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Taxonomic Revision of *Chironius bicarinatus* (Wied 1820) (Serpentes: Colubridae), with Description of a New Species

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ABSTRACT: *Chironius bicarinatus* is a conspicuous colubrid snake species, widely distributed in northeastern, southeastern, central-western, and southern Brazil, as well as Paraguay, Argentina, and Uruguay. On the basis of new morphological data of individuals from previously unsampled regions and deoxyribonucleic acid sequences, we reviewed the taxonomy of populations previously referred to as *C. bicarinatus*, revisiting the species definition with an updated diagnosis, inferring its phylogenetic relationships with closely related lineages in southern Brazil, herein described as a new species restricted to Pampa forests or grasslands and Atlantic Forest semideciduous forests in southern Brazil. The new species can be readily diagnosed from *C. bicarinatus* and all other congeners on the basis of internal (hemipenis unilobed, unicalyculate, cylindrical, apex with smooth calyces, with spinules restricted to proximal portion, near the medial area; lacrimal foramen with small projection on the anteroventral margin) and external morphology (ventrals 153–165 [153–165 in males, 155–164 in females]; subcaudals 103–146 pairs [129–142 in males, 103–146 in females]); adult dorsal pattern with dark green background, scales sometimes with light blue margin, two conspicuous black dorsal stripes with light green vertebral stripe between them that gradually dissipates to the tail, ventrals with black margin on its edges) and molecular evidence.

Key words: Micro-CT; Molecular; Morphology; Neotropical; Osteology; Phylogeny; Squamata; Taxonomy

THE SIPO RACERS of the genus *Chironius* Fitzinger are diagnosed as medium- to large-sized, terrestrial–arboreal, aglyphous, oviparous colubrids, being the only Neotropical snake genus with 10–12 dorsal scale rows at midbody; its hemipenis has a single sulcus and lobe, proximal naked pocket, is centrally spinous, distally calyculate, acapitate, and without apical disks (Dixon et al. 1993). Currently the genus includes 22 species, distributed from Central America, in the northern coast of Honduras, to most of South America at the east of the Andes, in Uruguay, and northeast Argentina (Dixon et al. 1993; Hollis 2006; Fernandes and Hamdan 2014; Klaczko et al. 2014; Wallach et al. 2014; Hamdan and Fernandes 2015), of which 15 are known to occur in Brazil (Costa and Bérnils 2018). The genus has presented significant taxonomic instability in previous centuries, being previously referred to as *Coluber* (Linnaeus 1758; Wied 1820), *Natrix* (Wagler 1824), *Erpetrodryas* (Boie 1826, 1827), *Herpetodryas* (Wagler 1830 in Spix 1830), *Macrops* (Wagler 1830 in Spix 1830), *Hylophis* (Fitzinger 1843), *Dendrophis* (Duméril et al. 1854), *Phyllosira* (Cope 1862), *Spilotes* (Peters and Orejas-Miranda 1970), and *Zaocys* (Werner 1896). In the first comprehensive taxonomic revision of *Chironius* sensu stricto (Bailey 1955), seven taxa and a new subspecies for the genus were recognized; this work was followed by an extensive systematic and morphological revision based solely on external and internal morphological characters (Dixon et al. 1993), where the authors described four new species. Later, Hollis (2006) conducted a morphological phylogeny based largely on the data of Dixon et al. (1993), the results of which supported the monophyly of *Chironius*. This work was then succeeded

by a phylogeny of combined morphological and molecular data of Klaczko et al. (2014), which also supported the previous arrangements. In a more recent work, Hamdan et al. (2017) provided a coalescent-based and a dated phylogeny of the genus, unraveling its putative origin in the early Miocene, and highlighting some cryptic lineages within it.

Chironius bicarinatus Wied 1820 is a conspicuous, small to medium-sized colubrid species, described on the basis of an unknown type specimen, from “sand beach of Lagoa, near the Rio Jacú, within 5 legoas of Villa do Espírito-Santo,” in the state of Espírito Santo, southeastern Brazil (Dixon et al. 1993:59). On the basis of literature records, this species is known to inhabit gallery and coastal forests, tropical rain forests, and deciduous mesophytic subtropical forests in northeastern, southeastern, central-western, and southern Brazil, as well as Paraguay, Argentina, and Uruguay (Bailey 1955; Dixon et al. 1993; Guedes et al. 2014; Cacciali and Cabral 2015). It has diurnal, terrestrial, and arboreal habits, preying upon amphibians, birds, and lizards, which it actively forages over the forest substrate (Dixon et al. 1993). *Chironius bicarinatus* was briefly mentioned in its original description (Wied 1820:181), with a holotype said to have 155 ventrals and 137 subcaudals; further works from the author (Wied 1824) do assist in diagnosing the species (a colored plate is presented in Wied [1824]; four specimens are mentioned in Wied [1825], although none of them has the same counts as the holotype).

Subsequent works (e.g., Bailey 1955; Dixon et al. 1993) have addressed it as an easily diagnosable, common, and widely distributed species. Dixon et al. (1993:66) remarks, “Two subspecies may be represented in *C. bicarinatus*: a southern form inhabiting gallery forest and available coastal forests and a northern form in tropical rain forest and

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deciduous mesophytic subtropical forest. Further studies incorporating more specimens from the southern part of the range are necessary to clarify this situation.” Dixon’s remark would prove to be particularly provocative, as upon encountering a specimen of *C. bicarinatus* during the 7th Brazilian Congress of Herpetology, hosted in Gramado, Rio Grande do Sul, southern Brazil, discussion arose among the authors as to whether it was actually a *C. bicarinatus* or not—the specimen, from the Araucaria moist forests of southern Brazil, indeed differed from those usually found at the Atlantic tropical rain forests at southeastern and northeastern Brazil. Prompted by such discussion, we revisit the definition of *C. bicarinatus* on the basis of the examination of new specimens, providing an emended diagnosis for the species, while investigating its phylogenetic and taxonomic relationships with formerly assigned populations in southern Brazil that are herein described as a new species on the basis of the integrative approach of molecular and morphological data.

MATERIALS AND METHODS

Molecular Analysis

For our molecular analyses we obtained sequences for new specimens of *C. bicarinatus* from the lowland Atlantic Forests of southeastern Brazil and from the Pampa grasslands of southern Brazil, in addition to other *Chironius* species. We pooled the new sequences with GenBank data of several *Chironius* taxa, avoiding combining sequences from different vouchers of the same *Chironius* species. Our final data set comprises 62 samples, representing 16 nominal species of *Chironius* and 9 outgroups (Appendix I).

We extracted total genomic deoxyribonucleic acid from liver or muscle tissues using a standard ethanol precipitation method adapted for microcentrifuges (ammonium acetate protocol, Maniatis et al. 1982). We generated sequences of two mitochondrial genes (12S ribosomal ribonucleic acid [rRNA] gene and 16S rRNA gene) and one nuclear gene fragment (oocyte maturation factor *mos*; *c-mos*). Primers and protocols follow Klackzko et al. (2014), except for 12Sa and 12Sb primers, based on Reeder (1995). We purified amplification products with enzymatic reactions and sequenced at Macrogen Inc. (Seoul, South Korea). Chromatograms were quality checked and trimmed with Geneious v6.0 (Biomatters, Ltd., Auckland, New Zealand). All sequences were deposited in GenBank.

Sequences were aligned using MAFFT v7.245 (Katoh 2013) with default parameters for gap opening and extension. The phylogenetic inferences were conducted under a maximum parsimony and maximum likelihood framework. The maximum parsimony analysis was performed in TNT v1.1 software (Goloboff et al. 2008) considering gaps either as a fifth state or as missing data, using equally weighted parsimony, traditional search, and 1000 bootstrap replicates. The maximum likelihood analysis was computed using RAxML software (Stamatakis 2014) in CIPRES Science Gateway (available at <https://www.phylo.org/>), considering each gene fragment as a different partition and searching the most likely tree 100 times and conducting 1000 nonparametric bootstrap replicates. The run was performed with the GTR + Γ model for all partitions.

Examined Specimens and Morphological Characters

We examined a total of 279 specimens formerly assigned to *C. bicarinatus*. In the field, we euthanized two specimens (CHFURG 4354, ZFMK 103132) with an injection of xylocaine to the heart, fixed them in 10% formalin, and preserved them in 70% ethanol. Ventral scales were counted according to Dowling (1951). A small scale between the temporals and postoculars, given its shape and size, is herein considered as a third or second postocular. Meristic and morphometric characters were selected on the basis of the nomenclature used by Dixon et al. (1993), and are as follows: head length, measured from center of rostral to the corner of mouth; head width, measured at the corner of mouth; snout-vent length (SVL), ventrally measured from center of rostral to the posterior margin of cloacal scale; tail length, measured from posterior margin of cloacal scale to terminal scale. Coordinates are given in WGS84 Datum. Head and tail measurements were taken with a dial caliper to the nearest 0.01 mm; for others, a flexible ruler was used. Speciation concepts follow de Queiroz (2005, 2007). Acronyms follow Sabaj (2016), except for Coleção Herpetológica, Universidade Federal de Rio Grande (CHFURG), Rio Grande, RS, Brazil; Coleção Herpetológica Universidade Federal do Ceará (CHUFC), Fortaleza, CE, Brazil; Coleção Zoológica Norte Capixaba (CZNC), São Mateus, ES, Brazil; Instituto Nacional da Mata Atlântica, previously known as Museu Biológico Mello Leitão (MBML), Vitória, ES, Brazil. Geographic distribution maps were performed with ArcMap 10 (ESRI, Redlands, CA, USA).

We conducted interspecific comparisons and tested for sexual dimorphism in meristic and morphometric data using Student’s *t* test and analysis of covariance (ANCOVA), respectively. We used an ANCOVA to test for differences in relative sizes of tail length and head length, using SVL as a covariate. We tested assumptions of normality and homogeneity of variance with the Shapiro-Wilk and Levene’s tests, respectively. In cases where characters showed insufficient variation to justify these assumptions, we performed the nonparametric Mann-Whitney *U* test (Zar 1999). Sample sizes are given as subscript before test values. We established $\alpha < 0.05$ for the statistical tests and performed all statistical inferences in R software v3.2.3 (R Core Team 2015).

Osteological descriptions of the skull of the new species were based on a high-resolution micro-computed tomography (CT) scan of the paratype specimen ZFMK 103132 performed with a Bruker SkyScan 1173 at ZFMK. The scan was conducted in 180° at rotation steps of 0.3° with a tube voltage of 43 kV and a tube current of 114 μ A, without the use of a filter, at an image resolution of 14.91 μ m. Scan duration was 39.44 min with an exposure time of 500 ms. The CT data set was reconstructed using N-Recon software v1.7.1.6 (Bruker MicroCT, Kontich, Belgium) and rendered in three dimensions through the aid of CTVox v2.6 for Windows 64 bits (Bruker MicroCT). Osteological terminology follows Bullock and Tanner (1966), Cundall and Irish (2008), and Hamdan and Fernandes (2015). We compared our osteological description with data available for Colubridae of Klackzko (2007), Klackzko et al. (2014), and Hamdan and Fernandes (2015).

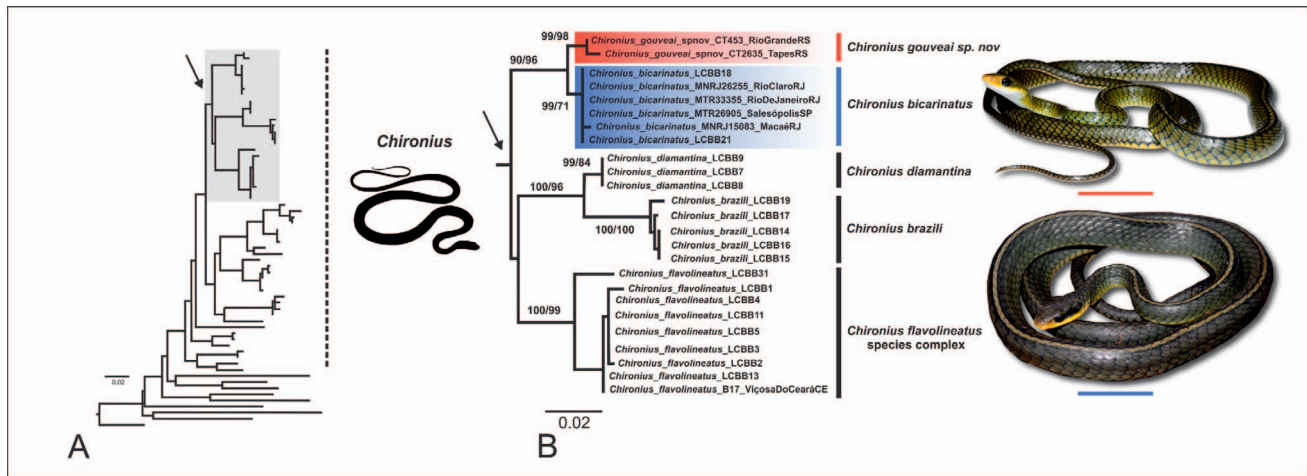


FIG. 1.—Maximum likelihood phylogenetic tree of *Chironius*, as inferred from molecular data. (A) Full topology, dashed line indicating *Chironius* genus terminals, arrow indicating clade of interest; (B) clade of interest, encompassing *C. bicarinatus*, *C. brazili*, *C. diamantina*, *C. gouveai*, and *C. flavolineatus* species complex. Node support values (bootstrap) of maximum likelihood/maximum parsimony are shown nearby nodes (values under 50 are not shown). Inset pictures: *C. gouveai* (green) and *C. bicarinatus* (red). Photos by D. Loebmann (top) and O. Marques (bottom).

