



<http://dx.doi.org/10.11646/zootaxa.3620.3.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:03B8D237-7C7D-4E79-A020-4305ACF119B7>

Taxonomy of the super-cryptic *Hyperolius nasutus* group of long reed frogs of Africa (Anura: Hyperoliidae), with descriptions of six new species

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Table of contents

Abstract	302
Introduction	302
Material and methods	303
Results	306
Taxonomy	310
<i>Hyperolius acuticeps</i> Ahl, 1931	310
<i>Hyperolius adspersus</i> Peters, 1877	314
<i>Hyperolius benguellensis</i> (Bocage, 1893)	317
<i>Hyperolius dartavellei</i> Laurent, 1943	319
<i>Hyperolius friedemanni</i> sp. nov. Mercurio & Rödel	320
<i>Hyperolius howelli</i> sp. nov. Du Preez & Channing	322
<i>Hyperolius igbettensis</i> Schiøtz, 1963	324
<i>Hyperolius inyangae</i> sp. nov. Channing	326
<i>Hyperolius jacobseni</i> sp. nov. Channing	327
<i>Hyperolius lamottei</i> Laurent, 1958	329
<i>Hyperolius lupiroensis</i> sp. nov. Channing	330
<i>Hyperolius nasicus</i> Laurent, 1943	333
<i>Hyperolius nasutus</i> Günther, 1865	334
<i>Hyperolius poweri</i> Loveridge, 1938	335
<i>Hyperolius rwandae</i> sp. nov. Dehling, Sinsch, Rödel & Channing	337
<i>Hyperolius viridis</i> Schiøtz, 1975	339
Incertae sedis	341
Species distribution model	341
Discussion	341
Acknowledgements	343
References	343

Abstract

Specimens from across the range of the *Hyperolius nasutus* species group were sequenced for two mitochondrial genes and one nuclear gene. Advertisement calls were recorded from the same specimens where possible, and morphological characters were compared. Bayesian inference and maximum likelihood produced a tree indicating 16 clades. The clades show little or no overlap in combinations of 16S sequence difference, shared *tyr* haplotypes, advertisement call parameters, snout profiles and webbing. On the basis of these data we recognise *H. acuticeps*, *H. adspersus*, *H. benguellensis*, *H. dartevellei*, *H. igbettensis*, *H. nasutus*, *H. nasicus*, *H. poweri*, *H. viridis* and describe six new species: *Hyperolius friedemanni* sp. nov. Mercurio & Rödel, *Hyperolius howelli* sp. nov. Du Preez & Channing, *Hyperolius inyangae* sp. nov. Channing, *Hyperolius jacobsoni* sp. nov. Channing, *Hyperolius rwandae* sp. nov. Dehling, Sinsch, Rödel & Channing, and *Hyperolius lupiroensis* sp. nov. Channing. *Hyperolius lamottei* is confirmed to be outside the *H. nasutus* group clade. *Hyperolius granulatus*, *H. oxyrhynchus*, *H. punctulatus* and *H. sagitta* are assigned as junior synonyms. As our results are based on a small number of specimens, these hypotheses await testing with larger sample sizes and more characters. A species distribution model suggests where outlier populations might be found.

Key words: *Hyperolius nasutus* group, new species, phylogeny, taxonomy, advertisement calls, biogeography, molecular genetics, morphology, species distribution model

Introduction

African reed frogs in the genus *Hyperolius* Rapp, 1842 are highly speciose, with 128 species currently recognised (Frost 2011). Many of them are brightly patterned and polymorphic (Schiøtz 1975, 1999), but all are poor in external diagnostic morphological characters, making it difficult to identify preserved material. Many of the original descriptions are not diagnostic which makes it difficult to assign names reliably. The advent of sound analysis that had become popular from the 1960s allowed the use of this non-morphological technique to identify *Hyperolius* species in the field (Schiøtz 1975, Köhler *et al.* 2005a, Dehling 2012). More recent phylogenetic studies have used DNA to help delimit *Hyperolius* species (Rödel *et al.* 2010, Schick *et al.* 2010, Conradie *et al.* 2012, Dehling 2012), and to even identify cryptic genera (Rödel *et al.* 2009). These studies are examples of an approach that has led to a huge increase in the number of amphibian species recognised worldwide (Köhler *et al.* 2005b). Mercurio (2011) provides illustrations and calls of some cryptic *Hyperolius* species.

Within *Hyperolius*, there are a number of proposed species groups (Schiøtz 1975). One of these, the long reed frogs in the *Hyperolius nasutus* group is widespread in sub-Saharan Africa. Recent molecular work revealed that these frogs are basal in a clade of some *Hyperolius* species (Rödel *et al.* 2009, Veith *et al.* 2009). Within this group many species have been described, and currently 15 species names are available (Amiet 2005). Channing *et al.* (2002) recognised three different advertisement call types across the range of the complex, and suggested that these represented three species (*H. nasutus*, *H. acuticeps*, *H. viridis*), with others regarded as *incertae sedis* as no calls were known for them. They proposed *H. lamottei* to be a junior synonym of *H. nasutus*, on the basis of a similar advertisement call. In addition they confirmed *H. viridis* as valid, based on calls and material from near Sumbawanga in Tanzania.

Schiøtz & Van Daele (2003) identified two species in north-western Zambia, using advertisement calls, which they referred to *H. nasutus* and *H. benguellensis*, in contrast to Channing *et al.* (2002) who had assigned two call types from the same locality to *H. acuticeps* and *H. nasutus*.

In Cameroon, two species were recognised by Amiet (2005), *H. adspersus* and *H. igbettensis*, which he distinguished using morphological features such as the snout shape and differences in webbing. There were also two species tentatively recognised in central Democratic Republic of Congo (hereafter DRC) (Schiøtz 2006a), *H. adspersus* and *H. nasicus* with a sharp snout tip.

Recently, Schiøtz (2006b) reviewed the state of the taxonomy of the group. He noted that the various characters used to separate the species often delimited different sets of specimens. His main conclusions were that *H. lamottei* was not part of the *H. nasutus* group, based on consistent call and colour pattern differences. He showed that the specimens that Channing *et al.* (2002) collected near Sumbawanga in Tanzania and identified as *H. viridis* (based on advertisement call), were actually not 'true' *H. viridis*, but other members of the *H. nasutus* group.

In the molecular hyperoliid phylogeny of Veith *et al.* (2009), having a limited sample size of long reed frogs at hand, three well supported lineages (of one specimen each) were evident, which the authors referred to as *H.*

acuticeps (Kenya) and *H. nasutus* complex A (Ivory Coast) and B (Namibia). In a tree based on mitochondrial (mt) and nuclear markers, the single representative of long reed frog (*H. nasutus* complex B) appeared as a sister taxon to *Morerella*, which could neither be confirmed nor rejected by Rödel *et al.* (2009). As only 25% of *Hyperolius* species were included in their analysis, the position of the *Hyperolius nasutus* clade is not yet confirmed.

The IUCN recognises eight species in the group (IUCN 2011): *Hyperolius acuticeps* Ahl, 1931 (type locality Konde-Nyika, = Poroto Mts, Tanzania) extending from northern coastal South Africa to Ethiopia, including much of Mozambique, Zimbabwe, Zambia, Malawi, Tanzania, south-eastern DRC, Burundi, Rwanda, Kenya, Uganda and south-eastern Sudan (Amiet 2006b); *Hyperolius adpersus* Peters, 1877 (type locality Chinchoxo, Cabinda, Angola) distributed from central Cameroon south to the Congo River (Schiøtz 2006b); *Hyperolius benguellensis* (Bocage, 1893) (type locality Caota, Angola) overlaps both *H. nasutus* and *H. acuticeps* in Angola, Zambia, Zimbabwe, northern Mozambique and south-eastern DRC (Schiøtz & Poynton 2008); *Hyperolius igbettensis* Schiøtz, 1963 (type locality Igbetti, Nigeria) distributed from the savannas of the Ivory Coast east to central Cameroon (Schiøtz *et al.* 2008a); *Hyperolius lamottei* Laurent, 1958 (type locality Mt Nimba area) known from Ivory Coast to southern Senegal (Rödel & Schiøtz 2004); *Hyperolius nasicus* Laurent, 1943 (type locality Kasiki, DRC) only known from the type material, (Schiøtz 2006b); *Hyperolius nasutus* Günther, 1865 “1864” (type locality Calandula, Angola) covering Angola but extending north into the Congo Basin, east into western Zambia and south into northern Namibia and the Okavango Swamps of Botswana (Amiet 2006a); *Hyperolius viridis* Schiøtz, 1975 (type locality near Sumbawanga, Tanzania) from a restricted area in Tanzania, possibly extending into adjacent countries (Schiøtz 2006b).

The current debate has raised a number of questions. In the framework of a taxonomic review, we attempt to answer them, based largely on molecular data. These include: Is *H. lamottei* a distinct species? Is *H. lamottei* part of the *H. nasutus* clade? Can the species outlined above be confirmed using molecular data? Are the disputed species assignments of Channing *et al.* (2002) resolved? Are there unrecognised cryptic species?

The confusion due to colour polymorphism and the paucity of calls and DNA sequences from material referable to types has considerably muddied the waters of this ubiquitous species complex. Where two or more species of the group may be sympatric, it is essential to record calls and take tissue samples from the same voucher specimen. This molecular project was initiated to provide a testable hypothesis of species boundaries and provide a framework for future studies, as more data become available.

Material and methods

Approach. We use the accepted species assemblage that makes up the *Hyperolius nasutus* group (IUCN 2011, Schiøtz 1999). Our approach was to sequence fragments of two mitochondrial genes (12S, 16S) and to use the sequence information to identify potential species. A phylogeny was constructed and we included genetic distances calculated for the 16S fragment. In amphibians, this is a widely accepted marker in DNA bar-coding (e.g. Vences *et al.* 2005). We also sequenced 40 specimens for the nuclear gene Tyrosinase exon 1, separated into the most likely haplotype phases as explained below. Once the species boundaries were hypothesised, the sequenced specimens were examined for advertisement calls and morphological characters that are elsewhere considered useful to recognize long reed frog taxa, such as snout shape and general body proportions (see Amiet 2005). The discovered clades were then compared to the type descriptions and the type specimens, in order to match the available names to the suggested species clades as defined by the molecular study.

Specimens for which only a single gene sequence, for example 12S, was available, were not included in the initial clade recognition. They were subsequently assigned to the discovered clades based on close sequence similarity.

Advertisement calls, most recorded from the same specimens that were sequenced, were analysed (see below). These specimens provide a positive link between gene sequence, morphology and advertisement call, as proposed by Channing *et al.* (2002).

Sampling. Tissue samples were obtained from field-collected specimens and preserved in 95% ethanol. Usually more than one specimen per locality was sampled. All available GenBank (<http://www.ncbi.nlm.nih.gov/>) 12S and 16S sequence pairs from the group were checked and incorporated, and unpublished sequences were kindly made available by A. van der Meijden and M. Vences. Samples for which sequence data are available were

collected from Angola, Botswana, Central African Republic, DRC, Congo-Brazzaville, Gabon, Ghana, Guinea, Ivory Coast, Kenya, Malawi, Mozambique, Namibia, Rwanda, South Africa, Sierra Leone, Tanzania, Zambia and Zimbabwe. The outgroup (*Hyperolius angolensis*) was represented by a specimen from Humpata, Angola (PEM A10106), GenBank accession number JQ513623. Additional specimens and/or tissues were generously provided by the United States National Museum, Washington (USNM), Museum of Comparative Zoology, Harvard (MCZ), Copenhagen Natural History Museum (ZMUC), the South African Institute of Aquatic Biodiversity, Grahamstown (SAIAB), E. Netherlands (EN), J. Harvey (JH) and N. Jacobsen (NJ).

Type material was examined from the Natural History Museum, London (NHM), the Museum für Naturkunde, Berlin (ZMB) and the Royal Museum for Central Africa, Tervuren (RMCA). Photographs of the type of *Hyperolius poweri* were made available by the MCZ. Call recordings were made available through the courtesy of ZMUC, NJ and Colin Tilbury. Voucher specimens collected as part of this project have been deposited at ZMB, Port Elizabeth Museum (PEM), National Museums of Kenya, Nairobi (NMK) and SAIAB. Field numbers include LdP (L. Du Preez), AC (A. Channing), LOM and MTN (A. Hillers).

Morphology. These small frogs have few useful features for diagnosing species. The snout shapes have been used, but these show a surprising range of variation (Amiet 2005). Snout shape in lateral view can be rounded, angular or angular with a protruding tip. Poynton (1964:193) illustrates the need to understand variation and the difficulty of using morphological characters to separate species in this group. A detailed discussion was presented in Poynton & Broadley (1987).

We used the following characters and abbreviations which have been used in previous work (Poynton 1964, Schiøtz 1975, Amiet 2005, Dehling 2012): snout-urostyle-length (SUL, from tip of snout to posterior end of urostyle); tibiofibula-length (TFL, measured by both knee and tibio-tarsal articulation flexed); total leg length (LEG, from vent to tip of fourth toe with leg fully extended at right angle to body axis); foot length (FOT, from proximal end of inner metatarsal tubercle to tip of fourth toe); hand length (HND, from proximal end of thenar tubercle to tip of third finger); head width (HW, measured at corners of the mouth); head length (HL, from posterior end of mandible to tip of snout); eye diameter (ED, horizontal diameter of the eye); eye-to-nostril distance (EN, from anterior edge of orbit to centre of nostril); nostril-snout distance (NS, from centre of nostril to tip of snout); internarial distance (NN, distance between centres of nostril); snout length (SL, from anterior edge of orbit to tip of snout); eye distance (EE, distance between anterior edges of eyes); interorbital distance (IO, shortest distance between upper eyelids); upper eyelid width (EW, maximum width of upper eyelid); length of thigh (THL). All measurements are given in mm. Webbing was illustrated using a diagram, following Biju *et al.* (2011); snout shape was described; and the dorsal pattern elements were noted.

Advertisement call. Calls were recorded in the field, and analysed using RavenPro 1.4 with the following settings: Hann type spectrogram, with a DFT size of 128, and a 50% time grid overlap.

DNA extraction and sequencing: Tissues were digested using standard Proteinase-K protocol, and DNA was extracted using phenol-chloroform (Hillis *et al.* 1996). A 550 bp fragment of the mt 16S gene was amplified using the primers 16SaR-F and 16SbR-R of Kocher *et al.* (1989), as modified by Bossuyt & Milinkovitch (2000) annealing at 51°C, and a 450 bp fragment of the mt 12S gene using the primers 12SA-F and 12SB-R (Goebel *et al.* 1999), annealing at 56°C. A 530 bp fragment of the nuclear tyrosinase exon 1 (Bossuyt & Milinkovitch 2000) annealing at 55°C, was sequenced for one or more representatives of each species. We used Fast Taq readymix (Kapa Biosystems) for PCR, using the manufacturer's recommended protocol; an initial denaturing step of 1 minute at 95°C, followed by 35 cycles of denaturing for 10 seconds at 95°C, annealing for 10 seconds, extension for 1 second at 72°C. There is no final extension step. Primer sequences are given in Table 1.

TABLE 1. Primer sequences used in this study.

Name and source	Sequence (5' to 3')
12SA-F (Goebel <i>et al.</i> 1999)	AAACTGGGATTAGATACCCCACTAT
12SB-R (Goebel <i>et al.</i> 1999)	GAGGGTGACGGGCGGTGTGT
16SaR-F (Bossuyt & Milinkovitch 2000)	CGCCTGTTTAYCAAAAACAT
16SbR-R (Bossuyt & Milinkovitch 2000)	CCGGTYTGAACCTCAGATCAYGT
TyrC-F (Bossuyt & Milinkovitch 2000)	GGCAGAGGAWCRTGCCAAGATGT
TyrG-R (Bossuyt & Milinkovitch 2000)	TGCTGGCRTCTCTCCARTCCCA

Sequencing reactions and electrophoresis were carried out by the University of Stellenbosch Central Analytical Facility. Forward and reverse strands were sequenced for all samples. Both sequences were checked against the chromatograms, trimmed, and combined into a single contig for each fragment using Sequencher 5.1 (GeneCodes Corporation). All mt and nuclear sequences were checked using BLAST to confirm their placement in the ingroup (<http://blast.ncbi.nlm.nih.gov/>). All new sequences were deposited in GenBank (Benson *et al.* 2012). Appendix 1 is a gazetteer of the collection localities. The nuclear *tyr* gene was phased into the most likely two haplotypes for each individual by first submitting the edited sequences including IUPAC polymorphism symbols, to SeqPhase step 1 (Flot 2010) an online service that prepares a simplified output file. The output from SeqPhase is then used as input to PHASE (Stephens & Donnelly 2003), which computes the likelihood of possible haplotypes. The output from PHASE is converted to full sequences through SeqPhase step 2.

Molecular analysis. Sequences were trimmed and concatenated using Sequencher 5.1, then aligned using Clustal W2 (2.0.12) with default settings. JModelTest was used to determine the appropriate model of evolution under AIC. The aligned sequences were input into MrBayes 3.2.1, and run for 10 million generations, with three attempted swaps each iteration, with the temperature set at 0.1, and using the GTR + G + I model. Two independent runs were analysed, each with one hot and three cold chains. The data were partitioned into three separate gene fragments (12S, 16S and *tyr*), and each partition was treated independently. The default burn-in value of 25% was used. A second analysis only using all available 16S sequence data was analysed in a similar manner.

Maximum likelihood (ML) models were analysed using Garli 2.0. Bootstrap support was determined using 1000 bootstrap repetitions each with three search repetitions. Uncorrected 16S sequence divergence was determined using PAUP*.

A haplotype network was constructed for the *tyr* sequences, using TCS 1.21 (Clement *et al.* 2000) that implements statistical parsimony to estimate gene genealogies (Templeton *et al.* 1992).

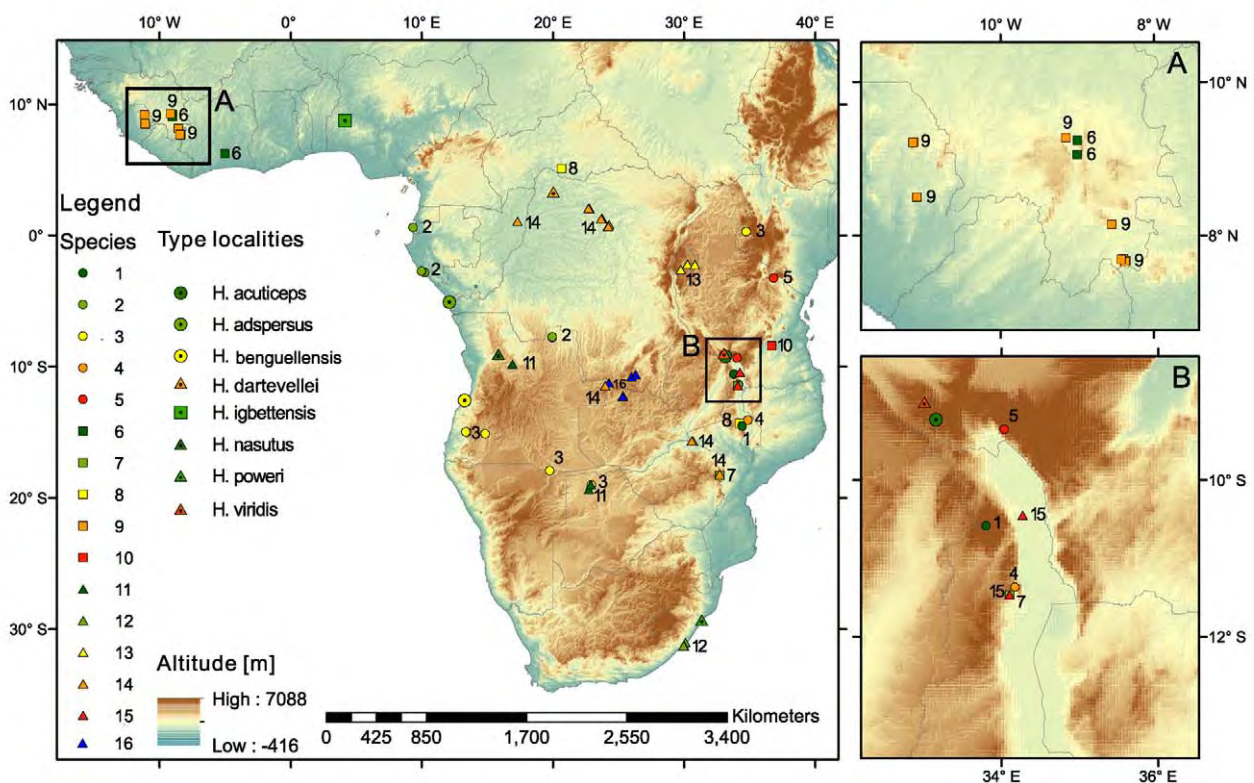


FIGURE 1. Map showing the distribution of the sequenced specimens of recognised species in the *Hyperolius nasutus* group plus *H. lamottei*. Species numbers represent the following: 1—*H. acuticeps*, 2—*H. adpersus*, 3—*H. benguellensis*, 4—*H. friedemanni* sp. nov., 5—*H. howelli* sp. nov., 6—*H. igbettensis*, 7—*H. inyangae* sp. nov., 8—*H. jacobseni* sp. nov., 9—*H. lamottei*, 10—*H. lupiroensis* sp. nov., 11—*H. nasutus*, 12—*H. poweri*, 13—*H. rwandae* sp. nov., 14—*H. dartevellei*, 15—*H. viridis*, 16—*H. nasicus*.

Species distribution modelling. The potential distribution of the whole *nasutus* group was assessed within a GIS-based analysis using the CRAN-R package 'dismo' (version 07.17; Hijmans *et al.* 2012). We obtained information on long-term climatic conditions within sub-Saharan Africa from the Worldclim database as interpolated average conditions within the time period 1950–2000 (Hijmans *et al.* 2005). Nineteen bioclimatic variables (Nix 1986) at all available records of long reed frog localities were extracted and a BIOCLIM (Nix 1986) model was computed. This model describes the environmental space occupied by all available species records of the group shown in Figure 1.

Results

The available genetic material and specimens are listed under the relevant species below. Most tissue samples were accompanied by voucher specimens, while a few were not vouchered, although these were usually duplicates of voucher specimens, which had been toe-clipped in the field and released. The DNA sequences are accessioned in GenBank, (JQ863547–JQ863780; KC409065–KC409087). The 131 samples resolve into 16 terminal groups in a phylogeny based on 16S sequences. The arrangement is congruent with a smaller set of 87 specimens using both 12S and 16S sequences. Table 2 shows the minimum and maximum uncorrected *p* distance values for 16S and summarises all the differences between the species pairs.

A real difficulty faced us in determining the species names that should be applied to the recognised clades (discussed below). The original descriptions are largely undiagnostic, but we adopted the pragmatic approach to best link existing names to the clades we recognize as species. Frost (2011) presents details of older synonymies, which are not repeated here. We assign the clades within the *H. nasutus* group to the following 16 species: *H. acuticeps*, *H. adspersus*, *H. benguellensis*, *H. friedemanni* **sp. nov.**, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus*, *H. nasicus*, *H. poweri*, *H. rwandae* **sp. nov.**, *H. dartevellei* and *H. viridis*. *Hyperolius lamottei* makes up the 16th species.

The phylogenetic analysis including the nuclear gene in addition to the two mitochondrial genes using Bayesian Inference showed an average standard deviation of split frequencies of 0.0032 after 10 million generations. At this point all parameters reported a potential scale reduction factor of 1.000, indicating that the two runs had converged. The tree topology is congruent for both Bayesian Inference and Maximum Likelihood. The Bayesian tree based on the 16S sequences (Fig. 2) is displayed with terminal substructure collapsed. Many of the clades show polytomies, which we interpret as evidence of a recent radiation, when read with the uncorrected *p* distances which vary from 1.4 to 14.4 across the group (Table 2). Although an uncorrected *p* distance of 3% or more is regarded as indicating a species-level difference (eg Fourquet *et al.* 2007), the present study shows that individuals of many species pairs can fall both below and above the 3% mark, such as *H. acuticeps/H. dartevellei* (2.3–3.5); *H. adspersus/H. howelli* (1.6–3.3); *H. nasicus/H. poweri* (2.7–3.1). The species pairs with low differences show differences in other characters.

The species were recognised by combinations of unique advertisement calls and mitochondrial haplotypes supported by morphological differences. A haplotype network for the nuclear gene *tyr*, is shown in Fig. 3. The heterozygosity *H* is 0.6 for the group, with a sample of 40 individuals across the species, with 47 *tyr* haplotypes. Two haplotypes are shared across the hypothesised species boundaries (one includes *H. rwandae* and *H. howelli*; and the other *H. acuticeps*, *H. friedemanni*, *H. dartevellei* and *H. howelli*).

Taxonomy should not be based on sequence differences alone (Moritz & Cicero 2004), although in the *H. nasutus* group there are few morphological characters that can support taxonomic decisions.

Although the sample size is too small for any statistical support, there is little inter-species difference in traditional body proportions such as TFL/SUL or HW/SUL. Although these values are not statistically relevant here, they do indicate potentially useful proportions to investigate with larger sample sizes.

The major elements of the dorsal pattern include pale lateral stripes, pale paravertebral stripes, and a dark mid-dorsal line. The pale stripes may have a dark border. The pale stripes are sometimes formed by an absence of dark spots, and sometimes by a very white pigment that remains even after preservation. The dorsum may be speckled or stippled to various degrees. Pale lateral stripes are common in males, with spotted patterns common in females. However, stripes or spots may be found in both sexes. The results of the morphological study are included with the relevant species below, and the measurements are summarised in Appendix 2.

TABLE 2. Summary of the differences between the species, in the form: 16S/tyr/call/snout/webbing. For 16S the range of differences is given; 'tyr' indicates that no tyrosine exon 1 haplotypes are shared, but is absent where a haplotype is shared; no overlap in advertisement call parameters is indicated by D (duration), P1 (only phase 1 present in one of the pair), PIN (number of pulses in phase 1), P2N (number of pulses in phase 2), P1R (pulse rate of phase 1), P2R (pulse rate of phase 2); difference in snout profile is indicated by SP; difference in webbing is indicated by W.

