A New Species of *Hyperolius* (Amphibia: Hyperoliidae) from Príncipe Island, Democratic Republic of São Tomé and Príncipe

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ABSTRACT: I describe a new species of reed frog (Hyperolius: Hyperoliidae) from the island of Príncipe in the Gulf of Guinea archipelago. The new species is within the Hyperolius cinnamomeoventris species complex, which includes four described species: H. cinnamomeoventris, H. veithi, H. molleri, and H. thomensis. The new species is sexually monochromatic (males and females have green dorsal coloration) and is thus distinguished from H. cinnamomeoventris, which is sexually dichromatic, and from H. veithi, in which both males and females are tan with yellow dorsolateral lines. The new species is smaller in size than H. thomensis, and differs in coloration from H. molleri and H. thomensis by lacking a black contour along the edges of the green/yellow band of coloration that extends down the dorsal side of the thigh, by lacking red/orange coloration on the dorsal and ventral sides of the thigh, and in the mitochondrial 16s and cytochrome-b genes. Furthermore, previous work indicates that the new species is distinct from H. molleri and H. thomensis in analyses of genome-wide single-nucleotide polymorphisms. This new species is the third endemic amphibian described from this small oceanic island. The type material for the closely related H. molleri and H. thomensis was destroyed or lost; therefore, I designate neotype material for these two species to enable the description of the new species.

Key words: Anura; Gulf of Guinea; Hyperolius drewesi sp. nov.; Hyperolius molleri; Hyperolius thomensis

The Islands of São Tomé and Príncipe in the Gulf of Guinea archipelago host seven endemic amphibian species, including two species of reed frogs, genus Hyperolius (Rapp 1842) (Hyperoliidae): Hyperolius molleri (Bedriaga 1892), found on both islands, and Hyperolius thomensis Bocage (1886), restricted to São Tomé (Jones 1994; Drewes and Stoelting 2004; Drewes and Wilkinson 2004; Uyeda et al. 2007). São Tomé and Príncipe arose as volcanoes along the Cameroon Volcanic Line and have never been connected to continental Africa; thus the prevailing hypothesis for the presence of endemic amphibians on these islands is assisted dispersal via vegetation rafts that are swept down major river drainages into the gulf following large rain events (Measey et al. 2007). A recent multilocus phylogeographic study of the island Hyperolius and their mainland sister taxon, the Hyperolius cinnamomeoventris species complex, indicated that Hyperolius dispersed from West-Central Africa in the last several million years and subsequently diversified within the archipelago (Bell et al. 2015a). São Tomé Giant Reed Frogs, H. thomensis, and Moller's Reed Frogs, *H. molleri*, are considered distinct species based on differences in body size, coloration, and breeding ecology (Drewes and Wilkinson 2004). In contrast, the populations of H. molleri on São Tomé and Príncipe are currently considered a single species, although populations on the two islands are reciprocally monophyletic at mitochondrial and nuclear loci (Bell et al. 2015a,b).

Herein I describe a new species of reed frog from the island of Príncipe, which represents the third endemic amphibian for Príncipe, and designate neotypes for *H. thomensis* and *H. molleri* to enable the description of the new species. The type material of *H. thomensis* was collected on São Tomé Island and housed in the Museu Bocage in Lisbon, Portugal (Drewes and Wilkinson 2004). All herpetological material at the Museu Bocage was destroyed in a fire in 1978 (Almaça and Neves 1987). The type material of

H. molleri was collected on São Tomé Island, sent to Bedriaga by Adolfo Moller (Universidade de Coimbra), and remained in Bedriaga's private collection (L. Ceríaco, personal communication; Museu Nacional de História Natural e da Ciência). There are no records of Bedriaga's private collection being deposited in a museum after his death, and the material is presumed lost. Additionally, there is a hybrid zone between \tilde{H} . thomensis and H. molleri on São Tomé that coincides with environmental transitions from agriculture to primary forest (Bell et al. 2015b) and the original type localities for H. thomensis and H. molleri are vague and/or include sites where hybridization is likely. Therefore, based on previous molecular work I selected neotypes for H. thomensis and H. molleri from sites outside of the hybrid zone and chose specimens with no evidence of hybrid ancestry (Bell et al. 2015b).

Materials and Methods

My colleagues and I collected specimens during April—May 2001, May 2006, April 2008, April 2012, and April—May 2013. Specimens were fixed in 10% buffered formalin after preserving livers in 95% ethanol or RNAlater (Ambion), and later transferred to 70% ethanol. Specimens and tissue samples were deposited at the California Academy of Sciences (CAS). Comparative material was examined in the holdings of this institution (Appendix).

Measurements were taken with dial calipers (±0.1 mm): snout–vent length (SVL); head length from tip of snout to rear of jaws (HDL); maximum head width (HDW); snout length from tip of snout to anterior corner of eye (SNT); eye diameter (EYE); interorbital distance (IOD); internasal distance (IND); shank length (SHK); thigh length (TGH); forearm length, from elbow to base of thumb (LAL); manus length from tip of third digit to base of thumb (HND); pes length from tip of fourth toe to base of inner metatarsal tubercle (FTL). I followed Myers and Duellman (1982) to describe the webbing formulae.