RESULTS

Genetic Divergency and Monophyly Tests

The phylogenetic trees inferred using maximum likelihood and maximum parsimony (Fig. 1) recovered two strongly supported clades for *C. bicarinatus*: one from the Atlantic Forest lowlands of southeastern Brazil and the other from the Pampa grasslands of southern Brazil. We recovered a clade encompassing *C. bicarinatus*, a candidate new species, *C. brazili*, *C. diamantina*, and *C. “flavolineatus”* (Fig. 1B); this clade of interest will be referred to from now on as the “*C. bicarinatus* clade.” It should be noted that,

according to other studies (e.g., Hamdan et al. 2017), *C. flavolineatus* possibly represents a cryptic species complex, therefore justifying its relatively distant clade structure; it is treated here as the “*C. flavolineatus* species complex.” The relationships between other *Chironius* species were in general not well supported, as in previous works (Klackzko et al. 2014; Hamdan et al. 2017). The maximum parsimony analysis resulted in eight most parsimonious trees of length 1262 steps considering gaps as fifth state and in three most parsimonious trees of length 1133 considering gaps as missing data, and the maximum likelihood resulted in a final tree topology with a score $-lnL = -6786.3828$.

Our molecular analysis provided evidence for two monophyletic lineages of *C. bicarinatus*. We conducted a morphological revision to evaluate for morphological congruence among these individuals, which revealed that populations assigned to these clades are allopatric (Fig. 2) and have substantial morphological characterization (Fig. 3). In light of this, we provide a diagnosis for these two clades on the basis of internal and external morphology, and molecular evidence, considering as *C. bicarinatus* the lineages in southeastern, northeastern, central, and southern Brazil. We describe a new species restricted to the Araucaria moist forests and Pampas grasslands of southern Brazil and Uruguay.

Taxonomic Identity

According to Dixon et al. (1993:59), “A type specimen [for *Chironius bicarinatus*] was not found. It is not clear whether a holotype was designated,” and type series mentioned by Wallach et al. (2014) was not collected or used by Wied (M. Franzen, personal communication); however, as pointed out by Dixon et al. (1993), the description in Wied (1820) and the plate in Wied (1824) seem to perfectly match the general aspects of populations historically recognized as *C. bicarinatus*, “Corps élancé, comprimé un peu triangulaire; une série longitudinale d’écailles carenées de chaque côté du dos; partie supérieure du corps couleur d’un vert foncé d’olive ou de serin, partie

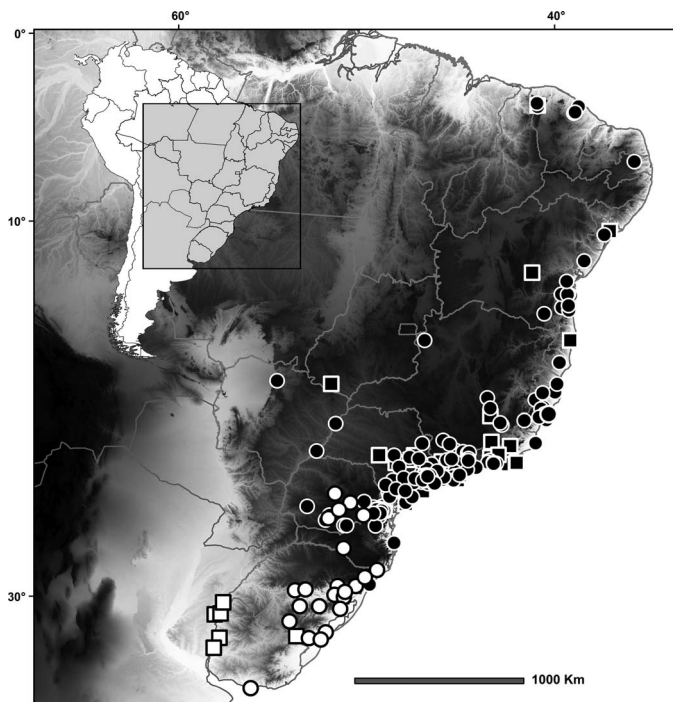


FIG. 2.—Geographic distribution of *Chironius bicarinatus* (black) and *Chironius gouveai* (white). Circles = examined specimens; squares = literature records.

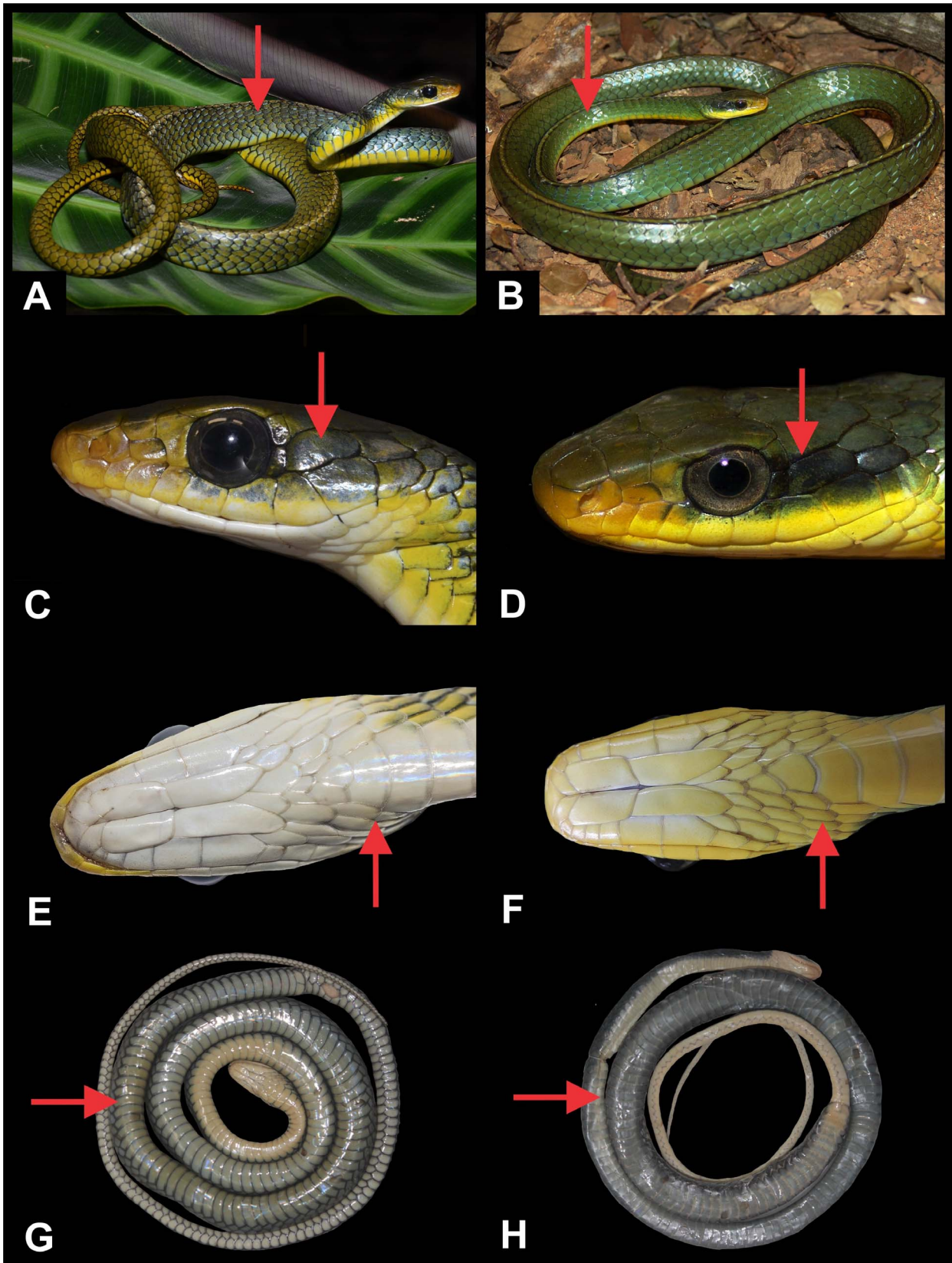


FIG. 3.—Comparative morphology of *Chironius gouveai* and *C. bicarinatus*. (A) Dorsal view of adult *C. gouveai* (ZFMK 103132, paratype, snout–vent length [SVL] 720 mm); (B) dorsal view of adult *C. bicarinatus* (unvouchered, Instituto Butantan); (C) lateral head view of same *C. gouveai* individual; (D) lateral head view of same *C. bicarinatus* individual; (E) ventral head view of *C. gouveai* (CHFURG 4394, holotype, head length 14 mm); (F) ventral head view of *C. bicarinatus* (unvouchered, Instituto Butantan); (G) ventral view of *C. gouveai*, with conspicuous ventral black scale margins (MCP 8968, paratype, SVL 840 mm); (H) ventral body view of *C. bicarinatus*, with uniform unmarked pattern (ZUFSM 1571, SVL 680 mm). Photos by D. Loebmann (A, B, C, D), G. Puerto (F), and O.M. Entiauspe-Neto (E, G, H). A color version of this figure is available online.



FIG. 4.—Illustration of *Chironius bicarinatus*, reproduced from Wied (1824). This individual has a dark green dorsum and immaculate yellow tail, characteristic of the Atlantic rain forest specimens. A color version of this figure is available online.

inférieure d'un j'aune pâle; dessous de la tête, de la queue et le gosier d'un jaune vif [...] 155 à 159 plaques abdominales; 101 à 137 paires de plaques caudales" (Wied 1820 in Wied 1824, in litteris); English translation, "Slender body, compressed in a triangular shape; a longitudinal series of carinated scales in each side of the body; upper body surface dark olive green or canary, inferior surface pale yellow; under the head, head and tail bright yellow [...] 155 to 159 abdominal (ventral) plates; 101 to 137 pairs of caudal (subcaudal) plates."

The type locality is given as "a sand beach of Lagoa, near the Rio Jacú, within '5 legoas' (leagues) of Villa do Espírito-Santo (sic), Estado Espírito Santo, Brazil." It is unclear whether the authors were referring to a municipality named "Lagoa," or actually attributing its type locality to a lagoon (in Portuguese, called "Lagoa") near the Rio Jacú (Dixon et al. 1993:59). According to Bailey (1955:8), the said locality is "a few miles south of Victória, Espírito Santo."

The original description (Fig. 4) allows us to safely identify individuals of *C. bicarinatus*; in light of this, we present here an emended diagnosis, morphological description (based on [CHFURG 4882, Ex-MNRJ 10976, from Parque Natural Municipal Serra do Mendanha, Nova Iguaçu 22°45'37.1"S, 43°26'51.8"W], Rio de Janeiro state, southeastern Brazil), hemipenis description, and updated geographic distribution for the species. This specimen was selected for being an adult individual (as the original type series), collected close to its type locality, and in good

preservation state, which should better represent the morphological characteristics from this species.

