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Bryconops colaroja and *B. colanegra*, two new species from the Cuyuní and Caroní drainages of South America (Teleostei: Characiformes)

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Two new, colorful, blackwater species of the genus *Bryconops*, subgenus *Creatochanes* are described. *Bryconops colanegra* is an Orinocoan endemic from Venezuela inhabiting tributaries of the Río Caroní. *Bryconops colaroja* may be endemic to the upper Essequibo River basin, in small tributaries of the Río Cuyuní in Venezuela and Guyana. *Bryconops colaroja* and *B. colanegra* belong to the subgenus *Creatochanes* based upon apomorphies of their jaws and infraorbital bones. Within the subgenus, *B. colaroja*, *B. colanegra*, and *B. melanurus* are the only species to lack both well-delveloped caudal fin ocellus and a humeral mark. These three species are distinguishable based upon coloration, meristic features and the structure of their gill rakers.

Dos nuevas y altamente coloridas especies del género *Bryconops*, subgénero *Creatochanes* son descritas. *Bryconops colanegra* es una especie endémica del Orinoco venezolano habitante de tributarios de Río Caroní. *Bryconops colaroja* aparentemente es endémica de la parte superior del Río Essequibo, habitante de pequeños tributarios del Río Cuyuní en Venezuela y Guyana. Comparaciones con otros miembros del subgénero *Creatochanes* fueron realizadas y los patrones de cambios de forma son discutidos.

Introduction

In this paper we make known two new characid fishes of the genus *Bryconops*. The genus contains 12 valid species, including the two described herein, and is broadly distributed east of the Andes in the Orinoco, Amazon, and Upper Paraguay-Parana watersheds, as well as in many independent Atlantic Coastal drainages of the Guyanas and Brazil. No species of *Bryconops* has yet been identified from rivers north or west of the Andes.

The two new species have been collected in black-water rivers from the Guyana Shield of Venezuela. *Bryconops colanegra* is found in small to medium-sized tributaries of the Río Caroní, part of the Río Orinoco drainage basin (Fig. 1). *Bryconops colaroja* is a common inhabitant of small quebradas and streams that drain into the Río Cuyuní, upper Essequibo River basin, near the

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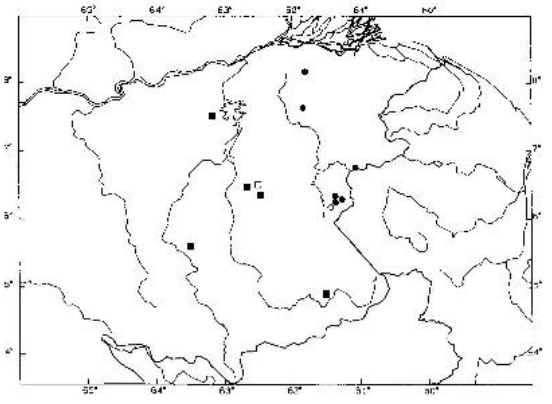

Venezuelan-Guyanan border (Fig. 1). Though the phylogenetic relationships of the two new species are not fully resolved, they share the synapomorphies of the monophyletic subgenus *Creatochanes*. Within that subgenus, they seem to belong to a clade that also contains *B. melanurus*, which inhabits the Guyanas from the Essequibo

Fig. 1. Distribution map of localities of *Bryconops colaroja* (circles) in the Río Cuyuní basin and *B. colanegra* (squares) in the Río Caroní basin. Each symbol represents at least one collection; open symbols indicate type localities.

Table 1. Descriptive measurements of *Bryconops colaroja*, n=89, and *B. colanegra*, n=114. Sample sizes for fin lengths and least depth caudal peduncle are 49 and 94, respectively. Standard length given in mm, all other values expressed in thousandths of standard length.

	B. colaroja			*B. colanegra*		
	holotype	range	mean	holotype	range	mean
Standard length	67.6	23.7-77.9	42.2	71.0	29.1-87.8	48.7
Snout – occiput	203	203-277	242	231	216-268	239
Snout – dorsal fin	468	448-505	481	479	445-505	486
Snout – anal fin	661	607-691	654	652	624-678	653
Snout – pectoral fin	239	239-306	268	273	247-291	265
Snout – pelvic fin	502	476-535	509	503	483-528	504
Head length	219	207-281	252	264	232-283	261
Postorbital head length	84	78-111	92	103	79-110	96
Orbit diameter	96	87-140	118	102	90-140	115
Snout length	41	29- 77	47	62	40- 77	53
Upper jaw length	129	108-157	141	161	124-167	149
Body depth	281	210-313	261	247	212-289	251
Interdorsal length	275	221-279	255	252	217-279	254
Caudal peduncle length	133	98-150	125	126	107-142	125
Caudal peduncle depth	84	65-270	89	75	66- 96	76
Dorsal-fin base	131	101-150	131	123	108-153	127
Anal-fin base	252	244-297	262	261	232-289	257
Dorsal-fin length	67	67-239	210	218	184-260	207
Anal-fin length	126	111-157	136	127	92-160	137
Pectoral-fin length	188	155-225	198	213	162-218	193
Pelvic-fin length	149	106-170	149	158	118-174	141
Additional truss elements						
Max – ant. orbit	94	68-122	103	111	80-123	108
Max – post. orbit	87	85-117	101	99	80-120	97
Max – pelvic fin	392	349-429	388	362	347-401	370
Pectoral – pelvic	272	219-289	251	241	227-269	248
Dorsal orig. – pectoral	342	283-368	330	324	295-352	328
Dorsal orig. – anal orig.	327	236-353	299	292	244-330	291
Dorsal term – pelvic fin	283	240-309	271	254	227-302	260
Dorsal term – anal origin	254	198-280	235	226	186-263	224
Dorsal term – anal termination	338	277-345	321	319	285-341	315
Adipose – anal orig.	290	270-313	292	279	257-307	283
Adipose – anal term.	116	98-135	118	107	96-126	109
Adipose – hypural base	156	142-180	161	168	142-177	161

River south and east to the Oyapock River (Machado et al., 1993; Chernoff et al., 1994). If the hypothesis of these relationships hold, then these three species may be very informative about the vicariance biogeographies of their river basins. The Caroní and the Cuyuní drainages were once thought to be confluent (Lasso et al., 1990: figs. 5-7); and *B. colaroja* and *B. melanurus* of the Essequibo drainage are seemingly restricted to the northeastern and southwestern portions of the drainage basin, respectively.

The purpose of this paper is to describe the two new species of *Bryconops*, compare them with other members of the subgenus *Creatochanes*, to discuss certain morphometric aspects of form change in the new species and to present a key for the currently recognized species of the genus.

Methods

Thirty-three morphometric and 22 meristic traits were enumerated according to definitions in Fink & Weitzman (1974), Chernoff & Machado (1990), Chernoff et al. (1991), and Machado et al. (1996) for almost all specimens examined. Samples of 40 individuals per species were sexed to determine if there were merisitic, morphometric or color differences associated with sex. No significant differences were found (P>.14).

The measurements (Table 1) comprise both traditional and truss measurements. Twenty-eight measures were calculated as interlandmark distances among the following fourteen landmarks: tip of snout, posterior tip of supraoccipital bone, origin of dorsal fin, posterior base of dorsal fin, anterior margin of adipose fin, posterocentral margin of hypural plate, posterior margin of anal fin, origin of anal fin, insertion of pelvic fin, insertion of pectoral fin, posterior margin of opercle, anterocentral and posterocentral margins of orbit, and distal tip of maxilla (Machado et al. 1996: fig. 2). The coordinates for these landmarks were obtained by optical digitizing. The landmark positions were identified by inserting 0000 insect pins into the specimens. The equipment and method for optical digitization was described in Chernoff et al. (1991), with an accuracy of 0.05 mm. Least depth of the caudal peduncle and the lengths of the dorsal, anal pectoral and pelvic fins were measured with needle-point dial calipers to the nearest 0.1 mm.