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Table 1.—Measurements (mm) of adult holotype and paratypes of $Hyperolius\ drewesi$ sp. nov and adult neotypes of $Hyperolius\ molleri$ and H. thomensis. Mean values are reported $\pm 1\ SD$; see text for measurement descriptions.

Measurement ^a	H. drewesi			H. molleri	H. thomensis
	Holotype male (CAS 253051)	Paratype males $(n = 16)$, range; mean	Paratype female (CAS 219205)	Neotype male (CAS 253073)	Neotype male (CAS 251637)
SVL	27.3	$24.8-30.9; 27.8 \pm 1.5$	32.7	26.9	38.6
HDL	5.9	$5.8-7.2$; 6.4 ± 0.4	7.1	6.3	8.3
HDW	9.7	$9.3-11.0;\ 10.1\ \pm\ 0.4$	11.7	9.4	13.5
SNT	4.3	$3.7-4.4$; 4.0 ± 0.2	4.8	4.2	5.8
EYE	2.7	$2.7-3.6; 3.0 \pm 0.2$	3.5	3	3.6
IOD	5.5	$5.1-6.0$; 5.7 ± 0.2	6.9	5.1	7.9
IND	2.3	$2.0-2.5$; 2.3 ± 0.2	2.6	2.6	3.5
SHK	13.8	$12.9-15.6$; 14.3 ± 0.6	15.6	13.1	19.8
TGH	13.5	$12.6-15.4$; 13.9 ± 0.7	15.4	13.0	18.9
LAL	5.9	$5.8-6.8$; 6.2 ± 0.3	6.9	5.9	7.3
HND	7.6	$7.3-8.5$; 8.0 ± 0.4	8.5	7.3	12.1
FTL	12.2	$11.4 - 13.2; 12.4 \pm 0.5$	13.4	11.6	18.5

a SVL, snout-vent length; HDL, head length from tip of snout to rear of jaws; HDW, maximum head width; SNT, snout length from tip of snout to anterior corner of eye; EYE, eye diameter; IOD, interorbital distance; IND, internasal distance; SHK, shank length; TGH, thigh length; LAL, forearm length, from elbow to base of thumb; HND, manus length from tip of third digit to base of thumb; FTL, pes length from tip of fourth toe to base of inner metatarsal tubercle.

I obtained sequence data from two mitochondrial genes for the type specimen of the new species and the neotypes of *H. molleri* and *H. thomensis* (GenBank accession numbers 16s: KP137129, KP137172, KP137217; cytochrome b: KP137243, KP137277, KP137316; Bell et al. 2015b) and calculated uncorrected pairwise distance between the sequences in Geneious v8.0.4.

Species Description

Hyperolius **drewesi** sp. n (Table 1; Figs. 1–3)

Holotype.—CAS 253051 (field no. RCB 0352), adult male, São Tomé and Príncipe, Príncipe Island, Road to Bom

Bom Resort, 1.6883°N, 7.4022°E (in all cases, datum = WGS84), 15 m elevation; collected by Rayna C. Bell, Robert C. Drewes, Velma Schnoll, and Andrew Stanbridge on 30 August 2013.

Paratypes.—CAS 219128–29 (field no. RCD 14048–49), two adult males, São Tomé and Príncipe, Príncipe Island, Agua Doutor, 1.6521°N, 7.4161°E, 178 m elevation, collected by Robert C. Drewes and Ricka E. Stoelting, 19 April 2001; CAS 219148 (field no. RCD 14068), adult male, São Tomé and Príncipe, Príncipe Island, Army depot at airport, 1.6685°N, 7.4128°E, 181 m elevation, collected by D. J. Long and F. Penny, 3 May 2001; CAS 219203 (field no. RCD 14125), adult male and CAS 219205 (field no. RCD 14127), adult female, São Tomé and Príncipe, Príncipe Island, Baia das Agulhas, 1.6009°N, 7.3531°E, 14 m

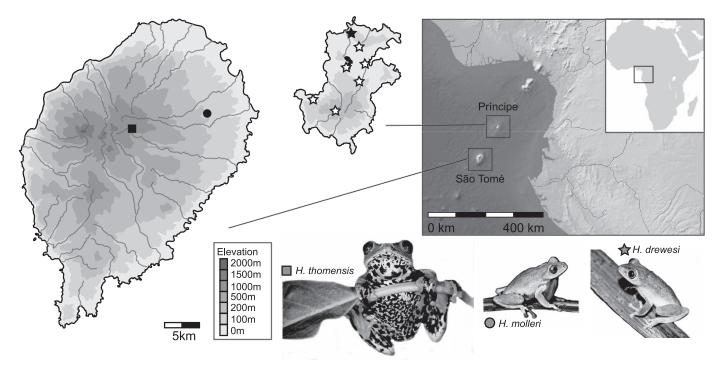


Fig. 1.—Distribution of localities for *Hyperolius drewesi* sp. nov. on Príncipe Island (filled symbol indicates type locality), and neotype localities for *Hyperolius molleri* and *Hyperolius thomensis* on São Tomé Island. Photos by D. Lin (*H. thomensis*) and A. Stanbridge (*H. molleri* and *H. drewesi*). A color version of this figure is available online.