Species Accounts

We detected sexual dimorphism in the *C. bicarinatus* clade in the number of ventral scales ($U_{24,29} = 812$, $P < 0.001$). Therefore, we treat this variable separately between sexes in subsequent interspecific analyses. The number of ventral scales was less numerous in *C. gouveai* males ($t_{15,8} = 2.311$, $P = 0.031$), but we failed to find a difference between females of *C. gouveai* and *C. bicarinatus* ($U_{12,16} = 232$, $P = 0.292$). We failed to encounter differences between *C. gouveai* and *C. bicarinatus* in number of subcaudal scales ($U_{22,25} = 350$, $P = 0.110$), tail length ($F_{19,20} = 0.596$, $P = 0.445$), or head length ($F_{19,20} = 0.419$, $P = 0.521$). We did not detect sexual dimorphism in *C. gouveai* for ventral ($t_{15,12} = 1.620$, $P = 0.117$) and subcaudal scales ($t_{13,9} = 0.740$, $P = 0.467$), tail length ($F_{9,10} = 2.795$, $P = 0.115$), or head length ($F_{9,10} = 1.248$, $P = 0.281$). We detected sexual dimorphism for *C. bicarinatus*, as females have a higher number of ventrals ($t_{8,16} = 4.702$, $P < 0.001$) and males have a higher number of subcaudals ($U_{9,16} = 20$, $P = 0.003$), although we failed to encounter difference for tail length ($F_{10,10} = 0.332$, $P = 0.573$) or head length ($F_{10,10} = 0.997$, $P = 0.332$).

It should be noted that Almeida-Santos and Marques (2002) reported a marked sexual dimorphism for SVL in field-collected specimens of *C. bicarinatus* related to male-male ritual combat in this species. For our analyzed specimens, the maximum SVL for males (840 mm in *C. gouveai*, 700 mm in *C. bicarinatus*) and females (860 mm in *C. gouveai*, 890 mm in *C. bicarinatus*) present very similar values between both species.

Chironius bicarinatus (Wied 1820)

(Figs. 1–5, 8)

Coluber bicarinatus Wied 1820:181. Unknown type series, likely lost, from "sand beach of Lagoa, near the Rio Jucú, within 5 leagues of Villa do Espírito Santo, Espírito Santo, Brazil," restricted to "south of Victória, Espírito Santo" by Bailey (1955). Merrem 1820:177; Boie 1826:237; Wagler 1830:180; Bailey 1955:8; Dixon et al. 1993:59.

Emended diagnosis.—*Chironius bicarinatus* can be distinguished from all its congeners by the following combination of characters: (1) 12/12/10 dorsal rows, two keeled rows, and two apical pits (sometimes 13/13/10, 14/13/10, 12/10/10, 10/10/10); (2) preoculars usually one (rarely two); (3) postoculars usually two (rarely three); (4) loreal present, single, rectangular; (5) temporals 1+1 or 1+2 (rarely 1+1+1, 1+1+2); (6) supralabials eight to nine, with fourth, fifth, and sixth in contact with orbit; (7) infralabials 7–10, with 1–4 in contact with chin shield; (8) ventrals 146–172 (146–163 in males, 157–172 in females); (9) subcaudals 129–155 pairs (136–155 in males, 132–172 in females); (10) adults have dorsal pattern with dark green background, scales sometimes with light blue margin, two conspicuous black dorsal stripes with light green vertebral stripe between them that gradually dissipates to the tail, snout orange or yellow, supralabials and infralabials vivid yellow, ventrally uniform yellow or dark green, juveniles with alternating dark green and white crossbands (in preservative, green surfaces turn



FIG. 5.—Specimens in life of *Chironius bicarinatus*. (A) Adult individual, unvouchered, São Roque, SP, Brazil; (B) subadult individual (IB 17044, snout-vent length [SVL] 480 mm), São Paulo, SP, Brazil; (C) adult individual (IB 59416, SVL ca. 800 mm), Araçariçuama, SP, Brazil; (D) newborn individual, unvouchered, Natividade da Serra, SP, Brazil; (E) subadult individual, São Paulo, SP, Brazil; (F, G) adult individual, unvouchered, SVL ca. 1000 mm, Ubatuba, SP, Brazil). Photos by O. Marques (A, B, C, D), A. Abegg (E, F), and E. Muscat (G, H). A color version of this figure is available online.

gray or blue, and yellow surfaces turn white); (11) ventral pattern immaculate yellow on the first body third, gradually turning light green to tail; (12) body size moderate, SVL 220–890 mm; (13) head length 2.5–4.5% of SVL; (14) tail length large, 59–62% of SVL; (15) hemipenis unilobed, unicalyculate, cylindrical, covered with spinulate calyces on apex and second body third.

Description.—Cervical construction distinct; head well distinct from neck, narrow anteriorly, slightly triangular in dorsal view, arched in lateral view, widest at parietal region; snout round in dorsal and lateral view; rostral broader than long, visible from above; internasals square shaped, slightly smaller than prefrontals, in contact with nasals, symmetric at both medial sutures; prefrontals larger than internasals, as long as wide, wide, separated from eye by supraocular and preocular; frontal pentagonal and bell shaped; nasal divided; nostril located between prenasal and postnasal; loreal in contact with second and third supralabials; eye large, round pupil; postoculars 1+1 (94.1%), 1+2 (5.9%); temporals 1+1 (79%), 1+2 (15%), 1+1+1 (3%), or 1+1+2 (3%); supralabials eight (61%), nine (39%), with fourth to sixth in contact with orbit, first in contact with nasals, second in contact with loreal, third in contact with loreal and preocular, fourth in contact with preocular and eye orbit, fifth in contact with orbit, sixth in contact with orbit, postocular and temporal, seventh, eighth, and ninth in contact with temporals; infralabials seven (5%), 8 (72%), 9 (20.4%), 10 (2.6%), with first five in contact with chin shield; three to six gular scale rows; one to four preventral scales; 12/10/10 (34%), 12/12/10 (56%), 13/13/10 (5%), 10/10/10 (2.5%), 14/13/10 (2.5%), keeled dorsal scales rows; ventrals 146–172 (146–163 [157 ± 5.19] in males, 157–172 [162 ± 3.6] in females); subcaudals 129–158 pairs (136–155 [143 ± 4.9] in males, 132–172 [134 ± 5] in females). Body size moderate, SVL 220–890 mm (460–700 in males, 550–890 in females).

Coloration in preservative.—Dorsal surface of head uniform dark gray, up to parietals; rostral, nasals, loreal, and supralabials have white coloration; supralabials 2–9 display dark gray and blue pigmentation in almost straight longitudinal line; ventral head surface is immaculate white, except for gray pigmentation on gular scale rows; first third of ventral coloration is white, with vestigial gray pigmentation on the edges of ventral scales, from 3 to 20, where these become uniform bluish gray to caudal scale; tail is ventrally white, with black margins restricted to suture between subcaudal scale pairs; dorsal coloration uniform bluish gray; after the 10th dorsal scale rows behind the neck there are two black stripes with a clear vertebral stripe, which gradually dissipates to the tail.

Distribution and natural history.—*Chironius bicarinatus* is currently endemic to Brazil, being recorded in central-western (Mato Grosso do Sul, Goiás states), northeastern (Bahia, Ceará, Paraíba, Sergipe states), southeastern (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo states), and southern (Paraná, Rio Grande do Sul, Santa Catarina states) regions. It should be noted that, in its southernmost range, in Rio Grande do Sul, this species occurs strictly on the Atlantic tropical rain forest of Dom Pedro de Alcântara and Torres municipalities, being sympatric with *C. cf. exoletus* and *C. foveatus*. For accounts on its natural history, see Marques and Duleba (2004).

In addition to localities of examined specimens (Appendix II), *C. bicarinatus* has also been recorded by other authors to Bahia (Andaraí, Dixon et al. 1993; Porto Seguro, Franco et al. 1998); Ceará (Ubajara, Loebmann and Haddad 2010); Goiás (Aporé, Vaz-Silva et al. 2007); Minas Gerais (Caman-ducaia, Juiz de Fora, Passa Quatro, Dixon et al. 1993); Rio de Janeiro (Cabo Frio, Cantagalo, Teresópolis, Dixon et al. 1993; Maricá, Rocha and Vrcibradic 1998; Nova Iguaçu, Realengo, Rio de Janeiro, Bailey 1955); and São Paulo (Botucatu, Bailey 1955; Cabrália Paulista, Dixon et al. 1993; Ilha do Cardoso, Cananéia, Rocha et al. 2008; Caraguatatu-ba, Dixon et al. 1993; Cordeirópolis, Dixon et al. 1993; Embu, Dixon et al. 1993; Ilhabela, Dixon et al. 1993; Jandira, Dixon et al. 1993; Natividade da Serra, Marques and Duleba 2004; Juréia-Itatins, Peruíba, Marques and Duleba 2004; Piracicaba, Dixon et al. 1993; Salesópolis, Dixon et al. 1993; Paranapiacaba, Santo André, Bailey 1955; Dixon et al. 1993; Ilha de Búzios, São Sebastião, Dixon et al. 1993; São Luís do Paraitinga, Serra do Mar, Hartmann et al. 2009; São Miguel Arcanjo, Dixon et al. 1993).

Hemipenis (Fig. 8).—Organ unilobed, unicalyculate, cylindrical. Apex with large spinulate calyces throughout its whole surface. Second third of hemipenis bearing a strong constriction, with small spines covering its entire surface. Large to medium-sized hooked spines on the first third of the organ that abruptly reduce in size into small spines on the medial constriction. Sulcus spermaticus simple, centro-lineal, located at the concave surface of the organ, positioned laterally at the basal portion of hemipenis, more centralized at the apical portion. Basal portion naked.

Chironius gouveai sp. nov.
(Figs. 1–3, 6–9)

Chironius bicarinatus: Dixon et al. 1993:59; Achaval and Olmos 1997:68; Lema 2002:55; Carreira et al. 2005:99 (in part, misidentification).

Holotype.—CHFURG 4394 (tissue sample CT2635), collected by Fernando Marques Quintela, an adult male from Tapes (30°28'46.7"S; 51°23'46.1"W), Rio Grande do Sul, Brazil (Figs. 1, 2, 4).

Paratypes.—ZUFMS 2908, roadkill adult male, collected by Vinícius Caldart and Samanta Iop on 25 April 2011 on Bagé municipality, Rio Grande do Sul, Brazil; ZFMK 103132 (Ex-CHFURG 1504; Fig. 6C,D; tissue sample CT453), adult male collected by Daniel Loebmann on 3 February 2012, Rio Grande municipality, Rio Grande do Sul, Brazil; MCP 2631, an adult female collected by Marcos Di-Bernardo on 17 October 1987 at Rodeio Bonito, São Francisco de Paula municipality, Rio Grande do Sul, Brazil; CHFURG 4823, 4824, adult male and female collected by Marcelo Burns on an unknown date of 2016 at Ilha da Torotama, Rio Grande municipality, Rio Grande do Sul, Brazil; MCP 8968 an adult male collected by students of the Gomerinda Dornelles Fountoura school on an unknown date, Encruzilhada do Sul municipality, Rio Grande do Sul, Brazil; MCP 12762, an adult male collected by Felipe Quadros on 24 January 2002 at Corsan-Sitel, Triunfo municipality, Rio Grande do Sul, Brazil.

Common name.—Proposed standard English name: Gouvea's Sipo. Proposed standard Portuguese name: Cobra-cipó de Gouvêa.