Differences in shape were estimated both from scatter plots of the logs of mensural variables against the log of standard length and from principal components analysis (PCA). Principal components (PCs) were calculated from the covariance matrix of 27 log-transformed variables, not including fin lengths (Table 2). In the among species analysis, the PC coefficients were scaled

Table 2. Principal components analysis of covariance matrix of log-transformed morphometric variables of *Bryconops colanegra* (*Bcn*; n=114) and *B. colaroja* (*Bcr*; n=89). Among species analysis: coefficients are scaled as a unit vector; asterisks indicate variables with high coefficients. Within species analyses: the coefficients are scaled to a mean square of 1 so that values > 1.03 are positively allometric, values 0.97-1.03 are isometric, values < 0.97 are negatively allometric; * and ** indicate significant differences between species allometries at the P<.05 and P<.01 levels, respectively. (Abbreviations: spec., species; orig., origin; term., termination)

	among spec.		within spec.	
	PC1	PC2	PC1 *Bcr*	PC1 *Bcn*
% variance	97.4	1.2	98.5	95.4
Eigenvalue	2.34	0.40	3.64	1.04
Variables				
Standard length	.189	.041	.977	.966
Snout – occiput	.158	.151	.795	.821 *
Snout – dorsal fin	.188	.096	.956	.972**
Snout – anal fin	.194	.022	1.00	.987
Snout – pectoral fin	.175	.104	.894	.904
Snout – pelvic fin	.185	.027	.961	.951
Head length	.173	.318**	.852	.894**
Postorbital head length	.178	.346**	.889	.883
Orbit diameter	.156	.184	.774	.868**
Upper jaw length	.190	.409**	.941	.951**
Body depth	.219	-.224	1.17	1.16
Interdorsal length	.195	-.042	1.02	.982
Caudal peduncle length	.196	.097	1.01	1.02
Dorsal-fin base	.201	-.112	1.09	.966
Anal-fin base	.184	-.058	.961	.946
Maxilla ant. orbit	.195	.376**	.982	.998 *
Maxilla – post. orbit	.175	-.039	.873	1.03**
Maxilla – pelvic fin	.181	-.138	.956	.946
Pectoral – pelvic	.196	-.064	1.03	.987
Dorsal orig. – pectoral	.205	-.056	1.07	1.07
Dorsal orig. – anal orig.	.223	-.200	1.19	1.15
Dorsal term. – pelvic orig.	.212	-.205	1.13	1.12
Dorsal term. – anal orig.	.222	-.274**	1.19	1.19
Dorsal term. – anal term.	.196	-.102	1.03	1.01
Adipose – anal orig.	.198	-.141	1.05	1.01
Adipose – anal term.	.204	-.305**	1.10	1.02
Adipose – hypural base	.188	.068	.951	1.01**

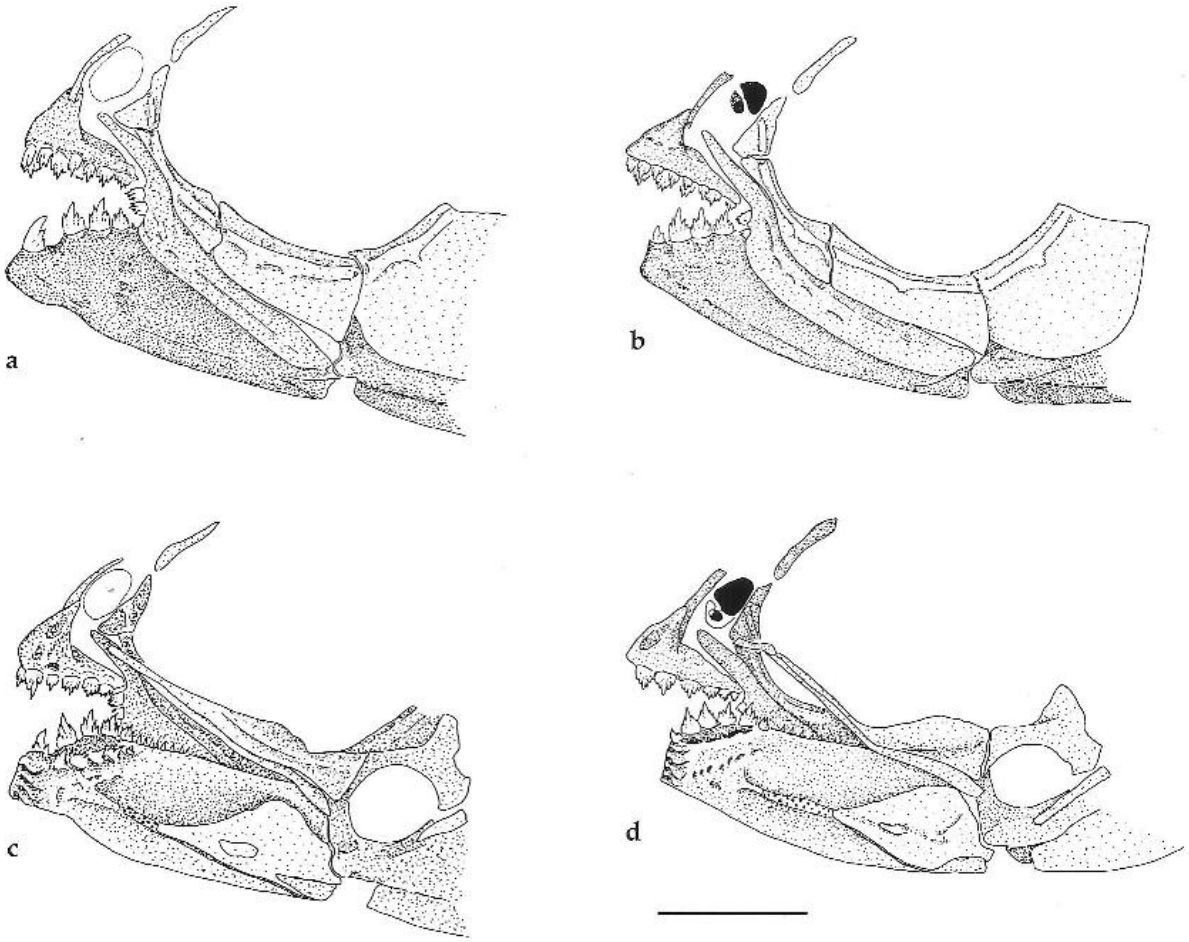

Fig. 2. Lateral and medial views, respectively, of jaws and infraorbital series of: **a, c,** *Bryconops colaroja*, paratype, FMNH 106509; and **b, d,** *B. colanegra*, paratype, FMNH 106511. Scale bar 10 mm.

to a unit vector – sum of squared coefficients equals 1.0. Because the axes of size and shape discrimination were largely parallel to the axes of PC1 and PC2, respectively, the shear method (Bookstein et al., 1985) was not required to clarify the interpretation of shape-differences. Principal component scores were calculated for each specimen and the resulting scatter plots were examined for separation according to species, population or sex. This method provides a weak test of the null hypothesis that only a single statistical population is present in the data. Non-random assortment of phenotypes on these or other grouping variables suggests that the null hypothesis should be rejected.

In order to understand the contribution of allometric growth to shape differences, PC1 was calculated within each species separately as a robust estimate of a general size factor (Bookstein et al., 1985). The coefficients on this size factor bear the allometric relationships of the measured variables, i.e., the relative scalings of the variables with respect to size change. The coefficients were scaled to a mean-square vector of 1.0. Variables with coefficients > 1.03 are positively allometric, those with values 0.97-1.03 are isometric and those with coefficients <0.97 are negatively allometric. Because these coefficients are proportional to the reduced major axis regression coefficients of the log variables on the log of size (scores on within-group PC1), the statistical difference between the coefficients of *B. colanegra* and *B. colaroja* were tested using Analysis of Covariance (ANCOVA). The null hypotheses were that the coefficients (slopes) for each species were homogeneous. The repetition of the ANCOVA for each allometric coefficient was equivalent to a test of repeated measures. Thus,

the sequential Bonferoni correction was applied to the probability level of obtaining the test statistic according to the method of Rice (1989).

