Zootaxa 2391: 47–60 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A new species of *Rhinatrema* Duméril & Bibron (Amphibia: Gymnophiona: Rhinatrematidae) from Guyana

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Abstract

The first new species of rhinatrematid caecilian in more than 50 years, *Rhinatrema shiv* **sp. nov.**, is described from Guyana. The type series of 10 specimens differs from the only other species in the genus, *R. bivittatum*, in having a longer tail, different colour pattern, more acuminate and relatively shorter head, and in several features of the skull and mandible including dentition. Sequence data for 1572 aligned base pairs of mitochondrial DNA are > 15% different between the two species. *Rhinatrema shiv* is known only from Guyana, and *R. bivittatum* from French Guiana and far northeastern Brazil. The only reported specimen of the genus from Suriname is not clearly referable to either of the named species.

Key words: Brazil, caecilians, French Guiana, Guiana Shield, herpetology, HRXCT, Kaieteur, South America, Suriname, systematics, taxonomy

Introduction

The family Rhinatrematidae Nussbaum, 1977 comprises the two Neotropical genera *Rhinatrema* Duméril & Bibron, 1841 and *Epicrionops* Boulenger, 1883 and is the sister group of all other living caecilian amphibians (e.g., Wilkinson & Nussbaum 2006). *Rhinatrema*, hitherto known only from the type species *R. bivittatum* (Guérin-Méneville, 1838) itself described from a single specimen from “L’Amérique Méridionale” (Cayenne, French Guiana according to Taylor, 1968), has been considered particularly poorly known because very few additional specimens have been reported in the more than 150 years since its discovery and description. Taylor (1968) listed only two specimens, and, in the most recent revision, Nussbaum & Hoogmoed (1979) summarized variation among the four specimens of *R. bivittatum* known to them, including new locality records for Suriname and Guyana (although they overlooked a few additional specimens in Brazilian collections). Since then, substantial additional but largely unreported collections of *R. bivittatum* have been made from French Guiana. Recently, Kok & Kalamandeen (2008) reported *Rhinatrema* from Kaieteur National Park, Guyana and noted that there were differences between this population and *R. bivittatum* that likely warranted the description of a new species, which is the purpose of this paper.

Material and methods

Recently collected specimens were killed by lethal anaesthesia (Xylocaine or MS222), fixed in formalin for several days, washed in water and stored in 70% ethanol or industrial methylated spirits, and deposited in the collections of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (IRSNB) and the Natural

Accepted by S. Carranza: 29 Jan. 2010; published: 8 Mar. 2010

History Museum, London, UK (BMNH). Tissue samples were removed immediately after lethal anaesthesia, preserved in 95% ethanol and deposited in the Amphibian Evolution Lab, Biology Department, Vrije Universiteit, Brussel. We also examined comparative material from the collections of the American Museum of Natural History, New York, USA (AMNH), Muséum national d'Histoire naturelle, Paris, France (MNHN), Museu Nacional Rio de Janeiro, Brazil (MNRJ), Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP), and Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands (RMNH), including type material of *R. bivittatum*. Several specimens of *R. bivittatum* from French Guiana bearing field tags with an MW prefix were examined; these will be accessioned into the collections of BMNH, MNHN and IRSNB. Measurements were taken to the nearest 0.1 mm using a vernier caliper, except total length and circumference, which were measured to the nearest 1 mm using a ruler and piece of thread. Where the phallus of males was not everted, sex was determined by examining the gonads through a small midventral incision in the posterior third of the specimen. Numbers of vertebrae were determined from radiographs. Total numbers of annuli were counted just dorsal to the lateral stripe. Terminology for phallus anatomy follows Gower & Wilkinson (2002).

Skulls and mandibles were visualised with high-resolution x-ray computed tomography (HRXCT), a non-destructive process enabling examination of bone *in situ*. The heads of whole spirit-preserved specimens (see Appendix) were scanned using a Metris X-Tek HMX ST 225 System by ES at the Natural History Museum, London. The scan parameters for each specimen, maximising the differentiation of bone tissue, were as follows: a molybdenum target set at 113 & 95kV and 130 & 190µA; scan data were collected at 2 frames per second over 3142 projections in 360˚; reconstructed voxel size of 8 & 10µm. Reconstructed HRXCT slices in the transverse plane were rendered as a three-dimensional volume using VGStudio MAX v2.0 (Volume Graphics, http://www.volumegraphics.com). In this software, the user can digitally dissect the specimens and view each element separately. We dissected the vertebral column and the mandible from the cranium using the *region grower tool*, which selects across slices all the voxels of a particular grey value (corresponding to x-ray attenuation and density) such that they can be rendered transparent. This allows regions to be removed from the rendered 3D volume until only elements intended for display (here crania and mandibles) are visible. This method is preferred over a *cutaway* of the 3D volume, which renders transparent whole sections of the volume in a plane and can lead to areas of interest being cut or missing.

Making tooth counts in caecilians is challenging without causing extensive damage to preserved specimens, and reported data are often approximate. Counting teeth in *Rhinatrema* is particularly difficult because the heterogeneous dentition (in size) and notably dynamic replacement makes it difficult to differentiate empty sockets from gaps between adjacent teeth in a row. Here we present tooth counts made from images assembled from HRXCT data, but these are also approximate because the same difficulty persists. Nussbaum & Hoogmoed (1979) did not count teeth for *Rhinatrema* specimens that had not had their jaws cut open.

We analysed the type series of the new species for sexual dimorphism in meristic and morphometric data and tested the significance of differences between numbers of annuli/vertebrae in the two species of *Rhinatrema* using Welch's t-test in order to cope with small and unequal sample sizes, and to reduce the likelihood of type I error (Welch 1947). Statistical analyses were carried out using the software JMP v.7 (SAS Institute Inc.).

