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A New Species of *Helicops* (Serpentes: Dipsadidae: Hydropsini) from Southeastern Brazil

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ABSTRACT: *Helicops* is a genus of Neotropical watersnakes containing 16 species. Based on morphological (scale counts, dentition, coloration, and hemipenis anatomy) and genetic data (16S rRNA and C-mos genes), we identify a new species of this genus. The new taxon is diagnosed by having 17-17-15 dorsal scale rows; 111–117 ventral plates; 41–56 subcaudals without keels; nasal entire; 18–21 + 2 maxillary teeth; hemipenis bilobed, semicalyculate, and semicapitate; dorsum uniformly medium brown or dark brown; venter cream or light brown with two medial rows of black markings, usually semilunar in shape. The new species occurs from southeastern to northern Minas Gerais state, Brazil.

Key words: 16S rRNA; C-mos DNA; Integrative taxonomy; Morphology; Phylogeny; Squamata

HYDROPSINI is a lineage of aquatic and semiaquatic South American snakes. It is composed of three genera: *Helicops* Wagler 1828, *Hydrops* Wagler 1830, and *Pseudoeryx* Fitzinger 1826 (Zaher et al. 2009). Morphologically, the Hydropsini share the character of significant enlargement of the m. *adductor mandibulae externus superficialis* at its origin (Zaher 1999). Viviparity has also been considered a diagnostic character of this tribe (Zaher et al. 2009), but *Hydrops*, *Pseudoeryx*, and some *Helicops* spp. are oviparous (Scartozzoni 2009), and *Helicops angulatus* is facultatively viviparous (Rossman 1984; Ford and Ford 2002).

Helicops is the most diverse genus of Hydropsini with 16 extant species (Kawashita-Ribeiro et al. 2013), diagnosed by the presence of nude flounces on the lobes of the hemipenis (Zaher 1999). Externally, *Helicops* species can be easily identified by the position of the eyes and nostrils toward the top of the head, single internasal scale, cloacal shield divided, and some or all dorsal scales keeled (Peters and Orejas-Miranda 1970).

Twelve species of *Helicops* have been recorded in Brazil (Costa and Bérnils 2015), six of them considered endemic to that country: *H. apiaka* Kawashita-Ribeiro, Ávila and Morais 2013, *H. carinicaudus* (Wied 1824), *H. gomesi* Amaral 1922, *H. modestus* Günther 1861, *H. tapajonicus* Frota 2005, and *H. trivittatus* (Gray 1849; Kawashita-Ribeiro et al. 2013). Herein we describe a new Brazilian species of *Helicops* based on morphological and molecular characters.

MATERIALS AND METHODS

Specimens Examined and Morphological Characters Analyzed

Museum abbreviations follow Sabaj Pérez (2014), with the addition of UFVCF (Universidade Federal de Viçosa, Campus Florestal, MG, Brazil). The specimens examined are listed in the Appendix.

Morphological characters examined include morphometrics, maxillary dentition, coloration, scale counts, and hemipenial morphology. Sex was determined by the presence

or absence of hemipenes through a ventral incision at the base of the tail. Ventral scale counts follow Dowling (1951); hemipenial characters follow Dowling and Savage (1960). Hemipenes were prepared following Nunes et al. (2012). Hemipenial comparisons were based on the descriptions provided by Yuki (1994), Frota (2005), Yuki and Lema (2005), Nunes (2006), and Kawashita-Ribeiro et al. (2013), except for *H. carinicaudus* and *H. infrataeniatus*, which were examined by the authors. Measurements were taken with an analog caliper (± 0.1 mm) or with a stereo microscope, except for snout–vent length (SVL) and tail length (TL), which were measured with a flexible ruler (± 1.0 mm). Asymmetrical measurements are reported as left:right sides of the body; mean values are reported ± 1 SD.

Sequence Data Collection

Whole genomic DNA of the new species of *Helicops* was taken from one preserved voucher specimen (ZUFMS-REP 2291) using the QIAGEN DNeasy Blood and Tissue Kit (QIAGEN). Our DNA sequences were compared to, and evaluated together with, mtDNA and nuDNA fragments of four *Helicops* species obtained from GenBank (Table 1). Although *H. pictiventris* and *H. infrataeniatus* are considered synonymous (Yuki and Lema 2005), we treated them as distinct in the molecular analysis because they are registered as such in the GenBank database. Additional sequences of *Hydrops triangularis* (Wagler 1824) and *Pseudoeryx plicatilis* (Linnaeus 1758) were used as outgroups (Lawson et al. 2005; Grazziotin et al. 2012).

Polymerase Chain Reaction (PCR) amplification and sequencing with primers 16Sa (5-CGC CTG TTT ATC AAA AAC AT-3) and 16Sb (5-CCG GTC TGA ACT CAG ATC ACG T-3) of Palumbi et al. (2002), and S77 (5-CAT GGA CTG GGA TCA GTT ATG-3) and S78 (5-CCT TGG GTG TGA TTT TCT CAC CT-3; Lawson et al. 2005) were performed to amplify a section of the mitochondrial 16S ribosomal RNA gene and oocyte maturation factor (C-mos) coding gene, respectively. PCR conditions for amplification consisted of 1× buffer, dNTP at 0.2 mM, each primer at

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TABLE 1.—Species of hydropsine snakes from Brazil for which molecular data were obtained for analysis.

Current genus and species name	GenBank accession numbers		Reference
	16s rRNA	C-mos	
<i>Helicops nentur</i> sp. nov.	KT453992	KT453991	This study
<i>Helicops hagmanni</i>	JQ598878	JQ598985	Grazziotin et al. (2012)
<i>Helicops angulatus</i>	AF158478	AF471160	Vidal et al. (2010)
<i>Helicops gomesi</i>	GQ457739	GQ45858	Zaher et al. (2009)
<i>Helicops infrataeniatus</i>	GQ457740	GQ457859	Zaher et al. (2009)
<i>Helicops pictiventris</i>	GQ457741	GQ457860	Zaher et al. (2009)
<i>Helicops carinicaudus</i>	—	JQ598984	Grazziotin et al. (2012)
<i>Hydrops triangularis</i>	AF158499	AF471158	Vidal et al. (2010)
<i>Pseudoeryx plicatilis</i>	AF158500	GQ45886	Vidal et al. (2010)

0.2 μ M, MgCl₂ at 2 mM, 1 unit Taq polymerase, and 2 μ L of template DNA, in a total reaction volume of 25 μ L. The PCR cycling program was as follows: 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 50°C and 54.4°C for 16S and C-mos, respectively, and 72°C for 1 min, concluding with a 7-min extension at 72°C. PCR products were purified by ammonium acetate/ethanol and sequenced at Macrogen Inc. (Seoul, South Korea). Sequences were edited by aligning forward and reverse reads using Geneious v7.1.7 (available at <http://www.geneious.com/>; Kearse et al. 2012).

Phylogenetic Analysis

The best-fit models of evolution (GTR + G for 16S rRNA and HKY for C-mos) were identified using JModeltest v2.1.7 (Darriba et al. 2012). Bayesian Information Criteria was chosen to select a model because of its high accuracy and precision (see Luo et al. 2010). Genetic divergences were estimated with MEGA (v6.06; Tamura et al. 2013). For pairwise distance comparisons we have chosen the uncorrected (p) model of nucleotide substitution because complex models might not be well-suited to specimen identification from short DNA fragments and do not provide better resolution than uncorrected p-distance (Srivathsan and Meier 2012).