Abbreviations: Ac—H. acuticeps, Ad—H. adspersus, Be—H. benguelensis, Da—H. dartevellei, Fr—H. friedemanni **sp. nov.**, Ho—H. howelli **sp. nov.**, Ig—H. igbettensis, In—H. inyangae **sp. nov.**, Ja—H. jacobsoni **sp. nov.**, Lu—H. lupitensis **sp. nov.**, La—H. lamottei, Na—H. nasutus, Ni—H. nasicus, Po—H. poweri, Rv—H. rwandae **sp. nov.**, Vi—H. viridis.

	Ac	Ad	Be	Da	Fr	Ilo	Ig	In	Ja	La	Lu	Na	Ni	Po	Rv
Ad	16S: 2.1–2.9/tyr/D, P1/SP/W														
Be	16S: 6.0–6.2/tyr/P2 R/ SP/ W	16S: 4.2–4.8/tyr/D, P1/ SP/ W													
Da	16S: 2.3–3.5//P1/ SP/ W	16S: 1.4–2.5//P1/ PIN// W	16S: 3.9–4.8/tyr/D, P1, P1R/ SP/ W												
Fr	16S: 2.5–3.5//D, P2R/ SP/ W	16S: 1.4–2.5//tyr/D, P1, P1R/ SP/ W	16S: 4.8–5.1/tyr/D, P2R/ SP/ W	16S: 1.5–2.5//D, P1, P1R/ SP/ W											
Ho	16S: 2.7–4.1//D, P1R, P2R// W	16S: 1.6–3.3/tyr/D, P1, P1R/ SP/ W	16S: 5.2–5.4/tyr/D, P2N/ SP/ W	16S: 1.2–2.7//D, P1, P1R/ SP/ W	16S: 1.6–2.7//P1R, P2R/ SP/ W										
Ig	16S: 5.2–5.8// D, P1R, P2R/ SP/ W	16S: 3.5–4.6/tyr/D, P1, P1R/ SP/ W	16S: 6.0–6.2/tyr/D, P1R, P2N/ SP/ W	16S: 3.9–5.2//D, P1, P1R/ SP/ W	16S: 4.6–5.0//P1R/ SP/ W	16S: 4.3–5.6//P1R, P2R/ SP/ W									
In	16S: 4.5–5.2/tyr// SP/ W	16S: 3.3–4.2/tyr/D, P1, P1R/ SP/ W	16S: 4.0–4.8/tyr/D, P2N/ SP/ W	16S: 3.5–4.7/tyr/D, P1, P1R/ SP/ W	16S: 3.9–4.4/tyr/D, PIN, P2R/ SP/ W	16S: 4.3–5.4/tyr/P1 N, P2N/ SP/ W	16S: 5.6–6.4/tyr/P1 N, P2R/ SP/ W								

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TABLE 2. (Continued)

Ac	Ad	Bc	Da	Fr	Ho	Ig	In	Ja	La	Lu	Na	Ni	Po	Rw
Ja	16S: 3.1–3.7/tyr/D, P1, P1R/ SP/W	16S: 5.4/tyr/D, P1, P1R/ SP/W	16S: 2.7–3.5/tyr/D, P1R/ SP/W	16S: 2.7–3.1/tyr/D, P1, P1R/ SP/W	16S: 3.1–3.7/tyr/D, P1, P1R/ W	16S: 4.6/tyr/P1, P1R/W	16S: 5.0–5.2/tyr/D, P1, P1R/ SP/W							
La	16S: 13.1–14.4/tyr/D, P1, P1R/ SP/W	16S: 14.2–14.8/tyr/D, P1, P1R/ SP/W	16S: 10.9–13.4/tyr/D, P1N/ SP/W	16S: 13.3–14.0/tyr/D, P1, P1R/ W	16S: 13.8–15.0/tyr/D, P1, P1R/ SP//	16S: 13.4–14.0/tyr/D, P1, P1R/ SP/W	16S: 13.1–15.1/tyr/D, P1, P1R/ SP/W	16S: 14.5–15.1/tyr/P1 N, P1R/ SP/W						
Lu	16S: 12.0–12.2/tyr/D, P1, P1R/ SP/W	16S: 11.4–11.7/tyr/D, P1, P1R/ SP/W	16S: 10.9–11.6/tyr/ SP/W	16S: 11.1–11.6/tyr/D, P1, P1R/ SP/W	16S: 12.0–12.8/tyr/D, P1R/ SP/ W	16S: 13.5/tyr/D, P1, P1R/ W	16S: 11.9–12.0/tyr/D, P1, P1R/ SP/W	16S: 13.6–14.0/tyr/ SP/W						
Na	16S: 2.5–2.8/tyr/D, P2R/ SP/ W	16S: 4.1–4.6/tyr/D, P2R/ SP/ W	16S: 1.2–2.5/tyr/D, P1, P1R/ SP/W	16S: 1.6–2.5/tyr/D, P2R/ SP/ W	16S: 2.0–3.1/tyr/P2 R/ SP/W	16S: 4.4–5.2/tyr/P2 R/ SP/ W	16S: 3.3–4.3/tyr/P1 N, P2R/ SP/W	16S: 2.7–3.1/tyr/D, P1, P1R/ SP/W	16S: 11.8–12.0/tyr/D, P1, P1R/ SP/W					
Ni	16S: 2.7–3.3/tyr/D, P1, P1R/ SP//	16S: 4.0–4.4/tyr/D, P1/ SP/W	16S: 1.8–3.1/tyr/D, P1R/ SP/ W	16S: 2.1–2.7/tyr/D, P1, P1R/ SP/W	16S: 2.5–4.1/tyr/D, P1, P1R/ SP/ W	16S: 4.5–4.8/tyr/P1, P1R/ SP/ W	16S: 3.9–5.2/tyr/D, P1, P1N/ SP/W	16S: 1.5–2.3/tyr/P1, P1R/ SP/ W	16S: 11.2–12.0/tyr/D, P1R/ SP/ W					
Po	16S: 2.9–3.1/tyr/D, P1R, P2R/ W	16S: 2.1–2.9/tyr/D, P1, P1R/ SP/W	16S: 2.7–3.5/tyr/D, P1, P1R/ SP/W	16S: 2.3–2.7/tyr/P1 R, P2R/ SP/W	16S: 3.0–4.1/tyr/P1 N// W	16S: 4.4–4.6/tyr/D, P1R// W	16S: 4.8–5.0/tyr/D, P2R/ SP/ W	16S: 2.7–3.1/tyr/P1, P1N/ SP/ W	16S: 14.0–14.6/tyr/D, P1, P1R/ SP/W					
Rw	16S: 2.7–3.3/tyr/D, P2R/ SP/ W	16S: 1.6–2.1/tyr/D, P1, P1R/ SP/W	16S: 1.8–2.7/tyr/D, P1, P1R/ SP//	16S: 2.3–2.7/tyr/P2 R/ SP/W	16S: 2.7–3.7/tyr/P1 R// W	16S: 4.1–4.3/tyr/P1 R, P2R/ SP/W	16S: 4.1–4.5/tyr/P1 N, P2N/ SP/W	16S: 1.9–2.3/tyr/P1, R/ SP/W	16S: 13.4–14.0/tyr/D, P1, P1R/ SP/W				16S: 1.9–2.7/tyr/P1 R/ SP/W	
Vi	16S: 6.8–7.2/tyr/D, P1R, P2R/ SP/W	16S: 6.6–7.0/tyr/D, P1/ W	16S: 5.8–6.8/tyr/D, P1R/ SP/ W	16S: 6.4–6.8/tyr/D, P2R/ SP/ W	16S: 7.0–8.0/tyr/D, P1R, P2R/ SP/W	16S: 8.5–8.7/tyr/D, P1R, P2R/ SP//	16S: 6.7–7.0/tyr/D, P1R, P2R/ SP/W	16S: 6.6–7.1/tyr/D, P1R, P2R/ SP/W	16S: 14.4–15.1/tyr/D, P1, P1R/ SP/W				16S: 6.8–7.2/tyr/D, P1, P1R/ SP/W	16S: 6.6/tyr/D, P1R, P2R/ SP/W

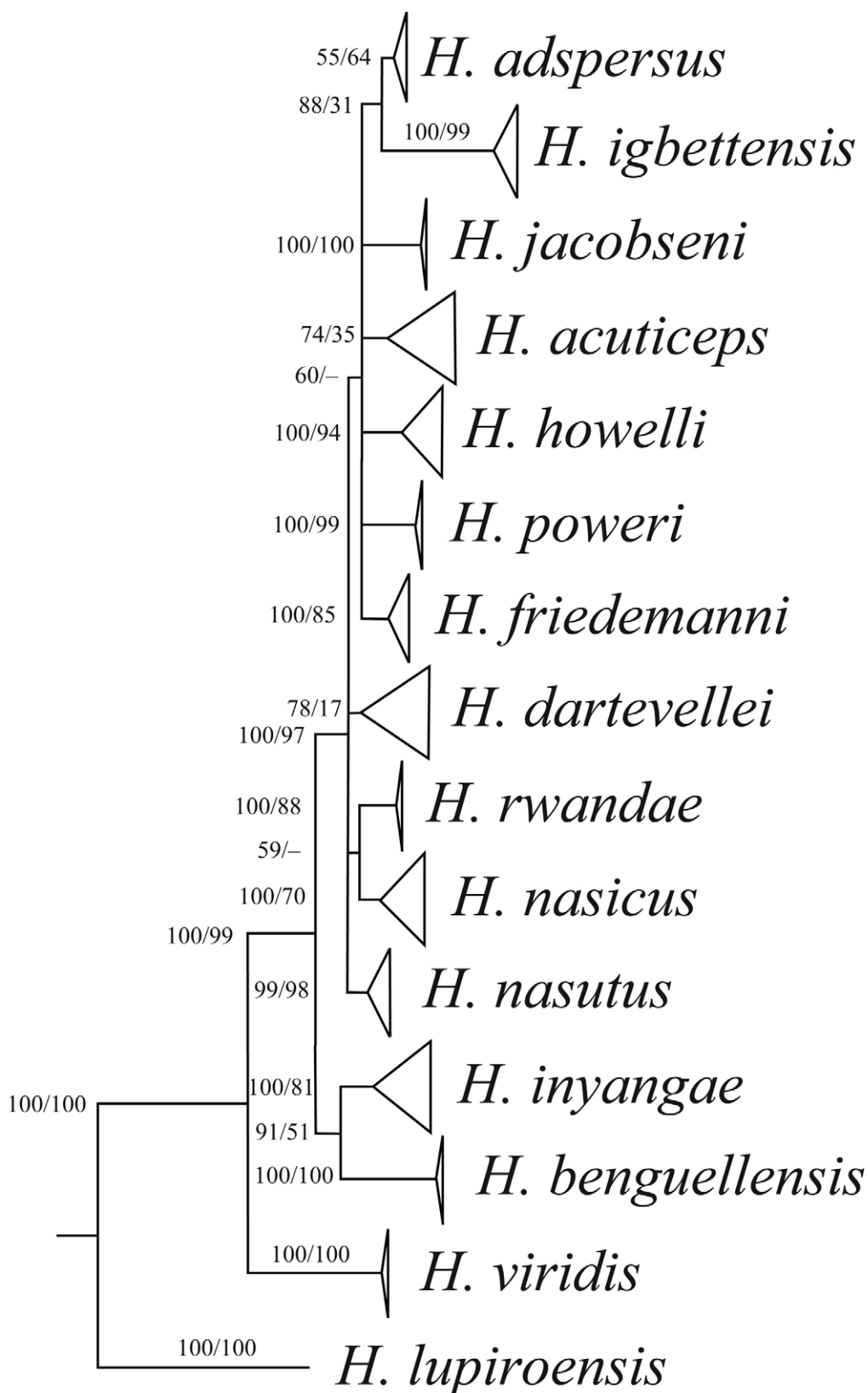


FIGURE 2. Phylogeny of the recognised species, based on 16S. Tree support is given as posterior probability/ML bootstrap. *Hyperolius lamottei* is basal to the group, and is not shown.

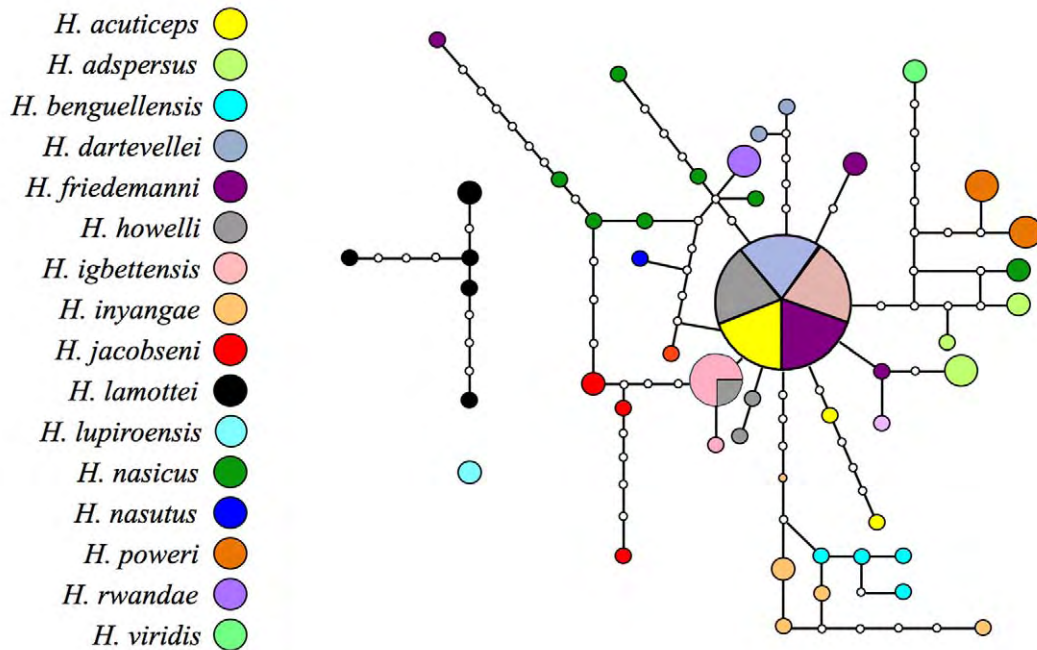


FIGURE 3. Haplotype network of the nuclear *tyr* gene. Each circle represents a unique haplotype. Species are indicated in colour, and hypothesised intermediates are shown as solid circles. The size of the circle indicates the number of individuals sharing the haplotype. One haplotype (large circle) is shared by individuals from five species, and a second is shared by two species. *Hyperolius lamottei* and *H. lupiroensis* haplotypes are more than nine changes different from the network.

Taxonomy

Hyperolius acuticeps Ahl, 1931

Sharp-headed Long Reed Frog
(Fig. 4)

Genetic material. MCZ A-137085–86 (Chelinda Camp, Nyika Plateau, Malawi); ZMB 76103, 76107, 76109 (Chongoni Forest Reserve, Malawi); ZMB 76097–98 (Kaningina Forest Reserve, Malawi) (Fig. 1).

Diagnosis. The illustrated advertisement call (Fig. 5) has a duration of 0.22 s,

consisting of 25 pulses, with a slower pulse rate at the end. This differs from the brief single notes of *H. adspersus*, *H. lupiroensis* **sp. nov.**, and the brief note consisting of a few initial pulses, followed by a number of pulses at a much slower pulse rate, such as *H. benguellensis*, *H. friedemanni* **sp. nov.**, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. rwandae* **sp. nov.**, *H. viridis* and *H. poweri*. The structure of the call of *H. jacobseni* **sp. nov.** and *H. nasutus* is similar to that of *H. acuticeps*, but the former consists of only five pulses with a duration of 0.07 s, while the latter consists of eight pulses in 0.1 s. The call of *H. dartavellei* consists of 13 pulses in 0.1 s. See Table 3 for a summary of call parameters. The snout is sharply rounded in profile and from above, differing from the truncated snout of *H. dartavellei* and the sharp, shark-like profile of *H. benguellensis*, *H. inyangae* **sp. nov.** or the bluntly rounded snout profile of *H. adspersus*, *H. igbettensis*, *H. jacobseni* **sp. nov.** and *H. poweri*. Although the webbing is variable, a typical specimen has one phalanx of the fifth toe free, while the fourth toe is webbed with half to just more than the first phalanx free, and the third toe likewise. It can be distinguished from species with less than one phalanx of the fifth toe free, such as *H. adspersus*, *H. friedemanni* **sp. nov.**, *H. igbettensis*, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*. It differs from those species with more than one phalanx free; *H. howelli* **sp. nov.** and *H. inyangae* **sp. nov.** It differs from *H. benguellensis* which has webbing on the third toe extending to the disc, from *H. nasutus* which has webbing on the fourth toe reaching the disc, and from *H. dartavellei* which has half a phalanx of the fourth toe free.

TABLE 3. Summary of advertisement calls. For each parameter the mean, (range) and sample size are given.

Species	Emphasised frequency (Hz)	Duration (s)	First phase length (s)	First phase number of pulses	First phase pulse rate (s ⁻¹)	Second phase length (s)	Second phase number of pulses	Second phase pulse rate (s ⁻¹)
<i>H. acuticeps</i>	4207 (3949–4443) n=7	0.354 (0.306–0.395) n=7	0.026 (0.025–0.028) n=7	5 (5–5) n=7	193 (179–200) n=7	0.329 (0.279–0.367) n=7	10 (9–11) n=7	30 (29–32) n=7
<i>H. adpersus</i>	4631 (4511–4692) n=3	0.037 (0.036–0.038) n=3	0.037 (0.036–0.038) n=3	15 (13–17) n=3	414 (351–447) n=3			
<i>H. benguelensis</i>	4211 (4148–4363) n=5	0.399 (0.372–0.422) n=5	0.038 (0.034–0.041) n=5	5.6 (5–7) n=5	147 (121–179) n=5	0.37 (0.336–0.420) n=5	12.8 (12–14) n=5	34 (33–35) n=5
<i>H. dartevillei</i>	4752 (4556–4907) n=4	0.052 (0.045–0.056) n=4	0.052 (0.045–0.056) n=4	19.5 (19–20) n=4	373 (351–422) n=4			
<i>H. friedemannii</i>	4497 (4381–4545) n=8	0.143 (0.104–0.156) n=8	0.042 (0.037–0.050) n=8	8.5 (7–10) n=8	202 (166–219) n=8	0.103 (0.064–0.116) n=8	6.3 (4–7) n=8	60 (57–62) n=8
<i>H. howelli</i>	4271 (4187–4331) n=6	0.161 (0.132–0.193) n=6	0.06 (0.05–0.07) n=6	9 (8–10) n=6	151 (142–160) n=6	0.102 (0.079–0.142) n=6	3.7 (3–5) n=6	36 (34–37) n=6
<i>sp. nov.</i>	4467 (4348–4616) n=7	0.142 (0.088–0.198) n=7	0.051 (0.039–0.063) n=7	12.4 (10–15) n=7	245 (233–260) n=7	0.092 (0.050–0.155) n=7	5.1 (3–8) n=7	57 (51–64) n=7
<i>H. igbettensis</i>	4064 (3846–4385) n=8	0.295 (0.177–0.332) n=8	0.026 (0.021–0.031) n=8	4.6 (4–6) n=8	138 (129–238) n=8	0.271 (0.168–0.309) n=8	8.8 (6–10) n=8	32 (29–35) n=8
<i>H. inyangae</i>	3640 (3538–3702) n=7	0.078 (0.067–0.089) n=7	0.078 (0.067–0.089) n=7	5.7 (5–7) n=7	73 (69–79) n=7			
<i>H. jacobsoni</i>	3545 (3500–3679) n=6	0.073 (0.068–0.077) n=6	0.073 (0.068–0.077) n=6	28.3 (28–29) n=6	388 (376–426) n=6			
<i>sp. nov.</i>	3693 (3529–3823) n=8	0.058 (0.040–0.072) n=8	0.058 (0.040–0.072) n=8	23.3 (17–30) n=8	401 (362–450) n=8			
<i>H. lupiroensis</i>	3508 (3430–3535) n=7	0.121 (0.086–0.217) n=7	0.121 (0.086–0.217) n=7	13.7 (10–22) n=7	116 (101–135) n=7			
<i>H. nasutus</i>	4484 (4213–4600) n=4	0.159 (0.145–0.179) n=4	0.054 (0.053–0.055) n=4	10 (8–13) n=4	186 (151–236) n=4	0.104 (0.086–0.124) n=4	5 (4–6) n=4	48 (46–49) n=4
<i>H. poweri</i>	4558 (4389–4860) n=6	0.137 (0.113–0.150) n=6	0.048 (0.039–0.071) n=6	6.7 (5–9) n=6	139 (113–159) n=6	0.088 (0.068–0.110) n=6	3.8 (3–5) n=6	43 (36–52) n=6
<i>H. rwandae</i>	4766 (4728–4846) n=7	0.137 (0.108–0.183) n=7	0.058 (0.050–0.071) n=7	12 (10–15) n=7	205 (181–232) n=7	0.079 (0.049–0.112) n=7	3 (2–4) n=7	38 (34–41) n=7
<i>sp. nov.</i>	3500	0.473	0.131	11	84	0.347	5	14.4
<i>H. viridis</i>								

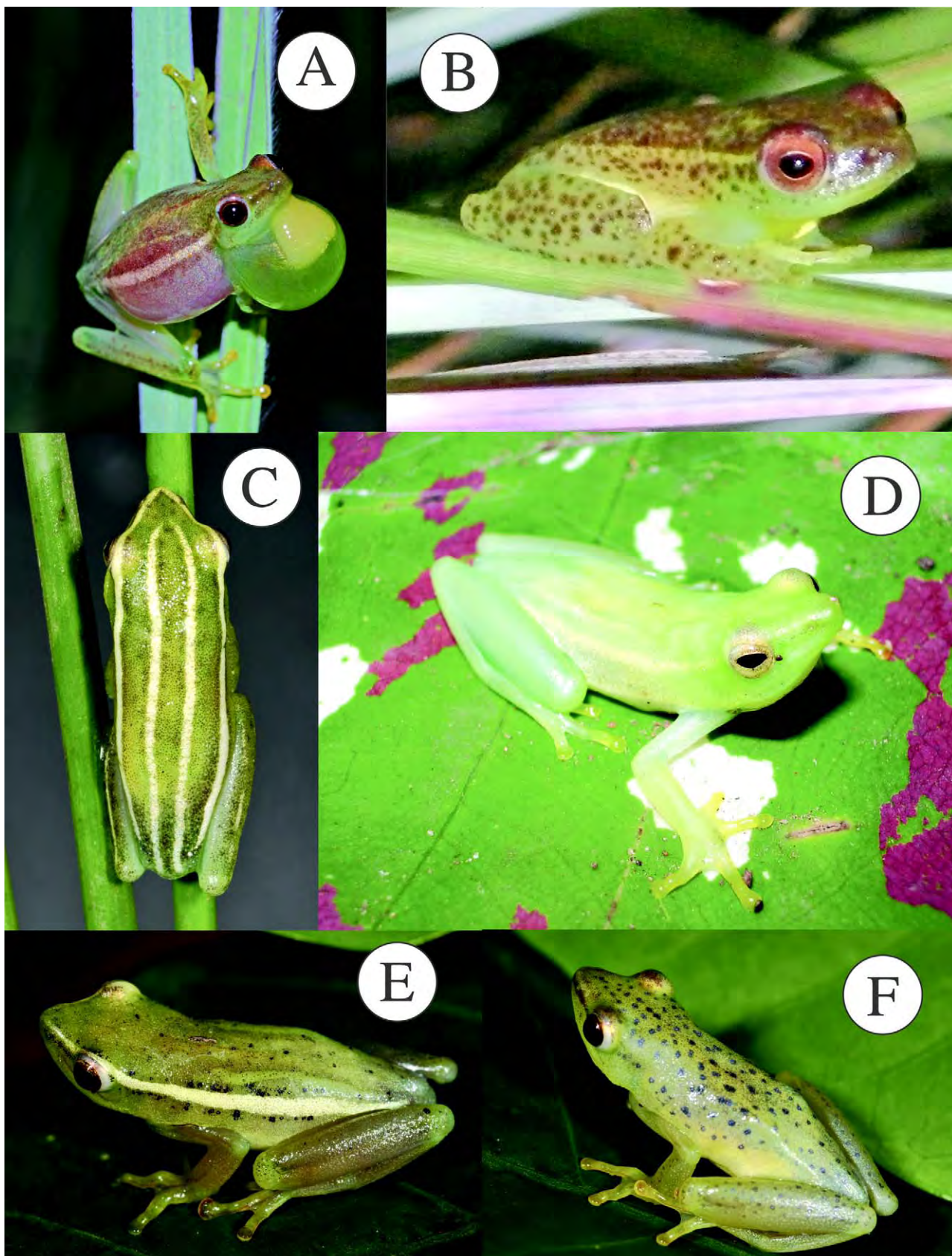


FIGURE 4. *Hyperolius acuticeps* Chongoni, Malawi, photo V. Mercurio (A); *H. adspersus* Bateka Nature Reserve, Gabon, photo G. Jongsma (B); *H. benguellensis*, Humpata, Angola, photo A. Channing (C); *H. friedemanni* **sp. nov.**, Karonga, Malawi, photo V. Mercurio (D); *H. howelli* **sp. nov.** holotype, SAIAB 118979, Arusha, Tanzania, photo A. Channing (E); *H. howelli* **sp. nov.** female paratype, SAIAB 118980-1, Arusha, Tanzania, photo A. Channing (F).