Following Kamei *et al.* (2009), abbreviations used for anatomical features and ratios of measures are: CM = corner of the mouth; C1 = first collar; C2 = second collar; IM = inner mandibular (= 'splenial') tooth; NG1 = first nuchal groove (between head and collars); NG2 = second nuchal groove (between first and second collars); NG3 = third nuchal groove (between collars and anteriormost annulus); ST = snout tip; TG = transverse groove (on dorsal surface of collar); TL = total length.

***Rhinatrema shiv* sp. nov.**

(Figs. 1–4; Tables 1, 2)

Rhinatrema bivittatum (Guérin-Méneville, 1838) in part; Nussbaum & Hoogmoed (1979: 219, 221, fig.1, Table 1)
Rhinatrema cf. *bivittatum* (Guérin-Méneville, 1838); Kok & Kalamandeen (2008: 246–247, figs. 17, 151)

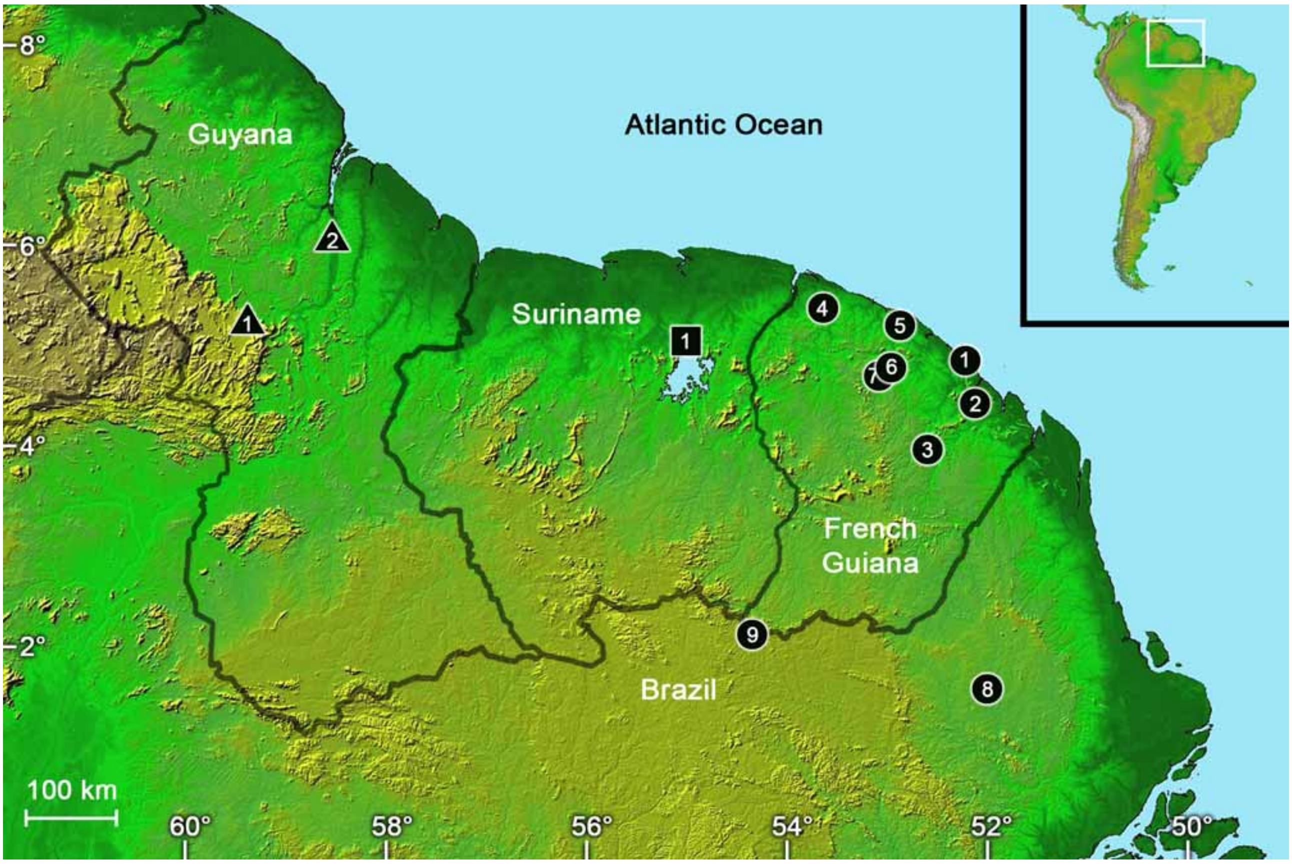

FIGURE 1. Map showing *Rhinatrema* localities. Circles = *R. bivittatum*: 1) Cayenne, 2) Kaw Mountains, 3) Nouragues, 4) Angoulême, 5) Paracou, 6) Courcibo, 7) Sait Eugène, 8) Rio Cassiporé, 9) Tumuc-Humac Mountains = *R. shiv* **sp. nov.**: 1) Kaieteur, 2) Wineperu. Square = *R.* sp.: Brownsberg. See Appendix for specimen data. Localities 8 and 9 are approximate because available data are not precise.

Holotype. IRSNB 1991 (field number PK 1569), transformed male, collected along Sir Donald's trail ca. 2 km from a tributary of the Elinkwa River, ESE Kaieteur National Park, Guyana, ca. 540 m elevation (5°08' N, 59°25' W) by Philippe J.R. Kok, Paul Benjamin and G. Seegobin on 23 June 2006, 1:00 PM.

Paratypes (n = 9). IRSNB 1992, collected in the vicinity of the type locality by G. Seegobin in May 2006, IRSNB 1993-94, collected at the type locality by G. Seegobin in September 2006, IRSNB 1995-96 and 1998-99 and BMNH 2008.602, collected in the vicinity of the type locality by G. Seegobin in 2008. BMNH 2008.601 collected in the vicinity of the type locality by G. Seegobin in 2007. All paratypes are transformed, and all are male except IRSNB 1993, 1994, 1999 and BMNH 2008.601.

Referred material (n = 1). BMNH 1976.102 transformed female, collected in 1976 by D. Healey, Wineperu, Guyana (6°10' N, 58°34' W).

