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Description of Two New Species of *Rhinatrema* (Amphibia: Gymnophiona) from Brazil and the Return of *Epicrionops niger* to *Rhinatrema*

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Abstract. We present a molecular phylogeny of Rhinatrematidae on the basis of three mitochondrial and four nuclear genes and describe two new species of *Rhinatrema* from the Guianan region of Brazil, both of which were previously conflated with *R. ron*. Our phylogenetic results show that at least one species of *Epicrionops* is nested within the *Rhinatrema* clade. Although our taxon sampling is limited, we reallocated *E. niger* in the genus *Rhinatrema* in order to avoid paraphyly. The phylogeny supports our new species described here. One of the new species is closely related to *R. bivittatum* in a clade that also includes *R. shiv*. The other new species is sister to all other sampled *Rhinatrema* and is morphologically similar to *R. ron* but differs in number of annuli and in the condition of the oral mucosa. The known distribution of *R. ron* is now restricted to the type locality.

Keywords. Amazonia; Caecilians; Guianan region; Nomenclature; Phylogenetic analysis; Taxonomy.

INTRODUCTION

Nussbaum (1977) described Rhinatrematidae to accommodate the species of two genera of South American caecilians (*Rhinatrema* Duméril and Bibron, 1841; and *Epicrionops* Boulenger, 1883), at that time classified as Ichthyophiidae Taylor, 1968. Despite the strong morphological support for the monophyly of Rhinatrematidae, which has been corroborated by later molecular phylogenetic studies (Pyron and Wiens, 2011; Kamei et al., 2012; San Mauro et al., 2014), Nussbaum (1977) presented few differences between *Rhinatrema* and *Epicrionops* additional to those provided by Taylor (1968).

Taylor (1968) resurrected *Epicrionops* from the synonym of *Rhinatrema* mainly based on the shape of the vent (longitudinal in the former and transverse in the latter), and in the size of the tail (much shorter in *Rhinatrema*). Nussbaum (1977) added the difference in the number of ceratobranchial arches in the glossal skeleton (three in *Epicrionops,* two in *Rhinatrema*) and the extension of the tentacular opening over the eyes, stating "In *Epicrionops,* the opening is in contact with the clear tissue covering the eye, and in *Rhinatrema* the opening projects well into the window over the eye" (Nussbaum, 1977:7).

Wilkinson and Nussbaum (2006) cited the number of scale rows per annular groove as a diagnostic character for the rhinatrematid genera (more than one in *Epicrionops,* a single row in *Rhinatrema*), but in the subsequently described *R. ron* Wilkinson and Gower, 2010 and *R. shiv* Gower et al., 2010 more than one row can be found, depending on the region of the body. More recently, Maciel et al. (2012) observed in what they (incorrectly) considered *R. ron* that the number of ceratobranchial arches in the glossal skeleton varies among adult specimens of one population, which can have two or three arches. Further, the condition of the tentacle apertures cited by Nussbaum (1977) was disregarded by later publications on rhinatrematids (Wilkinson and Nussbaum, 2006; Gower et al., 2010; Wilkinson and Gower, 2010; Wilkinson et al., 2011), and Maciel and Hoogmoed (2011) noted that a longitudinal vent also can be found in *Rhinatrema*. Thus, to date only tail length seems to remain as a useful character to distinguish the two rhinatrematid genera morphologically.

The few available phylogenetic studies that have included rhinatrematid species found *Epicrionops* to be paraphyletic, recovering *E. niger* (Dunn, 1942) as closely related to *Rhinatrema bivittatum* (Guérin-Méneville, 1838) (e.g., Pyron and Wiens, 2011; San Mauro et al., 2014). However, as these studies are limited in the number of relevant taxa considered (only *E. marmoratus* Taylor, 1968, *E. niger* and *R. bivittatum* were sampled) no nomenclatural

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changes were proposed. Recently, Wilkinson and Gower (2010) described *R. ron* on the basis of a single specimen from the state of Amazonas, Brazil. A year later, Maciel and Hoogmoed (2011: 45, see map in fig. 23) reported 31 specimens of *R. ron* from three more localities, including one in the state of Amazonas and two in the state of Pará, Brazil. They also noted that the color pattern distinguished the holotype of *R. ron* and the specimen from Urucará, Amazonas from the specimens from the two localities in Pará, but they considered all their specimens as *R. ron*.

We now have more specimens and new morphological and molecular data that support the description of two new species of *Rhinatrema* on the basis of specimens formerly identified as *R. ron* (Maciel and Hoogmoed, 2011; Maciel et al., 2012). Further, we can now include all but one of the species of *Rhinatrema* in a phylogenetic analysis, leading us to re-allocate *E. niger* in *Rhinatrema*.

MATERIALS AND METHODS

Morphological study

We examined specimens of *Epicrionops* and *Rhinatrema* from the following collections (for specimens of previously described species, see Appendix): AMNH (American Museum of Natural History), IEPA (Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá), INPA (Coleção Herpetológica do Instituto Nacional de Pesquisas Amazônicas), MNRJ (Museu Nacional do Rio de Janeiro, MPEG (Museu Paraense Emílio Goeldi), MZUSP (Museu de Zoologia da Universidade de São Paulo), and PUCMG (Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais).

Morphometric and meristic characters

The following characters were used: SVL (snout–vent length measured as the distance between the tip of snout and the anterior border of the vent), TL (total length), HH (head height level with corner of mouth), TSFN (distance between the tip of snout and first nuchal groove measured dorsally), HW (head width at jaw articulation), EE (distance between the inner edges of the eyes), ECM (distance between eye and corner of mouth), EMM (shortest distance between eye and margin of mouth), EN (distance between eye and nostril), NN (distance between inner edges of nostrils), NMM (shortest distance between nostril and margin of mouth [= lip]), LCR (length of the collar region measured dorsally), WNC (width at first nuchal collar), BH (body height at midbody), BW (body width at midbody), WS (width of the lateral stripe at midbody), WV (width of the body at vent), TAL (tail length measured from the posterior edge of the vent to the tip of the tail). Meristic: TBAD (total body annuli count made dorsally), TBAV (total body annuli count made ventrally), GIV (grooves interrupted by the vent), TF (tail folds counted behind vent). Dentition: DT (dentary teeth), PMT (premaxillary-maxillary teeth), PPT (prevomerine-palatine teeth), ST (splenial [= inner mandibular] teeth).

The third nuchal groove was identified following Wilkinson and Gower (2010: 64 as "arbitrarily the first dorsal groove that clearly crosses stripe onto venter." All measurements were made using a dial caliper to the nearest 0.1 mm, except total length, which was measured with a ruler to the nearest 1 mm. Sex was determined by direct observation of the gonads. Specimens with well-developed gonads and associated structures were considered to be adult. Dentition characters were examined under a stereozoom microscope.