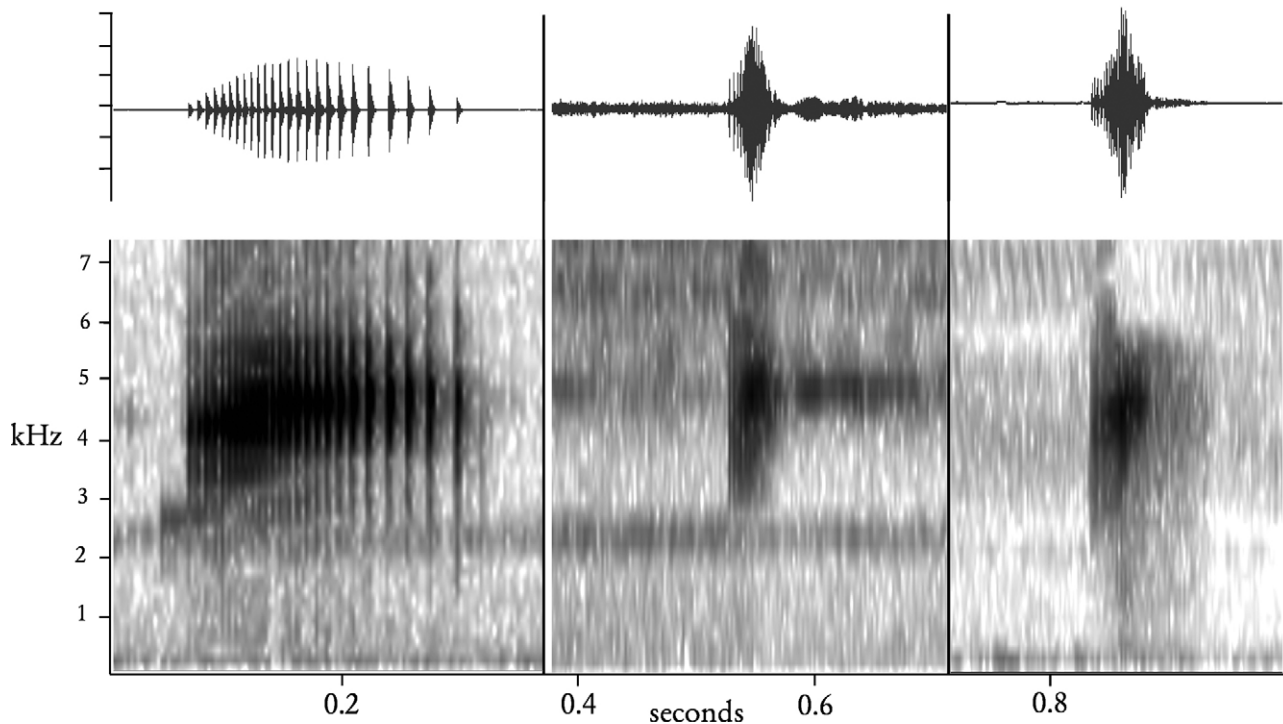


FIGURE 5. Advertisement calls of *H. acuticeps* Kaningina (left), *H. adspersus* Bateka Nature Reserve (center) and *H. dartvellei* Carumbo (right).

Description of a *Chelinda* specimen. This description is based on a female MCZ A-137085 from Chelinda on Nyika Plateau. Body long and slender, widest at temporal region, slightly tapering to groin; head comparatively small (HL/SUL 0.33, HW/SUL 0.30), not wider than trunk, longer than wide (HL/HW 1.10) although slightly wider than long in specimen MCZ A-137086; snout long (SL/HL 0.43), pointed in dorsal view, acute in profile (Fig. 6), considerably projecting beyond lower jaw, wider than long (SL/EE 0.72); canthus rostralis distinct, rounded, slightly concave from eye to nostril, concave near tip of snout; loreal region almost vertical, slightly concave; nostril directed laterally; situated much closer to tip of snout than to eye (EN/NS 1.43), separated from each other by distance less than distance between eye and nostril (NN/EN 0.9); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.26); eye diameter shorter than snout (ED/SL 0.61); interorbital distance as wide as upper eyelid (IO/EW 1.0), and greater than internarial distance (IO/NN 1.67); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 4.8, and wide (3.7 at widest point), free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent.

Dorsal surfaces of head, trunk and limbs smooth; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolated.

Fore limbs slender; hand moderately large (HND/SUL 0.27); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand II-2III1-2.5III2-1IV (after Myers & Duellman [1982]); thenar tubercle indistinct, low; palmar tubercles absent; inner metacarpal tubercle small, rounded, outer metacarpal tubercle absent.

Hind limbs slender, moderately long (LEG/SUL 1.45); tibio-tarsal articulation reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.49), longer than thigh (TFL/THL 1.07); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.82); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) I1.5-2II1-2III1-2IV2-1.5V; inner metatarsal tubercle small, oval, prominent; outer one

larger, almost circular, low and almost indistinct. Measurements of a second specimen from Chelinda MCZ A-137086 are included in Appendix 2.

Colouration in preservative. The pattern elements that remain after the green has faded are a dark vertebral stripe made up of a single row of chromatophores, with pale lateral bands bordered by irregular dark spots, and a row of dark chromatophores forming a dorsolateral stripe. A male is illustrated in Fig. 4.

Eggs and tadpoles. Unknown.

Distribution. This species is presently only confirmed from northern Malawi on the Nyika Plateau and Chongoni and Kaningina Forest Reserves, and the type locality in southern Tanzania.

Remarks. This study restricts the distribution of the species from the wide range presently attributed to it (Schiøtz *et al.* 2004), suggesting that its conservation status should be changed from Least Concern to Data Deficient, pending the collection of more data.

Hyperolius adpersus Peters, 1877

Sprinkled Long Reed Frog

(Fig. 4)

Synonymy. *Hyperolius granulatus* (Boulenger, 1901).

Genetic material. USNM 578140, 578144, 578166 (Plain of Vera, 15 km south east of Gamba, Gabon); USNM 578157 (Uemba Road, 2 km south of Gamba, Gabon); USNM 578142 (Setecama Road, 3 km west of Gamba, Gabon); USNM 578165 (National Forestry School, Gabon) (Fig. 1). Specimens examined as above, including the type (ZMB 917).

Diagnosis. The advertisement call consists of a brief note, duration 0.04 s, and indistinguishable pulses (Fig. 5). It can be distinguished from the call consisting of a brief note comprising a few initial pulses, followed by a number of pulses at a much slower pulse rate, such as *H. benguellensis*, *H. friedemanni* **sp. nov.**, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. rwandae* **sp. nov.**, *H. viridis* and *H. poweri*. It differs from the longer calls consisting of a number of pulses at a more or less constant rate, such as *H. acuticeps*, *H. jacobseni* **sp. nov.**, *H. nasutus*, *H. nasicus* and *H. dartevellei*. See Table 3 for a summary of call parameters. The snout is truncated to bluntly rounded, which differs from the sharp, shark-like profile of *H. benguellensis* and *H. inyangae* **sp. nov.**, and the sharply rounded snout profile of *H. acuticeps*, *H. friedemanni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus* and *H. rwandae* **sp. nov.** The fifth toe has about half a phalanx free of web. This distinguishes it from those species that have one or more phalanges of the fifth toe free, *H. benguellensis*, *H. howelli*, *H. inyangae*, *H. lamottei* and *H. nasicus*; and those with the fifth toe fully webbed, *H. friedemanni*, *H. jacobseni*, *H. lupiroensis* and *H. rwandae*. It has one phalanx free of webbing on the fourth toe, which distinguishes it from *H. dartevellei*, which has less than a phalanx free; nasutus which is webbed to the disc at least on one side; and *H. poweri* and *H. viridis* which have more than one phalanx free. It has no more than one phalanx free on the second toe, at least on one side, which distinguishes it from *H. igbettensis* which has more than one phalanx free of the second toe at least on one side.

Description of a specimen from Gamba, Gabon. An adult male USNM 578142 (measurements presented in Appendix 2) measuring 19.5 mm SUL; body long and slender, widest just behind orbital region, tapering to groin; head relatively small (HL/SUL 0.27, HW/SUL 0.33), wider than long (HL/HW 0.82); snout long (SL/HL 0.51, truncated in dorsal view (Fig. 6), just protruding just beyond lower jaw, wider than long (SL/EE 0.64); canthus rostralis rounded; loreal large and oval in shape; nostril directed laterally, elliptical slit, situated just behind the tip of the snout (EN/NS 1.60), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.19); eyes large (ED 2.0), directed anterolaterally, protruding outwards and forward, pupil is horizontal to circular, visible from below, eye diameter shorter than snout (ED/SL 0.74); interorbital distance much wider than upper eyelid (IO/EW 1.46), and equal to internarial distance (IO/NN 1.0); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae large, oval, vomer processes and teeth absent; tongue long and broad, mostly free except for first quarter, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular; large granular gular flap covering thin vocal sac (4.3 wide).

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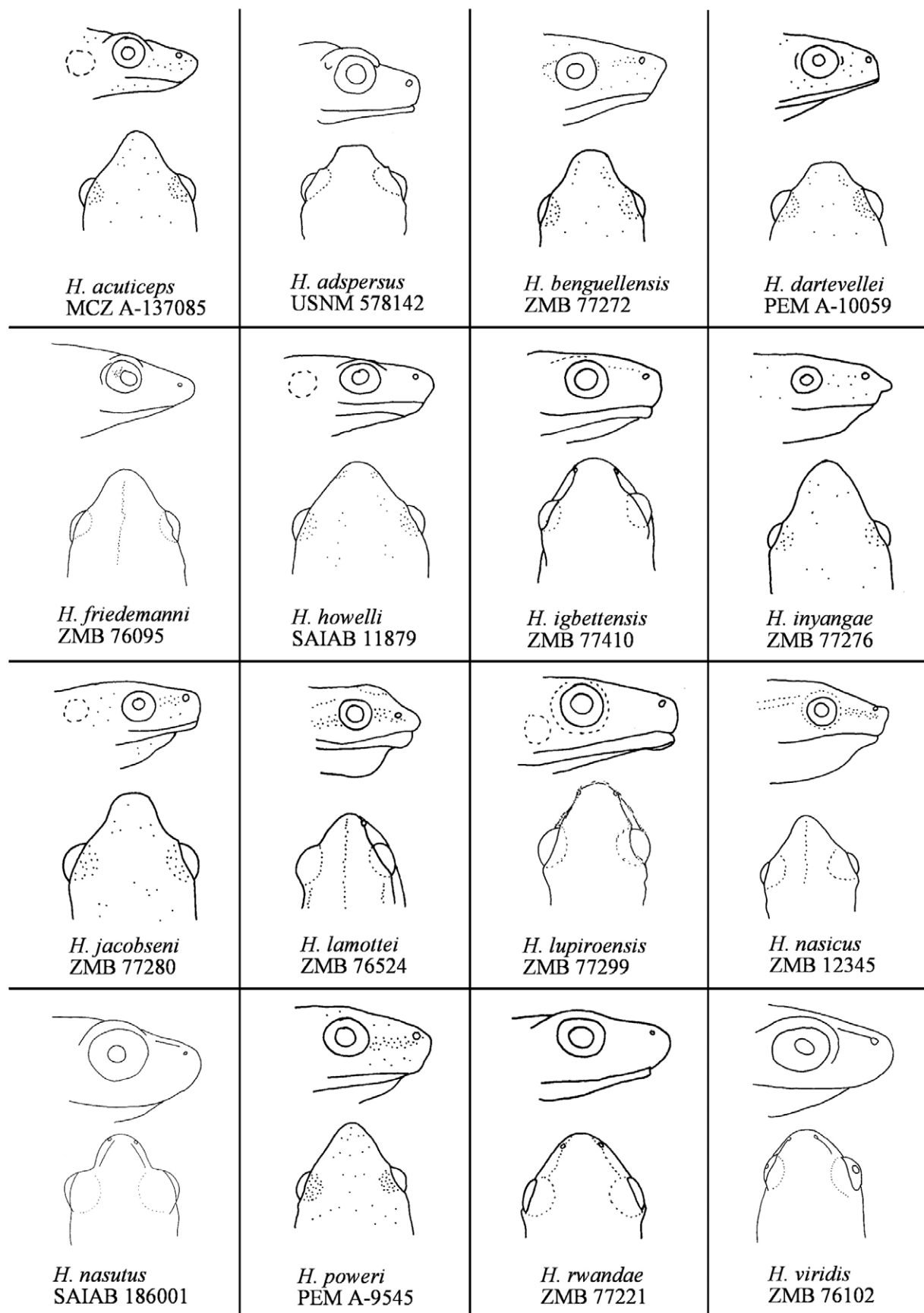


FIGURE 6. Snout profiles of representatives of the species in the *Hyperolius nasutus* group.

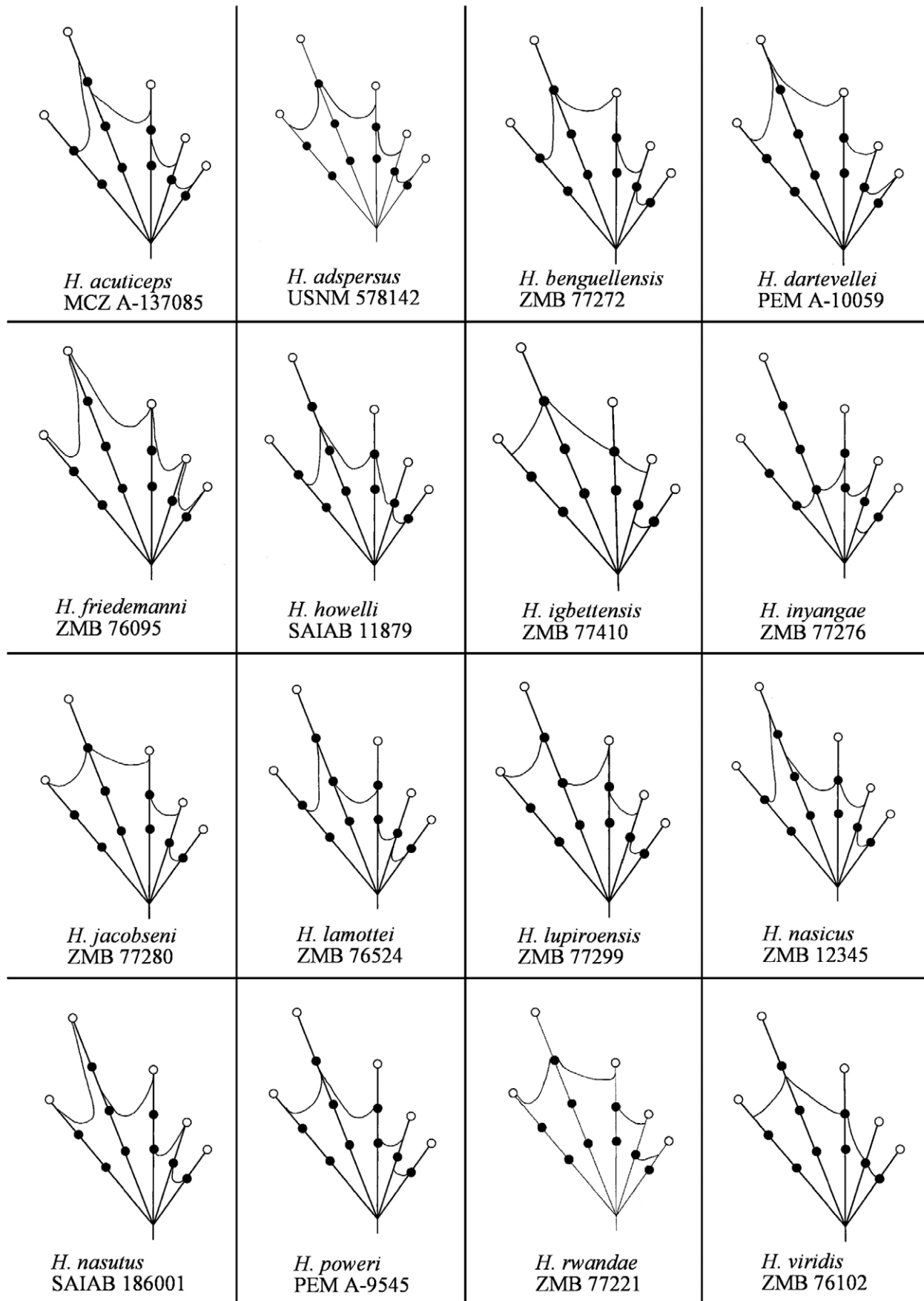


FIGURE 7. Webbing diagrams of representatives of the species in the *Hyperolius nasutus* group.

Dorsal surfaces of head, trunk and limbs generally appearing smooth but with many densely and more or less evenly scattered tiny, melanophores; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate; supratympanic fold absent.

Fore limbs slender; hand moderately large (HND/SUL 0.28); tips of fingers enlarged into broad oval disks, thin circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one per phalange; webbing formula of the hand $I2.5-2.5II2-2.25III2.25-2IV$; thenar tubercle indistinct; palmar tubercles absent.

Hind limbs slender, moderately long; tibiofibula moderately long (TFL/SUL 0.54), longer than thigh (TFL/THL 1.08); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.85); relative length of toes: I<II<III<V<IV; discs of toes similar in size to those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $I1-2II1-2III1-2IV2-1V$; inner metatarsal flat; outer metatarsal tubercle absent.

Colouration in life. No information, but see the photo (Fig. 4) of an unvouchered individual from the Bateka Nature Reserve, Gabon. **Colouration in preservative.** All colours have faded to a beige yellow with evenly spaced black dorsal melanophores.

Eggs and tadpoles. Unknown.

Habitat. Specimens were collected in grassland.

Distribution. Southern Cameroon, east and south through Gabon to the lower Congo Basin.

Remarks. The synonymy of *H. granulatus* (the holotype RMCA-152 was examined) is supported by the absence of dorso-lateral stripes and a short rounded snout. The species is presently only confirmed from northern Angola, the Cabinda enclave, and Gabon. There is little doubt that existing records refer to this species, and we suggest that its conservation status of Least Concern remains unchanged.

Hyperolius benguellensis (Bocage, 1893)

Benguella Long Reed Frog

(Fig. 4)

Synonym. *Hyperolius oxyrhynchus* (Boulenger, 1901)

Genetic material. ZMB 77271–2, ZMB 77318 (Humpata, Angola); ZMB 77273–4 (Bicuar National Park, Angola); ZMB 77275 (Zootecnica Plateau, Humpata, Angola); AACRG 1030 (Kaparotta, Botswana); GenBank AF215224, AF215442 (Rundu, Namibia) (Fig. 1).

Diagnosis. The advertisement call (Fig. 8) is a brief note consisting of five pulses, followed by 14 pulses at a slower rate, with a duration of 0.41 s. It can be distinguished from the brief calls consisting only of a single note, *H. adpersus* and *H. lupiroensis* **sp. nov.** and those consisting only of a series of pulses, *H. acuticeps*, *H. jacobseni* **sp. nov.**, *H. nasutus* and *H. dartevellei*. The other species with advertisement calls consisting of an initial note followed by some discrete pulses can be distinguished either by their short duration, less than 0.2 s, as in *H. friedemanni* **sp. nov.**, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. poweri* and *H. rwandae* **sp. nov.**, or by the lower number of slow pulses, less than 10, as in *H. inyangae* and *H. viridis*. See Table 3 for a summary of call parameters. The snout is shark-like in profile, protruding forward of the mouth in a straight line, before forming a sharp tip. It can be distinguished from the truncated, sharply- or bluntly rounded snout profiles as in *H. acuticeps*, *H. adpersus*, *H. friedemanni* **sp. nov.**, *H. igbettensis*, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus*, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*.

Description of a Humpata specimen. Body long and slender, widest at mid-body, slightly tapering to groin; head comparatively small (HL/SUL 0.33, HW/SUL 0.30), not wider than trunk, longer than wide (HL/HW 1.11); snout long (SL/HL 0.42), bluntly rounded in dorsal view, acute, sharklike in profile (Fig. 6), considerably projecting beyond lower jaw, wider than long (SL/EE 0.68); canthus rostralis distinct, moderately sharp, slightly concave from eye to just beyond nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 1.64), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.11); eyes directed

anterolaterally, moderately protruding, relatively small (ED/HL 0.33); eye diameter shorter than snout (ED/SL 0.78); interorbital distance much wider than upper eyelid (IO/EW 1.71), and greater than internarial distance (IO/NN 2.1); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth, vomer processes and teeth absent; tongue long 5.8, and narrow (2.7 at widest point), free for about three-fourths of length, bifurcated distally for about one-third of length; median lingual process absent; vocal sac single, median, subgular, mostly unpigmented and translucent when fully inflated; gular flap cream-coloured, granular; vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like, long, directed posterolaterally.

Dorsal surfaces of head, trunk and limbs smooth; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate.

Fore limbs slender; hand moderately large (HND/SUL 0.30); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand I2–2.5II2–3III2.5–2.5IV (after Myers & Duellman [1982]); thenar tubercle absent; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.55); tibio-tarsal articulation reaching to level of snout tip when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.53), shorter than thigh (TFL/THL 0.91); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.83); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) I1–III0.75–1III0–1IV1–1V; inner metatarsal tubercle small, oval, prominent; outer one low, almost indistinct.

Colouration in life. Skin more or less translucent. Dorsum and dorsal surface of head and limbs dark green (Fig 4); lateral sides of head and scapular region dark green; light, yellowish-white, moderately broad dorsolateral stripe running along each side of the body from snout tip, over the eye to vent; Pale paravertebral stripes originating on posterior of snout, diverging to level of eyes, and then running parallel to vent; small dark brown to black dots and on dorsum, most densely bordering both sides of dorsolateral stripes; distal portions of fingers and toes, especially the tips, yellow; ventral side and parts of dorsal side of thigh and upper arm largely unpigmented but with irregular dark spots, appearing bluish-green; peritoneum white, shining through the translucent belly skin. Iris reddish-brown. **Colouration in preservative.** All colours have faded to yellow; gular flap whitish-yellow.

Variation. The female ZMB 77271 is similar to the male in measurements (Appendix 2). The female is larger than the male (SUL 23.5). Colouration is variable; ZMB 77271 has a pale green dorsum with irregular darker marks, and yellow eyelids, with fingers and toes also yellow, and a white underside. AC 3073 has pale dorsolateral stripes on a dark green background.

Eggs and tadpoles. Unknown.

Habitat. We found the species only in open grassy habitats, along stream banks and man-made impoundments where sedges and other tall emergent vegetation were present (Humpata, Bicuar NP). Specimens were observed on leaves and stems of vegetation between 5 cm and 1.0 m above water level. Males called from elevated positions. The following species were found sympatrically or even syntopically with the new species: *Hyperolius marmoratus* and *Xenopus laevis*.

Remarks. The species is confirmed using molecular data from Rundu in the Caprivi Strip of Namibia, northern Botswana, and southern Angola.

The type locality of *H. benguellensis* is Caota, Angola. The type series (MBL 17.220-223; now Museu Bocage, National Museum of Natural History, University of Lisbon) has been destroyed (Frost 2011).

Our specimens agree with the original description of a sharp snout and small dorsal speckles. The specimens from Humpata show a range of colour patterns, from a uniform finely spotted dorsum, to pale dorsolateral stripes, to dorsolateral and paravertebral stripes. This variation was absent from the type description. The genetic material is from the same drainage basin as the type. *Hyperolius oxyrhynchus* is regarded as a synonym as the type description matches this species. The species is presently only confirmed from southern Angola, northern Namibia, and northern Botswana. We suggest that the conservation status Least Concern be maintained.

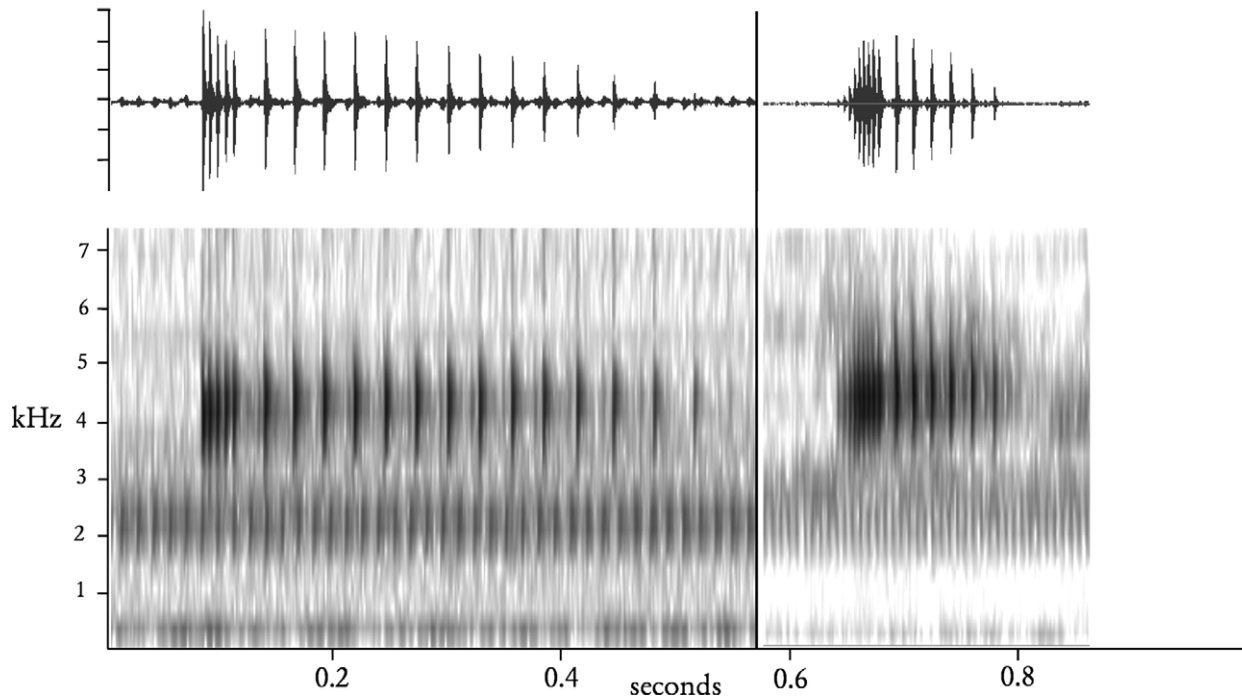


FIGURE 8. Advertisement calls of *H. benguellensis* Humpata (left) and *H. friedemanni* Karonga (right).

Hyperolius dartevellei Laurent, 1943

Dartevelle's Reed Frog

(Fig. 9)

Synonymy. *Hyperolius sagitta* Laurent, 1943

Genetic material. ZMB 77303 Ikelenge, Zambia; USNM 576167–70 (Impongui, Republic of Congo); field numbers A27, CRT 3577-9, 3604-6 (Congo River near Yekela, DRC); CRT 3730, 3798 (Congo River, near Nganda Kona, DRC); CRT 3838-9 (Congo River near Ngengele, DRC); CRT 3975–89 (Congo River near Bomani, DRC); CRT 4024, 4027 (Congo River, near Lulu, DRC); CRT 4205–10 (Congo River, near Lieki, DRC) (Fig. 1).