Diagnosis. A *Rhinatrema* differing from the only other known species (*R. bivittatum*) in having a longer tail (6.5–9.5 vs. 4–6.5 annuli posterior to the vent; 1.5–2% vs. 0.8–1.6 % of TL), lacking pale spots on dorsal and ventral surfaces of the tail, generally having more irregular, patchy and narrow pale lateral stripes (midbody width/median width of stripe 4.6–7.2 vs. 2.9–4.6), a proportionately shorter head (ST-CM as % of TL 2.9–3.5% vs. 3.1–4.4%), a more acuminate head in dorsal view, a shorter dentary tooth row and smaller difference between numbers of IMs and dentary teeth (2–3 vs. 5–10), narrower temporal fenestrae (= upper openings of adductor chambers), differently shaped and relatively sized cranial bones (see below), and substantially different (ca. 15 %) nucleotide sequences for 1572 base pairs of 12S, 16S and cytochrome b (Cytb) mitochondrial genes. Other colour pattern features that largely serve to distinguish *R. shiv* from *R. bivittatum* are pale blotches on dorsal surface of the head (much more extensive patch between eyes; continuous eye-naris stripe in *R. bivittatum*), pigmentation on denticulations around vent (dark in *R. shiv*, absent in *R. bivittatum*), pale stripes on upper and lower jaws (joined behind CM in *R. bivittatum*; not in *R.*

shiv), form of lateral stripes on and just behind collars (incomplete in *R. shiv*, complete in *R. bivittatum*). There are substantial overlaps in the numbers of vertebrae and annuli between *R. shiv* (range = 95–99 and 335–382, mean = 97 and 354, st. dev. = 1.8 and 16.3, n = 9 and 12, respectively) and *R. bivittatum* (range = 88–99 and 273–384, mean = 92.5 and 334.8, st. dev. = 2.7 and 29.4, n = 26 and 24, respectively). Data for these meristics are significantly different (at the 0.05 level) for the two species for both vertebrae (t = 5.6303, $p < 0.001$) and annuli (t = 2.5217, p = 0.0166), though we note that the size and geographical range size of the two samples is much greater for *R. bivittatum*.

Description of holotype. Some meristic and morphometric data are presented in Table 1. Male (cloaca everted) in good condition, small patches of stratum corneum missing, few scale pockets opened, ventral incision into coelom (for tissue sample) from 40 to 45 mm behind ST, narrow constriction caused by tag string 68 mm behind ST. Body subcylindrical, slightly dorsoventrally compressed, widest at midbody, very gently tapering towards head and tail, posteriormost 5 mm tapering more abruptly, in lateral view tail end tapers along dorsal edge, underside of tail flat.

Head more V- than U-shaped in dorsal view, very gently tapering in lateral view. In ventral view lateral edges of mandibles barely inset from sides of upper jaw, slightly more so anteriorly. Ventral surface between and behind back of mandibles puffed out artefactually, otherwise distance from CM to top of head about twice greater than to bottom. Eyes marginally closer to lips than top of head, distances between eye and lip almost twice diameter of eye (ca. 0.4 mm). In dorsal view, eyes less than one eye diameter from edge of head. Eye slightly bulging from surface of head, lying in posteroventral ‘corner’ of larger (ca. 0.5 mm) clear window, tentacle barely visible as small bump at anterior margin of clear window. Nares small (ca. 0.1 mm), very marginally closer to lips than are eyes, positioned anterolaterally on snout tip level with anterior margin of mouth, barely visible dorsally, clearly visible laterally and anteriorly, not ventrally.

From HRXCT data, inner mandibular and vomeropalatine teeth uniformly small; those of the outer series comprise small teeth anteriorly and posteriorly, with five or six much larger teeth in between. Dentary tooth series extend about three quarters the length of the IM series beyond the posteriormost IMs (with 5 or 6 small dentary teeth behind posteriormost IM on each side). Tongue obtusely pointed, anterior part swollen, posterior part sunken, anterior part with darker anterior edge and few longitudinal plicae. Choanae subcircular, separated by 1 to 1.5 times the width of each choana.

Collar region weakly differentiated. NG1 barely visible as very faint ventral and dorsal (not lateral) creases that are not aligned (ventral crease further anterior). NG2 not visible dorsally, faint ventrally, posterodorsally oblique laterally, with posterodorsal tip lying posterior to anteriormost of five TGs on dorsal surface of collars. First TG faint and not extensive, next four cross entire dorsal surface and reach lateral stripe, fourth crosses lateral stripe on left. NG3 narrowly incomplete midventrally, anteriormost AGs complete behind this. AGs almost all orthoplicate, posteriormost four with slight anteromedial curvature ventrally. Terminal annulus about as long as preceding annuli. Single row of large (1.1 mm diameter) rounded subquadrangular scales middorsally in deep (more than twice as long as annuli) pockets at 12th annulus anterior to tail tip. At 10th annulus behind collars, single row of smaller scales in pockets about one annulus deep.

A pair of small papillae present on edge of dilated vent. Phallus (Figs. 2, 3) about 7 mm long, perhaps not quite fully everted. Terminal surface of distal end shaped as isosceles trapezium with maximum width x depth dimensions of 2.9 x 4.2 mm, wider dorsally than ventrally. Single pair each of dorso- and ventrolateral longitudinal ridges, dorsolateral pair extends closer to vent. Single pair of lateral longitudinal ridges same length as ventrolateral pair, narrower and less prominent than both dorso- and ventrolateral pairs. Single middorsal and single midventral ‘ridge’ wider than other ridges and barely prominent. Lateral (5 to 6), dorsolateral (7) and ventrolateral (5 to 6) longitudinal ridges with narrow transverse, slightly raised bands, whiter than rest of phallus. Middorsal and midventral ‘ridges’ lack transverse bands but instead have less regular midline pale dots, also slightly raised. Anterior ends of dorsolateral ridges lead into opening at terminal end of phallus where each becomes smooth and has a major longitudinal sulcus, homologous with that seen in other caecilians (Gower & Wilkinson 2002). A photograph showing an approximately left ventrolateral view of the everted phallus in the anaesthetized holotype is given by Kok & Kalamandeen (2008: fig. 17).