Molecular study

Taxon sampling and DNA dataset

Our molecular dataset comprises nine rhinatrematids and eight representatives of other Gymnophiona families (Table 1). We used sequences of 13 terminal taxa available from GenBank and produced new sequences for four specimens of *Rhinatrema*. We generated sequences for three mitochondrial DNA genes—12S (using primers L1091 and H1478; Kocher et al. 1989), 16S (16Sar-L and 16Sbr-H; Palumbi et al., 1991), and cytochrome c oxidase subunit 1 (CO1; Amp-P3 F and Amp-P3 R; San Mauro et al., 2004)—and four nuclear genes—chemokine receptor type 4 (CXCR4-N and CXCR4-L; Roelants et al., 2007), histone H3 (H3F and H3R; Colgan et al., 1999), recombination-activating gene 1 (Amp-RAG1 F and Amp-RAG1 R1; San Mauro et al., 2004), and two fragments of the member 3 of the solute carrier family 8 (part1: Slc8a3-E and Slc8a3-B; part 2: Slc8a3-C and Slc8a3-J; Roelants et al., 2007).

DNA extraction, sequencing, concatenation, partitioning

DNA was extracted from ethanol-preserved tissues using the Wizard Genomics DNA Purification Kit (Promega, Madison, WI, USA). Polymerase chain reaction (PCR) was carried out in 14 µL reactions using the kit (5U/µL). Amplification employed specific protocols for each primer (Kocher et al., 1989; Palumbi et al., 1991; Colgan et al., 1999; San Mauro et al., 2004; Roelants et al., 2007) and the sequencing reaction with the BigDye (Applied Biosystems). The sequences were generated using an ABI 3500 (Applied Biosystems) sequencer and edited using BioEdit (Hall, 1999).

Table 1. List of species used in this study and their representation in the data set. Codes in the columns below molecular marks are GenBank accession numbers. Taxa labeled in bold were sequenced exclusively for this study.

	Locality data	Voucher Number	16S	12S	CO1	CXCR4	H3	Slc8a3	Rag1
Atretochoana eiselti (Taylor, 1968)	Belém, Pará, Brazil	MPEG 39586	KX757082	KX757071	KX757090	KX757097	KX757110	KX757134	KX757122
Caecilia gracilis Shaw, 1802	Maués, Amazonas, Brazil	MPEG 28603	KX757086	KX757076	–	KX757102	KX757108	KX757142	KX757117
Chikila fulleri (Alcock, 1904)	Assam, India	BNHS 5514	NC021369.1	NC021369.1	NC021369.1	–	–	–	HQ456772.1
Dermophis mexicanus (Duméril and Bibron, 1841)	Unavailable	1195DerMex	EF107197.1	–	–	–	–	EF107423.1	EF107320.1
Epicrionops marmoratus Taylor, 1968	Cotopaxi, Ecuador	UMMZ 190478	AY101226	AY101206	–	–	–	–	–
Epicrionops niger (Dunn, 1942)	Guyana	CPI103W8	GQ244468	GQ244468	GQ244468	–	–	–	–
Herpele squalostoma (Stutchbury, 1836)	Unavailable	1198HerSqu	EF107200.1	–	–	EF107485.1	–	EF107426.1	EF107323.1
Ichthyophis bannanicus Yang, 1984	Unavailable	0697IchBan	EF107165.1	–	–	EF107451.1	–	EF107358.1	EF107288.1
Rhinatrema bivittatum (Guérin-Méneville, 1838)	Ferreira Gomes, Amapá, Brazil	MBS 169	KX757089	KX757079	KX757095	KX757101	KX757107	KX757141	KX757120
Rhinatrema bivittatum (Guérin-Méneville, 1838)	Kaw, French Guiana	BMNH 2002.6	EF107191	–	–	EF107478	–	EF107417	EF107314
***Rhinatrema uaiuai* sp. nov.**	Serra do Acaraí, Oriximiná, Pará, Brazil	MPEG 26477	MH177828	MH177826	MH177832	MH177834	MH177836	MH177840	MH177841
***Rhinatrema gilbertogili* sp. nov.**	Oriximiná, Pará, Brazil	MPEG 16975	MH177829	–	–	–	MH177839	–	–
***Rhinatrema gilbertogili* sp. nov.**	Urucará, Amazonas, Brazil	MPEG 26945	MH177830	MH177827	MH177833	MH177835	MH177838	MH177844	missing
***Rhinatrema gilbertogili* sp. nov.**	Manaus, Amazonas, Brazil	INPA-H036015	–	MH177825	MH177831	–	MH177837	MH177843	MH177842
Rhinatrema shiv Gower, Wilkinson, Sherratt, and Kok, 2010	Guyana	IRSNB:1991	GU566189	GU566188	–	–	–	–	–
Scolecomorphus uluguruensis Barbour and Loveridge, 1928	Unavailable	1199ScoUlu	EF107201.1	–	–	EF107486.1	–	EF107427.1	EF107324.1
Siphonops paulensis Boettger, 1892	Mato Queimado, Rio Grande do Sul, Brazil	UFRGS 5100	KX757081	KX757080	KX757094	KX757105	KX757114	KX757133	KX757119

Sequences were aligned using MAFFT v.7 (Katoh et al., 2002; Katoh and Standley, 2013). The strategy Q-INS-I was used for the ribosomal 12S and 16S because this method considers the secondary structure of RNA, and the strategy G-INS-I for coding genes, since it is recommended for alignment with < 200 sequences and no long gaps.

Sequences of all sampled genes were concatenated in Sequence Matrix version 1.7.8 (Vaidya et al., 2011) and the final dataset had 4,704 sites [12S: 415 base pairs (bp), 16S: 562 bp, CXCR4: 695, CO1: 809 bp, H3: 328 bp, Rag1: 784 bp, and Slc8a3: 1,111 bp]. Stop codon positions were verified for coding genes with Mesquite version 3.04 (Maddison and Maddison, 2015).

Prior to data partitioning, we divided our alignment into 17 data blocks (12S, 16S, and separated three codon positions of the protein coding genes CO1, CXCR4, H3, Rag1, and Slc8a3). Then, we defined the following seven alternative partitioning schemes of variable complexity for model testing: (1) all loci in a single partition; (2) mitochondrial genes in one partition and nuclear genes in another partition (= two partitons); (3) one partition for each gene (= 7 partitons); (4) each ribosomal gene in a separate partition, each protein coding gene divided into one partition for codon position 1 and another partition containing codon positions 2 and 3 together (= 12 partitions); (5) each ribosomal gene in a separate partition, each protein coding gene divided into separate partitions, one containing codon positions 1 and 3 together and another partition for codon position 2 (= 12 partitions); (6) each ribosomal gene in a separate partition, each protein coding gene divided into separate partitions, one containing codon positions 1 and 2 together and another partition for codon position 3 (= 12 partitions); (7) each ribosomal gene in a separate partition, each protein coding gene divided into separate partitions for codon positions 1, 2, and 3 (= 17 partitions). We used PartitionFinder v.1.1.1 (Lanfear et al., 2012) under the Bayesian Information Criterion (BIC) to select the best partitioning scheme and the best substitution models for each partition. These partitions and models were then used in the phylogenetic analysis.

Phylogenetic analysis and pairwise comparisons

Phylogenetic relationships were inferred using maximum likelihood (ML) in RAxML v.7.2.6 (Stamatakis, 2006). The search for the best tree was implemented with 100 search replicates. For the bootstrap analysis we used 1,000 pseudoreplicates. Finally, the bipartition support was drawn on the best likelihood tree. For genetic comparisons among specimens we made a matrix of uncorrected pairwise distances using Mega v.6 (Tamura et al., 2013).