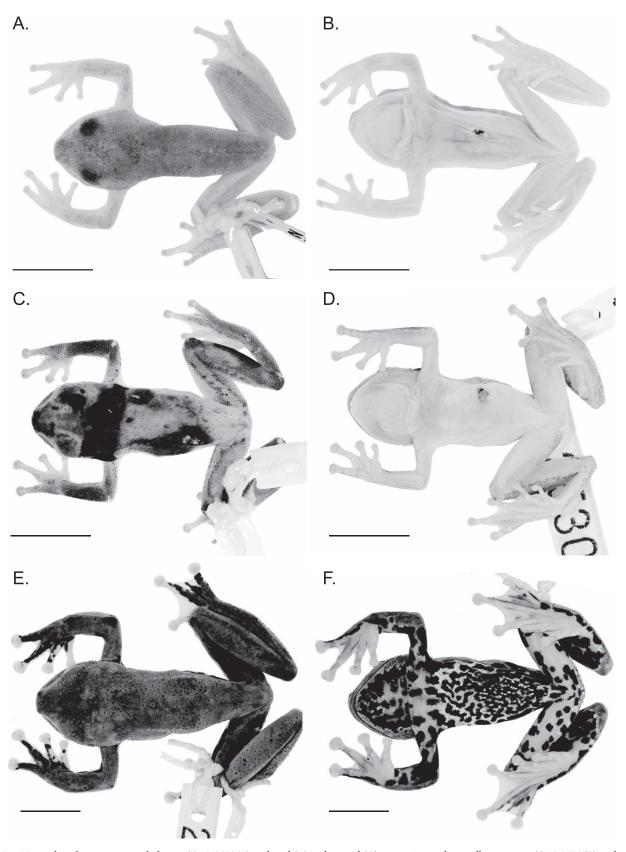


Fig. 2.—Hyperolius drewesi sp. nov. holotype (CAS 253051) in dorsal (A) and ventral (B) views; Hyperolius molleri neotype (CAS 253073) in dorsal (C) and ventral views (D); Hyperolius thomensis neotype (CAS 251637) in dorsal (E) and ventral (F) views. Scale bars = 10 mm. Photos by K. Whitney. A color version of this figure is available online.

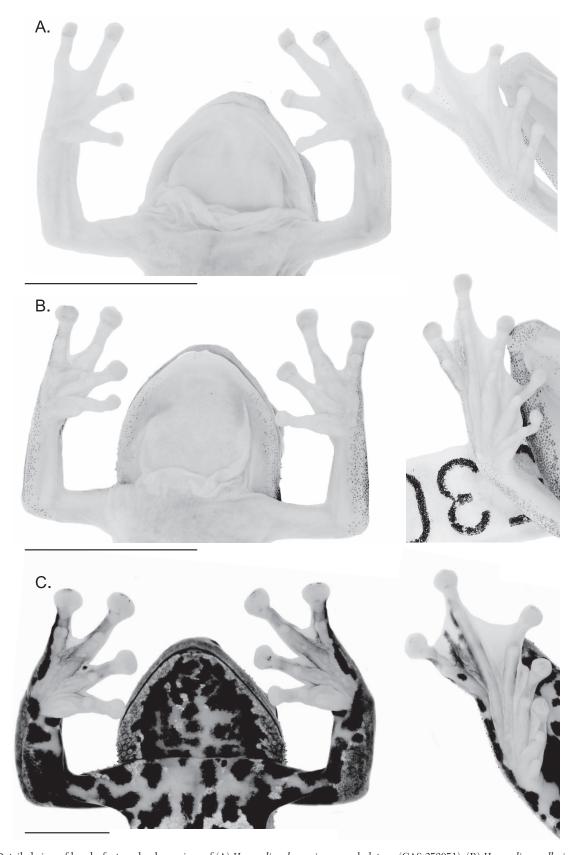


Fig. 3.—Detailed view of hands, feet, and gular regions of (A) $Hyperolius\ drewesi$ sp. nov. holotype (CAS 253051); (B) $Hyperolius\ molleri$ neotype (CAS 253073); (C) $Hyperolius\ thomensis$ neotype (CAS 251637). Scale bars = 10 mm. Photos by K. Whitney. A color version of this figure is available online.

elevation, collected by Robert C. Drewes and Ricka E. Stoelting, 3 May 2001; CAS 233444 (field no. RCD 14484), adult male, São Tomé and Príncipe, Príncipe Island, base camp of Pico de Príncipe, 1.5881°N, 7.3808°E, 620 m elevation, collected by Josef Uyeda, 22 May 2006; CAS 233491–94 (field no. RCD 14402–05), four adult males, São Tomé and Príncipe, Príncipe Island, road along Papagaio River, 1.6259°N, 7.4166°E, 6 m elevation, collected by Robert C. Drewes, Josef Uyeda, and Jens V. Vindum, 22 May 2006; CAS 253047–50, 253052–54 (field no. RCB 348–51, RCB 353–55), seven adult males, same data as holotype.