FIGURE 2. Preserved holotype (IRSNB 1991) of *Rhinatrema shiv* **sp. nov.** Photos by Harry Taylor (BMNH). Scale bar gradations = 1 mm.

FIGURE 3. Anaesthetized holotype (IRSNB 1991) of *Rhinatrema shiv* **sp. nov.** A) Right dorsolateral view. B) Ventral view, with phallus seen in left (slightly dorso-) lateral view. C) Head and anterior of body in right lateral view. Photos by PJRK.

TABLE 1. Variation in meristic and morphometric data of the type series of *Rhinatrema shiv* **sp. nov.** Holotype is IRSNB 1991; all other specimens are paratypes. Tooth counts taken from HRXCT data. “-” indicates data not taken; “?” indicates data could not be taken because of condition of specimen. Numbers separated by a comma are values for left, right sides. AG = annular groove; E = eye; L = lip; N = naris; V = ventrally; W = width. See Material and Methods for other abbreviations. Notes: a) immediately behind collar region; b) at midbody.

	IRSNB 1991	IRSNB 1993	BMNH 2008.601	IRSNB 1994	IRSNB 1992	IRSNB 1995	IRSNB 1996	BMNH 2008.602	IRSNB 1998	IRSNB 1999
Sex	m	f	f	f	-	m	m	m	m	f
TL	151	138	127	184	150	150	131	162	167	178
Tail length	2.8	2.6	2.6	2.9	2.6	2.8	2.3	2.5	2.8	3
Vertebrae	95	98	97	99	-	96	-	95	95	99
Total annuli	346	370	382	361	378	340	335	342	338	364
Annuli behind front of vent	12	11	12.5	12	12.5	11	10	12	11	13
Annuli behind back of vent	8	6.5	8	8	8.5	8	7	8.5	8	9.5
TG	5	4	4	5	5	4	5	5	4	5
V incomplete AGs [a]	1	1	1	2	1	1	0	0	1	1
E-E	2.5	2.3	2.2	2.7	2.3	2.7	2.5	2.7	2.8	3
N-N	0.9	0.9	0.9	1.1	0.9	1.1	1	1.1	1.1	1.1
E-N	2.2	2.2	2	2.6	2.2	2.2	2.2	2.3	2.3	2.4
Head width (HW) at CM	4.1	3.5	3.6	4.8	3.5	4.4	3.8	4.2	4.3	4.7
HW at N1	4.6	4.2	4.2	5.1	3.8	4.8	4	4.7	4.8	5.2
Length of collar region	2.4	2.5	2.5	2.4	-	3.1	3.1	2.7	2.7	3.8
ST-N1, laterally	7.5	7	6.8	7.2	6.8	6.4	5.6	6.5	6.5	7.4
ST-E	2.8	2.6	2.5	2.9	2.7	2.8	2.6	2.7	2.8	3
ST-CM	4.9	4.6	4.4	5.5	4.6	4.8	4.5	4.8	4.8	5.6
E-CM	1.9	1.8	1.9	2.4	1.7	1.8	1.7	2	1.8	2.5
E-L	0.6	0.5	0.6	0.6	0.4	0.6	0.5	0.6	0.6	0.6
N-L	0.6	0.4	0.5	0.6	-	0.5	0.5	0.6	0.6	0.6
Head depth behind CM	3	2.9	2.8	3.2	-	3.3	2.9	3.1	3.2	3.6
Minimum W of stripe [b]	0.6	0.8	0.6	0.5	0.6	0.5	0.6	0.7	0.8	0.6
Maximum W of stripe [b]	1	1	1	1	1	1.2	1.2	1.2	1.3	1.7
Annuli behind end of stripe	8,9	6,6	9,11	8,9	8.5	8,8	8,7	8,8	?	11,10
Midbody width	5.2	4.7	4.7	5.4	4.6	5.9	5.1	6.2	6.2	5.7
Body width at vent	3	2.5	2.3	2.7	2.7	3.5	2.9	2.9	3.3	3.6
Midbody circumference	18	18	14	16	16	19	16	20	20	19
Premaxillary-maxillary teeth	26	-	-	26	-	-	-	-	-	-
Vomeropalatine teeth	36	-	-	38	-	-	-	-	-	-
Dentary teeth (Ds)	28	-	-	30	-	-	-	-	-	-
Inner mandibular teeth (IMs)	25	-	-	28	-	-	-	-	-	-
Ds behind IMs on each side	5–6	-	-	5–7	-	-	-	-	-	-

In preservation grey-brown with off-white markings, body browner where stratum corneum missing, generally darker dorsally. Ventrally very few pale speckles but with whitish glands at anterior margin of each annulus. Dorsally slightly fewer, smaller glands at annular margins but many more and larger irregular pale speckles. Fewer to no speckles on dorsal surface of collars and especially posteriormost 15 mm of body. Pale lateral stripe widest at C1, narrower and partly broken on C2, patchy and irregular just behind collars, then more constant but narrow, irregular and slightly patchy on body until last quarter, increasingly faint and patchy posteriorly, stopping level with vent, absent on tail. Lateral stripe absent at back of head but present boldly on lower jaw where inset from lip by distance less than width of stripe, subparallel to lateral margin of lower jaw from behind CM almost to mentum, prevented from contacting opposite stripe by narrow, tapering brown stripe on mentum. Stripe on upper jaw continuous with margin of mouth from CM to underside of snout tip, widest just anterior to eye. Pale spot around and in front of nares. Narrow pale area around upper half of eye. Dorsal surface of head mostly grey/brown except for largely symmetrical pale blotches, three behind level of CM, anteriorly-open U-shape between eyes (with pale dot inside the U), and irregular blotch halfway between eye and naris on each side. Lower jaw more grey and less brown laterally behind CM back to anterior of C1 and between anterior ends of lateral stripes. Upper surface of head more grey than brown everwhere except centre of posterior half of head and between eye and naris. Annuli with generally darker posteriors because pale glands and speckles concentrated towards anterior of annuli. AGs whitish but not obviously so except where scale pockets opened. In life specimen brown with vivid yellow stripes and speckles.