RESULTS

Phylogenetic results and taxonomic decisions

The optimal partition scheme selected in PartitionFinder was number 7, which consisted of 17 partitions. The best-fit model for these partitions was GTR (Rodríguez et al., 1990) + G (Yang, 1994), with the exception of 16S, the first codon position of CO1, and the second codon position of SLC8A3, for which the best model was GTR (Rodríguez et al., 1990) + I (Fitch and Margoliash, 1967; Fitch, 1986) + G (Yang, 1994).

The ML analysis resulted in a well-supported phylogeny that recovered *Epicrionops marmoratus* as sister of a clade formed by *E. niger* within a group of species of *Rhinatrema* (Fig. 1). Specimens identified as *R. ron* by Maciel and Hoogmoed (2011) from two Brazilian localities (Urucará, state of Amazonas, and Porto Trombetas, Oriximiná, state of Pará), together with a specimen from Manaus, state of Amazonas, are close relatives (Fig. 1), forming the clade sister of a group composed of *E. niger, R. shiv, R. bivittatum* (the type species of *Rhinatrema*), and a specimen previously reported as *R. ron* from Serra do Acaraí, Oriximiná, state of Pará (Maciel and Hoogmoed, 2011).

In light of our phylogenetic results, we refer *Epicrionops niger* to the genus *Rhinatrema* to avoid paraphyly, returning this taxon to the original combination *Rhinatrema nigrum* Dunn, 1942. *Rhinatrema ron* is restricted to the type locality, and the other specimens previously identified as *R. ron* by Maciel and Hoogmoed (2011) are now considered to belong to new species, described in the following section. We did not observe any differences in the condition of the tentacle aperture among the species of *Epicrionops* and *Rhinatrema* we examined.

Species accounts

Rhinatrema uaiuai sp. nov.

Rhinatrema sp. nov.—Avila-Pires et al., 2010.
Rhinatrema ron—Maciel and Hoogmoed, 2011 (in part).

Holotype (Fig. 2; Table 2). MPEG 26477, an adult male from Serra do Acaraí, ESEC Grão-Pará Norte (01°17′7.51″N, 58°41′45.24″W; 500 m elevation), municipality of Oriximiná, State of Pará, Brazil, collected by T.C.S. Avila-Pires, W.A. Rocha, and M.A. Ribeiro-Junior on 30 August 2008.

Diagnosis. A species of *Rhinatrema* that differs from *R. bivittatum* mainly in the head being mostly brownish with small yellow spots (a conspicuous large yellow cephalic spot is present in *R. bivittatum*), the absence of

a yellow spot on dorsum and venter of the tail (present in *R. bivittatum*), and genetic divergence (e.g., *R. uaiuai* **sp. nov.** diverges 9.4% in 16S mitochondrial gene from a specimen of *R. bivittatum* from Kaw, French Guiana; Table 3).

Rhinatrema uaiuai **sp. nov.** differs from *Rhinatrema ron* in having darker head coloration composed of small yellow dots on a dark background (yellowish mottled with brownish spots in *R. ron*), a yellow stripe on each side of the head between the eye and the nostril (absent in *R. ron*), a narrow yellow stripe on each mandible (mandibles yellowish, mottled with brownish spots in *R. ron*), unpigmented and smooth palatine mucosa (slightly pigmented and strongly plicate in *R. ron;* see Wilkinson and Gower, 2010: fig. 2), a lower TBAD (333 versus 347 in *R. ron*), a narrower yellow lateral stripe (ratio between width at midbody and width of the lateral stripe at midbody 4.1 versus 2.4 in *R. ron*), and a transverse vent (longitudinal in *R. ron*); it further differs from *R. ron* in having a smaller difference between TBAD and TBAV counts (5 annuli versus 26 annuli), and TBAD < TBAV (TBAD > TBAV in *R. ron*).

Rhinatrema uaiuai **sp. nov.** differs from *R. nigrum* mainly in color pattern (entire body dark with no yellow lateral stripes in *R. nigrum*) and in having a shorter tail with eight folds (> 20 tail folds in *R. nigrum;* Taylor, 1968; Donnelly and Wake, 2013). Finally, *R. uaiuai* **sp. nov.** differs from *R. shiv* in having a slightly thicker yellow lateral stripe along the body (ratio between width at midbody and width of the stripe at midbody 5.2–7.2 in *R. shiv;* Wilkinson and Gower, 2010) and unpigmented denticulations around the vent (pigmented dark in *R. shiv*), as well as genetic divergence (e.g., *R. uaiuai* **sp. nov.** diverges