Phylogenetic relationships among species were estimated using maximum likelihood (ML) and Bayesian inference (BI). ML was performed by heuristic search methods using PhyML software (Guindon and Gascuel 2003) with 1000 bootstrap replicates. BI was generated using MrBayes v3.2.2 (Huelsenbeck and Ronquist 2001) with 20 million generations. We sampled a tree every 5000 generations and calculated a consensus topology after discarding the first 20,000 trees (burn-in = 2,000,000).

SPECIES DESCRIPTION

Helicops nentur sp. nov.
(Figs. 1–3; Table 2)

Helicops sp. Costa et al. 2010:359.

Helicops sp. Costa et al. 2014:118.

Holotype.—UFMG 2486, an adult female collected on 8 November 2013 by Fernando Leal at a swamp in Fazenda Papa Capim (18.329398°S, 42.092017°W, 260 m above sea level [a.s.l.]; in all cases, datum = WGS84), São José da Safira, state of Minas Gerais, Brazil (Figs. 1–2).

Paratypes.—Four specimens, all from the Brazilian state of Minas Gerais, as follows: MZUFV 742, an adult female collected by Lício W. Assad, date unknown, at Jaíba (15.340270°S, 43.676862°W, ca. 480 m a.s.l.); MZUFV 960,

a young male, collector unknown, February 1998 at CBIA (20.713650°S, 42.864917°W, ca. 640 m a.s.l.), urban area of Viçosa; UFMG 175, an adult female collected by V.X. Silva on 6 January 1999 at the campus of Universidade Federal de Minas Gerais (19.869395°S, 43.966480°W, ca. 820 m a.s.l.), Belo Horizonte; ZUFMS-REP 2291, a young female collected by Carmen Côrtes Santana Silva on 4 March 2013 at District of Macuco (21.145255°S, 42.493443°W, ca. 224 m a.s.l.), Muriaé.

Diagnosis.—*Helicops nentur* sp. nov. can be diagnosed by the following combination of characters: (1) dorsal scale rows 17–17–15, smooth on the anterior third of body, becoming weakly keeled posteriorly; (2) ventral plates in the male 115, in females 111–117; (3) subcaudals in the male 56, in females 41–52; (4) subcaudal keels absent, dorsal caudal scales keeled; (5) supralabials 8, third and fourth contacting orbit; (6) infralabials 9–10, the first to fifth contacting the first pair of chinshields, the fifth and sixth contacting the second pair of chinshields; (7) intergenials absent; (8) nasal entire; (9) preocular one; (10) postoculars two; (11) temporals 2 + 2 or 2 + 3; (12) maxillary teeth 18–21 + 2; (13) hemipenis bilobed, semicalyculate, semicapitate, with lobes covered by encircling rows of spinulate flounces, body covered by numerous spinules and a few spines arranged in more or less oblique rows; (14) dorsum uniformly medium brown or dark brown; (15) venter cream, yellow, or light brown (sometimes mottled with gray) with two medial rows of black markings, usually semilunar in shape.



FIG. 1.—Holotype of *Helicops nentur* sp. nov. (UFMG 2486): dorsal (A) and ventral (B) view. Scale bar = 20 mm. A color version of this figure is available online.

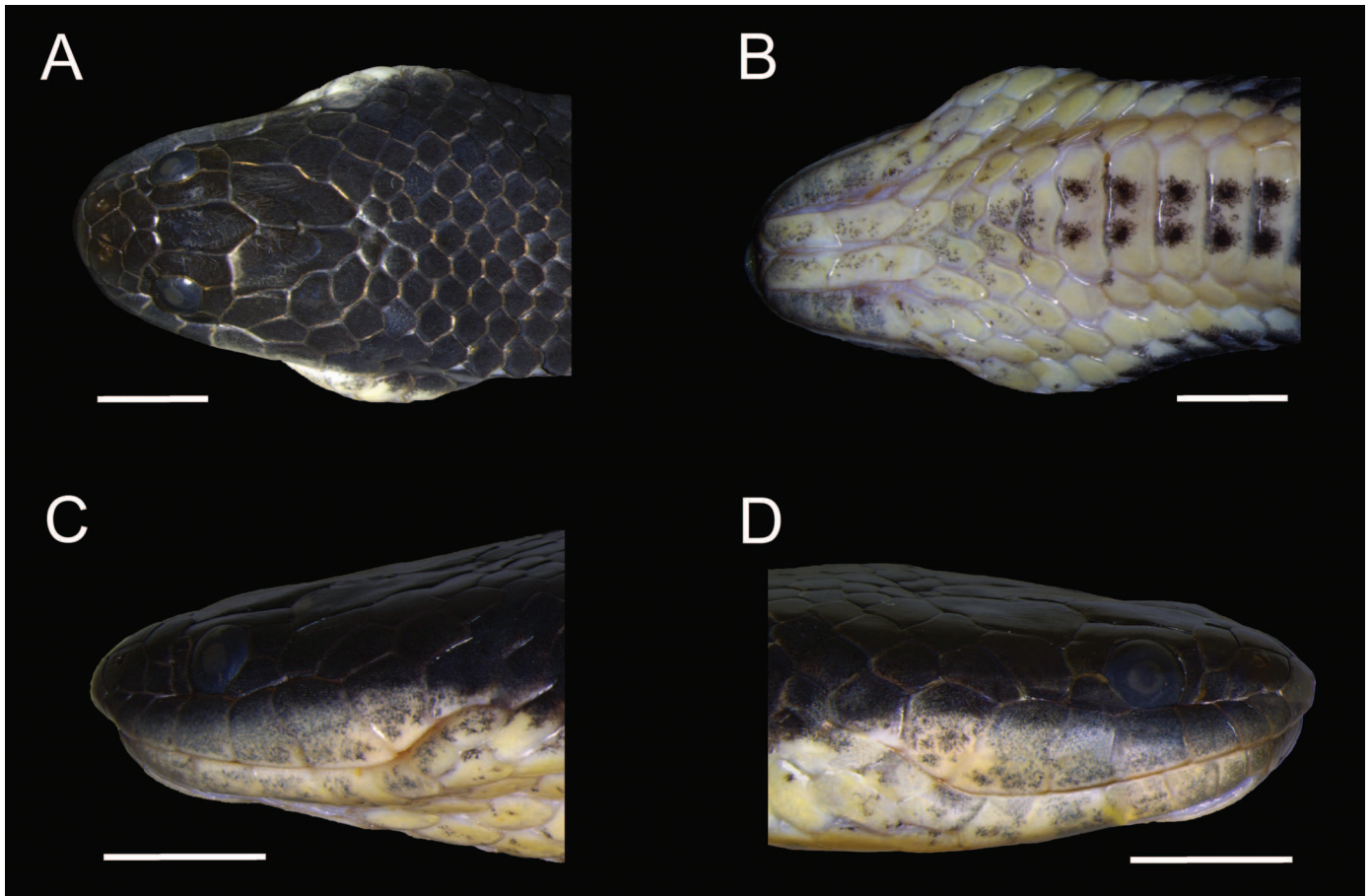


FIG. 2.—Holotype of *Helicops nentur* sp. nov. (UFMG 2486): head in dorsal (A), ventral (B), left (C), and right (D) view. Scale bar = 5 mm. A color version of this figure is available online.