Referred material.—CAS 219125–27, 219130–34, 219136-42 (field no. RCD 14045-47, 14050-54, 14055-62), 16 adult males, São Tomé and Príncipe, Príncipe Island, Agua Doutor, 1.6521°N, 7.4161°E, 178 m elevation, collected by Robert C. Drewes and Ricka E. Stoelting, 19 April 2001; CAS 219192-96 (field no. RCD 14114-18), five adult males, São Tomé and Príncipe, Príncipe Island, Conceição, 1.6441°N, 7.3978°E, 181 m elevation, collected by Robert C. Drewes and Ricka E. Stoelting, 21 April 2001; CAS 219204, 219206–07 (field no. RCD 14126, 14128–29), three adult males, São Tomé and Príncipe, Príncipe Island, Baia das Agulhas, 1.6009°N, 7.3531°E, 14 m elevation, collected by Robert C. Drewes, Ricka E. Stoelting, 3 May 2001; CAS 238886-91 (field no. RCD 14662-67), six adult males, São Tomé and Príncipe, Príncipe Island, Road to Bom Bom Resort, 1.6892°N, 7.4027°Ê, 25 m elevation, collected by Robert C. Drewes, 30 April 2008.

Diagnosis.—Multilocus molecular data indicate that H. drewesi is in the genus Hyperolius and is part of the H. cinnamomeoventris species complex, which includes four described species: H. cinnamomeoventris Bocage (1866) and H. veithi Schick, Kielgast, Rödder, Muchai, Burger, Lötters (2010) from continental Africa, and H. molleri and H. thomensis endemic to São Tomé Island in the Gulf of Guinea archipelago (Schick et al. 2010; Bell et al. 2015a). Hyperolius drewesi is sexually monochromatic (both sexes are green) and differs in color from H. cinnamomeoventris, which is sexually dichromatic (females are green and males are tan with bright yellow dorsolateral lines), and from H. veithi, which is sexually monochromatic (both sexes are tan with bright yellow dorsolateral lines). Hyperolius drewesi differs from H. thomensis in male body size (H. drewesi SVL 24.8-30.9 mm, H. thomensis SVL 36.1-41.2 mm), in the distal portion of the terminal phalanx (H. drewesi disc shaped, H. thomensis oval/wider in horizontal plane), and in ventral coloration (H. drewesi white/translucent, H. thomensis marbled black/orange). Hyperolius drewesi differs from H. molleri by lacking a black contour along the edges of the green/yellow band of coloration that extends down the dorsal side of the thigh (always present in H. molleri), by lacking red/orange coloration on the dorsal and ventral sides of the thigh (always present in *H. molleri*), and in the mitochondrial 16s and cytochrome-b genes (below).

Description of holotype.—Habitus moderately slender; head length less than width; snout short, obtusely pointed in dorsal view, round in profile; nostrils lateral, closer to tip of snout than eye, visible in dorsal view; canthus rostralis distinct, slightly constricted behind nostrils; lores concave, oblique; eye diameter less than snout length; interorbital distance greater than width of upper eyelid; pineal body not visible; tympanum indistinct, round, half of eye diameter;

tympanic annulus raised relative to tympanum, visible on anterior and ventral margin; vomerine teeth absent; tongue heart-shaped, notched.

Tips of all four fingers expanded with circummarginal grooves; width of Finger III disc $\sim\!1.6$ times width of phalanx; relative finger lengths I < II < IV < III; metacarpal, palmar, and thenar tubercles absent; subarticular tubercles on Fingers I–IV round, distal tubercle on Finger IV bifid; finger webbing formula I 2 – 2 II 2 – 3 II 2 – 1 IV; ulnar tubercle absent.

Tips of all five toes expanded; width of Toe IV disc ~ 1.5 times width of phalanx; relative toe lengths I < II < III < V < IV; outer metatarsal tubercle ill-defined, inner metatarsal tubercle distinct, ovoid; plantar surfaces smooth; well-developed subarticular tubercles on toes, round; toe webbing formula I 1-1 II $\frac{1}{2}-1$ III 0-1 IV 1-0 V.

Skin on dorsum finely granular; skin on limbs smooth; skin on ventral surface smooth, increasingly granular posteriorly; dorsolateral fold absent; fine dorsal asperities.

Nuptial pad absent; elongated vocal sac openings, located on either side of the floor of the mouth; vocal sac median; small, rounded gular gland occupies less than half of gular area.