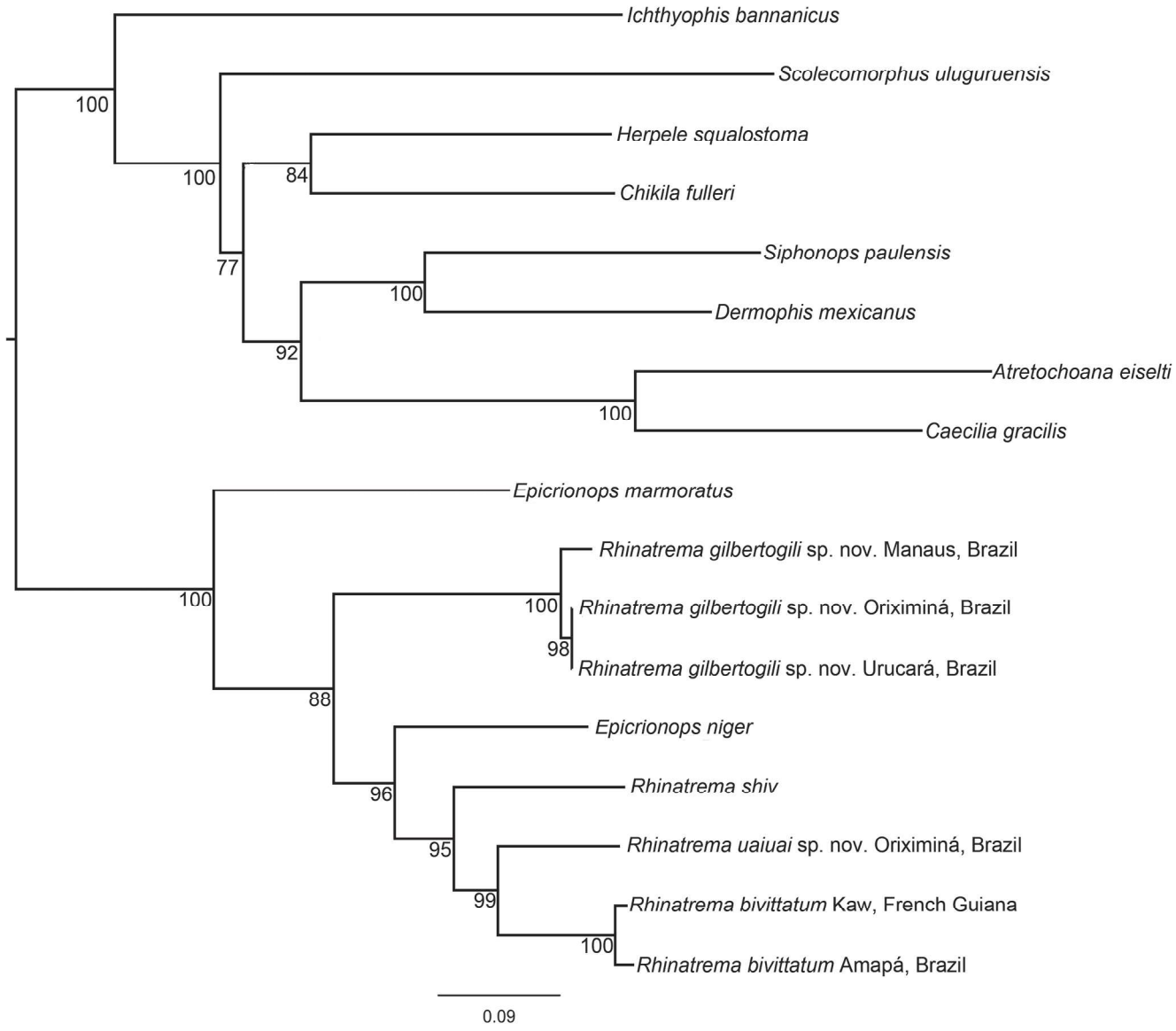

Figure 1. Maximum likelihood phylogram of Gymnophiona (1,000 searches, loglikelihood = -17937.768881), with main focus on Rhinatrematidae.

Figure 2. Holotype of *Rhinatrema uaiuai* **sp. nov. (A)** Dorsal (top), lateral (middle), and ventral (bottom) views of head and anterior body. **(B)** Dorsal (top), lateral (middle), and ventral (bottom) views of terminal region of body. **(C)** Dorsal and **(D)** ventral views of body. Scale bars = 5 mm.

Table 2. Morphometric (in mm) and meristic data (see text for definitions) for the types of *Rhinatrema uaiuai* **sp. nov.** and *Rhinatrema gilbertogili* **sp. nov.** Data reported in the fourth column are: range; mean; standard deviation (sample size).

	MPEG 26477 Holotype of *R. uaiuai* sp. nov.	**MPEG 19966 Holotype of *R. gilbertogili* sp. nov.**	**Paratypes of *R. gilbertogili* sp. nov.**
TL	151	195	97–278; 183; 37 (38)
SVL	146.3	190	94.6–272; 174; 36 (31)
TSFN	8.4	8.7	5.4–14.2; 8.5; 1.8 (30)
HW	5.4	5.5	3.7–8.8; 5.7; 1 (39)
HH	3.8	3.4	2.4–5.3; 3.8; 0.7 (39)
EE	3.2	3.4	2.2–5.1; 3.3; 0.6 (38)
EN	2.8	2.4	1.8–4.1; 2.7; 0.5 (38)
ECM	3	2.9	1.6–6; 3.1; 0.8 (37)
EMM	0.6	0.8	0.5–1.3; 0.8; 0.1 (38)
NN	1.3	1.3	0.9–1.8; 1.4; 0.2 (36)
NMM	0.6	0.6	0.3–1; 0.6; 0.1 (36)
WNC	5.5	5.7	3.8–8.2; 5.9; 0.9 (31)
LCR	2.7	3.5	2.2–4.1; 3.2; 0.5 (17)
BH	5.4	6.3	3.9–12.3; 6.7; 1.7 (32)
BW	6.6	7.1	4.3–12.2; 7.3; 1.5 (34)
WS	1.6	2.5	1.6–5.1; 2.8; 0.7 (31)
WV	3.3	3.8	2–6.3; 3.7; 0.8 (32)
TAL	3.5	2.4	1.4–2.6; 2.1; 0.3 (37)
GIV	5	4	3–6; 5; 0.7 (31)
TBAD	333	303	270–309; 292; 10.5 (38)
TBAV	338	276	254–293; 270; 10.6 (31)
TF	8	4	3–5; 4; 0.5 (39)
PMT	25	26	18–32; 24; 2.9 (31)
PPT	23	36	22–39; 28; 5 (22)
DT	14	18	14–28; 18; 3.3 (27)
ST	15	18	14–33; 20; 6 (12)

10.5% in 16S mitochondrial gene from the holotype of *R. shiv* from Guyana; (Table 3).

Description of holotype. Adult male, 151 mm total length, with multiple white testis lobes and abundant fat bodies. Total length 22.8 times body width. Head slightly narrower than body. Snout rounded in dorsal, ventral, and lateral views. Nostrils oval, laterally positioned, visible from above, not from below, close to the mouth margin (NMM = 0.6 mm). Eyes small (diameter = 0.5 mm), covered by a translucent epidermis, visible in lateral and dorsal view of head, as close to the mouth margin as the nostrils (EMM = 0.6 mm), slightly closer to corner of mouth than to the nostrils.

Tentacle apertures small, semicircular slits in skin (ca. 0.3 mm long), projecting anteriorly from anterior part of eye. First nuchal groove discernible dorsally only; second nuchal groove indistinct dorsally, distinct laterally and ventrally. First nuchal collar shorter (1.2 mm) than second (1.9 mm); second nuchal collar with four transverse grooves.

Body sub-cylindrical, slightly wider than deep. Width along body slightly variable, narrower close to vent. Ventral and dorsal counts of total annuli differ dorsally and ventrally, TBAD fewer (333) than TBAV (338). Most annular grooves completely encircling body, some bifurcated at dorsum and on venter. Vent transverse with 10 denticulations, 4 and 6 on anterior and posterior margins, respectively. Two anterior denticulations incompletely divided. Scales beginning in first transverse groove of second nuchal collar, trapezoidal, wider than long (e.g., 0.6 × 0.4 mm), arranged in single row; scales at midbody ovate (e.g., 1 × 0.7), in two rows; scales at tenth annulus anterior to the vent ovate (e.g., 1.2 × 0.8), in two rows; scales in the penultimate tail annulus in single row (e.g., 0.7 × 0.5 mm).

Table 3. Uncorrected pairwise distances between 16S sequences of 16 specimens of caecilians included in the phylogenetic analysis.

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
1	*Ichthyophis bannanicus*															
2	*Scolecomorphus uluguruensis*	0.179														
3	*Herpele squalostoma*	0.152	0.188													
4	*Chikila fulleri*	0.150	0.155	0.135												
5	*Siphonops paulensis*	0.179	0.186	0.177	0.150											
6	*Dermophis mexicanus*	0.143	0.168	0.159	0.126	0.130										
7	*Atretochoana eiselti*	0.161	0.195	0.177	0.150	0.168	0.148									
8	*Caecilia gracilis*	0.186	0.209	0.197	0.186	0.202	0.177	0.168								
9	*Epicrionops marmoratus*	0.166	0.197	0.191	0.166	0.197	0.177	0.206	0.211							
10	*Rhinatrema gilbertogili* Urucará, Amazonas	0.126	0.184	0.141	0.137	0.182	0.157	0.182	0.193	0.130						
11	*Rhinatrema gilbertogili* Oriximiná, Pará	0.126	0.184	0.141	0.137	0.182	0.157	0.182	0.193	0.130	0.000					
12	*Epicrionops niger*	0.150	0.179	0.170	0.148	0.173	0.161	0.179	0.202	0.108	0.112	0.112				
13	*Rhinatrema shiv*	0.141	0.200	0.152	0.150	0.179	0.173	0.173	0.191	0.143	0.123	0.123	0.096			
14	*Rhinatrema uaiuai*	0.152	0.188	0.161	0.132	0.184	0.168	0.186	0.211	0.152	0.128	0.128	0.112	0.105		
15	*Rhinatrema bivittatum* Kaw, French Guiana	0.166	0.206	0.177	0.152	0.184	0.164	0.186	0.193	0.150	0.143	0.143	0.123	0.103	0.094	
16	*Rhinatrema bivittatum* Amapá, Brazil	0.166	0.206	0.177	0.157	0.188	0.168	0.191	0.200	0.150	0.143	0.143	0.123	0.105	0.090	0.013

Choanae 1.5 mm apart, diameter ca. 1 mm. Palatine mucosa yellowish, smooth. Tongue fully attached to mandibular mucosa, with longitudinal plicae, slightly pigmented dark, narial plugs absent. Teeth in all series monocuspid, pointed, strongly recurved. Premaxillary-maxillary teeth 25; vomeropalatine teeth 23, dentary teeth 14; inner mandibular teeth (splenials) 15 (all tooth counts approximate because mouth was closed and a forceps was needed to open it partially and make counts).