Several variables that had large coefficients on PC2 in the among species analysis, which presumably bore information about shape differences between the new species, were discovered to have interesting non-log-linear distributions with respect to each other. The species differences were thereby obscured in standard scatter plots. To correct the distributions for size dependent nonlinearities, the values of the log-transformed variables were treated as rectangular coordinates (x,y) and then converted to polar coordinates (r, θ) according to the formulae:

$$x = r \cos \theta \text{ and } y = r \sin \theta$$

where r is the distance (hypotenuse) from the origin to the rectangular coordinates and θ is the angle expressed in radians between the x-axis and the hypotenuse. For example, if an individual had a body depth of 13.6 mm and a SL of 54.6 mm with natural logs, 2.61 and 4.00, respectively, the rectangular coordinates are (2.61, 4.00) and its polar coordinates are (4.78, .993). The polar coordinates are then plotted on a circular graph where the isopleths can be rescaled to original log values.

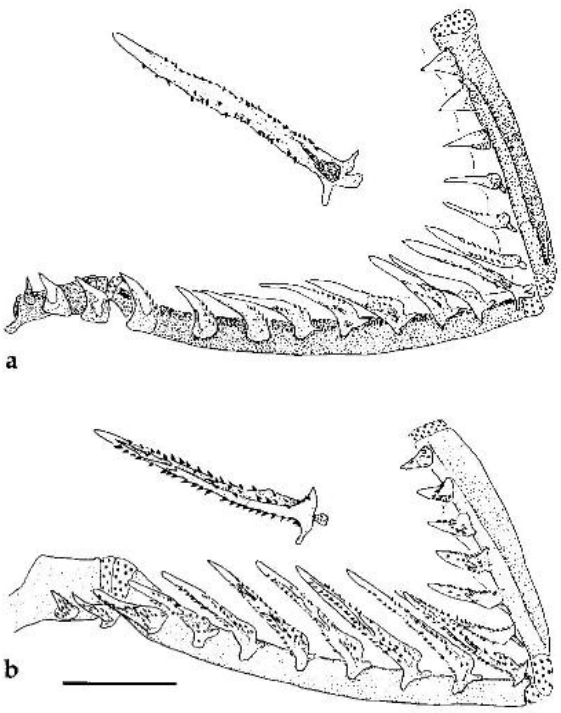

Fig. 3. Lateral view of first branchial arch of: **a,** *Bryconops colaroja*, paratype, FMNH 106509; and **b,** *B. colanegra*, paratype, FMNH 106511. Inset are expanded drawings of gill rakers at junction of cerato-and epibranchial elements. Scale bar for entire arch is 10 mm. Inset raker length is 26.3 mm for *B. colaroja* (a) and 25.0 mm for *B. colanegra* (b).

Bryconops Kner

Type species. *Bryconops alburnoides* Kner, 1858: 80.

Diagnosis. Distinguished from other characidae and related genera by three synapomorphic characters: (i) ventral edge of maxilla curves sharply posteriorly, almost 90°, extending to or beyond the quadrate socket of the articular; (ii) antorbital with well developed infraorbital sensory canal; and (iii) supraorbital sensory canal extending onto nuchal scales.

Comparisons

The genus *Bryconops* contains two monophyletic groups that we regard as subgenera: (i) the subgenus *Bryconops* sensu stricto (see key for included species); and (ii) the subgenus *Creatochanes*. *Bryconops colaroja* and *B. colanegra* belong to the subgenus *Creatochanes* based upon the extreme posterior extension of the maxilla to the junction of the second and third infraorbital bones, as well as the vertical junction of the second and third infraorbital bones (Fig. 2; Chernoff et al., 1994); both of these are derived conditions. Our research further indicates that within *Creatochanes*, *B. colaroja* and *B. colanegra* may belong in a clade with *B. melanurus* based upon apparently derived conditions of the armature of the gill rakers. In these three taxa, the gill raker at the junction of the ceratobranchial and the epibranchial of the first arch is ossified almost to its tip and the denticles extend well beyond the midpoint of the gill raker (Fig. 3). In the relatively plesiomorphic condition, the gill raker at the angle is less well ossified and the denticles do not extend beyond the midpoint of the gill raker.

Bryconops colaroja and *B. colanegra* can be distinguished from all other members of the genus based upon coloration and pigmentation. Characteristics of the pigmentation can easily be dis-

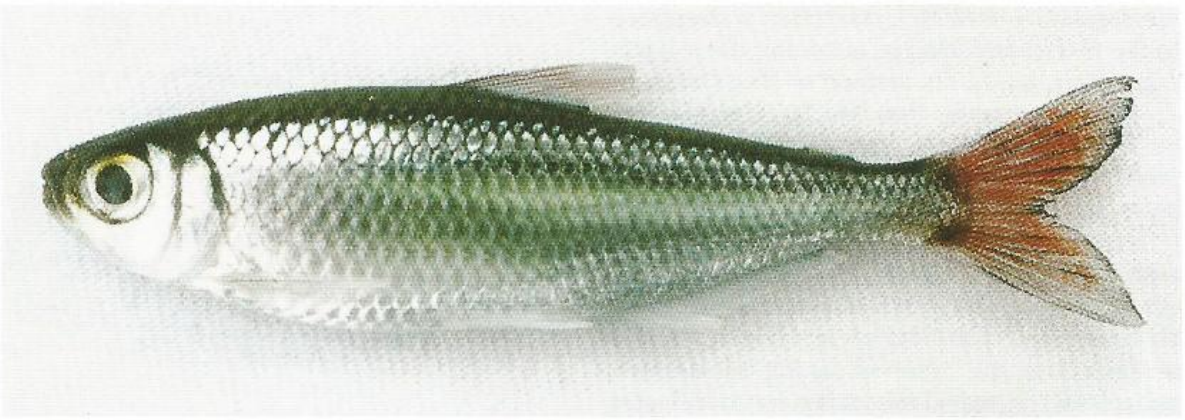

Fig. 4. *Bryconops colaroja*, holotype, MBUCV-V-27717, 67.6 mm SL; Venezuela: Bolivar: Río Las Claritas.

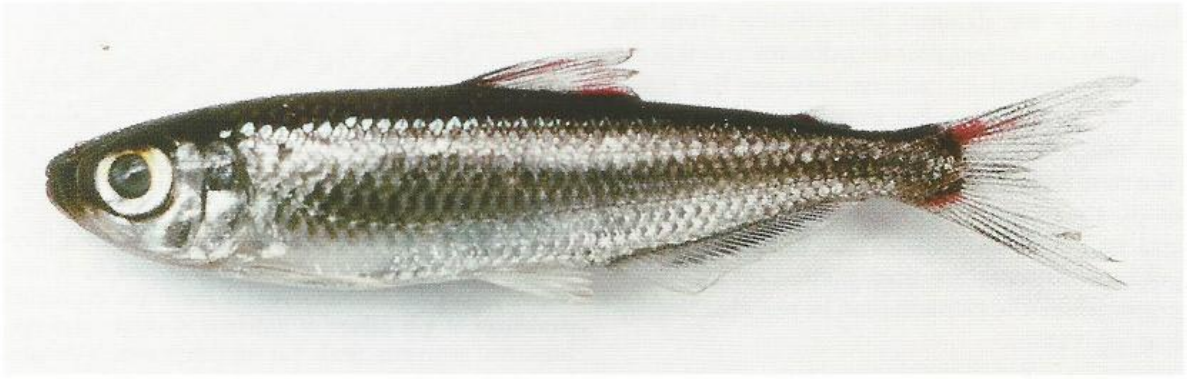

Fig. 5. *Bryconops colanegra*, holotype, MBUCV-V-27716, 71.0 mm SL; Venezuela: Bolivar: Río Carrao.

cerned in preserved specimens collected in the early 1900's. *Bryconops colaroja*, *B. colanegra*, *B. inpai*, and *B. melanurus* are the only members of *Creatochanes* to lack a well developed ocellus on the dorsal lobe of the caudal fin. Although the color within the ocellus can vary from yellow to bright red, the ocellus is always bordered distally by a more darkly pigmented section (e.g., see Chernoff, et al., 1994: fig. 1; Machado et al., 1996: figs. 3,6). This pattern that grades distally from a dark black to a duskier black has been termed a watermark by Eigenmann & Myers (1929). *Bryconops affinis*, which may be restricted to the Guyanas, has almost symmetric ocelli on each caudal-fin lobe. Furthermore, *B. humeralis*, *B. vibex* and *B. inpai* have one, one and two well-developed, vertically-oriented humeral marks, respectively (Machado et al., 1996: figs. 3, 4, 6). The other members of the subgenus, including *B. colaroja* and *B. colanegra*, lack these marks.

