

Describing the smaller majority: integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar

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Abstract

The genus *Stumpffia* BOETTGER, 1881 currently contains 15 named, small to miniaturized frog species, classified in the endemic Malagasy subfamily Cophylinae of the family Microhylidae. *Stumpffia* are terrestrial frogs with a largely unknown biology, probably due to their small size and secretive habits. Previous studies have suggested a large proportion of undescribed diversity in the genus. We revise the genus on the basis of a combination of molecular, bioacoustic, and morphological data and describe 26 new species that are all genetically divergent, almost all of them with high pairwise genetic divergences > 4% p-distance in a segment of the mitochondrial 16S rRNA gene and concordant differentiation in a segment of the nuclear Rag-1 gene. The majority of the new species can also be distinguished by the structure of their advertisement calls (where bioacoustic data are available), and in most comparisons the species can also be distinguished morphologically. Furthermore, a molecular phylogeny reconstructed from DNA sequences of one nuclear and four mitochondrial gene segments revealed that in many cases, morphologically similar species are not each other's closest relatives, thus confirming their identity as independent evolutionary lineages and revealing repeated phenotypic divergence and convergence among and within clades. The phylogeny distinguishes four main clades in the genus: Clade A containing 17 species (*Stumpffia be*, *S. hara*, *S. megsoni*, *S. staffordi*, *S. psologlossa*, *S. analamaina*, *S. gimmeli*, *S. madagascariensis*, *S. pygmaea*, *S. angeluci* **sp. nov.**, *S. huwei* **sp. nov.**, *S. iharana* **sp. nov.**, *S. larinki* **sp. nov.**, *S. maledicta* **sp. nov.**, *S. mamitika* **sp. nov.**, *S. sorata* **sp. nov.**, and *S. yanniki* **sp. nov.**) mostly from northern and northwestern Madagascar, generally characterized by limited digital reduction and divided in subclades of comparatively large, small, and miniaturized body size, respectively; Clade B with four species (*S. miery*, *S. meikeae* **sp. nov.**, *S. obscoena* **sp. nov.**, and *S. davidattenboroughi* **sp. nov.**) morphologically ranging from miniaturized with strong digital reduction to comparatively large-sized; Clade C with 18 species (*S. grandis*, *S. kibomena*, *S. roseifemoralis*, *S. tetradactyla*, *S. nigrorubra* **sp. nov.**, *S. achillei* **sp. nov.**, *S. diutissima* **sp. nov.**, *S. pardus* **sp. nov.**, *S. edmondsi* **sp. nov.**, *S. fusca* **sp. nov.**, *S. jeannoeli* **sp. nov.**, *S. spandei* **sp. nov.**, *S. garraffoi* **sp. nov.**, *S. analanjirofo* **sp. nov.**, *S. miovaova* **sp. nov.**, *S. makira* **sp. nov.**, *S. betampona* **sp. nov.**, and *S. dolchi* **sp. nov.**) mostly distributed in eastern and northeastern Madagascar, containing species of compara-

tively large size as well as small-sized species, many of which are characterized by a moderate degree of digital reduction; and Clade D with two miniaturized species (*S. tridactyla* and *S. contumelia* **sp. nov.**) with strong digital reduction, which form the sister group of all other *Stumpffia*. Two of the newly described species (*S. angeluci* and *S. maledicta*) are not separated by the 4% threshold in the 16S gene but occur in sympatry and do not share Rag-1 haplotypes. To achieve a comprehensive review of this species-rich genus, we provide simplified differential diagnoses and descriptions and abbreviated descriptions of morphological variation. Despite the large number of *Stumpffia* species newly described herein, we identify several additional candidate species with currently insufficient data to warrant formal description, and highlight that some species such as *S. analanjirofo*, *S. gimmeli*, *S. kibomena*, *S. madagascariensis*, *S. roseifemoralis* and *S. obscoena* are composed of two or more deep mitochondrial lineages that might also turn out to be distinct taxa after in-depth study. We confirm *Stumpffia* as a genus of highly microendemic frogs with many species apparently restricted to very small ranges, and provide evidence that two of the new species (*S. achillei* and *S. davidattenboroughi*) do not construct foam nests but lay their eggs in wet places in the leaf litter, or in cavities such as empty snail shells. We propose a conservation status for all the described species according to IUCN Red List Criteria, but also discuss several problems applying these criteria to such microendemic and poorly known frogs.

Key words

Amphibia; Anura; Microhylidae; diversity; systematics; bioacoustics; molecular genetics; morphology; microendemism.

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Introduction

An accurate and complete species inventory is the basis for ecological and evolutionary studies, as well as for conservation management, and has also been proposed as the moral counterweight that humankind can offer to life's runaway exploitation (DIJKSTRA, 2016). As with many other groups of organisms, the past three decades have seen a steep increase in the discovery and description of new amphibian species (KÖHLER *et al.*, 2005), mostly due to intensified exploration of tropical regions and application of an integrative taxonomic approach combining molecular, bioacoustics, and morphological characters (PADIAL *et al.*, 2010). Paradoxically, while more amphibian species are being discovered than any time before in taxonomic history, amphibians are also undergoing serious population declines and extinctions worldwide (HANKEN, 1999; STUART *et al.*, 2004; 2008). Among the numerous threats leading to these declines (MENDELSON *et al.*, 2006; WAKE & VREDENBURG, 2008) are the degradation and destruction of natural habitats and the introduction of invasive species (CUSHMAN, 2006), but also the rapid spread of emerging infectious diseases such as chytridiomycosis and ranavirus (DASZAK *et al.*, 2003; SKERRATT *et al.*, 2007; DUFFUS & CUNNINGHAM, 2010; OLSON *et al.*, 2013).

Madagascar is a global hotspot for biodiversity conservation in which amphibians have long been mainly threatened by deforestation, which progresses at alarming rates (HARPER *et al.*, 2007). Disease-related threats appeared minor (WELDON *et al.*, 2008; WOLLENBERG *et al.*, 2010; VREDENBURG *et al.*, 2012; CROTTINI *et al.*, 2011; 2014) but after the recent discovery of the pathogen *Batrachochytrium dendrobatidis* (KOLBY, 2014; BLETZ *et al.*, 2015), chytridiomycosis-related declines may occur at any time and at any rate, as has been seen elsewhere (e.g., HIRSCHFELD *et al.*, 2016). Additional threats are posed by two invasive amphibian species, *Hoplobatrachus tigrinus* (GUIBÉ, 1953; GLAW & VENCES, 2007), and especially *Duttaphrynus melanostictus* (MOORE *et al.*, 2015; GOODMAN *et al.*, 2017; VENCES *et al.*, 2017). While the conservation status of Madagascar's amphibians has continued to deteriorate, the numbers of newly discovered and described species per year have experienced an almost constant increase since the 1980s (e.g., KÖHLER *et al.*, 2005), and many additional species have already been identified but await description (e.g., VIEITES *et al.*, 2009). As of 2014, in addition to the 290 described Malagasy frog species, over 200 undescribed candidate species of frogs were known (CROTTINI *et al.*, 2012; PERL *et al.*, 2014).

As in many animal groups, the detection of the massive proportion of undescribed diversity in Malagasy frogs was boosted by the routine application of genetic screening approaches. Such DNA barcoding studies have often detected high levels of cryptic diversity (e.g., SMITH *et al.*, 2005; MONAGHAN *et al.*, 2009; RAMASINDRAZANA *et al.*, 2011), and in Malagasy amphibians were based both on the mitochondrial 16S rRNA gene (e.g., VIEITES

et al., 2009) but also on the standard barcoding marker cytochrome oxidase subunit I (COI or Cox-1) (VENCES *et al.*, 2005; NAGY *et al.*, 2012; PERL *et al.*, 2014). These studies confirmed that many species thought to be widespread are genetically diverse and contain additional, undescribed lineages (e.g., BOUMANS *et al.*, 2007; LEHTINEN *et al.*, 2007; GEHRING *et al.*, 2011; 2012). Many of the newly discovered candidate species had remarkably small distribution ranges, fitting an overall pattern of microendemism in Madagascar (WILMÉ *et al.*, 2006; VENCES *et al.*, 2009; BROWN *et al.*, 2016) and thereby posing additional challenges for conservation (ANDREONE *et al.*, 2008).

A large proportion of the cryptic and microendemic amphibian diversity of Madagascar is made up by the cophyline frogs. Cophylinae COPE, 1889 is a Madagascar-endemic subfamily of the pantropical family Microhylidae GÜNTHER, 1858, representing a morphologically diverse group characterised by several osteological characters, which comprise arboreal, terrestrial, fossorial, and rupicolous frogs (BLOMMERS-SCHLÖSSER & BLANC, 1991; GLAW & VENCES, 2007). The typical mode of reproduction is a nidicolous one, with non-feeding tadpoles developing in tree holes and other phytotelmata, or in terrestrial foam or jelly nests (BLOMMERS-SCHLÖSSER, 1975; BLOMMERS-SCHLÖSSER & BLANC, 1991; GLAW & VENCES, 1994), and cophyline advertisement calls mostly consist of long series of single tonal notes (BLOMMERS-SCHLÖSSER, 1975; VENCES *et al.*, 2006; GLAW & VENCES, 2007). Most cophyline genera have been shown to be monophyletic (ANDREONE *et al.*, 2005b; WOLLENBERG *et al.*, 2008; SCHERZ *et al.*, 2016), but the intergeneric relationships are largely unresolved (PELOSO *et al.*, 2015; 2017; SCHERZ *et al.*, 2016; 2017). Although it was recently suggested (PELOSO *et al.*, 2015; 2017) that *Stumpffia* should be synonymized with *Rhombophryne*, SCHERZ *et al.* (2016; 2017) provided genetic, morphometric, and osteological grounds for the rejection of this proposal. We therefore follow the genus-level classification of SCHERZ *et al.* (2016; 2017) herein.

Of the eight currently recognized cophyline genera, *Stumpffia* BOETTGER, 1881, is the most diverse and most urgently in need of taxonomic revision; together, GLAW & VENCES (2007), VIEITES *et al.* (2009), KÖHLER *et al.* (2010), KLAGES *et al.* (2013), PERL *et al.* (2014) and SCHERZ *et al.* (2016) have recognized over 60 candidate species of *Stumpffia*, in addition to the 15 currently recognized species (AMPHIBIAWEB, 2017). This genus is notable for containing most of the smallest cophyline frogs. These truly miniaturized frogs number among the smallest vertebrates in the world (GLAW & VENCES, 2007; KLAGES *et al.*, 2013; but see also SCHERZ *et al.*, 2016 for mention of *Stumpffia*-like genera that are also extremely small but remain to be taxonomically addressed) and are an important but underappreciated ecological guild (RITTMAYER *et al.*, 2012). Many *Stumpffia* show some degree of reduction of digits on fingers and toes (GLAW & VENCES, 1994) which have been flagged as possible taxonomic characters (KLAGES *et al.*, 2013). The mode of reproduction is known only for a few members of the genus; these lay eggs in foam nests in

the leaf litter, where non-feeding tadpoles develop (GLAW & VENCES, 1994; Klages et al., 2013).

The high proportion of cryptic diversity and the increasing threats facing Malagasy frogs demand the prioritization of taxonomic revisions (NDRIANTSOA *et al.*, 2015). These amphibians are a prime example of vertebrates in which traditional taxonomic practice may not be able to catch up with the rate of candidate species detection. While uncommon in vertebrates, such a situation is the rule in invertebrates, especially tropical insects, most groups of which are extremely species-rich. To tackle this diversity, various practices of fast-track taxonomy have been proposed. At the core of these is the routine use of molecular screening techniques (e.g., HEBERT *et al.*, 2003; RATNASINGHAM & HEBERT 2007; 2013) but also a focus on molecular diagnoses and concise and short morphological descriptions (RIEDEL *et al.*, 2013; RENNER *et al.*, 2016), and on online journals specifically adapted to fast species descriptions (SMITH *et al.*, 2013). Such fast-track taxonomy has the potential drawback of undetected errors: depending on the methods adopted, species may be overlooked, or synonyms produced (MIRALLES & VENCES, 2013), and an integrative approach using a variety of approaches and data sets is most suitable for fast elaboration of species hypotheses without compromising their quality (DAYRAT, 2005; PADIAL *et al.*, 2009; 2010; MIRALLES *et al.*, 2011).

In the present paper, using data from our own previous studies as well as newly collected material, we present a complete revision of the genus *Stumpffia* and describe 26 new species within this genus. We follow a simplified approach, wherein we present much less morphological detail on each species than in previous studies (e.g., KLAGES *et al.*, 2013), and instead base our species delimitation on integrating evidence from external morphology, natural history, DNA barcoding, congruence between mitochondrial and nuclear DNA differentiation, and bioacoustic analyses. We first identify clusters based on genetic distances, then discuss the genetic, morphological and bioacoustic evidence for their distinct taxonomic status, and proceed with the formal description of the 26 new species.

Materials and Methods

Specimens were collected at night or day by searching in the leaf litter guided by the calling of males and through opportunistic searches. The search was conducted using torches and headlamps at night. Specimens were euthanized in MS-222 solution, fixed in 90% ethanol and preserved in 70% ethanol.

Vouchers were deposited in the Zoological Collection of the Kyoto University Museum, Japan (KUZA), Université d'Antananarivo, Mention Zoologie et Biodiversité Animale, Antananarivo, Madagascar (UADBA), Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK), Museum für Naturkunde, Berlin, Germany (ZMB), the Zoologische Staatssammlung

München, Munich, Germany (ZSM), and the Museo Regionale di Scienze Naturali, Torino, Turin, Italy (MRSN). Additional voucher specimens were examined from the Naturhistorisches Museum Bern, Bern, Switzerland (NMBE), Muséum National d'Histoire Naturelle, Paris, France (MNHN), Senckenberg Museum Frankfurt, Frankfurt, Germany (SMF), and the Zoologisch Museum Amsterdam (ZMA), Netherlands (collections currently integrated in the Naturalis Biodiversity Center of Leiden). MNCN is used to refer to the Museo Nacional de Ciencias Naturales in Madrid, Spain. ACZCV, FAZC and FN, FG/MV, FGZC, DRV, NSH, JCR, RDR, and ZCMV refer to A. Crottini, F. Andreone, F. Glaw, D.R. Vieites, S.H. Ndriantsoa, J.C. Riemann, R.D. Randrianiana, and M. Vences field numbers, respectively. In some cases, specimens deposited in UADBA have not received final catalogue numbers yet; these are cited as UADBA followed by the respective field number in parentheses.

Tissue samples were taken by cutting pieces of leg muscle, tongue, or whole limbs (depending on specimen size) from the euthanized animals, and preserved separately in 99% ethanol. Males and females were distinguished based on field observations (calling behavior) or presence of a vocal sac in males, or eggs in females. Geographic regions are named according to BOUMANS *et al.* (2007) and BROWN *et al.* (2016); we follow BROWN *et al.* (2016) in defining “northern Madagascar” as an area roughly delimited by a diagonal spanning from 15.5°S on the east coast to ca. 15.0°S on the west coast.

Morphological measurements and descriptions

The following morphological measurements on preserved specimens were taken by the first author with digital callipers to the nearest 0.1 mm (Fig. 1): snout-vent length (SVL), maximum head width (HW), head length (HL), horizontal tympanum diameter (TD), horizontal eye diameter (ED), eye-nostril distance (END), nostril-snout tip distance (NSD), nostril-nostril distance (NND), forelimb length (FORL), hand length (HAL), hindlimb length (HIL), foot length including tarsus (FOTL), foot length (FOL), and tibia length (TIBL). Terminology and description scheme follow VENCES *et al.* (2010) and GLAW *et al.* (2012). Body parts used for the description of color and pattern are as in Fig. 2. Description of color in life is generally based on a single specimen, preferably the holotype when photos of it were available, with some reference to variation if known. In some cases where color or pattern is especially variable, a total-variation description is given instead, as the pattern of individual specimens is less informative.

Bioacoustics

Advertisement calls were recorded in the field using different digital or analogue devices such as: Sony WM-

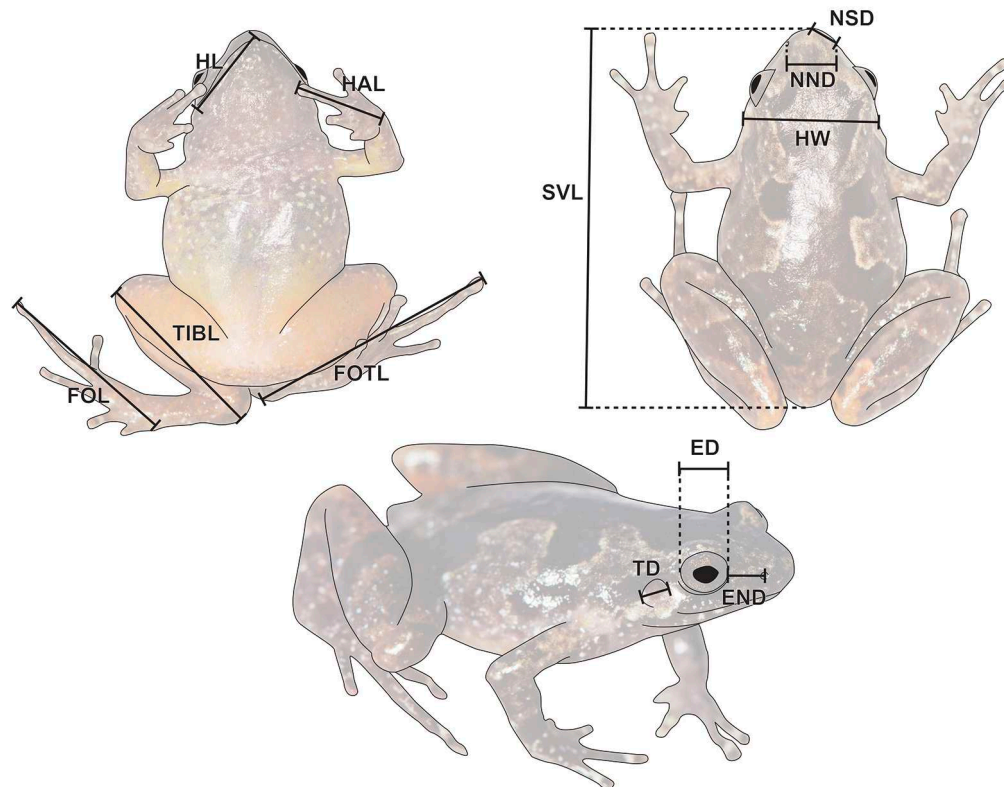


Fig. 1. Reduced morphological scheme indicating the measurements used herein. Abbreviations are given in the text. FORL and HIL are not shown.

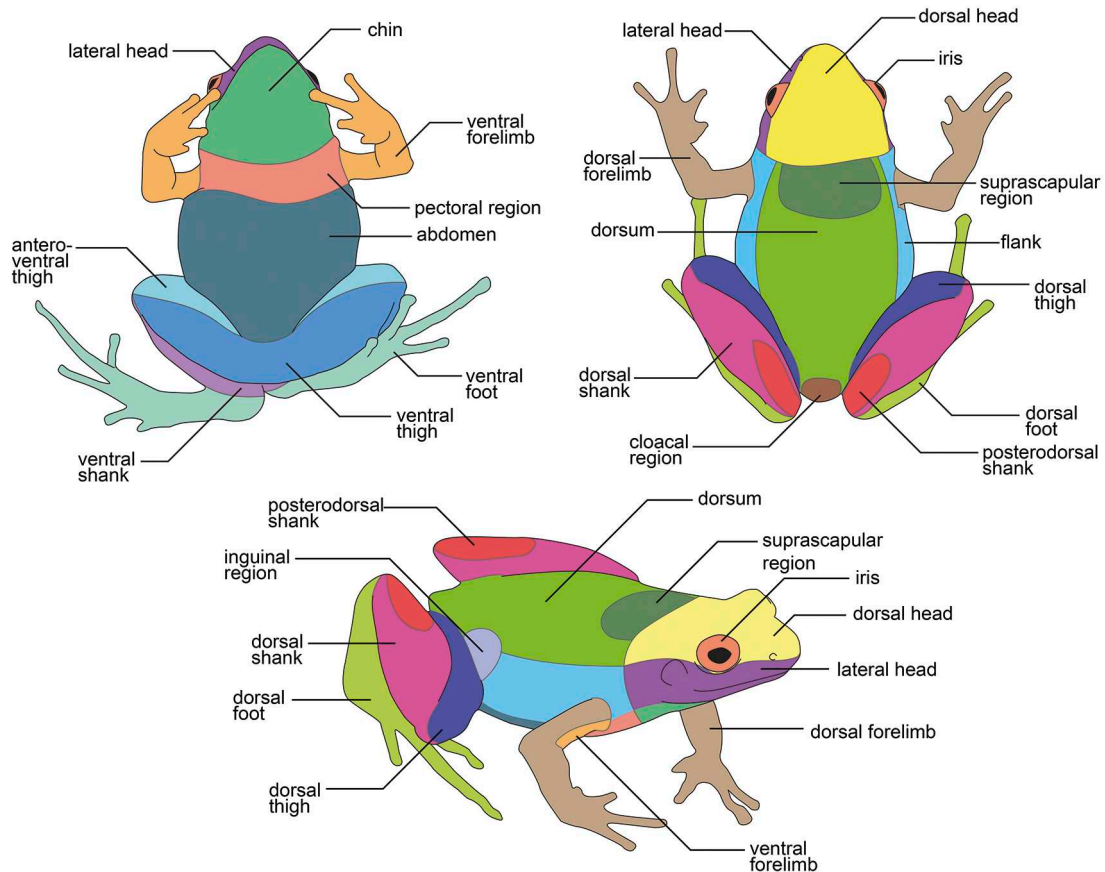


Fig. 2. Graphic scheme indicating regions of the body of *Stumpffia* specimens, as referred to in the descriptions of coloration throughout the manuscript. Labels and colors refer to regions of the body and not necessarily to anatomical features, and are used to simplify the description scheme of color patterns.

D6C and Tensai RCR-3222 tape recorders with external microphones (Sennheiser Me-80, Vivanco EM 238), and Tascam DR07, DR05, Marantz PMD 660, PMD 661 MkII, or Roland EDIROL R-09 digital recorders, with built-in microphones (Tascam) or accessorized with a semi-directional (Marantz and Roland) or supercardioid (Sennheiser) microphone. Digital recordings were obtained at a sampling rate of 44.1 kHz and 24-bit resolution and saved as uncompressed files. A number of recordings were done with a damaged Tascam DR07 recorder and contain an artificial initial high amplitude peak and possibly other artifacts; where used, these recordings are clearly indicated as such in the text. Recordings were sampled or resampled at 22.05 kHz and 16-bit resolution and computer-analyzed using the software CoolEdit Pro version 2000. Frequency information was obtained through Fast Fourier Transformation (FFT, width 1024 points); the audiospectrograms were obtained at Hanning window function with 256 bands resolution using the seewave package (SUEUR *et al.*, 2008) in R (R DEVELOPMENT CORE TEAM, 2015). Amplitude in spectrograms is color-coded with relative dB values referring to the loudest sound in the recording. Temporal measurements are given in milliseconds (ms) or seconds (s), as range, with mean \pm standard deviation in parentheses. Terminology in call descriptions follows the call-centered terminology of KÖHLER *et al.* (2017). All call recordings used for analysis were deposited in the Animal Sound Archive (Tierstimmenarchiv) at the Museum für Naturkunde in Berlin (accession numbers Ven1_1–Ven1_64).