In life, the holotype was predominantly brownish with yellow stripes and irregular spots along head and body (see Avila-Pires et al., 2010:37). Each side of the head had a yellow stripe between the eye and the nostril, both fusing into a yellow, irregular blotch on the tip of the snout; two larger yellow stripes extended along the mandibles from approximately the level of the corners of mouth to near the tip of the jaw, parallel to the margins of the mouth but not touching the lip and not fusing to each other on the tip of the jaw. A yellow blotch was present laterally in the nuchal region on the first collar at same level of the yellow lateral stripe, beginning as a homogeneously yellowish stripe in the third transverse groove of the second collar and extending to the fifteenth annulus anterior to the vent, where it becomes mottled with irregular brown spots extending to the tail tip. In preservative the brownish coloration became greyish brown and the yellowish coloration became pale yellow.

Geographic distribution. The species is known only from the type locality (Fig. 3).

Etymology. The name of the species is given as a noun in apposition, honoring the Uaiuai Indians (also called Waiwai), which include indigenous communities in southern Guyana and the southeastern part of the state of Roraima, the northeastern part of the state of Amazonas, and

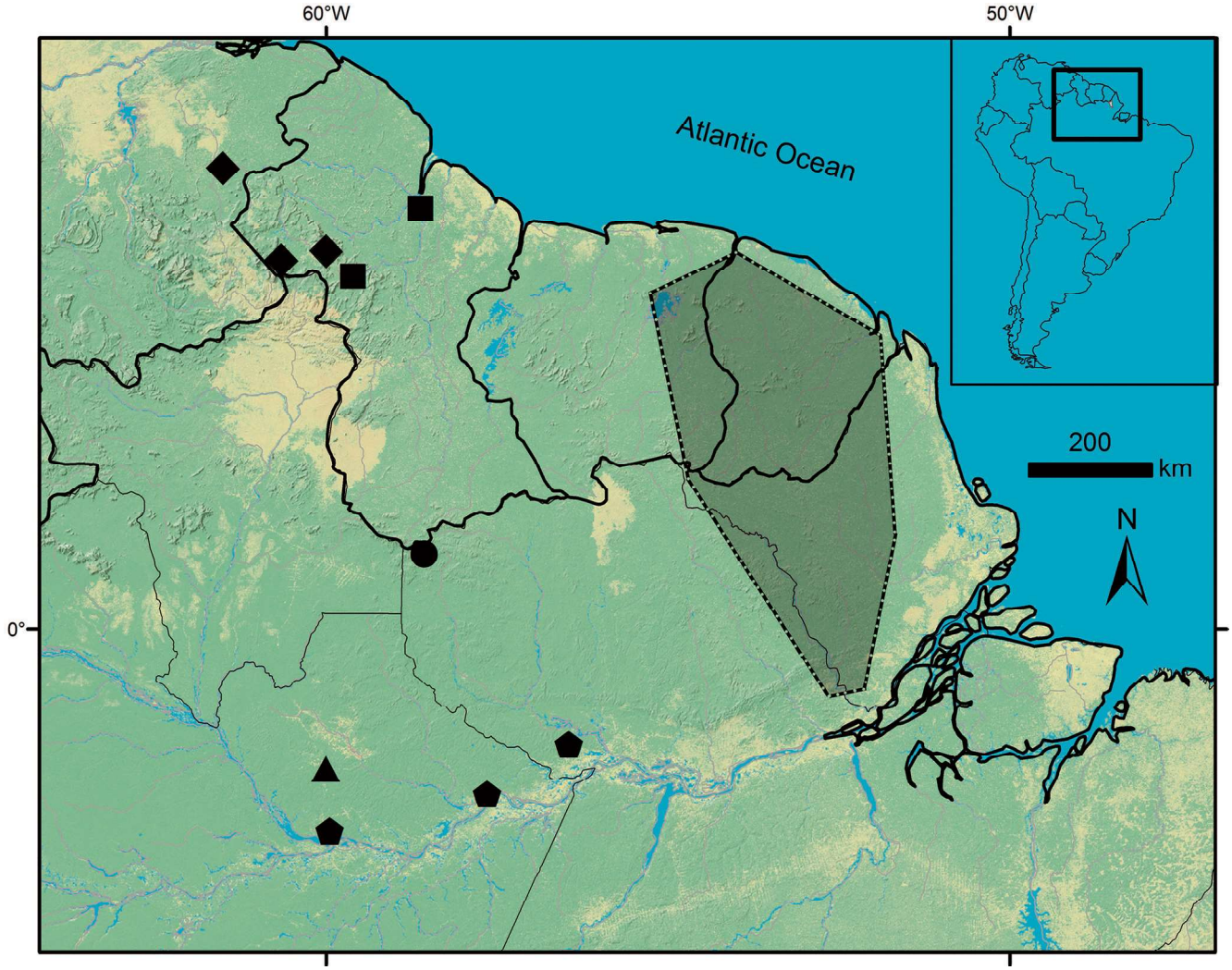

Figure 3. Distribution of the genus *Rhinatrema*. Lozenges represent *R. nigrum*. Squares represent *R. shiv*. Circle represents *R. uaiuai* **sp. nov.** Triangle represents *R. ron*. Pentagons represent *R. gilbertogili* **sp. nov.** The gray dashed polygon represents the distribution of *R. bivittatum*. Distribution data for *R. nigrum* are from Taylor (1968), MacCulloch and Lathrop (2009), and Donnelly and Wake (2013).

the northwestern part of the state of Pará in Brazil. All of these localities border on the Serra do Acaraí, which was historically inhabited by the Uaiuais. The Uaiuais are known to be great travelers and to organize expeditions to contact other communities in order to exchange objects and animals.

By naming this species after the Uaiuai Indians, we also call attention to the present problematic (financial and political) situation of FUNAI, the National Indian Foundation, which is the Brazilian government body responsible for policies relating to indigenous groups.

***Rhinatrema gilbertogili* sp. nov.**

Rhinatrema ron—Maciel and Hoogmoed, 2011.
Rhinatrema ron—Maciel et al., 2012.
Rhinatrema ron—Morato et al., 2014.

Holotype (Fig. 4; Table 2). MPEG 19966, mature male (Fig. 4), Porto Trombetas, Plateau Almeidas, municipality of Oriximiná, state of Pará, Brazil (01°40′S, 56°27′W); collected by U. Galatti, J.A.R. Bernardi, and F. Sarmento on 4 February 2006.

