



Taxonomic status and morphological variation of *Hydrodynastes bicinctus* (Hermann, 1804) (Serpentes: Dipsadidae)

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Abstract

Hydrodynastes bicinctus was described with no type material or locality and it has two subspecies currently recognized that are not taxonomically well defined. We tested the validity of the two subspecies through meristic, morphometric, and color pattern characters. Two apparently distinct color patterns of *H. bicinctus* were noticed, one from the Cerrado open formations and the other from the Amazon rainforest. These aforementioned patterns, however, exhibited a high degree of geographic overlap and many specimens showed a blended pattern. Based on these results we propose synonymizing *H. bicinctus schultzi* with the nominal taxon. Furthermore, we designate a neotype for the species, present data on geographic distribution, and provide morphological descriptions of the hemipenis, cephalic glands, and skull.

Key words: Species boundaries, External morphology, Cephalic glands, Hemipenis, Skull

Resumo

Hydrodynastes bicinctus foi descrita sem referência a material ou localidade-tipo e apresenta duas subespécies atualmente reconhecidas que não são bem definidas taxonomicamente. Nós testamos a validade das duas subespécies através de caracteres merísticos, morfométricos e de padrão de coloração. Dois padrões de coloração aparentemente distintos de *H. bicinctus* foram encontrados, um proveniente de formações abertas do Cerrado e o outro da região da floresta Amazônica. Esses padrões, entretanto, apresentaram um grande grau de sobreposição geográfica e muitos espécimes exibiram um padrão intermediário entre estes. Baseado nestes resultados, propomos a sinonimização de *H. bicinctus schultzi* com o táxon nominal. Além disso, nós designamos um neótipo para a espécie, apresentamos dados de distribuição geográfica e fornecemos descrições morfológicas de hemipênis, glândulas cefálicas e crânio.

Palavras-chave: Delimitação de espécies, Morfologia Externa, Glândulas cefálicas, Hemipênis, Crânio

Introduction

The genus *Hydrodynastes* Fitzinger, 1843, currently comprises three species: *Hydrodynastes gigas* (Duméril, Bibron & Duméril, 1854) distributed through Suriname, French Guiana, Venezuela, Peru, eastern Bolivia, Paraguay, Argentina, and Brazil (Carvalho & Nogueira 1998; Yuki *et al.* 1999; Giraudo & Scrocchi 2002; Franco *et al.* 2007; Toro *et al.* 2010); *Hydrodynastes melanogigas* Franco, Fernandes & Bentim, 2007, described from the municipality of Palmas, state of Tocantins, Brazil, and known from two other localities of that state, in addition to the municipality of Carolina, state of Maranhão, Brazil (Silva *et al.* 2012); and *H. bicinctus* (Hermann, 1804), which has two subspecies, *H. bicinctus bicinctus* and *H. bicinctus schultzi* Hoge, 1966. *Hydrodynastes bicinctus* was described without indication of a type-locality and occurs, according to literature, in Colombia, Venezuela,

French Guiana, Guyana, Suriname, and Brazil (Spix 1824; Duméril *et al.* 1854; Dunn 1944; Peters & Orejas-Miranda 1986; Abuys 2003; Franco *et al.* 2007; Avila-Pires *et al.* 2010).

Hermann (1804) briefly described *Coluber bicinctus* without designation of type specimens or any mention of its provenance. Wagler in Spix (1824) described *Elaps schrankii* on the basis of an illustration (Spix 1824:1, table 1) of a specimen supposedly from Japurá River, state of Amazonas, Brazil, that was registered as ZSM 1847/0 and is apparently lost (Hoogmoed & Gruber 1983). Schlegel (1837) transferred *Co. bicinctus* to the genus *Xenodon* Boie, 1827, with no further explanations. Fitzinger (1843) erected the genus *Hydrodynastes* to accommodate *Elaps schrankii*. Duméril *et al.* (1854), in the same study in which *X. gigas* was described, considered *Co. bicinctus* and *X. bicinctus* as synonyms of *Liophis bi-cinctus*. Jan (1863) synonymized *Co. bicinctus* with *E. schrankii* and proposed the genus *Lejosophis* to include *Co. bicinctus* and *X. gigas*. Cope (1885) considered *Lejosophis* a homonym of *Liophis*, due to similar pronunciation, and proposed the genus *Cyclagras* to embrace them. Boulenger (1894) accepted *Cy. gigas* but transferred *Co. bicinctus* to the genus *Urotheca* Bibron in de la Sagra (1843). Dunn (1944) proposed a new genus, *Dugandia*, to allocate *Co. bicinctus*. Hoge (1958) considered *Lejosophis* a valid genus to include *X. gigas*. Hoge (1958) also considered *Dugandia* a junior synonym of *Hydrodynastes*, since the later genus was proposed to accommodate *E. schrankii*, which is synonym of *Co. bicinctus*, resulting in the following taxonomic arrangement: *Le. gigas* and *H. bicinctus*. Hoge (1966) transferred *Le. gigas* to the genus *Hydrodynastes* with no further explanations and described *H. bicinctus schultzi*. Dowling & Gibson (1970) corroborated the allocation of *X. gigas* in the genus *Hydrodynastes*, along with *H. bicinctus*, without mentioning the study of Hoge (1966).

The diagnose and comparisons of *Hydrodynastes bicinctus schultzi* made by Hoge (1966) were very brief, distinguishing it from *H. bicinctus bicinctus* only by showing a larger first dorsal blotch and venter checkered with black and white (*vs.* black spots more or less arranged in cross bars in *H. bicinctus bicinctus*). Moreover, although Hoge (1966) mentioned the type-locality of the new taxon (municipality of Presidente Epitácio, state of São Paulo, Brazil), he provided no further information on the distribution of *H. b. schultzi*. Franco *et al.* (2007) mentioned specimens of *H. bicinctus bicinctus* from the Brazilian states of Amazonas, Pará, Rondônia, Tocantins, Goiás, and Mato Grosso, as well as specimens from French Guiana and Venezuela. In the same study, these authors cited specimens of *H. bicinctus schultzi* from the Brazilian states of Tocantins, Goiás, Mato Grosso do Sul, Minas Gerais, and São Paulo. These patterns of distribution suggest the parapatry between both subspecies, limiting *H. b. bicinctus* to the Amazon rainforest and surroundings and *H. b. schultzi* to the Cerrado open formations.

In the present study, we aim to test the validity of the current subspecies of *Hydrodynastes bicinctus* on the basis of quantitative analyses of meristic, morphometric, and color pattern variables and to provide detailed descriptions of the external and internal (skull, cephalic glands, and hemipenis) morphology for the recognized species.

Material and methods

We examined 134 specimens of *Hydrodynastes bicinctus*. Specimens and additional material examined are listed in Appendix I. Museum acronyms follow Sabaj Pérez (2014), except for Universidade Luterana do Brasil (MZCEUPL), municipality of Palmas, state of Tocantins, Brazil, and Munich Museum (ZSMH), municipality of Munich, Germany. Comparisons with the other species of the genus *Hydrodynastes* are based on data from Franco *et al.* (2007).

Franco *et al.* (2007) found secondary sexual dimorphism with regard to the number of ventral and subcaudal scales for species of the genus *Hydrodynastes*. Therefore, these data are here presented separated for males and females. The species was examined for meristic and morphometric characters, hemipenis, cephalic glands, skull morphology, and color patterns. Terminology for cephalic shields follows Peters (1964), whereas the method of counting ventral scales follows Dowling (1951). Dorsal scales row formula according to Peters & Orejas-Miranda (1986). Anterior dorsal scales counted about one head length posterior to the head, midbody dorsals counted halfway between the head and the cloaca, and posterior dorsal scales counted about one head length anterior to the cloaca. Sex was determined by the presence or absence of hemipenes through a ventral incision at the base of the tail. Measures of snout-vent (SVL) and tail length (TL) were taken with a flexible ruler to the nearest millimeter. We follow Dowling & Savage (1960), Myers & Campbell (1981), and Zaher (1999) for hemipenial terminology. Techniques for preparation follow Pesantes (1994), with modifications proposed by Myers & Cadle (2003),

Dowling (2004), and a coloration technique proposed by Uzzel (1973). We follow Taub (1966), Kochva (1978), and Zaher (1997) for cephalic glands terminology. We examined cephalic glands in preserved specimens after removal of head skin. We follow Hangay & Dingley (1985) and Cundall & Irish (2008) for skull preparation and terminology, respectively.

We examined in detail specimens of *Hydrodynastes bicinctus* with respect to eight color pattern variables: shape of postocular stripe (continuous “C” shaped stripe directed to gular region—Fig. 1A/small black postocular dot not connected to “C” shaped stripe directed to gular region—Fig. 1B); pale dorsal band on the posterior portion of head (present/absent); size of first dorsal blotch (measured by counting the number of scales in a longitudinal row situated in the largest portion of the blotch); extension of dorsal blotches (reach the venter/do not reach the venter); number of dorsal blotches in the body and tail; pale band surrounding dorsal blotches (present—Fig. 3/absent—Fig. 4); degree of definition of lateral blotches positioned between dorsal blotches on the paraventral region (conspicuous—Fig. 1C/inconspicuous—Fig. 1D); and ventral color pattern (checkered pattern—Fig. 1E/with a set of dots reaching the lateral portion of the body—Fig. 1F).