We here also report data from a survey of calling activity in *S. analamaina*, conducted at a dry deciduous forest of Ampijoroa, Ankarafantsika National Park (S16.3, E46.816). The annual precipitation of the region is between 1000 and 1500 mm. The rainfall occurs from November through April (rainy season), without water bodies at the study site. Mean air temperature and precipitation were obtained from the Durrell Wildlife Chelonian Breeding Center in Ampijoroa station. Call activity was recorded in the forest every night from 2 December 2010 to 7 February 2011 and 13 January to 12 February 2013. The recordings were obtained at 07:00, 12:00, 17:00, and 21:00 each day, and were identified among one of the following six level categories: level 0: no vocalizations were heard; level 1: single or a few calls were heard, but did not form a chorus; level 2: calls or choruses were heard intermittently, but in most of the time no vocalizations occurred; level 3: calls or choruses were frequently heard, but silent intervals were still obvious; level 4: intensive choruses were heard during most of the census, but several occasional cessation of the chorus was recognized; level 5: choruses were intensive and never ceased.

Molecular data sets

We assembled three different but partly overlapping data sets for the purpose of assessing the phylogenetic

relationships among species of *Stumpffia*, and delimiting species. Our rationale (reiterated in more detail below) is to first delimit species by a congruence approach of integrative taxonomy, i.e., finding evolutionary entities identifiable by at least two, if possible more, independent lines of evidence. For this purpose we separately analyze data sets of one mitochondrial and one nuclear gene and integrate these with further evidence from bioacoustics and morphology. We then infer the phylogeny among the delimited species-level entities by concatenating multiple mitochondrial and one nuclear gene from single representatives of each unit.

Molecular dataset A. As mitochondrial marker we used a 5' segment of the 16S rRNA gene (16S) that we have previously used to assess mitochondrial differentiation in microhylids, including *Stumpffia* (e.g., VENCES *et al.*, 2010; KÖHLER *et al.*, 2010; KLAGES *et al.*, 2013; RAKOTOARISON *et al.*, 2015). This segment differs from the one traditionally used for DNA barcoding across all Malagasy frogs (e.g., VIEITES *et al.*, 2009) but was chosen to combine newly generated data with the large sequence set of this gene from the work of KLAGES *et al.* (2013). We present these data as a phylogenetic tree from a simplified analysis (i.e., a maximum likelihood without exclusion of poorly aligned data) but emphasize that the goal of this tree is to visualize clustering of genetically similar individuals and their differentiation from other individuals, and not an accurate reconstruction of the *Stumpffia* phylogeny. Altogether, 281 sequences of *Stumpffia* were available for this segment (length of aligned sequences: 657 bp), and *Anilany helenae* (VALLAN, 2000) was used as the outgroup (SCHERZ *et al.*, 2016).

Molecular dataset B. As a nuclear marker, we selected a segment of the single-copy protein-coding nuclear recombination-activating gene 1 (Rag-1), which is known to often show distinct haplotypes for closely related species, including *Stumpffia* (e.g., KLAGES *et al.*, 2013; NDRINTSOA *et al.*, 2013). We used a nested primer approach (RAKOTOARISON *et al.*, 2015) to amplify a rather long stretch of this gene but trimmed it to 338 bp to allow analysis together with the extensive set of sequences available from the work of KLAGES *et al.* (2013). We represented variation among the sequences of a total of 163 specimens of *Stumpffia* as a haplotype network (after separating alleles by phasing), which in this case is appropriate due to the small number of mutations among species and the relatively high allele variation within species.

Molecular dataset C. To resolve the phylogenetic relationships among species-level units, we concatenated four mitochondrial and one nuclear gene segments: two segments of 16S, and one segment each of the 12S rRNA (12S), cytochrome oxidase subunit 1 (Cox-1) and Rag-1. A partitioned Bayesian Inference analysis was carried out after removing hypervariable stretches of 12S and 16S, and using *Scaphiophryne* as outgroup. This dataset included 49 terminals (of which 48 *Stumpffia*) for a total of 3325 bp.

For a series of new specimens collected in November 2016 in the Marojejy massif, we sequenced a 250 bp

highly variable segment of 16S by an Illumina amplicon approach (VENCES *et al.*, 2016) to identify them to species level; these short sequences were from a different segment of the 16S gene and are therefore not included in dataset A.

DNA sequence analysis

We extracted genomic DNA from muscle tissue samples preserved in 99% ethanol using a standard salt extraction protocol (BRUFORD *et al.*, 1992). All PCR protocols followed RAKOTOARISON *et al.* (2015). Standard PCRs were carried out to amplify the mitochondrial DNA segments whereas the Rag-1 segment was amplified using a nested PCR approach. Primer sequences, primer references, and cycling protocols are found in RAKOTOARISON *et al.* (2015). PCR products were cleaned with enzymatic purification: 0.15 units of Shrimp Alkaline Phosphatase (SAP) and 1 unit of Exonuclease I (New England Biolabs, Frankfurt am Main, Germany) incubated for 15 min at 37°C followed by 15 min at 80°C. Purified PCR products were sequenced on an automated DNA sequencer (Applied Biosystems ABI 3130XL). Sequencing reaction (10 µl) contained 0.2 or 0.3 µl of PCR product, 0.5 µl of BigDye 3.1 (Applied Biosystems, Darmstadt, Germany) and 0.3 µmol of primer. The mitochondrial segment was sequenced using the forward primer while Rag-1 was sequenced in both directions to allow for more reliable identification of heterozygote sites. Sequences were checked and edited, and heterozygous positions in Rag-1 inferred, in the software CodonCode Aligner 3.7.1 (Codon Code Corporation, Dedham, MA, USA). All 167 newly determined sequences were submitted to GenBank (accession numbers MF768086–MF768252).

Sequences were aligned with those from previous studies in MEGA 6 (TAMURA *et al.*, 2013). For **dataset A** we inferred a phylogenetic tree under the Maximum Likelihood optimality criterion in MEGA 6, under a substitution model suggested by the Bayesian Information Criterion in jModelTest 2.1.4 (DARRIBA *et al.*, 2012). For **dataset B** we first trimmed all sequences to equal length and removed sequences containing ambiguities that could not be interpreted as heterozygotes. We then separated sequences into haplotypes using the Phase algorithm (STEPHENS *et al.*, 2001) as implemented in DNAsp 5 (LIBRADO & ROZAS, 2009). Phased sequences were subsequently used to construct a haplotype network following the approach of SALZBURGER *et al.* (2011) with the program Haplotype Viewer. (<http://www.cibiv.at/~greg/haploviewer>) based on a Neighbour-joining tree computed with MEGA 6 from uncorrected p-distances.

For **dataset C** we first concatenated DNA sequences of four mitochondrial and one nuclear gene segments: two non-overlapping segments of 16S, and one segment each of 12S, Cox-1, and Rag-1. We then determined the best-fitting partition scheme and substitution models with PartitionFinder (LANFAR *et al.*, 2012), defining each codon position of the two protein-coding genes as separate char-

acter sets, and the whole 12S/16S segments as one further character set. We removed all gapped and hypervariable regions of the 12S and 16S segments after visual inspection because usage of a software for this task was complicated by the different sequence lengths and missing data for some of the species and segments. We then computed a phylogenetic tree by Bayesian inference with MrBayes 3.2 (RONQUIST *et al.*, 2012). Results of two independent runs of 20 million generations, each comprising four Markov Chains (three heated and one cold), were sampled every 10,000 generations. Chain mixing and stationarity was assessed by examining the standard deviation of split frequencies and by plotting the -lnL per generation using Tracer 1.5 software (RAMBAUT & DRUMMOND, 2007). Results were combined to obtain a 50%-majority rule consensus tree and the respective posterior probabilities of nodes, after discarding 25% of the generations as burn-in (all compatible nodes with probabilities < 0.5 were also kept).

Rationale for species delimitation

We here follow an approach of integration by congruence as defined by PADIAL *et al.* (2010), i.e., we define species as independent evolutionary lineages in the framework of the general lineage or evolutionary species concept (MAYDEN, 1997; DE QUEIROZ, 1997; 2007) if two or more independent lines of evidence support their distinctness. We start the species delimitation procedure by seeking mitochondrial clades divergent from other mitochondrial clades by sequence divergences > 3% in the 16S gene 5' fragment, given that this degree of divergence has been found to often correspond to species-level units in anurans (FOUQUET *et al.*, 2007; MALONE & FONTENO, 2008; VIEITES *et al.*, 2009). As cophyline microhylids, in general are characterized by quite high intra- and interspecific divergences (e.g., VENCES *et al.*, 2010; KLAGES *et al.*, 2013), and as this segment is slightly more variable than the 3' segment used for defining candidate species in Malagasy frogs (VIEITES *et al.*, 2009), we elevated this threshold to 4% uncorrected pairwise sequence divergence (p-distance), with some exceptions explained below. To identify lineages at this threshold we used the SpeciesIdentifier 'Cluster' algorithm in Taxon DNA 1.7 (MEIER *et al.*, 2006) to automatically cluster taxa according to pairwise distances for every sequence within each cluster, wherein the maximum pairwise distance within each cluster (possible species-level lineage) should not exceed a given threshold.

We subsequently tested if the individuals belonging to these mitochondrial lineages are also separated in a nuclear gene (Rag-1) given the important differences in inheritance between the nuclear and mitochondrial genomes, and the absence of any recombination between mitochondrial and nuclear genes. Genealogical concordance between such largely independent genetic markers has been long recognized as an important species criterion (AVISE & BALL, 1990), and can be highly informa-

tive even in the absence of monophyly (WEISROCK *et al.*, 2010), i.e., by strongly different allele frequencies or unique haplotypes not forming a clade. Such concordance between nuDNA and mtDNA, especially, can help to conclusively refute the possibility of mitochondrial introgression influencing the species delimitation process.

Furthermore, we examined external morphology of voucher specimens, using especially body size, digital reduction and specific distinctive color pattern as diagnostic characters. To compare the highly distinctive advertisement calls of *Stumpffia*, we considered in decreasing order of importance (1) general call structure, i.e., pulsed vs. unpulsed, (2) call duration, and (3) inter-call interval. For the last two characters, we considered a bioacoustic difference as conclusive if, with a comparable recording temperature, the respective values of two lineages do not overlap.

Hence in our species delimitation approach, we consider groups of individuals as species if they (1) form a monophyletic group based on mtDNA and (2) differ from other such groups by > 4% sequence divergence (mean p-distance), and fulfil at least one of the following additional criteria: (3a) exclusively private (unique) haplotypes in the analysed Rag-1 segment, (3b) bioacoustically distinct from other *Stumpffia*, (3c) morphologically and/or chromatically distinct from other *Stumpffia*. For some species with incomplete data or small sample sizes, we restrict the comparisons to their respective sister species, or related species belonging to an inclusive subclade, and consider the criteria of unique Rag-1 haplotypes and morphological and bioacoustic distinctness to be satisfied when they apply to this set of relatives rather than to all other *Stumpffia* species.

In a few cases we furthermore take a number of ad hoc taxonomic decisions deviating from this species delimitation rationale. This concerns a few species that we describe despite low sample size or missing data, if they are characterized by extremely high mitochondrial divergences and unclarified relationships to other *Stumpffia*. In several other cases, we allow for substantial mitochondrial divergence within our species units to avoid describing poorly defined species from well-defined mitochondrial clades, thereby leaving these probable species complexes for further study. In this we follow the argument of MIRALLES & VENCES (2013) who suggested that a false negative (failure to detect and describe a species) can more easily be corrected by future researchers than a false positive (wrongly describing an intraspecific lineage as a species).

Results

Molecular species delimitation

Maximum Likelihood (ML) analysis of DNA sequences (657 bp aligned) of the 5'-segment of the mitochondrial

16S rRNA gene for 281 individuals of *Stumpffia* yielded a tree with a clear pattern of clusters of identical or near-identical sequences, separated by long branches (and thus high genetic distances) from other such clusters (Fig. 3). The analysis with SpeciesIdentifier at the 4% threshold level for uncorrected p-distances yielded 53 clusters, not counting the outgroup and short sequences with inadequate sequence overlap. All nominal species of the genus were included in the analysis, all (except *S. miery* and *S. tridactyla*) with sequences of multiple individuals. No case of two or more nominal species of *Stumpffia* lumped in the same cluster was detected. Anticipating the results of our species delimitation procedure (specified in detail below), only in one case were units described as new species although they are lumped into one cluster (the sympatric *S. angeluci* **sp. nov.** and *S. maledicta* **sp. nov.**). On the contrary, SpeciesIdentifier suggested assignment of individuals to distinct clusters in numerous cases, which we herein consider, in a conservative approach, deep conspecific lineages (DCLs). Species including additional DCLs aside from the main species lineage were *S. analanjirofo* **sp. nov.** (1 extra DCL), *S. gimmeli* (2), *S. kibomena* (1), *S. madagascariensis* (1), *S. obscoena* **sp. nov.** (1), *S. roseifemoralis* (1), *S. sp. Ca30* (1). In all these cases, the mitochondrial data suggest the possibility of additional undescribed species hidden under these taxa, but we refrain from describing them due to insufficient information as discussed in the respective species accounts below.

The Rag-1 haplotype network reconstructed from a DNA sequence segment of 338 bp from 163 specimens presented a high amount of variation with a total of 146 haplotypes, including a large number of singletons (Fig. 4). This variation was caused by an overall high number of ambiguities in the chromatograms interpreted by the phasing algorithm as heterozygotes. While in many cases these positions refer to true heterozygotes, others might have different underlying causes but were in many cases confirmed as ambiguous in amplification and sequencing repeats. Distinct and unambiguous mutations separated numerous haplotype groups in the network, which in most cases corresponded to lineages identified also by the mitochondrial analysis. In a direct comparison to the mitochondrial clustering, and considering that for five mitochondrial clusters no Rag-1 sequence was available, 26 of the mitochondrial clusters were in unique haplogroups (originating from a single branch that does not also lead to another haplogroup), three haplogroups contained the representatives of 2 or 3 mitochondrial lineages, and the representatives of a few other mitochondrial lineages were distributed over various haplogroups, or grouped in 'non-monophyletic' haplogroups. Many of the haplogroups were separated from each other by a substantial number of five or more mutations. Haplotype sharing among individuals of different mitochondrial lineages was observed in only three instances: between the lineage pairs *S. pardus* **sp. nov.**/*S. diutissima* **sp. nov.**, *S. gimmeli*/*S. mamitika* **sp. nov.**, and *S. tetradactyla*/*S. nigrorubra* **sp. nov.**

Table 1. Between-group mean distance in percent (number of base differences per site from averaging over all sequence pairs between groups, multiplied by 100) for species and candidate species of *Stumpffia*, based on 574 bp of the mitochondrial 16S rRNA gene (3' end of the gene). All ambiguous positions were removed for each sequence pair.

	<i>achillei</i>	<i>analama- ina</i>	<i>anal- anji- rofo</i>	<i>ange- luci</i>	<i>be</i>	<i>contu- melia</i>	<i>diutis- sima</i>	<i>ed- mondsi</i>	<i>fusca</i>	<i>garraf- foi</i>	<i>gim- meli</i>	<i>gran- dis</i>	<i>hara</i>	<i>ihara- na</i>	<i>jean- noeli</i>	<i>kibo- mena</i>	<i>kibo- mena (2)</i>	<i>larinki</i>	<i>mada- gasca- riensis</i>	<i>mada- gasca- riensis (2)</i>	<i>male- dicta</i>	<i>megs- oni</i>	<i>miery</i>
<i>achillei</i>	—																						
<i>analama- ina</i>	7.8	—																					
<i>anal- anji- rofo</i>	3.0	9.4	—																				
<i>angeluci</i>	11.8	8.3	9.8	—																			
<i>be</i>	9.0	8.5	9.0	9.1	—																		
<i>contumelia</i>	14.8	13.7	14.2	14.9	12.8	—																	
<i>diutissima</i>	8.9	11.2	9.2	12.6	11.0	13.7	—																
<i>edmondsi</i>	10.2	10.6	8.5	13.7	9.0	15.0	7.7	—															
<i>fusca</i>	8.0	9.6	7.7	10.6	8.5	13.1	10.9	10.7	—														
<i>garraffoi</i>	11.4	12.6	9.2	11.3	10.8	14.6	9.9	5.5	11.4	—													
<i>gimmeli</i>	11.1	8.6	11.7	7.5	9.7	14.5	10.6	12.5	11.3	12.2	—												
<i>grandis</i>	9.6	10.4	7.8	13.1	9.1	13.9	11.9	9.6	7.0	9.5	11.4	—											
<i>hara</i>	9.8	10.3	10.8	9.8	4.9	13.6	11.5	11.1	10.3	11.3	10.1	10.0	—										
<i>iharana</i>	10.8	8.5	11.1	6.3	9.1	14.3	11.2	13.0	10.6	12.4	4.1	11.9	10.0	—									
<i>jeannoeli</i>	11.0	12.1	10.3	12.4	11.5	18.7	11.8	7.0	12.5	7.6	12.1	9.4	13.2	12.1	—								
<i>kibomena</i>	6.8	8.3	6.5	9.0	8.5	12.9	9.6	8.3	6.7	9.3	10.2	7.1	9.6	8.8	8.4	—							
<i>kibomena (2)</i>	6.7	6.7	6.2	6.7	8.2	11.3	8.2	6.7	6.2	7.0	9.3	5.1	11.4	8.3	6.3	4.6	—						
<i>larinki</i>	11.3	8.7	10.4	5.4	8.1	13.4	11.2	11.5	10.6	10.8	6.2	9.8	9.1	5.4	11.0	8.3	8.8	—					
<i>madagascari- ensis</i>	9.4	7.9	10.4	9.6	8.3	14.7	10.3	10.5	9.6	11.2	10.4	10.4	9.6	9.6	13.8	8.5	6.2	9.1	—				
<i>madagascari- ensis (2)</i>	10.4	7.5	10.6	10.1	8.9	15.3	10.1	10.2	10.8	10.8	10.2	11.3	11.5	10.1	13.2	10.0	7.8	9.8	4.0	—			
<i>maledicta</i>	10.2	8.1	9.6	1.9	8.1	13.9	9.9	10.6	10.4	11.7	5.5	11.1	9.1	4.8	12.4	9.6	7.8	5.8	10.4	10.0	—		
<i>megsoni</i>	9.3	8.8	8.6	9.0	3.8	13.9	11.5	9.3	9.9	9.7	9.8	9.9	3.7	8.8	11.3	9.0	9.4	8.3	9.4	9.2	8.8	—	
<i>miery</i>	11.1	8.8	11.0	11.0	9.7	15.9	13.5	11.6	11.0	12.8	10.3	13.1	10.6	10.0	13.1	10.1	6.5	9.1	9.1	8.4	10.0	10.1	—
<i>mirovaova</i>	10.5	11.9	9.1	13.2	12.1	15.8	11.3	10.2	9.5	11.9	11.7	11.2	14.2	12.7	11.1	9.3	5.2	12.7	10.6	11.3	12.9	13.5	11.6
<i>nigrorubra</i>	10.2	9.8	8.2	12.7	9.2	13.1	8.8	4.6	10.2	6.2	10.6	8.7	10.6	12.5	7.3	7.4	6.7	9.8	9.6	9.5	10.1	9.7	10.8
<i>obscoena</i>	10.2	9.1	11.2	13.8	9.9	15.8	11.0	11.4	10.2	11.5	10.7	11.1	10.0	10.2	11.5	8.6	6.7	9.6	8.6	10.0	11.2	10.3	10.8
<i>pardus</i>	10.0	9.6	7.9	10.9	10.6	12.9	8.5	7.9	9.1	8.5	11.2	8.7	10.3	11.2	10.3	7.6	4.6	8.9	9.3	10.5	9.0	10.1	11.3
<i>psologlossa</i>	9.1	8.3	9.6	7.8	7.6	13.7	9.0	10.8	10.3	11.1	7.2	10.4	8.8	6.3	11.0	8.8	7.3	5.4	9.0	8.6	5.5	9.0	8.8
<i>pygmaea</i>	8.6	7.6	8.3	10.8	8.0	13.3	9.0	9.0	11.0	10.4	10.1	10.6	8.8	9.2	10.1	7.8	6.2	9.2	6.5	5.9	9.2	7.8	7.4
<i>roseifemoralis</i>	9.5	9.0	9.6	11.2	10.7	15.7	9.6	9.6	10.6	9.8	9.6	9.6	11.1	10.0	7.9	8.3	6.2	9.0	10.0	9.6	9.5	11.2	8.9
<i>sorata</i>	10.0	7.9	9.8	5.2	8.3	13.3	9.0	9.5	10.2	10.4	6.4	10.7	8.4	6.5	11.3	9.4	7.3	6.7	8.1	8.4	4.4	8.6	8.5
sp_Ca11	6.8	8.5	6.5	10.5	8.9	14.6	10.6	8.8	6.1	9.0	9.5	6.5	10.8	10.2	7.1	5.5	2.1	9.8	9.4	9.6	9.4	9.2	10.1
sp_Ca29	7.9	6.4	8.8	9.3	7.9	13.0	11.1	10.5	9.2	10.4	9.1	10.6	9.6	8.6	9.9	7.7	6.2	7.1	9.0	9.2	7.3	9.0	8.5
sp_Ca30	10.8	10.8	11.3	11.5	12.4	14.7	13.3	11.6	12.5	11.9	12.8	10.8	13.5	12.1	13.2	9.6	7.2	12.5	8.9	10.0	12.1	13.0	12.5
sp_Ca42	10.5	10.4	9.3	11.1	10.0	13.8	8.7	4.2	10.8	5.9	11.3	9.9	11.8	11.5	7.3	8.3	7.2	10.2	9.2	8.6	10.7	9.7	11.3

Table 1 continued.