Holotype coloration in preservative.—Dorsum light gray, side of head, dorsal surface of forelimb and hindlimb cream with fine black speckling; ventral surfaces cream; dorsal asperities light.

Holotype coloration in life.—Iris gold; dorsum green, dorsal surface of forelimb and hindlimb green; dorsal surface of thigh translucent with thin green medial band extending from dorsum to lower limb; side of head green; dorsal surface of fingers and toes green; ventral surfaces translucent, chest white; dorsal asperities light.

Variation.—The new species is sexually dimorphic. Males with round gular gland that occupies less than half of gular area, vocal sac, and dorsal asperities (all absent in female). SVL of male paratypes 76–94% SVL of female paratype (Table 1). No variation in color or pattern noted among paratypes.

Molecular divergence.—The holotype of *H. drewesi* (CAS 253051) has an uncorrected pairwise distance of 1.5% in the 16s fragment and 1.6% in the cytochrome-b fragment to *H. molleri* (CAS 253073), and an uncorrected pairwise distance of 1.3% in the 16s fragment and 2.8% in the cytochrome-b fragment to *H. thomensis* (CAS 251637). Pairwise distances between *H. molleri* and *H. thomensis* are 1.7% and 2.8% at 16s and cytochrome b, respectively.

Distribution.—The new species was collected at seven localities spanning much of the altitudinal and ecological variation across Príncipe Island (Fig. 1).

Natural history.—We found the species breeding near slow-moving streams and temporary ponds in primary forest and in marginal habitats with high levels of human disturbance. The type locality of the species is next to a small landfill in secondary forest along the road to the Bom Bom Resort. Specimens at all sites were found during visual surveys at night approximately 1–2 m above the ground on leaves and thin branches overhanging streams or small pools of standing water. As in *H. molleri*, females deposit eggs on the surface of leaves overhanging water (Fig. 4G.) The eggs observed at the type locality were white with faint pigmentation on the animal pole and ~2 mm in diameter.

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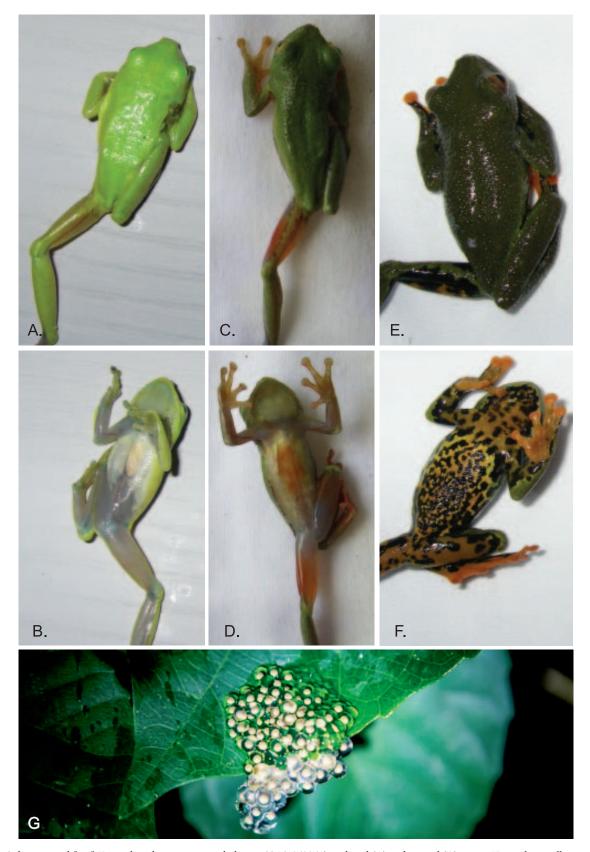


Fig. 4.—Coloration in life of $Hyperolius\ drewesi\ sp.\ nov.$ holotype (CAS 253051) in dorsal (A) and ventral (B) views; $Hyperolius\ molleri\ neotype\ (CAS\ 253073)$ in dorsal (C) and ventral views (D); $Hyperolius\ thomensis\ neotype\ (CAS\ 251637)$ in dorsal (E) and ventral (F) views. Egg mass at the type locality of $H.\ drewesi.$ Photos A–F by R.C. Bell; photo G by A. Stanbridge.

Etymology.—The specific name is a patronym for Robert C. Drewes, acknowledging his extensive contributions to herpetological research in Africa and in particular, his contributions to documenting biodiversity in São Tomé and Príncipe. The suggested common name is Drewes' Reed Frogs.

Hyperolius molleri (Bedriaga 1992) (Table 1; Figs. 1–3)

Neotype.—CAS 253073 (field no. RCB 0374), adult male, São Tomé and Príncipe, São Tomé, Caxão Grande, 0.29687°N, 6.70376°E, 141 elevation; collected by Rayna C. Bell, Quintino Cabral Quade, and Andrew Stanbridge on 5 May 2013.