Comparisons (Tables 3–4).—*Helicops nentur* sp. nov. differs from all congeners except *H. infrataeniatus* by having 17–17–15 dorsal scale rows. It also differs from all other *Helicops* except *H. modestus*, *H. tapajonicus*, *H. trivittatus*, and some *H. carinicaudus* by the presence of weak dorsal keels on the posterior third of body (character

unknown in *H. yacu*). *Helicops nentur* sp. nov. differs from *H. carinicaudus*, *H. danieli*, *H. gomesi*, *H. pastazae*, *H. petersi*, and *H. yacu* by having fewer than 119 ventral scales in both sexes. It further differs from *H. apiaka*, *H. hagmanni*, and *H. tapajonicus* by having fewer than 117 ventrals in males and fewer than 121 in females.

Helicops nentur sp. nov. differs from *H. angulatus*, *H. apiaka*, *H. danieli*, *H. gomesi*, *H. pastazae*, *H. petersi*, *H. polylepis*, *H. scalaris*, *H. tapajonicus*, and *H. yacu* by having fewer than 60 subcaudals in both sexes. The presence of 56 subcaudals in the male and 41–52 in the females of *H. nentur* sp. nov. also distinguishes it from *H. trivittatus* (subcaudals 67–80 in males and 56–66 in females) and *H. leopardinus* (64–89 in males and 53–76 in females). The absence of subcaudal keels distinguish *H. nentur* sp. nov. from *H. angulatus*, *H. apiaka*, *H. gomesi*, and *H. scalaris* (character unknown in *H. yacu*).

In *H. nentur* sp. nov., the third and fourth supralabials contact the eye, whereas in *H. danieli*, *H. hagmanni*, *H. pastazae*, *H. petersi*, and *H. tapajonicus* only the fourth supralabial contacts the eye. This character also distinguishes *H. nentur* sp. nov. from *H. angulatus* (fourth, fourth + fifth or fifth supralabial[s] contacting the eye), *H. gomesi* and *H. trivittatus* (fourth or fifth supralabial contacting the eye), *H. scalaris* (fourth or fourth + fifth supralabial[s] contacting the eye), and *H. yacu* (fourth + fifth supralabials contacting the eye).

The presence of 9–10 infralabials distinguishes *H. nentur* sp. nov. from *H. polylepis* (11–13), *H. trivittatus* (11–14), and

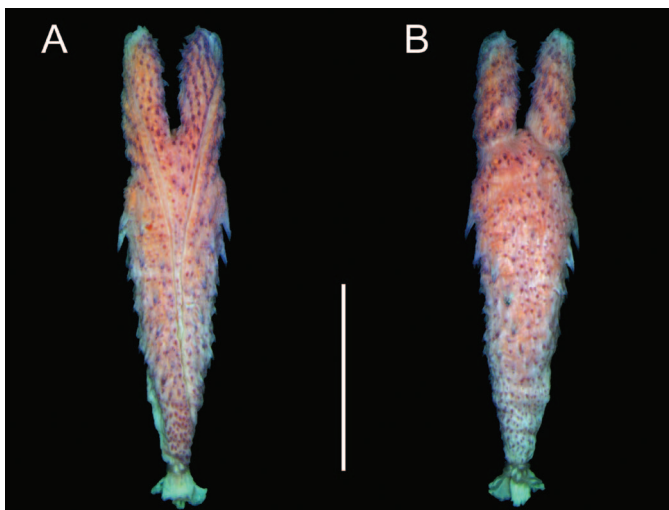


FIG. 3.—Right hemipenis of a paratype of *Helicops nentur* sp. nov. (MZUFV 960) fully everted and almost maximally expanded: sulcate (A) and asulcate (B) side. Scale bar = 10 mm. A color version of this figure is available online.

TABLE 2.—Meristic and morphometric characters in *Helicops nentur* sp. nov. PV = preventrals, VE = ventrals, C = cloacal shield, SC = subcaudals, SL = supralabials, SL + E = supralabials in contact with eye, IL = infralabials, IL + G1 = infralabials in contact with first pair of genials, IL + G2 = infralabials in contact with second pair of genials, NA = nasal (entire = E or semidivided = S), Pe = preocular, Po = postocular, AT = anterior temporals, PT = posterior temporals, MXT = maxillary teeth, SVL = snout-vent length (mm), TL = tail length (mm).

Specimen	Sex	Dorsals	PV	VE	C	SC	SL	SL + E	IL	IL + G1	IL + G2	NA	Pe	Po	AT	PT	MXT	SVL	TL
UFMG 2486 (holotype)	F	17-17-15	2	117	divided	41	8	iii-iv	10	i-v	v-vi	E:S	1	2	2	2	19 + 2	334	77
MZUFV 960	M	17-17-15	2	115	divided	56	8	iii-iv	10	i-v	v-vi	E	1	2	2	3:2	21 + 2	318	108
MZUFV 742	F	17-17-15	1	116	divided	44	8	iii-iv	10	i-v	v-vi	E	1	2	2	2:3	18 + 2	432	106
UFMG 175	F	17-17-15	1	117	divided	40 + n	8	iii-iv	10	i-v	v-vi	E	1	2	2	2	20 + 2	650	140 + n
ZUFMS-REP 2291	F	17-17-15	1	111	divided	52	8	iii-iv	9/10	i-v	v-vi	E	1	2	2	2	19 + 2	153	45

H. yacu (11-12). *Helicops nentur* sp. nov. can be further distinguished from *H. hagmanni*, *H. pastazae*, *H. petersi*, *H. scalaris*, *H. trivittatus*, and *H. yacu* by the absence of intergenials separating the second pair of chinshields.

An undivided nasal distinguishes *H. nentur* sp. nov. from all other *Helicops* with the exception of *H. yacu*. A single preocular distinguishes *H. nentur* sp. nov. from *H. trivittatus* (two preoculars), and the presence of two anterior temporals distinguishes *H. nentur* sp. nov. from *H. gomesi*, *H. petersi*, *H. tapajonicus*, *H. trivittatus*, and *H. yacu* (one anterior temporal). The presence of ≥ 18 (up to 21) prediastemal maxillary teeth distinguishes *H. nentur* sp. nov. from *H. angulatus*, *H. apiaka*, *H. hagmanni*, *H. pastazae*, *H. petersi*, *H. polylepis*, *H. scalaris*, and *H. yacu*, all of which have fewer than 18 teeth.

The uniformly colored dorsum of *H. nentur* sp. nov. is also present in some specimens of *H. carinicaudus*, *H. modestus*, and *H. tapajonicus*. A cream venter with two rows of black semilunar markings is present only in *H. nentur* sp. nov., *H. carinicaudus*, *H. danieli*, and *H. trivittatus*. In the latter three species the black ventral markings are strong and well-defined, whereas in *H. nentur* sp. nov. they are usually less well-defined. In preserved specimens of *H. nentur* sp. nov., the first dorsal scale row (DSR1) is cream colored, as is the adjacent venter, on the anterior third of the body; posteriorly, the scales of DSR1 become gray dorsally, and occasionally totally gray. In *H. carinicaudus* DSR1 is cream colored, whereas DSR2 is gray anteriodorsally, usually becoming totally gray posteriorly; in *H. danieli* DSR1 and DSR2 are white or cream colored, similar to the venter (Rossman 2002a); in *H. trivittatus* the scales of DSR1 are cream colored dorsally along the entire body (Rossman 2010).