Variation. See Tables 1 and 2 for meristic and morphometric data. The 10 type specimens range in TL from 127–184 mm (mean = 153.8), with the two largest specimens (> 167 mm) both female. Sexual dimorphism was tested for most (23) of the meristic and morphometric characters (except tooth counts) listed in Table 1. Significant differences at the 0.05 level between males and females were found only in numbers (greater in females) of vertebrae ($t = 5.5549$, $p = 0.036$) and annuli ($t = 2.8539$, $p = 0.0215$), but these were not significant at the Bonferroni-corrected 0.002 level, and the same sexual dimorphisms in caecilians have been found previously only in Scolecomorphidae (Nussbaum 1985; Kupfer 2009). The collar region is weakly demarcated, especially anteriorly, in all specimens. No variation in numbers of scale rows or depth of scale pockets posterior was observed. A pair of small papillae close to the midline are present just anterior to halfway along the disc surrounding the vent of two male (IRSNB 1997, 1998) and one female (BMNH 2008.601) paratypes. Numbers of denticulations around the vent seemed to depend partly on the condition of specimens, but varies from 11 to 13, generally with four or six anteriorly and seven posteriorly. Apart from their innermost portions, the denticulations at the margin of the vent are darkly pigmented in all specimens where this can be clearly assessed. The colour pattern of the paratypes is overall very similar to that of the holotype. The most divergent specimen (IRSNB 1993) has larger pale blotches on the dorsal surface of the head, a complete pale tentacle-naris stripe, lateral stripe unbroken immediately behind the collars, and less anteriorly extensive mandibular stripes and more brown chin. At the other end of the spectrum, the pale blotches on the dorsal surface of the head of BMNH 2008.601 are very slight.

Referred material. BMNH 1976.102 is from a locality in Guyana between the type locality and the northern coast of South America (Fig. 1), further down the Essequibo drainage and almost at sea level. This specimen is clearly more similar to the type series of *R. shiv* than to *R. bivittatum* in head shape, lack of dorsal (although there are some small flecks here) and ventral pale spots at the tail end, and in the length of the tail and head (Table 2). We have included this as referred rather than type material because it is a single specimen (lacking a tissue sample or DNA data) from a slightly outlying locality, and it is beyond the range of variation of the type series in some characters including width of stripe and number of annuli between anterior end of vent and tip of tail (Table 1). The pale blotches on the dorsal surface of the head are larger than in the type series, and the lateral stripe is broader, more regular and complete, being unbroken across and just behind the collars.

Cranial and mandibular osteology. Skulls of *R. bivittatum* and *R. shiv* differ substantially in their overall shape (Fig. 4). The snout tip is more acuminate in *R. shiv* and unlike *R. bivittatum* the premaxilla extends slightly anteriorly beyond the mouth. In dorsal view, the cranium of *R. shiv*, narrows rather uniformly from its widest point (at the jaw articulation) to just behind the external nares. In *R. bivittatum*, the anterior narrowing of the skull is much less uniform, its rate decreasing between the anterior limit of the squamosal to a little anterior to the orbit, making the snout relatively broader. This difference is reflected also in the shape of the paired frontal bones, the lateral margins of which are more or less sub-parallel in dorsal view in *R. bivittatum*, but narrow anteriorly in *R. shiv*, and in the maxillopalatine, the dorsal margins of which curve posterolaterally away from the frontals in *R. bivittatum*. The latter has the effect of making the temporal fenestrae far more extensive and very much wider anteriorly in *R. bivittatum* than in *R. shiv*.

TABLE 2. Variation in meristic and morphometric data of *Rhinatrema shiv* (type series[1] and referred specimen BMNH 1971.102[2]), *R. bivitattum* (including holotype – see Appendix) and *R.* sp. (RMNH 17667). Values given as means (with range in parentheses). Values in square parentheses from Nussbaum & Hoogmoed (1979). * the means for some characters were calculated from raw data for less than 10 specimens – see Table 1 for details. ** Means for *R. bivittatum* from data for 20–28 specimens except means for tooth counts (7 specimens). Note: c) measured as number of annuli. See caption to Table 1 for abbreviations and other notes.

