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TAXONOMIC STATUS OF *CHIRONIUS MULTIVENTRIS* AND *CHIRONIUS COCHRANAE* (SERPENTES)

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ABSTRACT: Recently four subspecies of *Chironius multiventris* were recognized as valid distinct species: *C. m. foveatus*, *C. m. multiventris*, *C. m. cochranae*, and *C. m. septentrionalis*. Although *C. foveatus* and *C. septentrionalis* clearly deserve specific status, a re-evaluation of the characters pointed in the literature as diagnostic of *C. multiventris* and *C. cochranae* does not support their recognition as valid distinct taxa. Additionally, our analysis of the scutellation pattern, continuous characters, and hemipenial morphology of 34 specimens, and of the available data in literature, shows that there are no significant differences between them. We therefore suggest that *C. cochranae* should be synonymized with *C. multiventris*.

Key words: Colubridae; Colubroides; External morphology; Hemipenis; Taxonomy

CHIRONIUS is a Neotropical genus of long and slender snakes distributed from southern Central America to southern South America. The genus is easily diagnosed by the presence of 12 or 10 rows of dorsal scales at midbody. All species of *Chironius* are diurnal arboreal snakes inhabiting preferably lowland tropical rainforests, but being also found in humid montane forests as well as open-formation biomes (Dixon et al., 1993; Marques et al., 2001; Marques and Sazima, 2003).

Recently, Hollis (2006) analyzed the phylogenetic affinities of 20 nominal taxa of the genus *Chironius* with the use of 36 hemipenial and external morphological characters, of which 34 were drawn directly from the Dixon et al. (1993) monographic review of the genus. According to Hollis (2006: Fig. 3), *C. multiventris foveatus* is the sister group of a clade comprising *C. vincenti* and *C. m. septentrionalis*. These three taxa cluster as the sister group of a clade formed by *C. m. cochranae* and *C. m. multiventris*. Based on these recovered affinities, Hollis (2006) concluded that all four subspecies of *C. multiventris*, *C. m. foveatus*, *C. m. multiventris*, *C. m. cochranae*, and *C. m. septentrionalis*, should be given full specific status. *Chironius foveatus* is the only species restricted to the Atlantic Forest biome, the other three being Amazonian components.

Although *C. foveatus* and *C. septentrionalis* have been convincingly demonstrated to be distinct valid species (Bailey, 1955; Hollis, 2006), the remaining two forms of *C. multiventris* (*C. m. multiventris* and *C. m. cochranae*) could still be arguably treated as subspecies or even as synonyms (see Cunha and Nascimento, 1982). Schmidt and Walker (1943) described *C. multiventris* based on two specimens from Peru, and distinguished it from the other species of the genus by the presence of a high number of ventral and subcaudal scales. *Chironius foveatus* was originally described as a distinct species by Bailey (1955), who based his description on 10 specimens from the Atlantic forest of the Brazilian states of Bahia, Espírito Santo, Rio de Janeiro, São Paulo, and Santa Catarina. Similarly, *C. cochranae* was described as a distinct species by Hoge and Romano (1969), who had at their disposal 10 specimens from the eastern Amazonian basin (Brazil, Guiana, and Surinam). Later, Cunha and Nascimento (1982) synonymized *C. cochranae* with *C. multiventris*. These authors analyzed 75 specimens from the Brazilian states of Amapá, Maranhão, and Pará, and concluded that there were no significant differences between *C. multiventris* and *C. cochranae*. Dixon et al. (1993) considered *C. cochranae* and *C. foveatus* as subspecies of *C. multiventris*, and added *C. m. septentrionalis* to this group, which has its population restricted to high