	<i>achillei</i>	<i>anala- maina</i>	<i>ana- lanji- rofo</i>	<i>ange- luci</i>	<i>be</i>	<i>contu- melia</i>	<i>diutis- sima</i>	<i>ed- mondsi</i>	<i>fusca</i>	<i>garraf- foi</i>	<i>gim- meli</i>	<i>gran- dis</i>	<i>hara</i>	<i>ihara- na</i>	<i>jean- noeli</i>	<i>kibo- mena</i>	<i>kibo- mena (2)</i>	<i>larinki</i>	<i>mada- gasca- riensis</i>	<i>mada- gasca- riensis (2)</i>	<i>male- dicta</i>	<i>megs- oni</i>	<i>miery</i>
<i>dolchi</i>	8.7	9.5	9.7	12.1	10.4	15.1	9.0	8.2	10.4	8.6	10.9	8.6	11.6	10.7	7.8	7.7	5.1	10.7	11.6	11.0	10.3	10.7	11.9
<i>huwei</i>	12.3	9.8	11.7	3.0	10.4	14.7	11.7	12.6	11.7	13.0	6.6	12.4	11.3	5.4	13.8	11.3	8.8	7.1	11.4	11.5	2.5	10.8	11.0
<i>davidattenbor- oughi</i>	9.5	9.9	9.9	10.2	9.2	13.6	10.8	11.0	10.7	10.9	9.7	10.5	9.0	9.1	10.6	7.1	6.7	9.4	9.4	10.6	10.1	9.8	9.2
<i>sp_Ca7</i>	9.5	9.5	10.6	8.2	9.0	13.5	7.6	10.1	12.1	11.6	7.9	11.7	8.8	7.5	11.3	9.0	5.2	7.0	8.8	8.9	6.3	9.6	10.9
<i>spandei</i>	10.8	11.2	8.1	10.3	10.4	14.9	9.5	8.1	9.9	6.5	12.6	11.0	11.2	11.9	7.8	7.5	5.1	9.8	10.1	11.0	10.8	9.6	13.8
<i>staffordi</i>	11.4	10.2	11.5	9.4	7.3	15.4	12.2	11.9	10.6	12.8	8.8	11.1	8.6	9.6	14.6	11.3	8.9	9.0	8.8	10.0	9.0	8.5	11.6
<i>mamitika</i>	10.8	9.4	11.5	6.2	10.1	14.6	9.8	12.3	11.5	13.8	6.5	12.5	10.7	6.3	13.3	10.3	8.3	6.6	11.5	11.5	3.7	11.3	11.3
<i>tetradactyla</i>	12.9	13.1	9.3	10.4	9.1	16.0	10.1	7.9	10.6	7.5	11.9	10.5	9.6	10.3	9.8	7.3	7.1	8.8	9.4	10.0	10.1	8.8	11.3
<i>tridactyla</i>	13.4	12.8	12.4	14.5	11.7	10.7	13.2	12.6	11.9	14.3	14.0	13.4	12.1	14.3	17.0	12.7	11.3	14.0	13.4	13.6	13.2	12.0	12.7
<i>yanniki</i>	7.6	6.2	8.6	8.7	8.5	12.2	10.6	10.4	9.6	12.1	9.7	10.2	9.3	9.2	11.5	8.1	7.3	8.1	7.9	8.1	8.9	9.0	9.7
	<i>mio- vaova</i>	<i>nigro- rubra</i>	<i>ob- scoena</i>	<i>pardus</i>	<i>psolo- glossa</i>	<i>pyg- maea</i>	<i>roseife- mora- lis</i>	<i>sorata</i>	<i>sp_Ca11</i>	<i>sp_Ca29</i>	<i>sp_Ca30</i>	<i>sp_Ca42</i>	<i>dolchi</i>	<i>huwei</i>	<i>davi- datten- boroughi</i>	<i>sp_Ca7</i>	<i>span- dei</i>	<i>staf- fordi</i>	<i>mami- tika</i>	<i>tetra- dactyla</i>	<i>tri- dactyla</i>		
<i>miovaova</i>	—																						
<i>nigrorubra</i>	9.9	—																					
<i>obscoena</i>	9.7	11.6	—																				
<i>pardus</i>	10.5	7.1	11.1	—																			
<i>psologlossa</i>	11.6	9.7	8.5	10.2	—																		
<i>pygmaea</i>	11.6	8.4	8.5	9.4	8.4	—																	
<i>roseifemoralis</i>	9.4	9.4	8.7	9.4	7.8	7.7	—																
<i>sorata</i>	11.1	8.8	10.7	8.1	4.8	8.3	9.3	—															
<i>sp_Ca11</i>	8.7	8.6	9.9	8.5	9.0	8.5	7.5	8.8	—														
<i>sp_Ca29</i>	11.5	10.5	7.4	9.2	6.5	8.1	7.9	7.5	7.2	—													
<i>sp_Ca30</i>	12.9	9.6	12.0	10.6	10.7	8.9	11.4	10.2	9.1	10.4	—												
<i>sp_Ca42</i>	9.9	5.7	9.9	8.9	10.3	7.2	7.3	9.0	8.4	10.0	10.8	—											
<i>dolchi</i>	10.1	7.6	10.6	9.9	9.1	9.1	8.5	10.0	6.0	10.2	10.7	8.6	—										
<i>huwei</i>	14.0	11.6	13.3	10.0	7.6	10.7	10.2	6.0	10.8	9.4	13.1	11.5	11.9	—									
<i>davidattenbor- oroughi</i>	10.3	10.9	7.2	9.3	8.6	9.4	7.7	8.8	8.9	7.6	12.0	10.5	10.0	10.9	—								
<i>sp_Ca7</i>	10.8	9.4	10.0	9.3	4.0	7.5	8.7	3.3	8.8	8.6	11.3	8.8	8.8	7.8	7.6	—							
<i>spandei</i>	9.9	7.8	11.8	9.2	9.9	10.8	10.6	9.4	9.3	10.9	11.4	6.9	8.0	12.2	9.9	9.4	—						
<i>staffordi</i>	12.9	10.7	9.7	11.3	9.0	8.7	10.5	8.1	10.6	9.4	12.9	11.3	12.6	10.6	9.7	9.3	11.2	—					
<i>mamitika</i>	12.4	11.0	12.2	10.8	6.5	9.7	10.2	6.0	10.8	9.2	12.6	11.5	10.3	5.1	10.6	5.8	12.0	10.3	—				
<i>tetradactyla</i>	12.8	6.5	11.2	8.1	8.5	9.1	10.9	9.5	9.1	10.7	11.5	7.9	9.6	11.2	9.8	9.3	8.1	12.1	12.0	—			
<i>tridactyla</i>	13.1	12.6	14.7	12.4	13.2	11.5	13.5	12.4	12.3	13.6	14.4	12.7	13.4	14.5	12.9	11.6	13.4	14.1	13.2	13.6	—		
<i>yanniki</i>	11.9	9.6	7.3	9.8	7.0	7.2	8.3	8.5	8.5	4.6	10.0	9.6	10.5	10.8	9.0	8.8	10.4	9.4	9.6	11.9	12.6		

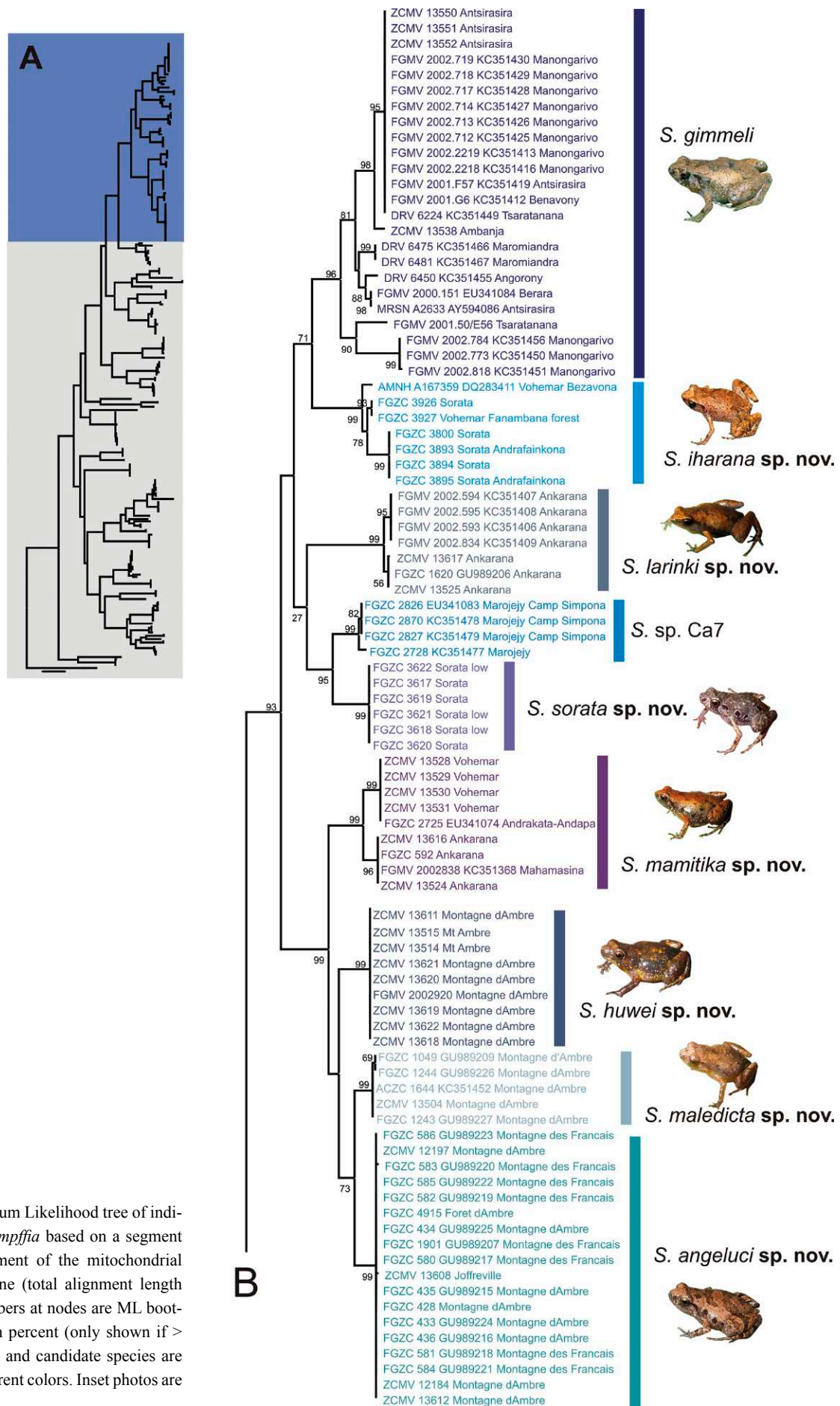


Fig. 3. Maximum Likelihood tree of individuals of *Stumpffia* based on a segment of the 5'-segment of the mitochondrial 16S rRNA gene (total alignment length 657 bp). Numbers at nodes are ML bootstrap values in percent (only shown if > 50%). Species and candidate species are shown in different colors. Inset photos are not to scale.

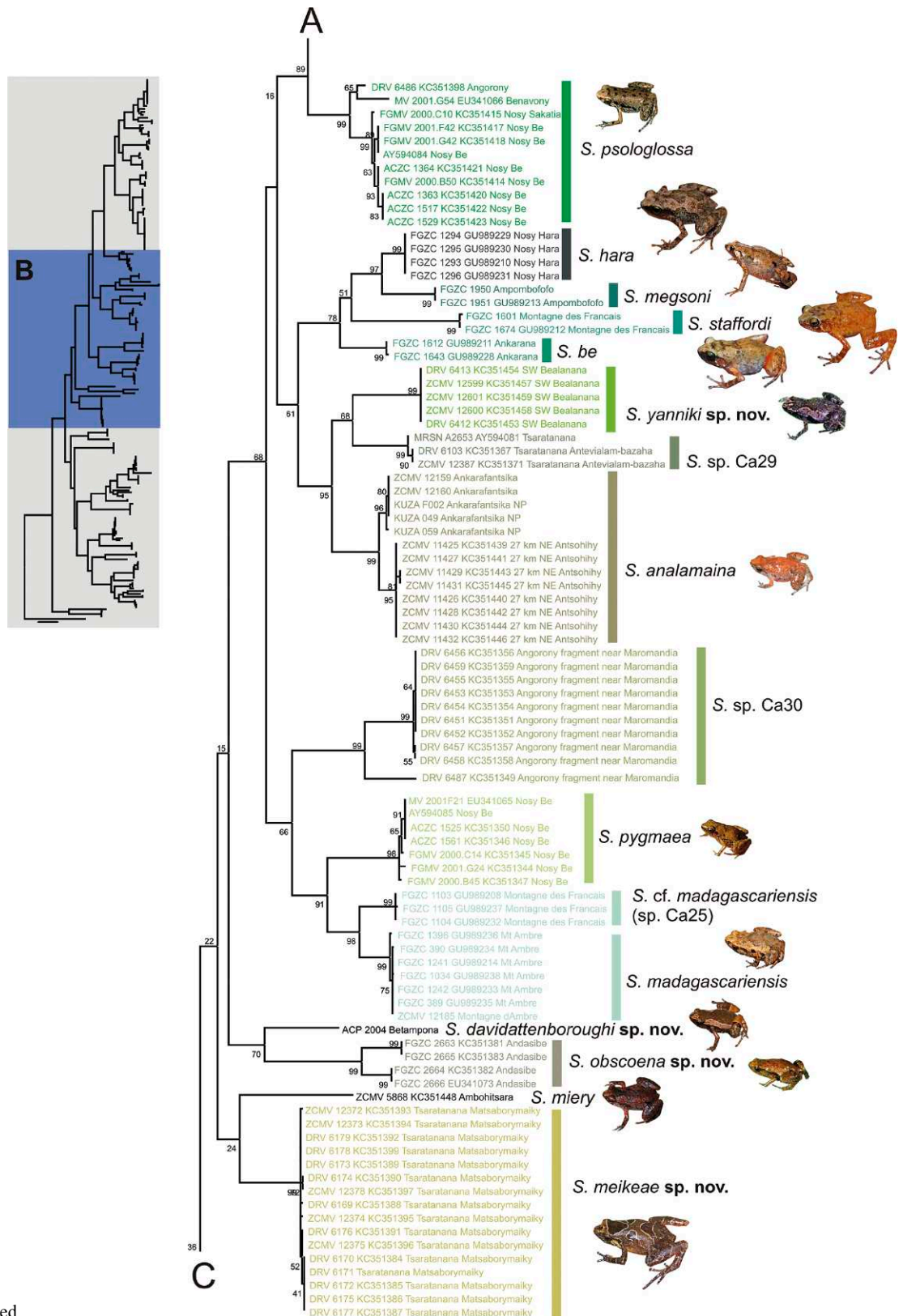


Fig. 3. Continued.

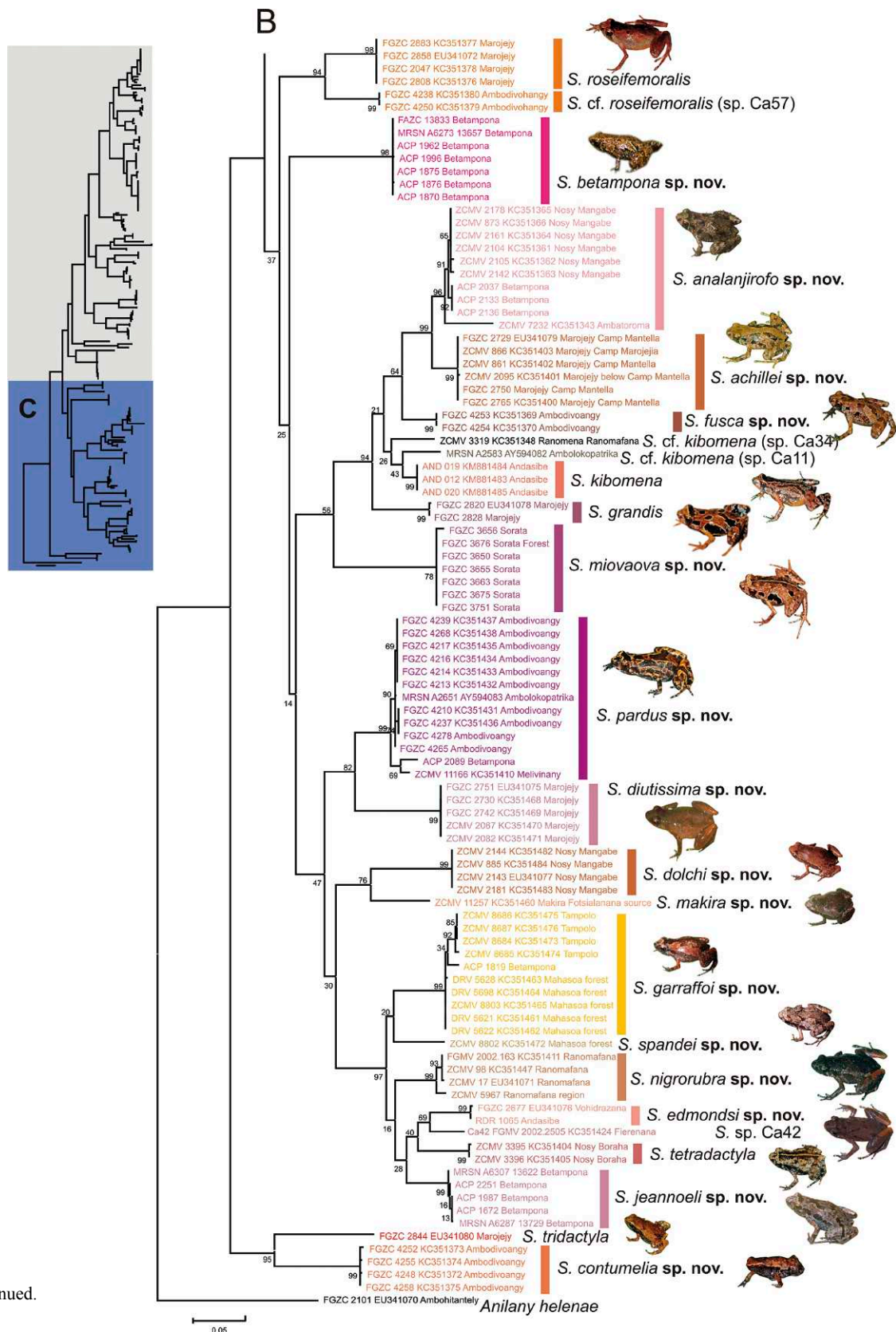


Fig. 3. Continued.

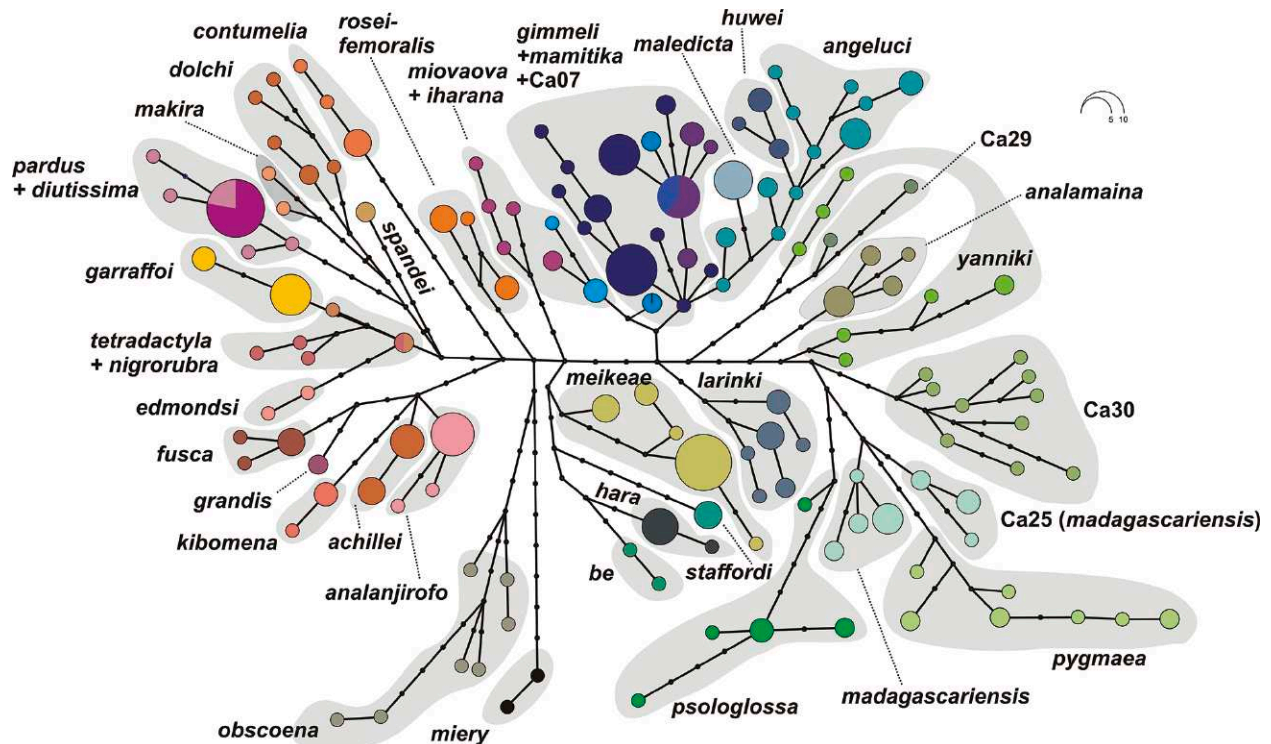


Fig. 4. Haplotype network constructed from sequences of the nuclear Rag-1 gene (338 bp, haplotypes inferred using the Phase algorithm). Colors correspond to the grouping as in the mitochondrial analysis (Fig. 3). Small dots represent unsampled or extinct haplotypes; whereas bars represent mutational steps. *Stumpffia tridactyla*, *S. betampona* sp. nov., *S. jeannoeli* sp. nov., *S. davidattenboroughi* sp. nov. and *S. sorata* sp. nov. could not be sequenced for Rag-1 and are therefore absent from this network.

Molecular phylogeny

The concatenated alignment of 12S, the two 16S fragments, Cox-1, and Rag-1, after exclusion of hypervariable regions of 12S and 16S, consisted of 3325 characters, of which 2315 were constant, 1010 were variable, and 714 of these were parsimony-informative. Partitioned Bayesian Inference analysis resulted in a well-resolved tree in which many nodes received maximum posterior probability (PP) support (Fig. 5). Four main clades were distinguished, of which three received maximum support (PP=1.0) and one was weakly supported (PP=0.94). These clades are here named A–D.

Clade A corresponded to a previously recovered group that has been named the northern/northwestern clade (KÖHLER *et al.*, 2010; KLAGES *et al.*, 2013; NDRINTSOA *et al.*, 2013) because most of the included species are exclusively distributed in these regions of Madagascar. All nodes within this clade were resolved with PP > 0.95, and the majority of nodes received maximum support. The three subclades splitting off the basalmost nodes within this clade are here denoted as subclades A1–A3. Of these, subclade A1 contains *S. gimmel* as well as the type species of the genus, *S. psologlossa*, plus eight further deep lineages of which seven are herein described as new species. The species in this subclade are small but not truly miniaturized (see below for definition of size ranges in *Stumpffia* used herein). Subclade A2 contains the smallest species within clade A, with three

described species (*S. analamaina*, *S. madagascariensis*, and *S. pygmaea*), one species newly described herein, and three further candidate species. Subclade A3 contains the four large-sized species described by KÖHLER *et al.* (2010), which probably are specialized to karst environments and at least partly are cave-dwellers. This subclade contains the *Stumpffia* species with the largest overall body sizes.