Diagnosis. A typical advertisement call (Fig. 5) consists of 13 pulses in 0.1 s, with an emphasised frequency of 4.8 kHz. It differs from those species with a brief note consisting of a few initial pulses, followed by a number of pulses at a much slower pulse rate, such as *H. benguellensis*, *H. friedemanni* **sp. nov.**, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. rwandae* **sp. nov.**, *H. viridis* and *H. poweri*, and those with a longer call consisting of multiple pulses that may change tempo, such as *H. acuticeps*, *H. jacobseni* **sp. nov.**, and *H. nasutus*. See Table 3 for a summary of call parameters. The advertisement call structure is similar to that of *H. adspersus* and *H. lupiroensis* **sp. nov.**, while the 16S sequence of *H. lupiroensis* **sp. nov.** differs by more than 11%.

The snout is truncated, distinguishing it from the species with shark-like or rounded snout profiles: *H. acuticeps*, *H. adspersus*, *H. benguellensis*, *H. friedemanni* **sp. nov.**, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus*, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*. The webbing shows a phalanx free on the first, third and fifth toes, with half a phalanx free on the other two. It can be distinguished from the species that have less than a phalanx of the fifth toe free: *H. adspersus*, *H. friedemanni* **sp. nov.**, *H. igbettensis*, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus*, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*. It differs from the species that have one phalanx or more of the fourth toe free of web: *H. acuticeps*, *H. benguellensis*, *H. howelli* **sp. nov.**, and *H. inyangae* **sp. nov.**

Description of a Carumbo specimen. An adult male PEM A 10059 (measurements presented in Appendix 2) measuring 18.6 mm SUL; body long and slender, widest just behind orbital region, tapering to groin; head relatively small (HL/SUL 0.32, HW/SUL 0.34), not much wider than long (HL/HW 0.95); snout long (SL/HL

0.46), bluntly pointed in dorsal view (Fig. 6), protruding just beyond lower jaw, wider than long (SL/EE 0.72); canthus rostralis distinct; loreal large and oval in shape; nostril directed dorsolaterally, moderately large vertical slit (0.4 mm in length), situated much closer to tip of snout than to eye (EN/NS 1.60), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.60); eyes large (ED 1.8), directed anterolaterally, protruding outwards and forward, pupil is horizontal to circular, visible from below, eye diameter shorter than snout (ED/SL 0.64); interorbital distance much wider than upper eyelid (IO/EW 1.50), and greater than internarial distance (IO/NN 1.41); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae large, oval, vomer processes and teeth absent; tongue long 3.9 and broad 2.8, mostly free except for first quarter, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular; large granular gular flap covering thin vocal sac (5.9 wide)

Dorsal surfaces of head, trunk and limbs generally appearing smooth but with many densely and more or less evenly scattered tiny, asperities; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate; supratympanic fold absent.

Fore limbs slender; hand moderately large (HND/SUL 0.26); tips of fingers enlarged into broad oval disks, no circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one per phalange; webbing formula of the hand $I1.5-0.25II0.25-0.25III0.25-0.25IV$ (after Myers & Duellman 1982) thenar tubercle indistinct; palmar tubercles absent.

Hind limbs slender, moderately long (LEG/SUL 1.50); tibio-tarsal articulation reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.52), longer than thigh (TFL/THL 1.07); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.77); relative length of toes: I<II<III<V<IV; discs of toes similar in size to those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $IO.25-1III0.25-1IIII0.25-1IV1-0.25V$; inner metatarsal absent; outer metatarsal tubercle large, almost circular, low and not distinct.

Colouration in life. Below translucent silvery-white, above uniform translucent green to brown, scattered darker spots, clear yellow-white dorsolateral line from snout to vent, forming a light canthus on the snout, darker pigmentation anterior-lateral from snout tip to above eye, upper jaw nearly free of any pigmentation, eye iris is yellow to brown; dorsal surface of arms and legs with scattered dark spots, inner thighs unmarked. **Colouration in preservative.** All colours have faded to a beige yellow with brown dorsal spots still visible.

Eggs and tadpoles. Unknown.

Habitat: Specimens were collected in the grassland floodplain wetlands surrounding a large natural lake (350 ha) at daytime. Specimens were found half a meter to a meter above water level on vegetation. The only other amphibians found were *Phrynobatrachus mababiensis*. Additional material was collected at a small pond (<0.5 ha) covered by tick marginal vegetation. Specimens were calling low down on the edge of the open water. Two other *Hyperolius* species were present in the same area, *Hyperolius angolensis* and *Hyperolius* cf. *cinereus*, both species were calling further away and higher up the vegetation. *Hoplobatrachus occipitalis* was present in the pond.

Distribution. Southern Cameroon, east and south through Gabon to the lower Congo Basin and the most northern parts of Angola, and the north-western Zambian highlands.

Remarks: The synonymy of *H. granulatus* (the holotype RMCA-152 was examined) is supported by the absence of dorso-lateral stripes and a short rounded snout. The species is presently only confirmed from northern Angola, the Cabinda enclave, and Gabon. There is little doubt that existing records refer to this species, and we suggest that its conservation status of Least Concern remains unchanged.

***Hyperolius friedemanni* sp. nov. Mercurio & Rödel**

Friedemann's Long Reed Frog (Fig. 4)

Holotype. SMF 85694 (tissue VM11), an adult male, collected at Karonga, Malawi, 7 February 2007 by V. Mercurio, 9°55'59.6" S, 33°56'44.6" N, 472 m a.s.l.

Paratypes. ZMB 76095 (tissue VM12), an adult female, with the same details as the holotype; SAIAB 186000, two juvenile specimens (Monkey Bay, Malawi) (Fig. 1).

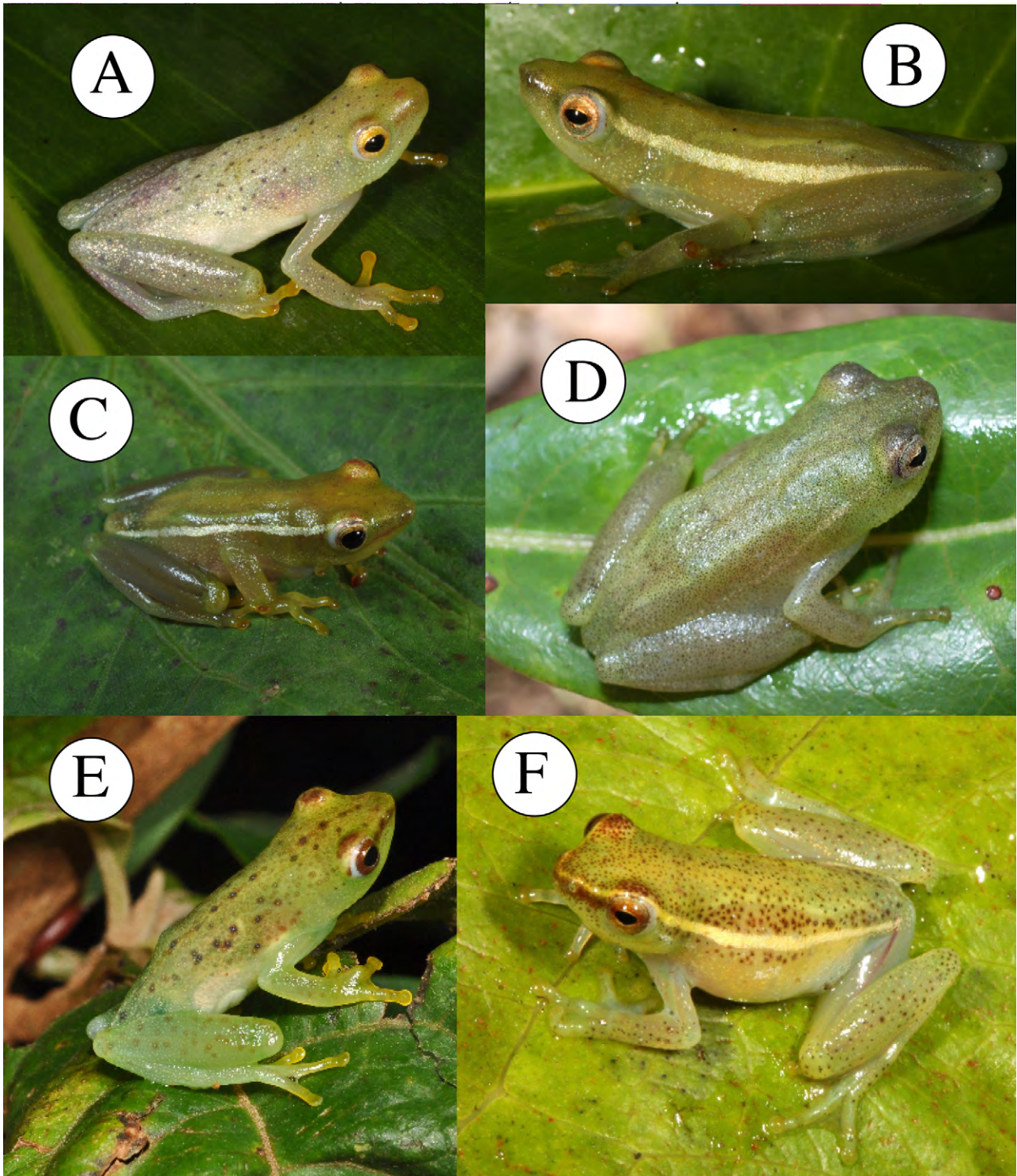


FIGURE 9 *Hyperolius nasutus*, Calandula, Angola, ZMB 77311, photo A. Channing (A); *Hyperolius poweri*, Mkambati NR, South Africa, photo W. Conradie (B); *Hyperolius rwandae* **sp. nov.**, Butare, Rwanda, ZMB 77221, holotype, photo J.M. Dehling (C); *Hyperolius viridis*, Kaningina, Malawi, photo V. Mercurio (D), *Hyperolius rwandae* **sp. nov.**, female paratype ZMB 77223, photo J.M Dehling (E), *Hyperolius dartevellei*, Carumbo, Angola, PEM A 10035, photo W. Conradie (F).

Genetic material. SMF 85694, ZMB 76095 (holotype and paratype) SAIAB 186000 (two specimens) Monkey Bay, Malawi.

Diagnosis. The advertisement call (Fig. 8) consists of a brief initial note of eight pulses, followed by six pulses at a slower rate. The duration of the call is 0.12 s. It can be distinguished from species that produce only a buzz, such as *H. acuticeps*, *H. jacobseni* **sp. nov.** and *H. nasutus*. It can also be distinguished from *H. adspersus*, *H.*

dartevellei and *H. lupiroensis* **sp. nov.**, which produce only a brief single note. It differs from those species with calls longer than 0.2 s, such as *H. benguellensis*, *H. inyangae* **sp. nov.** and *H. viridis*. It can be distinguished from those species where the slower part of the call consists of less than half the pulses of the initial note, such as *H. howelli* **sp. nov.**, *H. igbettensis* and *H. rwandae* **sp. nov.** Finally, although the structure of the call of *H. poweri* is similar, the two differ in pitch, *H. poweri* having the dominant frequency of 5.9 kHz, while *H. friedemanni* **sp. nov.** has a dominant frequency of 4.3 kHz. The snout is sharply rounded in profile, which distinguishes it from species with truncated, bluntly rounded, or shark-like snouts; *H. adspersus*, *H. benguellensis*, *H. howelli* **sp. nov.**, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. jacobsoni* **sp. nov.**, *H. poweri*, *H. dartevellei* and *H. viridis*. It is the only species in the study where the webbing reaches the disc on all toes, at least on one side. This distinguishes it from all other species.

Description of Holotype. The width of the gular flap is 5.1, hand 5.5. The top of the snout is flat, with the tip of the snout acutely rounded from above and from the side (Fig. 6) (HW/SUL 0.29). The snout is 1.4x eye. The tympanum is not visible. The nostrils are positioned near the snout tip (EN/SL 0.5), nostril opening rounded, slightly protruding. Fine teeth are present on the upper jaw. The choanae are small, round. The tongue is long, with the posterior as wide as the length, with the terminal 20% bifurcated. Vomerine processes absent. The hand is 25.5% of the SUL. A small inner metacarpal tubercle is present. The relative finger lengths are $1 < 4 < 2 < 3$. The foot is 0.4 of SUL, and the tibia is 0.52 of SUL. The webbing is shown in Fig. 7. The skin is smooth on the dorsum and limbs, coarsely granular under the thighs. In preservative the skin becomes transparent. In life the body is pale green, tinged with blue along the legs, and yellow-tipped fingers and toes. There are pale dorsolateral stripes without dark borders that originate at the nostril and run back over the eye to continue to the groin. The iris is golden.

Paratype variation. The female paratype is similar to the holotype. Tympanum not visible. The paratypes from Monkey Bay collected by EN are subadults, with skin that is transparent in preservative, showing large numbers of subdermal parasite eggs.

Advertisement call. Recorded at Karonga, on 7 February 2002 at 23:40 h, 27°C air temperature, voucher specimen SMF 85694. The call (Fig. 8) consists of the regular repetition of one single biphasic pulsed note with a duration 110–190 ms. Interval between notes is 180–360 ms. The note repetition rate is 1.4 s^{-1} . The dominant frequency is 3900–4500 Hz. The specimen was calling at night from dense grassy vegetation within a swamp in an exposed position about 400 mm above the water. See Table 3 for a summary of call parameters.

Eggs and tadpoles. Unknown.

Habitat. Swamp along the lakeshore with abundant grassy vegetation and sandy soil. Other common species were: *Afrivalus fornasini*, *Hyperolius pusillus*, *H. viridiflavus nyassae*, *H. tuberilinguis*, *Phrynobatrachus acridoides*, *P. mababiensis*, *Ptychadena* cf. *mascareniensis*, *P. anchietae*, *Kassina senegalensis*, *Amietophrynus gutturalis*, *A. maculatus*, *Xenopus muelleri*, *Arthroleptis stenodactylus*, and *Hemisus marmoratus*.

Etymology. We dedicate this new species to Friedemann Schrenk in recognition of his enthusiastic and tireless work for the research and protection of the natural history heritage of Malawi.

Remarks. The species is only known from the shores of Lake Malawi, and we suggest that it be regarded as Data Deficient, in terms of the IUCN criteria.

***Hyperolius howelli* sp. nov. Du Preez & Channing**

Howell's Long Reed Frog

(Fig. 4)

Holotype. SAIAB 118979, collected at Himo Road, Arusha, Tanzania (3°21' 29.6" S; 36°50'15.3" E), collected 12 April 2008 by L.H. du Preez.

Paratypes. SAIAB 118980–1, female, and SAIAB 118980–2, male, collected at Himo Road, near Arusha, Tanzania (3°21' 29.6" S; 36°50'15.3" E), collected 12 April 2008 by L.H. du Preez; NMK 39221 from Kakamega Forest.

Genetic material. SAIAB 118979–80 (Himo Road, Arusha) and a specimen from Madehani, Tanzania (no voucher), NMK 39221 (16S sequence accessioned as AY323926, 12S sequence determined as part of this study) Kakamega Forest, Kenya (Lötters *et al.* 2004) (Fig. 1).

Diagnosis: The advertisement call (Fig. 10) consists of an initial brief note, followed by three slower pulses, with a duration of 0.12 s. It can be distinguished from species producing only a single note and those producing only a buzz: *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. jacobsoni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, and *H. nasutus*. It differs from species producing a call over 0.2 s: *H. benguellensis*, *H. inyangae* **sp. nov.** and *H. viridis*. It differs from those species where the slower, pulsed part of the call has five or more pulses: *H. friedemanni*, *H. igbettensis*, and *H. poweri*. The initial note consists of eight pulses, while the superficially similar call of *H. rwandae* **sp. nov.** has an initial note consisting of 13 pulses.

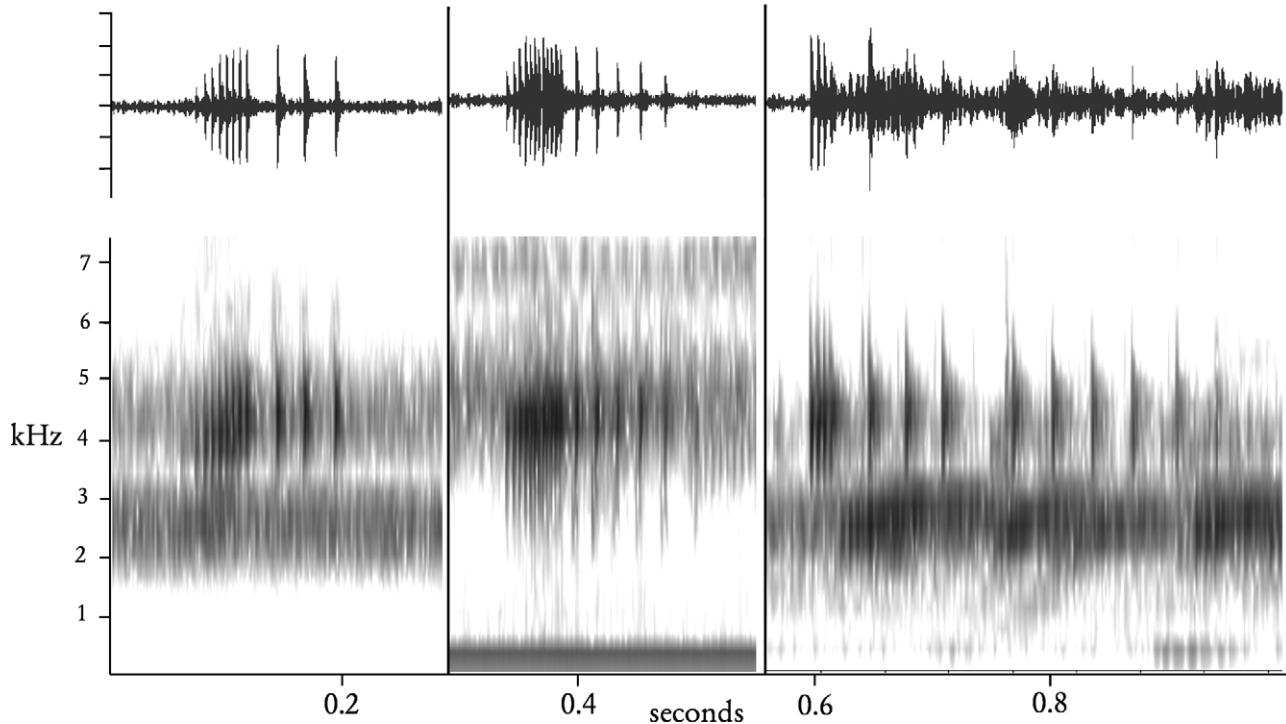


FIGURE 10. Advertisement calls of *H. howelli* Arusha (left), *H. igbettensis* Comoé National Park, Ivory Coast (center) and *H. inyangae* Rhodes Dam (right).

The shark-like profile of the snout distinguishes it from species with truncated or rounded snouts; *H. acuticeps*, *H. adspersus*, *H. friedemanni* **sp. nov.**, *H. igbettensis*, *H. jacobsoni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus*, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*. The foot has at least one phalanx free of webbing on every toe. This distinguishes it from species where at least one toe is webbed to the disc, at least on one side: *H. adspersus*, *H. benguellensis*, *H. friedemanni*, *H. jacobsoni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus* and *H. rwandae* **sp. nov.**. It also differs from those species that have less than one phalanx free, on at least one toe: *H. acuticeps*, *H. igbettensis*, *H. inyangae* **sp. nov.**, *H. poweri*, *H. dartevellei* and *H. viridis*.

Description of Holotype. Body slender, widest at temporal region, slightly tapering to groin; head comparatively small (HL/SUL 0.32, HW/SUL 0.31), not wider than trunk, slightly longer than wide (HL/HW 1.03); snout top flat, tip of snout rounded (SL/HL 0.48), from above the snout is triangular with a rounded tip (Fig. 6), considerably projecting beyond lower jaw with a shark-like profile, wider than long (SL/EE 0.76); canthus rostralis rounded, almost straight-lined from eye to just beyond nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed laterally; situated much closer to tip of snout than to eye (EN/NS 2.00), separated from each other by distance nearly equal to distance between eye and nostril (NN/EN 1.06); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.36); eye diameter much shorter than snout (ED/SL 0.74); interorbital distance much wider than upper eyelid (IO/EW 0.96), and greater than internarial distance (IO/NN 1.59); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 4.6, and narrow (2.3 at widest point), free for about three-fourths of length, bifurcated distally for about one-third of length; median lingual process absent; vocal sac single, median, subgular, yellow in colour; gular flap consisting of two areas of thickened skin, the anterior thicker, cream coloured, and the

posterior thinner, smooth and white; vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like, long.

Dorsal surfaces of head, trunk and limbs generally smooth; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate.

Fore limbs slender; hand moderately large (HND/SUL 0.24); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: $I < II < IV < III$; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand $I2^+ - 2II2 - 2.75III2 - 2.5IV$; thenar tubercle indistinct, low; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.36); tibio-tarsal articulation passing level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.56), longer than thigh (TFL/THL 1.27); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.70); relative length of toes: $I < II < III < V < IV$; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $I1 - 2II2 - 1III1 - 1.5IV1.5 - 1.25V$; inner metatarsal tubercle small, oval, prominent; outer one indistinct.

Colouration in life. Holotype was a brown-green overall, with white lateral stripes running from the snout, through the top of the eye, to the groin. The lateral stripe is lined with irregular large melanophores. The top of each eye has a smudge of golden brown. The back has many small dark melanophores, with a few irregularly spaced larger pigment cells. The limb joints are pale green, with the limbs showing a brown tinge. The fingers and toes are green with yellow tips. The skin is smooth above and on the limbs, while the ventrum is rough with large flat granules. **Colouration in preservative.** The dorsal pattern shows two pale lateral stripes edged with large dark melanophores, filled with opaque white pigment. The head and dorsum is uniformly speckled with small melanophores, with a few irregularly spaced larger pigment cells. A thin dark line runs from the nostril to the eye.

Paratype variation. The female has a similar body shape to the holotype, Skin texture the same as the holotype. Colour in preservative: pale yellow background with large irregular melanophores on the dorsum, overlaying a uniform fine speckling. A dark line runs from eye to eye below the snout tip, running through the nostril. In life the body is pale green with yellowish sides, with darker leaf green around the eyes. The top of the eye has a brown smudge. The line running from eye to eye below the snout tip is reddish brown, with a faint brown band around the top of the snout. The irregular large black spots are less dense posteriorly. The tibia has many large melanophores, with very small speckles on the forearm. The snout profile is rounded, with the nostrils behind the tip. Paratype measurements are included in Appendix 2.

Advertisement call. The call is a harsh insect-like chirp. Males call from elevated positions on vegetation (Fig 5). See Table 3 for a summary of call parameters.

Eggs and tadpoles. Lötters *et al.* (2004) found egg clutches attached to submerged vegetation. The larvae are omnivorous, found in quiet water.

Habitat. The type locality was a pond of roughly 20 m x 40 m with deep clear water. Along the periphery were dense stands of *Typha* sp. where the frogs were present from water level to about one meter above water level. Other species present included *Amietia angolensis*. In Kakamega, *H. cinnamomeoventris*, *H. kivuensis*, *H. lateralis* and *H. viridiflavus* were present (Lötters *et al.* 2004)

Etymology. We have pleasure in honouring Kim M. Howell for his contributions to East African zoology, made during a long career at the University of Dar-es-Salaam.

Remarks. The species is known from western Kenya, and southern and northern Tanzania. Due to its wide range and large populations, we suggest that it be regarded as Least Concern in terms of the IUCN criteria.

Hyperolius igbettensis Schiøtz, 1963

Igbetti Long Reed Frog

(Fig. 12)

Genetic material. Two samples without vouchers, and ZMB 76542–43 (Lamto, Ivory Coast); ZMB 77415 (Kérouane, Guinea); ZMB 77416 (Konsankoro, Guinea); ZMB 77410 (Dantilla, Guinea) (Fig. 1).

Diagnosis. The advertisement call (Fig. 10) consists of an initial brief note with 12 pulses, followed by five slower pulses, with a duration of 0.12 s. It can be distinguished from species producing only a single note, and those producing only a buzz: *H. acuticeps*, *H. adpersus*, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.** and *H. nasutus*. It differs from species producing a call over 0.2 s; *H. benguellensis*, *H. inyangae* **sp. nov.** and *H. viridis*, and from those where the initial note consists of less than 10 pulses: *H. friedemanni*, *H. howelli*, and *H. poweri*. The snout is bluntly round in profile, which distinguishes it from species with truncated, shark-like, or sharply rounded profiles; *H. acuticeps*, *H. adpersus*, *H. benguellensis*, *H. dartevellei*, *H. friedemanni*, *H. howelli*, *H. inyangae* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus* and *H. rwandae* **sp. nov.** The foot is webbed with one or more phalanges free of web on the first four toes, and half free on the fifth toe. This distinguishes it from species where at least one toe is webbed to the disc, at least on one side: *H. adpersus*, *H. benguellensis*, *H. friedemanni*, *H. jacobseni* **sp. nov.**, *H. lupiroensis* **sp. nov.**, *H. nasutus* and *H. rwandae* **sp. nov.** It differs from species that have at least one phalanx free on the fifth toe; *H. acuticeps*, *H. dartevellei*, *H. howelli*, *H. inyangae* and *H. nasutus*. Finally, it differs from the two species that have one or less phalanges of the second toe free of web: *H. poweri* and *H. viridis*.