Bryconops melanurus is easily distinguished from *B. colaroja* and *B. colanegra* on the basis of pigmentation as well as by meristic and morphometric characters. Interestingly, each of these species has some red suffused through the caudal fin but *B. colaroja* is the only species in the genus to have an entirely red caudal fin (Fig. 4); dark melanophores are restricted to margins of the fin rays giving rise to an appearance of dark striations radiating through the fin. *Bryconops melanurus* has its principal caudal-fin pigmentation appearing as a thick, more or less central, stripe offset by lighter or clear dorsal and ventral lobes (Bloch 1794; Chernoff et al., 1991: fig. 2). Upon careful inspection, the caudal stripe of *B. melanurus*, ca. the width of the iris, is primarily expressed on and between the rays of the dorsal lobe, extending ventrally only to the second fin ray from the middle (Eigenmann & Myers, 1927). *Bryconops colanegra* has an entirely blackened caudal fin (Fig. 5) though there is the suggestion of a central stripe on the caudal fin. The stripe

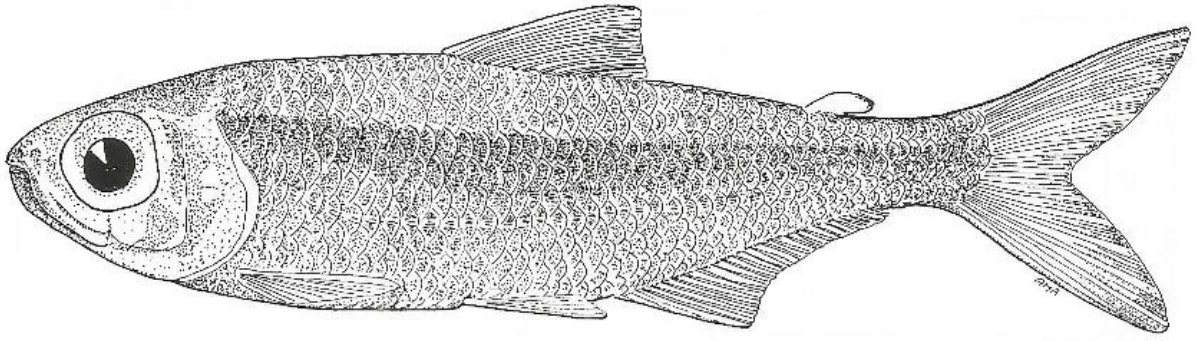

Fig. 6. *Bryconops colaroja*, holotype, MBUCV-V-27717, 67.6 mm SL; Venezuela: Bolivar: Río Las Claritas.

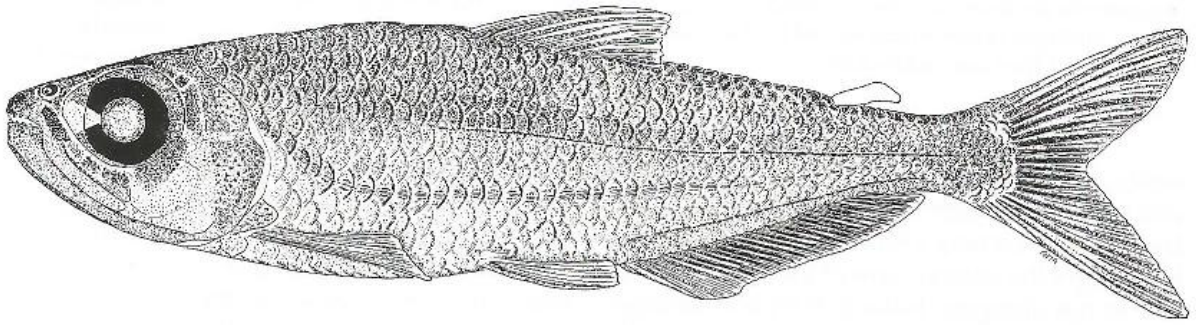

Fig. 7. *Bryconops colanegra*, holotype, MBUCV-V-27716, 71.0 mm SL; Venezuela: Bolivar: Río Carrao.

differs from that of *B. melanurus* because in *B. colanegra* it is very thin and is symmetric about the two central caudal-fin rays in the upper and lower lobes. *Bryconops colanegra* is the only species in the genus to possess a wide, blackened, proximal stripe that traverses almost the entire anal fin (Fig. 5). *Bryconops colaroja* and *B. melanurus* lack such a stripe – anal fin pigment is not distinct and is either restricted to the edges of fin rays or to the fin margin. In *B. colaroja* the cheek and lower opercular regions are silvery or immaculate (Fig. 6); whereas in *B. colanegra* (Fig. 7) and *B. melanurus* there is a distinct blotch of pigment.

Bryconops colaroja and *B. colanegra* are almost entirely differentiable from *B. melanurus* by the number of precaudal vertebrae and the vertebral centrum under which the anal fin originates. *Bryconops colaroja* and *B. colanegra* have 18-20 precaudal vertebrae, each with a strong modal value of 19; only 8 of 70 and 9 of 130 have 18 precaudal vertebrae, respectively. *Bryconops melanurus* has 17-19 precaudal vertebrae but only 1 specimen of 54 had 19. In *B. colaroja* and *B. colanegra*, the anal fin originates under the 18th-20th vertebral centrum, each with a strong modal value of 19; only 8 of 70 *B. colaroja* and 9 of 130 *B. colanegra* have the anal fin originating under the 18th vertebral centrum. In *B. melanurus*, the anal fin originates under the 17th or 18th centrum, modally 18.

In addition to the striking differences in coloration and pigmentation, *B. colaroja* and *B. colanegra* differ by the osteology of their jaws and cheeks and in certain aspects of their form. *Bryconops colaroja* has a larger 3rd infraorbital that contacts the preopercle at the angle and leaves only a small naked area anteriorly where it contacts the second infraorbital (Fig. 2a). In *B. colanegra*, the 3rd infraorbital is entirely free of the preopercle leaving a naked area at the angle which extends anteriorly to a larger naked area beneath the junction with the 2nd infraorbital (Fig. 2b). The larger size of the naked area is due to the fact that the anterior margin of the 3rd infraorbital curves away from the shorter junction with the 2nd infraorbital at a more dorsal position than that seen in *B. colaroja*.

Bryconops colaroja has a slightly more slender dentary than does *B. colanegra* (Fig. 2). But impor-

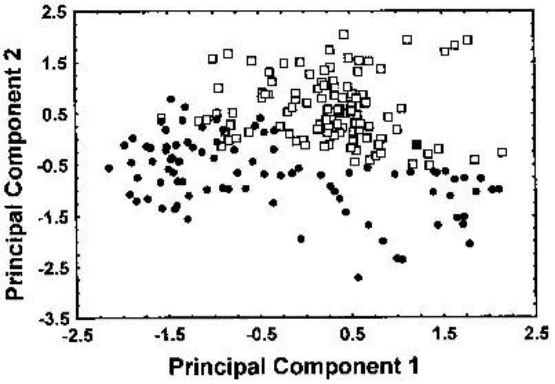

Fig. 8. Scatterplot of scores on the first two principal components for *Bryconops colaroja* (solid circles), n=89, and *B. colanegra* (open squares), n=114. Each symbol represents at least one individual.

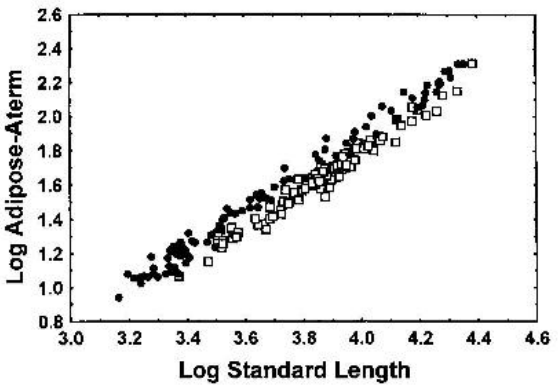

Fig. 9. Scatter plot of log adipose-anal fin terminus length (adipose-aterm) versus log SL for *Bryconops colaroja* (solid circles), n=89, and *B. colanegra* (open squares), n=114. Each symbol represents at least one individual.

tantly, the angular-articular of *B. colaroja* has an elongate anterior arm that leaves Meckel's cartilage exposed for only a short distance (Fig. 2c). In *B. colanegra* the anterior arm of the angular-articular is not elongate, leaving Meckle's cartilage exposed for approximately one-quarter the length of the dentary (Fig. 2d).