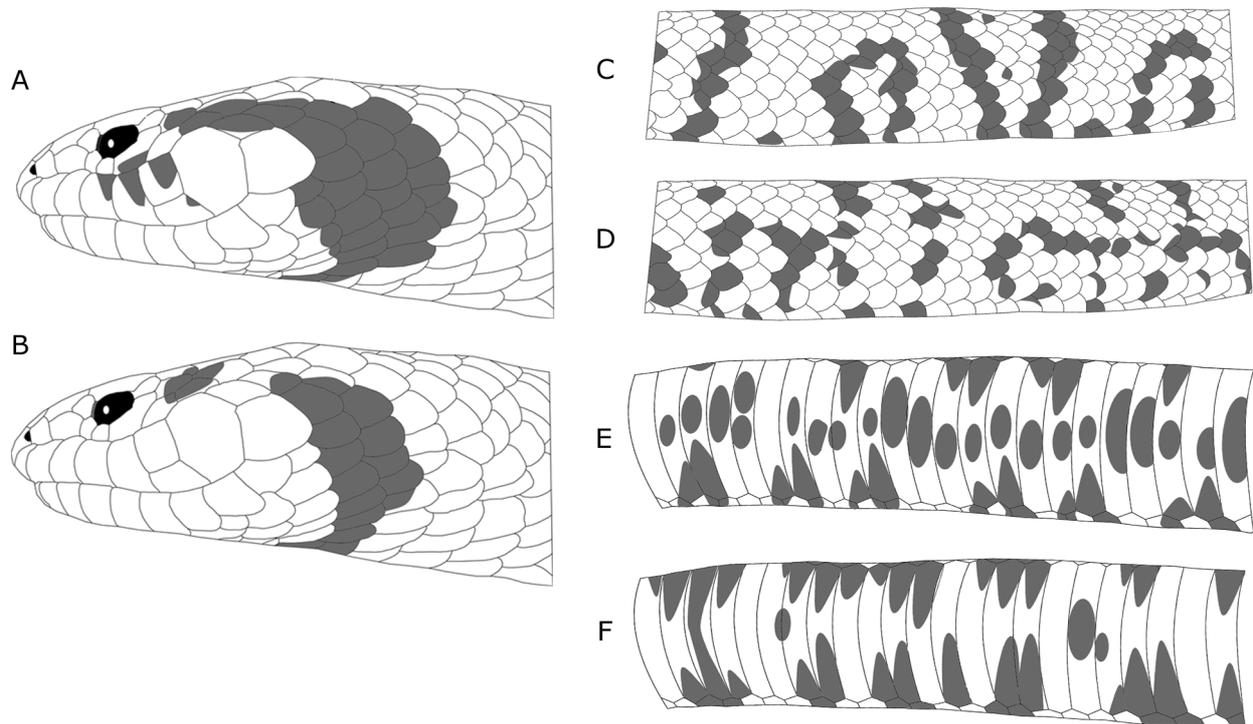


FIGURE 1. Color pattern variables observed in *Hydrodynastes bicinctus*. Lateral view of head, showing shape of the postocular stripe—continuous “C” shaped directed to gular region (A), and as small black postocular dot not connected to “C” shaped stripe directed to gular region (B). Lateral view of the body, showing degree of definition of lateral blotches positioned between dorsal blotches on the paraventral region—conspicuous (C), and inconspicuous (D). Ventral view of body showing color pattern—checkered pattern (E) or with a set of dots reaching the lateral portion of the body (F).

Based on observations of color pattern variation over the course of the study, we split individuals of *Hydrodynastes bicinctus* into operational taxonomic units (OTUs) according to the hydrographic basin and biome in which they occur. We considered that these two parameters (watersheds and biomes) could represent distinct potential physical and/or ecological barriers to the analyzed OTUs and we intended to evaluate this hypothesis. In the first approach, we lump specimens based on hydrographic basins according to the Brazilian National Agency of Water (ANA 2001), in which specimens fall into three major hydrological systems: Amazon River basin, Tocantins River basin, and Paraná River basin. A second approach considered the biome, defined by Ab’Saber (1970), along which these specimens are distributed (Cerrado open formations or Amazon rainforest). We performed the descriptive statistics of the variables number of ventral and subcaudal scales, and size of first dorsal blotch for each OTU (Zar 1999). The 95% confidence limits of these variables were compared among the OTUs to evaluate the level of overlap. We considered only specimens of *H. bicinctus* with unambiguous locality data ($n = 113$) for statistical analyzes. We performed statistical through the software Statistica version 7.0 (Statsoft 2010).

We here adopted the general lineage concept of species (De Queiroz 2007), considering species as unique evolving metapopulation lineages. The limits of a given species were herein established allowing some level of polymorphism in the diagnostic characters, as stated by Wiens & Servedio (2000). Based on this criterion, the limits of a given species are determined when 95% or more of its examined members hold a unique combination of one or more fixed states of characters. Hence, if an OTU shows a unique combination of state(s) of character(s) distributed in 95% or more of its representatives, we considered this OTU a valid species. Considering statistical data, variables with 95% confidence limits with no overlap among the OTUs correspond to diagnostic or taxonomically informative characters.

Results

Considering the three hydrographic basins together or the biomes, the three variables statistically analyzed showed amplitude of variation and 95% confidence limits with overlap among the OTUs (or the values were very close), precluding the differentiation of these OTUs based on such characters. Meristic data variations of the grouped specimens based on hydrographic basins and biomes are summarized in Table 1.

Furthermore, we identified two apparently distinct color patterns, corresponding roughly to the biomes of Amazon rainforest and Cerrado open formations. Specimens of *Hydrodynastes bicinctus* from the Amazon rainforest—here defined as "Amazon pattern"—usually present well-defined saddle-shaped dorsal blotches reaching the venter, interspersed with well-defined rounded lateral blotches (Fig. 1C); number of dorsal blotches varies from 28–34 (mean = 29.5; $s = 3.6$; $n = 18$). Individuals from the Cerrado open formations—here named "Cerrado pattern"—usually show ill-defined saddle-shaped dorsal blotches not reaching the venter, and ill-defined rounded lateral blotches (Fig. 1D); number of dorsal blotches varies from 18–31 (mean = 25.4; $s = 3.4$; $n = 31$). Despite these apparently distinct color patterns, there is a high degree of overlap of these traits, with specimens from the Amazon rainforest with the "Cerrado pattern" and individuals from the Cerrado open formations presenting the "Amazon pattern". Moreover, specimens with a blended pattern (showing features of both patterns) occur over the entire distribution of examined specimens. Of the 34 specimens examined from the Cerrado open formations for color pattern, 55.8% presented the "Cerrado pattern", 11.7% the "Amazon pattern", and 32.3% a blended pattern. In contrast, from the 12 analyzed individuals from the Amazon rainforest, 50% presented the "Amazon pattern", 25% the "Cerrado pattern" and 25% a blended pattern (Fig. 2). Considering these results, we were unable to recognize *Hydrodynastes bicinctus schultzi* as a distinct taxon based on the criterion here adopted, since we found no single apparently fixed feature or unique combination of states of characters in the OTUs sampled. Therefore, we propose synonymizing *H. b. schultzi* with the nominal subspecies.

The synonymization of these taxa, which were originally poorly described, clearly demonstrated existence of nomenclatural problems involving these entities and we intend to settle this issue with the present study. Furthermore, in order to achieve taxonomic stability, we believe the designation of a neotype for *Coluber bicinctus* Hermann, 1804 is required and we will argue that this approach meets the qualifying conditions expressed in the International Code of Zoological Nomenclature (ICZN 1999; Article 75.3; pp. 84–85). Firstly, Hermann (1804) designated no type material and locality in the original description of *Coluber bicinctus* (ICZN 1999; 3.1). Secondly, we here describe the neotype in detail and provide diagnostic characters that unequivocally allows the identification of all species of the genus *Hydrodynastes* (ICZN 1999; 3.2, 3.3). Hermann (1804) designated no holotype or syntypes in the original description of *Coluber bicinctus*, therefore there are no type specimens that could be deposited in any scientific collection (ICZN 1999; 3.4). The specimen we designated as the neotype is consistent with data from the original description and, as stated above, there are no data on type specimens for establishing other comparisons (ICZN 1999; 3.5). Considering the results here presented, *H. bicinctus* has two color patterns with some association to the Cerrado open formations of Brazil and the Amazon rainforest. We argue that the original description of *C. bicinctus* by Hermann (1804) was almost surely based on a specimen from the Amazon region since, at that time (early 19th century), the Brazilian Cerrado was an unexplored region, while the Amazon Forest region already harbored one of the three most important ports of Brazil (Lavilla *et al.* 2013). Based on these arguments we chose a specimen from the municipality of Novo Progresso, state of Pará, Brazil, with a typical "Amazon pattern", as the neotype of the species (ICZN 1999; 3.6). Finally, the neotype is deposited in the MPEG herpetological collection, a century-old institution holding the largest Amazonian natural history collection of Brazil (ICZN 1999; 3.7).

TABLE 1. A summary of variation of the meristic data for specimens of *Hydrodynastes bicinctus* from biomes and hydrographic basins. Ventral scales = VE; subcaudal scales = SC; first dorsal blotch = FDB; sample size = *n*; mean = *x*; standard deviation = *s*; range = *r*; 95% confidence limits = *cl*; females = *f*; males = *m*. The biomes definition follows Ab'Saber (1970) and hydrographic basins are according to ANA (2001).