	R. shiv [1]	*R. shiv* [2]	*R. bivittatum*	*R.* sp.
Number of specimens	10*	1	28**	1
Sex	-	f	11m, 11f	m
TL	153.8 (127–184)	172 [175]	176 (127–219)	168 [163]
Tail Length	2.69 (2.3–3)	2.7 [2.4]	2.19 (1.4–2.7)	3.1 [3.5]
Tail Length as % of TL	1.76 (1.54–2.01)	1.6 [1.37]	1.25 (0.8–1.59)	1.85 [2.15]
Vertebrae	97 (95–99)	[99]	93 (88–99)	[85]
Total annuli	356 (335–378)	347 [345]	335 (273–384)	382 [384]
Annuli behind front of vent	12 (10–13)	10	8.6 (7–10.5)	13.5
Annuli behind back of vent	8 (6.5–9.5)	7 [7]	5 (4–6.5)	10 [11]
TG	4.6 (4–5)	3	4.1 (3–6)	4 [3]
V incomplete AGs [a]	0.9 (0–2)	2	2.7 (1–5)	9
E-E	2.6 (2.2–2.8)	2.8 [3]	3.7 (2.9–4.4)	3.2 [2.8]
N-N	1 (0.9–1.1)	0.9 [0.9]	1.4 (1–1.7)	1.1 [1.2]
E-N	2.3 (2–2.6)	2.3 [2.4]	2.9 (2.2–3.4)	2.8 [3.2]
Head width (HW) at CM	4.1 (3.5–4.7)	4.4	5.3 (3.5–6.4)	5 [5.1]
HW at N1	4.5 (4–5.2)	4.8 [4.8]	5.6 (4.5–7.4)	5.5
Length of collar region	2.8 (2.4–3.8)	2.9	3.1 (2.3–4.3)	3.6
ST-N1, laterally	6.8 (5.6–7.4)	6.6 [8.7]	8.6 (6.7–10.6)	7.8 [8.9]
ST-E	2.7 (2.5–3)	2.9	3.5 (2.5–4.3)	3.5
ST-CM	4.9 (4.5–5.6)	5.6	6.6 (4.6–8.3)	6.6
ST-CM as % of TL	3.2 (2.9–3.6)	3.1 [3.2]	3.8 (3.1–4.4)	3.9
E-CM	2 (1.7–2.5)	2.3	2.7 (1.7–3.7)	2.7
E-L	0.6 (0.4–0.6)	0.5	0.5 (0.4–0.7)	0.5
N-L	0.5 (0.4–0.6)	ca. 0.6	0.6 (0.4–0.7)	0.6
Head depth behind CM	3.1 (2.8–3.6)	3.1	3.5 (2.4–4.6)	3.2
Range in stripe width [b]	(0.5–1.7)	1.3–1.7	(0.80–3.5)	1.8–2.5
Midbody W/median W stripe [b]	6.1 (5.2–7.2)	4.6	3.6 (2.9–4.6)	3.9
Annuli behind end of stripe	8.4 (6–11)	6	4.5 (2–7.5)	9,7
L dorsal pale spot on tail [c]	0 (0)	0	(3–12)	6
Midbody width	5.4 (4.7–6.2)	6.9 [6]	7.1 (4.2–10)	8.4 [8]
Body width at vent	2.9 (2.3–3.6)	3.6	2.9 (1.8–4.1)	3.4
Midbody circumference	17.6 (14–20)	19	21.2 (12–28)	23
Premaxillary teeth	26 (26)		26.3 (24–28)	
Vomeropalatine teeth	37 (36–38)		35.9 (31–39)	
Dentary teeth (Ds)	29 (28–30)		32.9 (30–35)	
Inner mandibular teeth (IMs)	26.5 (25–28)		25.7 (24–28)	
Ds minus IMs	2.5 (2–3)		7.1 (5–10)	
Ds behind IMs on each side	5–6.5 (5–7)		7.4–8.7(6–10)	

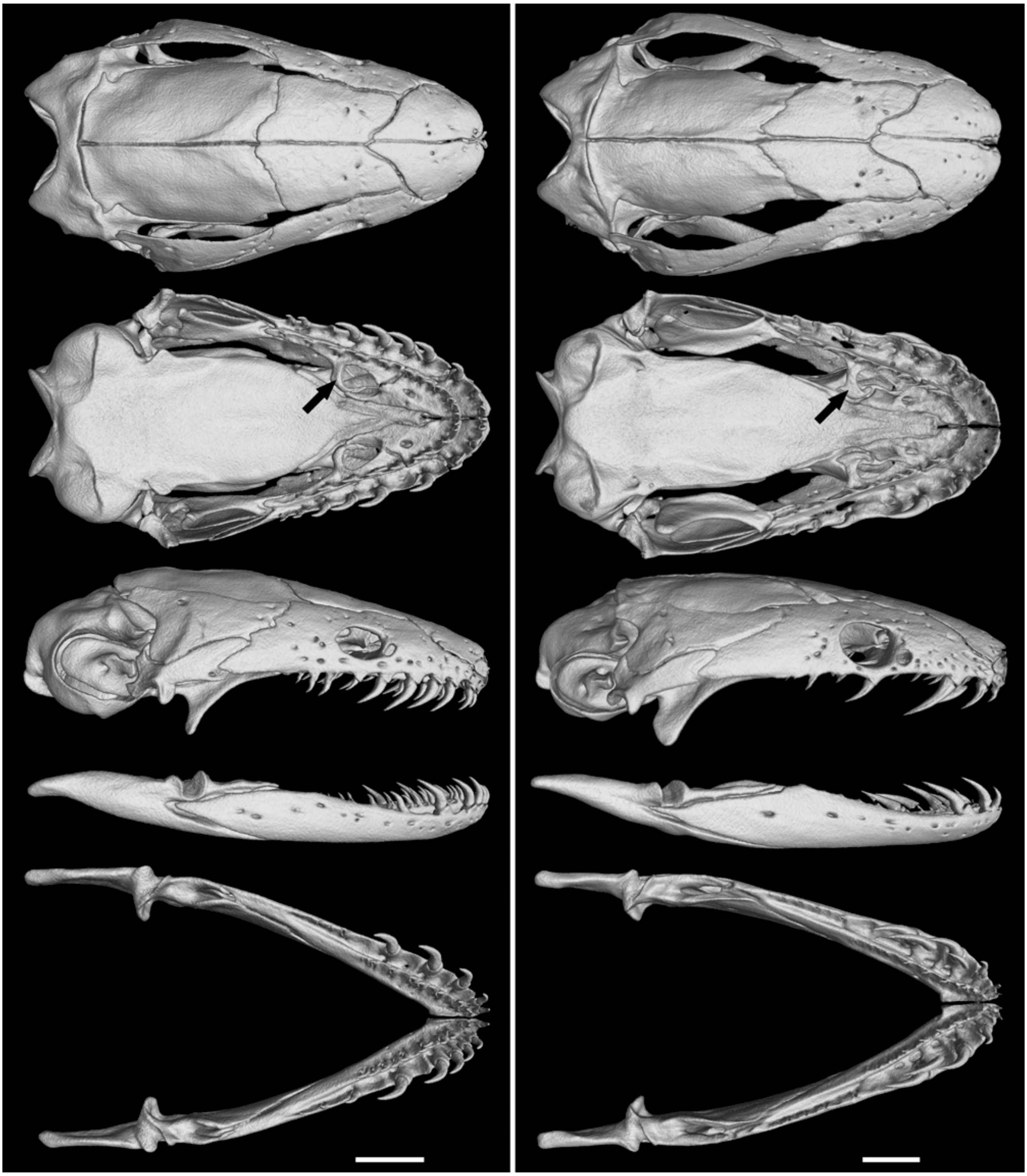

FIGURE 4. Volume reconstruction of HRXCT data showing *Rhinatrema shiv* **sp. nov.** (holotype IRSNB 1991: left column) and *R. bivittatum* (MW2051: right column). From top to bottom: crania in dorsal, palatal, lateral view and mandibles in lateral and dorsal view. Arrows in palatal views point to postchoanal processes of right maxillopalatines. See Nussbaum (1977) for figures and description of the cranial and mandibular osteology of rhinatrematids. Scale bar = 1mm.