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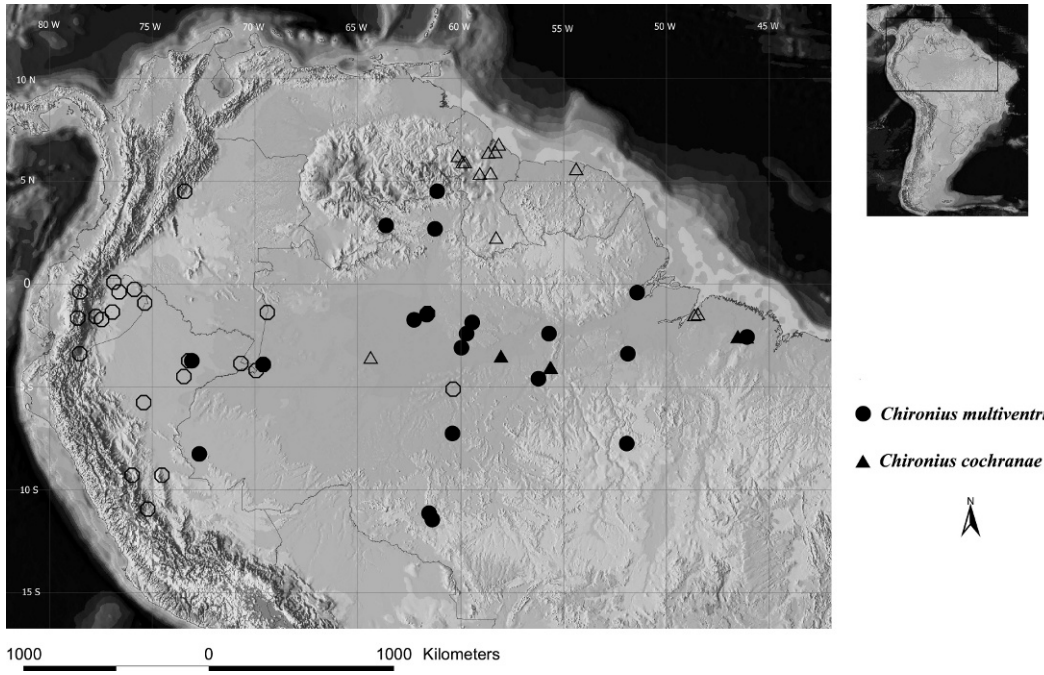

FIG. 1.—Distribution of *Chironius multiventris* and *C. cochranae*. Open circles and triangles are based on specimens analyzed by Dixon et al. (1993). Closed circles and triangles represent specimens analyzed in the present study.

elevations (above 1200 m) in the north of Venezuela and Trinidad. According to Dixon et al. (1993), *C. m. cochranae* is distributed through northeastern Brazil, eastern Venezuela, Surinam, and French Guiana (Chippaux, 1986; Starace, 1998), and *C. m. multiventris* is found in northwestern Brazil, eastern Peru and Ecuador, southeastern Colombia, and southern Venezuela (Fig. 1).

In an attempt to find additional specific characters to diagnose *C. cochranae* and *C. multiventris*, we analyzed the external morphology of a total of 34 specimens belonging to both species, compared their hemipenial morphology, and reevaluated critically the characters pointed out by Hollis (2006) as diagnostic for these two taxa.

MATERIALS AND METHODS

We examined 28 specimens of *C. multiventris*, and 6 specimens of *C. cochranae* (Appendix 1) from the following institutions: Instituto Butantan, São Paulo (IBH); Museu de História Natural do Capão da Imbuia, Curitiba (MHNCI); Museu de Zoologia da Universidade de São Paulo (MZUSP). We also analyzed one hemipenis of *C. cochranae*, and two of *C. multiventris* (Appendix 2).

Hemipenial preparations followed the procedure described by Zaher (1999) and Zaher and Prudente (2003). We counted ventral scales from the first scale wider than long (i.e., including "preventrals") to the last scale before the anal plate (Vanzolini et al., 1980). We measured snout–vent length and tail length to the nearest 1 mm by carefully stretching specimens along a ruler. We also photographed specimens and hemipenes with a Nikon Coolpix digital camera and mounted the photos on plates with the aid of Adobe Photoshop 7.0.1. We performed morphometric analyses on both meristics (ventral, subcaudal, postcephalic, and postocular scales) and continuous characters (snout–vent length [SVL], tail length [TL], and eye diameter). To assess the possibility of using parametric tests on SVL, TL, ventrals, and subcaudal counts, we tested these variables for normality and equality of variances with the use of a one-sample Kolmogorov-Smirnov test and a Bart-

TABLE 1.—Autapomorphic characters used by Hollis (2006) as diagnostic of *Chironius multiventris* and *C. cochranae*. The first column shows the character description, the second column the character number, and finally the third one shows the state transformation.