		Hydrographic basins															
Biomes		Amazon				Amazon				Tocantins				Paraná			
Cerrado		f		m		f		m		f		m		f		m	
VE	<i>n</i>	24	40	21	26	14	14	18	18	14	14	18	18	15	15	21	21
	<i>x</i>	171.9	169.7	172.4	170.8	172.8	172.8	170.9	170.9	171.0	171.0	170.9	170.9	171.9	171.9	169.9	169.9
	<i>s</i>	3.9	3.7	4.3	2.4	4.4	4.4	2.6	2.6	2.9	2.9	2.6	2.6	4.4	4.4	2.0	2.0
	<i>r</i>	165–179	154–179	164–180	166–176	164–180	164–180	166–176	166–176	166–175	166–175	166–176	166–176	165–179	165–179	165–173	165–173
	<i>cl</i>	170.2–173.5	168.5–170.9	170.5–174.4	169.8–171.7	170.2–175.3	170.2–175.3	169.6–172.2	169.6–172.2	169.3–172.7	169.3–172.7	169.6–172.2	169.6–172.2	169.5–174.3	169.5–174.3	168.9–170.8	168.9–170.8
SC	<i>n</i>	17	34	19	23	13	13	17	17	9	9	17	17	12	12	21	21
	<i>x</i>	72.4	80.1	76.8	84.0	76.9	76.9	84.5	84.5	75.8	75.8	84.5	84.5	71.8	71.8	80.5	80.5
	<i>s</i>	4.7	4.0	4.3	4.1	4.7	4.7	4.2	4.2	3.7	3.7	4.2	4.2	5.2	5.2	2.5	2.5
	<i>r</i>	62–80	63–87	69–85	75–93	69–85	69–85	75–93	75–93	71–82	71–82	75–93	75–93	62–80	62–80	75–85	75–85
	<i>cl</i>	70.0–74.8	78.7–81.5	74.7–78.9	82.2–85.7	74.1–79.8	74.1–79.8	82.3–86.6	82.3–86.6	72.9–78.6	72.9–78.6	82.3–86.6	82.3–86.6	68.4–75.0	68.4–75.0	79.3–81.6	79.3–81.6
FDB	<i>n</i>	7	18	9	14	4	4	6	6	11	11	6	6	1	1	4	4
	<i>x</i>	5.8	7.2	5.8	7.1	6.0	6.0	6.8	6.8	5.8	5.8	6.8	6.8	7.1	7.1	7.7	7.7
	<i>r</i>	5–6	6–9	5–7	6–9	5–7	5–7	6–7	6–7	5–6	5–6	6–7	6–7	6–9	6–9	6–9	6–9

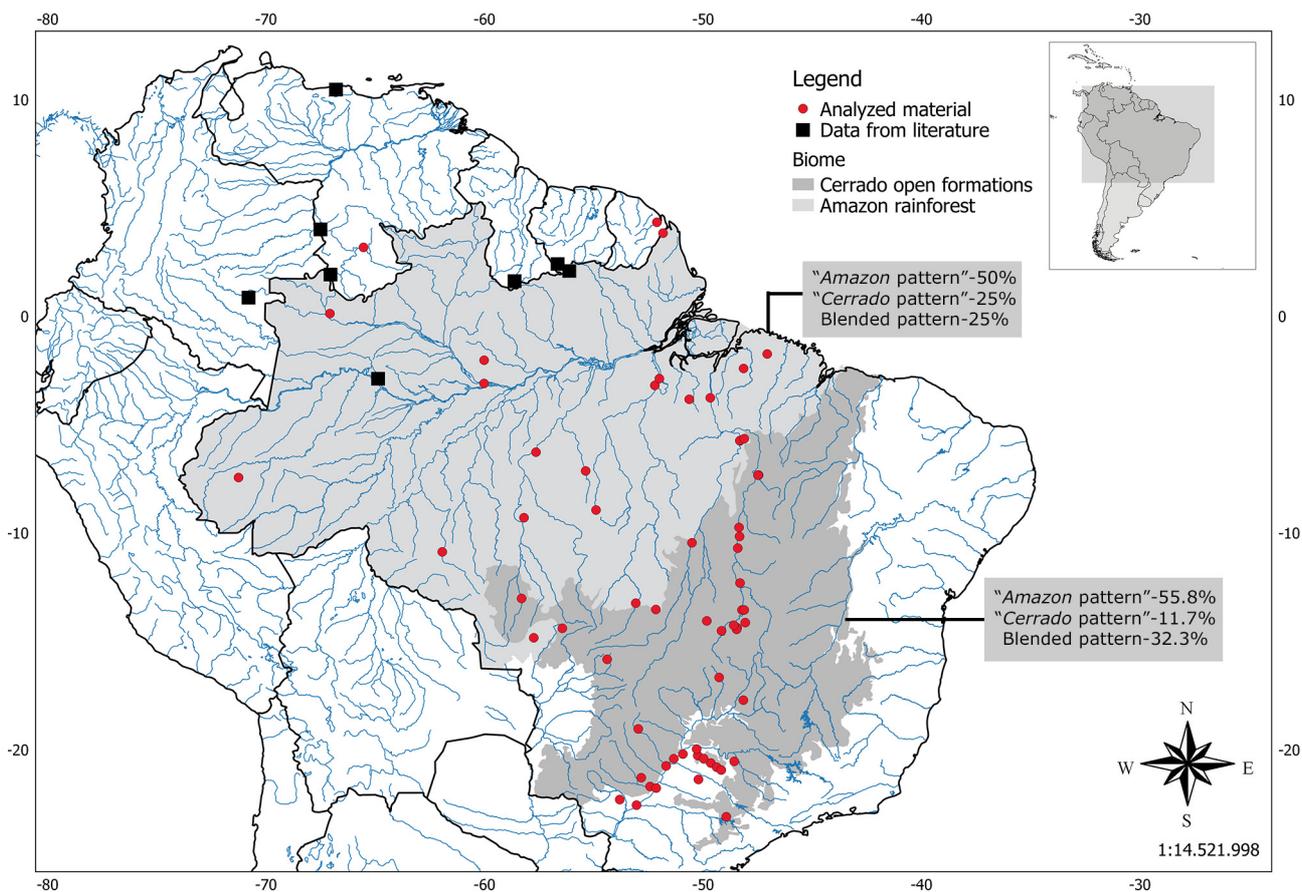


FIGURE 2. Geographic distribution of *Hydrodynastes bicinctus*. Squares represent data from the literature and circles material examined.

Hydrodynastes bicinctus (Hermann, 1804)

Figs. 3–5

Coluber bicinctus Hermann 1804. *Observationes Zoologicae*:276.

Elaps schrankii Wagler in Spix 1824. *Serpentum brasiliensium species novae*:1.

Xenodon bicinctus—Schlegel 1837. *Essai sur la physionomie des serpents*:95.

Hydrodynastes schrankii—Fitzinger 1843. *Systema Reptilium*:25.

Liophis bi-cinctus—Duméril, Bibron and Duméril 1854. *Erpétologie générale* vol. 7: 716.

Lejosophis bicinctus—Jan 1863. *Archives of Zoology, Anatomy and Fisiology*:324.

Cyclagras bicinctus—Cope 1885. *Proceeding of the American Philosophical Society*:185.

Urotheca bicincta—Boulenger 1894. *Catalogue of the snakes in the British Museum* vol. 2: 184

Dugandia bicincta—Dunn 1944. *Caldasia*:70.

Hydrodynastes bicinctus—Hoge 1958. *Papéis Avulsos de Zoologia*:222.

Hydrodynastes bicinctus bicinctus—Hoge 1966. *Ciência e Cultura*:143.

Hydrodynastes bicinctus schultzi—Hoge 1966. *Ciência e Cultura*: 143. **New synonymy.**

Holotype. Not designated in the original description.

Neotype (Fig. 4). Adult male, MPEG 24628, collected on 24 November 2005 by M.S. Hoogmoed, M.A. Ribeiro Jr., and C. Oliveira Araújo, in the municipality of Novo Progresso (07°02'25"S, 55°24'55"W, about 240m above sea level), state of Pará, Brazil.

Diagnosis. *Hydrodynastes bicinctus* is distinguished from its congeners by the following combination of states of characters: dorsal scales usually in 19/19/15 rows; ventral scales 164–180 in females and 154–179 in males; subcaudals 60–85 in females and 63–93 in males; prediastemal teeth 11–13; no apical pits; dorsum of body brown with darker saddle-shaped blotches; venter checkered with black and cream; postocular stripe “C” shaped, reaching gular region.

Comparisons. *Hydrodynastes bicinctus* is distinguished from *H. gigas* and *H. melanogigas* by having 11–13 prediastemal maxillary teeth (vs. 14–17 in *H. gigas* and *H. melanogigas*) and lacking apical pits (vs. apical pits present in the other two species). Additionally, *H. bicinctus* has a "C" shaped postocular stripe reaching gular region (vs. postocular stripe longitudinally extended but not reaching gular region in *H. gigas* and no distinct postocular stripe in *H. melanogigas*); venter with checkered pattern (vs. venter composed by black dots distributed in two longitudinal lines along lateral regions in *H. gigas* and *H. melanogigas*).