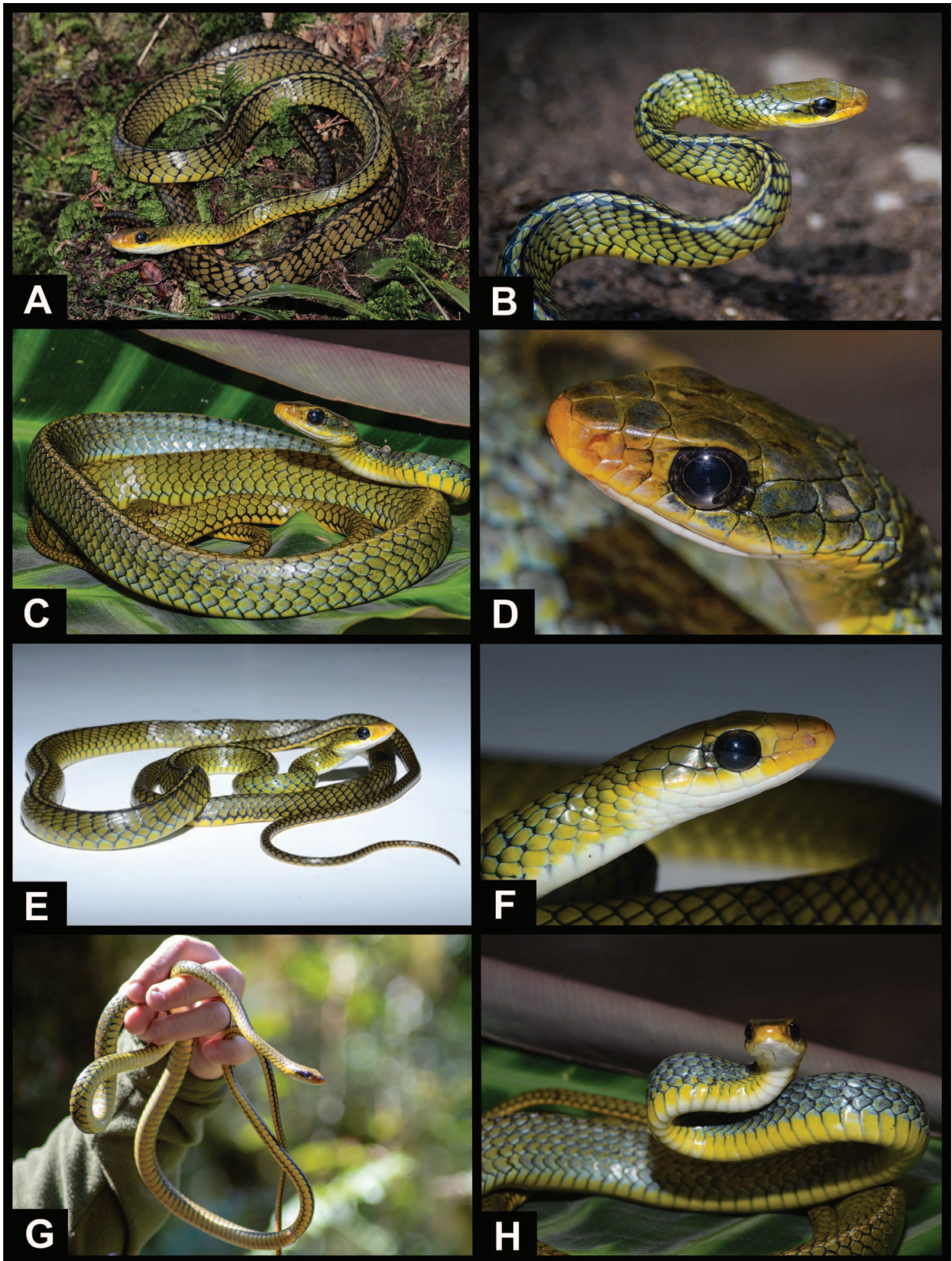


FIG. 6.—Specimens in life of *Chironius gouveai*. (A, B) Unvouchered, Cambará do Sul, RS, Brazil; (C, D) paratype (ZFMK 103132, snout–vent length [SVL] 670 mm), Rio Grande, RS, Brazil; (E, F) holotype (CHFURG 4394, SVL 790 mm), Tapes, RS, Brazil; (G) ventral view of unvouchered individual, Cambará do Sul, RS, Brazil; (H) striking posture, paratype (ZFMK 103132, SVL 670 mm). Photos by O.M. Entiauspe-Neto (A), L.M. Borges (B, G), D. Loebmann (C, D, E, F, H). A color version of this figure is available online.

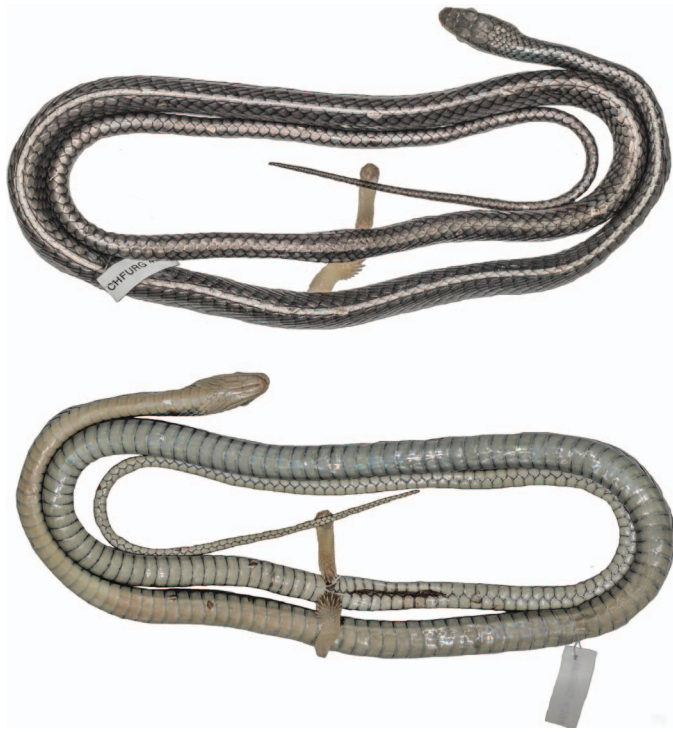


FIG. 7.—Holotype of *Chironius gouveai*. Dorsal (top) and ventral (bottom) views (CHFURG 4394). Photos by O.M. Entiauspe-Neto. A color version of this figure is available online.

Etymology.—The species etymology *gouveai* honors Paulo Roberto Cardoso Gouvêa, first author's grandfather, who is largely responsible for his scientific career, and has been the most significant source of inspiration, ethics, and funding for the author's research since then. The name is treated as a noun in apposition.

Definition and diagnosis.—*Chironius gouveai* is distinguished from all its congeners by the following combination of characters: (1) 12/12/10 dorsal scales; (2) preocular single; (3) two postoculars; (4) loreal present, single, rectangular; (5) temporals 1+1 (rarely 1+2); (6) supralabials 8–10, with fourth to sixth in contact with orbit; (7) 8–10 infralabials, with first to sixth in contact with chin shields; (8) ventrals 153–165 (153–165 in males, 155–164 in females); (9) subcaudals 103–146, paired (129–142 in males, 103–146 in females); (10) dorsal coloration background olive green, with black margins and diffuse blue pigmentation, with two longitudinal black stripes and light yellow vertebral stripe, which gradually dissipates to the tail (in preservative, olive green surfaces turn metallic gray and yellow surfaces turn white); (11) ventral surface immaculate white, with discrete black margins on the ventral scales, second third with olive green background, gradually becoming yellow, and black margins on ventral scales, last third with yellow background coloration and strong black margins, on ventral and subcaudal scales; (12) body length moderate, SVL 170–860 mm; (13) head length moderate, 2.44–5.45% of SVL; (14) tail length large, 47–63% of SVL; (15) hemipenis unilobed, unicalyculate, cylindrical, apex with smooth calyces, with spinules restricted to proximal portion, near the medial area; (16) lacrimal foramen with small projection on the anteroventral margin.

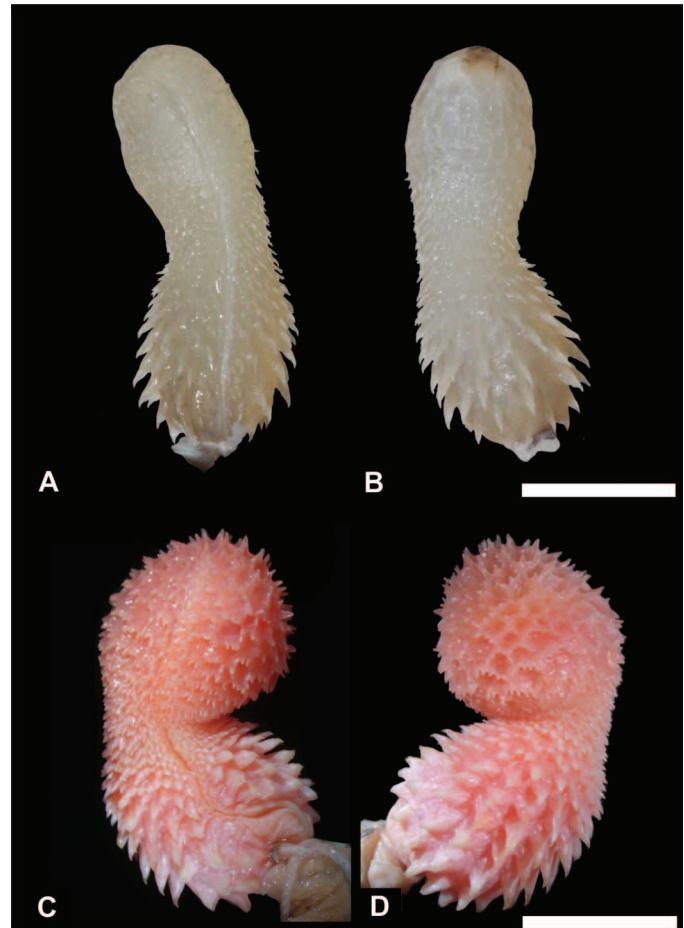


FIG. 8.—Hemipenis of *Chironius gouveai* and *C. bicarinatus*. (A) Sulcate side, (B) asulcate side (CHFURG 4394, holotype of *C. gouveai*); (C) sulcate side, (D) asulcate side (IB 55660, *C. bicarinatus*). Scale bars = 1 cm. Photos by O.M. Entiauspe-Neto (A, B) and J. Klaczko (C, D). A color version of this figure is available online.

Comparisons.—The new species is distinguished from *C. bicarinatus* (characters in parentheses) on the basis of the presence of strong black margins on the ventral scales, usually more visible near the tail (absent), white gular coloration in life (yellow), reticulated dorsal pattern in adults (uniform green), dorsal pattern with scattered black blotches in juveniles (black transversal bars), absent or vestigial postocular stripe (present on adults and juveniles, rarely vestigial on juveniles), hemipenis smooth calyculate apex (spinulate calyces), presence of lacrimal foramen with a small projection on the anteroventral margin (absent), presence of ventral expansion of the septomaxillary wall (absent), anterior portion of the supratemporal bone surpassing the parietal–pro-otic suture (posterior or above suture), posterior portion of supratemporal slightly curved (straight). Further comparisons are made in Table 1. It is also noteworthy that the new species is, to our current knowledge, not sympatric with *C. bicarinatus* in most of its range, having a small contact zone in the Araucaria moist forests of Paraná, southern Brazil.

The new species differs from *C. fuscus*, *C. leucometapus*, *C. grandisquamis*, and *C. scurrulus* in having 12/12/12 or 12/12/10 dorsal scale rows ([16–13]/12/[10–8]; 10/12/10; 10/10/10; 10/10/8); from *C. brazili*, *C. carinatus*, *C. diamantina*, *C.*

TABLE 1.—Comparative character set and variation between *Chironius gouveai* and *C. bicarinatus*. We present ranges followed by mean \pm 1 SD in parentheses.

	<i>C. gouveai</i> (n = 35)				<i>C. bicarinatus</i> (n = 44)			
	Males (n = 15)	Females (n = 12)	Unsexed juveniles (n = 8)	Males (n = 12)	Females (n = 17)	Unsexed juveniles (n = 15)		
Maximum snout-vent length (SVL)	840	860	340	700	890	300		
Minimum SVL	590	780	170	460	550	220		
Ventrals	153–165 (158 \pm 4.64)	155–164 (160 \pm 4.72)	153–160 (156 \pm 5)	146–163 (157 \pm 5.19)	157–172 (162 \pm 3.6)	147–168 (155 \pm 5.2)		
Subcaudals	129–142 (134 \pm 5.90)	103–146 (127 \pm 2)	136–141 (139 \pm 2)	136–155 (143 \pm 4.9)	132–172 (134 \pm 5)	129–158 (144 \pm 11.5)		
Postoculars	1+1	1+1	1+1	1+1	1+1 (94.1%)	1+1		
Temporals	1+1 (93.3%), 1+2 (6.66%)	1+1 (66.6%), 1+2 (33.3%)	1+1	1+1 (50%), 1+2 (41.7%), 1+1+2 (8.3%)	1+1 (88%), 1+2 (12%)	1+1 (93.3%), 1+1+1 (6.6%)		
Supralabials	9 (93.3%), 10 (6.6%), 4–6 in contact with orbit	8 (8.3%), 9 (91.6%), 4–6 in contact with orbit	9, 4–6 in contact with orbit	8 (33.3%), 9 (66.7%), 4–6 in contact with orbit	8, 4–6 in contact with orbit	8 (40%) 9 (60%), 4–6 in contact with orbit		
Infralabials	8 (93.3%), 10 (6.7%)	8 (91.7%), 9 (8.3%)	8 (12.5%), 9 (87.5%)	8	7 (5.8%), 8 (35.3%), 9 (52.9%), 10 (5.8%)	7 (6.66%), 8 (93.3%)		
Dorsal scale rows	12/12/10	12/12/10	12/12/10	12/12/10	12/10/10 (88.4%), 13/13/10 (5.8%), 10/10/10 (5.8%)	12/12/10 (86.6%), 13/13/10 (6.66%), 14/13/10 (6.66%)		
Strong black margin on ventrals	Present	Present	Present	Absent	Absent	Absent		
Black margins on dorsal scale rows	Present	Present	Present	Absent	Absent	Absent		
Hemipenis apex	Smooth calyculate	—	—	Spinulate calyces	—	—		

dixonii, *C. flavolineatus*, *C. flavopictus*, *C. foveatus*, *C. maculiventris*, *C. laevicollis*, *C. monticola*, *C. multiventris*, *C. quadricarinatus*, *C. spixii*, and *C. vincenti* in having a unique dorsal coloration composed of olive green background, with black margins and diffuse blue pigmentation, with two black stripes with a clear vertebral stripe, which gradually dissipates to the tail (distinct combinations of uniform green, black, red, olive or brown, with vertical bands, horizontal stripes, light markings or fleckings).