The ossification and denticulation of the gill rakers differs between these species. In *B. colaroja* the gill rakers have relatively less denticulation and smaller tooth plates than do those in *B. colanegra* (Fig. 3). In *B. colanegra* denticles can be found on all the gill rakers of the epibranchial and hypobranchial of the first arch; whereas in *B. colaroja* the gill rakers bearing denticles are located primarily on the ceratobranchial, only the gill raker at the angle and one or two rakers above the angle on the epibranchial are armed (Fig. 3).

There are subtle but consistent differences in the body shapes of *B. colaroja* and *B. colanegra* that can be summarized by PCA. The first two principal components explain 94.2% of the variance in the morphometric variables and summarize the majority of the size-change and linear shape-change information (PC1 and PC2, respectively) between these species (Table 2). The scatter of scores on the first two PCs (Fig. 8) shows that the sample of *B. colaroja* is almost entirely distinct from that of *B. colanegra*. The majority of the overlap is found among smaller individuals (SL<40 mm). The principal variables contributing to the shape differences on PC2 (Fig. 8) indicate that *B. colaroja* has relatively longer posterior body depths between the anal fin and the dorsal or adipose fins. In contrast, *B. colanegra* has a larger head that is manifest particularly in the head length, postorbital head length, upper jaw length and the distance from the distal end of the maxilla to the landmark on the anterior margin of the orbit.

Many of the differences in form between these species can be identified by comparing their patterns and rates of allometric growth (Table 2). Overall, the species share the following aspects of allometric growth: (i) almost all measurements of the head or those that largely comprise the head, i.e., prepectoral length, are negatively allometric; (ii) the region between the pectoral fin and the vertical between the dorsal-fin terminus and the anal-fin origin grows positively allometrically; (iii) the anal fin base is negatively allometric; (iv) the region above the anal fin is isometric to positively allometric; and (v) caudal peduncle length is isometric. The tests of homogeneity of the allometric coefficients, however, indicate that there are also significant differences in rates of growth between these species (Table 2). In general, the head measurements of *B. colanegra* scale more rapidly with size (are less negatively allometric) than do the head measurements of *B. colaroja* (Table 2). These differences in growth rate lead to the larger head sizes of *B. colanegra*.

The variables bearing the shape discrimination do not differentiate these species when expressed as ratios of SL due to overlapping ranges among juveniles less than 40 mm SL (Table 1).

However when plotted against SL, the differences in proportion between the species is clarified (Fig. 9). The ANCOVA of the distance between the terminus of the anal fin and the adipose fin (adipose-aterm) versus SL fails to reject the null hypothesis of homogeneity of slopes (F=.476, P=.491, error df = 199), but rejects the null hypothesis of equality of group means (F=232.2, P<.0001, error df = 200). Thus, the mean depth of *B. colaroja* for this posteriorly oblique measurement is significantly deeper than that of *B. colanegra*, and the species can be discerned from the scatter plot but not from the summary ratios. Similar results are obtained for the other variables bearing large coefficients on PC2.

Not all of the variables that are diagnostic for each of the species scale linearly in the same mathematical space. An example can be noted by examining the relationship between adipose-anal terminus length which is larger and grows more quickly in *B. colaroja* and postorbital head length which is larger and grows more quickly in *B. colanegra*. A scatter plot of these variables does not discriminate the species but illustrates a slightly s-shaped distributions that cross. To correct for the distributions, the values were transformed to polar coordinates and the shape differences between *B. colanegra* and *B. colaroja* are clarified (Fig. 10). *Bryconops colanegra* consistently has a longer postorbital head length for a given adipose-anal terminus length but the lengths of these variables are not linear with respect to each other. This non-linearity results because the head and mid-body develop according to species-specific growth stanzas. That is, the growth of the head and of the mid-body are accelerating and decelerating at different rates and at different sizes in the two species. This would also lead to misleading information about species differences when the variables are expressed as ratios to each other or as ratios of SL. The effects of growth stanzas across different regions of the body has been discussed for another characoid, *Leporinus brunneus*, by Chernoff et al. (1991), and is also documented in other teleosts (Martin, 1949). This demonstrates not only that the allometric effects of shape-change must be analyzed in order to accommodate the growth biology but also that the differences between classes of forms can be obscured if the analysis is not congruent with patterns of growth.

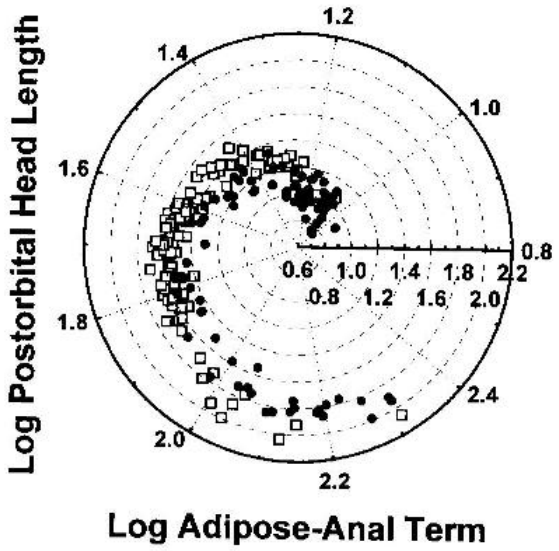

Fig. 10. Scatterplot of polar coordinates of log adipose-anal fin terminus (anal term) length (circumference) versus log postorbital head length (radius) for *Bryconops colaroja* (solid circles), n=89, and *B. colanegra* (open squares), n=114. Each symbol represents at least one individual.

Bryconops colaroja, new species
(Figs. 4, 6)

Holotype. MBUCV-V-27717, 67.6 mm SL; Venezuela: Bolivar: Río Las Claritas at Puente Las Claritas, at km 86 on the El Dorado-Sta. Elena Hwy, 6°10'16.4"N 61°25'33.9"W; A. Machado-Allison, B. Chernoff, H. Lopez, A. Bonilla, T. Bert, C. Silvera, 13 Feb 1997.

Paratypes. All localities in Venezuela: Estado Bolivar: Río Cuyuní basin. MBUCV-V-27966, 33 ex., 12.0-56.5 mm SL; FMNH 106507, 24 ex., 22.6-53.4 mm SL; captured with the holotype. - MBUCV-V-27967, 46 ex., 15.3-77.9 mm SL; FMNH 106508, 33 ex., 12.7-77.0 mm SL; Quebrada Araima at km 74 on El Dorado-Sta. Elena Hwy, 6°14'28.7"N 61°20'46.0"W, B. Chernoff et al., 13 Feb 1997. – ANSP 168000, 21 ex., 21.2-35.3 mm SL; Río Coruco, ca. 40 min downstream from Puerto Turuban, 6°45'00"N 61°04'00"W; F. Provenzano et al., 23 Jan 1991. -ANSP 168001, 8 ex., 28.9-75.0 mm SL; FMNH 106509, 1 ex., 85.3 mm SL; MBUCV-V-20770, 6 ex., 28.8-69.6 mm SL; Quebrada at km 72 on El Dorado-Sta. Elena Hwy, 6°18'00N 61°23'00"W; F. Provenzano et al., 26 Jan 1991. – ANSP 168005, 43 ex., 22.1-36.2 mm SL;

MBUCV-V-26509, 47 ex., 13.0-44.8 mm SL; border of Delta Amacuro, Río Grande at Campamento de Río Grande, 20 km E el Palmar, 8°10'00"N 61°45'00"W; F. Provenzano et al., 19 Jan 1991. – ANSP 168890, 2 ex., 32.7-43.1 mm SL; MBUCV-V-26309, 2 ex., 35.5-38.5 mm SL; Río Miamo, ca. 20 km W El Miamo, 7°38'00"N 61°50'00"W; F. Provenzano et al., 24 Jan 1991.