FIGURE 3. Color in life of *Hydrodynastes bicinctus*: juvenile (A) from Juruena National Park, state of Mato Grosso, and adult (B) from municipality of Peixes, state of Tocantins, both in Brazil. Photos by P.S. Bernarde (A) and P.H. Bernardo (B).

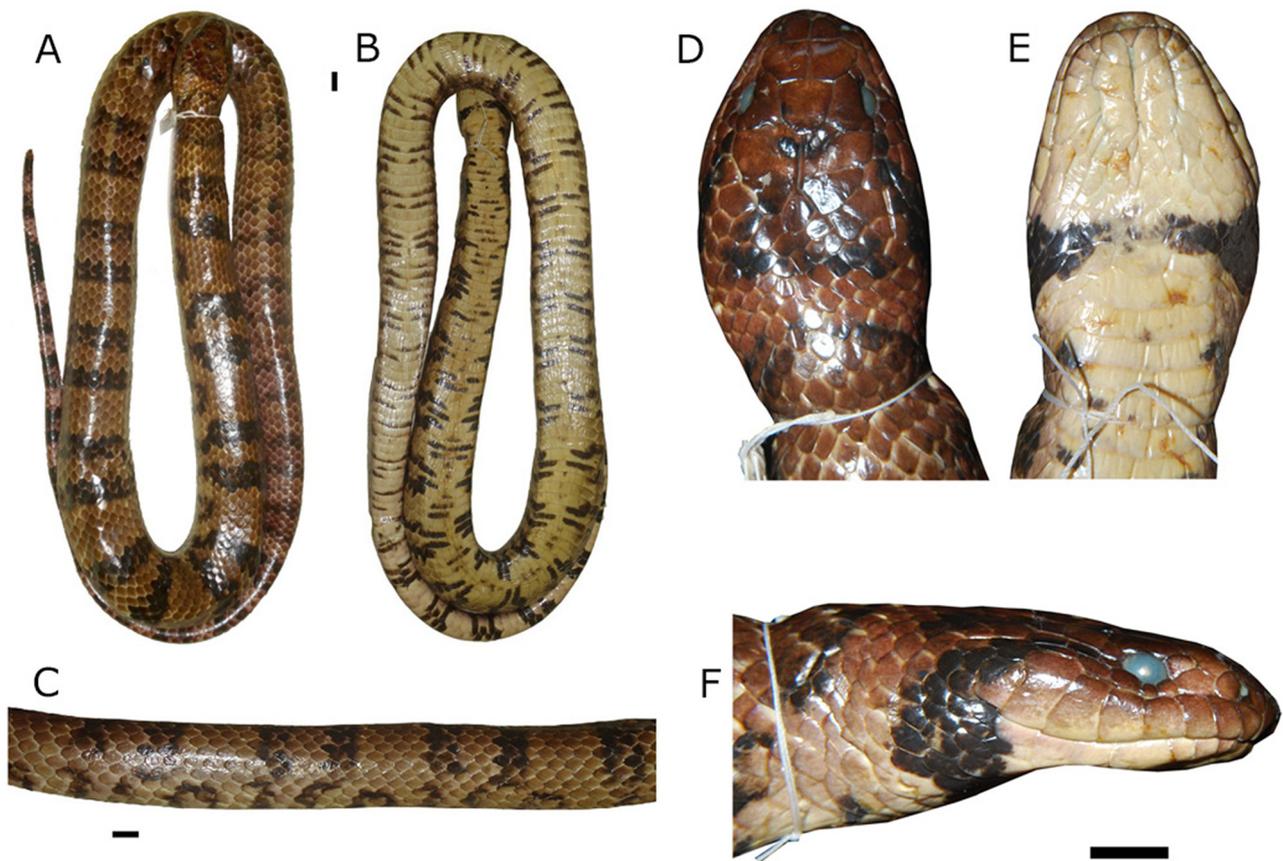


FIGURE 4. Dorsal (A), ventral (B), and lateral (C) views of body and dorsal (D), ventral (E), and lateral (F) views of head of the neotype of *Hydrodynastes bicinctus* (MPEG 24628) from municipality of Novo Progresso, state of Pará, Brazil. Scale = 10 mm.

Description of the neotype (Fig. 4). Adult male, SVL 1280 mm; TL 355 mm (27.7% SVL); head length 42.8 mm (3.3% SVL) from tip of snout to quadrate articulation; broadest head width 28.8 mm; interocular distance 13.9 mm; snout-orbit distance 10.6 mm (0.76 times interocular distance); rostral visible from above; two internasals 0.95 times as broad as high; right prefrontal 0.98 and left prefrontal 0.92 times as long as broad; frontal 1.19 times as long as broad, pentagonal-shaped in dorsal view; each parietal 1.2 times as long as wide; nasal divided; loreal pentagonal-shaped, 1.4 times as long as high; eye diameter 4.2 mm; pupil rounded; three suboculars, third larger than others; preocular single, two postoculars, and supraocular single; temporal 2+2+3/2+2+3; eight supralabials, none contacting orbit; ten infralabials, first to sixth contacting chin shields, except for the fifth scale on right side; three pairs of chin shields, anterior pair smaller than others; gular scale rows six between first ventral and infralabials; thirteen prediastemal maxillary teeth on right side and eleven on left side; two enlarged postdiastemal teeth on each side; dorsal scales 19/19/15, smooth, with no apical pits; ventrals 171; cloacal shield single; subcaudals 85, paired and unkeeled.

Color of the neotype in preservation (ethanol 70%) (Fig. 4). Head dark brown; two small black spots in anteromedial portion of parietals; two black spots (one on each side) on the level of third scale after parietals; black “C” shaped postocular stripe reaching gular region; supralabials brown; infralabials and chin shields creamish-white; ventral surface of head with two black blotches (one on each side), on the level of second scale before first ventral scale; dorsum of body brown with 30 dark brown, saddle-shaped blotches reaching the venter, alternating with well-defined dark brown rounded lateral blotches, also reaching venter; ventrals creamish-white with black spots irregularly distributed in a checkered pattern.

Color pattern variation of adults in preservation (ethanol 70%) (Fig. 1). Two basic patterns of dorsal coloration were observed, the “Cerrado pattern” and the “Amazon pattern”. In some individuals the postocular stripe is divided, with a small black postocular dot not connected to the “C” shaped stripe (Fig. 1B). Venter often with dots reaching the lateral portion of the body (Fig. 1F).

Juvenile color pattern in preservation (Fig. 5). Juveniles with dorsum of body brown, dark brown saddle-shaped dorsal blotches bordered by pale lines (these lines are usually vestigial or absent in adults). Rounded lateral blotches usually well-defined in all individuals, regardless of geographic origin. Postocular stripe frequently divided into a small black postocular dot not connected to the “C” shaped stripe.



FIGURE 5. Dorsal color pattern of a juvenile of *Hydrodynastes bicinctus* (MZUSP 16976). Scale = 10 mm.

Morphometric and meristic variation. Largest female SVL 1960 mm and TL 575 mm (IBSP 13824; TL/SVL = 0.29); largest male SVL 1930 mm and TL 530 mm (MNRJ 4741; TL/SVL = 0.27); TL/SVL 23–38% for females and 23–39% for males; dorsal scales row formula 17/17/15 ($n = 1$), 19/15/13 ($n = 1$), 19/15/14 ($n = 1$), 19/15/15 ($n = 10$), 19/16/15 ($n = 1$), 19/17/13 ($n = 5$), 19/17/14 ($n = 2$), 19/17/15 ($n = 35$), 19/18/13 ($n = 1$), 19/18/15 ($n = 4$), 19/19/13 ($n = 1$), 19/19/15 ($n = 59$), 21/17/15 ($n = 2$), 21/18/15 ($n = 1$), or 21/19/15 ($n = 8$); ventral scales in females 164–180 (mean = 172.2; $s = 4.2$; $n = 48$), males 154–179 (mean = 170.1; $s = 2.7$; $n = 81$); subcaudals in females 60–85 (mean = 74.1; $s = 5.5$; $n = 38$), males 63–93 (mean = 80.9; $s = 6.3$; $n = 70$); usually single preocular, three suboculars, and two postocular scales ($n = 78$); temporal scale formula extremely variable, with 51 distinct combinations; supralabials 7 ($n = 1$), 8 ($n = 111$), 9 ($n = 24$) or 10 ($n = 1$), usually with different numbers on each side; infralabials 9 ($n = 3$), 10 ($n = 62$), 11 ($n = 62$) or 12 ($n = 3$), generally with different numbers on each side; maxillary teeth 13–15.

Hemipenis ($n = 2$, Fig. 6). Organ deeply bilobed, lobes occupying about $\frac{1}{4}$ of total length of hemipenis. Sulcus spermaticus divides near the base of organ, adopting a centrolineal position until proximal region of lobes, where branches diverge to a centrifugal position, ending on lateral tip of lobes. Organ semicapitate and semicalyculate. Capitulum formed by papillate calyces on the sulcate and papillate calyces and body calyces on the asulcate side. Hemipenis with large, calcified lateral spine rows, beginning at the level of bifurcation of sulcus spermaticus and extending along apical portion of hemipenial body, immediately proximal to the beginning of lobes, lateral to asulcate side. Hemipenial body covered with spinules on both sides.