	Character number	Transformation
Chironius multiventris		
Maximum SVL[a]	1	7 ⇒ 8
Apical pits	7	1 ⇒ 3
Mean number of postcephalics	16	3 ⇒ 2
Mean number of central spines on dorsal surface of hemipenis	32	4 ⇒ 3
Mean number of distal calyces on dorsal surface of hemipenes	34	3 ⇒ 2
Chironius cochranae		
Tail length as percent of total length	2	7 ⇒ 8
Mean number of ventrals	3	5 ⇒ 6
Mean number of paired subcaudals	4	7 ⇒ 8
Apical pits	7	1 ⇒ 0
Mean number of postoculars	13	1 ⇒ 6
Mean ratio of eye diameter to snout length	19	7 ⇒ 8
Ratio of maximum male SVL to maximum female SVL	24	7 ⇒ 8
Ratio of male tail percent to female tail percent	25	2 ⇒ 1
Mean of subcaudal number to which everted hemipenis extends	26	2 ⇒ 1

[a] SVL = snout-to-vent length.

lett test, respectively. No variable violated significantly either one of these assumptions (Kolmogorov-Smirnov test $P > 0.25$, for all analyses; Bartlett test $P > 0.17$, for all analyses). Additionally, we tested ventral scales and subcaudal scales for correlation with snout–vent length and tail length, respectively, but did not obtain any significant results (Pearson's product-moment correlation $P > 0.13$; for all analyses). We did not include in the analysis the sexual dimorphism in keeled scale rows reported by Dixon et al. (1993) because that character does not help resolve species identity in the group as a whole. We performed all of these exploratory tests with *C. multiventris* and *C. cochranae* used as distinct groups.

To test the difference between *C. multiventris* and *C. cochranae* we employed an analysis of variance (ANOVA) for ventral and subcaudal scales. To test for sexual dimorphism in TL and SVL within each species we used analyses of covariance (ANCOVA), with sex as the factor and total length as the covariate. To investigate the differences in SVL, TL, and eye diameter between species, we used ANCOVAs with total length as the covariate for the former two variables and snout length as the covariate for the last variable. We analyzed postoculars and postcephalic scale counts with the use of a nonparametric Wilcoxon rank test. We ran all statistical analyses with R 2.11.1 (R Development Core Team, 2010).

RESULTS AND DISCUSSION

According to Hollis (2006), *C. multiventris* and *C. cochranae* are diagnosed by five and nine autapomorphies, respectively (Table 1). Hollis (2006) did not explicitly define the states of the characters used. Therefore, we could not carry out a more effective analysis of her results. Because Hollis (2006) drew her analysis directly from the Dixon et al. (1993) study, we reanalyzed the list of autapomorphic characters as described by them, evaluating the data gathered from the 34 specimens analyzed by us. The Dixon et al. (1993) data were used only for qualitative comparison, because they were not promptly available in the literature. Even though the data from Cunha and Nascimento (1982) were available, they could not be included in our analyzes because these authors named all specimens as *C. multiventris*.

Hollis (2006) used both ratio of maximum male SVL to maximum female SVL and ratio of male tail percent to female tail percent in the phylogenetic analysis of *Chironius*. The reasons for such character formulation are not clear: it relates not only to an ensemble property, but it also scores phenotypes that

TABLE 2.—Summary of ANCOVAs used to investigate sexual dimorphism.