In *H. carinicaudus* there is no gray pigmentation on the outer edges of the ventrals, and sometimes there is a midventral row of poorly defined black semilunar markings (Yuki and Lema 2005; present study); in *H. danieli* there is no gray pigmentation on the ventrals, and the black semilunar markings sometimes fuse midventrally (Rossman 2002a); in *H. trivittatus* the black markings are proportionally larger than those of *H. nentur* sp. nov., and there is no gray pigmentation on the ventrals (Rossman 2010).

Among the species of *Helicops* whose hemipenis morphology is described (all but *H. petersi* and *H. yacu*), the organ of *H. nentur* sp. nov. is readily distinguishable from that of *H. infrataeniatus*, *H. leopardinus*, *H. modestus*, and *H. tapajonicus* in having well-developed lobes. The asulcate side having lateral spines larger than central spines distinguishes the hemipenis of *Helicops nentur* sp. nov. from that of *H. hagmanni*, *H. infrataeniatus*, *H. leopardinus*, *H. modestus*, and *H. trivittatus* (small spines of uniform size). In *H. pastazae*, the central spines on the asulcate side are considerably longer than in *H. nentur* sp. nov. Lobes

covered with spinulate flouces distinguish the organ of *H. nentur* sp. nov. from that of *H. apiaka* (lobes with plicae), *H. danieli*, and *H. polylepis* (lobes with small papillae). The spines bordering the sulcus spermaticus in the hemipenis of *H. nentur* sp. nov. are smaller than those of *H. apiaka*. The less developed basal pocket in *H. nentur* sp. nov. distinguishes its hemipenis from that of *H. scalaris*.

Description of holotype.—Adult female, SVL 334 mm, tail length 77 mm (23% SVL); head rounded in dorsal view, flattened in lateral view, head length 19.13 mm (5.8% SVL), head width 11.92 mm (61.8% head length); no evident cervical constriction; snout rounded in dorsal and lateral views; rostrum-orbit distance 4.1 mm (21.2% head length); nasal-orbit distance 2.37 mm (12.3% head length); interorbital distance 4.64 mm (38.9% head width); eye diameter 2.65 mm, pupil round; rostral subtriangular in frontal view, wider (3.22 mm) than high (1.78 mm), visible from above; internasal single, diamond-shaped, longer (2.2 mm) than wide (1.98 mm); prefrontals two, hexagonal, longer (2.34:2.35 mm) than wide (1.46:1.49 mm), in medial contact (prefrontal suture 0.81 mm); frontal pentagonal, longer (4.84 mm) than wide (2.56 mm); supraoculars rectangular, longer (3.89:3.98 mm) than wide (1.61:1.63 mm); parietals longer (6.18:6.23 mm maximum length) than wide (3.47:3.52 mm maximum width); parietal suture 3.95 mm; nasals quadrangular, separated by prefrontal, well visible from above; left nasal semidivided, right nasal entire; loreal quadrangular, contacting nasal anteriorly, prefrontal above, second and third supralabials below, and preocular posteriorly; preocular single, higher (1.90:1.97 mm) than wide (0.65:0.60 mm), contacting loreal and prefrontal anteriorly, supraocular above, third supralabial below, and the eye posteriorly; postoculars two; upper postocular (1.33:1.35 mm high; 1.48:1.50 mm wide) contacting the eye anteriorly, supraocular and parietal above, lower postocular below, and upper anterior temporal posteriorly; lower postocular (2.17:2.17 mm high; 1.14:1.14 mm wide) contacting the eye anteriorly, upper postocular above, fourth to sixth supralabials below, and upper anterior temporal posteriorly; temporals 2 + 2, longer than wide; upper anterior temporal (1.97:1.96 mm high; 3.56:3.58 mm long) contacts the postoculars anteriorly, parietal above, sixth supralabial below, lower anterior temporal and upper posterior temporal posteriorly; lower anterior temporal (2.06:1.65 mm high; 3.67:3.15 mm long) contacts upper anterior temporal above and anteriorly, sixth and seventh supralabials below, upper posterior temporal above, and lower posterior temporal posteriorly; upper posterior temporal (2.56:2.59 mm high; 2.92:2.92 mm long) contacting both anterior temporals anteriorly, parietal above, lower anterior and posterior temporals below, and two small head scales posteriorly; lower posterior temporal (2.2 mm high; 2.45:2.52 mm long)

TABLE 3.—Summary of morphological characters of *Helicops* species. AD = anterior dorsal scale rows, MD = midbody dorsal scale rows, PD = posterior dorsal scale rows, DK = dorsal keels on posterior third of body (medium = M, strong = S, or weak = W), V = ventral plates, SC = subcaudal plates, SCK = subcaudal keels (present = Yes or absent = No), SL = supralabials, SL + E = supralabials contacting the eye, IL = infralabials, IL + G1 = infralabials contacting the first pair of genials, IG = intergenials (present = Yes or absent = No), NA = nasal (entire = E or semidivided = S), Pe = precoculars, Po = postoculars, AT = anterior temporals, PT = posterior temporals, MXT = maxillary teeth.