FIGURE 6. Asulcate (A) and sulcate (B) views of the entirely expanded and completely filled hemipenis of *Hydrodynastes bicinctus* (MNRJ 4770). Scale = 5 mm.

Cephalic glands ($n = 2$, Fig. 7). *Premaxillary gland*: triangular, contacting anterior region of supralabial glands. *Nasal glands*: pentagonal, limited by prefrontal bone posteriorly and by nasal capsule anteriorly; the dorsal limit of the nasal glands goes beyond the nostril and dorsal margin of orbit. *Supralabial glands*: slender glands contacting premaxillary gland anteriorly and rear end overlapped by Duvernoy's gland. *Harderian glands*: orbital and postorbital lobes about same size; orbital lobes rounded, completely filling orbit space; postorbital lobes with

irregular rectangular shape, showing a constriction on medial portion, limited by *musculus adductor mandibulae externus medialis* (amem) posteriorly and overlapped by Duvernoy's gland ventrally. *Duvernoy's glands*: large, elliptical, overlapping posterior region of supralabial glands anteriorly, and limited posteriorly by *musculus adductor mandibulae externus superficialis* (ames). *Rictal glands*: absent or indistinct. *Infralabial glands*: cover lateral portions of ventral surface of head, reaching the level of amem; mesoposterior portion enlarged; anterior portion of infralabials glands touch each other in the region adjacent to symphyseal. *Sublingual glands*: medial sublingual gland elongated, positioned between lateral sublingual glands, and not extending beyond posterior limit of infralabial glands; lateral sublingual glands ellipsoidal, not in contact. *Supralingual gland*: absent or indistinct.

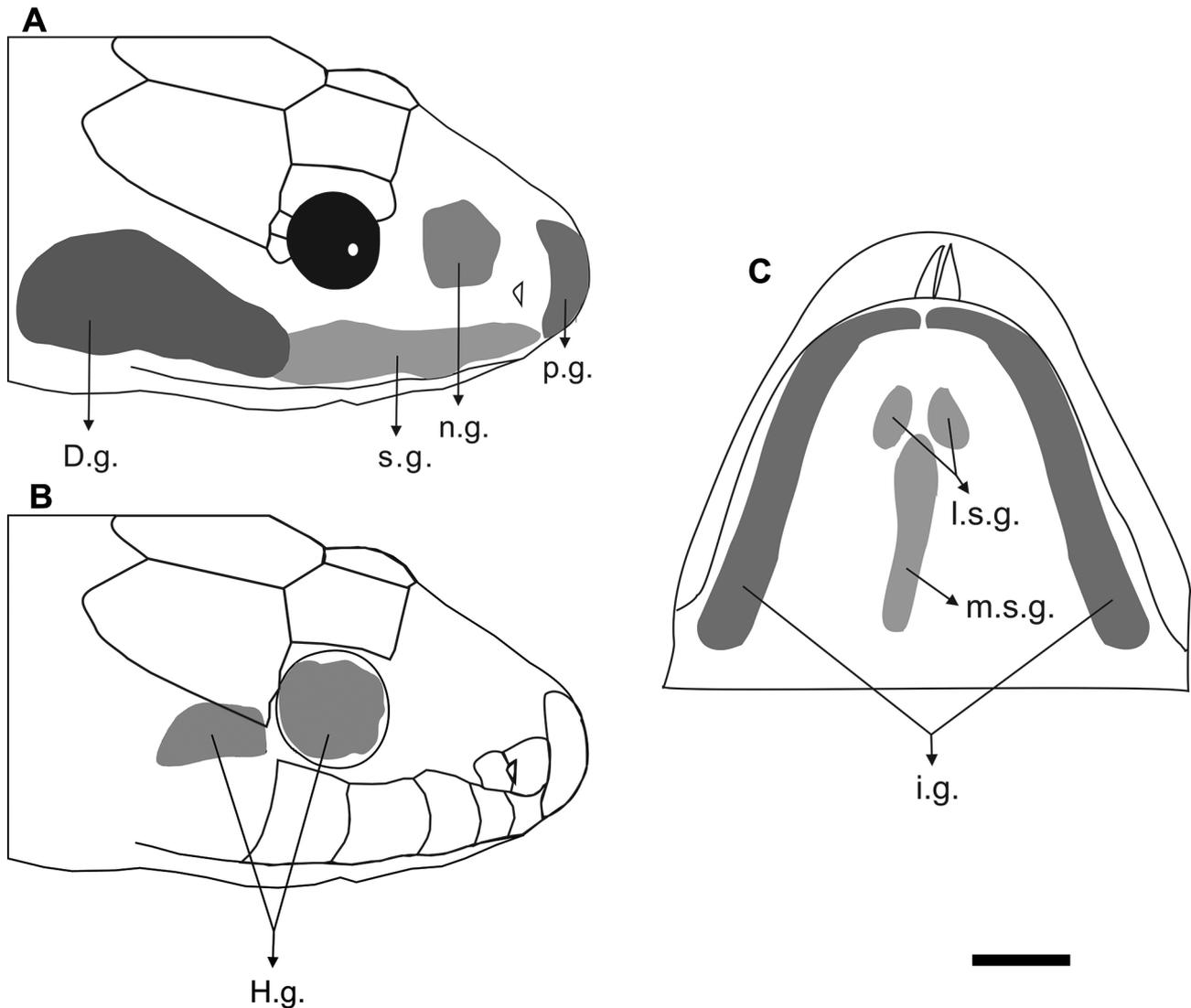


FIGURE 7. Cephalic glands of *Hydrodynastes bicinctus* (MNRJ 4769). Lateral view after removing the skin (A), lateral view after removing the orbit, Duvernoy's gland and *adductor externus medius* (aem), *adductor externus superficialis* (aes), and *levator anguli oris* (lao) muscles (B), and ventral view exposing infralabial and sublingual glands (C). Duvernoy's gland = D.g.; supralabial gland = s.g.; nasal gland = n.g.; premaxillary gland = p.g.; Harderian gland = H.g.; lateral sublingual gland = l.s.g.; medial sublingual gland = m.s.g.; infralabial gland = i.g. Scale = 5 mm.

Skull ($n = 2$, Figs. 8–10). SNOOUT: Premaxilla (Figs. 8–9): triangular in frontal view with slender transverse process slightly oblique ventrally, not reaching anterior portion of maxilla; basal portion of ascending process large and apical portion straight, slightly narrower than base; ascending process not touching nasals; vomerine processes divergent in ventral view overlapping vomer. Septomaxillae (Fig. 9): positioned ventral to nasals, dorsal to vomers and posterior to premaxilla; anterior edge simple embedded in the angle formed by ascending and vomerine processes of premaxilla; along with vomer, septomaxilla forms capsule of vomeronasal organ; anterolateral process

oblique dorsally, with rounded edge, not overlapping anterior portion of maxilla or transverse process of premaxilla; septomaxilla contacts nasals laterally. Vomers (Figs. 8–9): positioned anteroventrally in midline of skull, posteriorly to premaxilla; anterior process overlapped by vomerine process of premaxilla; posterior process of vomer with large foramen in ventral view and with vertical portion perpendicular to horizontal portion. Nasals (Figs. 8–9): joined medially and with dorsal position in skull, between premaxilla and frontals; lateral edges more slender than medial edges, with pair of nasals forming a diamond shape; anterior and posterolateral margins slightly concave; nasal with elongated posteroventral process in lateral view (the frontal process of nasal) which contacts vertical lamina of frontals; anteriorly, nasals do not contact ascending process of premaxilla.