	Chironius multiventris				*Chironius cochranae*			
ANCOVA	df	Sum of squares	*F*	*P*	df	Sum of squares	*F*	*P*
SVL[a]	Males = 13; females = 5				Males = 4; females = 5			
Total length	1	6776.6	1175.0616	4.105e-08*	1	1196.64	910.5641	7.994e-05*
Sex	1	1.5	0.2523	0.6333	1	2.49	1.8965	0.2622
Total length:sex	1	3.2	0.5578	0.4834	1	3.86	2.9335	0.1853
Residuals	6	34.6			3	3.94		
TL[b]	Males = 7; females = 3				Males = 3; females = 4			
Total length	1	1796.20	311.4605	2.125e-06*	1	369.74	281.3509	0.0004614*
Sex	1	1.46	0.2523	0.6333	1	2.49	1.8965	0.2622366
Total length:sex	1	3.22	0.5578	0.4834	1	3.86	2.9335	0.1852765
Residuals	6	34.60			3	3.94		

* $P < 0.0001$.
[a] SVL = snout-to-vent length.
[b] TL = tail length.

are not representative of a given biological population, because it evaluates outlier individuals. Because these characters express a relationship between sexes, they can be interpreted as a measure of sexual dimorphism. The ANCOVAs between sexes found no significant differences for both variables (Table 2), showing that there is no sexual dimorphism in *C. cochranae* and *C. multiventris*. Furthermore, these analyses allowed us to pool both sexes together in the other analysis.

The following characters show significant overlap between their states and cannot be used to diagnose both species: SVL (Fig. 2A); TL (Fig. 2B); eye diameter (Fig. 2C); number of ventral scales and number of paired subcaudal scales (Fig. 2D); number of postocular scales (Fig. 3A); and apical pits (Fig. 3B). Statistical tests are summarized in Table 3. These characters are further detailed below.

Hollis (2006) considered the maximum value of SVL as diagnostic of *C. multiventris*. However, she did not consider the length range. According to data obtained by Dixon et al. (1993), plus our data, the highest SVL for *C. multiventris* is 2611 mm and the length ranges from 476 mm to 2611 mm, whereas the *C. cochranae* highest SVL is 2359 mm, with the variation in length ranging from 829 mm to 2359 mm. Although *C. multiventris* seems to reach larger values of SVL, *C. cochranae* is placed within the range of *C. multiventris*, thus preventing the use of this character to discriminate between these taxa. Furthermore, the ANCOVA of SVL using total length as a covariate could not detect the presence of any significant difference between these groups (Table 3).

Hollis (2006) suggested the following characters as being diagnostic of *C. cochranae*: tail length as a percent of total length, mean number of ventrals, mean number of paired subcaudals, number of postocular scales, and eye/snout ratio. Again, Hollis (2006) did not provide the variation of these characters within and between groups. *Chironius cochranae* shows an average tail length of 37.5% of the total length, ranging from 35.6 to 39.5%, and *C. multiventris* shows an average tail length of 37.1%, ranging from 35.1 to 38.9%. The ANCOVA of tail length using total length as a covariate showed no significant differences between the groups (Table 3). The eye/snout ratio of *C. cochranae* shows an average of 0.942, varying between 0.722 and 1.234, whereas *C. multiventris* has an average of 0.912, varying between 0.704 and 1.196. The ANCOVA of eye diameter using snout length as a covariate exhibited no significant difference between groups (Table 2).

Hollis (2006) found a positive correlation between the number of subcaudals and TL, thus justifying the use of the residuals as phylogenetic characters. However, our data indicate that neither ventral scales nor subcaudal counts present any correlation with SVL or TL (Pearson's product-moment cor-