Clade B is a weakly supported assemblage of morphologically and biogeographically disparate species. It contains on the one hand a rather large-sized new species from high elevations in the Tsaratanana Mountains (*S. meikeae* sp. nov.), and on the other hand, three species from the Southern Central East and Northern Central East that are small to miniaturized and show distinct to extreme digital reduction.

Clade C contains the bulk of remaining species of *Stumpffia*, most of which are distributed in either eastern or northeastern Madagascar (including the regions North-East, Northern Central East, and Southern Central East). This clade contains 4 previously described species, 14 new species described herein, and 3 additional candidate species. Relationships within clade C in general are poorly resolved, but to facilitate further discussion we here name two main subclades C1 and C2, both of which received maximum support. Clade C contains rather large-sized species (e.g., *S. grandis*) as well as numerous small-sized species, some of which show a moderate degree of digital reduction (e.g., *S. tetradactyla*).

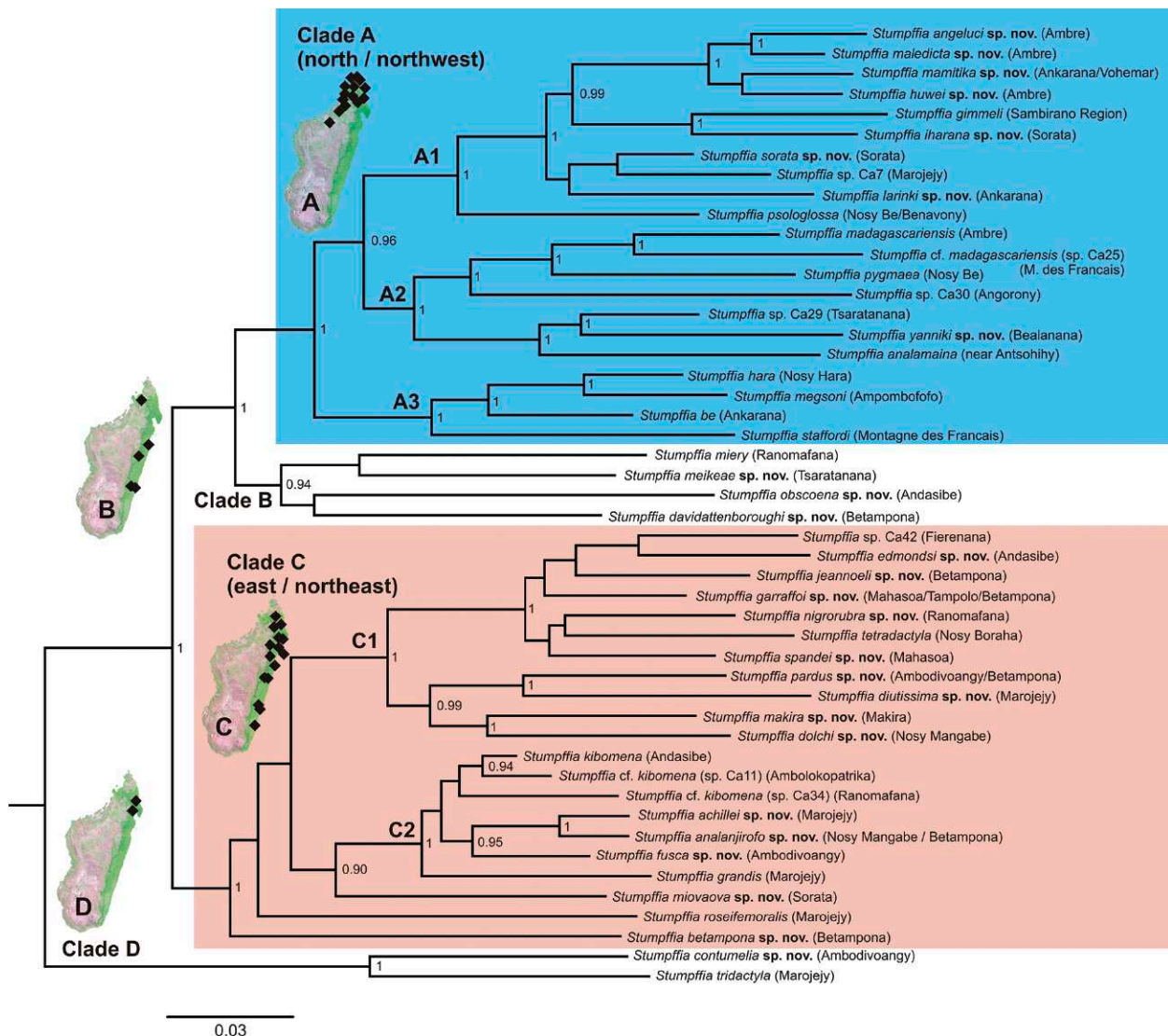


Fig. 5. Majority-rule consensus tree from a Bayesian Inference analysis of the concatenated dataset of one nuclear (Rag-1) and four mitochondrial (12S and 16S rRNA, Cox-1) gene fragments (3325 nucleotides). Major clades denoted A–D and subclades (A1–A3, C1–C2) are as discussed in the text. Clade A contains mostly species distributed in northern and north-western Madagascar whereas clade C mostly contains species from eastern and northeastern Madagascar. Numbers at nodes are posterior probabilities; not shown for values < 0.9. For each species or candidate species, up to three representative collection localities are mentioned. Inset maps summarize distribution records of all species in each of the four clades.

Clade D splits off the basalmost node within *Stumpffia* and contains two miniaturized species with a strong digital reduction that are genetically highly divergent from other *Stumpffia*. The genus-level classification of this clade will be reassessed in forthcoming publication in the light of a much-needed comprehensive screening of osteological variation in *Stumpffia*.

Morphological and bioacoustic comparisons

Given the difficulties in examining external morphological features in these miniaturized frogs, and our goal to reach a comprehensive review of the genus in a reasonable time frame, we focused on a limited number of traits that had previously proven to be informative in *Stumpffia*

fia, and partly in other small to miniaturized frogs and that are easily reproducible: (1) body size, (2) externally visible digital reduction, (3) dorsal and ventral color, and (4) advertisement call. In addition we also scored (5) relative length of hands and feet, which in the past have been found to differ among species of *Stumpffia* (KLAGES *et al.*, 2013), and (6) the texture of the dorsal skin. Altogether, our result suggest that the majority of molecular lineages of *Stumpffia* can be reliably distinguished from each other by a combination of these six characters, although some lineages (especially those with missing data on bioacoustics) were indistinguishable from a few others. However, often the morphologically most similar lineages were not direct phylogenetic sister lineages, thus not jeopardizing our taxonomic conclusion of assigning species status to them. Furthermore, such lineages that

Small-sized species of clade B, C and D

Clade B



Stumpffia miery
ZMB 77453



Stumpffia davidattenboroughi **sp. nov.**
ACZCV 0106

Clade D



Stumpffia tridactyla
FGZC 2844



Stumpffia contumelia **sp. nov.**
FGZC 4258, 4248, 4252

Clade C



Stumpffia tetradactyla
ZCMV 3395, ZFMK 52746



Stumpffia makira **sp. nov.**
ZCMV 11257



Stumpffia obscoena **sp. nov.**
FGZC 2666, 2664



Stumpffia betampona **sp. nov.**
ACZCV 0046, 0210



Stumpffia dolchi **sp. nov.**
ZCMV 2143



Stumpffia miovaova **sp. nov.**
FGZC 3751, 3656, 3676



Stumpffia spandei **sp. nov.**
FGZC 2677



Stumpffia garraffoi **sp. nov.**
ZCMV 8687, 8685, 8803

Fig. 6. Comparative view of ventral surfaces of hands of preserved specimens of small-sized *Stumpffia* species of Clade B, C and D. Not to scale.

Small-sized/miniaturized species of clade A



Stumpffia psiloglossa
FGMV 2000.279



Stumpffia analamaina
ZCMV 10034, 12159



Stumpffia gimmeli
DRV 6475, FGMC 2000. 0151



Stumpffia madagascariensis
FGZC 0390



Stumpffia pygmaea
ZFMK 53769



Stumpffia angeluci **sp. nov.**
FGZC 433, 580, 434



Stumpffia maledicta **sp. nov.**
FGZC 1049, ZCMV 13504



Stumpffia mamitika **sp. nov.**
ZCMV 13524, FGZC 2725



Stumpffia larinki **sp. nov.**
FGMV 2002.594, 2002.834, FGZC 1620



Stumpffia yanniki **sp. nov.**
ZCMV 12600, DRV 6413



Stumpffia sorata **sp. nov.**
FGZC 3618, 3621, 3622



Stumpffia iharana **sp. nov.**
FGZC 3927, 3800



Stumpffia huwei **sp. nov.**
ZCMV 13514, ZCMV 13515

Fig. 7. Comparative view of ventral surfaces of hands of preserved specimens of miniaturized/small-sized species of Clade A. Not to scale.

Large-sized species of clade B and C

Clade B



Clade C



Fig. 8. Comparative view of ventral surfaces of hands of preserved specimens of large-sized species of Clade B and C. Not to scale.

Small-sized species of clade B, C and D

Clade B



Clade C



Clade D



Fig. 9. Comparative view of ventral surfaces of feet of preserved specimens of small-sized species of Clade B, C and D. Not to scale.

Small-sized/miniaturized species of clade A

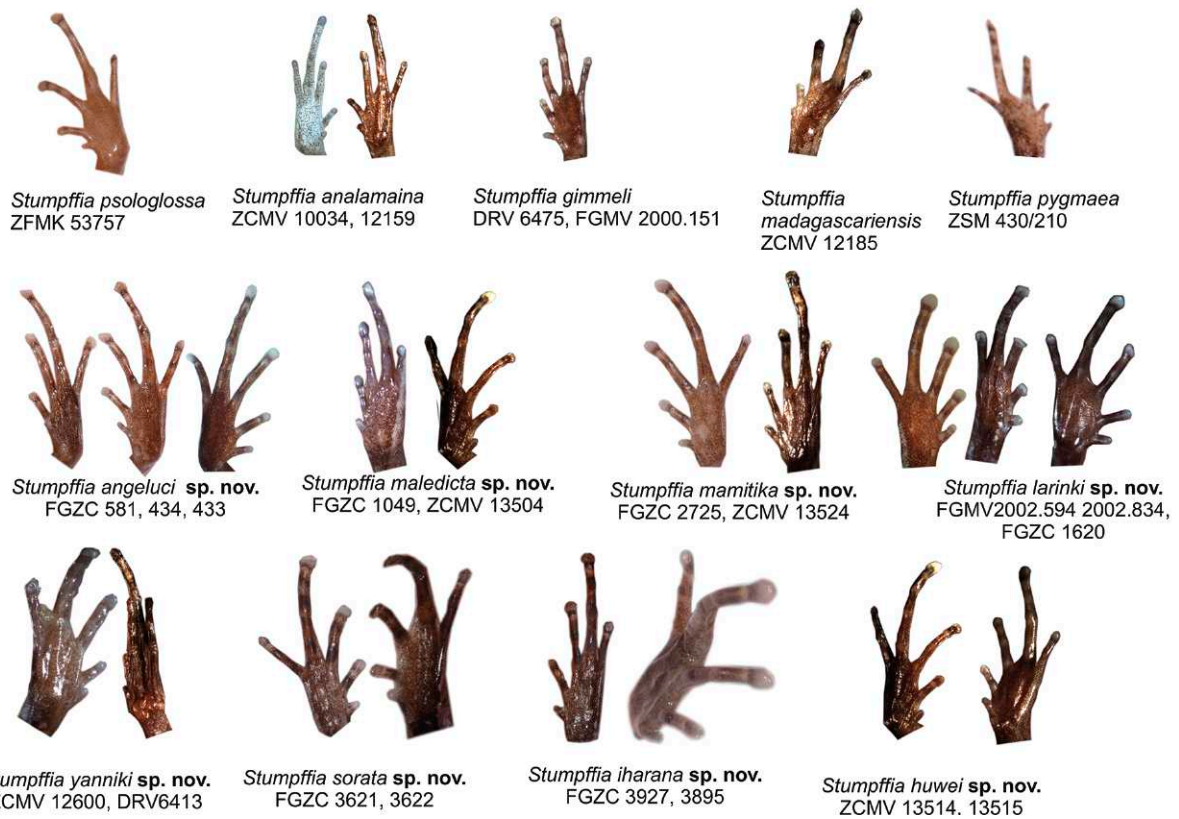


Fig. 10. Comparative view of ventral surfaces of feet of miniaturized/small-sized species of Clade A. Not to scale.

Large-sized species of clade B and C

Clade B



Clade C



Fig. 11. Comparative view of ventral surfaces of feet of large-sized species of Clade B and C. Not to scale.

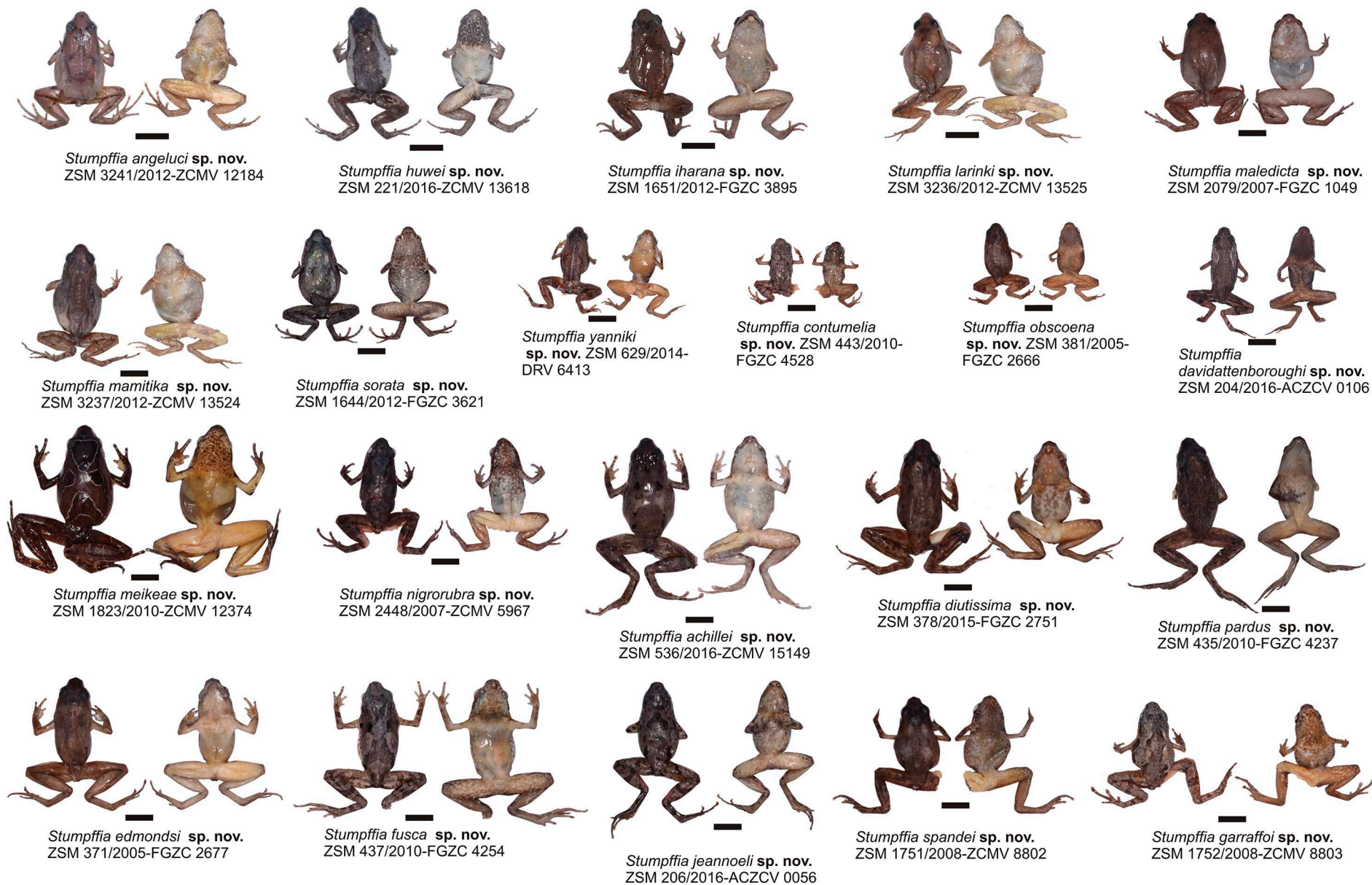


Fig. 12. Dorsal and ventral views of preserved name-bearing type specimens of newly described *Stumpffia* species. Scale bars equal 5 mm.



Fig. 12. Continued.

cannot be morphologically distinguished typically do not occur in close geographical proximity to one-another, meaning that field identification is unlikely to be hampered by this morphological similarity.

We found body size (Fig. 12) a useful means to define major clusters of *Stumpffia* species. These clusters often corresponded to clades in the phylogeny, but in some cases species of very different body sizes were grouped in the same clade. Body sizes range from 8–9 mm SVL in adult males of *S. contumelia* **sp. nov.** to a maximum of 28 mm in *S. staffordi*. For the purpose of this study and restricting our perspective to this genus alone, we define moderately to large-sized *Stumpffia* as those reaching regularly more than 17 mm snout-vent length. Species that typically reach 12–16 mm SVL are referred to as small-sized, and species below 12 mm are considered as miniaturized. This categorization is however not applied very strictly because there are species ranging inbetween the categories and exceptionally sized individuals of some species that we have disregarded for the categories. Our categorization is used primarily to facilitate comparisons among *Stumpffia*, and differs from previous work that defined, for frogs overall, miniature frogs as those ≤ 20 mm (CLARKE, 1996), or considering species < 14 mm as extremely miniaturized (TRUEB & ALBERCH, 1985). In clade A, there is a clear distinction of subclades in body size, with A1 containing mostly small species, A2 consisting of small to miniaturized species, and A3 containing moderate-sized to large species. Clade D contains only miniaturized species, clade C contains small to moderate/large-sized species and clade B shows a large variation despite few included species, from miniaturized and small species to one large-sized species.

In *Stumpffia*, miniaturized species < 12 mm SVL are also those that most commonly show extreme degrees of digital reduction (Fig. 6–11). *Stumpffia tridactyla* and two new species described herein, have the most strongly reduced condition, with only one finger and three toes recognizable and represent the smallest body sizes in *Stumpffia* (*S. contumelia* **sp. nov.**, probable calling males 8–9 mm). However, digital reduction is not strictly linked to body size, and is distinctly expressed in the four major clades. For instance, species of clade A show only very limited degrees of digital reduction even if miniaturized (e.g., *S. analamaina*, *S. pygmaea* and *S. yanniki* **sp. nov.**) whereas in clade C, the majority of species, even if large-sized, show a distinct length reduction at least of the first toe and a strong or complete reduction of this toe if small-sized. This character thus allows a quick distinction of all small-sized species of clade A from those in clade C, while the rather strong reduction pattern at the hand in the small-sized species of clade B (*S. miery* and *S. davidattenboroughi* **sp. nov.**) allows distinguishing these from both clade A and clade C species.

Aside from these morphological characters, the advertisement call is the most obvious character to diagnose species of *Stumpffia*. Unlike body size and digital reduction, the advertisement call often differs strongly between closely related lineages and direct sister line-

Table 2. Locality records of *Stumpffia* species with geographical coordinates.