Paratypes. MPEG 16975, MPEG 17435, Porto Trombetas, Plateau Almeidas (01°40′S, 56°27′W), State of Pará, Brazil, collected by R.A.T. Rocha, J.A.R. Bernardi and G.L.F. Silva, resp. on 29 September 2003 and 14 June 2004. MPEG 19967, same data as holotype. MPEG 20167–20177, Porto Trombetas, State of Pará, Brazil, collected by R. Carvalho Jr. on 10–21 May 2006. MPEG 21912, Porto Trombetas, Plateau Bacaba, State of Pará, Brazil, collected by G.F. Maschio and team on 8 November 2007. MPEG 26478, Porto Trombetas, State of Pará, Brazil, collected by J.A.R. Bernardi and F. Sarmento on 1 February 2009. MPEG 26942, Porto Trombetas, Plateau Saracá, State of Pará, Brazil, collected by D. Baêta and team on 14 March 2008. MPEG 26943 and 26944, Porto Trombetas, Platô Aviso, State of Pará, Brazil, collected by D. Baêta and team on 19 March 2008. MPEG 26945, municipality of Urucará, State of Amazonas, Brazil, 02°24′54″S; 57°38′22″W, collected by E.G. Pereira and team on 10 February 2009. MPEG 27864, Flona Saracá-Taquera, Porto Trombetas, Platô Almeidas, State of Pará, Brazil, collected by Sérgio Morato on 12 May 2009. MPEG 39991–39997, Reserva Florestal Adolpho Ducke, municipality of Manaus, State of Amazonas, Brazil, collected by Márcio R.C. Martins on 27 August 1993. MNRJ 47921, 48248 from Porto Trombetas, State of Pará, Brazil, collected by E.G. Pereira and team on 16 December 2006 and 30 January 2007; MNRJ 52982–52987; PUCMG 10114, 10115, 10134, 10178, Porto Trombetas, State of Pará, Brazil, collected by D. Baêta and team 4 March 2008–28 June 2008. INPA-H036015, Reserva Florestal Adolpho Ducke, municipality of Manaus, State of Amazonas, Brazil, collected by E. Pontes and L. Viegas on 10 July 2015. All paratypes are fully metamorphosed specimens, most are males except MPEG 16975, 17435, 20173, 26945, MNRJ 47921, 52982–52985, and PUCMG10114.

Diagnosis. This new species of *Rhinatrema* differs from *R. uaiuai* **sp. nov.** in having a shorter tail with a maximum of five folds (eight in the holotype of *R. uaiuai* **sp. nov.**), a thicker lateral yellow stripe along the body (ratio between width at midbody and width of the stripe at midbody 1–3 in *R. gilbertogili* **sp. nov.,** 4.1 in the holotype of *R. uaiuai* **sp. nov.**), and in having a longitudinal vent (transverse in *R. uaiuai* **sp. nov.**).

The new species differs from *Rhinatrema bivittatum* mainly in having the head mostly brownish with small, irregularly, scattered yellow spots (a large yellow cephalic spot is present in *R. bivittatum*), in the absence of a yellow spot on dorsum and venter of the tail (present in *R. bivittatum*), and in genetic divergence (e.g., a paratype of *R. gilbertogili* **sp. nov.**—MPEG 16975, from Oriximiná, Pará, Brazil—diverges 14.3% in 16S mitochondrial gene from a specimen of *R. bivittatum* from Kaw, French Guiana; Table 3). It differs from *Rhinatrema nigrum* mainly in color pattern (entire body dark with no yellow lateral stripes in *R. nigrum*) and in having a shorter tail with at most five folds (> 20 in *R. nigrum;* Taylor, 1968; Donnelly and Wake, 2013). *Rhinatrema gilbertogili* **sp. nov.** differs from *R. ron* mainly in having an unpigmented and smooth palatine mucosa (slightly pigmented and strongly plicate in *R. ron;* Wilkinson and Gower 2010: fig. 2 of) and fewer TBAD (270–309, n = 38; 347 in *R. ron*). *Rhinatrema gilbertogili* **sp. nov.** differs from *R. shiv* in having fewer TBAD (270–309, n = 38; 335–378 in *R. shiv;* Gower et al. 2010), a slightly thicker yellow lateral stripe along the body (ratio between width at midbody and width of the stripe at midbody is 1–3 in *R. gilbertogili* **sp. nov.,** 5.2–7.2 in *R. shiv;* Wilkinson and Gower, 2010).

Description of holotype. An adult male, 195 mm total length, with multiple white testis lobes and abundant fat bodies. Total length 27.5 times body width. Head slightly narrower than body. Snout rounded in dorsal, ventral, and lateral views. Nostrils oval, laterally positioned, visible from above and laterally but not below, close to the mouth margin (NMM = 0.6 mm). Eyes small (0.5 mm), covered by a translucent epidermis, visible in lateral and dorsal view of head, farther from the mouth margin than the nostrils (EMM = 0.8 mm), slightly closer to nostrils than to corner of mouth.

Tentacle apertures small semicircular slits in skin (ca. 0.3 mm long), projecting anteriorly from anterior part of eye. First nuchal groove discernible dorsally only; second nuchal groove indistinct dorsally, distinct laterally and ventrally. First nuchal collar shorter (1.7 mm) than second (2.0 mm); second nuchal collar with four transverse grooves.

Figure 4. Holotype of *Rhinatrema gilbertogili* **sp. nov. (A)** Dorsal (top), lateral (middle), and ventral (bottom) views of head and anterior body. **(B)** Dorsal (top), lateral (middle), and ventral (bottom) views of terminal region of body. **(C)** Dorsal and **(D)** ventral views of body. Scale bars = 5 mm.

Body sub-cylindrical, slightly wider than deep. Width along body slightly variable, narrower near vent. Ventral and dorsal counts of total annuli differ dorsally and ventrally, TBAD greater (303) than TBAV (276). Most annular grooves encircle body completely, some bifurcated at dorsum and on venter. Vent longitudinal with 13 denticulations. Scales begin in the second transverse groove of the second nuchal collar, three times wider than long (e.g., 0.6 × 0.2 mm), in a single row of scales; scales at midbody ovate (e.g., 1.1 × 0.7), in two rows of; scales at tenth annulus anterior to the vent ovate (e.g., 1.6 × 1.2), in two rows; scales in penultimate tail annulus in single row (e.g., 0.8 × 0.6 mm).

Choanae 1.6 mm apart, diameter ca. 1 mm. Palatine mucosa not pigmented, smooth. Tongue fully attached to mandibular mucosa, with longitudinal plicae, slightly dark pigmented, narial plugs absent. Teeth in all series monocuspid, pointed, strongly recurved. Premaxillary-maxillary teeth 26; vomeropalatine teeth 36, dentary teeth 18; inner mandibular teeth (splenials) 18 (all tooth counts approximate because mouth was closed and a forceps was needed to open it partially and make counts).

In preservative, the body of the holotype is predominantly greyish brown with pale yellow stripes and irregular spots along head and body. The dorsum of the head and the mandibles are slightly lighter than the body, greyish brown mottled with small, sparse, pale-yellow spots. The throat and ventral parts of the nuchal collars and the body are more brownish than the dorsum. A yellow blotch is present at the corners of the mouth (larger on the left side). There are yellow spots, larger than those on the body, in the lateral portion of the nuchal region at the same level as the yellow lateral stripe, which begins as a homogeneously yellowish stripe in the first transverse groove of the second collar and extends to the level of the posterior edge of the vent.

