTON, D.C. 20013-7012. E-mail: (RPV) varir@si.edu; and (CJF) carlferraris@comcast.net. Send reprint requests to RPV. Submitted: 22 March 2005. Accepted: 22 Nov. 2005. Section editor: J. W. Armbruster.