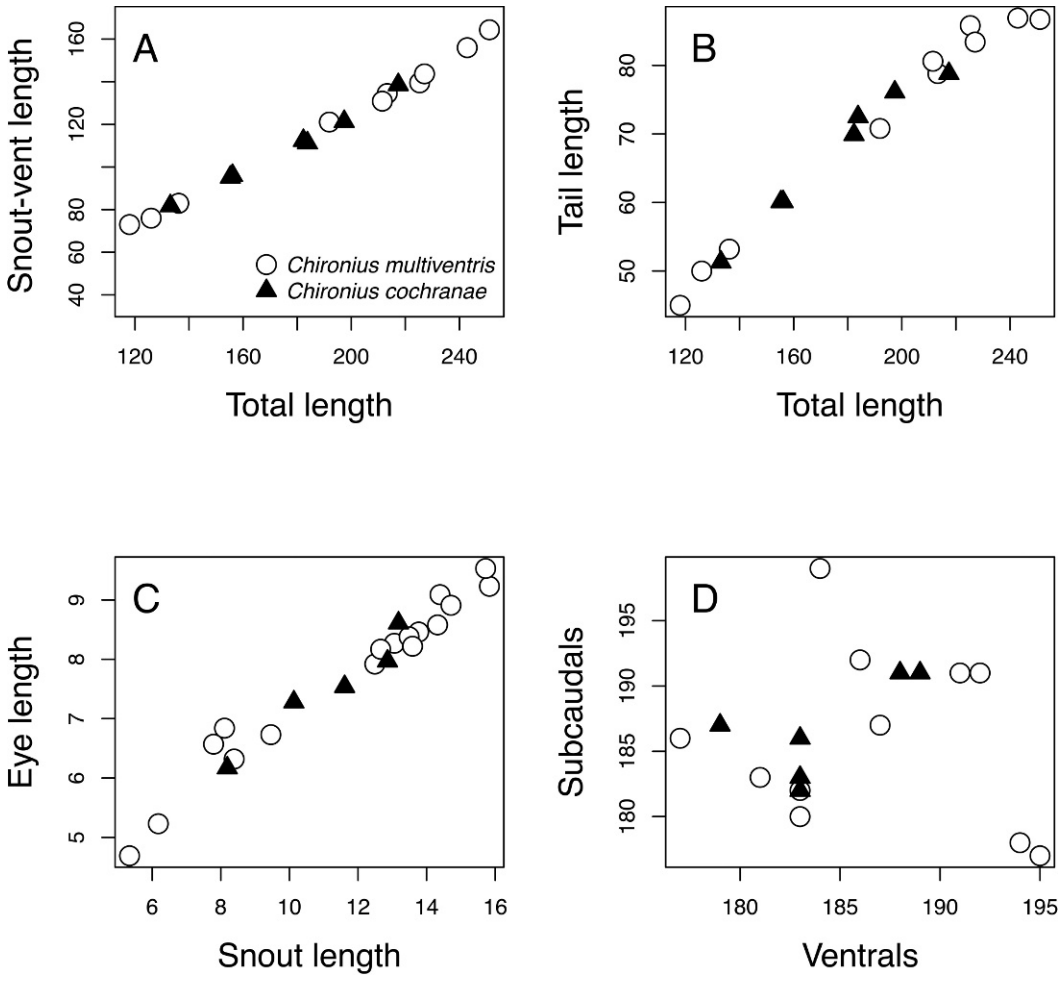

FIG. 2.—Dispersion plots. (A) Snout–vent length against total body length; (B) tail length against total body length; (C) eye diameter against snout length; (D) ventrals by subcaudals.

relation—P value > 0.13 for all analyses), allowing us to access the difference between taxa for this variable on the raw data. *Chironius cochranae* shows 178–196 ventrals and 180–197 paired subcaudals, and *C. multiventris* has 166–192 ventrals and 158–208 paired subcaudals, evidencing a great overlap between the groups. The ANOVA over both scale-count variables found no significant difference between them (Table 3).

Moreover, the number of postocular scales varies in the genus from 1–4 scales. Among the 48 specimens of *C. cochranae* (the Dixon et al. [2003] data plus our data), 24 specimens have 2 postocular scales, 19 specimens have 3 scales, and 5 specimens have 4 scales, thus overlapping with the analyzed specimens of *C. multiventris*, which have 2 or 3 postoculars, with 84 out of 90 specimens showing only 2 scales (Fig. 3A). The Wilcoxon rank test failed to find any significant differences for this character between the two groups (Table 3). Likewise, the mean number of postcephalic was used as a diagnostic character for *C. multiventris*. However, analyzing the range of variation with a Wilcoxon rank test showed no significant divergence for this character (Table 3).