Description of a Dantilla specimen. This is based on ZMB 77410, an adult female. The ranges are given from three specimens (ZMB 77410–412; 1 female, 2 males), with single measurements from the sequenced specimen. Elongate, fragile frogs; Body long and slender (SUL 21.1), widest at temporal region (HW 5.8–7.0; 7.0), slightly tapering to groin; head comparatively small (HL/SUL 0.33, HW/SUL 0.26), not wider than trunk, longer than wide (HL/HW 1.27); snout long (SL/HL 0.43), subelliptical in dorsal view and protruding in lateral view (Fig. 6), projecting beyond lower jaw, wider than long (SL/EE 0.73); canthus rostralis indistinct, roundish, straight-lined from eye to just beyond nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril round, directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 1.91), separated from each other by distance slightly less than distance between eye and nostril (NN/EN 0.90); eyes directed anterolaterally, protruding, relatively small (ED/HL 0.29); eye diameter shorter than snout (ED/SL 0.67); interorbital distance narrower than upper eyelid (IO/EW 0.8), and greater than internarial distance (IO/NN 1.11); tympanum barely visible, very small with tympanum-eye distance equal to half diameter of eye; upper jaw with dentition; choanae small, oval, located far anterolaterally at margins of roof of the mouth, concealed by upper jaw for about the half in ventral view; vomer processes and teeth absent; tongue long 5.0, and wide (3.6 at widest point), free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single of males, median, subgular, mostly unpigmented and translucent when fully inflated; gular gland large covering 2/3 to almost entire throat, dilatable skin visible posterior to gland; width of male gular flap 3.6–4.8; gular flap consisting of two medially arranged, heart shaped and triangular areas of thickened skin, immediately adjacent to each other; anterior, heart shaped, light yellow, larger, more granular, and thicker than posterior, triangular white-coloured part; in resting position only anterior part visible from ventral;

Dorsal surfaces of head, trunk and limbs generally smooth; ventral surface of limbs and gular smooth, lower belly slightly more areolate; a few warts in angle of mouth; supratympanic fold absent.

Fore limbs slender; hand moderately large (HND/SUL 0.28); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: $1 < 2 < 4 < 3$; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; finger webbing reaches the proximal subarticular tubercle between fingers 2 and 3, and between 3 and 4, with only traces of webbing on the other fingers; thenar tubercle indistinct, low; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.58); tibio-tarsal articulation almost reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.58), longer than thigh (TFL/THL 1.13; TFL 10.7–11.0); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.86; FOT 10.5–15.3); relative length of toes: $I < II < III < V < IV$; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $I1^+ - 1.25II0.25 - 2III2 - 1IV1 - 0.3V$; no visible internal or external metatarsal tubercles.

Colouration in life. The basic colour of live frogs ranges from a light bluish green, to grass green or almost green-brown; shanks, lower and upper arms are almost transparent blue-green; flanks, back and thighs darker green with many small dark spots, sometimes arranged along vertebral line into a broken line; eyelids usually lighter than

rest of head and dorsum, yellowish to reddish brown; sometimes head darker (reddish brown) than rest of dorsal surfaces; in some animals, mostly males, light white to yellow dorsolateral stripe, rarely bordered by two dark lines; dark canthal stripe, reddish iris bordered by narrow blue line; gular gland of males yellowish or like rest of vocal sac skin light green-blue; ventral surfaces light, belly whitish, often almost transparent; toe and finger tips yellow to orange; females are usually more “transparent” than males, with eggs visible through the body wall. **Colouration in preservative.** Very pale beige in preservation with small dark spots scattered over back and extremities, with or without a distinct white dorsolateral band.

Eggs and tadpoles. Unknown.

Remarks. The biology of this species was discussed by Rödel *et al.* (2006). The species is now known from Guinea to Cameroon, and perhaps occurs further east (Amiet 2006a). We suggest that the IUCN status of Least Concern be maintained.

***Hyperolius inyangae* sp. nov. Channing**

Nyanga Long Reed Frog

(Fig. 12)

Holotype. ZMB 77276, a male, collected at Rhodes Dam in the Nyanga National Park, Zimbabwe, 18°17'20.3" S, 32°43'24.4" E, 14 November 2009.

Paratypes. A female, ZMB 77277, and two males, ZMB 77278–9, with the same collecting details as the holotype.

Genetic material. ZMB 77277–8, ZMB 77276 (Rhodes Dam, Nyanga National Park, Zimbabwe); ZMB 76099–101 (Kanungu, Malawi).

Diagnosis: The advertisement call (Fig. 10) consists of a brief initial note of four pulses, followed by nine slower pulses, with a duration of 0.35 s. It can be distinguished from species producing only a single note, and those producing only a buzz: *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. jacobseni* sp. nov., *H. lupiroensis* sp. nov., and *H. nasutus*. It can be distinguished from those species with short calls under 0.2 s: *H. friedemanni*, *H. howelli*, *H. igbettensis*, *H. poweri* and *H. rwandae* sp. nov. It differs from *H. viridis*, which has an initial note consisting of 26 pulses. See Table 3 for a summary of call parameters. It has a shark-like snout profile, which distinguishes it from those species that have truncated or rounded snouts; *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. friedemanni*, *H. igbettensis*, *H. jacobseni* sp. nov., *H. lupiroensis* sp. nov., *H. nasutus*, *H. poweri*, *H. rwandae* sp. nov., and *H. viridis*. The webbing is characterized by three phalanges free of the fourth toe, and two phalanges free of the fifth toe. This distinguishes it from all other species (which have more webbing).

Description of Holotype. Body long and slender, widest at mid-body, slightly tapering to groin; head comparatively small (HL/SUL 0.37, HW/SUL 0.29), not wider than trunk, longer than wide (HL/HW 1.27); snout long (SL/HL 0.46), sharply rounded in dorsal view, acute in profile with a distinct protruding tip (Fig. 6), considerably projecting beyond lower jaw, wider than long (SL/EE 0.82); canthus rostralis distinct, sharp, almost straight-lined from eye to nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed dorsolaterally; situated midway between tip of snout and eye (EN/NS 1.0), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.15); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.23); eye diameter shorter than snout (ED/SL 0.51); interorbital distance much wider than upper eyelid (IO/EW 1.14), and greater than internarial distance (IO/NN 1.04); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, slightly oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 4.6, and narrow (2.9 at widest point), free for about one-quarter of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular, mostly unpigmented and translucent when fully inflated; gular flap consisting of thickened granular skin, vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like, long, directed posterolaterally.

Dorsal surfaces of head, trunk and limbs finely granular with minute tubercles visible under magnification; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate.

Fore limbs slender; hand moderately large (HND/SUL 0.24); tips of fingers enlarged into broad oval disks,

each with circummarginal groove; relative length of fingers: $I < II < IV < III$; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand $I2^+ - 2II2 - 3III2.5 - 2.5IV$ (after Myers & Duellman [1982]); thenar tubercle absent; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.42); tibio-tarsal articulation not reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.48), subequal to thigh (TFL/THL 0.97); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.85); relative length of toes: $I < II < III < V < IV$; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $I1.5 - 1.5II0.75 - 2III1.5 - 3IV3 - 2V$; inner metatarsal tubercle absent; outer one almost circular, flattened.

Colouration in life. head green, overlain with brown pigment which extends over the back and exposed surfaces of limbs. Tibia reddish-brown. Iris and eyelid pale brown. The vocal sac is pale green. **Colouration in preservative.** a yellow-brown background, covered dorsally with a dense speckling of small black and brown melanophores and chromatophores. No pale lateral stripes, pigmentation over snout and head more dense than dorsum. Upper exposed surfaces of limbs and digits pigmented.

Paratype variation. The paratypes are similar to the holotype in measurements (Appendix 2). The two males are similar in proportions, including the sharp protruding snout tip, but both have pale lateral stripes. The female, 21.6 SUL, is gravid, with a mid-body width of 10.2. The female also has a sharp shark-like snout, although it is not as acute as those of the males.

Eggs and tadpoles. A female (ZMB 77277) has enlarged ovarian eggs with a diameter of ca. 1.3. Eggs are darkly pigmented on the animal pole and white on the vegetative pole. Tadpoles are unknown.

Etymology. The species is named for the Nyanga National Park, Zimbabwe.

Remarks. The species is known from the Eastern Highlands of Zimbabwe and northern Malawi. The distribution of this species appears to cover at least 900 km of highlands between the collecting localities. Due to the extensive range we suggest that this species be regarded as Least Concern in terms of the IUCN criteria.

***Hyperolius jacobseni* sp. nov. Channing**

Jacobsen's Long Reed Frog

(Fig. 12)

Holotype. ZMB 77280, a male, collected near Gatiko, Central African Republic, 5°4'43" N, 20°40'2" E, by N. Jacobsen, 29 August 2006.

Paratypes. A female, ZMB 77281, with the same details as the holotype; 16 males and one female, ZMB 77282–298, collected at the same locality, and within a few days of the holotype.

Genetic material. ZMB 77280–1 (holotype and paratype) (Fig. 1).

Diagnosis. The advertisement call (Fig. 11) consists of a short buzz with five pulses, with a duration of 0.06 s. This distinguishes it from the species with a single unpulsed note, and those with both an initial note and a series of slow pulses: *H. adspersus*, *H. benguellensis*, *H. dartevellei*, *H. friedemanni*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. lupiroensis* **sp. nov.**, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*. It can be distinguished from the other species with a buzz call by the number of pulses: 25 pulses in *H. acuticeps*, and eight pulses in *H. nasutus*. See Table 3 for a summary of call parameters. The snout is bluntly round in profile, distinguishing it from those with truncated, shark-like or sharply rounded snouts: *H. acuticeps*, *H. benguellensis*, *H. dartevellei*, *H. friedemanni*, *H. howelli*, *H. inyangae*, *H. lupiroensis* **sp. nov.**, *H. nasutus* and *H. rwandae* **sp. nov.** The toes are webbed with one phalanx of the third and fourth toes free, and the fifth toe webbed to the disc. This pattern distinguishes it from those species that do not have the fifth toe webbed to the disc: *H. acuticeps*, *H. benguellensis*, *H. dartevellei*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. nasutus*, *H. poweri*, and *H. viridis*. It differs from *H. friedemanni* which has all the toes webbed to the disc, and from *H. rwandae* **sp. nov.** which has two phalanges of the third toe free. The webbing is similar to that of *H. lupiroensis* **sp. nov.**

Standard measurements of the holotype are compared with the other species in Appendix 2.

Description of Holotype. Body long and slender, widest at temporal region, slightly tapering to groin; head comparatively small (HL/SUL 0.34, HW/SUL 0.28), not wider than trunk, longer than wide (HL/HW 1.22); snout long (SL/HL 0.43), bluntly rounded in dorsal view, truncated in profile (Fig. 6), not significantly projecting beyond lower jaw, wider than long (SL/EE 0.74); canthus rostralis distinct, rounded, strongly concave from eye to nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed laterally; situated much closer to tip of snout than to eye (EN/NS 1.6), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.31); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.25); eye diameter shorter than snout (ED/SL 0.58); interorbital distance much wider than upper eyelid (IO/EW 2.9), and greater than internarial distance (IO/NN 1.38); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 4.7, and narrow (2.8 at widest point), free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular; gular flap consisting of two medially arranged, subcircular areas of thickened skin, immediately adjacent to each other; anterior part cream-coloured, larger, more granular, and thicker than posterior white-coloured part; vocal sac aperture on each side of the mouth, slit-like, long.

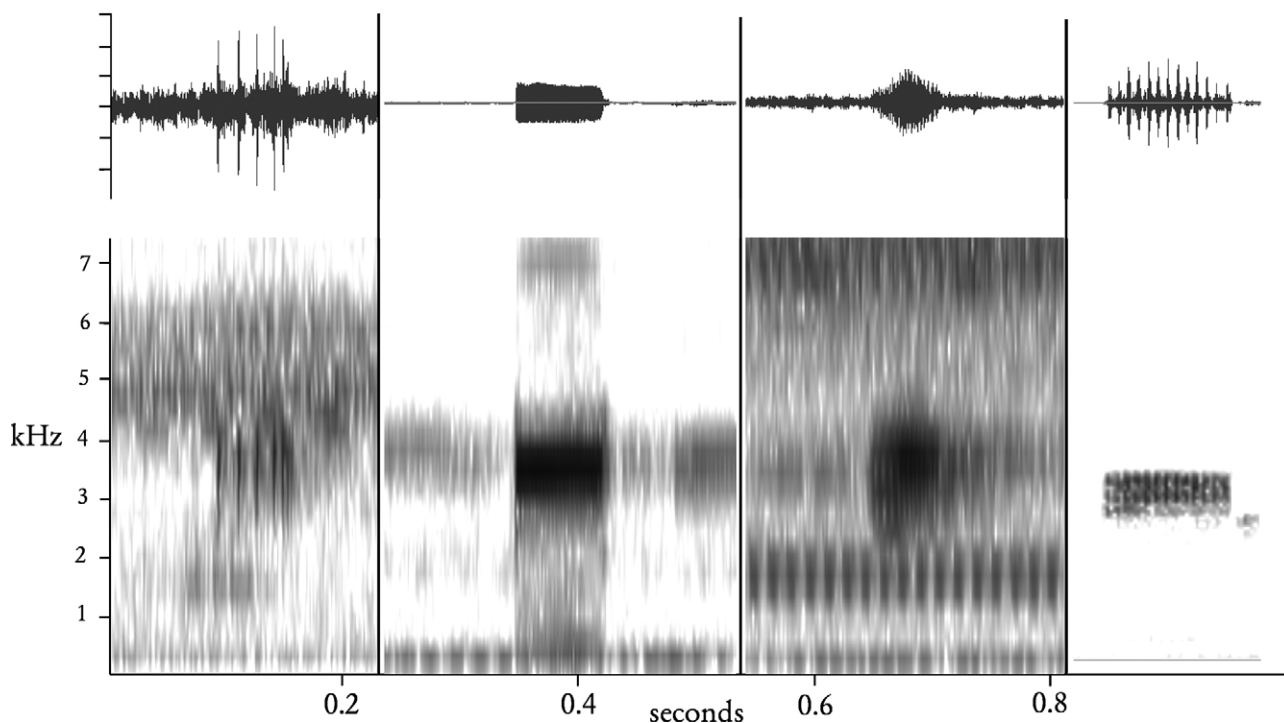


FIGURE 11. Advertisement calls of *H. jacobseni* Gatiko (left), *H. lamottei* Nimba (center left), *H. lupiroensis* Lupiro (center right) and *H. nasicus* Fungurume (right).

Dorsal surfaces of head, trunk and limbs smooth but with many densely and more or less evenly scattered tiny, low, spine-like tubercles; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate.

Fore limbs slender; hand moderately large (HND/SUL 0.28); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand I2–2.5II2.5–3III2.5–2IV; thenar tubercle indistinct, low; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.60); tibio-tarsal articulation reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.52), longer than thigh (TFL/THL 1.05); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.78); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal

webbing formula (Fig. 7) **I1–II0.25–III0.25–IV1–0V**; inner metatarsal tubercle small, oval, prominent; outer circular, low and less distinct.

Colouration in life. The body is an overall yellow-brown, with a green tinge visible through the skin of the sides of the body. The lateral stripes are bright white, edged with brownish pigment spots. **Colouration in preservative.** Colour in preservative pale yellow, with pigmented snout, a blotch of pigment on top of the eye, and minute black melanophores on the back, more dense anteriorly, with larger brown spots irregularly scattered. White lateral lines run from the top of the eye to the groin, bordered by dark lines of spots and melanophores. The belly is white.

Paratype variation. The paratypes are similar in size and proportions to the holotype, with the large female ZMB 77281 having SUL 19.5 and with HW 6.2, with the largest female having SUL 21.5. The male paratypes have a conspicuous muscle (*m. ileolumbaris*) running from behind the tympanum to the groin, visible under the skin. The inner metatarsal tubercle is flattened, while the outer metatarsal tubercle is absent. The discs on the toes are slightly wider than the width of the toes.

Eggs and tadpoles. A female paratype ZMB 77281 contains enlarged ovarian eggs with a diameter of ca. 1.1. Eggs are darkly pigmented on the animal pole and white on the vegetative pole. Tadpoles are unknown.

Habitat. The types were found on emergent grass and other plants around temporary pools.

Etymology. This species is named for the collector, the South African herpetologist Niels Jacobsen.

Remarks. The species is only known from southern Central African Republic, although it is probably widespread. It should be regarded as Data Deficient in terms of the IUCN criteria.

Hyperolius lamottei Laurent, 1958

Lamotte's Reed Frog

(Fig. 12)

Synonymy: *Hyperolius nasutus* Channing *et al.*, 2002 (part)

Genetic material. ZMB 76536–7 (Loma Mountains, Sierra Leone); ZMB 76535 (Nimini Forest Reserve, Sierra Leone); ZMB 76525 (Korombadou/ Tourou, Guinea); ZMB 76532 (Mont Béro Forest Reserve, Guinea); ZMB 76526–27 (Nimba Mountains, Guinea); three samples (no vouchers), (Mare d'hivenage, Nimba, Guinea); ZMB 76516 (Savanne de But, Nimba, Guinea); ZMB 76523–24 (Nimba Mountain, Guinea) (Fig. 1).

Diagnosis. It is distinguished on the overall yellow background colour pattern, rounded body shape and advertisement call from the species in the *H. nasutus* clade. The call (Fig. 12), recorded at Lamto by Arne Schiøtz, is a brief unpulsed whistle that has a duration of 0.08 s, and a dominant frequency of 3.5 kHz. See Table 3 for a summary of call parameters. It is known mostly from high altitude grassland, in Senegal, Sierra Leone, Guinea, Liberia and Ivory Coast (e.g. Rödel & Ernst 2003, Rödel *et al.* 2004, Adeba *et al.* 2010). The night-time colour pattern is shown in Figure 12, and the day-time pattern is illustrated in Schiøtz (1999) and Rödel & Ernst (2003). In our dataset, *H. lamottei* is outside the *H. nasutus* group, with a genetic distance for the 16S fragment of 13.2–16.4% to the species inside the group. Tissues were available from near the type locality.

Description of Nimba material. A male ZMB 76526, from the type locality, Mount Nimba, Guinea: Body long and slender, widest at temporal region, almost parallel to groin; head comparatively small (HL/SUL 0.33, HW/SUL 0.28), not wider than trunk, longer than wide (HL/HW 1.14); snout long (SL/HL 0.44), subelliptical in dorsal view, protruding in profile (Fig. 6), considerably projecting beyond lower jaw, almost as wide as long (SL/EE 0.97); canthus rostralis indistinct, round, very slightly concave from eye to nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 1.6), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.19); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.38); eye diameter shorter than snout (ED/SL 0.87); interorbital distance almost equalling upper eyelid (IO/EW 0.94), and greater than internarial distance (IO/NN 1.53); tympanum not visible externally; upper jaw with dentition; choanae small, oval, located far anterolaterally at margins of roof of the mouth, completely concealed by upper jaw in ventral view; vomer processes and teeth absent; tongue broad and heart shaped, free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular, mostly

unpigmented and translucent when fully inflated; The gular flap is glandular, white in preservative, with folded skin posteriorly. width of gular flap 4.6, gular flap consisting of one round areas of thickened skin, cream-coloured; vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like, long, directed posterolaterally.

The skin of the dorsum and upper limbs is smooth, with a flat granular belly; supratympanic fold absent.

Fore limbs slender; hand short (HND/SUL 0.18); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV; basal webbing only lacking between fingers I and II; thenar tubercle distinct; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, comparatively short (LEG/SUL 1.18); tibio-tarsal articulation almost reaching to level of tip of snout when legs are adpressed to body; tibiofibula short (TFL/SUL 0.41), shorter than thigh (TFL/THL 0.96); heels in contact when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.81); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles indistinct: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $II.5-2.5III-2^{+}III^{+}-2IV1-1.25V$; inner and outer metatarsal tubercle indiscernible.

Colouration in life. The back and flanks are dark beige to yellow and densely covered with minute melanophores, bands of more densely arranged melanophores border broad white dorsolateral bands; the back with a narrow black vertebral line, a white longitudinal band on upper surfaces of tibia, slightly bordered darker, not very distinct. The colour pattern may be either fainter or with much more contrasting darker stripes and lines in different individuals. **Colouration in preservative.** All colours fade, but the pattern remains distinct.

Eggs and tadpoles. The eggs were described by Schiøtz (1967). The tadpole was described by Arnoult & Lamotte (1958). See Rödel (2000).

Habitat. Humid savanna habitats close to forest belt, mostly in mountainous areas. Reaching altitudes of above 100 m asl. Often in areas with low grasses and rocky ground.

Distribution. Recorded from Senegal, though Sierra Leone, Liberia, southern Guinea into western Ivory Cost (Rödel 2000, Rödel & Ernst (2003). A population from Central Ivory Coast, Lamto Reserve, may be extinct (Adeba *et al.* 2010).

Remarks. Channing *et al.* (2002) suggested that this species should be regarded as a junior synonym of *H. nasutus*, based on similarity of colour pattern and advertisement call structure, which view was disputed by Rödel & Agyei (2003) and Schiøtz (2006b). Molecular evidence presented in this paper shows that it is not in the *H. nasutus* species group. The sequences of 13 specimens of *Hyperolius lamottei* all group together forming a clade outside the *nasutus* group, with little variation. The intraspecific differences in the sample range from 0.0–0.63% for 16S. The conservation status of this species is Least Concern (IUCN 2011).

Hyperolius lupiroensis sp. nov. Channing

Lupiro Long Reed Frog

(Fig. 12)

Holotype. ZMB 77299, a gravid female collected near Lupiro, 8°25'29.3" S, 36°41'33.1" E, Ifakara district, Tanzania, by A. Danby, 9 July 2007.

Paratype. ZMB 77300, a subadult male, with the same collecting details as the holotype.

Genetic material. The holotype and paratype (Fig. 1).

Diagnosis. The advertisement call (Fig. 11) consists of a single unpulsed note, with a duration of 0.06 s. It can be distinguished from the species with calls consisting of a few initial pulses, followed by a number of pulses at a much slower pulse rate, such as *H. benguellensis*, *H. friedemanni*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. rwandae* sp. nov., *H. viridis*, and *H. poweri*. It is different from the longer calls consisting of a number of pulses at a more or less constant rate, such as *H. acuticeps*, *H. dartevellei*, *H. jacobseni*, and *H. nasutus*. See Table 3 for a summary of call parameters. The snout is sharply rounded in profile, which distinguishes it from those species with truncated, shark-like, or bluntly rounded snouts: *H. benguellensis*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. jacobseni*, *H. poweri*, *H. dartevellei* and *H. viridis*. The toes are webbed with one phalanx of the third and fourth

toes free, and the fifth toe webbed to the disc. This pattern distinguishes it from those species that do not have the fifth toe webbed to the disc: *H. acuticeps*, *H. benguellensis*, *H. dartavellei*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. nasutus*, *H. poweri* and *H. viridis*. It differs from *H. friedemanni* which has all the toes webbed to the disc, from *H. rwandae* **sp. nov.** which has two phalanges of the third toe free, and from *H. adspersus* which has the fourth toe webbed nearly to the disc.

Description of Holotype. Body long and slender, widest at mid-belly, slightly tapering to groin; head relatively small (HL/SUL 0.32, HW/SUL 0.23), not wider than trunk, appreciably longer than wide (HL/HW 1.38); snout long (SL/HL 0.48), bluntly rounded in dorsal view, rounded in profile (Fig. 6), slightly projecting beyond lower jaw, longer than wide (SL/EE 1.1); canthus rostralis distinct, rounded, almost straight-lined from eye to nostril; loreal region almost vertical, slightly concave; nostril a thin slit directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 2.25), separated from each other by distance almost equal to the distance between eye and nostril (NN/EN 0.94); eyes directed

anterolaterally, moderately protruding, relatively small (ED/HL 0.35); eye diameter shorter than snout (ED/SL 0.72); interorbital distance about equal to upper eyelid (IO/EW 0.96), and greater than internarial distance (IO/NN 1.44); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 4.0, and narrow (2.5 at widest point), free for about three-fourths of length, bifurcated distally for about one-third of its length; median lingual process absent.

Dorsal surfaces of head, trunk and limbs generally smooth; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate.

Fore limbs slender; hand moderately large (HND/SUL 0.26); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand I2.5–3II2–3III2.5–2.5IV; thenar tubercle small, distinct; palmar tubercles absent; metacarpals without supernumerary tubercles.

Hind limbs slender, moderately long (LEG/SUL 1.64); tibio-tarsal articulation passing level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.52), subequal to thigh (TFL/THL 1.03); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.75; relative length of toes: I<II<III<V<IV; discs of toes subequal to those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) I1–1III0.5–2⁺III0.25–2IV1–0V; inner metatarsal tubercle small, oval, distinct; outer metatarsal tubercle absent.

Colouration in life. Generally weakly pigmented and skin more or less translucent. Dorsum and dorsal surface of head and limbs yellowish green; lateral sides of head and scapular region light green; light, yellowish-white, moderately broad dorsolateral stripe running along each side of the body from lateral edge of upper eyelid to groin, continued as faint, hardly discernible line from eyelid to tip of snout; very small dark brown to black dots and larger brown to reddish brown specks on dorsum, most densely along both sides of canthus rostralis and upper eyelid and to lesser extent on both sides of dorsolateral stripe; dots roundish, specks shaped like stars or neurons with many dendrites; distal portions of fingers and toes, especially the tips, yellow; ventral side and parts of dorsal side of thigh and upper arm largely unpigmented, appearing bluish-green; peritoneum white, shining through the translucent belly skin; most of internal organs covered with silvery-white tissue (only visible when dissected). Iris reddish-brown during the night, yellowish-brown during the day. **Colouration in preservative.** All colours have faded to yellow; gular flap whitish-yellow.

Paratype variation. The subadult male is considerably smaller than the type, SUL 14.2, and has bright white lateral stripes originating at the nostrils and running back through the top of the eye to the groin. A dark line runs below the pale band from the nostril to the eye. The pale bands have dark borders between the eye and the groin. The back is uniformly speckled, giving the back a brown colour in preservative.

Eggs and tadpoles. The type contains enlarged ovarian eggs with a diameter of ca. 0.7–0.8. Eggs are darkly pigmented on the animal pole and white on the vegetative pole. Tadpoles are unknown.

Remarks. Although it is common for males to have lateral stripes and the females to be spotted in this group, the gravid holotype shows distinct pale lateral stripes. The species is only known from eastern Tanzania, and should be regarded as Data Deficient in terms of the IUCN criteria.