BRAINCASE: Frontals (Figs. 8–9): joined medially, positioned dorsally between nasals and parietal; pair of frontals with trapezoidal shape in dorsal view and slightly longer than wide; anterolateral portion with prefrontal process, anterior margin wider than posterior margin; frontals, along with parietal, constitutes internal wall and dorsal border of orbit in lateral view; orbital foramen inserted in region of contact between frontal and parietal; most of the foramen inserted into parietal, occupying less than half of height of orbital internal wall in lateral view. Prefrontals (Figs. 8–9): with irregular shape, contacts frontal dorsally and maxilla ventrally, overlapping palatine process of maxilla, and delimiting orbit anteriorly; on its anterior portion, the bone has an acuminate projection; in frontal view, lacrimal foramen crosses the bone as far as its posterior portion; dorsal to this foramen, a lacrimal process is present. Parietal (Fig. 8): with subtriangular aspect in dorsal view; parietal contacts frontals anteriorly, postorbitals (by mean of a conspicuous postorbital process) anterolaterally, supraoccipital posteriorly, and prootics posterolaterally, where parietal is overlapped by supratemporals; two convergent well-developed dorsolateral crests emerge at the level of postorbital process up to region of contact with supraoccipital; dorsolateral crests not in contact. Postorbitals (Figs. 8–9): with tapered and curved shape; delimits orbital cavity posteriorly with ventral edge not reaching maxilla; extends parallel to anterolateral portion of parietal, not reaching frontals; anterior face concave and posterior convex laterally. Supraoccipital (Fig. 8): bone with irregular shape, projecting toward supratemporals and prootics laterally, and exoccipitals posteriorly; concave edge contacts parietal anteriorly; mesodorsal crest crosses supraoccipital longitudinally and its lateroposterior portion has two transverse crests. Exoccipitals (Fig. 8): bones with irregular shape, positioned at posterior portion of braincase, with anterior limit on supraoccipital and posterior limit adjacent to first vertebra (atlas), comprising dorsolateral edge of *foramen magnum*; exoccipitals contacting prootics anteriorly and basioccipital ventrally; transverse crests of supraoccipitals extending through exoccipitals, and laterally over the level of *fenestra ovalis*. Prootics (Fig. 10): contacting parietal anteriorly, exoccipitals posteriorly, and dorsal portion of supraoccipital and ventral portion of basioccipital posterolaterally; supratemporals overlap most of dorsal portion of prootics; lateral ridge divides prootic into dorsal and ventral portions; two foramina allow passage to maxillary and mandibular branches of trigeminal nerve lateroventrally; ventral to these foramina, next to region of contact with parabasisphenoid, there are multiple smaller foramina. Columella auris: paired small bones located on lateroposterior region of braincase, articulating with exoccipitals and prootics through *fenestra ovalis*; each *columella* consists of a small discoid footplate inserted in a *fenestra ovalis* and has an elongated shaft extending toward quadrate. Basioccipital (Fig. 8): bone with subtrapezoidal shape, located on ventral surface of skull and contacting parabasisphenoid anteriorly and atlas posteriorly; anterior margin wider than posterior margin, which has a slight bifurcation; anterior portion with inconspicuous dentigerous process, adjacent to suture with parabasisphenoid; basioccipital with slight longitudinal mesial crest. Parabasisphenoid complex (Fig. 8): composed of parasphenoid and basisphenoid, both fused without visible suture; spear shaped, positioned at mesoventral surface of braincase, with posterior portion broader and anterior portion tapering approximately on the level of posterior portion of palatines; the most tapered portion corresponds to anterior end of parasphenoid; posterior opening of Vidian canal situated posterolaterally, in the suture with parietal, next to prootics.

PALATOMAXILLARY APPARATUS: Maxillae (Figs. 8–9): located on anterolateral portion of skull, not contacting premaxilla; maxilla with elongated and arched shape; lateral portion convex and medial portion concave, extending to the level of postorbitals; palatine process completely overlapped by prefrontals, with broad base, extending from sixth up to ninth teeth, with medial edge narrowing at the level of eighth tooth; posterior edge enlarged in the region of contact with ectopterygoids; each maxilla bears twelve or thirteen curved prediastemal and two enlarged and ungrooved postdiastemal teeth (aglyphous); diastema equals size of one alveolus; anterior maxillary teeth smaller. Palatines (Figs. 8–9): elongated and narrow, located on the mesoventral portion of skull,

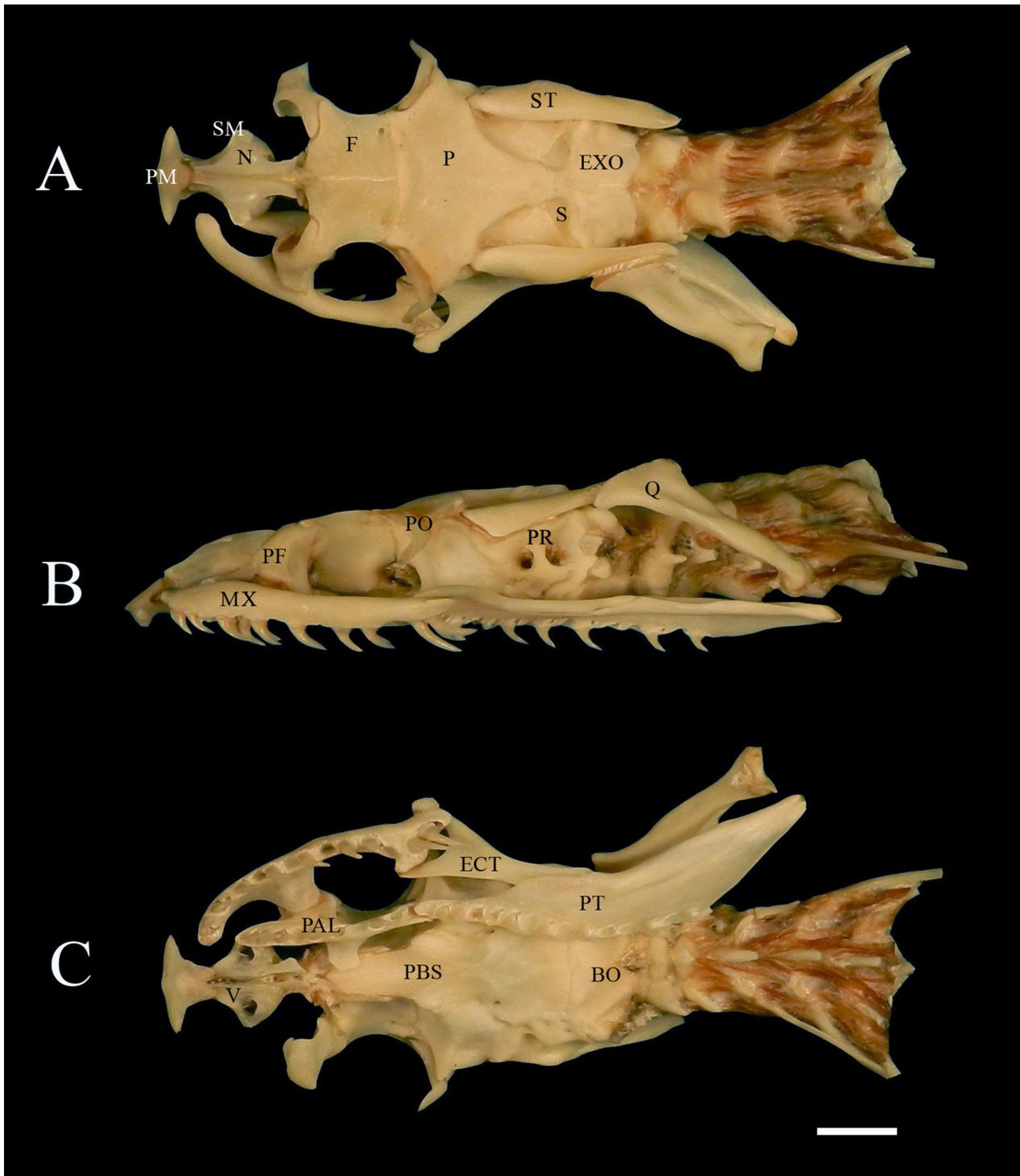


FIGURE 8. Dorsal (A), lateral (B), and ventral views (C) of the skull of *Hydrodynastes bicinctus* (MNRJ 4767). Premaxilla = PM; septomaxilla = SM; nasals = N; frontals = F; parietals = P; supratemporal = ST; exoccipital = EXO; supraoccipital = S; maxilla = MX; prefrontal = PF; postorbital = PO; prootic = PR; quadrate = Q; vomer = V; palatine = PAL; ectopterygoid = ECT; parabasisphenoid = PBS; pterygoid = PT; basioccipital = BO. Scale = 5 mm.

contacting vomer-septomaxilla complex anteriorly, maxillae laterally, and pterygoids posteriorly; lateral maxillary process overlapped by prefrontal, slightly anterior to choanal process, extending from fourth to sixth teeth; maxillary process with wide base and straight edge; choanal process extending from sixth to eighth teeth, close to parabasisphenoid, but not reaching it; posterior portion with small bifurcation where palatine articulates with anterior portion of pterygoid; each palatine bears ten or eleven curved teeth of nearly equal size. Pterygoids (Fig. 10): bones located medially on ventroposterior region of skull, elongated, tapered anteriorly, with length more than

50% of skull length; pterygoid contacts palatine anteriorly, ectopterygoid mesolaterally, and quadrate-compound bone joint posteriorly; anterolateral portion of pterygoid articulates with ectopterygoid at the level of seventh to fifteenth teeth; pterygoid becomes broader anteroposteriorly, up to the end of the row of teeth, where the bone tapers, directing laterally on the posterior portion; mesoposterior portion with dorsolateral longitudinal crest emerging just after joint with ectopterygoid and extending to its posterior edge; each pterygoid has fifteen to eighteen curved teeth of nearly equal size. Ectopterygoids (Fig. 10): located on the mesolateral portion of skull, elongated, with anterior edge bifurcated contacting posterior portion of maxilla and posterior portion contacting pterygoid, which has approximately two times the length of ectopterygoid.