Locality	Coordinates	Altitude (m a.s.l.)	Species
27 km from Ambanja (northeast of Ambanja towards Ambilobe)	—	—	<i>Stumpffia gimmeli</i>
27 km from Antsohihy	S15.0532, E48.2064	140	<i>Stumpffia analamaina</i>
Ambanja	S13.670, E48.463	—	<i>Stumpffia gimmeli</i>
Ambatolahidimy	S21.24831, E47.41987	—	<i>Stumpffia nigrorubra</i> sp. nov.
Ambatoroma (campsite in the Manompana / Befanjana forest area)	S16.66, E49.59	—	<i>Stumpffia analanjirofo</i> sp. nov.
Ambodivoangy (close to the Makira Reserve; sometimes spelled Ambodivoahangy)	S15.289944, E49.620278	ca. 100–287	<i>Stumpffia contumelia</i> sp. nov. <i>Stumpffia pardus</i> sp. nov. <i>Stumpffia fusca</i> sp. nov. <i>Stumpffia</i> sp. Ca57
Ambohitsara	S21.3571, E47.8153	294	<i>Stumpffia miery</i>
Ambolo forest fragment	S21.26359, E47.50921	—	<i>Stumpffia nigrorubra</i> sp. nov.
	S21.2625, E47.5068	660	<i>Stumpffia miery</i>
	S21.2639, E47.5092	700	<i>Stumpffia miery</i>
Ambolokopatrika (sometimes spelled Ambolokopatriky)	ca. S14.52, E19.43	810–1250	<i>Stumpffia</i> sp. Ca11
Ampombofofo	S12.0994, E49.3388	20	<i>Stumpffia megsoni</i>
An'Ala forest	S18.9166, E48.4833	ca. 850	<i>Stumpffia kibomena</i>
Ananitehana	S21.26549, E47.444296	—	<i>Stumpffia nigrorubra</i> sp. nov.
Andalangina	S21.2993, E47.5976	450	<i>Stumpffia miery</i>
	S21.29712, E47.59951	—	<i>Stumpffia nigrorubra</i> sp. nov.
Andapa	ca. S14.66, E49.66	—	<i>Stumpffia mamitika</i> sp. nov.
Andasibe (localities typically in Analamazaotra/Mantadia National Park or in Analamazaotra Forest Reserve)	S18.9333, E48.4166	900	<i>Stumpffia obscoena</i> sp. nov. <i>Stumpffia kibomena</i> <i>Stumpffia edmondsi</i> sp. nov.
Angorony forest fragment	S14.22111, E48.14211	115	<i>Stumpffia psiloglossa</i> <i>Stumpffia gimmeli</i> <i>Stumpffia</i> sp. Ca30
Ankarafantsika National Park	ca. S16.30, E46.81	—	<i>Stumpffia analamaina</i>
Ankarana National Park	—	—	<i>Stumpffia larinki</i> sp. nov.
	S12.9619, E49.1208	121	<i>Stumpffia mamitika</i> sp. nov.
	S12.95, E49.1166	90	<i>Stumpffia be</i>
Antsirasira	S13.9394, E48.559	—	<i>Stumpffia gimmeli</i>
Antaramananavana	S21.23997, E47.50647	—	<i>Stumpffia nigrorubra</i> sp. nov.
Benavony	S13.7, E48.4833	140	<i>Stumpffia psiloglossa</i> <i>Stumpffia gimmeli</i>
	S14.30917, E47.91528	170	<i>Stumpffia gimmeli</i>
Berara (forest in Sahamalaza Peninsula)	S17.9141, E49.21671	356	<i>Stumpffia pardus</i> sp. nov.
Betampona: Betakonana	S17.89383, E49.22508	274	<i>Stumpffia jeannoeli</i> sp. nov.
Betampona: Maintimbato	S17.92305, E49.20868	205	<i>Stumpffia jeannoeli</i> sp. nov.
Betampona: Rendrirendry: Piste Fotsimavo	S17.92682, E49.20777	287	<i>Stumpffia garraffoi</i> sp. nov.
Betampona: Sahabefoza	S17.91273, E49.21069	—	<i>Stumpffia jeannoeli</i> sp. nov.
Betampona: Sahaindrana	S17.89682, E49.19957	344	<i>Stumpffia jeannoeli</i> sp. nov.
	S17.89481, E49.20081	269	<i>Stumpffia betampona</i> sp. nov.
Betampona: Sahambendrana	S17.90137, E49.21098	558	<i>Stumpffia davidattenboroughi</i> sp. nov.
	S17.89905, E49.21635	455	<i>Stumpffia jeannoeli</i> sp. nov.
	S17.89916, E49.21650	447	<i>Stumpffia analanjirofo</i> sp. nov.
	S17.89848, E49.21470	476	<i>Stumpffia betampona</i> sp. nov.
Betampona: Vohitsivalana	S17.88501, E49.20339	481	<i>Stumpffia betampona</i> sp. nov.
	S17.88501, E49.20339	481	<i>Stumpffia jeannoeli</i> sp. nov.
	S17.88473, E49.20378	—	<i>Stumpffia analanjirofo</i> sp. nov.
Bezavona	ca. S13.52, E49.83	ca. 100	<i>Stumpffia iharana</i> sp. nov.
Fanambana forest	S13.6138, E50.0019	53	<i>Stumpffia iharana</i> sp. nov.
Fierenana	S18.54333, E48.44889	948	<i>Stumpffia</i> sp. Ca42
Forest fragment between Bealanana and Antsohihy	S14.72145, E48.56272	1187	<i>Stumpffia yanniki</i> sp. nov.
Forêt d'Ambre Special Reserve, ca. 5 km SW Sakaramy	S12.4714, E49.2204	487	<i>Stumpffia angeluci</i> sp. nov.
Gallery forest SE Andrafaïnkona	S13.7139, E49.4966	820	<i>Stumpffia iharana</i> sp. nov.
Ifanadiana	S21.2970, E47.5995	515	<i>Stumpffia miery</i>
Joffreville	S12.50175, E49.20206	796	<i>Stumpffia angeluci</i> sp. nov.
Mahaso Forest	S17.29769, E48.70199	1032	<i>Stumpffia spandei</i> sp. nov.
			<i>Stumpffia garraffoi</i> sp. nov.
Makira plateau, Fotsialanana source (within Makira Natural Park)	S15.4668, E49.1289	1067	<i>Stumpffia makira</i> sp. nov.
Manombo Special Reserve	S23.02521, E47.72515	—	<i>Stumpffia nigrorubra</i> sp. nov.
Manongarivo Special Reserve	S13.9755, E48.4266	688	<i>Stumpffia gimmeli</i>

Table 2 continued.

Marojejy National Park: ‘Camp 0’	S14.44633, E49.78523	310	<i>Stumpffia diutissima</i> sp. nov. <i>Stumpffia</i> sp. Ca7
Marojejy National Park: Camp Mantella	S14.4376, E49.7755	481	<i>Stumpffia roseifemoralis</i> <i>Stumpffia achillei</i> sp. nov. <i>Stumpffia diutissima</i> sp. nov.
Marojejy National Park: Camp Marojejia	S14.4333, E49.7666	746	<i>Stumpffia achillei</i> sp. nov. <i>Stumpffia diutissima</i> sp. nov.
Marojejy National Park: Camp Simpona	S14.4499, E49.7433	1326	<i>Stumpffia roseifemoralis</i> <i>Stumpffia grandis</i> <i>Stumpffia tridactyla</i> <i>Stumpffia</i> sp. Ca7
Marojejy National Park, high elevation site	S14.44064, E49.73995	1573	<i>Stumpffia tridactyla</i>
Marojejy National Park, high elevation <i>Pandanus</i> site	S14.44755, E49.73365	2026	<i>Stumpffia tridactyla</i>
Maromiandra	S13.99653, E48.21770	283	<i>Stumpffia gimmeli</i>
Melivinany (campsite in the Manompana / Befanjana forest area)	S16.66, E49.59	—	<i>Stumpffia pardus</i> sp. nov.
Montagne d’Ambre (localities refer to Montagne d’Ambre National Park or directly adjacent areas)	S12.5200, E49.1755	1052	<i>Stumpffia madagascariensis</i>
	S12.5134, E49.1835	ca. 975	<i>Stumpffia angeluci</i> sp. nov.
	S12.51483, E49.17617	1018	<i>Stumpffia huwei</i> sp. nov.
	S12.516667, E49.176667	1050	<i>Stumpffia maledicta</i> sp. nov.
Montagne des Français	S12.3258, E49.3380	—	<i>Stumpffia</i> cf. <i>madagascariensis</i> Ca25
	S12.333, E49.35	80–200	<i>Stumpffia angeluci</i> sp. nov.
	S12.3166, E49.333	260	<i>Stumpffia staffordi</i>
Near Ambodimandresy	ca. S13.7133, E49.4911	ca. 778	<i>Stumpffia iharana</i> sp. nov.
Nosy Be	S13.41333, E48.3341	110	<i>Stumpffia psologlossa</i>
Nosy Boraha	S13.3933, E48.3411	39	<i>Stumpffia pygmaea</i>
Nosy Hara	S16.9089, E49.8678	20	<i>Stumpffia tetradactyla</i>
Nosy Hara	S12.2497, E49.0077	20	<i>Stumpffia hara</i>
Nosy Mangabe Special Reserve	S15.5, E49.766	ca. 50–100	<i>Stumpffia dolchi</i> sp. nov. <i>Stumpffia analanjirofo</i> sp. nov.
Nosy Sakatia	S13.3141, E48.1555	0	<i>Stumpffia psologlossa</i>
Ranomafana village (village near Ranomafana National Park; coordinates correspond to village)	S21.262014, E47.459780	—	<i>Stumpffia nigrorubra</i> sp. nov.
Sahadikaina forest	S21.24658, E47.52178	—	<i>Stumpffia nigrorubra</i> sp. nov.
Sorata Forest	S13.6817, E49.4411	1339	<i>Stumpffia sorata</i> sp. nov.
Sorata Forest	S13.6744, E49.4403	1516	<i>Stumpffia miovaova</i> sp. nov.
Tampolo (Fenerive Est, Tamatave)	ca. S17.2887, E49.4116	ca. 10	<i>Stumpffia garraffoi</i> sp. nov.
Tsaranana Strict Nature Reserve: Manarikoba Forest, Andampy Campsite	S14.04222, E48.76167	730	<i>Stumpffia gimmeli</i>
Tsaranana Strict Nature Reserve: Antevialam-bazaha (Camp 1)	S14.17413 E48.94521	1589	<i>Stumpffia</i> sp. Ca29
Tsaranana Strict Nature Reserve: Matsabory Maiky (Camp 2; sometimes spelled Matsaborimaiky or Matsaborymaika)	S14.15256, E48.95728	2021	<i>Stumpffia meikeae</i> sp. nov. <i>Stumpffia</i> sp. Ca29
Vohemar	ca. S13.4289, 49.9629	—	<i>Stumpffia mamitika</i> sp. nov.
Vohidrazana	S18.95, E48.5	ca. 700–800	<i>Stumpffia edmondsi</i> sp. nov.

ages, thereby providing immediate evidence for their status as distinct species, if individuals with strongly divergent calls are encountered in sympatry (KÖHLER *et al.*, 2017). At the same time, the calls of *Stumpffia* have a very conserved general structure, consisting of a single chirp or whistle repeated at regular intervals, and only in one case (*S. psologlossa*) exhibit a distinctly pulsed note structure.

Taxonomic accounts

In this revision, we review all of the nominal species of *Stumpffia* (i.e., the ones with valid scientific names) and describe a total of 26 new species. Because this implies a total of around 40 species, it is impractical to provide de-

tailed differential diagnoses. Furthermore, not all species can be unambiguously diagnosed by morphology alone. We therefore provide comparative tables with details of important bioacoustic traits, comparative plates with views of hand and feet illustrating digital reductions, and a table with genetic distances in the fragment of the 3’-terminus of the mitochondrial 16S rRNA gene (Table 1).

The aim of this study is a revision of *Stumpffia* sensu stricto. We therefore do not consider species of *Anilany* (*A. helenae*, originally described as *Stumpffia helenae*) and do not discuss in detail those candidate species morphologically similar to *Stumpffia* but falling outside the main *Stumpffia* clade in molecular phylogenetics (SCHERZ *et al.*, 2016; 2017).

The species accounts are organized following first the phylogenetic subdivision of the genus into main clades,

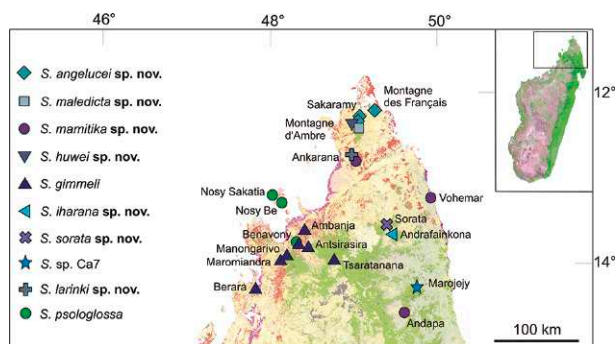


Fig. 13. Distribution map of *Stumpffia* species of clade A1. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, brown/orange colors deciduous dry and arid spiny forest.

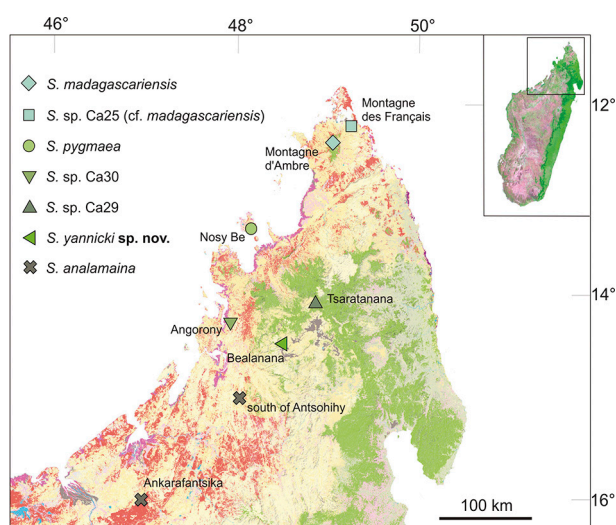


Fig. 14. Distribution map of *Stumpffia* species of clade A2. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, brown/orange colors deciduous dry and arid spiny forest.

and subsequently are subdivided based on body size, to facilitate comparisons. In each series of accounts, the nominal species are reviewed first, and the new species described subsequently. The nominal species in each cluster are listed alphabetically (except for the first cluster in which the type species *S. psologlossa* is listed first).

In the diagnoses, we briefly provide for each species a short non-differential diagnosis based on seven character sets: body size, digital reduction, terminal phalanges of digits relative hand and foot length, skin texture, color pattern, and call. The combination of these characters allows the vast majority of species to be distinguished from one another. We then give a very brief differential diagnosis. To avoid exceedingly long differential diagnoses, these were assembled in the following structure: (1) Each nominal species is compared only with those nominal species and newly described species mentioned in preceding accounts in this paper; i.e., the second species listed is compared only with the first, the third species

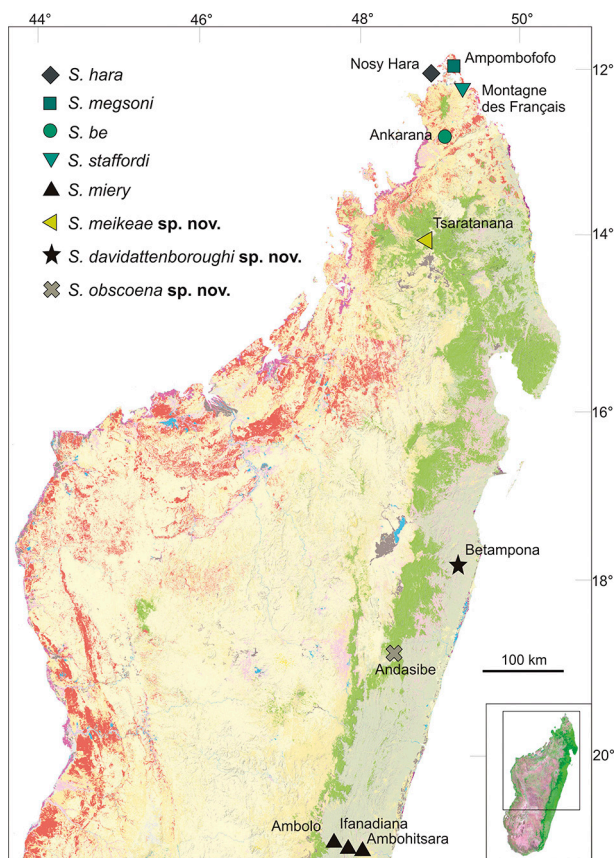


Fig. 15. Distribution map of *Stumpffia* species of clades A3 and B. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, brown/orange colors deciduous dry and arid spiny forest.

cies listed is compared with the first and the second, and so on. (2) Each newly described species is compared with all nominal species, and with the newly described species mentioned in preceding accounts in this paper. Where morphological and/or bioacoustic differences are absent or faint, we extend the respective differential diagnosis (and thus the species justification) to include also mitochondrial and nuclear genetic divergences, and especially, the phylogenetic position of the respective species. Figures 13–18 summarize the distribution of all species of *Stumpffia*, whereas living specimens and spectrograms/oscillograms of their calls are represented in Figs. 19–90. A set of representative preserved voucher specimens of most species is shown as Online Appendix (numbered as Supplementary Figs. S91–S125).

1. Small-sized or miniaturized species of clade A

Clade A is unambiguously supported by different sets of molecular markers and different analysis methods. This clade has previously been named the northern/north-western clade because all of the contained species occur in this area of Madagascar. Among nominal species of

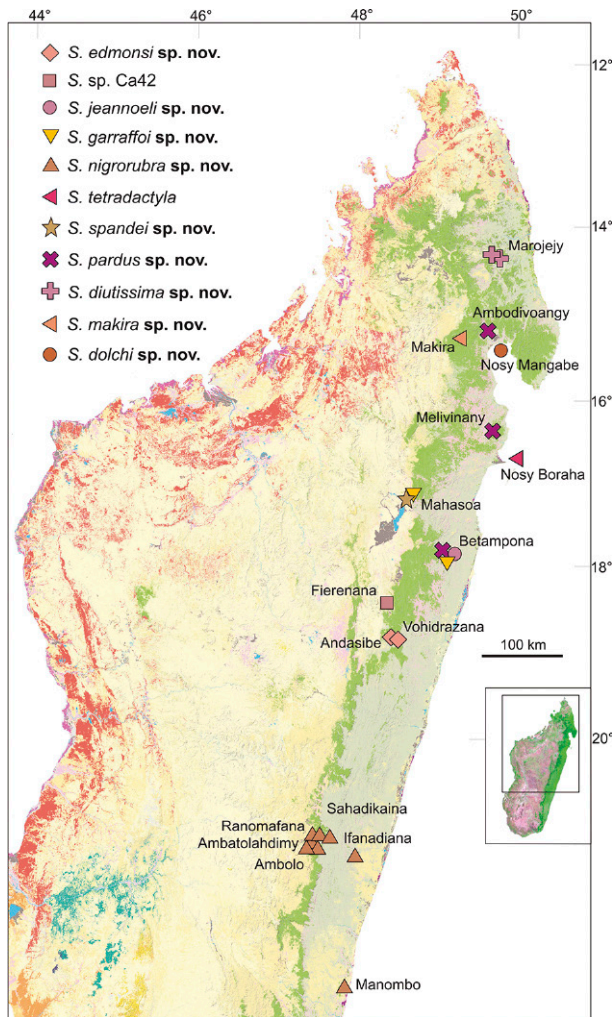


Fig. 16. Distribution map of *Stumpffia* species of clade C1. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, brown/orange colors deciduous dry and arid spiny forest.

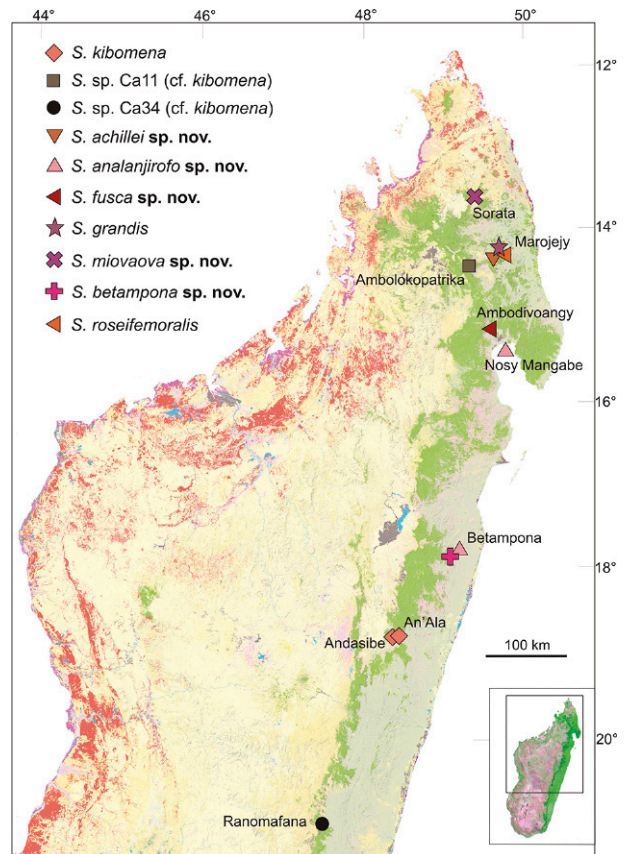


Fig. 17. Distribution map of *Stumpffia* species of clade C2 and remaining species of clade C. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, reddish colors deciduous dry forest, brown/orange colors deciduous dry and arid spiny forest.

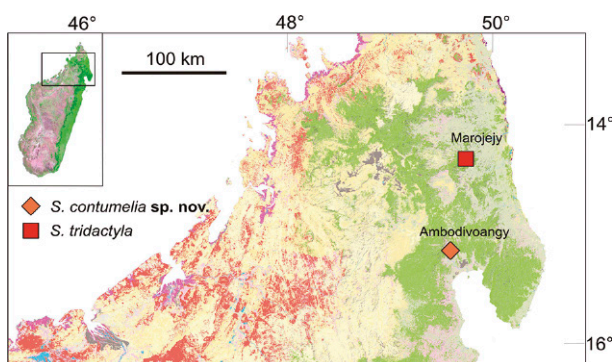


Fig. 18. Distribution map of species of *Stumpffia* in clade D. The map shows the remaining primary vegetation of Madagascar (www.vegmad.org), green colors indicating rainforest, brown/orange colors deciduous dry and arid spiny forest.

Stumpffia, five small-sized species and four large-sized species belong to this clade. We here first provide accounts for the small-sized species (clades A1 and A2)

and in the next section, the large-sized species (clade A3).

Stumpffia psologlossa BOETTGER, 1881

(Figures 19 and S91)

Name-bearing type. One specimen in SMF collected by A. Stumpff on “Nossi-Bé” (= Nosy Be), according to original description (BOETTGER, 1881), thus representing the holotype. BOETTGER (1892) lists six specimens in the SMF collection. MERTENS (1967) probably considered these wrongly as syntypes and designated SMF 7337 as lectotype; this specimen is here considered to correspond to the original holotype because it fits very well with the holotype drawing in the original description of BOETTGER (1881).

Identity and diagnosis. *Stumpffia psologlossa* is historically the first described species of *Stumpffia* and the type species of the genus. Despite some uncertainties regarding the holotype/lectotype of the species, the species identity is clear because only two species occur on Nosy Be, and in only one of them the typical “teddybear”-shaped

Table 3. Original morphometric measurements of representative specimens of *Stumpffia* examined. ND=not determined.