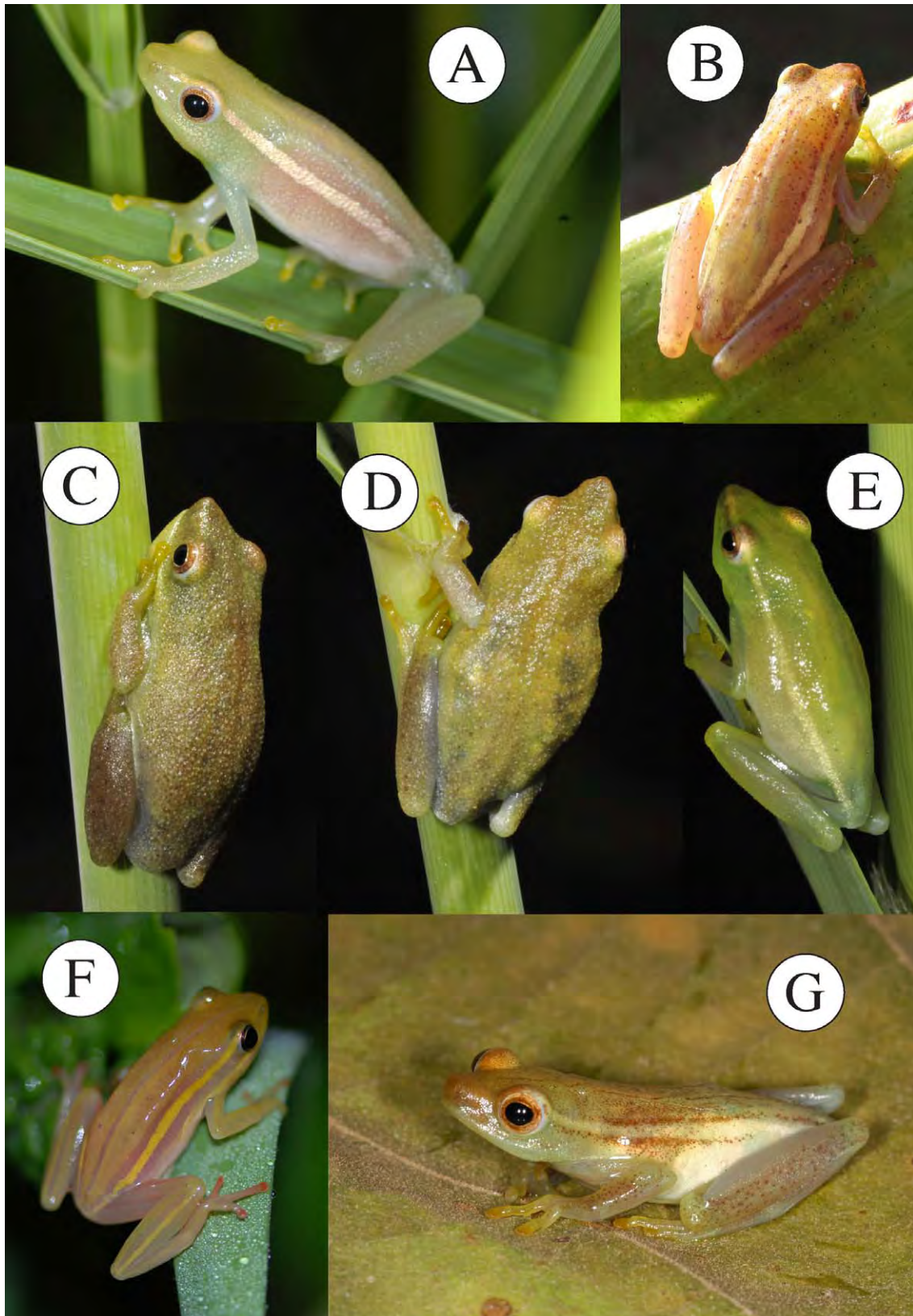


FIGURE 12. *Hyperolius igbettensis*, Lamto, Ivory Coast, photo M.-O. Rödel (A); *Hyperolius jacobsoni* **sp. nov.** holotype, ZMB 77280, Gatiko, Central African Republic, photo N. Jacobsen (B); *Hyperolius inyangae* **sp. nov.** male holotype, ZMB 77276, Rhodes Dam, Nyanga National Park, Zimbabwe, photo A. Channing (C); female paratype *H. inyangae*, ZMB 77277, same details (D); *Hyperolius nasicus*, Nyanga Flats, Zimbabwe, photo A. Channing (E); *H. lamottei*, night pattern, Mt Nimba, Guinea, photo M.-O. Rödel (F); *Hyperolius lupiroensis* **sp. nov.**, holotype ZMB 77300, Lupiro, Tanzania, photo A. Channing (G).

***Hyperolius nasicus* Laurent, 1943**

Pointed long reed frog (Fig. 12)

Genetic material. SAIAB A-136-1 (2 specimens, Elephant's Camp, Mozambique); SAIAB A-188 (Satellite Camp, Mozambique); SAIAB KU95952, KU96401, KU98212 (Quantum Mine & Kalumbila River, Zambia); ZMB 77308 (Kisanfu River, DRC); ZMB 77309 Fungurume, DRC; ZMB 77310 (Nyanga Flats, Zimbabwe); ZMB 77301–2, 77304–7, 77314 Ikelenge, Zambia.

Diagnosis. The advertisement call (Fig. 11) consists of a brief chirp-like note of about 10–20 constant-rate pulses with a duration of 0.09–0.2 s. It can be distinguished from species producing only a single note, and those producing only a buzz: *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. jacobseni*, *H. lamottei*, and *H. lupiroensis*. It differs from species producing a call over 0.2 s: *H. benguellensis*, *H. inyangae* and *H. viridis*. It differs from the species that have a number of slower pulses: *H. friedemanni*, *H. igbettensis*, *H. howelli* and *H. poweri*. The call is similar in structure to that of *H. nasutus*, but the latter call has a shorter duration and a higher pulse rate. See Table 3 for a summary of call parameters. The snout is sharply rounded from above, with a shark-like tip when viewed from the side, which distinguishes it from those species without truncated, shark-like, or bluntly rounded snouts: *H. adspersus*, *H. dartevellei*, *H. friedemanni*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. jacobseni*, *H. lamottei*, *H. lupiroensis*, *H. nasutus*, *H. poweri*, *H. rwandae* and *H. viridis*. The first, third and fifth toes have one phalanx free of webbing, distinguishing it from all the other species. Measurements of some individuals are compared with the other species in Appendix 2.

Description of a Nyanga Flats specimen. This is a male (ZMB 77310). Body long and slender, widest at mid-body, slightly tapering to groin; head comparatively small (HL/SUL 0.32, HW/SUL 0.27), not wider than trunk, longer than wide (HL/HW 1.22); snout long (SL/HL 0.45), pointed in dorsal view, acute in profile (Fig. 6), with a slightly upturned tip, considerably projecting beyond lower jaw, wider than long (SL/EE 0.78); canthus rostralis distinct, sharply rounded, almost straight-lined from eye to just beyond nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 1.7), separated from each other by distance equal to distance between eye and nostril (NN/EN 1.0); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.27); eye diameter less than snout length (ED/SL 0.61); interorbital distance subequal to upper eyelid (IO/EW 1.04), and greater than internarial distance (IO/NN 1.41); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 5.4, and narrow (2.2 at widest point), free for about three-fourths of length, bifurcated distally for about one-third of length; median lingual process absent; vocal sac single, median, subgular; gular flap consisting of thickened skin; anterior part cream-coloured, larger, more granular, and thicker than posterior white-coloured part; vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like, long.

Dorsal surfaces of head, trunk and limbs generally smooth; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate.

Fore limbs slender; hand moderately large (HND/SUL 0.28); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand I2–2II2–3III2.5–2.5IV; thenar tubercle indistinct, low; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.41); tibio-tarsal articulation not reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.48), longer than thigh (TFL/THL 1.14); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.84); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) II–1III0.5–1III1–1IV1–1V; inner metatarsal tubercle small, oval, prominent; outer one indistinct.

Colouration in life. Generally weakly pigmented. The frog was translucent green, with the pale dorsolateral bands originating at the snout tip. A thin dark middorsal line runs from the snout tip to between the eyes. The iris is dark brown. **Colouration in preservative.** The back is pale yellow with dense small dark chromatophores. The

pale dorsolateral bands originate at the nostril, run over the eye and continue to the groin. They are not bordered. A darkly pigmented band runs from the nostril to the eye. Ventrally unpigmented.

Eggs and tadpoles. Unknown.

Habitat. This species has been found in open savanna, through densely vegetated areas along the Congo River, to flooded swamp forest. They call from emergent vegetation bordering pools or flowing water up to a meter above the water surface.

Distribution. This species has been confirmed on molecular data from Mozambique, north-western Zambia, eastern Zimbabwe and Democratic Republic of Congo (Fig. 1).

***Hyperolius nasutus* Günther, 1865**

Large-nosed Long Reed Frog (Fig. 9)

Synonymy. *Hyperolius punctulatus* (Bocage, 1895)

Genetic material. ZMB 77311 (Calandula, Angola); AC2990 (Kangandala, Angola); LdP field specimen (Xigera, Botswana); SAIAB 186001 (Vumbura, Botswana) (Fig. 1).

Diagnosis. The advertisement call (Fig. 13) consists of a buzz with eight pulses, with a duration of 0.1 s. This distinguishes it from the species with a single unpulsed note, and those with both an initial note and a series of slow pulses: *H. adspersus*, *H. benguellensis*, *H. friedemanni*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. lupiroensis*, *H. poweri*, *H. rwandae* **sp. nov.** and *H. viridis*. It can be distinguished from the other species that have a buzz call by the number of pulses: 13 pulses in *H. dartevellei*, 25 pulses in *H. acuticeps*, and five pulses in *H. jacobseni*. See Table 3 for a summary of call parameters. The snout is sharply rounded in profile, which distinguishes it from those species with truncated, shark-like, or bluntly rounded snouts: *H. adspersus*, *H. benguellensis*, *H. dartevellei*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. jacobseni*, *H. poweri*, and *H. viridis*. The second to fifth toes are webbed to the disc, or just below the disc. This distinguishes it from those species with half or more of a phalanx of the fourth toe free: *H. acuticeps*, *H. benguellensis*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. jacobseni*, *H. lupiroensis*, *H. poweri*, *H. rwandae* **sp. nov.**, and *H. viridis*.

Description of a Vumbura specimen. A male, SAIAB 186001 has the body long and slender, widest at temporal region, slightly tapering to groin; head comparatively small (HL/SUL 0.28, HW/SUL 0.31), not wider than trunk, longer than wide (HL/HW 0.88); snout short (SL/HL 0.30), rounded to trapezium shaped in dorsal view (Fig. 6), (SL/EE 0.53); canthus rostralis fairly distinct, straight-lined from eye to nostril; nostril oval (0.13 X 0.10), directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 1.20), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.58); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.46); eye diameter exceeding than snout length (ED/SL 1.50); interorbital distance much wider than upper eyelid (IO/EW 1.91), and greater than internarial distance (IO/NN 2.32); tympanum not visible externally; upper jaw with dentition; choanae small, oval, located far anterolaterally at margins of roof of the mouth, concealed by upper jaw for about the half in ventral view; vomer processes and teeth absent; tongue long, free for about three-fourths of length, bifurcated distally for about one-fourth of length; vocal sac single, median, glandular, pale yellow, roughly triangular;

Dorsal surfaces of head, trunk and limbs finely granulated

Fore limbs slender; hand moderately large (HND/SUL 0.25); tips of fingers enlarged into broad rounded disks; relative finger lengths are I<IV<II<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on fingers III and IV hardly discernible; webbing formula of the hand I2⁺-2II2.5-2III1.5-2IV; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.48); tibio-tarsal articulation reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.48), longer than thigh (TFL/THL 1.14); foot shorter than tibiofibula (FOT/TFL 0.70); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) I1-1.5II2-1.5III2.5-2IV2.5-2.5V; inner metatarsal tubercle small, oval, prominent; outer one larger, almost circular, low and less distinct.

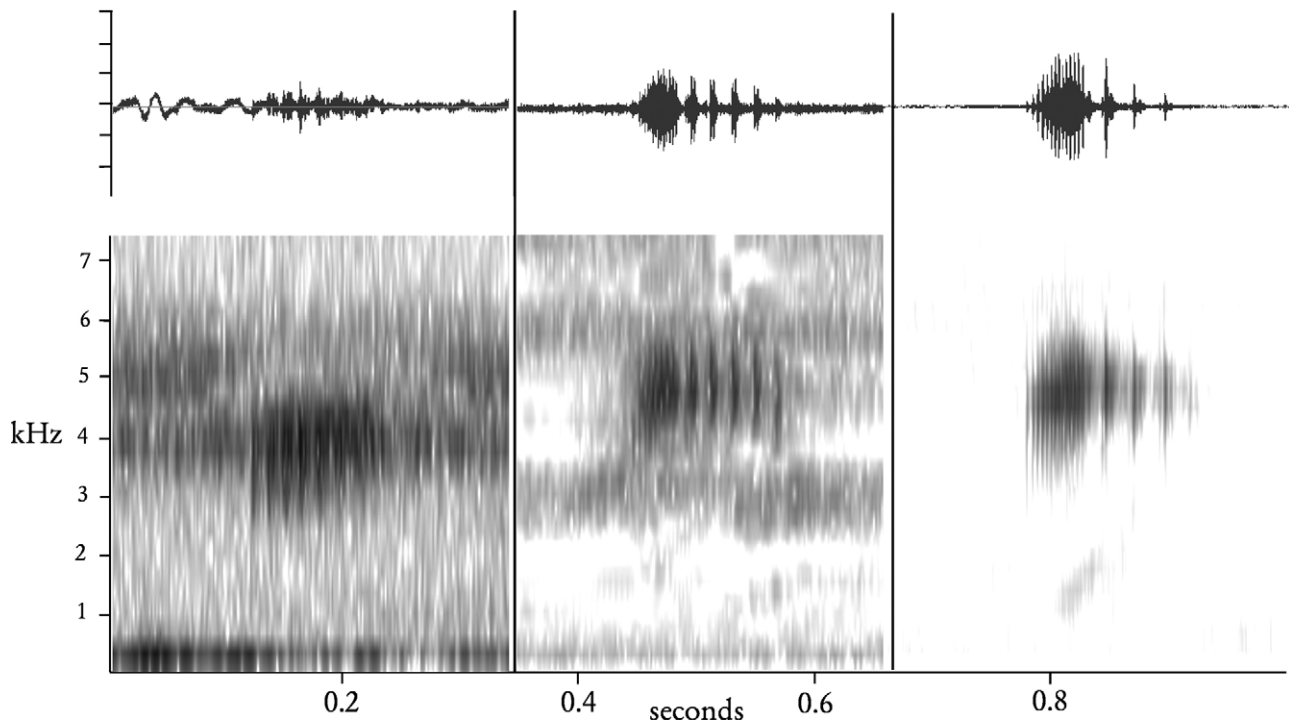


FIGURE 13. Advertisement calls of *H. nasutus* Kangandala (left), *H. poweri* Port Edward (center) and *H. rwandae* Gitarama (right).

Eggs and tadpoles. Unknown.

Colouration in life. Dorsal surface light green, skin more or less translucent. Dorsal surface of body and limbs with very small dark brown to black dots and slightly larger brown to reddish brown specks on dorsum; dots roundish, specks shaped like stars or neurons with many dendrites, limbs green; lateral sides of snout and area above eyes reddish brown, moderately broad dorsolateral stripe running along each side of the body from groin to eye extending to the snout as a thin white line; distal portions of fingers and toes, especially the tips, yellow; ventral side and parts of dorsal side of thigh and upper arm largely unpigmented. Iris reddish-brown. **Colouration in preservative.** The back is yellow brown with darker uniform speckles that extend on to the upper surfaces of the limbs.

Remarks. Specimens are similar to the type description, and one was collected from the type locality Calandula (Duque de Bragança). The back is covered with small and large spots. The synonymy of *H. punctulatus* is supported by the spotted back. The species is known from northern Botswana and northern Angola. Due to the extensive range and large population numbers, we suggest that the IUCN status of Least Concern be maintained.

Hyperolius poweri Loveridge, 1938

Power's Long Reed Frog

(Fig. 9)

Genetic material. ZMB 77312–3 (Port Edward, South Africa); PEM A 9545–6 (Mkambati Nature Reserve, South Africa) (Fig. 1).

Diagnosis: The advertisement call (Fig. 13) consists of an initial brief note with seven pulses, followed by five slower pulses, with a duration of 0.12 s. It can be distinguished from species producing only a single note, and those producing only a buzz: *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. jacobseni*, *H. lupiroensis*, and *H. nasutus*. It differs from species producing a call over 0.2 s; *H. benguellensis*, *H. inyangae* and *H. viridis*. See Table 3 for a summary of call parameters. The snout is bluntly rounded, distinguishing it from those with truncated, shark-like or sharply rounded snouts: *H. acuticeps*, *H. benguellensis*, *H. dartevellei*, *H. friedemanni*, *H. howelli*, *H. inyangae*, *H. lupiroensis*, *H. nasutus*, and *H. rwandae* **sp. nov.** There is a phalanx free of web on the first and third

toes, with slightly more than a phalanx free on the fourth toe. The second and fifth toes have about half a phalanx free of web. It can be distinguished from the species that have at least one toe webbed to the disc: *H. adspersus*, *H. benguellensis*, *H. friedemanni*, *H. jacobseni*, *H. lupiroensis*, *H. nasutus* and *H. rwandae* **sp. nov.** It differs from the species that have the fifth toe with one or more phalanges free of web: *H. acuticeps*, *H. dartevellei*, *H. howelli*, and *H. inyangae*.

Description of a specimen from Mkambati. This is a male, PEM A 9545, collected at the Mkombati Nature Reserve, Eastern Cape Province, South Africa by J. Venter and W. Conradie, 8 February 2011. Body long and slender, widest at mid-body, slightly tapering to groin; head comparatively small (HL/SUL 0.30, HW/SUL 0.30), not wider than trunk, length subequal to width (HL/HW 0.98); snout long (SL/HL 0.49), sharply rounded in dorsal view, blunt in profile (Fig. 6), projecting beyond lower jaw, wider than long (SL/EE 0.75); canthus rostralis distinct, rounded, slightly concave from eye to just beyond nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed laterally; situated much closer to tip of snout than to eye (EN/NS 1.46), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.16); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.34); eye diameter shorter than snout (ED/SL 0.70); interorbital distance wider than upper eyelid (IO/EW 1.14), and greater than internarial distance (IO/NN 1.09); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth; vomer processes and teeth absent; tongue long 5.1, and narrow (2.3 at widest point), free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular, mostly unpigmented and translucent when fully inflated; gular flap consisting of two areas of thickened skin, immediately adjacent to each other; anterior part cream-coloured, larger, more granular, and thicker than posterior white-coloured part; in resting position only a narrow band of the posterior part visible from below; vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like.

Dorsal surfaces of head, trunk and limbs generally smooth; ventral surface of limbs and gular smooth.

Fore limbs slender; hand moderately large (HND/SUL 0.27); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand I2–2II2.5–3III3–2.5IV; thenar tubercle indistinct, low; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.5); tibio-tarsal articulation passing level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.52), subequal to thigh (TFL/THL 1.04); heels overlapping each other when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.81); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) I1–1.5II0.75–2III1–2IV1.5–0.5V; inner metatarsal tubercle small, oval, prominent; outer one indistinct.

Colouration in life. In life the body is dark green with pale flecks, and fine brown pigment spots. The lateral stripes are shiny white, with a subdermal paradorsal band visible as an irregular pale green band. The toes have reddish tips. **Colouration in preservative.** In preservative the lateral stripes are shiny white, originating at the nostrils, being pale and subdermal before running over the eyes, and extending back to the groin. The back is densely covered in small chromatophores, with very dark pigment over the snout. The gular region is pale with a few dark spots

Eggs and tadpoles. The eggs are white with a grey animal pole, less than 1 mm in diameter, within capsules 2.2 mm in diameter (Wager 1986). Clutch size is about 200, with the eggs being deposited in small groups attached to vegetation under water (Wager 1986). Wager (1986) described the tadpoles.

Habitat. The frogs are found on reeds and other emergent vegetation around pools and swamps.

Distribution. This species is only confirmed from the east coast of South Africa, from Mkambati in the south, northwards to the Mozambique border. The northern extent of the distribution is unknown.

Remarks. The species is only known from the north-eastern coastal strip of South Africa. Due to the disturbed coastal habitat, this species should be regarded as Data Deficient in terms of the IUCN criteria, until further studies are carried out.

***Hyperolius rwandae* sp. nov. Dehling, Sinsch, Rödel & Channing**

Rwanda Long Reed Frog

(Fig. 9)

Holotype. ZMB 77221, adult male, from a pond in farmland on the eastern outskirts of Butare, Huye District, South Province, Rwanda (2°37'10.79" S, 29°45'08.45" E), collected 13 September 2010 by J.M. Dehling.

Genetic material. ZMB 77221–2 (Butare, Rwanda); ZMB 77223–4 (Mugesera wetland, Rwanda); ZMB 77225 (Akagera wetland, Rwanda) (Fig. 1).

Paratypes. ZMB 77222, adult male, same data as holotype; ZMB 77423–24, 77426–29, six adult males, ZMB 77425, adult female, all from farmland on the eastern outskirts of Butare, Huye District, South Province, Rwanda, collected in October 2009 by K. Lümekemann, K. Rosar and C. Schwartz; ZMB 77686–89, four adult males, from farmland on the eastern outskirts of Butare (2°35'44.1" S, 29°45'25.6" E), collected 27 February 2012 by J.M. Dehling; ZMB 77223, adult female, from the Mugesera wetland south of Lac Mugesera, Bugesera District, East Province, Rwanda (2°12'18.92" S, 30°16'18.18" E), collected 27 March 2011 by J.M. Dehling; ZMB 77224, adult male, from the Mugesera wetland, Bugesera District, East Province, Rwanda (2°12'15.95" S, 30°15'49.25" S), collected 27 March 2011 by B. Dumbo and J.M. Dehling; ZMB 77683 juvenile, ZMB 77684 adult female, ZMB 77685 adult male, all from the Mugesera wetland, Bugesera Province, southeastern Rwanda, collected 26 February 2012 by J.M. Dehling; ZMB 77225, adult male, from a wetland of the Akagera River, Kihere District, East Province, Rwanda (2°13'27.63" S, 30°49'39.06" E), collected 31 March 2011 by J.M. Dehling; ZMB 77746–48, three adult males, from a swamp in farmland on the eastern outskirts of Ruhengeri, Musanze District, North Province, Rwanda (1°30'25.73" S, 29°39'12.11" E), collected 30 March 2012 by J.M. Dehling.

Diagnosis: The advertisement call (Fig. 13) consists of an initial brief note of 13 pulses, followed by three slower pulses, with a duration of 0.14 s. It can be distinguished from species producing only a single note, and those producing only a buzz: *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. jacobseni*, *H. lupiroensis*, and *H. nasutus*. It differs from species producing a call over 0.2 s: *H. benguellensis*, *H. inyangae* and *H. viridis*. It differs from the species that have five or more slower pulses: *H. friedemanni*, *H. igbettensis* and *H. poweri*. The initial note of the call of *H. howelli* consists of only eight pulses, distinguishing it from *H. rwandae* with 13. See Table 3 for a summary of call parameters. The snout is sharply rounded in profile, which distinguishes it from those species with truncated, shark-like, or bluntly rounded snouts: *H. adspersus*, *H. benguellensis*, *H. dartevellei*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. jacobseni*, *H. poweri*, and *H. viridis*. The third and fifth toes webbed three-fourth the way between disc and distal subarticular tubercle, distinguishing it from the species where the webbing does not reach beyond the distal subarticular tubercles of the third and/or fifth toe: *H. acuticeps*, *H. benguellensis*, *H. dartevellei*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. nasutus*, *H. poweri*, and *H. viridis*. It differs from *H. friedemanni* which has all the toes webbed to the disc, and from *H. lupiroensis* and *H. nasutus* which have three phalanges free of web on the inner side of the fourth toe. Standard measurements of the holotype are compared with the other species in Appendix 2.

Description of Holotype. Body long and slender, widest at temporal region, slightly tapering to groin; head comparatively small (HL/SUL 0.33, HW/SUL 0.30), not wider than trunk, longer than wide (HL/HW 1.10); snout long (SL/HL 0.44), pointed in dorsal view, acute in profile (Fig. 6), considerably projecting beyond lower jaw, wider than long (SL/EE 0.77); canthus rostralis distinct, moderately sharp, almost straight-lined from eye to just beyond nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed dorsolaterally; situated much closer to tip of snout than to eye (EN/NS 1.42), separated from each other by distance greater than distance between eye and nostril (NN/EN 1.13); eyes directed anterolaterally, moderately protruding, relatively small (ED/HL 0.31); eye diameter shorter than snout (ED/SL 0.70); interorbital distance much wider than upper eyelid (IO/EW 1.71), and greater than internarial distance (IO/NN 1.16); tympanum not visible externally; upper jaw with dentition; teeth on premaxilla larger than those on maxilla; choanae small, oval, located far anterolaterally at margins of roof of the mouth, concealed by upper jaw for about the half in ventral view; vomer processes and teeth absent; tongue long 4.9, and narrow (2.4 at widest point), free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular, mostly unpigmented and translucent when fully inflated; gular flap consisting of two medially arranged, subcircular areas of thickened skin, immediately adjacent to each other; anterior part cream-coloured, larger, more granular, and thicker than posterior white-coloured part; in resting position only anterior part visible from ventral;

vocal sac aperture on each side of the mouth, situated lateral from and close to base of tongue, slit-like, long, directed posterolaterally.

Dorsal surfaces of head, trunk and limbs generally appearing smooth but with many densely and more or less evenly scattered tiny, low, spine-like tubercles, hardly visible with the naked eye; ventral surface of limbs and gular smooth, chin and abdomen slightly more areolate; supratympanic fold absent.

Fore limbs slender; hand moderately large (HND/SUL 0.29); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV, with proximal tubercle on finger IV hardly discernible; webbing formula of the hand $I2^+ - 2II2 - 2.75III2 - 2IV$ (after Myers & Duellman [1982]); thenar tubercle indistinct, low; palmar tubercles absent; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.63); tibio-tarsal articulation reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.54), longer than thigh (TFL/THL 1.11); heels overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.81); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) $I1.5 - 2^*II1.25 - 2^*III1.25 - 2IV2 - 1.25V$; inner metatarsal tubercle small, oval, prominent; outer one larger, almost circular, low and less distinct.