Diagnosis. A species of *Bryconops*, subgenus *Creatochanes*, that is distinguished from all other congeners by its unique red caudal fin and greenish-silver body. It is further distinguished from all other *Creatochanes* by the following combination of traits: humeral mark absent; caudal fin ocellus absent; pigment on anal fin restricted to margins of fin rays and not forming band; precaudal vertebrae 18-20; anal fin originates under 19th-20th centrum, rarely 18th; cheek lacking conspicuous blotch of pigment; upper lobe of caudal fin longer than lower lobe; third infraorbital contacting preopercle at angle.

Description. Morphometric data are given in Table 1. A moderate sized species of *Bryconops*, known from specimens less than 80 mm SL. Overall shape with convex dorsum and rounded belly, tapering to relatively thin caudal peduncle, < 10 % SL. Dorsal fin originates at or just anterior to mid-body, predorsal length 44.8-50.5 % SL, and anterior to vertical through insertion of pelvic fin.

Head 20.7-28.1 % SL; posterior margin of opercle sinusoidal. The border between second and third infraorbitals entire without a naked area between. Third infraorbital large, abuts preopercle without leaving a naked region. Eye large, 8.7-14 % SL, positioned within anterior 60 % of head. Snout bullet shaped; mouth terminal, opening just ventral to horizontal diameter through orbit; maxilla extending posteriorly to posterior margin of second infraorbital, ca. on vertical through midpoint of eye. When mouth closed, upper jaw projects just slightly beyond lower jaw; outer two rows of premaxillary teeth prominent, directed slightly forward. Premaxilla with 3-6 teeth bearing 3-5 cusps arranged in two loosely defined rows. Inner premaxillary teeth uniformly five with 5-7 cusps; teeth basically symmetric, exposed portions wider than high with concave outer surface. Maxilla with 1-2 teeth with 3-5 cusps. Dentary with 4-6 large teeth bearing 5-7 cusps, higher than wide, not symmetric; posterolateral edge prominent, cusps recurved posterolaterally. Smaller dentary teeth 6-8 in number with 1-2 cusps; if bicuspid, anteromedial cusp is minute.

Dorsal fin with straight to slightly convex distal margin; fourth ray, either first or second branched ray, longest. Posterior base of dorsal fin separated from anterior base of adipose fin by 12-14 scales, or 1.5 times dorsal fin height. Adipose fin with convex dorsal margin (anterior if elevated) and straight ventral margin (posterior if elevated). Upper lobe of caudal fin pointed to almost rounded and larger than pointed ventral lobe. Distal margin of anal fin straight in juveniles and slightly falcate in adults; fin height greater than half length of fin base. Pelvic fin not reaching origin of anal fin; distal margin rounded. Distal margin of pectoral fin pointed and slightly falcate; not reaching pelvic fin insertion.

Widths of scales on sides of body above lateral line and below row along dorsal fin greater than or equal to length; anterior margins almost circular to wavy with a central notch (Fig. 11a-b); rounded posterior margin; circuli present on anterior two-thirds of scale; posterior field lacking circuli, possessing 2-3 centrally-located almost parallel striae.

Dorsal-fin rays: unbranched 2*(70), 3(1); branched 7(1), 8(1), 9*(67), 10(2); total 9(1), 11*(68), 12(2). Anal-fin rays: unbranched 3(3), 4*(57); branched 22(4), 23(17), 24(25), 25*(13), 26(1); total 26(5), 27(17), 28(25), 29*(12), 30(1). Pectoral-fin rays 11(1), 12(28), 13*(37). Scales: predorsal rows 10(1), 11*(48), 12(1); lateral line 41(1), 42(1), 43(3), 44(23), 45(23), 46*(12), 47(1); rows above lateral line 6(1), 8*(61), 9(2); rows below lateral line 4(5), 5*(58). Gill rakers: upper 5(3), 6*(6), 7(49), 8(10); lower 9(1), 10(6), 11(31), 12*(28), 13(3); total 14(1), 15(1), 16(3), 17(5), 18*(26), 19(23), 20(9). Vertebrae: precaudal 18(8), 19*(62); caudal 22(14), 23*(54), 24(2); total 41(20), 42*(51); centrum under origin of dorsal fin 9(3), 10*(64), 11(3); centrum over origin of anal fin 18(8), 19*(62). Premaxillary teeth: outer 3(2), 4(19), 5*(48), 6(1); inner 5*(70). Maxillary teeth 0(1), 1*(34), 2(34). Large teeth on dentary 4(15), 5*(54), 6(1).

Pigmentation. Overall a moderately dusky species in preservation, countershaded above and below lateral stripe. Lateral stripe somewhat prominent in preservation, increasing in intensity just posterior to dorsal-fin origin, occupying three scale rows just behind midbody. Lateral-

line canals outlined with pigment. Below lateral line anterior to pelvic-fin insertion, melanophores may extend ventrally one-two scale rows; below devoid of pigment. Above lateral stripe, scales duskily pigmented, appearing crosshatched. A dark stripe on dorsum extends from supraoccipital region posteriorly to procurrent caudal fin rays. Posterior to anus and ventral to lateral line, scales peppered with small melanophores. One scale row above anal fin, melanophores forming stripe, extending entire length of fin. Ventral portion of caudal peduncle with melanohpores but lighter than lateral portions.

Top of head almost uniformly pigmented; ovate area about symphyseal bar lighter. Ethmoid region slightly darker, and dark streak extending laterally onto and down maxilla, as if a handle-bar moustache. Premaxilla lighter, uniformly flecked with small melanophores. Dorsal portion of lower lip darkly pigmented, but dusky ventrally towards gular region, forming a dusky muzzle. Pigment streaks on lower edge of dentary, extending below eye. Orbit outlined with melanophores, some spilling onto suborbital region; cheek largely devoid of pigment. Opercle more lightly pigmented below, peppered above.

Dorsal, anal, pectoral and pelvic fins with pigment flecked along rays, fin membranes clear. Caudal fin with melanophores along rays proximally; pigmentation becoming darker posteriorly forming a blackened marginal band.

Coloration. In bright sunlight, based upon reflectance, the color of the body varies from: (i) emerald green with a silver lateral stripe to darkish-green and silver above, and a silver belly; to (ii) a light green to emerald lateral stripe and bright silver below. Upper half of iris yellow. The dorsal fin and adipose fin is suffused with carmine red that fades immediately from the adipose fin. The caudal fin is carmine to vermilion red with blackened rays extending to the blackened marginal band and fin tips. Other than the pigmentation described above the anal, pectoral and pelvic fins lack color and are generally pale in appearance.

Distribution. This species is known only from the Río Cuyuní basin in the vicinity of the Venezuelan-Guyanan border. It has been collected in small streams and quebradas with black water that are tributaries to the Río Cuyuní over sand, gravel and rocky bottoms. This species has not been collected in the mainstem of the Río Cuyuní.

Etymology. The species-group name, *colaroja*, is taken from the Spanish words, *cola*, meaning tail, and *roja*, meaning red, in reference to its brilliant red tail. A noun in apposition.

Bryconops colanegra, new species
(Figs. 5, 7)

Holotype. MBUCV-V-27716, 71.0 mm SL; Venezuela: Bolivar: Río Carrao near base camp at Angel Falls; A. Machado-Allison & B. Chernoff, 22 Sept 1993.