Variation. Morphometric and meristic variation is summarized in Table 2. Color is variable among populations. Specimens from Urucará and Manaus have a predominantly yellow head mottled with brownish patches. The bodies of the specimen from Urucará (see Maciel and Hoogmoed, 2011: fig. 24) and of some specimens from Manaus (MPEG 39991–39997) are more yellowish than the bodies of specimens from Pará, which have the same pattern as the holotype. In four specimens from Manaus (MPEG 39992, 39993, 39995, and 39997), the yellowish lateral stripe is not interrupted in the nuchal region. Some specimens have a darker head and nuchal region because of the absence of yellowish spots or blotches in that area (MPEG 20167, 20174, 21912, and 26944; PUC-MG 10178). Maciel and Hoogmoed (2011) reported that the females (formerly identified as *Rhinatrema ron*) have larger means in morphometric characters than the males, indicating sexual size dimorphism in the species.

Distribution. The species is known from the municipality of Oriximiná, state of Pará, Brazil; and from the municipalities of Urucará, and Manaus, state of Amazonas, Brazil (Fig. 3).

Etymology. The name of the species is a noun in apposition, proposed in homage to the Brazilian musician (singer and composer), Gilberto Passos Gil Moreira, better known as "Gilberto Gil" (born in 1942), in recognition of his great contributions to Brazilian music. "Aqui e agora," "Drão," "Esotérico," "Estrela," "Palco," and "Tempo Rei" are some of the most beautiful songs produced by Gilberto Gil. The artist is also known for participating in environmental protection projects.

DISCUSSION

Despite using considerably fewer molecular markers and taxa (e.g., the complete mitochondrial genome and two nuclear markers were analyzed for 23 taxa by Kamei et al., 2012), our phylogenetic results are similar to those of previous studies (Pyron and Wiens, 2011; Kamei et al., 2012; San Mauro et al., 2014) in the interfamilial relationships with well-supported nodes. Our results also agree with those studies that sampled at least two species of the family (Pyron and Wiens, 2011; San Mauro et al., 2014) in finding the rhinatrematid genera to be non-monophyletic, with *Epicrionops niger* nested within *Rhinatrema*.

We performed an analysis with an unprecedented sample including almost all species of *Rhinatrema,* the results of which raised two main taxonomic issues. One is the possibility that *Epicrionops* should be placed in the synonymy of *Rhinatrema,* which was already discussed by other authors (Wilkinson and Gower, 2010; Wilkinson et al., 2011); however, unfortunately, we could not sample more species of *Epicrionops,* including its type species, so we do not consider that option to be viable at this time. The second issue concerns the consequences of the phylogenetic positioning of *E. niger,* which contrasts with the morphological diagnosis of *Rhinatrema* and *Epicrionops* (e.g., *E. niger* has a long tail like all other known *Epicrionops* spp., whereas *Rhinatrema* has a short tail). Because *E. niger* is positioned within a clade of *Rhinatrema* that includes the type species of this genus (*R. bivittatum*), we decided to re-allocate this species in *Rhinatrema* in order to avoid paraphyly. This decision was fully based on our phylogenetic evidence, which cannot be disregarded, although it contradicts the conclusion based on the few morphological characters which have been considered as differences between the genera. Thus, we do not have to date any known, differentiating morphological synapomorphies attributable to each of the two rhinatrematid genera. This fact might lead to hypothesize, for instance, that the tail size in *E. niger* and at least that in *E. marmoratus* may cor-

respond to a case of convergence, which should be tested in new studies including more species of *Epicrionops*.

One of our new species, *Rhinatrema uaiuai* **sp. nov.,** is sister to *R. bivittatum* in our phylogeny, with which it shares some similarities in external morphology, like the shape of the vent (transverse) and in the presence of a yellowish eye–nostril stripe, but diverges in the absence of the typical large yellow cephalic spot and other remarkable features. The other new species, *R. gilbertogili* **sp. nov.,** is quite similar to *R. ron*. Although we could not include a molecular sample of *R. ron,* we are convinced that it differs from *R. gilbertogili* **sp. nov.** on the basis of morphological characters only. The holotype of *R. ron* has 38 annuli more on the body (e.g., in the dorsal count), is much larger than any of the other species, and has a slightly pigmented palatine mucosa with strong plicae, neither of which occur in any of the other known species of *Rhinatrema*.

The continuous discovery of undescribed species in recent years (e.g., Maciel et al. 2009; Gower et al., 2010; Wilkinson and Gower, 2010; Wilkinson and Kok, 2010; Maciel and Hoogmoed, 2011; Donnelly and Wake, 2013; Maciel and Hoogmoed, 2013; Maciel et al., 2015) and the remaining problems in the classification within Rhinatrematidae presented here indicate that the systematics and classification of caecilians in the Neotropical region are still in their initial stage.

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REFERENCES

Alcock A.W. 1904. Description and reflections upon a new species of apodous amphibian from India. *Annals and Magazine of Natural History, Series 7* 14:267–273. DOI

Avila-Pires T.C.S., Hoogmoed M.S., Rocha W.A. 2010. Notes on the vertebrates of northern Pará, Brazil: a forgotten part of the Guianan Region, I. Herpetofauna. *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais* 5:1:13–112.

Barbour T., Loveridge A. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. *Memoirs of the Museum of Comparative Zoology* 50: 87–265. DOI

Boettger O. 1892. Katalog der Batrachier-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellshaft in Frankfurt am Main. *Bericht der Senckenbergischen Naturforschenden Gesellshaft in Frankfurt am Main* 1892:1–73.

Boulenger G.A. 1883. Description of a new genus of Coeciliae. *Annals and Magazine of Natural History* 11:202–203.

Colgan D.J., McLauchlan A., Wilson G.D.F., Livingston S.P., Edgecombe G.D., Macaranas J., … Gray M.R. 1999. Histone H3 and U2 sn-RNA DNA sequences and arthropod molecular evolution. *Australian Journal of Zoology* 46:419–437. DOI

Donnelly M.A., Wake M.H. 2013. A new *Microcaecilia* (Amphibia: Gymnophiona) from Guyana with comments on *Epicrionops niger*. *Copeia* 2013:223–231.

Duméril A.M.C., Bibron G. 1841. Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Tome Huitième. Librarie Enclyclopedique de Roret, Paris. DOI

Dunn E.R. 1942. The American caecilians. *Bulletin of the Museum of Comparative Zoology, Harvard* 91:439–540.

Fitch W.M., Margoliash E. 1967. A method for estimating the number of invariant amino acid coding positions in a gene using cytochrome c as a model case. *Biochemical Genetics* 1:65–71. DOI

Fitch W.M. 1986. An estimation of the number of invariable sites is necessary for the accurate estimation of the number of nucleotide substitutions since a common ancestor. *Progress in Clinical and Biological Research* 218:149–159.

Gower D.J., Wilkinson M., Sherratt E., Kok P.J.R. 2010. A new species of *Rhinatrema* Duméril & Bibron (Amphibia: Gymnophiona: Rhinatrematidae) from Guyana. *Zootaxa* 2391:47–60.