The distinction between the new species and *C. exoletus* has been proven as challenging in preserved specimens, considering the convoluted taxonomic status of the latter species; as pointed out by Giraud (2001), the diagnostic dorsal scale row formulae provided by Dixon et al. (1993) encompasses the intraspecific variation of *C. bicarinatus*. Considering that *C. exoletus* has an immense geographic distribution range, from Costa Rica and Panama to most of the South America east and west of the Andes, with its southernmost records at Argentina and southern Brazil, added to its extensive intraspecific variation, we herein refer to *C. exoletus* as strictly the type series of Linnaeus (1758), the specimen ZMUU 135, redescribed by Hoge et al. (1978), tentatively assigning the sympatric populations somewhat congruent with the former description as *C. cf. exoletus*, to avoid creating taxonomic instability within the group. A taxonomic revision of this species is currently underway, and this group likely constitutes a species complex (V. Sudre, personal communication).

The new species is distinguished from *C. exoletus* on the basis of its coloration pattern (uniform clear brown with bluish gray on the nuchal region), infralabial scale counts (11 infralabials with first five in contact with anterior mentonian scale), and dorsal scale counts (14/12/8 smooth dorsals).

Chironius gouveai can also be distinguished from the sympatric *C. cf. exoletus* populations on the basis of its dorsal scale rows (12/12/8 or 12/10/10), distinct dorsal coloration and pattern (uniform bluish gray top of head in preservative, dark olive green in life, with irregular black and white blotches over a brown and olive background on the dorsum), and hemipenis morphology (spinulate calyces on its distal portion).

Description of holotype.—Adult male; total length 1290 mm; SVL 790 mm; tail length 500 mm (38.75% of total length); head length 14.31 mm (18.11% of SVL, 11.09% of total length); head width 12.56 mm (87.77% of head length); interorbital distance 10.24 mm; rostro-orbital distance 9.58 mm; naso-orbital distance 5.28 mm; cervical construction distinct; head well distinct from neck, narrow anteriorly, slightly triangular in dorsal view, arched in lateral view, widest at parietal region; snout round in dorsal and lateral view; rostral broader than long, 4.27 mm wide, visible from above; internasals square shaped, 3.48 mm long, 3.65 mm wide, smaller than prefrontals, in contact with nasals, asymmetrical medial suture, slightly sinistral to prefrontal medial suture; prefrontals larger than internasals, as long as wide, 4.01 mm long, 4.01 mm wide, separated from eye by supraocular and preocular; supraocular 8.02 mm long, 4.05 mm wide; frontal pentagonal and bell shaped, 7.19 mm long, 5.06 mm wide; nasal divided; nostril located between prenasal and postnasal; loreal 2.32 mm long, 2.01 mm high, in contact with second and third supralabials; eye large, diameter 5.90 mm long; round pupil; parietal 8.71 mm long;

two postoculars; upper postocular 2.26 mm high, 1.89 mm wide; lower postocular 1.99 mm high, 2.02 mm wide; temporals 1+1, anterior temporal 4.20 mm long, 2.32 mm wide; posterior temporal 4.52 mm long, 3.57 mm wide, nine supralabial scales, with fourth to sixth in contact with orbit; eight largest, first contacting nasal, second contacting nasal and loreal, third contacting preocular and loreal, fourth and fifth contacting eye orbit, seventh in contact with postocular and eye orbit, eighth and ninth in contact with temporals; 10 infralabials, with first to sixth in contact with chin shield; chin shields 15.5 mm long, 5.25 mm wide; four gular scale rows; three preventral scale rows; 12/12/10 keeled dorsal scale rows; 139 subcaudal scales; 158 ventral scales; slender tail with apical disk.

Coloration in preservative.—Dorsal surface of head uniform dark gray, to parietals; rostral, nasals, loreal, and supralabials have white coloration; supralabials 2–9 display dark gray and blue pigmentation in almost straight longitudinal line; ventral head surface is immaculate white, except for gray pigmentation on gular scale rows; first third of ventral coloration is white, with vestigial gray pigmentation on edges of ventral scales from third to 20th, where ventral scales become uniform bluish gray to caudal scale and black margin of ventral scales becomes conspicuous; tail is ventrally white, with black margins restricted to suture between subcaudal scale pairs; dorsal coloration uniform bluish gray; after the 10th dorsal scale rows behind the neck there are two black stripes and white vertebral stripe, which gradually dissipates to tail.

Coloration of holotype in life.—Dorsal surface of head uniform olive green, from the neck to prefrontals; rostral and prefrontals have orange pigmentation, which gradually becomes yellow in lateral surfaces, on first four supralabials, nasals, loreal, and preocular; supralabials 5–9 display white pigmentation, which is gradually replaced by yellow and olive green; ventral head surface is immaculate white, except for small olive green pigmentations; first third of ventral coloration immaculate white, with discrete black margins on the ventral scales, which gradually expand to center; second third with olive green background, gradually becoming yellow, and black margins on ventral scales; last third with yellow background coloration and strong black margins, on ventral and subcaudal scales; dorsal coloration olive green, with black margins and diffuse blue pigmentation; after the 10th dorsal scale row below neck, there are two black stripes and olive green vertebral stripe, which gradually dissipates to the tail.

Hemipenis (Fig. 8).—Organ unilobed, unicalyculate, cylindrical. Apex with smooth calyces, with spinules restricted to its proximal portion. The organ bears strong constriction on its medial surface, at its middle half, with small spines covering its entire surface. Large to medium-sized hooked spines on the first and second thirds of the organ that gradually decrease in size into small spines near medial constriction. Sulcus spermaticus simple, centrolineal, located at the concave surface of the organ, with spinules on its borders, until proximal region, positioned laterally at basal portion of hemipenis, more centralized at the apical portion. Basal portion naked.

Variation.—Adult individuals may have the dorsal portion of the head uniform green, dark olive, or light green; rostral, nasals, loreal, and supralabials have light

orange and white coloration; ventral head surface is immaculate white or light yellow in all observed individuals, in both ontogenetic states; first third of ventral coloration is white, gradually becoming yellow to tail, with marked outer black margins on ventral scales; ventrally, tail might be either yellow or light green, subcaudals with conspicuous black margins; dorsal coloration may be light yellow, olive green, and blue, with a conspicuous white vertebral stripe or not. We have also observed an ontogenetic coloration shift, in which juveniles have a dorsal pattern composed of scattered irregular black blotches over an olive green background, gradually changing into a uniform pattern.

Ventrals 153–165 (153–165 [158 ± 4.64] in males, 155–164 [160 ± 4.72] in females); subcaudals 103–146 pairs (129–142 [134 ± 5.90] in males, 103–146 [127 ± 2] in females); postoculars 1+1; temporals 1+1 (62%) or 1+2 (38%); supralabials 9 (94%), 8 (3%), or 10 (3%); infralabials 8 (74.2%), 9 (22.8%), or 10 (3%).

Snout osteology (Fig. 9).—Based on ZFMK 103132, adult male. Premaxilla subtriangular in frontal view, with a posterodorsally oriented ascending process approaching, but not contacting, anterior end of nasals; in lateral view, ascending process with an almost straight anterior edge; transverse processes elongated, slightly shorter in length than ascending process; in ventral view, distance between both edges of transverse processes is 1.5 times longer than distance between the anterior tip of the premaxilla and the end of the vomerine processes; vomerine processes broad and comparatively long, posteriorly oriented, contacting anterior end of vomers. Septomaxillae slightly separated from each other, each with a long, broad ascending conchal process freely extending anterolaterally beyond lateral margins of nasals; prominent projection on the posterolateral edge of vomeronasal cupola of the septomaxilla present, approaching frontals posteriorly, remaining slightly separated from the right frontal and contacting left frontal, connected to vomers ventrally and posteromedially; this particular projection has been recorded to *C. bicarinatus*, *C. exoletus*, *C. flavolineatus*, *C. fuscus*, *C. laeicollis*, and *C. multiventris*, being absent in other congeners (Klaczko 2007; Klaczko et al. 2014; Hamdan and Fernandes 2015); ventrally, septomaxillar wall has a conspicuous extension in its medial portion, shared with *C. carinatus*, *C. dixonii*, *C. flavolineatus*, *C. fuscus*, *C. monticola*, *C. multiventris*, *C. scurrulus*, and *Leptophis* (Klaczko 2007); the nasal capsule internal groove is absent, as in *C. bicarinatus*, *C. dixonii*, *C. exoletus*, *C. flavolineatus*, *C. foveatus*, *C. laeicollis*, *C. monticola*, *C. multiventris*, *C. quadricarinatus*, and *C. scurrulus* (Klaczko 2007). Nasals in contact medially, each with a tapered anterior process; subtriangular horizontal laminae with anterolaterally oriented anterior margins; posterior processes of nasals approaching and almost contacting anterior part of frontals; vertical lamina of nasals approaching, but not contacting, medial part of septomaxillae. Vomers with globular mesoventral portion with rounded opening corresponding to exochoanal fenestra; in contact medially and almost contacting anterior region of palatine laterally; large vertical posteromedial laminae of about one-third length of vomers, with a large circular fenestra, approaching, but not contacting medially, diverging dorsally and ventrally; vomeronasal cupola bears a posterodorsally projected spine-shaped process above the circular fenestra, which is more