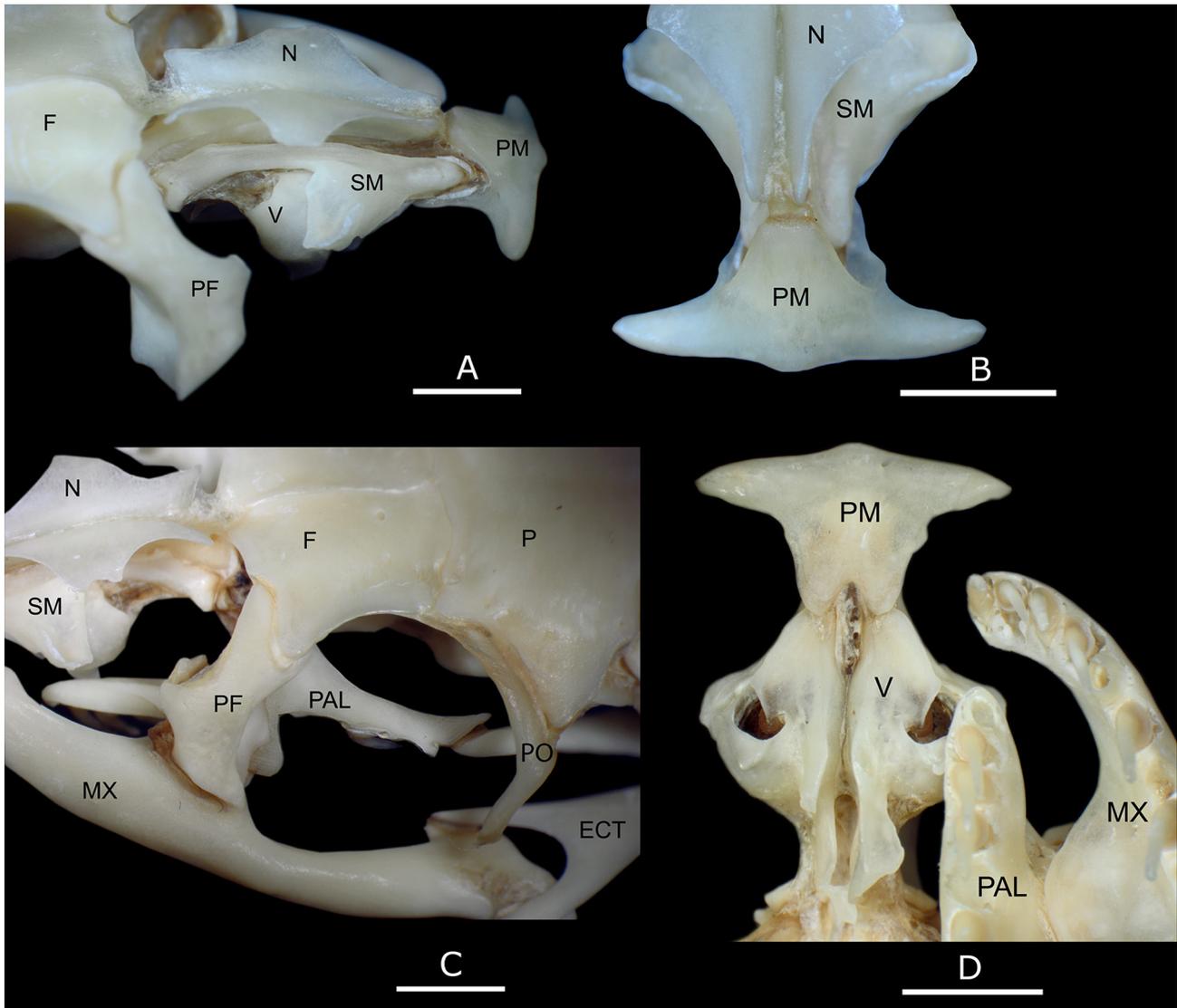


FIGURE 9. Lateral (A), dorsal (B), and ventral (D) views of the snout and detailed dorsolateral view of anterior region of skull (C) of *Hydrodynastes bicinctus* (MNRJ 4767). Frontal = F; nasal = N; prefrontal = PF; vomer = V; septomaxilla = SM; premaxilla = PM; palatine = PAL; maxilla = MX; parietal = P; postorbital = PO; ectopterygoid = ECT. Scale = 2.5 mm.

SUSPENSORIUM AND MANDIBLE: Supratemporals (Fig. 10): elongated, located on the posterodorsal portion of skull with anterior portion slightly wider than posterior portion; contacts parietal and prootic anteriorly, overlapping much of dorsal portion of prootic; posterior end extends beyond braincase, reaching the level of rear end of atlas. Quadrates (Fig. 10): well-developed bones located on the posterolateral portion of skull, lateral to supratemporals; articulates with supratemporal dorsally and glenoid cavity of compound bone ventrally, representing quadrate-articular joint; quadrate has about same length of supratemporal, elongated shape, and dorsal portion wider than ventral portion; anterolateral crest toward anterior portion of skull present; longitudinal and

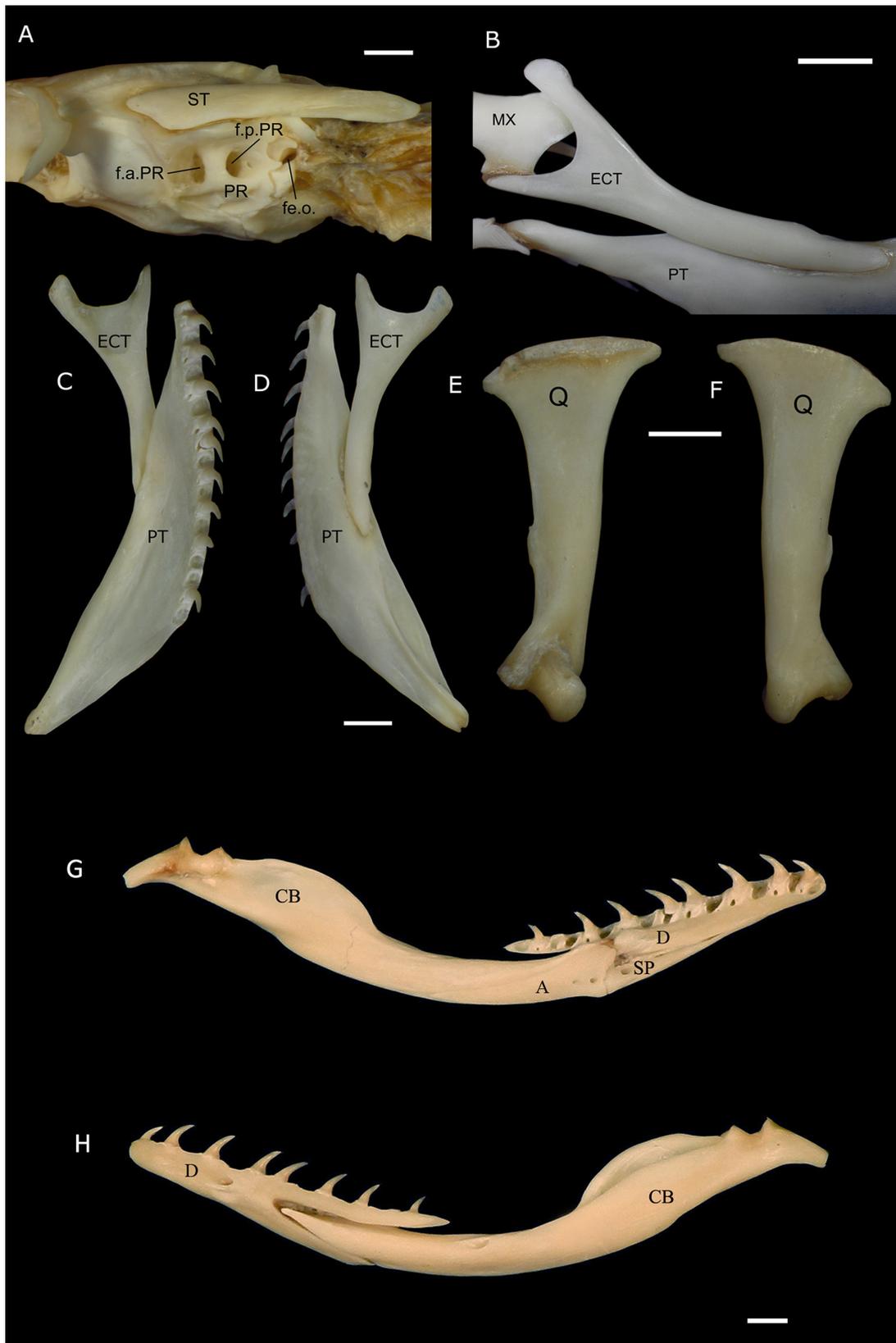


FIGURE 10. Lateral view of posterior region of the skull (MNRJ 4769 - A), detail of dorsal view of ectopterygoid (MNRJ 4767 - B), dorsal (C) and ventral (D) views of pterygoid and ectopterygoid (MNRJ 4769), medial (E), and lateral (F) views of quadrate (MNRJ 4769), and medial (G) and lateral (H) views of mandible of *Hydrodynastes bicinctus* (MNRJ 4767). Supratemporal = ST; prootic = PR; anterior foramen of prootic = f.a. PR; posterior foramen of prootic = f.p. PR; fenestra ovalis = fe.o.; Maxilla = MX; ectopterygoid = ECT; pterygoid = PT; quadrate = Q; compound bone = CB; articular = A; splenial = SP; dentary = D. Scale = 2.5 mm.

oblique rod-shaped process on posterior edge. Dentaries (Fig. 10): elongated, located on anterior edges of mandibles; posteroventral portion contacts dorsal surface of splenial and anterodorsal edge of angular in medial view; anterior portion medially curved toward opposite hemimandible; posterior edge bifurcated in lateral view, forming dorsal and ventral processes of dentary, between which the anterior edge of compound bone fits; dorsal process slightly longer than ventral; dentary forms—along with splenial—the Meckel groove; fifteen to seventeen curved teeth with nearly equal size distributed from anterior edge to the end of dorsal process; lateral face with a foramen on the level of seventh tooth. Splenials (Fig. 10): triangular with anterior edge tapered and posterior end vertical; in medial view, contacts posteroventral portion of dentary; mylohyoid anterior foramen close to posterior joint with angular. Angulars (Fig. 10): triangular, located on medial face, with anterior edge vertical and posterior end tapered, exceeding the level of posterior edge of dorsal process of dentary; anterior portion of angulars with mylohyoid posterior foramen; anterodorsal portion contacts posterior portion of dentary; angular contacts posterior portion of splenial anteriorly, and it is completely overlapped by anteroventral portion of compound bone dorsally; joint with splenial visible in medial and ventral views. Compound Bones (Fig. 10): corresponding to the largest bone of the mandible; contacts dentary, splenial, and angular anteriorly, and rear end articulates with quadrate; elongated, with narrow anterior portion fitting between dorsal and ventral process of dentary; posterior portion with glenoid cavity; after glenoid cavity, rear end of compound bone with narrow projection; articular and surangular crests well developed, first crest higher than second, lying anterior to glenoid cavity; posterior orifice of inferior dental canal located on anterior portion of a large cavity between articular and surangular crests; small crest on the posterior portion of compound bone in lateral view.