Paratypes. All localities in Venezuela: Estado Bolivar: Río Caroní basin. MBUCV-V-27714, 5 ex., 49.7-73.0 mm SL; FMNH 106510, 2 ex., 52.1-71.2 mm SL; collected with the holotype. - MBUCV-V-27718, 6 ex., 42.8-80.2 mm SL; Río Carapo near Guaquinima Tepuy; A. Machado-Allison & C. Ferraris, 1990. – MBUCV-V-6875, 12 ex., 21.7-68.7 mm SL; Morichal tributary to Río Tocome near Ciudad Piar; F. Mago & A. Machado-Allison, 20 June 1972. – MBUCV-V-26764, 1 ex., 55.5 mm SL; Río Carrao near Isla Orquidea; A. Machado-Allison & B. Chernoff, 21 Sept 1993. – MBUCV-V-26747, 20 ex., 36.0-59.4 mm SL; MBUCV-V-27715, 51 ex., 29.2-57.5mm SL; FMNH 106511, 33 ex., 40.0-54.9 mm SL; Río Carrao at Isla Orquidea; A. Machado-Allison & B. Chernoff, 21-22 Sept 1993. – MBUCV-V-26765, 6 ex., 34.3-57.7 mm SL; FMNH 106512, 6 ex., 32.4-56.9 mm SL; Río Cherun Meru near Angel Falls; A. Machado-Allison & B. Chernoff, 23 Sept 1993.- FMNH 45714; 2 ex., 26.4-87.8 mm SL; Río Abacapa, Chimantá Tepuy, 31 March 1953, J. Steyermark and C. Griffin.

Diagnosis. A species of *Bryconops*, subgenus *Creatochanes*, that is distinguished from all other congeners by the following unique traits: entirely black caudal fin with some red suffused in the upper and lower lobes; prominent black stripe across anal fin; presence of black and silver stripes above the lateral line; and orange-red coloration on the mandible. It is further distinguished from all other *Creatochanes* by the following combination of traits: humeral mark absent; caudal fin ocellus absent; precaudal vertebrae 18-20; anal fin originates under 19th-20th centrum, rarely

18th; cheek with conspicuous blotch of pigment; lower lobe of caudal fin longer than upper lobe; third infraorbital not contacting preopercle at angle.

Description. Morphometric data are given in Table 1. A moderate sized species of *Bryconops*, known from specimens less than 81 mm SL. Overall shape with straight to convex dorsum and rounded belly, tapering to relatively thin caudal peduncle, < 10 % SL. Dorsal fin originates anterior to mid-body, predorsal length 44.5-50.5 % SL, and anterior to vertical through insertion of pelvic fin.

Head 23.2-28.3 % SL. Posterior margin of opercle irregular to sinusoidal above; shield shaped below. Third infraorbital large and joining squarely with second infraorbital, leaving triangular naked area anteroventrally and a narrow naked strip between it and preopercle. Eye large, 9.0-14.0 % SL; distance from snout to posterior margin of orbit 66 % of head length. Snout produced slightly, conic to bullet-shaped anteriorly. Mouth terminal, opens just ventral to horizontal diameter of orbit. Maxilla extending to junction of second and third infraorbitals and posterior to vertical through midpoint of eye. When mouth closed, upper jaw projects slightly beyond lower jaw. Outer premaxillary teeth, number 3-6 with 3-5 cusps, directed outward slightly or downward. Inner premaxillary teeth, number 5-6 with 5-7 cusps, with very flat anterior surface and very symmetric about enlarged median cusp; exposed portion wider than tall. Maxilla with 1-3 teeth bearing 3 cusps. Dentary with 4-7 enlarged teeth bearing 5-7 cusps, exposed portion higher than wide and not symmetric with prominent posterolateral edge; 6-8 small dentary teeth with 1-2 cusps.

Posterior margin of dorsal fin straight; second branched ray (usually fourth overall) longest. Posterior base of dorsal fin separated from adipose fin by 12-16 scales. Dorsal margin of adipose fin convex; posterior margin straight. Caudal fin with pointed lobes; lower lobe longer than upper lobe. Anal fin with straight distal margin; fin height greater than half of the length of the fin base. Pelvic fin extending just beyond anal-fin origin; distal margin rounded. Pectoral fin slightly falcate, not reaching by 1-2 scale rows vertical through pelvic-fin insertion.

Scales above lateral line and below dorsal fin with wavy anterior margin, one or two central notches; circuli on anterior field; radii absent; posterior field naked; and two, shallow, almost parallel, posteriorly-directed striae (Fig.11c-d).

Dorsal-fin rays: unbranched 2*(130); branched 9*(125), 10(5); total 11*(125), 12(5). Anal-fin rays: unbranched 4*(117), 5(2); branched 22(1), 23(18), 24(56), 25*(38), 26(6); total 26(1), 27(18), 28(54), 29(40), 30(6). Pectoral-fin rays 12(20), 13*(77), 14(9), 15(1). Scales: predorsal rows 10(5), 11(63), 12*(33); lateral line 42(8), 43(12), 44(21), 45*(27), 46(20), 47(13), 48(1); rows above lateral line 7(2), 8*(104); rows below lateral line 4*(6), 5(100). Gill rakers: upper 6(9), 7*(60), 8(34), 9(4); lower 10(2), 11(32), 12*(60), 13(13); total 17(4), 18(26), 19*(46), 20(20), 21(9), 22(2). Vertebrae: precaudal 18(9), 19(102), 20*(19); caudal 21(1), 22(25), 23*(82), 24(22); total 40(5), 41(16), 42(78), 43*(31); centrum under origin of dorsal fin 10(34), 11*(96); centrum over origin of anal fin 18(9), 19(101), 20*(20). Premaxillary teeth: outer 3(1), 4(39), 5*(61), 6(6); inner 5*(106), 6(1). Maxillary teeth 1(4), 2*(84), 3(19). Large teeth on dentary 4(3), 5*(93), 6(9), 7(2).

Pigmentation. Overall a darkly pigmented species; darker to blackened above, lighter below. Lateral stripe either indistinct or absent; essentially as a border between lighter and darker regions. Dark posterior borders on scales above lateral line result in crosshatched appearance. Scale rows becoming more darkly pigmented towards dorsum; middorsal scales darkest but not appearing as a distinct stripe. Pigmentation along edges of lateral line canal on scales more distinct posteriorly. Anterior to anus, pigmentation becoming sparser towards belly; only midventral row of scales devoid of pigment. Posterior to anus and below lateral line, body almost uniformly peppered with melanophores; pigment along posterior scale margins resulting in herring-bone pattern; and a thin stripe parallel to anal-fin base, 1-2 scale rows above fin base. Ventral portion of caudal peduncle freckled with small melanophores.

Top of head is uniformly, darkly pigmented; in some specimens upper lip somewhat lighter. Melanophores becoming individually distinct as they extend laterally onto maxilla and second infraorbital. Melanophores becoming restricted to anterior edge of maxilla. Lower lip forming a dark border over dusky portion of lower dentary grading into lighter gular region peppered and streaked with large melanophores extending to