Species	AD	MD	PD	DK	V (male/female)	SC (male/female)	SCK	SL	SL + E	IL	IL + G1	IG	NA	Pe	Po	AT	PT	MXT
<i>H. angulatus</i>	19–21	19–20	17–19	S	105–123/109–123	74–96/66–84	Yes	7–9	iv; iv–v; v	9–11	i–iv; i–v; i–vi	No	S	1–2	2	2–3	3–4	15 + 2
<i>H. apiaka</i>	21–24	21–22	17–19	S	118–127/124–132	79–103/80–84	Yes	7–9	iii–iv	9–12	i–iv; i–v; i–vi	No	S	1	2	2–3	3	15–16 + 2
<i>H. carinicaudus</i>	19	19	17	W–S	130–141/135–148	48–69/48–73	No	7–8	iii–iv; iv	9–10	i–v	No	S	1	2	1–2	2–3	16–19 + 2
<i>H. danieli</i>	19–21	19–20	16–19	S	125–135/130–141	76–86/61–70	No	8–9	iv	10–11	i–v	No	S	1	2	1–2	2	16–20
<i>H. gomesi</i>	19	19	19	S	125–132/128–132	71–86/67–73	Yes	8–9	iv; v	10	i–iv; i–v	No	S	1	2	1	2–3	18
<i>H. hagmanni</i>	23–27	21–29	19–23	S	117–127/130–134	55–67/51–53	No	8	iv	10–12	i–v	Yes	S	1–2	1–2	1–2	3	15–17 + 2
<i>H. infrataeniatus</i>	17–19	17–19	15–19	S	115–138/117–138	52–88/50–83	No	7–9	iii–iv; iv	10–12	i–v; i–vi	No	S	1	2	1–2	2	17–20 + 2
<i>H. leopardinus</i>	15–22	19–22	17–19	M–S	108–126/108–130	64–89/53–76	No	8–10	iii–iv; iv; iii–v	8–11	i–iv; i–v	No	S	1–2	2	2	2–4	18 + 2
<i>H. modestus</i>	19	19	17–19	W–M	112–125/116–122	54–70/53–64	No	8	iii–iv; iv	9–11	i–iv; i–v; i–vi	No	S	1–2	2–3	2	2–4	19 + 2
<i>H. pastazae</i>	23	23–25	19	S	121–134/130–145	93–117/72–97	No	8–10	iv	9–13	i–iv; i–v	Yes	S	1	2	2	2–3	14–17 + 2
<i>H. petersi</i>	21	21–23	16	S	135–142/137–150	85–91/67–73	No	8	iv	9–12	i–v	Yes	S	1	2	1	2–3	16–17 + 2
<i>H. polyplepis</i>	23–25	23–25	19	S	112–131/121–133	70–102/71–81	No	8–9	iii–iv; iv	11–13	i–iv; i–v; i–vi	No	S	1	2	1–2	2–4	16 + 2
<i>H. scalaris</i>	21–25	19–21	16–19	S	110–119/113–125	83–95/67–81	Yes	8–9	iv; iv–v	10–14	i–v	Yes	S	1	2	1–3	3	15–17 + 2
<i>H. tapajonius</i>	19	19	17	W	118/121–123	79/67–76	No	8	iv	9–11	i–iv; i–v	No	S(?)	1	2	1	2	18 + 2
<i>H. trivittatus</i>	21–25	20–23	16–19	W	114–128/115–129	67–80/56–66	No	8–10	iv; v	11–14	i–v; i–vi	Yes	S	2	2	1	2	19–22 + 2
<i>H. yacu</i>	25–29	25–28	18–20	?	124/129–136	?	?	8–9	iv–v	11–12	i–v; i–vi	Yes	E	1	2	1	2–3	14–15 + 2
<i>H. nentur</i> sp. nov.	17	17	15	W	115/111–117	56/41–52	No	8	iii–iv	9–10	i–v	No	E	1	2	2	2–3	18–21 + 2

References: Amarel (1922, 1938), Boulenger (1893), Frota (2005), Griffin (1916), Kawashita-Ribeiro et al. (2013), Nunes (2006), Rossmann and Abe (1979), Rossmann and Dixon (1975), Rossmann (1975, 1976, 2002ab, 2010), Shreve (1934), Yuki and Lenka (2005), and the present study.

TABLE 4.—Descriptions of the color patterns seen in *Helicops* species.

Species	Dorsal color pattern	Ventral color pattern	Reference*
<i>H. angulatus</i>	Olive gray, tan or olive brown, with reddish brown to dark brown crossbands.	Cream to light tan, with or without extensions of dorsal crossbands, making a checkered pattern.	11, 16
<i>H. apiaka</i>	Approximately 15 dark crossbands.	Creamy white with the extensions of large black dorsal crossbands.	15
<i>H. carinicaudus</i>	Uniformly dark-brown or black, sometimes with broad longitudinal stripes lighter than ground color.	Cream with two (sometimes three) medial rows of black semilunar marks.	13, 16
<i>H. danieli</i>	Reddish-brown or olive-brown with 4–5 rows of alternating dark spots.	Cream with two medial rows of black semilunar marks, sometimes fused midventrally.	3, 9
<i>H. gomesi</i>	Olive-brown with irregular dark blotches.	Yellowish-brown or olive, with the extensions of dark dorsal blotches laterally.	2
<i>H. hagmanni</i>	Gray-brown with alternating light and dark blotches.	Irregularly checkered light/red and dark color.	5
<i>H. infrataeniatus</i>	Dark-brown with light-brown stripes.	Cream or red with 1–3 dark stripes or darkly checkered.	13, 16
<i>H. leopardinus</i>	Medium brown with dark brown or black blotches.	Checkerboard of black and red, banded black and red, or a combination of both.	11, 16
<i>H. modestus</i>	Dark brown with 2–3 narrow light brown stripes, or uniformly dark olive.	Cream, with or without faint brown flecks.	4, 15, 16
<i>H. pastazae</i>	Tan to gray brown with four or five rows of alternating dark spots, the paravertebral spots large and often fused transversely.	Cream with a series of dark crossbands or alternating checks, the light ventral color extending onto several dorsal scale rows.	7
<i>H. petersi</i>	Dark olive brown with four or five rows of alternating dark spots.	Cream with a lateral series of dark checks.	7
<i>H. polyplepis</i>	Brownish or olive gray, with blackish spots in five alternating rows.	Dark with pale spots.	1, 7
<i>H. scalaris</i>	Grayish tan with 3–5 rows of irregular dark blotches, the vertebral blotches larger than the laterals, and all 3 usually fused longitudinally on the neck to form short, broad stripes.	Cream medially with two rows of brown pigment forming either an irregular checkered pattern or broad ventrolateral stripes, at least anteriorly.	10
<i>H. tapajonius</i>	Uniformly moss-green.	Checkered light and dark brown.	12
<i>H. trivittatus</i>	Medium brown with five narrow longitudinal light stripes.	Cream with two medial rows of black semilunar markings.	14
<i>H. yacu</i>	Light to medium gray-brown, with four alternating rows of relatively small dark spots.	Cream with an irregular series of large black checks or a median row of black crescents.	6, 8
<i>H. nentur</i> sp. nov.	Uniformly dark-olive green, dark brown or dark gray.	Yellow (in life), cream or light brown (sometimes mottled with gray) with two medial rows of black semilunar markings.	16

* (1) Boulenger 1893; (2) Amarel 1922; (3) Amarel 1938; (4) Rossmann 1974; (5) Rossmann 1975; (6) Rossmann and Dixon 1975; (7) Rossmann 1976; (8) Rossmann and Abe 1979; (9) Rossmann 2002a; (10) Rossmann 2002b; (11) Bartlett and Bartlett 2003; (12) Frota 2005; (13) Yuki and Lenka 2005; (14) Rossmann 2010; (15) Kawashita-Ribeiro et al. 2013; (16) present study.

contacting lower anterior temporal anteriorly, upper posterior temporal above, seventh and eighth supralabials below, and two small head scales posteriorly; supralabials eight, the third and fourth contacting the eye; sixth supralabial higher (3.05:3.20 mm) and wider (3.25:3.26 mm) than the others; symphyseal triangular, wider (1.71 mm) than long (1.38 mm); infralabials 10, the first pair in contact behind symphyseal, preventing symphyseal–chinshield contact; first to fifth pair of infralabials contacting first pair of chinshields (genials); fifth and sixth pair of infralabials in contact with second pair of chinshields; intergenital scale absent; chinshields longer (first pair 4.62:4.50 mm; second pair 5.75:4.70 mm) than wide (first pair 1.60:1.62 mm; second pair 1.70:1.71 mm); dorsal scales in 17–17–15 rows, lacking apical pits, smooth behind the head, becoming weakly keeled posteriorly; keels are more visible on posterior-most region of body and on dorsal surface of tail; gular scales 4:5, between the last infralabial and first preventral; preventrals two, ventral scales 117; cloacal plate divided; 41 divided subcaudals; maxillary teeth 19 + 2.