The character apical pits was used to diagnose both species; defining *C. multiventris* as a species showing change from state 1

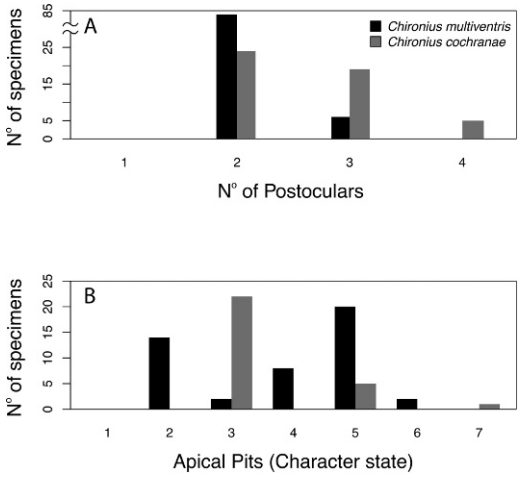

FIG. 3.—Distribution of frequencies of number of postoculars (A) and of character states related to apical pits (B) based on data from Dixon et al. (1993). See text for description.

to state 3, and *C. cochranae* as showing change from state 1 to state 0 (Table 1). Because Hollis (2006) did not provide the states that were used in the analysis, we analyzed the Dixon et al. (1993) classification of the condition of apical pits in *C. multiventris* and *C. cochranae*. The latter authors divided the apical pits condition in seven states: (1) absent; (2) neck only; (3) neck, paravertebral scales rows for length of body; (4) neck, paravertebral scales rows of tail only; (5) neck, paravertebral scales rows on posterior 1/2–1/3 of body and tail; (6) neck, paravertebral scales rows above anus only; (7) other. Among the 28 specimens of *C. cochranae* analyzed, 22 show state 3, 5 show state 5, and 1 shows state 7. Among the 46 specimens of *C. multiventris* analyzed, 14 show state 2, 2 show state 3, 8 show state 4, 20 show state 5, and 2 show state 6 (Fig. 3B). In

TABLE 3.—Summaries of statistics for the differences between *Chironius multiventris* and *C. cochranae*.

ANOVA	df	Sum of squares	*F*	*P*
Ventrals				
Taxa	1	37.02	1.7769	0.1941
Residuals	26	541.66		
Paired subcaudals				
Taxa	1	1.73	0.0483	0.829
Residuals	15	535.33		
ANCOVA	df	Sum of squares	*F*	*P*
SVL[a]				
Total length	1	7094.7	1508.9962	7.82e-15*
Taxa	1	0.2	0.0523	0.82274
Total length:taxa	1	0.9	0.1915	0.66883
Residuals	13	61.1		
TL[b]				
Total length	1	1830.61	389.3601	4.502e-11*
Taxa	1	0.25	0.0523	0.82274
Total length:taxa	1	0.90	0.1915	0.66883
Residuals	13	61.12		
Eye diameter				
Snout length	1	10.7769	151.7547	3.305e-10*
Taxa	1	0.0041	0.0575	0.8132
Snout length:taxa	1	0.0050	0.0700	0.7943
Residuals	18	1.2783		
Wilcoxon rank test			*W*	*P*
Postocephalics			64	0.1801
Postoculars			108	0.2411

* $P < 0.0001$.
[a] SVL = snout-to-vent length.
[b] TL = tail length.