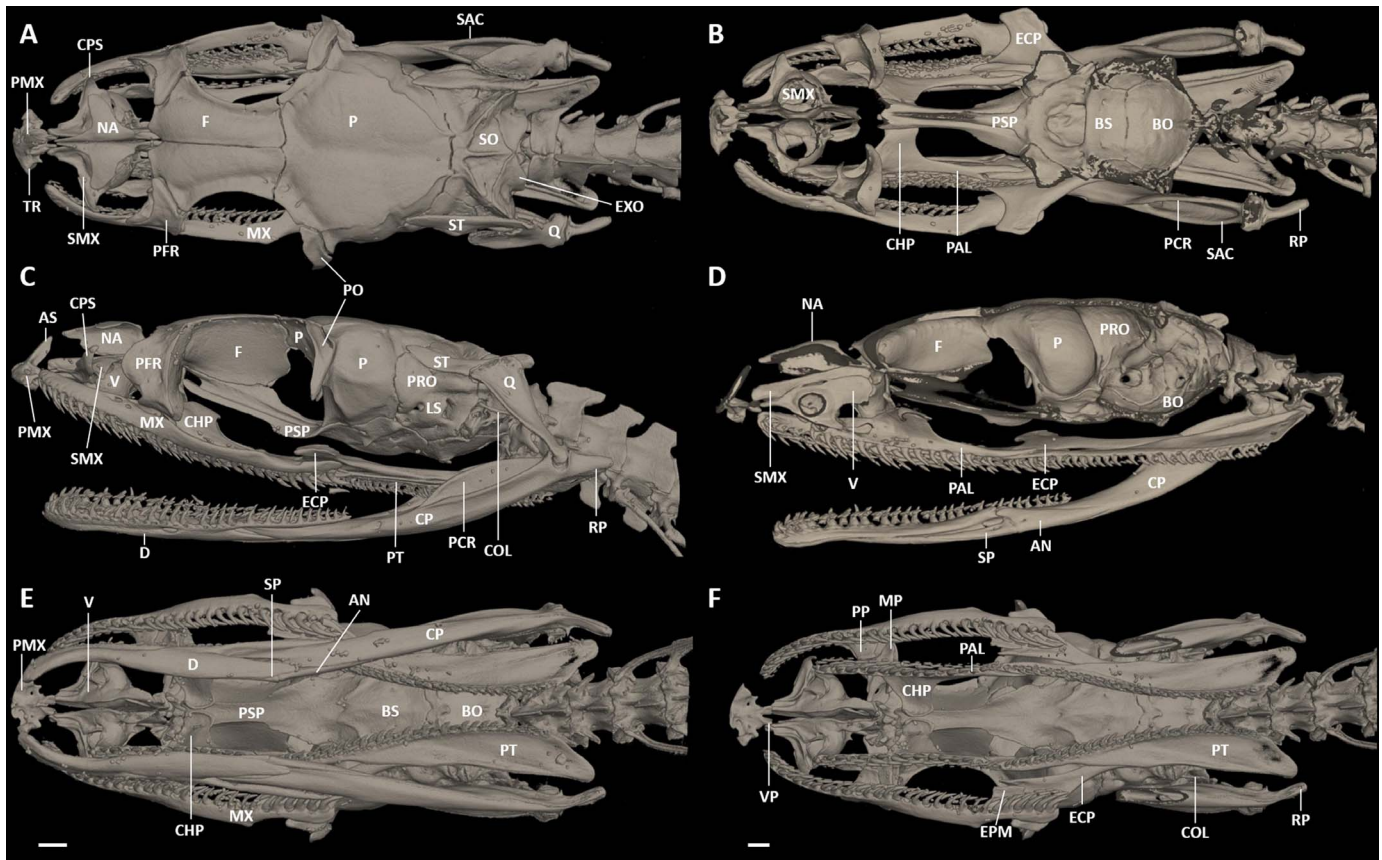


FIG. 9.—Micro-computed tomography images of the skull of *Chironius gouveai* (ZFMK 103132) in (A, B) dorsal, (C, D) lateral, and (E, F) ventral views; (B, D, F) cutaway views. AN = angular; AS = ascending process of premaxilla; BO = basioccipital; BS = basisphenoid; CHP = choanal process of palatine; COL = columella; CP = compound bone; CPS = conchal process of septomaxilla; D = dentary; ECP = ectopterygoid; EPM = ectopterygoid process of process of maxilla; EXO = exoccipital; F = frontal; LS = laterosphenoid; MP = maxillary process of palatine; MX = maxilla; NA = nasal; P = parietal; PAL = palatine; PCR = prearticular crest of compound bone; PFR = prefrontal; PMX = premaxilla; PO = postorbital; PP = palatine process of maxilla; PRO = pro-otic; PSP = parasphenoid rostrum; PT = pterygoid; Q = quadrate; RP = retroarticular process of compound bone; SAC = surangular crest of compound bone; SMX = septomaxilla; SO = supraoccipital; SP = splenial; ST = supratemporal; TR = transverse process of premaxilla; V = vomer; VP = vomerine process of premaxilla. Scale bars = 1 mm. Images by C. Koch. A color version of this figure is available online.

pronounced in the left vomer than in the right, a condition shared with *C. bicarinatus*, *C. exoletus*, *C. flavolineatus*, *C. fuscus*, *C. laeicollis*, and *C. multiventris*, but not with other congeners (Klaczko 2007).

Braincase osteology.—Based on ZFMK 103132, adult male. Prefrontals forming anterior margin of orbits; orbital lamina concave, with a large lacrimal foramen in most basal portion; lacrimal foramen with a small projection on the anteroventral margin, as in *Drymobius*, *Drymoluber*, *Mastigodryas*, *Palusophis*, but not in any *Chironius* species (Klaczko 2007); in lateral view, with broad and rounded prefrontal apex at about the median part of the lateral lamina; in contact with frontal dorsally; ventral surface contacts maxillary process of palatine; in posterior view, the prefrontal exhibits a small process directed medially or slightly anteromedially; frontals paired, in close contact, with a V-shaped anterior margin in medial region followed by a straight medial suture, forming anterodorsal margin of orbits; convex in dorsal view, with lateral margins oriented dorsolaterally; anterolateral edges of frontals forming an oblique suture with prefrontals; suture between frontals and parietals more or less straight in lateral half and curved anteriorward in medial half; posterolateral region, near

suture with parietal, with one to three foramina; ventral edges of orbital laminae of frontals in contact medially, contacting dorsal projection of parabasisphenoid ventrally. Parietal single, with a medial anterodorsally oriented depression, almost rounded in dorsal view, slightly broader than long, forming posterodorsal margin of orbit; bearing a triangular lateral process on each side anterior to level of midlength, of which the anterior edge contacts postorbital; lateral ridges visible in dorsal view, extending from region of contact with postorbitals to suture with supraoccipital, not contacting each other; parietal anteroventrally contacting posteriormost portion of parasphenoid rostrum, lateroventrally contacting basisphenoid portion of parabasisphenoid, posterolaterally contacting anterior margin of pro-otics and supratemporals and posteriorly contacting supraoccipital with a slightly curved suture. Postorbitals elongate, narrow, slightly curved, forming posterolateral margin of orbit; contacting lateral process of parietal medially and freely extending parietal ventrally; not in contact with frontals and broadly separated from region of contact between ectopterygoid and maxilla. Supraoccipital single, subpentagonal, broader than long, with a pointed posterior end, which is excluded from the border of the foramen magnum by a thin

contact of the pointed dorsomedial processes of the exoccipitals; contacting pro-otics laterally; not in contact with supratemporals; lateral regions each with a conspicuous and oblique ridge toward supratemporal that continues on exoccipital; among these side crests emerges a rather pronounced medial crest, which divides two depressions posteriorly. Exoccipitals irregularly shaped, each with a medial constriction and lateral ridge continuing lateral ridge of supraoccipital; exoccipitals contact basioccipital ventrally and pro-otics and supratemporals laterally; fenestra ovalis is situated at suture between pro-otic and exoccipital, and exoccipitals forming posterior margin of fenestra; posteriorly, exoccipitals forming dorsal, lateral, and lateroventral border of foramen magnum. Columellae with enlarged ovaloid foot plate and a thin stylus, which runs toward the inner surface of the quadrate, although still largely separated from the quadrate. Basioccipital somewhat heart shaped, contacting parabasisphenoid complex anteriorly, pro-otics anterolaterally, exoccipitals posterolaterally, and forming ventral border of foramen magnum posteriorly; anterior basioccipital with two short medially oriented oblique ridges; between those, a soft medial ridge crosses about most of basioccipital and features an almost spinelike projection at the anterior end, at the level of the oblique ridges. Pro-otics ovaloid in lateral view and uneven surface; each with large anterior and posterior trigeminal foramina, separated by comparatively broad laterosphenoid; two smaller foramina in lower part of pro-otic; overlain by supratemporals in dorsal region, contacting parietal dorsally and anteriorly and parabasisphenoid complex anteroventrally; posteriorly forming anterior margin of fenestra ovalis at suture with exoccipitals. Parasphenoid and basisphenoid fused; basisphenoid portion subhexagonal, with a large median cavity in dorsal view; anterior end of parasphenoid rostrum trifurcate, surpassing choanal process of palatine but not contacting it ventrally, not reaching posterior vomers, nasals, and septomaxillae; parasphenoid rostrum with lateral groove on each side along most of its length; anteromedial portion of basisphenoid with two lateral sigmoidal ridges extending posterolaterally to suture of basisphenoid with parietal and pro-otic; anterolateral to these ridges at about midlength of the ridges is a small foramen on each side of basisphenoid; two further foramina are present on each side of basisphenoid, posteriorly to ridges; posterior part of parasphenoid rostrum is lateroventrally extended.

Palatomaxillary arch osteology.—Based on ZFMK 103132, adult male. Maxillae long, extending from level of vomerine processes of premaxilla to posterior border of postorbital; anterior portion arched toward premaxilla, elongated and slightly extending medially beyond the tip of the palatine; posterior portion with a slight lateral twist between ectopterygoid and prefrontal, forming the inferior margin of orbit laterally; ventral surface of maxillae with 30–32 tooth loci; teeth subequal, curved, and rear facing, increasing in size posteriorly; palatine process situated slightly anterior to mid-region of maxilla at level between 12th and 14th tooth (left maxilla), facing medially, dorsally covered by prefrontal, but not contacting it; ectopterygoid process situated between 25th and 30th tooth (left maxilla), facing medioventrally, tip of process partly overlain by anteromedial process of ectopterygoid; posterior process of maxilla completely overlain by anterolateral process of

ectopterygoid; maxilla corresponds to more than half of length of braincase. Ectopterygoids axe shaped, with a triangular anteromedial process, an almost rectangular anterolateral process, and a rodlike, slightly curved posterior process; ventral surface of posterior half contacting dorsal surface of lateral portion of pterygoid. Pterygoids elongate, corresponding approximately to half-length of skull, ventral surface with 33 tooth loci; teeth subequal, slightly curved, and rear facing; anterior portion slender, dorsally overlain by posterior toothless portion of palatine up to level of fifth pterygoid tooth; gradually broadening in longitudinal direction from shortly before region of contact with ectopterygoid up to level of last tooth, tapering posterolaterally between last tooth and rounded posterior end; lateral borders of pterygoids nearly parallel; medial borders along tooth line curved, not parallel, with greatest distance between each other in anterior part and gradually approaching up to the level of 25th/26th tooth, where the distance between both tooth lines corresponds to the greatest width of the pterygoids; posterior to this the tooth lines move slightly laterally apart; posterior portion of pterygoid broad end approaching but not contacting posterior region of compound bone and ventromedial portion of quadrate; dorsal surface of posterior half with a lateral longitudinal ridge, beginning medially at level of contact zone with ectopterygoid, and ending at rounded end of pterygoid. Palatines slender, almost straight and parallel along tooth line, shortest of all toothed bones, ventral surface with 18 tooth loci; teeth subequal, slightly curved, and rear facing; anterior portion of palatines almost contacting globular portion of vomers dorsomedially; long trapezoidal choanal process dorsomedially directed toward parasphenoid rostrum, almost contacting its counterpart medially; short maxillary process situated at level of anterior border of choanal process on lateral surface of palatine, directed posterolaterally, anterior region almost contacting palatine process of maxilla, dorsal surface contacting medioventral region of prefrontal; posterior part bifurcating shortly before contact zone with pterygoid, with a short, lateral thornlike branch and a distinctly longer, rodlike medial branch, the latter flattened and tapering toward the posterior end, overlaying and contacting anterior part of pterygoid.

Suspensorium and mandible osteology.—Based on ZFMK 103132, adult male. Supratemporals laminar, elongate; anterior end surpassing suture of pro-otic and parietal; overlaying and firmly contacting pro-otic and anterolateral part of exoccipital; posterior half, except ultimate end, laterally articulating with quadrate; posterior end free, surpassing exoccipital and quadrate, ultimate part slightly laterally curved, as in *C. monticola*, *C. multiventris*, *C. quadricarinatus*, and *C. scurrulus*, but not other congeners (Klaczko 2007). Quadrate flattened and broad dorsally, with a slightly curved dorsal end, tapering dorsoventrally; obliquely oriented from anterodorsally to posteroventrally; medial portion with short process corresponding to region of contact with columella auris; ventral portion articulates with the saddle-shape notch of the articular part of the compound bone. Dentaries medially curved anteriorly; dorsal surface with 32–34 tooth loci; teeth subequal, slightly curved, rear facing, becoming gradually smaller posteriorly; lateral face convex with a mental foramen located at about level of 13th–15th tooth, slightly anterior to midregion of dental; at about

level of 21st tooth, dentary branches into a long slender dorsal process that overlays but only contacts compound bone in very anterior part, and a shorter broader ventrolateral process that contacts splenial and angular and anterior part of medioventral region of compound bone with its dorsal surface; at level of 24th tooth, dorsal process branches again into a short medial process and a much longer tooth-bearing dorsal process; meckelian fossa is delimited by the dentary, angular and splenial. Splenials elongate, triangular, with anterior mylohyoid foramen present, situated slightly anterior to the level of the summit, tapered anteriorly in region of contact with dentary; posterior part contacting anterior region of angular. Angulars elongate, triangular, tapered posteriorly; contacting compound bone laterally; anterodorsal process contacting medial process of dentary; posterior mylohyoid foramen present, as in all *Chironius* species and the genera *Dendrophidion*, *Drymarchon*, *Drymobius*, *Leptophis*, *Phrynonax*, *Spilotes sulphureus*, *Simophis*, and *Coluber*, but not in *Drymoluber*, *Mastigodryas*, *Palusophis*, *Oxybelis*, *Rhinobothryum*, *Spilotes pullatus*, and *Stenorhina*, and in anterior region near suture with splenial (Klaczko 2007). Compound bones elongate, approximately two-thirds length of mandible; prearticular crest prominent, visible in lateral view, distinctly higher than surangular crest, the latter not visible in medial view, proximally oriented, as in all *Chironius* species and the genera *Dendrophidion*, *Drymarchon*, *Drymobius*, *Leptophis*, *Oxybelis*, *Phrynonax*, *Rhinobothryum*, *Simophis*, *Spilotes*, *Stenorhina*, and *Coluber*, but not in *Drymoluber*, *Mastigodryas*, and *Palusophis* (Klaczko 2007); in lateral view, compound bone tapering anteriorly, fitting between dorsal and ventrolateral processes of dentary; dorsally oriented foramen at about level where posterior tip of angular meets compound bone; articular part, where it is joined to the quadrate, with a deep, saddle-shape notch; retroarticular process comparatively long, medially directed.