Description of neotype.—Habitus moderately slender; head length less than width; snout short, obtusely pointed in dorsal view, round in profile; nostrils lateral, closer to tip of snout than eye, visible in dorsal view; canthus rostralis distinct, slightly constricted behind nostrils; lores concave, oblique; eye diameter less than snout length; interorbital distance greater than width of upper eyelid; pineal body not visible; tympanum indistinct, round, half of eye diameter; tympanic annulus raised relative to tympanum, visible on anterior and ventral margin; vomerine teeth absent; tongue heart-shaped, notched.

Tips of all four fingers expanded with circummarginal grooves; width of Finger III disc \sim 1.9 times width of phalanx; relative finger lengths I < II < IV < III; metacarpal, palmar and thenar tubercles absent; subarticular tubercles on Fingers I–IV round, distal tubercle on Finger IV bifid; finger webbing formula I 2 – 2 II 2 – 3 II 2 – 1 IV; ulnar tubercle absent.

Tips of all five toes expanded; width of Toe IV disc ~ 1.7 times width of phalanx; relative toe lengths I < II < III < V < IV; outer metatarsal tubercle ill-defined, inner metatarsal tubercle distinct, ovoid; plantar surfaces smooth; well-developed subarticular tubercles on toes, round; toe webbing formula I 1 – 1 II $\frac{1}{2}$ – 1 III 0 – 1 IV 1 – 0 V.

Skin on dorsum finely granular; skin on limbs smooth; skin on ventral surface smooth, increasingly granular posteriorly; dorsolateral fold absent; fine dorsal asperities.

Nuptial pad absent; elongated vocal sac openings, located on either side of the floor of the mouth; vocal sac median; small, rounded gular gland occupies less than half of gular area.

Coloration in preservative.—Dorsum brown; side of head, dorsal surface of forelimb and hindlimb brown; dorsal surface of thigh cream with black speckling and thin brown medial band with black contour extending from dorsum to lower limb; ventral surfaces cream; dorsal asperities dark.

Coloration in life.—Iris gold; dorsum green, dorsal surface of forelimb and hindlimb green; dorsal surface of thigh red with thin yellow medial band with black contour extending from dorsum to lower limb; side of head green; dorsal surface of fingers and toes translucent and with green/red/yellow wash; ventral surfaces translucent, chest white with red/orange blotch, feet and thighs with red wash; dorsal asperities black.

Hyperolius thomensis Bocage, 1886 (Table 1; Figs. 1–3)

Neotype.—CAS 251637 (field no. RCB 0295), adult male, São Tomé and Príncipe, São Tomé, trail from Bom Sucesso Radio Tower, 0.27568°N, 6.60412°E, 1326 m elevation; collected by Rayna C. Bell and Andrew Stanbridge on 17 April 2012.

Description of neotype.—Habitus moderately slender; head length less than width; snout short, obtusely pointed in dorsal view, round in profile; nostrils lateral, closer to tip of snout than eye, visible in dorsal view; canthus rostralis distinct, slightly constricted behind nostrils; lores concave, oblique; eye diameter less than snout length; interorbital distance greater than width of upper eyelid; pineal body not visible; tympanum indistinct, round, less than half of eye diameter; vomerine teeth absent; tongue heart-shaped, notched.

Tips of all four fingers expanded with circummarginal grooves; width of Finger III disc ~ 1.8 times width of phalanx; relative finger lengths I < II < IV < III; metacarpal tubercle small and ovoid, thenar tubercle well developed; subarticular tubercles on Fingers I–IV, round, distal tubercle on Finger IV bifid; finger webbing formula I 1 – 1 II $\frac{1}{2}$ – 1 $\frac{1}{2}$ II 1 – $\frac{1}{2}$ IV; ulnar tubercle absent.

Tips of all five toes expanded; width of Toe IV disc ~ 1.7 times width of phalanx; relative toe lengths I < II < III < V < IV; outer metatarsal tubercle round, inner metatarsal tubercle distinct, ovoid; plantar surfaces smooth; well-developed subarticular tubercles on toes, round; toe webbing formula I $\frac{1}{2}$ – 1 II 0 – 1 III 0 – 1 IV 1 – 0 V.

Skin on dorsum finely granular; skin on dorsal side of limbs granular; skin on ventral surface coarsely granular, smooth on chest and ventral sides of limbs; dorsolateral fold absent; fine dorsal asperities.

Nuptial pad absent; elongated vocal sac openings, located on either side of the floor of the mouth; vocal sac median; small, rounded gular gland occupies less than half of gular area

Coloration in preservative.—Dorsum, side of head, dorsal surface of forelimb and hindlimb brownish grey; dorsal surface of thigh cream with black blotches and thin brown medial band with thick black contour extending from dorsum to lower limb; ventral surfaces cream with black blotches; dorsal asperities dark.