Species	Collection number-Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
<i>Stumpffia psologlossa</i>	SMF 7337	ND	14.6	4.9	ND	0.4	1.6	1.1	ND	1.8	ND	2.8	ND	ND	6.8	6.5
<i>Stumpffia psologlossa</i>	ZSM 479/2000 (FG/MV 2000.279)	ND	13.2	4.3	4.4	0.9	1.8	1.6	0.8	1.9	7.0	2.7	19.2	9.1	5.7	6.5
<i>Stumpffia psologlossa</i>	ZSM 480/2000 (FG/MV 2000.837)	ND	13.8	5.0	3.3		1.7	1.6	1.1	1.7	8.4	3.2	22.0	11.1	4.9	7.6
<i>Stumpffia psologlossa</i>	ZSM 483/2000 (FG/MV 2000.837)	Juvenile	10.1	3.9	3.1	0.6	1.5	1.2	1.1	1.9	6.3	2.3	15.0	6.6	4.5	5.0
<i>Stumpffia psologlossa</i>	ZSM 484/2000 (FG/MV 2000.837)	ND	11.6	4.3	2.8	0.8	1.2	1.0	0.8	1.4	7.2	2.9	16.4	8.9	5.3	5.8
<i>Stumpffia psologlossa</i>	ZSM 485/2000 (FG/MV 2000.837)	Juvenile	10.2	3.5	ND	0.7	1.5	ND	ND	ND	5.9	2.4	14.7	6.9	3.6	5
<i>Stumpffia psologlossa</i>	ZFMK 52530	ND	14.8	5.3	4.6	0.7	2.2	1.4	1.2	2	7.8	3	20.1	9.9	5.6	6.8
<i>Stumpffia psologlossa</i>	ZFMK 52532	ND	14.4	4.7	4.2	0.8	1.9	1.6	1.1	2	7.5	2.8	20.1	8.8	5.6	7.3
<i>Stumpffia psologlossa</i>	ZFMK 52531	ND	14.5	5.0	4.9		2.0	1.7	1	1.8	6.9	3	20.9	9.1	6	6.7
<i>Stumpffia psologlossa</i>	ZFMK 52533	ND	13.5	5.0	4.2	1.0	2.1	1.4	1.1	1.8	7.3	2.8	18.1	9.3	6.2	6.4
<i>Stumpffia psologlossa</i>	ZFMK 52534	ND	14.0	4.3	4.0		1.5	1.1	1	1.9	8.2	2.5	19.8	8.5	5.2	7
<i>Stumpffia psologlossa</i>	ZFMK 53750	ND	13.2	4.2	4.0	0.6	1.5	1.6	1	2	7.6	2.4	18.1	8.7	5.2	6
<i>Stumpffia psologlossa</i>	ZFMK 53751	ND	12.2	4.1	4.1	0.8	1.5	1.7	1	1.9	7.2	2.5	16.0	8.3	5	6
<i>Stumpffia psologlossa</i>	ZFMK 53752	ND	12.1	3.9	4.1	0.6	1.7	1.5	1.2	2	7.4	2.9	19.4	9.1	5.5	6.2
<i>Stumpffia psologlossa</i>	ZFMK 53753	Juvenile	8.7	3.2	3.6		1.3	0.9	0.7	1.2	5.2	2.1	13.5	6.7	4.8	5.1
<i>Stumpffia psologlossa</i>	ZFMK 53754	ND	11.6	4.3	3.8		1.1	0.9	1	1.6	7	2.7	16.3	8.7	5.3	5.7
<i>Stumpffia psologlossa</i>	ZFMK 53755	ND	10.2	4.0	4.1	1.0	1.3	0.8	0.8	1.1	7.2	2	18.3	8.3	4.2	5
<i>Stumpffia psologlossa</i>	ZFMK 53756	ND	10.2	4.1	3.8		1.4	1.1	1.1	1.7	7.4	2.1	18.8	8.5	4.6	6
<i>Stumpffia psologlossa</i>	ZFMK 53757	ND	10.9	3.7	3.9	0.7	1.4	1.5	1.1	1.8	6.3	2.3	17.5	7.2	4.9	5.9
<i>Stumpffia psologlossa</i>	ZFMK 53758	Juvenile	9.0	3.3	3.1		1.1	0.6	0.7	1.3	3.7	2.3	12.4	6.6	4.1	4.6
<i>Stumpffia psologlossa</i>	ZFMK 53759	Juvenile	8.2	3.0	ND		1.2	0.7	0.7	1.2	5	1.9	13.2	6.5	4.3	4.8
<i>Stumpffia psologlossa</i>	ZFMK 53760	ND	13.4	5.2	4.8	0.9	1.8	0.7	0.8	1.6	6.8	2.5	17.8	8.6	5.7	5.2
<i>Stumpffia psologlossa</i>	ZFMK 53761	Juvenile	7.4	3.2	3.3		1.2	0.7	0.7	1.3	7.2	2.8	10.8	4.3	2.7	3.4
<i>Stumpffia analamaina</i>	ZSM 542/2009 (ZCMV 11428)	Male	11.2	4.0	ND		1.4	0.8	ND	1.2	ND	2.6	ND	ND	5.8	5.6
<i>Stumpffia analamaina</i>	KUZA 0007-2011_Ad_059	ND	11.5	3.6	3.7	0.8	1.2	1.4	1	1.6	3.8	2.8	14.4	6.6	3.6	4.9
<i>Stumpffia analamaina</i>	KUZA 0004-2010_F005	ND	12.3	4.3	3.4	0.8	1.7	1.3	0.8	1.5	5.9	2.6	17.1	9.4	6.3	6.2
<i>Stumpffia analamaina</i>	KUZA 0001-2010_F002	ND	12.6	4.6	3.7	0.5	1.5	1.4	0.8	1.4	5.7	2.8	18.4	8.6	6	7
<i>Stumpffia analamaina</i>	KUZA 0003-2010-F004	ND	11.2	4.7	ND	ND	1.3	ND	ND	ND	ND	2.7	ND	8.2	6.2	6.3
<i>Stumpffia analamaina</i>	KUZA 0002-2010-F003	ND	12.1	4.1	ND	ND	1.3	ND	ND	ND	ND	2.8	ND	8.7	6.1	6.0
<i>Stumpffia analamaina</i>	KUZA 0006-2011-Ad-050	ND	13.4	4.2	4.5	ND	1.6	ND	ND	ND	6.9	2.8	19.5	8.4	6.3	6.3
<i>Stumpffia analamaina</i>	KUZA 0005-2011-Ad-049	ND	12.0	4.3	4.5	ND	1.8	ND	ND	ND	6.2	2.7	17.1	8.8	6.3	5.7
<i>Stumpffia analamaina</i>	KUZA 0010-2013-A (= 2013-NoCode)	ND	13.2	4.1	4.4	ND	1.5	ND	ND	ND	5.9	2.6	19.0	9.1	5.7	6.8
<i>Stumpffia analamaina</i>	KUZA 0008-2012-089	Female	13.2	4.3	4.3	ND	1.5	ND	ND	ND	6.4	2.7	17.6	8.6	6.0	5.9
<i>Stumpffia analamaina</i>	KUZA 0009-2012-090	Male?	12.6	4.4	4.5	ND	1.5	ND	ND	ND	6.1	2.6	18.9	8.6	5.7	5.9
<i>Stumpffia gimmeli</i>	ZSM 597/2001 (MV 2001.36)	ND	15.3	5.0	4.9	1.0	2.3	1.5	0.7	1.6	6.1	2.9	21.2	9.7	6.9	6.3
<i>Stumpffia gimmeli</i>	ZSM 412/2000 (FG/MV 2000.151)	ND	18.1	6.3	5.8	1.1	2.1	1.1	1.1	2.0	9.7	4.1	27.3	12.1	8.2	8.8
<i>Stumpffia gimmeli</i>	ZSM 833/2003 (FG/MV 2002.0784)	Male	14.5	4.7	4.5	1.0	1.7	0.9	0.9	1.8	7.4	3	20.1	9.6	6.4	6.7
<i>Stumpffia madagascariensis</i>	ZSM 3242/2012 (ZCMV 12185)	ND	11.2	3.8	4.1	0.7	1.3	0.8	0.8	1.3	4.8	1.8	ND	7.0	5.0	4.5
<i>Stumpffia madagascariensis</i>	ZSM 202/2004 (FGZC 390)	ND	10.0	3.3	3.8	1.0	1.3	0.9	0.8	1.3	4.4	1.8	11.9	5.4	3.9	4.2

Table 3 continued.

Species	Collection number (Field number)	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
<i>Stumpffia madagascariensis</i>	ZSM 201/2004 (FGZC 389)	ND	11.7	3.6	3.9	0.8	1.3	0.9	0.7	1.2	ND	1.8	13.9	6.7	4.5	4.4
<i>Stumpffia</i> cf. <i>madagascariensis</i> (sp. Ca25)	ZSM 2108/2007 (FGZC 1103)	ND	13.6	4.2	3.7	0.6	1.9	1.1	0.9	1.5	7.1	2.2	15.8	7.9	4.3	6.7
<i>Stumpffia</i> cf. <i>madagascariensis</i> (sp. Ca25)	ZSM 2109/2007 (FGZC 1105)	ND	11.0	3.7	3.7	0.5	1.8	1.2	0.9	1.3	4.6	1.9	15.7	6.8	4.3	5.1
<i>Stumpffia pygmaea</i>	ZSM 430/2010	ND	8.3	3.7	ND		1.4	0.8	0.8	1.2	3.6	1.5	12.9	5.5	3.2	4.3
<i>Stumpffia pygmaea</i>	ZSM 431/2010	ND	8.8	3.0	3.0		1.3	0.8	0.7	1.0	3.2	1.3	10.0	4.8	2.5	4.0
<i>Stumpffia pygmaea</i>	ZFMK 53767	ND	9.8	3.5	ND		1.2	ND	ND	ND	4.8	1.3	14.9	6.8	4.2	5.5
<i>Stumpffia pygmaea</i>	ZFMK 53762	ND	11.7	4.0	3.8	1.2	1.5	0.9	0.5	1.9	4.9	1.7	12.8	6.5	4.6	4.3
<i>Stumpffia pygmaea</i>	ZFMK 53763	ND	10.5	3.4	3.5	1.2	1.4	0.7	0.5	1.9	4.7	2.0	13.9	6.6	4.2	5.0
<i>Stumpffia pygmaea</i>	ZFMK 53768	ND	9.5	3.9	3.7	1.0	1.5	0.9	0.6	1.7	5.0	1.6	14.3	7.3	4.5	4.9
<i>Stumpffia pygmaea</i>	ZFMK 53766	ND	10.2	3.1	ND		1.4	ND	ND	ND	4.1	1.8	14.3	7.1	3.7	4.8
<i>Stumpffia pygmaea</i>	ZFMK 53764	ND	12.5	3.9	4.1	0.8	1.7	0.8	0.7	1.9	5.2	1.8	13.4	6.0	4.7	4.6
<i>Stumpffia pygmaea</i>	ZFMK 53765	Female	11.0	3.7	ND		1.6	ND	ND	ND	4.8	2.1	14.7	7.1	3.6	5.6
<i>Stumpffia pygmaea</i>	ZFMK 53769	ND	10.4	3.8	3.6	0.9	1.6	0.9	0.6	1.9	3.1	1.9	14.1	5.6	3.6	4.8
<i>Stumpffia pygmaea</i>	ZFMK 53772	ND	10.6	3.7	3.4	1.0	1.4	0.8	0.7	2	5.2	1.4	13.9	6.7	4.8	4.8
<i>Stumpffia pygmaea</i>	ZFMK 53773	ND	9.5	3.4	3.4	0.9	1.4	1	0.7	1.9	5.9	1.7	11.4	6	3.6	4.7
<i>Stumpffia angeluci</i> sp. nov.	ZSM 3241/2012 (ZCMV 12184)	Male	14.6	5.3	5.2	1.0	1.8	1.2	0.6	2.4	7.6	3.3	20.8	10.3	7.2	7.3
<i>Stumpffia angeluci</i> sp. nov.	ZSM 3243/2012 (ZCMV 12197)	Male	13.9	4.8	5.5	0.8	1.6	1	0.4	2.1	6.9	2.9	19.2	10.1	6.4	7.2
<i>Stumpffia angeluci</i> sp. nov.	ZSM 300/2004 (FGZC 580)	Male	13.7	5.0	4.5	0.8	1.4	1.0	0.6	1.7	6.3	3.0	18.4	8.7	4.6	5.7
<i>Stumpffia angeluci</i> sp. nov.	ZSM 224/2004 (FGZC 434)	Male	14.2	4.6	4.8	0.7	1.9	1.0	0.5	1.6	7.9	3.3	21.8	10.0	6.7	7.2
<i>Stumpffia angeluci</i> sp. nov.	ZSM 223/2004 (FGZC 433)	Male	16.1	5.5	5.1	0.8	2.1	1.3	1.2	1.8	8.2	3.7	21.6	10.6	7.4	7.4
<i>Stumpffia angeluci</i> sp. nov.	ZSM 301/2004 (FGZC 581)	Female	14.7	5.2	5.2	0.8	1.7	1.1	0.3	1.6	7.4	3.2	19.4	9.5	5.9	6.4
<i>Stumpffia angeluci</i> sp. nov.	ZSM 302/2004 (FGZC 583)	ND	12.0	4.3	4.1	0.6	1.6	1.0	0.5	1.8	7.4	3.0	19.1	8.8	6.0	6.2
<i>Stumpffia angeluci</i> sp. nov.	ZSM 303/2004 (FGZC 586)	ND	11.0	4.0	4.2	0.6	1.7	1.0	0.5	1.6	4.8	2.5	14.8	7.5	4.2	5.2
<i>Stumpffia angeluci</i> sp. nov.	ZSM 1671/2008 (FGZC 1901)	ND	11.2	4.1	4.0	1.5	1.5	0.9	0.5	1.8	5.6	2.2	16.9	7.8	4.6	5.9
<i>Stumpffia huwei</i> sp. nov.	ZSM 221/2016 (ZCMV 13618)	Male	12.8	4.3	4.5	1.4	1.6	1.7	0.7	1.5	5.2	2.8	20.1	8.8	5.5	6.5
<i>Stumpffia huwei</i> sp. nov.	ZSM 904/2003 (FG/MV 2002.920)	ND	12.8	4.1	4.3	1.1	1.9	1.2	0.9	1.5	4.8	2.5	17.8	8.0	4.4	6.2
<i>Stumpffia huwei</i> sp. nov.	UADBA-A 60282 (ZCMV 13619)	ND	15.0	4.4	4.7	1.4	1.7	1.3	1.0	1.5	6.1	2.6	19.0	8.6	6.3	6.3
<i>Stumpffia huwei</i> sp. nov.	UADBA-A 60281 (ZCMV 13515)	Male	12.7	4.2	4.6	1.0	1.8	1.2	0.7	1.6	4.1	2.6	17.7	8.1	4.4	6.0
<i>Stumpffia huwei</i> sp. nov.	ZSM 3245/2012 (ZCMV 13514)	Male	12.5	3.9	4.1	0.8	1.6	1.1	0.8	1.2	5.0	2.0	17.2	7.8	4.2	5.7
<i>Stumpffia huwei</i> sp. nov.	ZSM 224/2016 (ZCMV 13611)	Male	14.8	4.9	4.7	0.8	1.8	1.2	0.8	1.5	6.3	2.9	20.3	8.6	4.9	6.9
<i>Stumpffia iharana</i> sp. nov.	ZSM 1651/2012 (FGZC 3895)	ND	14.3	4.7	5.3	1.3	2.2	1.2	1.1	1.9	7.8	2.8	21.0	9.3	5.7	7.0
<i>Stumpffia iharana</i> sp. nov.	ZSM 1652/2012 (FGZC 3927)	Female	14.7	4.9	5.2	1.2	1.8	1.2	0.8	2.2	7.4	3.3	22.9	11.0	7.2	7.3
<i>Stumpffia iharana</i> sp. nov.	ZSM 1642/2012 (FGZC 3800)	ND	14.0	5.1	4.9	1.1	1.8	1.4	0.9	2.0	8.0	3.1	20.3	9.5	6.5	6.6
<i>Stumpffia iharana</i> sp. nov.	ZSM 1650/2012 (FGZC 3893)	ND	15.5	4.7	4.9	1.2	2.1	1.3	1.0	2.1	7.6	3.0	21	8.8	4.6	7.0
<i>Stumpffia larinki</i> sp. nov.	ZSM 3236/2012 (ZCMV 13525)	Male	12.6	4.1	4.3	0.9	1.6	0.9	0.5	1.6	5.8	2.8	17.4	6.4	4.7	5.9
<i>Stumpffia larinki</i> sp. nov.	ZSM 779/2003- (FG/MV 2002.0594)	ND	12.7	4.0	4.3	1.1	1.8	1.2	0.6	1.8	7.1	3.1	16.8	8.5	5.3	6.0
<i>Stumpffia larinki</i> sp. nov.	ZSM 861/2003- (FG/MV 2002.0834)	ND	12.5	4.4	4.2	0.8	1.7	0.9	0.3	1.8	7.4	2.8	18.0	8.7	5.1	6.1
<i>Stumpffia larinki</i> sp. nov.	ZSM 1669/2008 (FGZC 1620)	ND	12.8	4.6	3.8	0.8	1.9	0.9	0.4	1.6	6.2	3.1	16.9	7.5	5.0	6.3
<i>Stumpffia maledicta</i> sp. nov.	ZSM 2079/2007 (FGZC 1049)	ND	16.8	6.5	5.4	1.1	2.0	1.0	0.6	2.0	8.5	3.2	23.2	10.0	6.0	8.2

Table 3 continued.

Species	Collection number (Field number)	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
<i>Stumpfia maledicta</i> sp. nov.	ZSM 3244/2012 (ZCMV 13504)	Male	13.8	5.1	4.6	1.2	1.5	1.0	0.5	2.1	6.2	2.5	9.8	9.8	4.9	7.0
<i>Stumpfia maledicta</i> sp. nov.	ZSM 2169/2007 (FGZC 1244)	ND	14.2	5.4	5.1	1.1	2.1	1.1	ND	2.0	7.5	2.8	21.8	9.2	4.1	7.6
<i>Stumpfia mamitika</i> sp. nov.	ZSM 3237/2012 (ZCMV 13524)	Male	15.0	4.9	4.4	1.3	1.9	1.1	0.8	1.3	6.7	3.2	19.0	9.3	6.2	5.9
<i>Stumpfia mamitika</i> sp. nov.	ZSM 3232/2012 (ZCMV 13528)	Male	12.7	4.1	4.2	1.6	1.7	1.5	0.3	1.3	6.1	2.8	17.2	8.4	5.8	5.6
<i>Stumpfia mamitika</i> sp. nov.	UADBA-A 60278 (orig. ZSM 3233/2012, ZCMV 13529)	ND	12.5	3.8	3.9	1.1	1.6	1.2	0.9	1.4	5.2	2.8	17.7	8.3	5.6	5.8
<i>Stumpfia mamitika</i> sp. nov.	UADBA-A 60278 (orig. ZSM 3233/2012, ZCMV 13529)	ND	12.7	3.8	3.9	1.1	1.3	1.1	0.8	1.3	5.6	2.6	16.3	8.2	5.5	5.3
<i>Stumpfia mamitika</i> sp. nov.	UADBA-A 60284 (orig. ZSM 3234/2012, ZCMV 13530)	ND	12.3	4.0	4.3	0.9	1.8	1.0	0.8	1.4	4.9	2.9	17.4	9.1	5.8	6.2
<i>Stumpfia mamitika</i> sp. nov.	ZSM 862/2003 (FG/MV 2002.0838)	ND	14.2	4.5	4.3	1.4	1.8	1.1	0.3	1.6	7.3	2.7	19.8	10.1	6.5	6.5
<i>Stumpfia mamitika</i> sp. nov.	ZSM 375/2005 (FGZC 2725)	ND	14.4	5.4	4.7	1.2	1.9	0.9	0.4	1.6	7.1	2.3	22.5	10.8	7.2	7.1
<i>Stumpfia sorata</i> sp. nov.	ZSM 1644/2012 (FGZC 3621)	ND	16.0	5.5	5.3	1.5	2.0	1.1	1.0	1.9	8.3	3.1	22.1	10.1	6.9	7.1
<i>Stumpfia sorata</i> sp. nov.	ZSM 1645/2012 (FGZC 3622)	ND	15.8	5.5	5.1	1.0	1.8	1.1	0.9	1.7	8.1	2.9	23.4	10.1	4.7	7.4
<i>Stumpfia sorata</i> sp. nov.	ZSM 1643/2012 (FGZC 3618)	ND	15.6	5.4	5.3	1.3	2.3	1.3	1.2	1.9	8.7	3.6	22.1	10.2	6.3	7.8
<i>Stumpfia yanniki</i> sp. nov.	ZSM 629/2014 (DRV 6413)	ND	9.8	3.3	3.5	0.9	0.9	0.7	0.6	1.3	3.3	1.8	12.4	6.1	3.2	4.3
<i>Stumpfia yanniki</i> sp. nov.	ZSM 1825/2010 (ZCMV 12600)	ND	10.6	3.0	3.3	1.0	1.5	0.6	0.5	1.1	5.3	2.0	13.3	6.9	3.7	4.5
<i>Stumpfia tridactyla</i>	MNHN 1975.0028	ND	10.6	3.7	ND	0.8	1.5	0.5	ND	1.4	ND	1.5	ND	5.9	3.4	4.0
<i>Stumpfia tridactyla</i>	MNHN 1975.0029	ND	10.4	3.4	ND	0.7	1.2	0.6	ND	1.3	ND	1.4	ND	5.9	3.3	3.7
<i>Stumpfia tridactyla</i>	ZSM 382/2005 (FGZC 2844)	ND	9.8	3.2	ND	0.6	1.5	0.6	0.6	1.0	ND	1.5	ND	5.2	3.0	3.2
<i>Stumpfia tridactyla</i>	ZSM 527/2016 (ZCMV 15284)	ND	8.6	2.9	3.3	0.8	1.4	1	0.6	1.1	5.2	1.5	12.3	5.6	3.5	3.8
<i>Stumpfia contumelia</i> sp. nov.	ZSM 443/2010 (FGZC 4258)	Male	8.0	3.0	3.1	0.5	1.0	0.5	0.3	1.1	4.5	1.3	12.1	6.1	3.5	3.9
<i>Stumpfia contumelia</i> sp. nov.	ZSM 441/2010 (FGZC 4248)	ND	8.5	3.2	2.5	0.6	0.9	0.5	0.4	1.1	4.6	1.4	12.8	5.6	2.7	3.9
<i>Stumpfia contumelia</i> sp. nov.	ZSM 442/2010 (FGZC 4252)	Male	8.9	2.9	3.2	0.6	1.1	0.4	0.4	1.0	3.9	1.6	12.3	7.2	3.1	4.2
<i>Stumpfia davidattenboroughi</i> sp. nov.	ZSM 204/2016 (ACZCV 106)	ND	11.7	3.8	3.9	0.8	1.0	1.1	0.8	1.4	5.7	2.0	14.3	6.5	2.7	3.3
<i>Stumpfia meikeae</i> sp. nov.	ZSM 1823/2010 (ZCMV 12374)	Male?	21.3	6.5	6.4	1.1	2.2	1.1	1.3	2.3	ND	4.8	ND	15.9	10.2	11.0
<i>Stumpfia meikeae</i> sp. nov.	ZSM 617/2014 (DRV 6163)	Male	20.9	5.9	6.4	1.3	2.6	1.6	1.3	2.2	10.2	5.0	34.9	15.2	10.5	11.4
<i>Stumpfia meikeae</i> sp. nov.	ZSM 619/2014 (DRV 6171)	Male	23.4	6.4	6.8	1.4	2.2	1.7	1.4	2.1	10.3	5.1	33.6	15.3	9.4	12
<i>Stumpfia meikeae</i> sp. nov.	ZSM 620/2014 (DRV 6175)	Male	20.7	6.0	6.4	1.8	2.2	1.8	1.3	2.0	10.4	4.8	32.3	14.6	10	11.4
<i>Stumpfia meikeae</i> sp. nov.	ZSM 621/2014 (DRV 6177)	Male	21.6	6.6	6.3	1.6	2.2	1.4	1.4	2.0	11.6	5.1	35.6	15.7	9.4	11.7
<i>Stumpfia meikeae</i> sp. nov.	ZSM 1821/2010 (ZCMV 12372)	Male	19.2	6.3	6.4	1.2	1.8	1.6	1.1	1.6	10.9	4.6	32.1	15.4	10.7	10.8
<i>Stumpfia meikeae</i> sp. nov.	ZSM 1822/2010 (ZCMV 12373)	Female	21.5	6.1	6.5	1.3	2.2	2.5	1.4	2.0	11.2	4.6	33.4	15.7	10.1	11.8
<i>Stumpfia meikeae</i> sp. nov.	ZSM 624/2014 (DRV 6185)	Female	20.6	6.9	6.3	1.2	2.2	1.7	1.4	2.0	10.8	4.4	29.6	14.7	9.0	11.0
<i>Stumpfia meikeae</i> sp. nov.	ZSM 626/2014 (DRV 6189)	Female	21.7	6.8	6.8	1.7	2.3	1.5	1.1	2.2	11.6	5.2	34.6	14.3	10.2	11.0
<i>Stumpfia meikeae</i> sp. nov.	ZSM 622/2014 (DRV 6179)	Female	21.1	7.1	6.6	1.8	1.3	1.3	1.4	1.9	10.9	5.1	34.4	14.6	9.5	11.2
<i>Stumpfia obscoena</i> sp. nov.	ZSM 381/2005 (FGZC 2666)	ND	9.9	3.7	3.1	0.6	1.1	0.8	0.5	1.2	3.8	1.6	11.5	5.8	3.5	4.5
<i>Stumpfia obscoena</i> sp. nov.	ZFMK 52550	ND	9.7	3.4	2.9	1.0	1.3	0.8	0.6	1.3	4.3	1.3	12.0	5.7	3.4	4.0
<i>Stumpfia obscoena</i> sp. nov.	ZFMK 52552	ND	10.7	3.7	3.4	0.9	1.2	1.1	0.6	1.0	4.9	1.7	13.7	6.9	4.3	4.5
<i>Stumpfia obscoena</i> sp. nov.	ZFMK 59875	ND	11.1	3.7	3.5	0.6	1.2	0.9	0.9	1.5	4.5	1.6	13.5	6.1	3.7	4.3
<i>Stumpfia obscoena</i> sp. nov.	ZSM 380/2005 (FGZC 2664)	ND	10.3	3.0	3.2	0.5	1.1	1.0	0.6	1.1	4.9	1.4	12.9	5.5	3.8	4.2
<i>Stumpfia roseifemoralis</i>	ZSM 373/2005 (FGZC 2808)	ND	18.2	6.2	6.0	0.7	2.1	1.2	1.4	0.8	9.8	3.5	26.6	12.6	6.7	8.9
<i>Stumpfia roseifemoralis</i>	ZSM 374/2005 (FGZC 2883)	ND	16.2	6.5	5.9	0.5	1.9	1.4	1.2	0.8	9	4.0	28.0	12.1	7.6	8.8

Table 3 continued.