Distribution and natural history.—The new species has been recorded for 27 localities, of which 16 are at Rio Grande do Sul (Agudo, Arroio Grande, Bagé, Caçapava do Sul, Caxias do Sul, Encruzilhada do Sul, Cambará da Serra, Putinga, Porto Alegre, Rio Grande, Salvador do Sul, Santa Maria, São Francisco de Paula, São Leopoldo, Tapes, Triunfo), one at Santa Catarina (Campos Novos) in southern Brazil, and four at Uruguay (Cañada Vicharedo, Salto, Rio Negro, Montevideo). These localities encompass gallery and deciduous mesophytic subtropical forests of the Alto Parana and Araucaria moist forests provinces, as well as typical grasslands of the Uruguayan savanna domain (Fig. 2).

In its northernmost range, in Paraná State, *C. gouveai* is likely sympatric with *C. bicarinatus*; the records of *C. gouveai* are, however, restricted to the Araucaria moist forests, and the species does not occur in lowland Atlantic rain forest. In northern Rio Grande do Sul and southern Santa Catarina, it appears to be geographically isolated from *C. bicarinatus* through the White Stratigraphic Column, a mountain range elevated between the Carboniferous and Cretaceous periods, at northern Rio Grande do Sul and southern Santa Catarina (Orlandi Filho et al. 2006); *C. bicarinatus* is recorded in the lowland Atlantic Forest at Torres, on the right side of the column, and *C. gouveai* at Campos Novos and Cambará do Sul, in the Araucaria moist forests on the left side of the column. Carreira (2002) also

mentions the encounter of specimens at the Mercado Modelo (Montevideo), Uruguay accidentally introduced in banana shipments from São Paulo, Brazil; these specimens, although they could not be examined, likely represent *C. bicarinatus*.

In addition to the localities of examined specimens (Appendix II), this species was also recorded to Uruguay, in the departments of Artigas (Isla Zapallo, Rio Uruguay, Carreira et al. 2005), Cerro Largo (Cañada Vicharedo, Carreira et al. 2005), Salto (El Espinillar, Carreira et al. 2005; Salto Grande, Carreira et al. 2005), and Rio Negro (Estero Farrapos, Colonia San Javier, Carreira et al. 2005).

There was also an unvouchered specimen observed by the authors in Cambará do Sul, Rio Grande do Sul, in the border with the state of Santa Catarina. The specimen was observed basking on the ground at 1130 h, over a particularly wet area of Araucaria moist forests. Upon observation, it quickly displaced to nearby arboreal vegetation. The specimen from Quinta, Rio Grande, Rio Grande do Sul (ZFMK 103132) was encountered in activity, while crossing a dirt road, in a Uruguayan savannah restinga forest, around 1600 h. From personal experience, *C. gouveai* appears to be a particularly agile and defensive species, actively striking and quickly evading when threatened. Consecutive sampling over the course of 20 years has achieved no more than two specimens in Rio Grande, Rio Grande do Sul, southern Brazil (O.M. Entiauspe-Neto and D. Loebmann, personal observation). It would be possible to suggest that this could be related either to a low individual density or its cryptic coloration and secretive habits, considering this is a diurnal and large species. Considering its arboreal habits, the distribution of this species might be restricted by availability of adequate arboreal vegetation in most of its range, which has been largely deforested.

Achaval and Olmos (1997) report amphibians as its diet for Uruguayan specimens; Carreira (2002) recovered no stomach content from the Uruguayan specimens at the ZVC-R collection. Lema (2002) mentions frogs, lizards, and birds as prey items. There is no reproductive information available for this species.

DISCUSSION

In their revision, Dixon et al. (1993:66) provided a redescription for *C. bicarinatus* in which they partitioned the variation data in three samples, “based largely on vegetation and topography,” with the latter corresponding with specimens from between 29°30’S and 35°S latitude, from extreme southern Brazil, Uruguay, and Argentina in gallery forest, coastal forested areas, and some deciduous mesophytic subtropical forest. Although we could not examine the same specimens to which Dixon et al. (1993:66) referred in their “sample number three,” its general description and distribution provides a concise match with *C. gouveai*. The authors report “the southern sample is significantly different from the middle sample in ventrals plus subcaudals and number of maxillary teeth, although there is complete overlap in these characters” (Dixon et al. 1993:66). Since the sample was separated on the basis of geographic characters, specimens of *C. gouveai* from the semideciduous mesophytic forests of Rio Grande do Sul, Santa Catarina, and Paraná states, which were

inserted in sample two, could probably correspond to the reported overlap in overall morphology. Our sample also suggests that specimens encountered at coastal forests east and north of the White Stratigraphic Column, in the state of Santa Catarina and Rio Grande do Sul, southern Brazil, may be exclusively attributable to *C. bicarinatus*.

Several questions remain unanswered in the taxonomy of *Chironius*—the taxonomic status of *C. exoletus* and *C. flavolineatus* remains poorly resolved. We observed particular variation and diagnostic incongruence among these taxa, with noted molecular distance and phylogenetic structure among clades of *C. flavolineatus* (Fig. 1) and marked morphological distinction among examined specimens of *C. cf. exoletus* from southern Brazil and their respective type series (see Comparisons section), which agrees with the proposed recognition of cryptic candidate species complexes within these taxa by other authors (Hamdan et al. 2017).

Our comparisons corroborate the observations of Hamdan and Fernandes (2015), in which we also conclude that the unique combination of fixed characters in different geographically distinct morphotypes should be a strong indicator of speciation events in colubrids. Our results corroborate that integrative methods between molecular and morphological characters are essential in elucidating identity issues in complex species groups and help provide general taxonomic stability for the genus as a whole.

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RESUMO: *Chironius bicarinatus* é uma conspícua espécie de serpente Colubridae, amplamente distribuída no Nordeste, Sudeste, Centro-Oeste e Sul do Brasil. Com base em novos dados morfológicos de indivíduos advindos de áreas até então não avaliadas, revisamos a taxonomia de populações previamente referidas como *C. bicarinatus*, revisitando a definição desta espécie, fixando uma nova diagnose, e inferindo suas relações filogenéticas com linhagens próximas no Sul do Brasil, aqui descritas como uma nova espécie, restritas as Formações Florestais e Savanas de Pampa, assim como Florestas Atlânticas Semidecíduais do sul do Brasil. A nova espécie pode ser prontamente diagnosticada de *C. bicarinatus* e todas outras congêneres com base em morfologia interna (hemipênis unilobado, unicalculado, cilíndrico, ápice com cálices lisos, com espinulas restritas a sua porção proximal, próximo a área medial; fôramen lacrimal com uma pequena projeção na margem anteroventral),

externa (ventrais 153–165 [153–165 em machos, 155–164 em fêmeas; subcaudais em 103–146 pares [129–142 em machos, 103–146 em fêmeas]; padrão dorsal adulto com coloração de fundo verde escuro, escamas ocasionalmente com margem azul claro, duas faixas dorsais pretas conspícuas com uma faixa verde claro entre elas, que gradualmente se dissipa para a cauda, escamas ventrais com margem preta em suas extremidades), e evidência molecular.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/HERPMONOGRAPHS-D-19-00013.S1>.

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APPENDIX I.—GenBank accession numbers for colubrid deoxyribonucleic acid sequences used in this study. Sequences generated in this study are indicated by an asterisk.

Species	12S	16S	CMOS
<i>Chironius gouveai</i> (CHFURG 4394, holotype)*	MH602301	MH602314	MH603955
<i>Chironius gouveai</i> (ZFMK 103132, paratype)*	MH602302	MH602315	MH603956
<i>Chironius bicarinatus</i> (MNRJ 15083)*	MH602303	MH602316	MH603957
<i>Chironius bicarinatus</i> (tissue sample only, MTR3 3355)*	MH602304	MH602317	MH603958
<i>Chironius bicarinatus</i> (MNRJ 26255)*	MH602305	MH602318	MH603959
<i>Chironius bicarinatus</i> (tissue sample only, MTR2 6905)*	MH602306	MH602319	MH603960
<i>Chironius bicarinatus</i> (tissue sample only, LCBB18)	MF673186	MF673217	MF769829
<i>Chironius bicarinatus</i> (tissue sample only, LCBB21)	MF673189	MF673220	MF769832
<i>Chironius brazili</i> (tissue sample only, LCBB17)	MF673185	MF673216	MF769828
<i>Chironius brazili</i> (tissue sample only, LCBB16)	MF673184	MF673215	MF769827
<i>Chironius brazili</i> (tissue sample only, LCBB14)	MF673182	MF673213	MF769825
<i>Chironius brazili</i> (tissue sample only, LCBB15)	MF673183	MF673214	MF769826
<i>Chironius brazili</i> (IB 87467)	MF673187	MF673218	MF769830
<i>Chironius carinatus</i> (tissue sample only, MZUSP 14195)	HM565745	HM582207	HQ157810
<i>Chironius diamantina</i> (tissue sample only, LCBB7)	MF673176	MF673206	MF769818
<i>Chironius diamantina</i> (tissue sample only, LCBB8)	—	MF673207	MF769819
<i>Chironius diamantina</i> (tissue sample only, LCBB9)	MF673177	MF673208	MF769820
<i>Chironius exoletus</i> (tissue sample only, MZUSP11297)	HM565746	HM582208	HQ157812
<i>Chironius exoletus</i> (tissue sample only, LCBB12)	MF673180	MF673211	MF769823
<i>Chironius exoletus</i> (tissue sample only, LCBB10)	MF673178	MF673209	MF769821
<i>Chironius exoletus</i> (tissue sample only, C42)*	MH602307	MH602320	—
<i>Chironius exoletus</i> (tissue sample only, MCL216)*	MH602308	MH602321	MH603961
<i>Chironius exoletus</i> (MNRJ 25988)*	MH602309	MH602322	MH603962
<i>Chironius exoletus</i> (tissue sample only, MH602323)*	—	MH602323	MH603963
<i>Chironius flavolineatus</i> (tissue sample only, B17)*	MH602310	MH602324	MH603964
<i>Chironius flavolineatus</i> (tissue sample only, LCBB3)	MF673172	MF673203	MF769814
<i>Chironius flavolineatus</i> (tissue sample only, LCBB5)	MF673174	MF673205	MF769816
<i>Chironius flavolineatus</i> (tissue sample only, LCBB4)	MF673173	MF673204	MF769815
<i>Chironius flavolineatus</i> (tissue sample only, LCBB1)	MF673170	MF673201	MF769812
<i>Chironius flavolineatus</i> (tissue sample only, LCBB11)	MF673179	MF673210	MF769822
<i>Chironius flavolineatus</i> (tissue sample only, LCBB2)	MF673171	MF673202	MF769813
<i>Chironius flavolineatus</i> (tissue sample only, LCBB13)	MF673181	MF673212	MF769824
<i>Chironius flavolineatus</i> (tissue sample only, LCBB31)	MF673198	MF673225	MF769840
<i>Chironius fuscus</i> (MZUSP 11299)	HM565749	HM582211	HQ157815
<i>Chironius fuscus</i> (tissue sample only, LCBB26)	MF673193	—	MF769838
<i>Chironius fuscus</i> (tissue sample only, LCBB28)	MF673195	MF673223	—
<i>Chironius fuscus</i> (MTR 2269)*	MH602311	MH602325	—
<i>Chironius grandisquamis</i> (tissue sample only, CH528)	HM565750	HM582212	HQ157816
<i>Chironius laevicollis</i> (tissue sample only, IB 7194)	HM565751	HM582213	HQ157817
<i>Chironius laevicollis</i> (tissue sample only, LCBB20)	MF673188	MF673219	MF769831
<i>Chironius dixonii</i> (tissue sample only, 1478)	HM565752	—	HQ157818
<i>Chironius maculiventris</i> (tissue sample only, LCBB23)	MF673190	MF673221	MF769834
<i>Chironius monticola</i> (tissue sample only, JK5)	HM565753	HM582214	HQ157819
<i>Chironius foveatus</i> (tissue sample only, MTR 12348)*	MH602312	MH602326	MH603965
<i>Chironius foveatus</i> (tissue sample only, MTR 2414)*	MH602313	MH602327	MH603966
<i>Chironius foveatus</i> (tissue sample only, R6656)	HM565748	HM582210	HQ157814
<i>Chironius foveatus</i> (tissue sample only, LCBB25)	MF673192	—	MF769836
<i>Chironius multiventris</i> (tissue sample only, LCBB29)	MF673196	MF673224	—
<i>Chironius quadricarinatus</i> (tissue sample only, LCBB30)	MF673197	—	MF769839
<i>Chironius quadricarinatus</i> (tissue sample only, LCBB6)	MF673175	—	MF769817
<i>Chironius quadricarinatus</i> (tissue sample only, LCBB27)	MF673194	—	MF769837
<i>Chironius quadricarinatus</i> (MZUSP 14265)	HM565755	HM582215	HQ157820
<i>Chironius scurrulus</i> (tissue sample only, WED60)	HM565756	HM582216	HQ157821
Outgroups			
<i>Coluber constrictor</i> (tissue sample only, SR649)	AY122667	KX694632	AY486937
<i>Dendrophidion percarinatum</i> (tissue sample only, CTMZ000626)	HM565757	HM582217	HQ157822
<i>Drymarchon corais</i> (tissue sample only, JES1731)	HM565758	HM582218	HQ157823
<i>Drymobius rhombifer</i> (tissue sample only, WED59315)	HM565761	HM582220	GQ927313
<i>Leptophis ahaetulla</i> (tissue sample only, MZUSP 14269)	HM565762	HM582222	HQ157826
<i>Mastigodryas boddaerti</i> (tissue sample only, IBSP 279)	HM565764	HM582224	HQ157828
<i>Oxybelis aeneus</i> (tissue sample only, R6911)	HM565765	HM582225	HQ157829
<i>Oxybelis fulgidus</i> (tissue sample only AF158432)	AF158432	HM582226	HQ157830
<i>Spilotes pullatus</i> (tissue sample only, MZUSP 11969)	HM565768	HM582228	HQ157832

APPENDIX II

Specimens Examined

Material examined in this study. Specimens marked with an asterisk (*) were used in Table 1.