Color in life of holotype.—Dorsal and lateral surfaces of head dark olive-green; supralabials dark olive-green above, becoming yellowish-green below; infralabials and gular region yellow with scattered olive-green pigment. Ventrals yellow, with two medial rows of black round or semilunar marks (two marks on each ventral); gray pigment between the black marks on each ventral anteriorly; gray pigment more intense and covering entire ventral surface posteriorly. Subcaudals gray, with black medial markings on subcaudals 1–6. Dorsal ground color dark olive-green; DSR1 yellow with olive-green pigments anteriorly.

Color in preservative of holotype (Fig. 1).—Dorsal and lateral surfaces of head dark gray; supralabials 1–5 light gray; supralabials 6–7 cream with gray pigmentation, more intense above; supralabial 8 dark gray above and cream below; infralabials and gular region cream with scattered gray pigment. Ventrals cream, with two medial rows of black round or semilunar marks (two marks on each ventral); gray pigment between the black marks on each ventral anteriorly; gray pigment becoming more intense and covering entire ventral surface posteriorly. Subcaudals grayish, with black medial markings on subcaudals 1–6. Dorsal ground color dark gray; DSR1 cream with gray flecks anteriorly.

Description of hemipenis.—Based on the right hemipenis of the male paratype (MZUFV 960), which was fully everted and almost maximally expanded (Fig. 3). In situ, the everted organ extends to the 14th subcaudal. Hemipenis bilobed, semicalyculate, and semicapitate; body 12.9 mm long, with well-developed lobes (7.5 mm; 58% of hemipenial body length), distinct from the body by a constriction from lateral to asulcate side; lobular crotch with a line of small spines; lobes covered by encircling rows of horizontally oriented spinulate flounces, except at the apices, which are nude; sulcate side covered by several spinules and some small spines arranged in more or less oblique rows; sulcus spermaticus bifurcating in the proximal region, with branches having a S-shaped condition; the asulcate side is covered with spinules and bordered by lateral spines increasing in size from the base to the apex; a small oblique nude area is present in the left and right portions of the asulcate side, close to the edge of capitulum; a basal pocket is present.

Variation.—The single male 154 mm SVL, 45 mm TL; largest female UFMG 175, 650 mm SVL, 140+ mm TL



FIG. 4.—Paratype (ZUFMS-REP 2291) of *Helicops nentur* sp. nov. immediately postmortem in (A) dorsal view and (B) ventral view. A color version of this figure is available online.

(broken tail); tail 33.9% SVL in the male, 23–29.2% SVL (mean = $25.56 \pm 3.23\%$, $n = 3$) in females (UFMG 175 not included); ventrals in the male 115, in females 111–117 (mean = 115.2 ± 2.87 , $n = 4$); subcaudals 56 in the male, in females 41–52 (mean = 45.6 ± 5.68 , $n = 3$); preventrals 1–2 (mean = 1.40 ± 0.54 , $n = 5$); prediastemal maxillary teeth 18–21 (mean = 19.40 ± 1.14 , $n = 5$); infralabials on left side in the male 9.

The nasals are undivided in all specimens, with two exceptions: The right nasal of UFMG 2486 is semidivided and the right nasal of MZUFV 742 shows a small sulcus that does not reach the lower part of the nostril. All specimens have two anterior temporals, the upper longer than the lower. Usually there are two posterior temporals unequal in size, but MZUFV 742 has three posterior temporals on the right side, whereas MZUFV 960 has three posterior temporals on the left side.

Color pattern is similar among all examined specimens of *H. nentur* sp. nov., with few differences, probably of ontogenetic origin. The two smallest specimens—MZUFV 960 and ZUFMS-REP 2291—have less gray pigment in the medial region of the ventrals. In life, the venter was cream in the gular region, yellow on the anterior half of body, and light orange posteriorly in ZUFMS-REP 2291 (Fig. 4).

Natural history and habitat.—Available information (from the holotype and one paratype) suggests that *H. nentur*

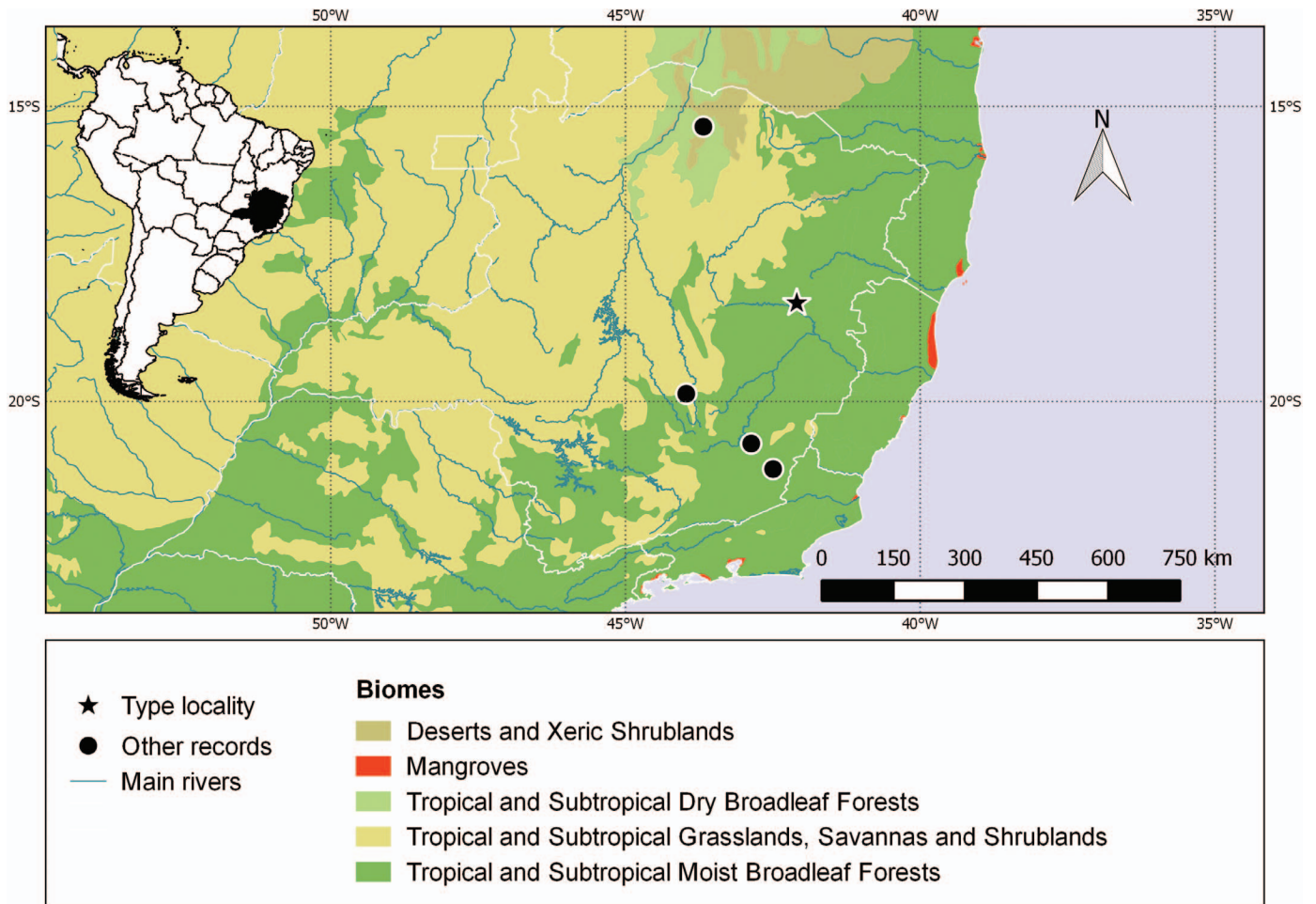


FIG. 5.—Locality records of *Helicops nentur* sp. nov. in the state of Minas Gerais, Brazil (insert). A color version of this figure is available online.

sp. nov. inhabits lentic water bodies such as swamps. The holotype was collected while active at 0300 h, partially submerged. After collection, it gave birth to two stillborn specimens not measured nor preserved. ZUFMS-REP 2291 has an umbilical scar on ventrals 91–95. Date of collection of these two specimens suggest that reproduction in *H. nentur* sp. nov. might occur during the rainy season (October–March).