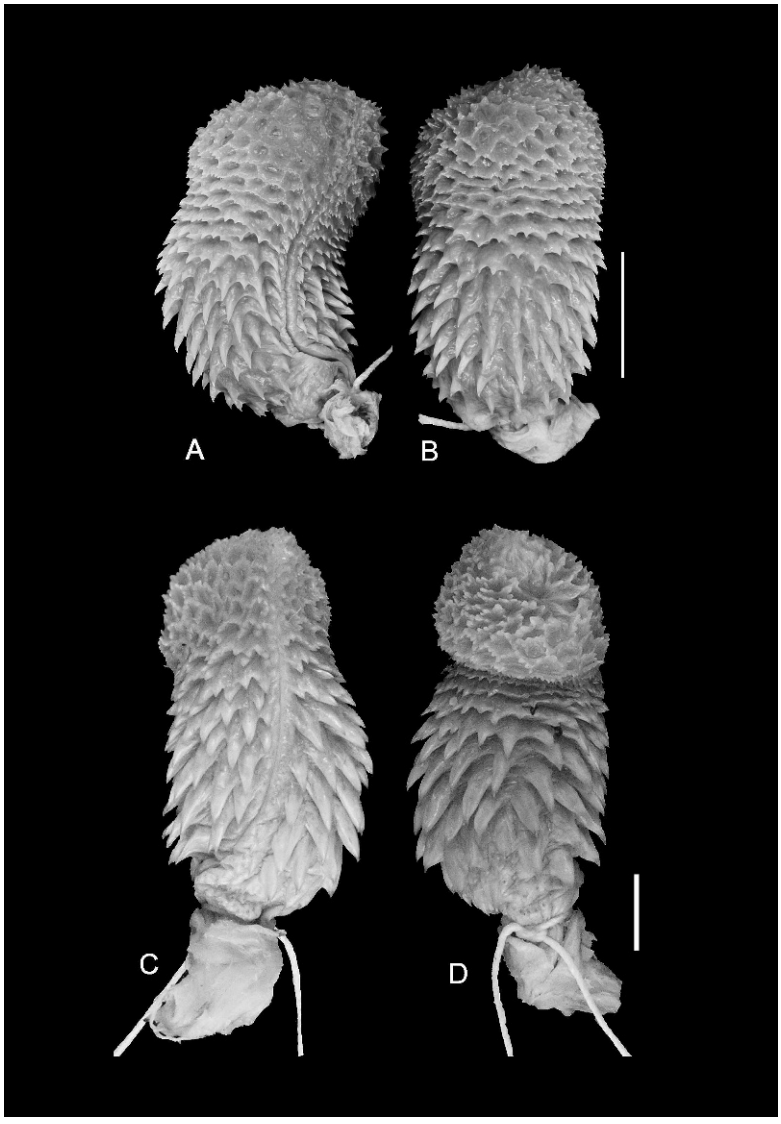

FIG. 4.—Hemipenis of *Chironius cochranae* in sulcate (A) and asulcate (B) views, and *C. multiventris* in sulcate (C) and asulcate (D) views. Both hemipenes are fully everted. However, although the hemipenis of *C. cochranae* is maximally expanded, the one of *C. multiventris* was only partially expanded during preparation, resulting in a distortion of the lobe due to an incomplete unfolding of the tissues at the base of the asulcate surface of the lobe (seen in D).

spite of results of Hollis' analysis, the overlap present on states 3 and 5 hinder the use of this character as diagnostic. It should be noted that polymorphic characters cannot support the differentiation between groups alone because the same character distribution could be more parsimoniously interpreted as evidence for the existence of only one polymorphic taxon, instead of the existence of two polymorphic, yet phenotypically overlapping, taxa.

Chironius multiventris and *C. cochranae* have the same hemipenial pattern: a unilobed, calyculate hemipenis, with a centrolineal sulcus spermaticus, and a globular lobe covered by papillate calyces. Calyces decrease in size toward the distal area of the hemipenis. Spines that gradually increase in size toward

the base uniformly cover the hemipenial body. The base is covered by spinules (Fig. 4). Despite general similarity, Hollis (2006) used three hemipenial characters to diagnose *C. multiventris* and *C. cochranae*: (1) the number of central spines on dorsal surface, (2) the number of calyces on the dorsal surface, and (3) the number of subcaudals to which the everted hemipenis extends. Our analysis reveals evident overlap between both species: in *C. cochranae*, the number of spines per row is 7, calyces on the dorsal surface are 9–11, and the everted hemipenis extends to subcaudals 5–6; in *C. multiventris*, the number of spines per row varies from 5–7, calyces on the dorsal surface are 8–10, and the everted hemipenis extends to subcaudals 5–7.