There are numerous other differences between the crania of the two species including: the lengths of the retroarticular processes, otic regions, pterygoid processes of the quadrates and quadrate processes of the pterygoids (all proportionately shorter *in R. bivittatum*); the sizes of the orbits (substantially larger and much closer to the margin of the mouth, in *R. bivittatum*); the form of the postchoanal process of the maxillopalatine (thicker and bearing a posterodistal process only in *R. bivittatum*); the angle formed middorsally by the posterior margins of the frontals (approximately 90˚ in *R. bivittatum*, more obtuse in *R. shiv*); the extent of the edentulous (adentigerous) palatine shelf medial to the tooth row (small in *R. shiv* but almost non-existent in *R. bivittatum*); and the position of the foramina in the spenethmoid for the passage of the dorsal roots of the olfactory nerve (distinctly more dorsal in *R. shiv*).

Differences in the overall shape of the lower jaws parallel those of the cranium with *R. bivittatum* having a larger space between the dentary and IM tooth rows anterolaterally, with more substantial neurovascular foramina in this space. Additionally, each mandible of *R. bivittatum* has a weaker subsplenial ridge (sensu Wilkinson & Nussbaum 1997) and a proportionately shorter distance between the canalis primordialis and jaw articulation. The dentary tooth rows of *R. bivittatum* extend further posteriorly, closer to the canales primordiales, and with more elements behind the proportionately shorter IM series. The greater relative length of the dentary rows explains the greater difference in numbers of dentary and IM teeth in *R. bivittatum*.

Genetics. Following the protocols outlined by Gower *et al.* (2002), 12S, 16S and Cytb mitochondrial (mt) DNA sequences were generated for the holotype of *R. shiv* (GenBank accessions GU566188 to 566190), and compared with other rhinatrematids. The comparison was made with the following three specimens: *R. bivittatum* from close to the type locality in French Guiana (San Mauro *et al.* 2004; GenBank accession AY456252); *Epicrionops marmoratus* from Ecuador (Gower *et al.* 2002; GenBank AY101206, AY101226, AY101246); *E. niger* from Guyana (Zhang & Wake 2009; GenBank GQ244468). The aligned sequences (excluding gaps and missing data) comprised a total of 1572 sites, 349 for 12S, 533 for 16S and 690 for Cytb. Pairwise differences were 15.3% for the two *Rhinatrema*, and 17.2/16.3 and 20.2/20.4 between *R. bivittatum/R. shiv* and *E. marmoratus* and *E. niger*, respectively, with the two *Epicrionops* differing by 18.2%. Thus, the genetic distance between *R. bivittatum* and *R. shiv* is not much less than between each of these species and two species of *Epicrionops*. These pairwise differences are substantial, all greater for the same mt genes than among species of Sri Lankan and Indian *Ichthyophis* (Gower *et al.* 2005), and similar to the greatest differences among species of *Boulengerula* and *Herpele* (Loader *et al.* submitted). We interpret the new data as strongly supporting the hypothesis that *R. shiv* is a valid species distinct from *R. bivittatum*.

Etymology. Named in honour of Shivnarine ‘Shiv’ Chanderpaul (born 1974), in recognition of his being the West Indies’ most capped and highest run-scoring Guyanese cricketer, and international cricketer of the year in 2008. The specific epithet is considered to be a noun in apposition.

Suggested common name. Shiv’s Rhinatrema.

Distribution, natural history and conservation. The type series was collected in submontane forest of the Pakaraima uplands on white sand dominated by clump wallaba (*Dicymbe* spp.) (ter Steege 2001). The holotype and two of the paratypes (IRSNB 1993-94) were collected in pitfall traps (plastic buckets of about 28 cm diameter at the top, 30 cm deep) that were buried into the ground at ca. 3 m intervals under a 60 m-long drift fence of plastic sheet (approximately 50 cm in height) positioned to run across the open midline top of the buckets. The other seven paratypes were collected by diamond miners in inundated mining pits (see Kok & Kalamandeen 2008: fig. 11), without precise data. Nychthemeral cycle is unknown, but all individuals collected in pitfall traps where found early morning or early afternoon (pitfall traps were checked two times a day, in early morning or early afternoon and late afternoon), consistent with nocturnal surface activity. The new species appears to be active during both the dry and the wet seasons given that specimens were collected in pitfall traps in May and June (long wet season) and in September (long dry season).

The new species is known with certainty only from Kaieteur, Guyana, although it possibly extends further down the Essequibo drainage in Guyana. Given the slight doubt that it has more than a point distribution, and that we lack data on ecological tolerance or requirement, *R. shiv* would probably qualify for Data Deficient status in the IUCN redlist. The occurrence of the type locality within a National Park, and possibility that the species occurs more widely offer hope that *R. shiv* could be upgraded to Least Concern status with a little more research. Habitat destruction (including mining activity) likely represents the major threat. Where known, rhinatrematids have a biphasic life history with larvae hatching from terrestrial eggs (Nussbaum 1977). All the known specimens of *R. shiv* are fully transformed, with no indication of larval features (lateral line organs, expanded lips, spiracles, tail fin).