Coloration in life.—Iris gold; dorsum dark green/brown, dorsal surface of forelimb and hindlimb green; dorsal surface of thigh marbled black/orange with thin green medial band with thick black contour extending from dorsum to lower limb; side of head green; dorsal surface of fingers and toes orange; ventral surfaces orange with large black blotches, chest white with orange wash and black blotches; dorsal asperities black.

DISCUSSION

Among São Tomé and Príncipe's endemic vertebrates, reed frogs are thought to be one of the only lineages that diversified within a single island and also dispersed between islands in the archipelago (Jones 1994; Bell et al. 2015b). Previous work indicates that *H. molleri* and *H. drewesi* represent evolutionarily distinct lineages, as they do not share mtDNA haplotypes and form entirely distinct genetic demes in a Bayesian clustering analysis of genome-wide single nucleotide polymorphisms (Bell et al. 2015b). Divergence between *H. molleri* and *H. drewesi* was previously estimated at ~1,100,00–270,000 yr ago (Bell et

al. 2015a), indicating that although dispersal between São Tomé and Príncipe occurred at least once in the history of this endemic radiation, there is no evidence of regular dispersal between the islands. Furthermore, although the islands are only separated by $\sim\!150$ km, none of the six other endemic amphibians that occur on Príncipe or São Tomé have successfully dispersed between the islands, providing further indication that such dispersal events are uncommon for amphibians.

Despite the relatively recent divergence between H. molleri and H. drewesi, the species differ in coloration, which is consistent with the seemingly rapid evolution of color differences within the H. cinnamomeoventris species complex (Schick et al. 2010) and across the genus Hyperolius (Schiøtz 1999). Sexual dichromatism, which is common in Hyperolius (Bell and Zamudio 2012), also appears to have been acquired and lost repeatedly across the genus (Veith et al. 2009), including at least two reversals to monochromatism within the H. cinnamomeoventris complex (Schick et al. 2010). Juvenile coloration in H. molleri and H. drewesi resembles the juvenile coloration in H. cinnamomeoventris (phase juvenile), which is retained in adult males of H. cinnamomeoventris and in both adult sexes of H. veithi (Schick et al. 2010). In contrast, the adult coloration of H. molleri and H. drewesi resembles the mature female coloration of H. cinnamomeoventris (phase female), which is absent in *H. veithi*. Finally, *H. thomensis* exhibit dramatic orange and black ventral coloration that has not been described in any members of the H. cinnamomeoventris species complex. Thus, extensive phenotypic variation within this recent radiation indicates that the \tilde{H} . cinnamomeoventris group is well suited for studying the heritability of coloration phenotypes and for investigating the evolutionary and ecological contexts underlying sexual dichromatism.

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RESUMO: Eu descrevo uma espécie nova de rã (Hyperoliidae: Hyperolius) da ilha de Príncipe, no arquipélago do Golfo da Guiné. A espécie nova está dentro do complexo de espécies H. cinnamomeoventris, a qual inclui quatro espécies descritas: H. cinnamomeoventris, H. veithi, H. thomensis, e H. molleri. Esta espécie nova é sexualmente monocromática (machos e fêmeas possuem coloração dorsal verde) e se distingue de H. cinnamomeoventris, a qual é sexualmente dicromática, e de H. veithi, ambos machos e fêmeas são marrom pálidos com linhas dorsolaterais amarelas. A espécie nova é menor em tamanho do que H. thomensis, difere em coloração de H. thomensis e H. molleri pela ausência do contorno preto ao longo das bordas da banda verde / amarela de

coloração que se estende atrás da coxa, devido a ausência da coloração vermelha / laranja nos lados dorsais e ventrais da coxa, e nos genes mitocondriais 16S e cytochrome-b. Além disso, o trabalho anterior indica que a espécie nova se distingue de *H. molleri* e *H. thomensis* em uma análise dos genes nucleares. Esta espécie nova é o terceiro anfíbio endêmico descrito desta pequena ilha oceânica. Os materiais originais das espécies mais próximas, *H. molleri* e *H. thomensis*, foram destruídos; portanto, eu designei materiais neótipo para estas duas espécies permitindo a descrição da espécie nova.

LITERATURE CITED

Almaça, C., and A. Neves. 1987. The Museu Bocage and the new series of its Arquivos. Arquivos do Museu Bocage, Nova Série 1:1–8.

Bedriaga, J.v. 1892. Notes sur les amphibiens et reptiles recueillis par M. Adolphe F. Moller aux îles de la Guinée. O Instituto Coimbra, Series 2, 39:642-648

Bell, R.C., and K.R. Zamudio. 2012. Sexual dichromatism in frogs: Natural selection, sexual selection and unexpected diversity. Proceedings of the Royal Society of London, B Biological Sciences 279:4687–4693.

Bell, R.C., R.C. Drewes, A. Channing, V. Gvozdik, J. Kielgast, S. Loetters, B.L. Stuart, and K.R. Zamudio. 2015a. Overseas dispersal of *Hyperolius* reed frogs from Central Africa to the oceanic islands of Sao Tome and Principe. Journal of Biogeography 42:65–75.