Geographic distribution.—*Helicops nentur* sp. nov. is known only from five localities in the Brazilian state of Minas Gerais: Belo Horizonte, Jaíba, Muriaé, São José da Safira, and Viçosa (Fig. 5). The distribution of this species (sensu Olson et al. 2001) is in the Bahia Interior Forest ecoregion (Tropical and Subtropical Moist Broadleaf Forests biome), its border with the Cerrado ecoregion (Tropical and Subtropical Grasslands, Savannas, and Shrublands biome), and the ecotone between the Atlantic Dry Forest and the Caatinga ecoregions (Tropical and Subtropical Dry Broadleaf Forests biome and Deserts and Xeric Shrublands biome). This indicates that *H. nentur* sp. nov. might occupy different environments and climatic conditions. The distance between collection localities also indicates that there are many distribution gaps in the range of the species.

Etymology.—The specific name *nentur* has its origin in Quenya, a fictional language created by the late writer and philologist J.R.R. Tolkien. In Tolkien's mythology, Quenya is

spoken by the Eldar, the High Elves of Valinor, which is a land in the blessed continent of Aman. The name *nentur* is formed by the words *nen* (water) and *tur* (ruler, master), meaning “master of waters,” which is a reference to the aquatic habits of *Helicops*. The name is treated as a noun in apposition.

Molecular phylogeny and genetic divergence of the new species.—Sequence divergences between *H. nentur* sp. nov. and other congeners range between 4.0% and 6.0% (mean 4.8%) for 16S rRNA and between 0.0% and 0.4% (mean 0.2%) for C-mos (Table 5). Among those species for which 16S genetic data are available, *H. nentur* sp. nov. is sister to a clade formed by *H. hagmanni*, *H. angulatus*, and *H. gomesi* (Fig. 6A) with high support (bootstrap value = 81%, and posterior probability = 0.99). A partial C-mos tree shows the new species as sister to *H. carinicaudus* with low bootstrap value (64%) but high posterior probability (0.99; Fig. 6B).

DISCUSSION

We have described the 17th extant species of *Helicops*. Most species of the genus occur in northern South America and have received more attention from taxonomists than the southern species (e.g., Rossman 1976, 2002a,b, 2010; Yuki 1994). Of the southern *Helicops*, only *H. carinicaudus* and *H. infrataeniatus* have had recent taxonomic revision (Lema et al. 1984; Deiques

TABLE 5.—Uncorrected pairwise distances of nucleotide substitution between 16S rRNA (below the diagonal) and C-mos (above the diagonal) sequences of some *Helicops* species.

	<i>Helicops nentur</i> sp. nov.	<i>Helicops hagdmani</i>	<i>Helicops angulatus</i>	<i>Helicops infrataeniatus</i>	<i>Helicops pictiventris</i>	<i>Helicops gomesi</i>	<i>Helicops carinicaudus</i>
<i>Helicops nentur</i> sp. nov.	—	0.004	0.002	0.002	0.002	0.002	0.000
<i>Helicops hagdmani</i>	0.040	—	0.002	0.002	0.002	0.002	0.004
<i>Helicops angulatus</i>	0.042	0.045	—	0.000	0.000	0.000	0.002
<i>Helicops infrataeniatus</i>	0.048	0.062	0.065	—	0.000	0.000	0.002
<i>Helicops pictiventris</i>	0.051	0.065	0.068	0.002	—	0.000	0.002
<i>Helicops gomesi</i>	0.060	0.054	0.022	0.071	0.074	—	0.002
<i>Helicops carinicaudus</i>	—	—	—	—	—	—	—

and Cechin 1991; Yuki and Lema 2005). The description of *H. nentur* sp. nov. is the first of a non-Amazonian *Helicops* since *H. gomesi*, >90 yr ago (Amaral 1922).

The new taxon can be distinguished from all other congeners by scale counts and color pattern. A specimen now referred to as *H. nentur* sp. nov. was first noted during an inventory of the snakes from Viçosa region (Costa et al. 2010, as “*Helicops* sp.”). At that time it was identified as having morphological characters between those of *H. carinicaudus* and *H. infrataeniatus*, but the lack of additional specimens had prevented further study. With the availability of new specimens, a better comparison could be made. *Helicops nentur* sp. nov. and *H. infrataeniatus* share many scale counts and are the only species of the genus with 17 dorsal scale rows—*H. infrataeniatus* can also present 19 dorsals—but have distinct color patterns and very different hemipenial morphology (Yuki and Lema 2005). Despite a superficial similarity, *H. nentur* sp. nov. and *H. carinicaudus* can be separated by the number of dorsal scale rows, ventral plates, and some details of color pattern.

The superficial similarity between *H. nentur* sp. nov. and *H. carinicaudus* led us to hypothesize a close phylogenetic

affinity between them. This assumption could not be tested with 16S rRNA because of the lack of 16S data for *H. carinicaudus* in GenBank. A genetic analysis based on C-mos indicates a close relationship between the two species (Fig. 6B), with low bootstrap (64%) but high posterior probability (0.99; see García-Sandoval 2014 for a discussion of this type of discrepancy). As well as morphological distinctiveness, these two species have different geographic distribution patterns: *H. carinicaudus* occurs in lowland ombrophilous forests, restingas, and mangroves in southeastern and southern Brazil (Yuki and Lema 2005; Bérnils 2009); whereas *H. nentur* sp. nov. has a more inland distribution, from southeastern to northern Minas Gerais state, in regions originally covered by deciduous or semideciduous seasonal forests.