Discussion

Cranial and mandibular osteology has been little used in low-level taxonomic analysis of caecilians, perhaps because of generally small sample sizes and the previous requirement of destructive sampling. HRXCT is a relatively new technique that offers the opportunity to examine skeletons without dissecting away or damaging soft tissues, and its effective use in this study suggests it will be a valuable tool in future caecilian systematics research.

Previous results suggest that the herpetofauna of Kaieteur National Park is a mix of widespread lowland species and upland endemics (Kok & Kalamandeen 2008, Kok unpubl. data). At least two species (one lizard and one frog) are currently not reported from outside the park, which also harbours at least 14 amphibian and reptile species that are considered strict Guyanese endemics. Our referral of BMNH 1976.102 to *R. shiv* suggests that this species is not endemic to Kaieteur and occurs also in the lowlands, but collection of additional specimens of *Rhinatrema* from Guyana is required to test this. The caecilians of the Guiana shield, and rhinatrematids in general, have mostly not been studied in detail. Our description of *R. shiv* is the first description of a new species of rhinatrematid for more than 50 years, and adds to two caeciliid caecilian species very recently described from the Guiana shield (Wake & Donnelly 2009; Wilkinson *et al.* in press). Additional new taxa almost certainly wait to be discovered in this region.

Nussbaum & Hoogmoed (1979) identified all four of the specimens of *Rhinatrema* known to them as *R. bivittatum*. These authors noted the longer tail of RMNH 17667 but, because this was the only male and the only Suriname record, they were unable to rule out sexual dimorphism and/or geographic variation. Our much larger sample of *R. bivittatum* (28 specimens, see Appendix) includes males and females from several localities (though no additional specimens from Suriname), and none of these specimens approaches RMNH 17667 in the length of its tail, which furthermore has even more annuli than any known specimen of *R. shiv.* Despite its long tail, RMNH 17667 resembles *R. bivittatum* more than *R. shiv* in having a broader (more U-shaped) and relatively longer head, a more extensive pale blotch between the eyes, complete eye-naris pale stripes, broader and more regular body stripes, and pale spots on the dorsal and ventral surfaces on the tail. Despite its long tail, RMNH 17667 has fewer vertebrae than other *Rhinatrema* specimens examined (Table 2). It might be that RMNH 17667 represents a third species of the genus but we refer to it here as *Rhinatrema* sp. because it is the only specimen known from Suriname, it is flattened and somewhat dehydrated making it difficult to compare readily with other specimens, and there are no HRXCT data for its skull and mandibles. Collection of fresh material from Suriname will aid a more precise identification of this population. Based on currently available material, *R. bivittatum* is restricted to French Guiana and far northeastern Brazil (Amapá state).

Acknowledgements

PJRK's fieldwork in Guyana was made possible with the generous financial support of the Belgian Directorate-General of Development Cooperation and the help and support of the Prime Minister of Guyana, the Honorable Samuel Hinds. PJRK expresses special thanks to Giuliano "Kinky" Seegobin for collecting a large part of the type series and for hospitality in his diamond mining camp, to his counterpart Paul Benjamin for field assistance, and to Michelle Kalamandeen, Kaslyn Holder and Calvin Bernard (University of Guyana) for help in obtaining export permits. PJRK's research permit in Guyana (030605BR006) and export permits (040406SP014, 010207SP001) were issued by the Guyana Environmental Protection Agency. For hospitality and help with collecting and exporting *Rhinatrema* samples from French Guiana, DJG, MW, and ES are very grateful to Jeannot and Odette (Camp Patawa), Céline Dupuy (Direction des Services, Vétérinaires de la Guyane), Alexander Kupfer (Friedrich-Schiller Universität Jena), and Jérôme Chave, Patrick Chatelet, and especially Philippe Gaucher (CNRS). Diego San Mauro generated and analysed DNA sequence data, and Richie Abel helped with HRXCT. Alexander Kupfer and Hendrik Müller provided constructive criticism on an earlier version of the paper. This work was supported, in part, by EU Synthesys grants to PJRK (to visit

BMNH) and DJG and MW (to visit IRSNB), and NERC studentship NE/F009011/1 to ES. DJG, MW and ES conducted fieldwork in French Guiana in 2008 thanks, in part, to an award from the CNRS Nouragues Research Grants Program. Georges Lenglet (IRSNB) is thanked for support and access to material. Curatorial and collections management staff of the herpetological collections of AMNH (Darrel Frost), MNHN (Alain Dubois and Ivan Ineich), MNRJ (Ulisses Caramaschi, José Pombal Jr and Ronaldo Fernandes), MZUSP (Paulo Vanzolini, Miguel Trefault Rodrigues and Hussam Zaher), and RMNH (Ronald de Ruiter) are thanked for granting access to specimens and/or loans to DJG and MW.

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Appendix. Specimens examined

All specimens fully transformed. * indicates specimens examined by HRXCT.

Rhinatrema bivittatum (n = 28)

FRENCH GUIANA: “Cayenne” (MNHN 585); Kaw Mountains (BMNH 2002.6; MW 2051*, 2393, 2395*, 2426, 3957, 3979*, 3980*, 4095, 5589*, 5695*, 5805, 6473); Nouragues (MW 5631*, 6480, 6482); Paracou, near Sinnamary (AMNH A139214); Courcibo, Adieu Vat (MNHN 1986.3169); Sait Eugène Museum fieldstation (MNHN 1999.8360); Angoulême (MW 5669, 6457, 6459); no precise locality (MNHN 1986.2497).

BRAZIL: *Amapá*: Upper Lumier River, Tumuc-Humac Mountains (MNHN 1899.101); Estrada T-11, Serra do Navio (MZUSP 57082, 57083); Rio Cassiporé or Rio Araguarí (MNRJ 24681).

Rhinatrema shiv (n = 11)

GUYANA: Kaieteur National Park (IRSNB 1991*, 1992, 1993, 1994*, 1995, 1996, 1998 and 1999; BMNH 2008.601 and 2008.602). Wineperu (BMNH 1971.102).

Rhinatrema sp. (n = 1)

SURINAME: Irene Falls, Brownsberg (RMNH 17667).