Chironius aff. *flavolineatus* ($n = 7$).—BRAZIL: CEARÁ: Planalto de Ibiapaba (IB 77058, 77059, 77113, 77114, 77529–77531).

Chironius brazili ($n = 4$).—BRAZIL: RIO GRANDE DO SUL: Santa Cruz do Sul (MCP 18429), Santiago (IB 87467), São Francisco de Assis (MCP 18430), Serra do Caverá, Rosário do Sul (IB 87468).

Chironius diamantina ($n = 2$).—BRAZIL: BAHIA: Mucugê (CZGB 2759), mountains at ca. 3 km West of “Cemitério Bizantino” (MZUSP, voucher unknown).

Chironius gouveai ($n = 36$).—BRAZIL: PARANÁ: Guarapuava, Guairaçá (MHNCI 10626*); Ivaí (MHNCI 8950*); Manoel Ribas (MHNCI 3257*); Reserva do Iguaçú, Rio Iguaçú (MHNCI 5332*); São João do Triunfo, Vila Palmira (MHNCI 11812*, 11852*); Siderópolis (MHNCI 12641*); RIO GRANDE DO SUL: Agudo (MCP 5995*); Arroio Grande (MCP 19117–19120*); Bagé (ZUFMS 2908*, paratype); Caçapava do Sul (ZUFMS 682); Caxias do Sul (MCP 14516); Encruzilhada do Sul (MCP 8968*, paratype); Cambará da Serra (Photographic voucher); Putinga (MCP 3073*); Porto Alegre (MCP 11850); Rio Grande, Ilha da Torotama (CHFURG 4823*, 4824*, paratypes), Quinta (ZFMK 103132*, paratype), Estação Ecológica do Taim (photographic voucher); Salvador do Sul (MCP 14419*); Santa Maria (ZUFMS 1168*); São Francisco de Paula (MCP 2649*, paratype; 10716*, 2631*); São Leopoldo (ZFMK 96439, 102609, 102463); Tapes (CHFURG 4394*, everted hemipenis—holotype); Triunfo (MCP 12762*, paratype; 7053*); SANTA CATARINA: Campos Novos (MCP 2813*, 2814*). URUGUAY: MONTEVIDEO: Montevideo (MHNCI 6028).

Chironius bicarinatus ($n = 243$).—BRAZIL: BAHIA: Alagoinhas (IB 48655); Barra do Choça (MZUESC 384, CZGB 6303, 6281); Camamu (MZUESC 5115); Coaraci (MZUESC 3902); Ibirataia (MZUESC 1272); Igrapiúna (MZUESC 1446); Ilhéus (CZGB 467); Teixeira de Freitas (IB 54676); Uruçuca (CZGB 1496); Valença (CZGB 2350); CEARÁ: Sítio Cantinho, Guarimiranga (photographic voucher); Guarimiranga (CHUFC 1389); Ibiapina (CHUFC 13300); Serra de Maranguape (CHUFC 2103); Pacoti (CHUFC 2597); Tianguá (CHUFC 3249); ESPÍRITO SANTO: Alegre (MBML 3942–3946); Baixo Guandu (IB 12740); Cariacica, Reserva Biológica Duas Bocas (MBML 3759); Domingos Martins (IB 69170); Guarapari (MBML 2159); Linhares (MBML 710); Santa Teresa (MBML 1741); São Mateus (CZNC 137); São Domingos do Norte (IB 25217); Santa Maria de Jetibá (MBML 3406); Marechal Floriano (MBML 4331, 4407); MATO GROSSO DO SUL: Anaurilândia (IB 64234); Coxim (IB 10908); Três Lagoas (IB 21568); MINAS GERAIS: Coimbra (MZUFV 45); Itamonte (IB 56049); Jaboticatubas (UFMG 1610); Machado (IB 18304); Mariana (Bailey, 1955); Santa Bárbara (IB 76875); Sapucaí-Mirim (IB 62094); Unai (MZUFV 642); Viçosa (MZUFV 46, 49, 51, 143, 145, 168); PARÁIBA: Arara (UFPB 77); PARANÁ: Parque Primavera, Almirante Tamandaré (MHNCI 4688*, 1854*, 1879*), Almirante Tamandaré (MHNCI 1826, 1827, 1878, 1840, 2037, 2038); Balsa Nova, São Luiz do Purunã (MHNCI 12303*, 12304*); Bocaiúva do Sul (MHNCI 2697); Campinhos (MHNCI 395*), Comunidade Cabeça D’Anta (MHNCI 1029); Taquari (MHNCI 4730); Campina Grande do Sul (MHNCI 8334*); Campo Largo, Bateias (MHNCI 4879); Campo Largo, Três Córregos (MHNCI 4838*); Campo Magro (MHNCI 10693*); Catanduvas (MHNCI 8428*, 11258*); Colombo (MHNCI 587, 1677); Curitiba (MHNCI 12300*), Barigui (MHNCI 393*, 1626), Campo Comprido (MHNCI 9179*), Pinheirinho (MHNCI 1357*); Mandirituba, Rodovia BR 116, Km 140 (MHNCI 6395); Rio Iguaçú, Mangueirinha (MHNCI 5328); Pinhais (MHNCI 6481*, 11787*); Piraquara (MHNCI 7842*, 7847*, 10739*); Quatro Barras (MHNCI 2174*, 8294*, 4799*,

8243*, 8929*, 10502*, 16467); União da Vitória (MHNCI 1662*); Porto Vitória (MCP 17291*); RIO GRANDE DO SUL: Unknown locality (ZFMK 96445*); Dom Pedro de Alcântara (MCP 6538*, 4283*, 4134*, 4199*, 4283*, 4199*, 4244*); SANTA CATARINA: Bombinhas (MCP 10301*); Fazenda Terra Nova, Rio Negrinho (MHNCI 10502); RIO DE JANEIRO: Angra dos Reis (IB 28044); Itatiaia (MZUSP 2442); Niterói (IVB 2796); Parque Natural Municipal Serra do Mendanha, Nova Iguaçu (CHFURG 4882*, Ex-MNRJ 10976); Parati (IB 56828); São João da Barra (MNRJ 17419); Resende (IB 46961); Tijuca, Rio de Janeiro (MCP 1167); Gávea, Rio de Janeiro (IB 22003); Rio de Janeiro (IB 2114); SÃO PAULO: Aparecida (IB 20771); Apiaí (IB 79155); Araçariçuama (IB 59416); Arujá (IB 67511); Barra Bonita (IB 19049); Barueri (IB 63637); Boracéia, Bertioga (IB 20755); Bertioga (IB 26168, MZUSP 5007, 5421); Boituva (MHNCI 11263); Bofete (IB 57329); Bom Jesus dos Perdões (IB 57739); Bragança Paulista (IB 16333); Buri (IB 17570); Caieiras (IB 12243, 54233, 54697, 60588, 62099, 68850, 69099); Cajamar (IB 69099); Campinas (ZUEC 925); Campo Limpo Paulista (IB 32018, 63715, 63716, 63929, 79872); Campos do Jordão (IB 21809, IB 56196, ZUEC 1346, 1347); Cananéia (IB 71178); Capão Bonito (ZUEC 1109); Mococa, Caraguatatuba (IB 26743); Caraguatatuba (IB 13025, 63066, 72870); Carapicuíba (IB 70551, 70557, MZUSP 14448); Cocais (IB 13816); Curucutu (IB 87938, 88356, 87380, IB 86994, everted hemipenes, 67987); Recreio, Charqueada (IB 15670); Caucaia do Alto, Cotia (IB 22256); Reserva Florestal Morro Grande, Cotia (IB 56033); Embu-Guaçu (IB 29617); Embu (IB 55660, Everted hemipenes); Guarulhos (IB 78679, 85567, 58420, everted hemipenis); Itapeverica da Serra (IB 82735, 84534, 81419, 81088, 81088, 78032, everted hemipenis, 82134, 84622, everted hemipenis); Juquitiba (MCP 7300*, IB 87570, 88102, 88084, 85605, everted hemipenis, 85234, everted hemipenis); Ibiúna (IB 23175, 23175, 52487, 55634); Iguape (IB 57180); Ilhabela (IB 58723, 72433, MZUSP 40131, 11525); Itapetininga (IB 29686); Itapeva (IB 27946); Itapevi (IB 17005); Jandira Natividade da Serra (Photographic voucher); Osasco (IB 12244); Piedade (IB 60607); Poá (IB 70932); Praia Grande (IB 67518); Ribeirão Grande, Intervalos (IB 64690, 65414, 65415); Salesópolis (IB 25220, MZUSP 2422, 2443, 2444, 3179, 4071, 4483, 4513, 13882, ZUEC 5555.); Santa Isabel (IB 62019, 62845); Parelheiros (IB 87502); Parque Intervalos (IB 64690*, everted hemipenis); Ribeirão Grande (MHNCI 16156), São Paulo (IB 17044, ZUFMS 1571*, MHNCI 7568, MZUSP 13236, 4829, 4316, 2585); São Bernardo do Campo (IB 55924, 60181, 79665); Fazenda Bonito, São José do Barreiro (MZUSP 10576); São José do Barreiro (IB 75410, 76061); São Lourenço da Serra (IB 23901); São Sebastião (IB 85454*); São Vicente (MZUSP 1369; IB 15850); Santos (IB 18761*); Sete Barras (IB 49877, 49878); Tabaão da Serra (IB 63833); Ubatuba (IB 16023); SERGIPE: Capela (Morato et al. 2011); Itabaiana (CHUFS 238).

Chironius cf. *exoletus* ($n = 5$).—BRAZIL: PARANÁ: UHE Santa Clara, Candói (MHNCI 12369); RIO DE JANEIRO: Unknown locality (MNRJ 8731); RIO GRANDE DO SUL: Osório (MCP 2423), São Francisco de Paula (MCP 14267); SANTA CATARINA: Itapoá (CHFURG 3201).

Chironius foveatus ($n = 5$).—BRAZIL: ESPÍRITO SANTO: Reserva Biológica Duas Bocas, Cariacica (MBML 3758); RIO GRANDE DO SUL: Canto dos Leffa, Dom Pedro de Alcântara (MCP 312), Dom Pedro de Alcântara (MCP 1711, 3724, 15530).

Chironius fuscus ($n = 2$).—BRAZIL: RIO DE JANEIRO: Caxias (CHFURG 4889), Guapimirim (CHFURG 4888).

Chironius laevis ($n = 1$).—BRAZIL: SANTA CATARINA: Itapoá (CHFURG 3110).

Chironius maculoventris ($n = 3$).—BRAZIL: RIO GRANDE DO SUL: Parque do Espinillo, Barra do Quaraí, Brazil/Argentina border (MCP 19319, 19322, 19329).

Chironius quadricarinatus ($n = 2$).—BRAZIL: SÃO PAULO: Unknown locality (CHFURG, voucher unavailable); BAHIA: Mucugê (MZUSP 15049).