Colouration in life. Generally weakly pigmented and skin more or less translucent. Dorsum and dorsal surface of head and limbs yellowish green; lateral sides of head and scapular region light green; light, yellowish-white, moderately broad dorsolateral stripe running along each side of the body from lateral edge of upper eyelid to groin, continued as faint, hardly discernible line from eyelid to tip of snout; very small dark brown to black dots and larger brown to reddish brown specks on dorsum, most densely along both sides of canthus rostralis and upper eyelid and to lesser extent on both sides of dorsolateral stripe; dots roundish, specks shaped like stars or neurons with many dendrites; distal portions of fingers and toes, especially the tips, yellow; ventral side and parts of dorsal side of thigh and upper arm largely unpigmented, appearing bluish-green; peritoneum white, shining through the translucent belly skin; most of internal organs covered with silvery-white tissue (only visible when dissected). Iris reddish-brown during the night, yellowish-brown during the day. **Colouration in preservative.** All colours have faded to yellow; gular flap whitish-yellow.

Paratype variation. The paratypes are similar to the holotype in measurements (Appendix 2). Female type specimens (SUL 18.2–20.4, mean 19.2, n=3) are about as large as males (SVL 18.4–22.0, mean 19.5, n=15). Colouration of male paratypes is similar to that of the holotype. In some specimens, however, the pattern of dots and speckles is more pronounced. In others, the lateral stripe is less distinct. The light canthal stripe is completely absent in ten male paratypes and in seven paratypes as faintly visible as in the holotype. All females observed in the field, including the female paratypes, lack the light dorsolateral and canthal stripes, gular sacs and flaps, and the spiny dorsal tubercles (Fig. 8). In life, the flanks of the body turn reddish in active males, especially those which are calling.

Eggs and tadpoles. Several females with enlarged ovarian eggs were observed but only three of them were collected (ZMB 77143, 77425, 77684). Their ovaries contain about 80 enlarged eggs with a diameter of ca. 0.7–0.8. Eggs are darkly pigmented on the animal pole and white on the vegetative pole. Tadpoles are unknown.

Habitat. We found the species only in open habitats, in natural wetlands (Mugesera, Akagera) as well as at the edge of ponds and other lentic water bodies in cultivated areas. Specimens were observed perching on leaves of vegetation between 5 cm and 1.2 m above the ground or the water level. Males called from elevated positions, sometimes in close proximity to each other (ca. 15 cm). Several males were found engaged in combat. They were holding, pushing, and kicking each other, apparently fighting over an apparently favoured calling site. They also emitted aggressive calls which differed markedly from the advertisement call. The male aggression call is shown in Fig. 14. The following species were found sympatrically or even syntopically with the new species: *Afrivalus quadrivittatus*, *Amietia* cf. *angolensis*, *Amietophrynus kisoensis*, *A. regularis*, *Hyperolius cinnamomeoventris*, *H. kivuensis*, *H. lateralis*, *H. viridiflavus*, *Kassina senegalensis*, *Leptopelis kivuensis*, *Phrynobatrachus* cf. *mababiensis*, *P. natalensis*, *Phrynobatrachus* sp., *Ptychadena anchietae*, *P. porosissima*, *P. cf. mascareniensis*, *Ptychadena* sp. and *Xenopus victorianus*.

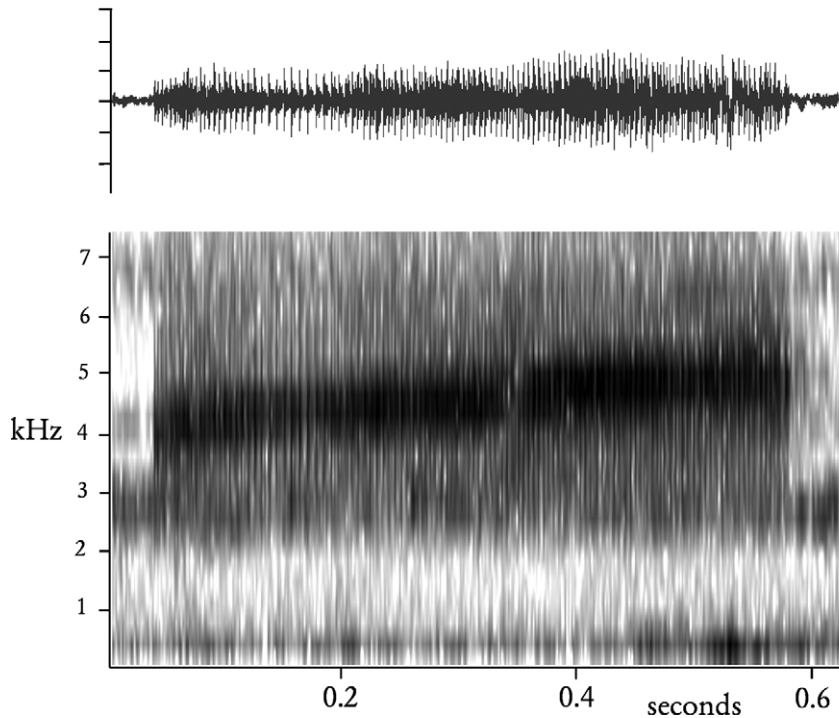


FIGURE 14. Aggression call of *H. rwandae*.

Distribution. We observed the species at three further locations in Rwanda, near Gitarama (2°05'57.14" S, 29°46'41.94" E, Muhanga District, Southern Province, central Rwanda) and west of Kigali (1°57'49.11" S, 30°00'05.87" E, Kamonyi District, Southern Province, central Rwanda; and 1°56'59.33" S, 30°00'48.97" E, Nyarugenge District, Kigali Province, central Rwanda). The localities from where the species is known are in the northern, central, southern and eastern parts of Rwanda. Elevations of the sites ranged from 1300 m (Akagera wetland) to 1800 m (Ruhengeri). Population size was high at all sites. Because the locations in Butare, Mugesera, and Akagera are only 17 km and 15 km from the border with Burundi and 1.6 km from the border with Tanzania, respectively, and especially because the wetlands of Mugesera and Akagera continue into Burundi and Tanzania, respectively, we assume that the species occurs in these countries as well.

Etymology. The species epithet derives from Rwanda. It is a noun in genitive singular.

Remarks. Although the species is so far only known from several localities in Rwanda, it is probably more widespread. The species occurs in both natural and cultivated areas. Therefore, we propose that it should be classified as Least Concern under the current criteria of the IUCN redlist.

Hyperolius viridis Schiøtz, 1975

Robust Long Reed Frog

(Fig. 9)

Genetic material. ZMB 76096 (Vintukutu Forest Reserve, Malawi); ZMB 76102 (Kaningina Forest Reserve, Malawi) (Fig. 1).

Diagnosis. The advertisement call (Fig. 15) consists of a brief initial note consisting of 26 pulses followed by five slower pulses, with a duration of 0.41 s. It can be distinguished from species producing only a single note, and those producing only a buzz: *H. acuticeps*, *H. adspersus*, *H. dartevellei*, *H. jacobseni*, *H. lupiroensis*, and *H. nasutus*. It can be distinguished from the other species producing a two-part call, which have a duration less than 0.4 s: *H. friedemanni*, *H. howelli*, *H. igbettensis*, *H. inyangae*, *H. poweri* and *H. rwandae*. It differs from *H. benguellensis* which only has five pulses in the initial note. See Table 3 for a summary of call parameters. The snout is bluntly rounded, distinguishing it from those with truncated, shark-like or sharply rounded snouts: *H. acuticeps*, *H. benguellensis*, *H. dartevellei*, *H. friedemanni*, *H. howelli*, *H. inyangae*, *H. lupiroensis*, *H. nasutus*,

and *H. rwandae*. The webbing has one phalanx free on the first to third toes, just more than one free on the fourth toe, and half a phalanx free on the fifth toe. It can be distinguished from the species that are webbed to the disc on the fifth toe: *H. adspersus*, *H. friedemanni*, *H. jacobsoni*, *H. lupiroensis*, and *H. rwandae*. It differs from the species that have more than half a phalanx free of web on the fifth toe: *H. acuticeps*, *H. benguellensis*, *H. dartevellei*, *H. howelli*, and *H. inyangae*. It can be distinguished from the remaining species that are webbed to the disc on the third or fourth toes: *H. adspersus* and *H. nasutus*. Our specimens show the stocky build noted by Schiøtz (1975).

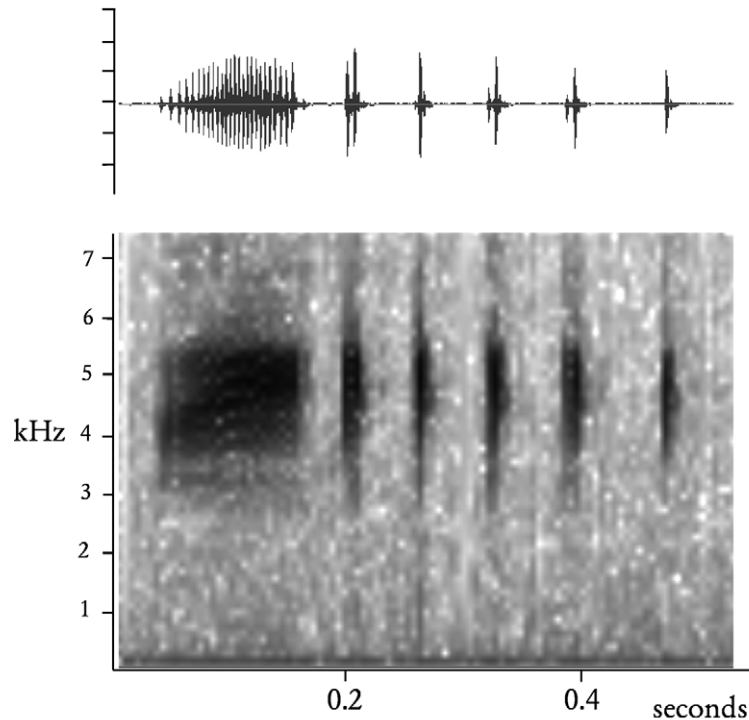


FIGURE 15. Advertisement call of *H. viridis* Sumbawanga (A. Schiøtz)

Description of a Vintukutu specimen. An adult male ZMB 76096, from Vintukutu Forest Reserve, Malawi. Body short and compact, widest at mid-body, tapering to head and neck; head very small (HL/SUL 0.22, HW/SUL 0.34), narrower than mid part of trunk, wider than long (HL/HW 0.64); snout short (SL/HL 0.59), subovoid in dorsal view, almost truncate in profile (Fig. 6), only slightly protruding beyond lower jaw, almost as long as wide (SL/EE 0.96); canthus rostralis distinct, rounded, slightly concave between eye to nostril, slightly convex near tip of snout; loreal region almost vertical, slightly concave; nostril directed dorsolaterally; situated closer to tip of snout than to eye (EN/NS 1.18), separated from each other by distance equal to distance between eye and nostril (NN/EN 0.94); eyes directed anterolaterally, moderately protruding, relatively large (ED/HL 0.59); eye diameter equal to snout length (ED/SL 1.0); interorbital distance much narrower than upper eyelid (IO/EW 0.36), but greater than internarial distance (IO/NN 1.3); tympanum not visible externally; upper jaw with dentition; choanae small, round, located far anterolaterally at margins of roof of the mouth, completely concealed by upper jaw in ventral view; vomer processes and teeth absent; tongue slightly longer than wide (2.1), free for about three-fourths of length, bifurcated distally for about one-fourth of length; median lingual process absent; vocal sac single, median, subgular; The gular flap is large (almost completely covering the throat), glandular and wider (4.7) than long (4.1), white in preservative with many minute melanophores.

The skin of the dorsum and upper limbs appears smooth, finely granular under dissecting microscope; flat granular belly; supratympanic fold absent.

Fore limbs slender; hand small (HND/SUL 0.19); tips of fingers enlarged into broad oval disks, each with circummarginal groove; relative length of fingers: I<II<IV<III; subarticular tubercles rounded, well developed, with one on fingers I and II, two on fingers III and IV; only basal webbing between fingers; thenar tubercle oval and prominent; palmar small, round and indistinct; metacarpals without supernumerary tubercles; nuptial pads or asperities absent.

Hind limbs slender, moderately long (LEG/SUL 1.45); tibio-tarsal articulation reaching to level of tip of snout when legs are adpressed to body; tibiofibula moderately long (TFL/SUL 0.54), longer than thigh (TFL/THL 1.09); heels only slightly overlapping each other considerably when knees are flexed and thighs are held laterally at right angle to body; foot shorter than tibiofibula (FOT/TFL 0.79); relative length of toes: I<II<III<V<IV; discs of toes smaller than those of fingers; subarticular tubercles: one on toes I and II, two on toes III and V, and three on toe IV; pedal webbing formula (Fig. 7) **I**0.5–**II**0.25–**III**0.25–**IV**1–**0.25V**; inner metatarsal tubercle small, oval, not very prominent; outer one not discernible.

Colouration in life. The dorsal and ventral surfaces are white, dorsal surfaces (including thighs) densely covered with minute melanophores. **Colouration in preservative.** All colours have faded to yellow; gular flap whitish.

Eggs and tadpoles. Unknown.

Remarks. The species is known from southern Tanzania and northern Malawi. We suggest that the IUCN status of Data Deficient be maintained until further studies are undertaken.

Incertae sedis

Hyperolius papyri Werner, 1908 is regarded as *incertae sedis*, as the original description is not sufficiently diagnostic, and we have no fresh material from Southern Sudan for DNA analysis.

Species distribution model

The potential distribution of the *H. nasutus* group (Fig. 16) is remarkably similar to the known distribution of the clade (IUCN 2011) comprising major parts of sub-Saharan Africa. The BIOCLIM model suggests a major connected part of the potential distribution in central Africa ranging from southern Cameroon southward to southern Angola and westward to the Kenyan highlands and southward to South Africa. The most humid areas within the central Congo basin and some parts of the West African coast are outside of the occupied climatic space. When interpreting the results, it needs to be acknowledged that the model can only be seen as a rough approximation of the distribution of the clades due to the very limited sample size. The potential distribution describes the climatic space occupied by all members in the group, so the niche of each single species might be much smaller. As soon as additional localities of species can be reliably determined, a model may be refined and computed separately for each species.

The model (Fig. 16) incorporates specimens that extend the range of the group. These are additional records of *H. igbettensis* from Guinea (number 6 in Fig. 1) and *H. jacobseni* from the Central African Republic (number 8 in Fig. 1).

Discussion

This group of long reed frogs is ubiquitous across the humid to semi-humid tropics of Africa (Fig. 16). We suggest that a combination of DNA barcoding, advertisement calls and some aspects of morphology such as webbing and snout shape, is useful in delimiting species. Scientists are univocal that such a pluralistic approach, elsewhere termed 'Integrative Taxonomy', improves our understanding of diversity in an evolutionary framework and helps to identify species. Padial *et al.* (2010) reviewed integration of taxonomically useful characters (i.e. data obtained through independent methodological approaches) via accumulation versus via congruence and concluded that they can lead to both over- and under estimation of species richness. Because long reed frogs are morphologically difficult to distinguish, we were careful to only recognise a species when molecular in combination with call differences could be shown. Snout shape and degree of webbing provided additional support (Table 2). This approach was termed congruence by Padial *et al.* (2010), leading to the tentative conclusion that our revision of long reed frogs may even underestimate true species diversity in this group. Cryptic species diversity may be present in character sets other than morphology, suggesting that more species await identification.

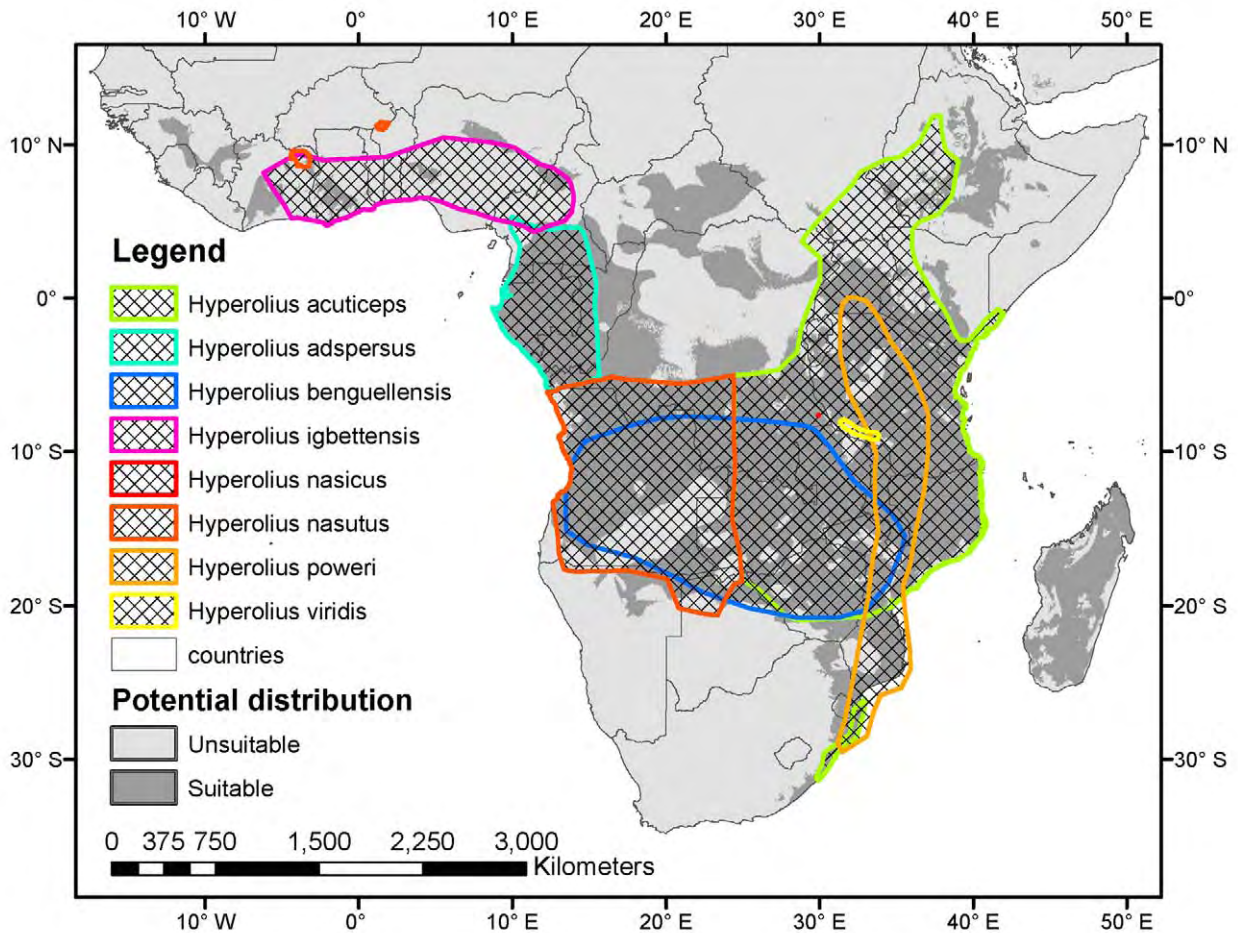


FIGURE 16. Potential distribution of the *H. nasutus* group derived from a BIOCLIM model. All grey areas are within the environmental envelope of the group, pale areas are outside of the envelope. Overlain is the distribution of the species as recognised by the IUCN (2011). Note that the IUCN taxonomy and species distributions are used purely for illustrating the overall range of the group as known before the present study.

The polytomies shown in Fig. 2 may indicate that some species recognised here split only recently (e.g. Schick *et al.* 2008). In such cases, introgression or incomplete lineage sorting, e.g. with Pleistocene interplay of cold and warm phases, may have occurred (e.g. Noonan & Gaucher 2005; Vences & Wake 2007). The 16S difference between our species is mostly moderate to high (Table 2), with the smallest distances reaching 2.5 % or more, in all but two species pairs. Some individuals show very low to low differences between species. A difference of 3% has been proposed as a rule of thumb as an operable value when distinguishing species using 16S sequences (e.g. Fouquet *et al.* 2007). This applies to most of the species we recognise here (which are otherwise confirmed on the basis of vocalisations, see above). However, it is known that *p* distances can be much lower between taxa that are otherwise confirmed as 'good' species (Vieites *et al.* 2009; Zimkus & Schick 2010).

There are three kinds of advertisement calls: those consisting of a brief single unpulsed note, those consisting of a pulsed initial note, and a number of slower pulses, and those consisting of a brief chirp. There are many subtle differences between the species, that were not appreciated in an earlier paper that divided the group into three species based on the three kinds of calls (Channing *et al.* 2002). Small differences in the pulse rate of the slower sections, the duration of the call, and the frequency modulation of the call, allow the species as recognised here to have unique advertisement calls. Advertisement call differences are generally associated with species differences. However, the calls of *H. lupiroensis* and *H. lamottei* overlap in all parameters, despite the significant genetic and morphological differences between these geographically widely separated species. This finding offers interesting opportunities to explore the relationship between speciation and advertisement call divergence.

To strictly operate with integration by congruence and our initial assumption that two or three species can be

breeding in the same area, made it imperative that the call and morphology results be based on exactly the specimens that had been sequenced. The exceptions are a call of *H. viridis* from the type locality, when no other recording from a sequenced specimen was available and a call of *H. dartevellei* from the Congo River, that cannot be linked to a sequenced voucher, although all 32 sequenced individuals from there fall into the same species. While we were certain to not mix characters of different species, this procedure limits our study (and species definitions) to a few specimens of each species. This offers opportunities for further work to investigate intra- and interspecific variation in the species recognised here. It is clear that, for example, the within-species variation in characters such as advertisement calls is understated here. Other challenging questions include the geographic distributions of all species, and the niche partitioning of those that are sympatric.

An important implication for future studies of intra- and interspecies variation in long reed frogs concerns the large amount of specimens in museum collections for which no recordings or DNA are available. Many will probably never be positively identified.

This study recognised two species from Ikelenge in north-western Zambia; *H. dartevellei* and *H. nasicus*. This is a positive step in solving what Schiøtz (2006b) called 'the Hillwood mystery'.

Acknowledgements

Arie van der Meijden provided sequences of material from Kenya. The United States National Museum, through Roy W. McDiarmid, kindly supplied tissues and loaned voucher material from Gabon and Congo-Brazzaville. The Congo-Brazzaville material was collected by Kate Jackson, and we thank her for permitting us to use it. Pedro vas Pinto made it possible for AC to visit Calandula, the type locality of *Hyperolius nasutus*. Colin Tilbury and James Harvey kindly provided tissues from the DRC. Ed Netherlands provided specimens from Monkey Bay in Malawi. Gregor Jongsma provided calls and photos of *H. adspersus* from Gabon. SAIAB is acknowledged, through Roger Bills, for material from north-western Zambia and Mozambique. We acknowledge the assistance of Barry Clarke and David Moyer. We thank Arne Schiøtz for helpful comments, and for assistance in obtaining call recordings. Martin Jansen kindly provided pictures, measurements and the webbing formula of the holotype of *H. friedemanni*. Jan Venter of the Eastern Cape Parks and Tourism Agency is thanked for providing logistical and financial support to collect *H. poweri*. JMD would like to thank Antoine Mudakikwa (Rwanda Development Board - Tourism & Conservation) for kindly issuing permissions for field studies, handling and exportation of specimens and Eberhard Fischer (University of Koblenz), Bonny Dumbo (Bukavu, DRC), and Siegmair Seidel (Butare Field Station, University of Koblenz) for logistic support and help during field work.

References

- Adeba, P.J., Kouassi, P. & Rödel, M.-O. (2010) Anuran amphibians in a rapidly changing environment – revisiting Lamto, Côte d'Ivoire, 40 years after the first herpetofaunal investigations. *African Journal of Herpetology*, 59, 1–16. <http://dx.doi.org/10.1080/04416651003595337>
- Amiet, J.-L. (2005) Les *Hyperolius* camerounais du groupe d' *H. nasutus* (Amphibia, Anura, Hyperoliidae). *Revue Suisse de Zoologie*, 112, 271–310.
- Amiet, J.-L. (2006a) *Hyperolius igbettensis*, In: IUCN 2008. IUCN Red List of Threatened Species. Version 2008. <www.iucnredlist.org>. Downloaded on 9 January 2012.
- Amiet, J.-L. (2006b) *Hyperolius adspersus*, In IUCN 2008. IUCN Red List of Threatened Species. Version 2008. <www.iucnredlist.org>. Downloaded on 9 January 2012.
- Benson, D.A., Karsch-Mizrachi, I., Clark, K., Lipman, D.J., Ostell, J. & Sayers, E.W. (2012) GenBank. *Nucleic Acids Research* 40 (Database issue), D48–53. <http://dx.doi.org/10.1093/nar/gkr1202>
- Biju, S.D., Van Bocxlaer, I., Mahoney, S., Dinesh, K.P., Radhakrishnan, C., Zachariah, A., Giri, V. & Bossuyt, F. (2011) A taxonomic review of the Night Frog genus *Nyctibatrachus* Boulenger, 1882 in the Western Ghats, India (Anura: Nyctibatrachidae) with description of twelve new species. *Zootaxa*, 3029, 1–96.
- Bossuyt, F. & Milinkovitch, M.C. (2000) Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proceedings of the National Academy of Sciences, USA*, 97, 6585–6590. <http://dx.doi.org/10.1073/pnas.97.12.6585>
- Channing, A., Moyer, D. & Burger, M. (2002) Cryptic species of sharp-nosed reed frogs in the *Hyperolius nasutus* complex: advertisement call differences. *African Zoology*, 37, 91–99.

- Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9, 1657–1660. <http://dx.doi.org/10.1046/j.1365-294x.2000.01020.x>
- Dehling, J.M. (2012) An African glass frog: a new *Hyperolius* species (Anura: Hyperoliidae) from Nyungwe National Park, southern Rwanda. *Zootaxa*, 3391, 52–64.
- Flot, J.-F. (2010) SeqPHASE: a web tool for interconverting PHASE input/output files and FASTA sequence alignments. *Molecular Ecology Resources*, 10, 162–166. <http://dx.doi.org/10.1111/j.1755-0998.2009.02732.x>
- Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M. & Gemmill, N.J. (2007) Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS ONE*, 2:e1109. <http://dx.doi.org/10.1371/journal.pone.0001109>
- Frost, D.R. (2011) *Amphibian Species of the World: an Online Reference, Version 5.5* (31 January, 2011) Electronic Database accessible at <http://research.amnh.org/vz/herpetology/amphibia/> American Museum of Natural History, New York, USA. <http://dx.doi.org/10.1126/science.os-1.19.223>
- Goebel, A.M., Donnelly, J.M. & Atz, M.E. (1999) PCR primers and amplification methods for 12S ribosomal DNA, the control region, cytochrome oxidase I, and cytochrome *b* in bufonids and other frogs, and an overview of PCR primers which have amplified DNA in amphibians successfully. *Molecular Phylogenetics & Evolution*, 11, 163–199. <http://dx.doi.org/10.1006/mpev.1998.0538>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. <http://dx.doi.org/10.1002/joc.1276>
- Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2012) Dismo: Species distribution modelling. R package version 0.7-17. <http://CRAN.R-project.org/package=dismo>.
- Hillis, D.M., Mable, B.K., Larson, A., Davis, S.K. & Zimmer, E.A. (1996) Nucleic acids IV: Sequencing and cloning, In Hillis, D.M., Moritz, C. & Mable, B.K (eds) *Molecular Systematics* 2nd ed. Sinauer Associates, Sunderland, Massachusetts, USA.
- IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2 <www.iucnredlist.org>. Downloaded on 06 April 2012.
- 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. <http://dx.doi.org/10.1073/pnas.86.16.6196>
- Köhler, J., Scheelke, K., Schick, S., Veith, M. & Lötters, S. (2005a) Contribution to the taxonomy of hyperoliid frogs (Amphibia: Anura: Hyperoliidae): advertisement calls of twelve species from East and Central Africa. *African Zoology*, 40, 127–142.
- Köhler, J., Vietes, D.R., Bonett, R.M., Hita Garcia, F., Glaw, F., Steinke, D. & Vences, M. (2005b) New amphibians and global conservation: a boost in species discoveries in a highly endangered vertebrate group. *BioScience*, 55, 693–696. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0693:NAAGCA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0693:NAAGCA]2.0.CO;2)
- Lötters, A., Schick, S., Scheelke, K., Teege, P., Kosuch, J., Rotich, D. & Veith, M. (2004) Bio-sketches and partitioning of sympatric reed frogs, genus *Hyperolius* (Amphibia: Hyperoliidae), in two humid tropical African forest regions. *Journal of Natural History*, 38, 1969–1997. <http://dx.doi.org/10.1080/00222930310001613584>
- Mercurio, V. (2011) *Amphibians of Malawi*. Edition Chimaira, Frankfurt am Main. <http://dx.doi.org/10.1086/659940>
- Moritz, C. & Cicero, C. (2004) DNA barcoding: promise and pitfalls. *PLoS Biology* 2(10), e354. <http://dx.doi.org/10.1371/journal.pbio.0020354>
- Myers, C.W. & Duellman, W.E. (1982) A new species of *Hyla* from Cerro Colorado, and other treefrog records and geographical notes from western Panama. *American Museum Novitates*, 2752, 1–32.
- Nix, H. (1986) A biogeographic analysis of Australian elapid snakes. In *Atlas of elapid snakes of Australia*, ed Longmore, R. Bureau of Flora and Fauna, Canberra, pp 4–15.
- Noonan, B.P. & Gaucher, P. (2005) Phylogeography and demography of Guianan harlequin toads (*Atelopus*): diversification within a refuge. *Molecular Ecology*, 14, 3017–3031. <http://dx.doi.org/10.1111/j.1365-294X.2005.02624.x>
- Padial, J.M., Miralles, A., de la Riva, I. & Vences, M. (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 7, article 16. <http://dx.doi.org/10.1186/1742-9994-7-16>
- Perret, J.-L. (1976) Revision des amphibiens Africaines et principalement des types conservés au Musée Bocage de Lisbonne. *Arquivos do Museu Bocage* ser 2, 6, 15–34.
- Poynton, J.C. (1964) The amphibians of southern Africa: a faunal study. *Annals of the Natal Museum*, 17, 1–334.
- Poynton, J.C. & Broadley, D.G. (1987) Amphibia Zambesiaca 3. Rhacophoridae and Hyperoliidae. *Annals of the Natal Museum*, 28, 161–229.
- Rödel, M.-O. (2000) *Herpetofauna of West Africa, Vol. I: Amphibians of the West African savanna*. Edition Chimaira, Frankfurt am Main.
- Rödel, M.-O. & Agyei, A.C. (2003) Amphibians of the Togo-Volta highlands, eastern Ghana. *Salamandra*, 39, 207–234.
- Rödel, M.-O., Bangoura, M.A. & Böhme, W. (2004) The amphibians of south-eastern Republic of Guinea (Amphibia: Gymnophiona, Anura). *Herpetozoa*, 17, 99–118.
- Rödel, M.-O. & Ernst, R. (2003) The amphibians of Marahoué and Mont Péko National Parks, Ivory Coast. *Herpetozoa*, 16, 23–39.
- Rödel, M.-O., Kosuch, J., Grafe, T.U., Boistel, R., Assemian, N.E., Kouamé, N.G., Tohé, B., Gourène, G., Perret, J.-L., Henle, K., Tafforeau, P., Pollet, N. & Veith, M. (2009) A new tree-frog genus and species from Ivory Coast, West Africa (Amphibia: Anura: Hyperoliidae). *Zootaxa*, 2044, 23–45.

- Rödel, M.-O., Lampert, K.P. & Linsenmair, K.E. (2006) Reproductive biology of the West African savannah frog *Hyperolius nasutus* Günther, 1864 (Amphibia: Anura: Hyperoliidae). *Herpetozoa*, 19, 3–12.
- Rödel, M.-O., Sandberger, L., Penner, J., Mané, Y. & Hillers, A. (2010) The taxonomic status of *Hyperolius spatzi* Ahl, 1931 and *Hyperolius nitidulus* Peters, 1875 (Amphibia: Anura: Hyperoliidae). *Bonn zoological Bulletin*, 57, 177–188.
- Rödel, M.-O. & Schiøtz, A. (2004) *Hyperolius lamottei*, In IUCN 2009. IUCN Red List of Threatened Species. Version 2009.1. <www.iucnredlist.org>. Downloaded on 19 January 2012.
- Schick, S., Kielgast, J., Rödder, D., Muchai, V., Burger, M. & Lötters, S. (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. (1975) *The treefrogs of Eastern Africa*. Steenstrupia, Copenhagen.
- Schiøtz, A. (1999) *Treefrogs of Africa*. Edition Chimaira, Frankfurt am Main.
- Schiøtz, A. (2006a) Notes on the genus *Hyperolius* (Anura, Hyperoliidae) in central République Démocratique du Congo. *Alytes*, 24, 40–60.
- Schiøtz, A. (2006b) Reflections on the *Hyperolius nasutus* group. *Alytes*, 24, 61–71.
- Schiøtz, A. (2008) *Hyperolius nasicus*. In: IUCN 2009. IUCN Red List of Threatened Species. Version 2009.1. <www.iucnredlist.org>. Downloaded on 9 January 2012.
- Schiøtz, A., Channing, A., Largen, M., Howell, K., Lötters, S. (2004) *Hyperolius acuticeps*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. <www.iucnredlist.org>. Downloaded on 24 September 2012.
- Schiøtz, A., Channing, A., Burger, M. & Largen, M. (2008a) *Hyperolius nasutus*, In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 9 January 2012.
- Schiøtz, A., Channing, A., Largen, M., Howell, K. & Lötters, S. (2008b) *Hyperolius acuticeps*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 9 January 2012.
- Schiøtz, A. & Poynton, J. (2008) *Hyperolius benguellensis*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 9 January 2012.
- Schiøtz, A. & van Daele, P. (2003) Notes on the treefrogs (Hyperoliidae) of North-Western Province, Zambia. *Alytes*, 20, 137–149.
- Stephens, M. & Donnelly, P. (2003) A comparison of Bayesian methods for haplotype reconstruction from population genotype data. *American Journal of Human Genetics*, 73, 1162–1169. <http://dx.doi.org/10.1086/379378>
- Templeton, A.R., Crandall, K.A. & Sing, C.F. (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics*, 132, 619–633.
- Veith, M., Kosuch, J., Rödel, M.-O., Hillers, A., Schmitz, A., Burger, M. & Lötters, S. (2009) Multiple evolution of sexual dichromatism in African reed frogs. *Molecular Phylogenetics & Evolution*, 51, 388–393. <http://dx.doi.org/10.1016/j.ympev.2008.12.022>
- Vences, M., Thomas, M., van der Meijden, A., Chiari, A. & Vieites, D.R. (2005) Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Frontiers in Zoology*, 2, 5. <http://dx.doi.org/10.1186/1742-9994-2-5>
- Vences, M. & Wake, D.B. (2007) Speciation, species boundaries and phylogeography of amphibians. In *Amphibian Biology*, eds Heatwole, H. & Tyler, M.J. pp 2613–2671, Surrey Beatty & Sons, Chipping Norton.
- Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F. & Vences, M. (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Science USA*, 196, 8267–8272. <http://dx.doi.org/10.1073/pnas.0810821106>
- Wager, V.A. (1986) *Frogs of South Africa*. Delta Books, Craighall.
- Zimkus, B.M. & Schick, S. (2010) Light at the end of the tunnel: insights into the molecular systematics of East African puddle frogs (Anura: Phrynobatrachidae). *Systematics and Biodiversity*, 8, 39–47. <http://dx.doi.org/10.1080/14772000903543004>

APPENDIX 1. Gazetteer of localities.

Locality	Latitude	Longitude
Akagera wetland, Rwanda	2°13'27.7" N	30°49'39.1" E
Bicuar National Park, Angola	15°06'03.4" S	14°50'21.0" E
Bumba, DRC	2°10'57.0" N	22°28'08.4" E
Butare, Rwanda	2°37'08.0" N	29°45'06.9" E
Bwindi Impenetrable Forest, Uganda	1°03'00.0" S	29°43'00.0" E
Calandula (Duque de Bragança), Angola	9°04'45.0" S	15°47'45.0" E
Camp Nimba, Guinea	7°41'54.9" N	8°23'55.1" W
Chelinda Camp, Malawi	10°34'59.9 S	33°48'00.0 E
Chongoni Forest Reserve, Malawi	14°19'59.9 S	34°15'00.0" E
Congo River near Yekela, site 1, DRC	0°47'25.7" N	24°17'52.5 E
Congo River near Yekela, site 2, DRC	0°49'42.6" N	24°16'26.5" E
Congo River near Yekela, site 3, DRC	0°49'18.7" N	24°16'40.1" E
Congo River near Nganda Kona, site 4, DRC	2°02'13.7" N	22°47'09.6" E
Congo River near Ngengele, site 5, DRC	2°03'32.2" N	22°42'08.4" E
Congo River near Bomani, site 6, DRC	1°16'35.8" N	23°45'38.3 E
Congo River near Bomani, site 7, DRC	1°17'28.9" N	23°45'41.0"E
Congo River near Bomani, site 8, DRC	1°15'18.5" N	23°44'03.4" E
Congo River near Lulu, site 9, DRC	1°15'11.4" N	23°39'49.3" E
Congo River near Lieki, site 10, DRC	0°39'33.3" N	24°11'08.3" E
Congo River near Lieki, site 11, DRC	0.°41'29.8" N	24°11'58.8" E
Congo River near Lieki, site 12, DRC	0.°41'05.1" N	24°13'29.0" E
Elephant's Camp, Mozambique	15°39'19.0" S	30°41'09.0" E
Fungurume, DRC	10°37'00.0" S	26°20'00.0" E
Gatiko, Central African Republic	5°04'43.0" N	20°40'02.0" E
Himo Road, Arusha, Tanzania	3°21'29.6" S	36°50'15.3" E
Humpata, Angola	14°14'17.3" S	13°25'59.9" E
Ikelenge Nature Reserve, Zambia	11°14'17.3" S	24°16'05.3" E
Impongui, Republic of Congo	1°04'36.6" N	17°17'58.8" E
Kakamega, Kenya	0°16'59.9" N	34°45'00.0" E
Kalumbila River bridge, Zambia	12°14'13.2" S	25°20'44.5" E
Kalumbila River, Zambia	12°16'45.1" S	25°19'06.7" E
Kangandala, Angola	9°49'30.4" S	16°54'44.1" E
Kaningina Forest Reserve, Malawi	11°28'00.0 S	34°06'00.0" E
Kaparotta, Botswana	19°00'24.0" S	22°55'36.6" E
Karonga, Malawi	11°22'00.0" S	34°10'00.0" E
Kérouané, Guinea	9°14'24.7" N	8°59'52.0" W
Kisanfu River, DRC	10°48'28.0" S	25°59'24.0" E
Kisangani, DRC	0°30'36.7" N	25°12'19.4" E
Konsankoro, Guinea	9°01'59.9" N	9°00'00.0" W
Korombadou/Tourou, Guinea	9°16'24.6" N	9°08'54.5" W
Lake Carumbo, Angola	7°43'59.9" S	19°55'59.9" E
Lamto, Ivory Coast	0°13'03.4"N	5°01'29.6" W

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APPENDIX 1. (Continued)

Locality	Latitude	Longitude
Loma Mountains Forest Reserve, Sierra Leone (LOM100)	9°12'45.6" N	11°08'40.1" W
Loma Mountains Forest Reserve, Sierra Leone (LOM99)	9°12'58.8" N	11°07'52.8" W
Lupiro, Tanzania	8°25'29.3" S	36°41'33.1" E
Madehani, Tanzania	9°21'00.0" S	34°01'59.9" E
Mare d'hivenage, Guinea	7°39'38.1" N	8°22'49.2" W
Mkambati Nature Reserve, South Africa	31°16'39.9" S	30°00'27.3" E
Monkey Bay, Malawi	14°04'37.0" S	34°55'34.2" E
Mont Béro Forest Reserve, Guinea	8°08'41.0" N	8°33'11.1" W
Mugesera wetland, Rwanda	2°12'34.1" N	30°15'26.4" E
National Forestry School, Libreville, Gabon	0°03'37.1" N	9°20'14.2" E
Himo Road, Arusha, Tanzania	3°21'29.6" S	36.83758 E
Mkambati Nature Reserve, South Africa	31°16'39.9" S	30°50'15.3" E
Nimba Mountains, Guinea (MTN255-256)	7°40'22.8" N	8°21'55.0" W
Nimba Mountains, Guinea (MTN93)	7°41'47.7" N	8°23'55.1" W
Nimini Forest Reserve, Sierra Leone	8°29'58.7" N	11°05'30.1" W
Nyanga Flats, low bridge, Zimbabwe	18°10'00.6" S	32°42'48.6" E
Plain of Vera, Gabon	2°49'43.0" S	10°12'57.2" E
Port Edward, South Africa	31°04'00.8" S	30°11'16.1" E
Quantum Mine Camp, Zambia	12°14'13.2" S	25°20'44.5" E
Rhodes Dam, Nyanga NP, Zimbabwe	18°17'20.3" S	32°43'24.4" E
Rundu, Namibia	17°55'12.0" S	19°45'00.0" E
Savanne de But, Guinea	7°41'17.1" N	8°25'44.5" W
Satellite Camp, Mozambique	15°39'11.0" S	30°35'14.0" E
Setecama Road, Gabon	2°43'58.9" S	9°58'41.8" E
Uemba Road, Gabon	2°44'49.4" S	10°00'17.9" E
Vintukutu Forest Reserve, Malawi	10°45'00.0" S	34°16'00.0" E
Vumbura, Botswana	18°58'38.0" S	22°53'41.3" E
Xigera, Botswana	19°23'03.8" S	22°43'44.6" E
Zootecnica Plateau, Angola	14°57'56.9" S	13°20'40.5" E

APPENDIX 2. Comparative measurements (in mm) of representative specimens. For abbreviations see Materials and Methods.

Specimen	SUL	TFL	LEG	FOT	HND	HW	HL	ED	EN	NS	NN	SL	EE	IO	EW	THL
<i>Hyperolius acuticeps</i> MCZ A-137085, female	22.0	10.7	31.8	8.8	5.9	6.6	7.3	1.9	2.0	1.4	1.8	3.1	4.3	3.0	3.0	10.5
<i>Hyperolius acuticeps</i> MCZ A-137086, female	21.4	11.4	32.9	9.9	5.8	7.0	6.4	2.2	1.6	0.9	2.2	3.0	4.5	2.6	1.4	10.9
<i>Hyperolius adpersus</i> USNM 578142, male	19.5	10.5		8.9	5.4	6.4	5.3	2.0	1.6	0.7	1.9	2.7	4.2	1.9	1.3	9.7
<i>Hyperolius benguellensis</i> ZMB 77272, male	19.3	10.2	29.9	8.5	5.7	5.7	6.4	2.1	1.8	1.1	1.9	2.7	4.0	4.0	2.4	11.2
<i>Hyperolius benguellensis</i> male	19.3	10.1	31.9	7.4	5.2	5.8	5.2	1.7	1.9	1.1	2.1	2.9	3.7	2.3	1.4	10.1
<i>Hyperolius benguellensis</i> ZMB 77275, female	23.7	12.0	34.3	9.7	6.2	7.4	6.3	2.1	1.9	1.3	2.2	3.3	4.5	3.1	1.2	11.0
<i>Hyperolius benguellensis</i> ZMB 77271, female	23.5	13.4	37.2	10.3	6.7	7.3	7.1	2.2	2.3	1.1	2.1	3.4	5.2	2.8	1.8	13.3
<i>Hyperolius friedemanni</i> ZMB 76095, paratype, female	21.0	11.7		14.9	6.0	5.1	7.1	1.8	2.3	1.2	1.7	2.8	5.7	2.7	2.5	11.0
<i>Hyperolius howelli</i> SAIAB 118979, holotype, male	20.2	11.3	27.5	7.9	4.9	6.2	6.4	2.3	1.6	0.8	1.7	3.1	4.1	2.7	2.8	8.9
<i>Hyperolius howelli</i> SAIAB 118980-1, paratype, female	19.0	11.0	29.7	8.7	4.0	5.5	6.7	2.1	1.6	0.8	1.7	2.6	3.8	2.7	2.8	8.1
<i>Hyperolius howelli</i> SAIAB 118980-2, paratype, male	21.0	10.3	32.6	8.5	5.6	6.1	7.1	2.2	1.5	0.9	1.9	2.0	3.8	2.8	1.0	9.6
<i>Hyperolius igbettensis</i> ZMB 77410, female	21.1	12.2	33.5	10.5	5.9	5.5	7.0	2.0	2.1	1.1	1.9	3.0	4.1	2.1	3.0	10.8
<i>Hyperolius inyangae</i> ZMB 77276, holotype male	21.7	10.4	31.0	8.8	5.2	6.4	8.1	1.9	2.0	2.0	2.3	3.7	4.5	2.4	2.1	10.7
<i>Hyperolius inyangae</i> ZMB 77277, paratype, female	21.6	11.1	31.9	7.0	5.3	7.0	7.4	2.2	1.9	1.3	2.1	3.4	4.1	2.5	1.3	11.1
<i>Hyperolius inyangae</i> ZMB 77278, paratype, male	19.7	10.3	27.7	8.8	5.1	6.5	6.8	2	1.8	1.3	1.9	2.9	3.9	2.4	1.7	10.2

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APPENDIX 2. (Continued)

Specimen	SUL	TFL	LEG	FOT	HND	HW	HL	ED	EN	NS	NN	SL	EE	IO	EW	THL
<i>Hyperolius inyangae</i> ZMB 77279, paratype, male	19.0	9.6	26.4	7.3	4.9	6.0	6.6	1.7	1.8	1.4	2.1	3.3	4.0	2.7	1.6	9.5
<i>Hyperolius jacobsoni</i> ZMB 77280, holotype, male	21.3	11.1	34.4	8.7	6.0	5.9	7.2	1.8	1.6	1.0	2.1	3.1	4.2	2.9	1.0	10.6
<i>Hyperolius jacobsoni</i> ZMB 77281, paratype, female	19.5	11.2	23.3	8.4	6.7	6.2	6.7	1.9	1.9	0.8	1.9	3.0	4.1	2.5	1.0	10.5
<i>Hyperolius lamottei</i> ZMB 76526, male	21.8	9.0	25.7	7.3	4.0	7.1	7.1	2.7	1.6	1.0	1.9	3.1	3.2	2.9	3.1	9.4
<i>Hyperolius lupiroensis</i> ZMB 77299, holotype, female	23.0	12.0	37.7	8.7	5.9	5.4	7.4	2.6	1.8	1.0	1.7	3.6	3.3	2.4	0.8	11.6
<i>Hyperolius nasicus</i> ZMB 77310, male	18.9	9.1	26.6	7.6	5.2	5.1	6.2	1.7	1.7	1.0	1.7	2.8	3.9	2.4	2.3	8.0
<i>Hyperolius nasutus</i> SAIAB 186001, male	16.6	7.9	24.7	5.5	4.1	5.2	4.6	2.1	1.2	1.0	1.9	1.4	2.6	4.4	2.3	6.9
<i>Hyperolius poweri</i> PEM A 9545, male	20.4	10.6	30.6	8.6	5.5	6.2	6.1	2.1	1.9	1.3	2.2	3.0	4.0	2.4	2.1	10.1
<i>Hyperolius poweri</i> PEM A 9546, male	19.1	10.8	33.5	9.1	5.4	6.9	6.2	2.1	1.7	0.8	1.8	2.5	4.2	2.7	1.0	9.6
<i>Hyperolius rwandae</i> ZMB 7721, holotype, male	18.9	10.2	30.7	8.3	5.5	5.8	6.3	2	1.7	1.2	1.9	2.8	3.6	2.2	1.3	
<i>Hyperolius rwandae</i> ZMB 77222, paratype, male	18.8	10	30.2	8.1	5.1	5.6	6.3	2	1.7	1.1	1.7	2.4	3.2	2.2	1.2	
<i>Hyperolius rwandae</i> ZMB 77224, paratype, male	19.2	9.7	30	8.1	4.8	5.9	6.1	1.8	1.7	1.1	1.8	2.8	3.4	2.3	1.1	
<i>Hyperolius rwandae</i> ZMB 77225, paratype, male	20.2	10.4	31.8	8.5	5.2	5.7	6.2	1.9	1.9	1	1.9	2.8	3.7	2.2	1.3	
<i>Hyperolius rwandae</i> ZMB 77423, paratype, male	19.3	10.1	29.8	8.5	5.4	5.7	6.5	2.3	1.7	1.3	1.9	2.8	3.7	2.5	1.1	
<i>Hyperolius rwandae</i> ZMB 77424, paratype, male	20.2	10.4	32	8.5	6.2	6	6.8	2.3	1.8	1.3	2	3.1	4	2.6	1.4	
<i>Hyperolius rwandae</i> ZMB 77426, paratype, male	19.4	10.6	32.5	8.2	5.2	5.9	6.5	2.2	1.9	1.2	2	3	3.9	2.3	1.4	

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APPENDIX 2. (Continued)

Specimen	SUL	TFL	LEG	FOT	HND	HW	HL	ED	EN	NS	NN	SL	EE	IO	EW	THL
<i>Hyperolius rwandae</i> ZMB 77427, paratype, male	19.9	10.5	33	9.1	5.9	5.8	6.9	2.3	1.9	1.2	2.1	2.9	4.1	2.5	1.3	
<i>Hyperolius rwandae</i> ZMB 77428, paratype, male	19.1	10.1	29.8	8.9	5.7	5.6	6.3	2.2	1.6	1.3	1.9	2.8	3.5	2.5	1.2	
<i>Hyperolius rwandae</i> ZMB 77429, paratype, male	18.6	10.3	31.9	8.7	5.4	5.3	6.1	2.4	1.8	1.2	1.8	2.7	3.9	2.4	1.3	
<i>Hyperolius rwandae</i> ZMB 77685, paratype, male	18.4	8.7	27.8	6.8	4.7	5	5.8	2	1.7	1.1	1.8	2.7	3.4	2	1	
<i>Hyperolius rwandae</i> ZMB 77686, paratype, male	20	9.9	30.7	8.5	5.8	5.9	6.5	2.3	1.7	1.2	1.8	3	3.6	2.2	1.4	
<i>Hyperolius rwandae</i> ZMB 77687, paratype, male	19.6	10	31.7	8.7	5.6	5.9	6.6	2.2	1.9	1.4	1.9	3.1	3.9	2.5	1.2	
<i>Hyperolius rwandae</i> ZMB 77688, paratype, male	21.3	11.3	33.9	8.9	5.7	6.2	6.6	2.5	2	1.4	2.1	3.1	4.1	2.6	1.2	
<i>Hyperolius rwandae</i> ZMB 77689, paratype, male	20.1	10.2	31.6	8.6	5.4	6	6.5	2.4	1.9	1.3	2.2	3.1	4.2	2.3	1.5	
<i>Hyperolius rwandae</i> ZMB 77746, paratype, male	22	11.7	34.4	9	6.1	6.9	6.5	2.3	2	1.4	2	3.1	4.1	2.5	1.6	
<i>Hyperolius rwandae</i> ZMB 77747, paratype, male	20	10.2	31.1	8.5	5.7	6.1	6.5	2.1	1.7	1.2	1.9	2.9	3.9	2.3	1.3	
<i>Hyperolius rwandae</i> ZMB 77748, paratype, male	20.6	10.5	31.8	8.4	5.5	6.3	6.6	3.3	1.9	1.3	2.1	2.9	4.1	2.5	1.3	
<i>Hyperolius rwandae</i> ZMB 77223, paratype, female	19	8.8	27.5	7.1	4.2	5.3	6.2	1.8	1.7	1	1.8	2.6	3.5	2.2	1.2	
<i>Hyperolius rwandae</i> ZMB 77425, paratype, female	18.2	10	29.7	8.2	4.8	5.2	5.6	2.2	1.5	1.1	1.8	2.8	3.2	2.1	1	
<i>Hyperolius rwandae</i> ZMB 77684, paratype, female	20.4	9.9	29.5	8.2	5.4	5.7	6.4	2.3	2	1.2	2	3	4	2.4	1.4	
<i>Hyperolius viridis</i> ZMB 76096, male	20.9	11.2	30.4	8.9	4.0	7.1	6.4	2.7	1.9	1.6	1.8	2.7	2.8	2.4	3.1	10.3