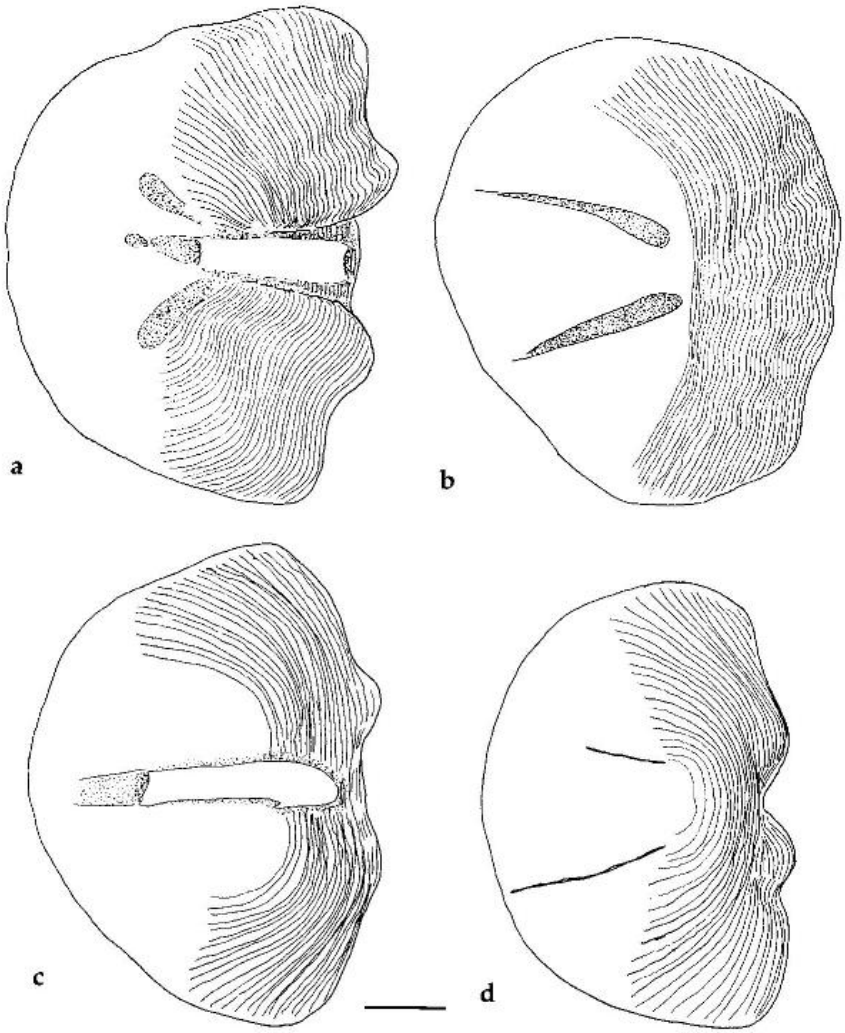

Fig. 11. Lateral line and mid-body scale from below middle of dorsal fin of: **a-b,** *Bryconops colaroja,* paratype, FMNH 106507; and **c-d,** *B. colanegra,* paratype, MBUCV-V-27714. Scale bar 10 mm.

distal tip of maxilla. Cheek dusky; lower portion of preopercle sparsely flecked. Posterior infraorbitals peppered, becoming more densely pigmented dorsally. Opercle darkly pigmented, appearing as a wide irregular vertical mark, offset by lighter infraorbital series anteriorly (Fig. 7).

Dorsal fin dark with melanophores on membranes between all rays; anterior portion of fin darkest. Anal fin with melanophores forming proximal stripe, half width of fin along entire length of fin, best developed posterior to first several fin rays; except for stripe, fin membranes clear or with a few scattered flecks; distal margin of posterior half of fin dusky. Pectoral and pelvic fins dusky with melanophores along fin rays, membranes generally lacking pigment. Adipose fin with highly pigmented base and fin margin; body of fin freckled. Overall, caudal fin darkly pigmented with melanophores along and on all fin rays and suffused in all interradial membranes; central caudal rays very dark forming thin stripe from base to end of fin fork; above and below central stripe small areas more diffuse and lighter, not appearing as ocelli; outer 3-4 principal rays also very dark, primarily along fin rays appearing as radiating streaks; distal margin dark.

Coloration. Overall body coloration with alternating black and silver stripes. Head and dorsum dark black then silver below for 1-2 scale rows, then a broad but ill-defined black lateral stripe bordered below by the outlined lateral line

scales, below which is silver. Snout and muzzle generally black; mandible orange/red below lips; opercular series silver with two large, black patches on upper and lower opercle and posterior infraorbital bones. Iris yellow. Dorsal fin with red suffused in membranes between black streaks along fin rays in anterior and posterior portions of the fin leaving a clear central area. Anal fin with proximal black stripe, contrasting with clear distal portion. Pectoral and pelvic fins light to dusky. Adipose fin with some red at base. Caudal fin with red extending distally in membranes of outer 3-4 principal rays in both lobes, appearing distinctive between darkly outlined fin rays; a narrow band of red along base of fin; thin blackened stripe between central fin rays.

Distribution. This species is apparently an endemic to the Río Caroní basin, found in upper and lower tributaries. So far it has not been captured below the falls from Guri dam in the Río Caroní. It inhabits medium to small blackwater rivers or morichales in forested habitat. We have captured this species over bottoms with sand, gravel and some rocks.

Etymology. The species-group name, *colanegra*, is formed from the Spanish words, *cola* meaning tail, and *negra* meaning black, in reference to the black caudal fin of this species. A noun in apposition.

Artificial key to the species of *Bryconops*

1. - Posterior extension of the maxilla not reaching the junction of the second and third infraorbital bones. Border between the second and third infraorbital bones leaving a small naked triangle between them. Maxilla without teeth, rarely a single small conical tooth, usually on just one side (subgenus *Bryconops*). 2
   - Posterior extension of the maxilla reaching the junction of the second and third infraorbital bone. Ventro-posterior margin of second infraorbital squared-off, forming a complete border with the third infraorbital without naked area between them. Maxilla with one to three teeth on both sides (subgenus *Creatochanes*). 4

2. - Snout pointed slightly. Lower jaw included in upper jaw when closed. Premaxillary teeth generally in three rows. Caudal fin with yellow in life on both dorsal and ventral portions, lacking any ocellus, posterior margin dusky to dark. Anal fin long with 32-37 branched rays. Pored lateral line scales 57-61. Scales above lateral line 9-10. Scales below lateral line 5-6. ..... *B. alburnoides*
   - Snout blunt and rounded. Lower jaw terminal or only slightly included in the upper jaw. Premaxillary teeth generally in two rows. Caudal fin with well formed ocellus on the dorsal lobe, intense red in life (clear in preserved material), remainder of fin dark to dusky. Anal fin with 22-30 branched rays. Pored lateral line scales 9-43. Scales above lateral line 7-8. Scales below lateral line 4-5. 3

3. - Lateral line missing on last four to five scales, 40-43 pored scales. ..... *B. caudomaculatus*
   - Lateral line not extending beyond second or third branched anal fin rays, 9-23 pored scales. ..... *B. disruptus*

4. - Humeral mark(s) present. 5
   - Humeral mark(s) absent. 7

5. - Two humeral marks. Dark to dusky pigment obscuring the caudal peduncle from over the middle of the anal-fin base onto the central part of the caudal fin. Caudal fin dusky without ocelli on either lobe. Metallic blue in life. ..... *B. inpai*
   - Single humeral mark. Caudal peduncle not obscured by pigment. Caudal fin with ocellus on dorsal lobe. 6

6. - Scales below lateral line 4-5. Gill rakers on the lower limb of the first arch 10-11. Caudal peduncle least depth 6.6-10.2 % SL ($\bar{x}$ = 10.0 % SL). Upper jaw length 11.8-16.9 % SL ($\bar{x}$ = 14.5 % SL). ..... *B. humeralis*

- Scales below lateral line 6. Gill rakers on the lower limb of the first arch 9-10. Caudal peduncle least depth 9.2-11.1 % SL ($\bar{x}$ = 10.0 % SL). Upper jaw length 15.2-20.6 % SL ($\bar{x}$ = 16.9 % SL).
  ..... B. vibex

7. - Caudal fin with well developed ocellus on dorsal lobe.
  8
  - Caudal fin pigmented but lacking a well formed ocellus.
  9

8. - Caudal fin with almost symmetric well-formed ocelli on both lobes.
  ..... *B. affinis*
  - Caudal fin with only a single, well-formed ocellus on the dorsal lobe.
  ..... *B. giacopinii*

9. - Caudal fin with prominent black stripe, width almost equal to the pupil, asymmetrically from the central fin rays onto the dorsal lobe; remainder of fin clear to lightly pigmented and with dusky margin. Outer teeth on premaxilla 3-6, modally 4. Precaudal vertebrae 17-18. Anal fin originates under 17th-18th centrum.
  ..... *B. melanurus*
  - Darkened central caudal rays not principal pigment pattern on fin; wide stripe absent. In life, caudal fin either completely blackened or carmine red with dusky posterior margin. In preservation, caudal fin with black striations along all fin rays. Outer teeth on premaxilla 4-6, modally 5. Precaudal vertebrae 18-20. Anal fin originates under 19th-20th centrum, rarely 18th centrum.
  10

10. - Caudal fin completely carmine red. Anal fin with pigment along fin rays, not in membranes, not forming prominent wide stripe along entire length of fin. Cheek lacking conspicuous blotch of pigment. Upper lobe of caudal fin longer than lower lobe. Third infraorbital contacting preopercle at angle.
  ..... *B. colaroja*
  - Caudal fin principally black with some red suffused among outer 3-4 principal rays of both lobes. Anal fin with broad prominent black stripe along entire base of fin. Cheek with conspicuous blotch of pigment. Lower lobe of caudal fin longer than upper lobe. Third infraorbital not contacting preopercle at angle.
  ..... *B. colanegra*

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