Moreover, all analyzed specimens show the same color pattern: a brownish-yellow head, especially around the temporal area, that turns into a greenish brown in the dorsum; two dark brown lines following the keels of the paravertebral scales; and ventral scales strongly angled, light yellow, darkening toward the edge of the scales.

Conclusion

Hollis (2006) proposed the separation of *C. multiventris* and *C. cochranae* mainly based on a phylogenetic analysis of gap-weighted and frequency-coded characters. The reanalysis of the autapomorphies pointed out by Hollis as diagnostic of these species shows that the selected characters are not able to distinguish one taxa from the other. The mismatch between our results and Hollis' could be due to "nonsense distinctions" (sensu Farris, 1990) introduced by the use of gap-weighted continuous characters. Gap-weighting has been criticized as being arbitrary, and possibly misleading in phylogenetic analyses and their subsequent conclusions (Rae, 1998). The use of polymorphisms has also been debated (e.g., Murphy and Doyle, 1998; Smith and Gutberlet, 2001; Wiens, 1995, 1999) and interpretations drawn from such analysis should be handled with care.

Each of the 14 characters analyzed supports the conclusion reached by Cunha and Nascimento (1982) that *C. multiventris* and *C. cochranae* are in fact conspecific. We thus suggest considering *C. cochranae* Hoge and Romano, 1969 as a junior synonym of *C. multiventris* Schmidt and Walker, 1943.

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APPENDIX 1

Specimens Examined

Chironius cochranae (n = *6*).—**BRAZIL:** AMAZONAS: Fortaleza, Paraná do Urariá, 03°30′S, 58°02′W (MZUSP 5239). MARANHÃO: Aldeia Araçu, Igarapé Gurupí-Una, 02°35′S, 46°05′W (MZUSP 4293, 4827). Rodovia Belém-Brasília, km 93 (MZUSP 3739). PARÁ: Canindé, Rio Gurupi, 02°33′S, 46°31′W (MZUSP 4258); Monte Cristo, Rio Tapajós, 04°04′S, 55°39′W (MZUSP 5151).

Chironius multiventris (n = *28*).—**BRAZIL:** ACRE: Porto Walter, 08°16′S, 72°44′W (MZUSP 7391). AMAPÁ: Rio Maracá (boca do Igarapé Camaipi), 00°26′S, 51°26′W (MZUSP 11717). AMAZONAS: Balbina, 01°53′S, 59°28′W (MZUSP 9641); Estrada ZF-3, km 13 (MZUSP 8473); Igarapé, Belém, 0355′S, 69°37′W (MZUSP 4413); Manaus, 03°07′S, 60°00′W (MZUSP 3716); Moura, 01°30′S, 61°40′W (MZUSP 5230); Prainha, Rio Aripuanã, 07°16′S, 60°24′W (MZUSP 5196); Reserva INPA-WWF, 02°25′S, 59°43′W (MZUSP 8472, MZUSP 8660). PARÁ: Juruá, Rio Xingu, 03°24′S, 51°53′W (MZUSP 9343); Serra de Kukoinhokren (MZUSP 10685, MZUSP 10976); Uruá (Parque Nacional da Amazônia), Rio Tapajós, 04°37′S, 56°15′W (MZUSP 7288, MZUSP 7289). RONDÔNIA: Cacoal, 11°27′S, 61°24′W (MZUSP 8732); Nova Brasília, 11°09′S, 61°34′W (MZUSP 8738). RORAIMA: Apiaú, 02°40′S, 61°15′W (MZUSP 9775, MZUSP 10295); BR-174, Marco de fronteira BV-8, 04°30′S, 61°09′W (MZUSP 10474); Serra dos Surucucus, 02°50′S, 63°38′W (MZUSP 10368); Cachoeira do Cujubim, Rio Catrimani, 1°45′S, 62°17′W (MZUSP 8027). **PERU:** LORETO: Rio Itaya, 03°45′S, 73°06′W (MZUSP 7846).

APPENDIX 2

Hemipenes Examined

Chironius cochranae (n = *1*).—MZUSP 10553.

Chironius multiventris (n = *2*).—MZUSP 7289; KU 126009.