Bell, R.C., R.C. Drewes, and K.R. Zamudio. 2015b. Reed frog diversification in the Gulf of Guinea: Overseas dispersal, the progression rule, and in situ speciation. Evolution 69:904–915.

Bocage, J.V.B. 1866. Reptiles nouveaux ou peu connus recueillis dans les possessions portugaises de l'Afrique occidentale, qui se trouvent au Muséum de Lisbonne. Journal de Sciências, Mathemáticas, Physicas e Naturaes. Academia Real das Sciencias de Lisboa 1:57–78.

Bocage, J.V.B. 1886. 2. Reptiles et batraciens nouveaux de l'île de St. Thomé. Journal de Sciências, Mathemáticas, Physicas e Naturaes. Academia Real das Sciencias de Lisboa 11:71–75.

Drewes, R.C., and R. Stoelting. 2004. The California Academy of Sciences Gulf of Guinea Expedition (2001) II. Additions and corrections to our knowledge of the endemic amphibians of São Tomé and Príncipe. Proceedings of the California Academy of Sciences 55:573–587.

Drewes, R.C., and J.A. Wilkinson. 2004. The California Academy of Sciences Gulf of Guinea expedition (2001) I. The taxonomic status of the genus *Nesionixalus* Perret, 1976 (Anura: Hyperoliidae), treefrogs of São Tomé and Príncipe, with comments on the genus *Hyperolius*. Proceedings of the California Academy of Sciences 55:395–407.

Jones, P.J. 1994. Biodiversity in the Gulf of Guinea: An overview. Biodiversity and Conservation 3:772–784.

Measey, G.J., M. Vences, R.C. Drewes, Y. Chiari, M. Melo, and B. Bourles. 2007. Freshwater paths across the ocean: Molecular phylogeny of the frog Ptychadena newtoni gives insights into amphibian colonization of oceanic islands. Journal of Biogeography 34:7–20.

Myers, C.W., and W.E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado and other tree frog records and geographical notes from western Panama. American Museum Novitates 2752:1–32.

Rapp, W.v. 1842. Neue Batrachier. Archiv für Naturgeschichte 8:289–291.
Schick, S., J. Kielgast, D. Rödder, V. Muchai, M. Burger, and S. Lötters.
2010. New species of reed frog from the Congo basin with discussion of paraphyly in Cinnamon-belly reed frogs. Zootaxa 2501:23–36.

Schiøtz, A. 1999. Treefrogs of Africa. Edition Chimaira, Germany.

Uyeda, J.C., R.C. Drewes, and B.M. Zimkus. 2007. The California Academy of Sciences Gulf of Guinea Expeditions (2001, 2006): A new species of *Phrynobatrachus* from the Gulf of Guinea Islands and a reanalysis of *Phrynobatrachus dispar* and *P. feae* (Anura: Phrynobatrachidae). Proceedings of the California Academy of Sciences 58:367–385.

Veith, M., J. Kosuch, M.-O. Rödel, A. Hillers, A. Schmitz, M. Burger, and S. Lötters. 2009. Multiple evolution of sexual dichromatism in African reed frogs. Molecular Phylogenetics and Evolution 51:388–393.

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Appendix

Specimens Examined

 $\begin{array}{c} \textbf{Hyperolius molleri.} \\ -\text{S\bar{a}o$ Tom\'e and Pr\'incipe: S\bar{a}o Tom\'e CAS 218850-} \\ 60, 218862-75, 218877-91, 218974, 218976-93, 219010-26, 219048-50, \\ 219054-59, 219068-69, 233464-68, 233703, 251579-82, 251584-88, \\ 251593-604, 251606-609, 251613-619, 251622-634, 252818, 252821, \end{array}$

 $\begin{array}{l} 253055-72 \ (158 \ \text{adult males}); \ \text{CAS} \ 218848-49, \ 218861, \ 218876, \ 218975, \\ 233463, \ 251583, \ 251589-90, \ 251610, \ 252819 \ (11 \ \text{adult females}); \ \text{CAS} \\ 218839-42, \ 219047, \ 233705, \ 253074 \ (7 \ \text{juveniles}). \\ \hline \textit{Hyperolius thomensis.} \quad \text{São} \ \text{Tom\'e} \ \text{ and } \ \text{Pr\'incipe: } \ \text{São} \ \text{Tom\'e} \ \text{CAS} \\ \end{array}$

Hyperolius thomensis.—São Tomé and Príncipe: São Tomé CAS 218926–37, 233470–72, 233475, 251635–36 (17 adult males); CAS 218925, 218934, 233473, 233474, 251605 (five adult females); CAS 233476 (one iuvenile).

Queries for herp-72-04-06

- 1. Author: This article has been lightly edited for grammar, style, and usage. Please compare it with your original document and make corrections on these pages. Please limit your corrections to substantive changes that affect meaning. If no change is required in response to a question, please write "OK as set" in the margin. Copy editor
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