Geographic distribution (Fig. 2). *Hydrodynastes bicinctus* occurs in the Amazon, Tocantins, Paraná and Atlantic, stretch North/Northeast, hydrographic basins, at Amazon rainforest and Cerrado open formations, through Colombia (Vaupés, Dunn 1944; Orinoco and Amazonas Rivers, Pérez-Santos and Moreno 1988), Guyana (no specific locality, Boulenger 1894; Onora Falls, Cole *et al.* 2013), Suriname (no specific locality, Duméril *et al.* 1854; Kwamalasemoetoe, Abuys 2003; Sipaliwini, Avila-Pires *et al.* 2010), Venezuela (Caracas, Jan 1863; between Guaramaco and San Fernando, and San Carlos, Negro River, Roze 1966), French Guiana (Amazon basin and Guianas Shield, Chippaux 1987), and Brazil (in the states of Amazonas, Amapá, Goiás, Maranhão, Mato Grosso do Sul, Mato Grosso, Minas Gerais, Pará, Rondônia, São Paulo, and Tocantins).

Discussion

Hydrodynastes bicinctus schultzi was described by Hoge (1966) who distinguished it from *H. b. bicinctus* by the size of the first dorsal blotch and ventral color pattern. Although in the present study we found differences between populations of *H. bicinctus* from Cerrado open formations and Amazon rainforest, it was not possible to recognize these taxa based on the criterion here adopted. A relevant point is that the characters used by Hoge (1966) to distinguish *H. b. schultzi* from *H. b. bicinctus* (size of first dorsal blotch and ventral pattern) showed overlap among the Amazon and Cerrado populations.

The species of the genus *Hydrodynastes* are considered as semiaquatic and closely associated with rivers (Strussman & Sazima 1990), being mostly found in the hydrographic basins of Amazonas, Tocantins and Paraná Rivers. We found no apparently fixed characters in the OTUs of *H. bicinctus* from Cerrado open formations and Amazon rainforest as well as in the OTUs from the three distinct hydrographic basins this taxon occurs. We hypothesize this fact could be explained by the connection of such populations through the watersheds, that instead of representing barriers act as corridors that allow for gene flow to sustain the distinction of *H. bicinctus* as a single evolutionary lineage. This idea is supported by data from different groups of South American fishes whose distribution extends beyond the boundaries of the Amazon or Tocantins watersheds, indicating that capture between adjacent river basins occurred in distinct regions of South America, including central Brazil (Ribeiro *et al.* 2011). We believe that studies of phylogeography focusing specifically on *H. bicinctus* could properly clarify this issue.

Considering the internal morphology of *Hydrodynastes bicinctus*, few efforts have been done to comprehend or to describe these sources of characters that often reveal useful in systematic studies (Taub 1966; Zaher 1999; Cundal & Irish 2008). Dowling & Gibson (1970) showed the sulcate view of the hemipenis of the species, while Zaher (1999) provided detailed description of the organ. The description here presented agrees with these previous

descriptions of the hemipenis of *H. bicinctus*. However, no detailed descriptions of cephalic glands or skull morphology were available for this taxon in the literature, making the present study an important contribution for the taxonomy and systematics of the genus *Hydrodynastes*.

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APPENDIX I. Specimens examined.

COUNTRY: Municipality: Locality.

Cephalic glands = **cg**; skull = **s**; hemipenis = **h**. All the specimens were examined for meristic and morphometric data. Specimens deposited in MNRJ, MZUSP, and MPEG were examined for color pattern characters.

Hydrodynastes bicinctus (n = 134). BRAZIL: RONDÔNIA: Ji-Paraná: IBSP 44538. AMAZONAS: Iauareté, Uaupés River: MPEG 17; Manaus: MZUSP 7635; Presidente Figueiredo: MPEG 17541, 17593; São João: MZUSP 5358; Uaupés: IBSP 31974, 31976, 31980, 31982, 31984, 31986, 31988, 31990, 31994, 31997, 32001–03, 32012, 33391; Km 195 of the AM 010 Highway: MZUSP 7643; Uaupés River, Salesian mission of Iauareté, Santa Cruz, Igarapé Tauré, right tributary of Pandurê River, right tributary of Uaupés River: MPEG 603. PARÁ: Altamira: MPEG 19871; Cachimbo: IBSP 18516; Capitão Poço: MPEG 1249; Jacareacanga: MNRJ 7869, 9051–52; Novo Progresso: MPEG 24628 (neotype); Palestina do Pará: MPEG 12745; Tomé-Açu: IBSP 14724; Tucumã: MPEG 16743; Tucuruí: MPEG 16642, 16688; Vitória do Xingú: MPEG 19879, 19881, 19918; Maria Juriti Island, Tocantins River: MZUSP 8019; Araguaia River, Porto Jarbas Passarinho, Transamazônica: MPEG 10163–64. AMAPÁ: Oiapoque: IBSP 13773; Igarapé Taperebá: MZUSP 11704. MARANHÃO: Carolina: MZUSP 18753. TOCANTINS: Angical: MZUSP 17427; Araguatins: MZUSP 3838; Filadelfia: MZUSP 15672; Palmas: MNRJ 330, MZCEUPL 413, 475, 890; Porto Nacional: IBSP 14180; hydroelectric power plant Peixe Angical: MZUSP 15560; hydroelectric power plant Luís Eduardo Magalhães: MZUSP 15670. GOIÁS: Colinas do Sul: MZUSP 15925; Goiania: IBSP 32560, 33323; Ipameri: IBSP 17112; Minaçú: MNRJ 4742 (**h**), 4863–64, MZUSP 16976; Minaçú, Tocantins River: MNRJ 4495, 4769, 7500; Minaçú, Serra Branca: MNRJ 4744, 4747; Niquelândia, Maranhão River, Porto Alfredinho: MNRJ 7866–67; Niquelândia, Traíras River: MNRJ 4741; Uruaçú: MNRJ 4746, 4862, Das Almas River: MNRJ 4916, 9928; Maranhão River, between the river mouth of the Bagagem and Tocantinzinho Rivers: MNRJ 7323; Tocantins River, mouth of the Preto River: MNRJ 4770 (**h**); Maranhão River, upstream of the mouth of the Peixe River: MNRJ 4767 (**cg**, **s**); Maranhão River, Castelão River: MNRJ 4768; Traíras River, Maranhão River tributary: MNRJ 7865; Serra da Mesa: MNRJ 4669 (**cg**, **s**), 4670–72, 4743, 4745, 9904, MZUSP 17428–29; hydroelectric power plant Serra da Mesa: MNRJ 7868. MATO GROSSO DO SUL: Bataguassu: IBSP 27652; Ivinhema: IBSP 37321; Paraíso das Águas, Paraíso River: MNRJ 6435; Tapyrapuã: MNRJ 195, 328–29; Três Lagoas: IBSP 32547; Xavantina (= Santa Rita do Pardo): IBSP 12707, 12808. MATO GROSSO: No specific locality: IBSP 22217, 22327, 22393, 27641; Arino: IBSP 22179; Canarana: IBSP 62873; Gaúcha do Norte: MZUSP 14280; Poxoreo: IBSP 42063; Juruena River: IBSP 41160; Santa Teresinha: IBSP 41232; Utiariti: MZUSP 4752. SÃO PAULO: No specific locality: IBSP 24289; Avaré: IBSP 27521; Barretos: IBSP 15707, 23690; Fernandópolis: IBSP 29905, 29930; Glicério, Tietê River: IBSP 19477–78; Ilha Solteira: IBSP 37637; Indaiaporã: IBSP 42136, 42167; Presidente Epitácio: IBSP 18128, 22956; Rosana, Porto Primavera: IBSP 53843; Santa Fé do Sul: MZUSP 4060; São José do Rio Preto: IBSP 17113; Uchoa: IBSP 28240; Votuporanga: IBSP 22914, 22933; Cachoeira dos Índios, Grande River: IBSP 13810, 29293–94; Cachoeira das Onças: IBSP 30119. FRENCH GUIANA: Crique Inery: IBSP 13824. VENEZUELA: upper Orinoco River: IBSP 25746.