Species	Collection number (Field number)	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
<i>Stumpffia roseifemoralis</i>	ZSM 487/2005 (ZCMV 2047)	ND	17.9	6.3	6.5	0.5	2.4	1.6	1.1	0.7	9.3	4.4	25.4	12.5	7.3	8.7
<i>Stumpffia roseifemoralis</i>	ZSM 0529/2016 (ZCMV 15172)	Male	18.4	7.1	6.1	1.5	2.7	1.1	1.3	2.6	10.1	4.9	26.3	11.5	5.9	7.8
<i>Stumpffia achillei</i> sp. nov.	ZSM 494/2005 (ZCMV 861)	Female	19.1	5.3	6.1	1.8	2.8	1.6	1.1	1.5	10.1	4.6	29.1	12.8	7.9	9.2
<i>Stumpffia achillei</i> sp. nov.	ZSM 493/2005 (ZCMV 860)	ND	18.3	5.6	5.5	1.7	2.1	1.6	0.9	1.6	10.4	4.0	27.3	12.7	8.2	9.0
<i>Stumpffia achillei</i> sp. nov.	ZSM 377/2005 (FGZC 2750)	ND	18.1	5.7	5.8	1.5	2.0	1.4	1.1	1.8	10.9	4.5	27.3	13.7	9.2	9.3
<i>Stumpffia achillei</i> sp. nov.	ZFMK 57461	ND	16.8	5.6	5.4	1.1	2.6	1.7	1.2	1.4	9.3	4.6	26.7	12.8	8.1	8.5
<i>Stumpffia achillei</i> sp. nov.	ZFMK 57460	ND	17.5	5.9	5.8	1.8	2.1	1.6	1.2	1.6	10.3	4.6	28.6	12.7	8.4	9.1
<i>Stumpffia achillei</i> sp. nov.	ZFMK 59893	Male	17.8	5.6	5.3	1.4	2.2	1.9	0.8	1.4	10.1	3.8	25.9	13.4	8.0	8.8
<i>Stumpffia achillei</i> sp. nov.	ZSM 0534/2016 (ZCMV 15141)	Male	15.6	5.4	5.7	1.3	2.2	1.2	1.2	1.9	9.6	4.3	27.1	12.6	7.8	8.6
<i>Stumpffia achillei</i> sp. nov.	ZSM 0535/2016 (ZCMV 15143)	ND	16.1	5.6	5.7	1.3	2.1	1.6	1.2	1.9	9.1	4	26.4	12.3	7.8	8.4
<i>Stumpffia achillei</i> sp. nov.	ZSM 0536/2016 (ZCMV 15149)	Male	14.6	4.8	5	1.2	1.9	1.3	1.4	1.6	9	3.9	26.9	11.3	7.6	8.1
<i>Stumpffia analanjirofo</i> sp. nov.	ZSM 489/2005 (ZCMV 873)	Female	20.3	6.5	6.3	1.2	2.2	1.1	0.9	2.0	12	4.9	33.6	15.2	9.4	10.3
<i>Stumpffia analanjirofo</i> sp. nov.	ZSM 492/2005 (ZCMV 2178)	Female	20.4	6.2	6.1	1.6	1.9	1.8	1.2	1.8	10.4	5.0	28.0	13.1	7.3	9.8
<i>Stumpffia analanjirofo</i> sp. nov.	ZSM 491/2005 (ZCMV 2104)	ND	15.7	4.8	5.3	1.5	1.5	1.7	1.0	1.5	8.1	3.7	24.3	11.8	7.4	8.1
<i>Stumpffia diutissima</i> sp. nov.	ZSM 378/2005 (FGZC 2751)	Male	13.6	4.8	4.6	0.7	2.0	1.3	0.5	1.9	8.0	3.3	22.7	9.8	5.8	7.1
<i>Stumpffia diutissima</i> sp. nov.	ZSM 376/2005 (FGZC 2742)	ND	19.4	6.4	7.2	1.4	2.7	1.5	0.9	2.3	10.7	4.4	28.1	11.7	8.7	9.3
<i>Stumpffia diutissima</i> sp. nov.	ZSM 496/2005 (ZCMV 2082)	ND	20.0	6.0	6.7	1.4	2.7	1.4	1.1	2.5	12.3	4.3	30.1	14.1	8.7	9.5
<i>Stumpffia diutissima</i> sp. nov.	ZSM 495/2005 (ZCMV 2067)	ND	16.9	5.2	4.1	0.9	2.4	1.4	1.0	1.8	8.1	3.9	23.9	11.7	6.8	9.1
<i>Stumpffia diutissima</i> sp. nov.	ZSM 546/2016 (ZCMV 15064)	ND	13.4	4.3	4.9	1.2	1.8	1.3	1.1	1.9	9.1	2.9	22.8	10.4	6.7	7.6
<i>Stumpffia diutissima</i> sp. nov.	ZSM 547/2016 (ZCMV 15117)	ND	15.8	5	5.7	1.4	2.3	1.4	1.3	1.8	9	3.4	25.4	11.4	6.8	7.8
<i>Stumpffia diutissima</i> sp. nov.	ZSM 549/2016 (ZCMV 15144)	Male	15.9	5	5.6	1.5	2.2	1.6	1.1	1.7	9.1	4.1	24	11.1	7	8.4
<i>Stumpffia edmonsi</i> sp. nov.	ZSM 0371/2005 (FGZC 2677)	ND	17.3	5.5	5.8	1.0	2.1	1.6	1.0	1.2	8.4	4.4	28.2	12.5	7.6	9.2
<i>Stumpffia edmonsi</i> sp. nov.	ZSM 1731/2012 (RDR 1065)	Male	17.4	4.9	5.5	0.8	2.1	1.5	1.0	1.5	9.5	4.4	28.2	10.7	8.0	9.4
<i>Stumpffia fusca</i> sp. nov.	ZSM 437/2010 (FGZC 4254)	Female	17.7	5.8	5.4	1.0	2.2	1.4	1.2	1.6	11.3	4.1	27.8	12.8	8.8	9.1
<i>Stumpffia fusca</i> sp. nov.	ZSM 436/2010 (FGZC 4253)	ND	14.4	5.2	4.6	0.7	2.0	1.5	1.1	1.8	9.0	3.8	24.3	11.2	7.3	8.1
<i>Stumpffia jeannoeli</i> sp. nov.	ZSM 206/2016 (ACZCV 56)	Male	17.1	6.0	5.7	1.2	1.9	2.1	1.1	1.9	9.2	3.7	25.0	12.3	7.0	8.9
<i>Stumpffia jeannoeli</i> sp. nov.	MRSN A6386 (FAZC 13903)	ND	18.6	6.3	6.1	2.0	2.2	1.2	0.9	2.3	8.3	3.2	29.0	12.8	8.2	8.4
<i>Stumpffia jeannoeli</i> sp. nov.	ZSM 207/2016 (ACZCV 167)	ND	16.3	5.3	5.8	1.1	2.1	1.7	1.4	1.9	9.4	3.3	26.2	11.9	6.8	8.9
<i>Stumpffia jeannoeli</i> sp. nov.	ZSM 208/2016 (ACZCV 218)	ND	19.7	6.1	6.5	1.9	2.2	1.7	1.2	2.2	11.6	4.3	28.8	13.6	6.8	9.9
<i>Stumpffia jeannoeli</i> sp. nov.	MRSN A6283 (FAZC 13682)	Male	17.1	5.7	5.8	0.5	2.0	1.6	1.2	1.6	7.9	3.7	24.9	9.4	6.2	8.7
<i>Stumpffia nigrorubra</i> sp. nov.	ZSM 2448/2007 (ZCMV 5967)	ND	20.0	6.2	6.5	1.6	2.6	1.5	0.8	1.7	10.9	4.6	28.1	11.7	12.6	9.7
<i>Stumpffia nigrorubra</i> sp. nov.	ZSM 640/2003 (FG/MV 2002.0162)	Male	17.4	5.7	5.7	1.2	2.2	1.4	1.2	1.7	8.4	4.0	28.8	12.5	8.0	10.2
<i>Stumpffia nigrorubra</i> sp. nov.	ZSM 641/2003 (FG/MV 2002.0163)	Male	17.7	5.9	6.3	1.4	2.0	1.5	0.9	1.3	9.8	4.2	27.3	12.4	8.9	9.6
<i>Stumpffia pardus</i> sp. nov.	ZSM 435/2010 (FGZC 4237)	Male	17.7	5.6	5.6	1.1	1.9	1.8	1.2	2.0	7.3	4.5	18.8	11.9	8.2	9.6
<i>Stumpffia pardus</i> sp. nov.	ZSM 230/2016 (ACZCV 0147)	Male	22.4	7.7	6.9	1.7	2.6	1.5	1.0	2.2	12.5	5.5	24.1	16.8	9.8	10.3
<i>Stumpffia pardus</i> sp. nov.	ZSM 439/2010 (FGZC 4268)	Female	18.4	6.2	5.9	1.5	2.1	1.6	1.2	2.0	11.4	4.3	27.3	13.8	8.2	9.4
<i>Stumpffia pardus</i> sp. nov.	MRSN A6276 (FAZC 13498)	ND	14.6	4.9	4.9	1.6	2.1	0.8	0.6	1.7	6.0	2.4	19.3	12.8	6.0	7.8
<i>Stumpffia pardus</i> sp. nov.	ZSM 432/2010 (FGZC 4210)	ND	16.2	5.2	5.8	1.5	2.4	1.2	0.9	1.7	10.2	4.0	26.0	12.5	7.7	8.6
<i>Stumpffia pardus</i> sp. nov.	ZSM 440/2010 (FGZC 4278)	ND	16.2	5.6	5.9	1.2	2.5	1.4	1.1	1.8	9.6	4.0	24.1	11.9	8.1	7.8

Table 3 continued.

Species	Collection number (Field number)	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL
<i>Stumpfia pardus</i> sp. nov.	ZSM 434/2010 (FGZC 4214)	ND	19.9	6.3	6.3	1.8	2.6	1.5	1.0	2.0	12.2	4.5	30.0	15.0	9.6	9.7
<i>Stumpfia pardus</i> sp. nov.	ZSM 438/2010 (FGZC 4265)	ND	18.0	6.3	5.9	1.4	2.6	1.2	1.1	2.0	11.9	4.4	28.6	13.5	8.9	9.1
<i>Stumpfia pardus</i> sp. nov.	ZSM 770/2009 (ZCMV 11166)	ND	16.6	5.5	4.1	1.3	2.4	1.5	1.3	1.8	9.2	3.1	23	11.2	7.5	7.9
<i>Stumpfia pardus</i> sp. nov.	ZSM 433/2010 (FGZC 4213)	ND	16.3	5.7	5.4	1.4	2.5	1.6	1.2	1.6	10	4.3	25.7	12.6	7.9	8.6
<i>Stumpfia tetradactyla</i>	ZSM 594/2006 (ZCMV 3396)	ND	13.9	4.6	4.4	0.3	1.6	0.4	0.3	1.1	7.7	2.7	20.5	8.4	4.6	6.2
<i>Stumpfia tetradactyla</i>	ZSM 593/2006 (ZCMV 3395)	ND	14.1	4.9	4.8	0.3	2.0	0.3	0.2	0.8	6.7	3.0	20.2	8.2	5.3	6.4
<i>Stumpfia betampona</i> sp. nov.	ZSM 214/2016 (ACZCV 210)	ND	13.2	4.5	4.3	0.9	1.2	1.1	0.7	1.7	4.5	2.3	19.0	8.8	5.2	6.0
<i>Stumpfia betampona</i> sp. nov.	ZSM 217/2016 (ACZCV 46)	ND	13.8	4.7	4.6	1.4	1.2	1.3	0.7	2.0	6.4	2.7	19.7	10.5	5.3	6.3
<i>Stumpfia betampona</i> sp. nov.	ZSM 219/2016 (ACZCV 103)	ND	13.6	4.1	4.6	1.1	1.4	1.3	0.8	1.4	6.9	2.8	ND	8.8	5.8	6.4
<i>Stumpfia betampona</i> sp. nov.	ZSM 218/2016 (ACZCV 47)	ND	12.1	4.1	4.4	1.1	1.0	1.3	0.5	1.7	5.9	2.5	19.7	8.6	5.3	6.7
<i>Stumpfia betampona</i> sp. nov.	ZSM 216/2016 (ACZCV 41)	ND	11.4	4.0	3.4	0.5	1.5	1.2	1.0	1.4	4.8	1.9	18.0	7.8	4.5	6.0
<i>Stumpfia dolchi</i> sp. nov.	ZSM 488/2005 (ZCMV 2143)	ND	11.6	4.1	3.9	0.6	1.5	1.1	1.2	1.4	6.7	2.1	18.7	8.7	5.3	5.6
<i>Stumpfia garraffoi</i> sp. nov.	ZSM 1752/2008 (ZCMV 8803)	Male	12.1	4.2	4.5	0.6	1.9	1.0	0.6	2.0	6.6	2.3	19.9	9.2	5.6	6.6
<i>Stumpfia garraffoi</i> sp. nov.	ZSM 220/2016 (ACZCV 6)	ND	16.2	4.7	5.5	1.1	1.6	1.4	0.8	1.7	7.8	2.3	23.5	9.7	5.1	6.0
<i>Stumpfia garraffoi</i> sp. nov.	ZSM 632/2009 (ZCMV 8685)	ND	13.5	5.2	4.4	0.8	2.0	1.0	0.8	1.8	6.8	2.6	19.6	8.9	5.8	6.6
<i>Stumpfia garraffoi</i> sp. nov.	ZSM 631/2009 (ZCMV 8684)	ND	13.9	5.0	4.9	0.7	2.3	0.8	1.0	1.7	6.1	2.7	20.6	9.5	6.2	7.3
<i>Stumpfia garraffoi</i> sp. nov.	ZSM 633/2009 (ZCMV 8687)	ND	13.2	4.5	4.7	0.7	2.1	1.0	0.8	1.7	7.4	3.0	18.5	9.2	5.6	7.0
<i>Stumpfia garraffoi</i> sp. nov.	MRSN A6278 (FAZC 13489)	Male	14.5	5.2	4.8	0.6	1.7	1.2	0.6	1.8	6.0	2.5	21.2	9.7	6.3	6.5
<i>Stumpfia makira</i> sp. nov.	ZSM 541/2009 (ZCMV 11257)	ND	12.1	4.1	3.9	0.8	1.4	1.1	0.8	1.7	5.2	1.9	16.2	7.7	4.3	5.5
<i>Stumpfia miovaova</i> sp. nov.	ZSM 1649/2012 (FGZC 3656)	Male	15.1	5.3	3.8	1.1	2.3	1.2	1.0	1.9	7.3	3.6	25.2	11.3	7.7	8.1
<i>Stumpfia miovaova</i> sp. nov.	ZSM 1640/2012 (FGZC 3650)	Female	14.8	5.3	5.1	0.9	2.1	1.4	1.1	1.9	8.9	3.0	25.7	11.2	6.8	7.9
<i>Stumpfia miovaova</i> sp. nov.	ZSM 1647/2012 (FGZC 3675)	Female	16.4	5.1	5.5	1.2	2.0	1.4	1.0	2.0	9.2	2.5	24.1	10.7	6.4	8.3
<i>Stumpfia miovaova</i> sp. nov.	UADBA-A 60280 (orig. ZSM 1648/2012, FGZC 3676)	Female	16.9	5.2	5.3	1.1	2.0	1.8	1.2	1.9	8.4	3.4	24.3	12.6	6.4	8.0
<i>Stumpfia miovaova</i> sp. nov.	ZSM 1646/2012 (FGZC 3751)	ND	18.2	5.7	6.2	1.2	1.8	1.5	1.2	2.0	9.0	3.2	27.4	11.6	7.2	9.0
<i>Stumpfia spandei</i> sp. nov.	ZSM 1751/2008 (ZCMV 8802)	ND	12.7	4.1	4.0	0.9	1.7	0.9	0.6	1.8	6.4	2.7	17.7	8.5	5.2	6.2
<i>Stumpfia</i> sp. Ca7	ZSM 379/2005 (FGZC 2826)	ND	14.6	5.1	4.9	1.1	1.6	1.3	0.9	2.1	7.9	2.7	21.1	10	6.0	7.4
<i>Stumpfia</i> sp. Ca7	ZSM 544/2016 (ZCMV 15181)	Male	15.3	5.1	5.1	1.5	2.1	1.3	1.2	1.8	8.2	3.5	22.8	11.4	6	7.5
<i>Stumpfia</i> sp. Ca7	ZSM 545/2016 (ZCMV 15182)	Male	15.5	5.3	5.2	1.3	2.1	1.2	1.1	1.6	7.4	2.9	22.5	9.9	5	7.3
<i>Stumpfia</i> sp. Ca29	ZSM 627/2014 (DRV 6103)	Male	11.8	4.3	4.0	0.8	1.5	1.4	0.8	1.4	5.2	2.3	16.9	7.7	5.5	5.8
<i>Stumpfia</i> sp. Ca29	ZSM 1824/2010 (ZCMV 12387)	Juvenile	7.6	2.5	ND		1.2	ND	ND	ND	2.6	3.0	9.0	4.1	2.6	3.5
<i>Stumpfia</i> sp. Ca30	ZSM 634/2014 (DRV 6453)	ND	9.7	3.3	3.0	0.4	1.1	1.6	0.6	1.4	4.5	2.1	10.7	7.5	3.8	4.3
<i>Stumpfia</i> sp. Ca30	ZSM 632/2014 (DRV 6451)	ND	9.7	3.9	3.6	0.6	1.1	1.0	0.6	1.7	5.1	1.7	12.4	5.4	4.4	5.6
<i>Stumpfia</i> sp. Ca30	ZSM 633/2014 (DRV 6452)	ND	9.6	3.4	3.2	0.6	1.0	1.0	0.5	1.6	5.0	2.1	11.2	6.2	4.0	5.1
<i>Stumpfia</i> sp. Ca30	ZSM 635/2014 (DRV 6454)	ND	10.1	3.8	3.7	0.6	1.0	1.1	0.6	1.7	5.1	1.7	12.2	5.6	4.5	5.2

Table 4. Body sizes, relative hand length, and relative length of foot (including tarsus) of adults of *Stumpffia* species, given as range with mean \pm standard deviation and sample size in parentheses. See Table 3 for original values and differences between sexes. ND=not determined.