Guérin-Méneville F.É. 1838. Iconographie du Règne Animal de G. Cuvier ou Représentation d'Après Nature de l'une des Espèces les plus Remarquables et Souvent non Encore Figurees, de Chaque Genre d'Animaux, avec un Texte Descriptif mis au Courant de La Science. Tome III (Part—Reptiles) J.B. Ballière, Paris. DOI

Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41:95–98.

Kamei R.G., San Mauro D., Gower D.J., Van Bocxlaer I., Sherratt E., Thomas A., … Biju S.D. 2012. Discovery of a new family of amphibians from Northeast India with ancient links to Africa. *Proceedings of the Royal Society of London B* 279:2396–2401. DOI

Katoh K., Misawa K., Kuma K., Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30:3059–3066. DOI

Katoh K., Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. DOI

Kocher T.D., Thomas W.K., Meyer A., Edwards S.V., Pääbo S., Villablanca F.X., Wilson A.C. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA* 86:6196–6200. DOI

Lanfear R., Calcott B., Ho S.Y.W., Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29:1695–1701. DOI

MacCulloch R.D., Lathrop A. 2009. Herpetofauna of Mount Ayanganna Guyana: results of the Royal Ontario Museum Ayanganna Expedition 2000. *Royal Ontario Museum Contributions in Science* 4:1–35.

Maciel A.O., Mott T., Hoogmoed M.S. 2009. A second species of *Brasilotyphlus* (Amphibia: Gymnophiona: Caeciliidae) from Brazilian Amazonia. *Zootaxa* 2226:19–27.

Maciel A.O., Hoogmoed M.S. 2011. Taxonomy and distribution of caecilian amphibians (Gymnophiona) of Brazilian Amazonia, with a key to their identification. *Zootaxa* 2984:1–53.

Maciel A.O., Hoogmoed M.S., Peloso P.L.V. 2012. Variation in the glossal skeleton arrangement of *Rhinatrema ron* (Gymnophiona: Rhinatrematidae) and its systematic implications. *Salamandra* 48:4:224–226.

Maciel A.O., Hoogmoed M.S. 2013. A new species of *Microcaecilia* (Amphibia: Gymnophiona: Siphonopidae) from the Guianan region of Brazil. *Zootaxa* 3693:387–394.

Maciel A.O., Leite J.M., Leite R.R.S., Leite J.R.S.A., Cascon P. 2015. A new species of *Chthonerpeton* Peters 1880 (Amphibia: Gymnophiona: Typhlonectidae) from the state of Piauí, Northeastern Brazil. *Journal of Herpetology* 49:308–313. DOI

Maddison W.P., Maddison D.R. 2015. Mesquite: a modular system for evolutionary analysis, Version 3.04. Available from: http://mesquiteproject.org.

Morato S.A.A., Calixto P.O., Mendes L.R.L.P., Gomes R., Galatti U., Trein F.L., ... Ferreira G.N. 2014. Guia Fotográfico de Identificação da Herpetofauna da Floresta Nacional de Saracá-Taquera, Estado do Pará. STCP Engenharia de Projetos Ltda., Curitiba; MRN – Mineração Rio do Norte S.A., Porto Trombetas.

Nussbaum R.A. 1977. Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona). *Occasional Papers of the Museum of Zoology, University of Michigan* 682:1–30.

Palumbi S.R., Martin A., Romano S., Owen MacMillan W., Stice L., Grabowski G. 1991. The Simple Fool's Guide to PCR. Department of Zoology, University of Hawaii, Honolulu.

Pyron R.A., Wiens J.J. 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61:543–583. DOI

Rodríguez F., Oliver J.L., Marín A., Medina J.R. 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* 142:85–501. DOI

Roelants K., Gower D.J., Wilkinson M., Loader S.P., Biju S.D., Guillaume K., ... Bossuyt F. 2007. Global pattern of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences USA* 104:887–892. DOI

San Mauro D., Gower D.J., Oommen O.V., Wilkinson M., Zardoya R. 2004. Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1. *Molecular Phylogenetics and Evolution* 33:413–427. DOI

San Mauro D., Gower D.J., Müller H., Loader S.P., Zardoya R., Nussbaum R.A., Wilkinson M. 2014. Life-history evolution and mitogenomic phylogeny of caecilian amphibians. *Molecular Phylogenetics and Evolution* 73:177–179. DOI

Shaw G. 1802. General Zoology or Systematic Natural History. Volume III, Part 1. Amphibia. Thomas Davison, London. DOI

Stamatakis A. 2006. Raxml-vi-hpc: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690. DOI

Stutchbury S. 1834. Description of a new species of the genus *Chameleon*. *Transactions of the Linnean Society* 17:361–362. DOI

Tamura K., Stecher G., Peterson D., Filipski A., Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30:2725–2729. DOI

Taylor E.H. 1968. The Caecilians of the World – A Taxonomic Review. University of Kansas Press, Lawrence.

Vaidya G., Lohman D.J., Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* 27:171–180. DOI

Wilkinson M., Nussbaum R.A. 2006. Caecilian phylogeny and classification. Pp. 39–78, in Exbrayat J.M. (Ed.), Reproductive Biology and Phylogeny of Gymnophiona (caecilians). Science Publisher Inc., Enfield.

Wilkinson M., Gower D.J. 2010. A new species of *Rhinatrema* Duméril & Bibron (Amphibia: Gymnophiona: Rhinatrematidae) from Amazonas, Brazil. *Zootaxa* 2650:63–68.

Wilkinson M., Kok P.J.R. 2010. A new species of *Microcaecilia* (Amphibia: Gymnophiona: Caeciliidae) from Guyana. *Zootaxa* 2719:35–40.

Wilkinson M., San Mauro D., Sherrat E., Gower D.J. 2011. A nine-family classification of caecilians (Amphibia: Gymnophiona). *Zootaxa* 2874:41–64.

Yang, D. 1984. A new species of *Ichthyophis—I. bannanica*. *Acta Herpetologica Sinica/Liangqi baxing dongwu yanjiu. New Series* 3:2:73–76.

Yang Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Journal of Molecular and Evolution* 39:306–314.

APPENDIX

Additional specimens analyzed (number of specimens in parentheses)

***Epicrionops* sp. (02). ECUADOR:** "San Ramon" (MZUSP 74373, 74374).

***Epicrionops bicolor subcaudalis* (03 by high-resolution photo). PERÚ:** Junin: Chanchamayo on Río Perene (AMNH 17304, 17305, 42858).

***Epicrionops lativittatus* (01 by high-resolution photo). ECUADOR:** East Ecuador (AMNH 46205).

***Epicrionops petersi noblei* (01 by high-resolution photo). PERÚ:** Southern Perú (AMNH 1454).

***Rhinatrema bivittatum* (11). BRAZIL:** AMAPÁ: Ferreira Gomes: Flona Amapá (IEPA/FL519; MPEG/MBS 169) Laranjal do Jari: BR 156 (MPEG 26941), Reserva de Desenvolvimento Sustentável do Rio Iratapuru (IEPA/RS215), Parque Nacional Montanhas do Tumucumaque, Igarapé Mapaoni (IEPA/TQ272, TQ287, TQ306, TQ347, TQ348), PARÁ: Almeirim, Monte Dourado (MPEG 23548, 23549).