No phylogeny of *Helicops* based on morphological characters has been published. Nunes (2006) reported on the systematics of hydropsine snakes based on examinations of morphological and meristic traits of 13 species of *Helicops* (all known species at that time other than *H. tapajonicus* and *H. yacu*). It is of interest to note that the phylogenetic relationships of *Helicops* described here (Fig. 6A), albeit

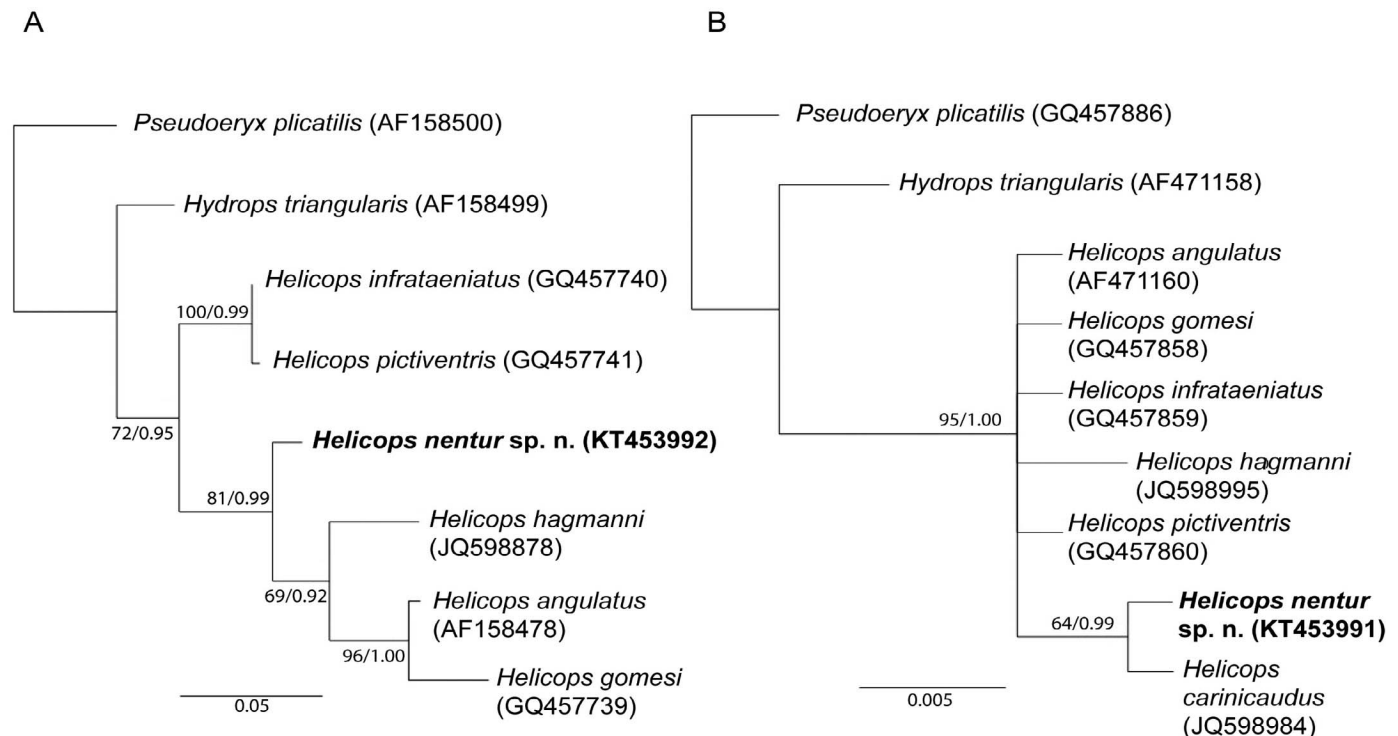


FIG. 6.—Phylogenetic relationships of sampled species of *Helicops* based on (A) 16s rRNA and (B) C-mos sequence data. Numbers at nodes indicate the bootstrap values/posterior probabilities; the bars below each cladogram indicate base substitution rate for each gene (# of substitutions per site). *Hydrops triangularis* and *Pseudoeryx plicatilis* were used as outgroups.

with limited taxon sampling, differ from Nunes (2006) only in the position of *H. hagmanni*.

Despite some recent studies (e.g., Rossman 1976, 2002a,b, 2010; Frota 2005; Yuki and Lema 2005; Kawashita-Ribeiro et al. 2013), an understanding of the taxonomy and systematics of *Helicops* needs further resolution. Widespread taxa such *H. angulatus* and *H. leopardinus* should be reviewed whereas less common taxa, such as *H. gomesi*, deserve redescription. Moreover, further sequencing of nuclear and mitochondrial genes of additional species could help improve the understanding of the evolution of morphological characters in *Helicops*.

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RESUMO: *Helicops* é um gênero neotropical de cobras-d'água com 16 espécies. Com base em dados morfológicos (contagens de escamas, dentição, coloração e anatomia do hemipênis) e genéticos (genes 16S rRNA e C-mos) nós identificamos uma nova espécie para o gênero. O novo táxon é diagnosticado pela presença de 17-17-15 fileiras de escamas dorsais, 111–117 escudos ventrais, 41–56 subcaudais sem quilhas, nasal inteira, 18–21 + 2 dentes maxilares, hemipênis bolobado, semicaliculado e semicapitado, dorso uniformemente marrom ou marrom-escuro, ventre creme ou marrom-claro com duas fileiras mediais de marcas negras, usualmente com forma semilunar. A nova espécie é conhecida do sudeste ao norte do estado de Minas Gerais, Brasil.

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APPENDIX

Specimens Examined (all from Brazil)

- Helicops angulatus*.—PARÁ: Marabá: Vila União (UFMG 1463 [male], 1523 [female], 1526 [female]).
- Helicops carinicaudus*.—ESPÍRITO SANTO: Anchieta: Barragem norte da lagoa de Maimbá (UFMG 174 [male]); RIO DE JANEIRO: Magé: Ponte Preta (MNRJ 15892 [female], 15893 [male]); Rio de Janeiro: Pedra de Guaratiba (MNRJ 15186 [male], 15187 [male]); Serra do Mendanha, estrada Guandu do Sena (MNRJ 14082 [male]); SÃO PAULO: Itanhaém (UFMG 178 [male], 179 [male], 180 [female]).
- Helicops infrataeniatatus*.—RIO GRANDE DO SUL: Balneário Pinhal: (MCP 18916 [female]); Magistério (MCP 18914 [female]); RS-040 (MCP 18867 [male]); Capivari do Sul: RS-040 (MCP 18288 [female]); RS-040, Km 54 (MCP 18433 [male]); Gravataí: Itacolomi, Sede do Sintai (MCP 15723 [male]); Passo Fundo: (MNRJ 10069 [female]); SANTA CATARINA: Porto União: Bairro Bela Vista (MCP 16046 [male]).
- Helicops leopardinus*.—MATO GROSSO: Poconé (UFMG 172 [male]); MINAS GERAIS: Januária: Pandeiros, Rancho do Chico (UFMG 1208 [female], 1209 [female]).
- Helicops modestus*.—MINAS GERAIS: Augusto de Lima: Fazenda Serra do Cabral Sul (UFMG 1630 [female]); Belo Horizonte: Bairro Pampulha, Av. Otacílio Negrão de Lima, Perto da "Toca da Raposa" (UFMG 184 [male]); Bairro Santa Amélia, Av. Sanitária (UFMG 176 [female]); Florestal (UFVCF 57 [male], 58 [female]); Sabará: Ravena (UFMG 1698 [female]); SÃO PAULO: Cotia (UFMG 177 [female]).
- Helicops nentur* sp. nov.—MINAS GERAIS: Belo Horizonte, Campus UFMG (UFMG 175 [female], paratype); Jaíba (MZUFV 742 [female], paratype); Muriaé, Distrito de Macuco (ZUFMS-REP 2291 [female], paratype); São José da Safira: Fazenda Papa Capim (UFMG 2486 [female], holotype); Viçosa, CBIA (MZUFV 960 [male], paratype).

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