	SVL	HAL/SVL	FOTL/SVL
<i>Stumpffia psologlossa</i>	10.2–14.8 mm (12.84 \pm 1.52, N=17)	0.18–0.25 (0.21 \pm 0.02, N=17)	0.61–0.83 (0.70 \pm 0.07, N=16)
<i>Stumpffia analamaina</i>	11.2–13.4 mm (12.30 \pm 0.79, N=11)	0.20–0.24 (0.22 \pm 0.02, N=11)	0.57–0.76 (0.69 \pm 0.06, N=10)
<i>Stumpffia gimmeli</i>	14.5–18.1 mm (15.97 \pm 1.89, N=3)	0.19–0.23 (0.21 \pm 0.02, N=3)	0.63–0.67 (0.65 \pm 0.02, N=3)
<i>Stumpffia madagascariensis</i>	10.0–13.6 mm (11.50 \pm 1.33, N=5)	0.15–0.18 (0.17 \pm 0.01, N=5)	0.54–0.63 (0.59 \pm 0.03, N=5)
<i>Stumpffia pygmaea</i>	8.3–12.5 mm (10.23 \pm 1.17, N=12)	0.13–0.19 (0.16 \pm 0.02, N=12)	0.48–0.77 (0.62 \pm 0.08, N=12)
<i>Stumpffia angeluci</i> sp. nov.	11.0–16.1 mm (13.49 \pm 1.73, N=9)	0.20–0.25 (0.22 \pm 0.02, N=9)	0.64–0.73 (0.69 \pm 0.03, N=9)
<i>Stumpffia huwei</i> sp. nov.	12.5–15.0 mm (13.43 \pm 1.14, N=6)	0.16–0.22 (0.19 \pm 0.02, N=6)	0.57–0.69 (0.62 \pm 0.04, N=6)
<i>Stumpffia iharana</i> sp. nov.	14.0–15.5 mm (14.63 \pm 0.65, N=4)	0.19–0.22 (0.21 \pm 0.02, N=4)	0.57–0.75 (0.66 \pm 0.07, N=4)
<i>Stumpffia larinki</i> sp. nov.	12.5–12.8 mm (12.65 \pm 0.13, N=4)	0.22–0.24 (0.23 \pm 0.01, N=4)	0.51–0.70 (0.61 \pm 0.09, N=4)
<i>Stumpffia maledicta</i> sp. nov.	13.8–16.8 mm (14.93 \pm 1.63, N=3)	0.18–0.20 (0.19 \pm 0.01, N=3)	0.60–0.71 (0.65 \pm 0.06, N=3)
<i>Stumpffia mamitika</i> sp. nov.	12.3–15.0 mm (13.40 \pm 1.10, N=7)	0.16–0.24 (0.21 \pm 0.03, N=7)	0.68–0.75 (0.68 \pm 0.05, N=7)
<i>Stumpffia sorata</i> sp. nov.	15.6–16.0 mm (15.80 \pm 0.20, N=3)	0.18–0.23 (0.2 \pm 0.02, N=3)	0.63–0.65 (0.64 \pm 0.01, N=3)
<i>Stumpffia yanniki</i> sp. nov.	9.8–10.6 mm (10.20 \pm 0.57, N=2)	0.18–0.19 (0.19 \pm 0.00, N=2)	0.62–0.65 (0.64 \pm 0.02, N=2)
<i>Stumpffia be</i>	25.2 mm (N=1)	0.3 (N=1)	0.6 (N=1)
<i>Stumpffia hara</i>	22.4–24.6 mm (23.50 \pm 1.50 mm, N=2)	0.2–0.3 (N=2)	0.5–0.6 (N=2)
<i>Stumpffia megsoni</i>	21.0–21.7 mm (21.30 \pm 0.50 mm, N=2)	0.2–0.3 (N=2)	0.7 (N=2)
<i>Stumpffia staffordi</i>	27.0–27.9 mm (27.40 \pm 0.60 mm, N=2)	0.3 (N=2)	0.6 (N=2)
<i>Stumpffia miery</i>	13.5–14.6 mm (14.00 \pm 0.50 mm, N=5)	0.15–0.18 (N=4)	0.5–0.6 (N=4)
<i>Stumpffia tridactyla</i>	8.6–10.6 mm (9.85 \pm 0.90 mm, N=4)	0.14–0.16 (0.14 \pm 0.05, N=4)	0.55–0.60 (0.57 \pm 0.36, N=4)
<i>Stumpffia contumelia</i> sp. nov.	8.0–8.9 mm (8.47 \pm 0.45 mm, N=3)	0.16–0.18 (0.17 \pm 0.01, N=3)	0.66–0.81 (0.74 \pm 0.08, N=3)
<i>Stumpffia obscoena</i> sp. nov.	9.7–11.1 mm (10.34 \pm 0.57 mm, N=5)	0.13–0.16 (0.15 \pm 0.01, N=5)	0.53–0.64 (0.58 \pm 0.04, N=5)
<i>Stumpffia davidattenboroughi</i> sp. nov.	11.7 mm (N=1)	0.17 (N=1)	0.55 (N=1)
<i>Stumpffia meikeae</i> sp. nov.	19.2–23.4 mm (21.20 \pm 1.06 mm, N=10)	0.21–0.24 (0.23 \pm 0.01, N=10)	0.65–0.80 (0.72 \pm 0.04, N=10)
<i>Stumpffia grandis</i>	19.3–23.7 mm (21.60 \pm 1.8 mm, N=4)	0.2–0.3 (N=4)	0.8 (N=4)
<i>Stumpffia kibomena</i>	17.0–21.0 mm	ND	ND
<i>Stumpffia roseifemoralis</i>	16.2–18.4 mm (17.67 \pm 1.00, N=4)	0.21–0.26 (0.23 \pm 0.59, N=4)	0.68–0.70 (0.68 \pm 0.49, N=4)
<i>Stumpffia achillei</i> sp. nov.	14.6–19.1 mm (17.10 \pm 1.44, N=9)	0.24–0.26 (0.25 \pm 0.2, N=69)	0.71–0.77 (0.74 \pm 0.4, N=9)
<i>Stumpffia analanjirofo</i> sp. nov.	15.7–20.4 mm (18.80 \pm 2.69, N=3)	0.24–0.25 (0.24 \pm 0.00, N=3)	0.64–0.75 (0.71 \pm 0.06, N=3)
<i>Stumpffia diutissima</i> sp. nov.	13.4–20.0 mm (16.48 \pm 2.38, N=8)	0.21–0.22 (0.23 \pm 0.21, N=8)	0.70–0.73 (0.69 \pm 0.52, N=8)
<i>Stumpffia edmondsi</i> sp. nov.	17.3–17.4 mm (17.35 \pm 0.07, N=2)	0.25–0.25 (0.25 \pm 0.00, N=2)	0.61–0.72 (0.67 \pm 0.08, N=2)
<i>Stumpffia fusca</i> sp. nov.	14.4–17.7 mm (16.05 \pm 2.33, N=2)	0.23–0.26 (0.25 \pm 0.02, N=2)	0.72–0.78 (0.75 \pm 0.04, N=2)
<i>Stumpffia jeannoeli</i> sp. nov.	16.3–19.7 mm (17.76 \pm 1.37, N=5)	0.17–0.22 (0.21 \pm 0.02, N=5)	0.55–0.73 (0.68 \pm 0.07, N=5)
<i>Stumpffia nigrorubra</i> sp. nov.	17.4–20.0 mm (18.37 \pm 1.42, N=3)	0.23–0.24 (0.23 \pm 0.00, N=3)	0.59–0.72 (0.67 \pm 0.07, N=3)
<i>Stumpffia pardus</i> sp. nov.	14.6–22.4 mm (17.63 \pm 2.23, N=10)	0.16–0.26 (0.23 \pm 0.03, N=10)	0.67–0.88 (0.75 \pm 0.06, N=10)
<i>Stumpffia tetradactyla</i>	13.9–14.1 mm (14.00 \pm 0.14, N=2)	0.19–0.21 (0.20 \pm 0.01, N=2)	0.58–0.60 (0.59 \pm 0.02, N=2)
<i>Stumpffia betampona</i> sp. nov.	11.4–13.8 mm (12.82 \pm 1.03, N=5)	0.17–0.21 (0.19 \pm 0.02, N=5)	0.65–0.76 (0.69 \pm 0.04, N=5)
<i>Stumpffia dolchi</i> sp. nov.	11.6 mm (N=1)	0.18 (N=1)	0.75 (N=1)
<i>Stumpffia garraffoi</i> sp. nov.	12.1–16.2 mm (13.90 \pm 1.38, N=6)	0.14–0.23 (0.19 \pm 0.03, N=6)	0.60–0.76 (0.68 \pm 0.05, N=6)
<i>Stumpffia makira</i> sp. nov.	12.1 mm (N=1)	0.16 (N=1)	0.64 (N=1)
<i>Stumpffia miovaova</i> sp. nov.	14.8–18.2 mm (16.28 \pm 1.38, N=5)	0.15–0.24 (0.19 \pm 0.03, N=5)	0.64–0.76 (0.71 \pm 0.06, N=5)
<i>Stumpffia spandei</i> sp. nov.	12.7 mm (N=1)	0.21 (N=1)	0.67 (N=1)
<i>Stumpffia</i> sp. Ca7	14.6–15.5 mm (15.16 \pm 1.11, N=3)	0.18–0.22 (0.11 \pm 3.3, N=3)	0.67–0.73 (0.3 \pm 11.09, N=3)
<i>Stumpffia</i> sp. Ca29	11.8 mm (N=1)	0.19 (N=1)	0.65 (N=1)
<i>Stumpffia</i> sp. Ca30	9.6–10.1 mm (9.78 \pm 0.22, N=4)	0.17–0.22 (0.19 \pm 0.03, N=4)	0.55–0.77 (0.63 \pm 0.10, N=4)

dorsal marking occurs that also characterizes the *S. psologlossa* holotype according to the original description.

Incidentally, this species is also diagnosed from all other nominal species of *Stumpffia* (as well as from all candidate species, as far as known) by its unique call consisting of a pulsed trill note. (1) Miniaturized to small-sized species (adult SVL 10.2–14.8 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers and toes without clearly enlarged discs but very slightly enlarged

and distally pointed teardrop-shaped in some specimens; (4) relative hand and foot length, HAL/SVL 0.18–0.25, FOTL/SVL 0.61–0.83; (5) dorsum, especially in life, often not completely smooth but slightly granular; (6) dorsally often brown with distinct dark brown patches on the back, sometimes with a large central dark teddybear-shaped marking, and with more or less complete dark brown bands along the flanks; without contrasted ventral coloration, red color elements on ventral side; (7) unique call among *Stumpffia*, consisting of a single regularly repeated long and strongly pulsed note.

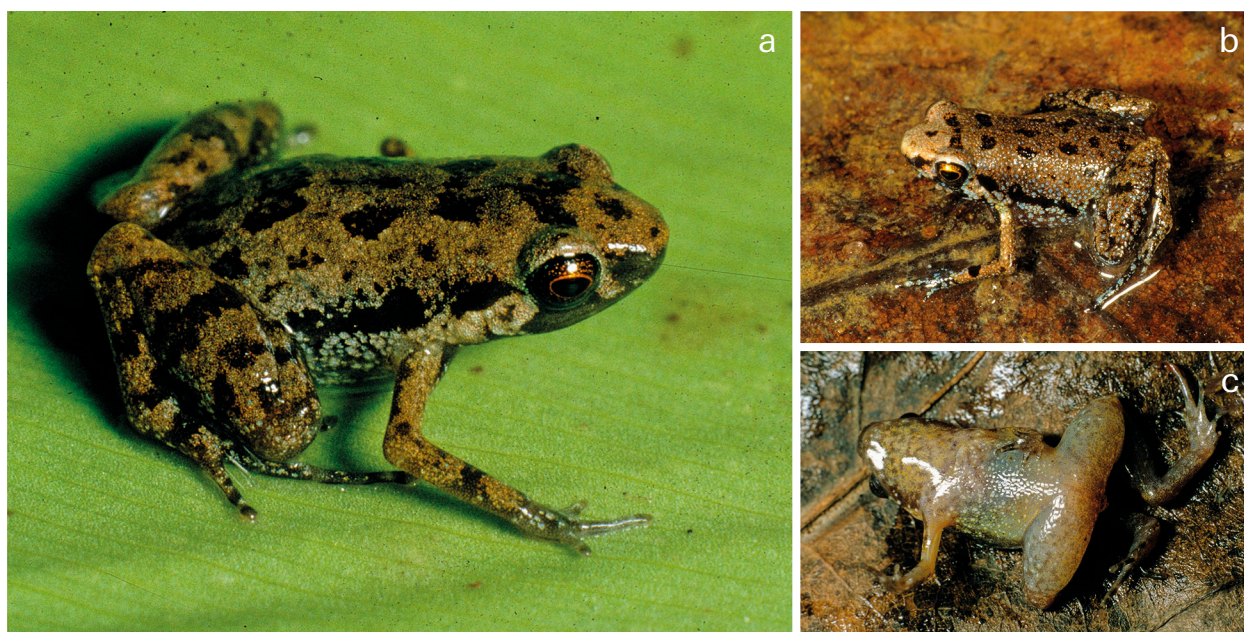


Fig. 19. *Stumpffia psologlossa* from Nosy Be in life: (a) a specimen for which no voucher number is known; (b–c) ZSM 479/2000 (FG/MV 2000.279).

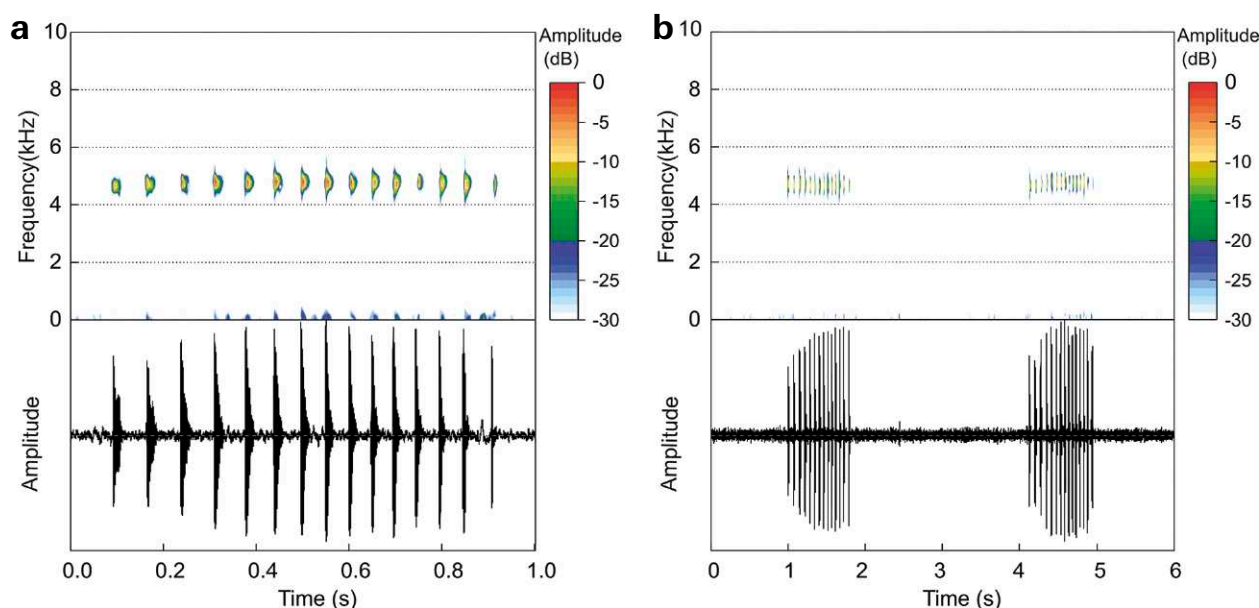


Fig. 20. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia psologlossa* from its type locality Nosy Be: (a) 1 s duration section, (b) 6 s duration section.

Specimens examined. Holotype SMF 7337 collected prior to 1881 on Nosy Be by A. Stumpff. Referred specimens: ZFMK 52530–52535 collected in March 1991 on Nosy Be by F. Glaw and M. Vences. ZFMK 53750–53754, 53756–53761, collected by F. Glaw and J. Müller in January/February 1992 on Nosy Be. ZSM 479/2000 (FG/MV 2000.279), collected on 11 March 2000, at eastern edge of Lokobe reserve on Nosy Be (S13.4133, E48.3341, 110 m a.s.l.) by F. Glaw, K. Schmidt, and M. Vences; ZSM 480/2000–485/2000 (all with field number FG/MV 2000.837), collected on 9 March 2000 on Nosy Sakatia (S13.3141, E48.1555, < 10 m a.s.l.) by F. Glaw and K. Schmidt. ZSM 616/2014 (DRV 6486), collected on 30 June 2010 in Maromandra forest fragment near Ankaramy (S13.99653, E48.21770, 283 m a.s.l.) by F.M. Ratsoavina, S. Rasamison, T. Rajoafiarison, and F. Randrianasolo.

Distribution. This species is known from (1) Nosy Be (type locality), (2) Nosy Sakatia (a small island west of Nosy Be), (3) Benavony, and (4) Maromandra (two localities on the Madagascan mainland) (Fig. 13). These four localities are all confirmed by molecular genetics, with the mainland populations being only slightly differentiated from the island populations (Fig. 3). A fifth locality, Nosy Komba (between Nosy Be and mainland Madagascar) was recently reported (BLUMGART *et al.*, 2017) and seems to be supported based on a photograph provided in that paper, but specimens from this locality have not yet been studied from a molecular

Table 5. Basic temporal and spectral variables of advertisement calls of *Stumpffia*.

Species	Call duration	Inter-call interval duration	Dominant frequency
<i>Stumpffia psologlossa</i>	791–871 ms (831 ± 25 ms; N = 11)	2210–5055 ms (2691 ± 860 ms; N = 10)	4651–6503 Hz (4955 ± 520 Hz)
<i>Stumpffia analamaina</i> (captive)	228–286 ms (260 ± 23.6 ms; N = 5)	1974–2260 ms (2242 ± 136 ms; N = 4)	6130–6330 Hz (6210 ± 80.4 Hz; N = 5)
<i>Stumpffia analamaina</i> (wild/Ankarafantsika)	134–175 ms (153 ± 13.5 ms; N = 10)	1055–1160 ms (1120 ± 30 ms; N = 9)	5343–5531 Hz (5399 ± 91 Hz, N = 10)
<i>Stumpffia gimmeli</i>	96–185 ms (126.8 ± 30 ms; N = 14)	1367–4204 ms (2362.5 ± 813.4 ms; N = 14)	4521–5211 Hz (4832.2 ± 302.4 Hz; N = 146)
<i>Stumpffia madagascariensis</i>	187–198 ms (195 ± 5 ms; N = 5)	4060–4427 ms (4224 ± 153 ms; N = 4)	3980–4579 Hz (4231 ± 197 Hz; N = 5)
<i>Stumpffia pygmaea</i>	185–210 ms (196 ± 10 ms; N = 5)	2900–3882 ms (3447 ± 419 ms; N = 4)	5986–6115 Hz (6054 ± 49 Hz; N = 5)
<i>Stumpffia angeluci</i> sp. nov.	179–187 ms (182 ± 6 ms; N = 6)	3174–3801 ms (3596 ± 254 ms; N = 5)	4565–4694 Hz (4651 ± 47 Hz; N = 6)
<i>Stumpffia huwei</i> sp. nov.	67–74 ms (70 ± 2.4 ms; N = 6)	2340–3117 ms (2687.5 ± 267 ms; N = 6)	4952–5061 Hz (5020 ± 39 Hz; N = 6)
<i>Stumpffia larinki</i> sp. nov.	114–155 ms (138 ± 21 ms; N = 3)	2143–2289 ms (2216 ± 103 ms; N = 2)	2842–3057 Hz (2914 ± 124 Hz; N = 3)
<i>Stumpffia maledicta</i> sp. nov.	98–104 ms (102 ± 2.8 ms; N = 4)	5167–5637 ms (5927 ± 735 ms; N = 3)	4823–4866 Hz (4833 ± 21.5 Hz; N = 4)
<i>Stumpffia mamitika</i> sp. nov.	90–124 ms (103 ± 9 ms; N = 20)	612–1510 ms (955 ± 264 ms; N = 19)	4435–5081 Hz (4749 ± 257 Hz; N = 20)
<i>Stumpffia be</i>	170–179 ms (174 ± 3 ms; N = 7)	784–1053 ms (919 ± 84 ms; N = 6)	3899–3928 Hz (3912 ± 11 Hz; N = 7)
<i>Stumpffia tridactyla</i>	101–198 ms (132 ± 23 ms; N = 18)	969–1121 ms (1012 ± 39 ms; N = 17)	6933–7835 Hz (7244 ± 200 Hz; N = 18)
<i>Stumpffia miery</i>	51–88 ms (73 ± 12; n = 10)	2679–4247 ms (3102 ± 456; n = 10)	7751–8225 Hz (8057 ± 136.9; N = 10)
<i>Stumpffia contumelia</i> sp. nov.	38–50 ms (42 ± 4 ms; N = 7)	508–580 ms (543 ± 27 ms; N = 6)	7450–7579 Hz (7493 ± 50 Hz; N = 7)
<i>Stumpffia obscoena</i> sp. nov.	137–154 ms (144 ± 8 ms; N = 6)	3948–6322 ms (4619 ± 990 ms; N = 5)	8225–8397 Hz (8361 ± 69 Hz; N = 6)
<i>Stumpffia kibomena</i>	70–76 ms (73 ± 2 ms; n = 9)	770–813 ms (797 ± 15 ms; n = 9)	3900–4300 Hz
<i>Stumpffia nigrorubra</i> sp. nov.	46–88 ms (67 ± 10 ms; N = 19)	1366–1720 ms (1472 ± 104 ms; N = 18)	5124–5426 Hz (5283 ± 70.5 Hz; N = 19)
<i>Stumpffia achillei</i> sp. nov.	36–52 ms (43 ± 3.4 ms; N = 20)	507–582 ms (530.4 ± 19.3 ms; N = 20)	5813–6459 Hz (6134.2 ± 235 Hz; N = 20)
<i>Stumpffia diutissima</i> sp. nov.	53–56 ms (54.6 ± 1 ms; N = 10)	1775–2200 ms (1924.1 ± 126.8 ms; N = 10)	6459–6632 Hz (6498.3 ± 51.8 Hz; N = 10)
<i>Stumpffia pardus</i> sp. nov.	35–44 ms (38.3 ± 2.3 ms; N = 12)	467–495 ms (479.3 ± 7.6 ms; N = 12)	5124–5383 Hz (5264.5 ± 73.3 Hz; N = 12)
<i>Stumpffia jeannoeli</i> sp. nov.	43–45 ms (44.2 ± 0.8 ms; N = 6)	1183–1220 ms (1195.2 ± 5 ms; N = 5)	6072–6244 Hz (6166.6 ± 76.9 Hz; N = 6)
<i>Stumpffia tetradactyla</i>	77–109 ms (92 ± 9 ms; N = 11)	741–1566 ms (959 ± 244 ms; N = 10)	5081–5555 Hz (5355 ± 138 Hz; N = 11)
<i>Stumpffia spandei</i> sp. nov.	43–49 ms (46 ± 1.8 ms; N = 11)	736–907 ms (801.8 ± 48.6 ms; N = 10)	5641–5857 Hz (5755 ± 69.8 Hz; N = 11)
<i>Stumpffia garraffoi</i> sp. nov.	101–107 ms (103.4 ± 2.5 ms; N = 7)	1553–1901 ms (1695.8 ± 150 ms; N = 6)	5813–6029 Hz (5936.7 ± 84.2 Hz; N = 7)
<i>Stumpffia roseifemoralis</i>	276–280 ms (278 ± 1.6 ms; N = 6)	2891–3304 ms (3073.8 ± 152 ms; N = 6)	4220–4306 Hz (4234.3 ± 35.1 Hz; N = 6)
<i>Stumpffia</i> Ca7	290–299 ms (293.8 ± 2.9 ms; N = 10)	2764–3250 ms (2929.3 ± 182.9 ms; N = 10)	3919–3962 Hz (3931.9 ± 20.7 Hz; N = 10)

perspective and the locality is therefore not included in Figure 13.

Natural history. Specimens were observed in the leaf litter of forested areas and plantations. On Nosy Be, often syntopic with *S. pygmaea*. Calling activity is predominantly in the evening and night (VENCES & GLAW, 1991).

Call. Calls were recorded at the type locality Nosy Be by F. Glaw in February 1992 (VENCES *et al.*, 2006: CD3,

track 35) and had already been previously described by VENCES & GLAW (1991) based on other recordings. Among calls of *Stumpffia* species, the call of *S. psologlossa* is unique in consisting of a rather long and distinctly pulsed note, with 13–16 pulses/note emitted at a repetition rate of approximately 17 pulses/second (Fig. 20). Additional parameters were as follows: call duration (= note duration) 791–871 ms (831 ± 25 ms; N = 11), inter-call intervals 2210–5055 ms (2691 ± 860 ms; N = 10), pulse duration 16–20 ms (17.2 ± 1.2; N = 23), and a dominant frequency at 4651–6503 Hz



Fig. 21. *Stumpffia analamaina*, specimens in life. (a) ZSM 3224/2012 (ZCMV 12159) from Ankarafantsika National Park; (b) holotype ZSM 542/2009 from near Antsohihy; (c) uncollected specimen from Ankarafantsika; (d) KUZA 0011 from Ankarafantsika; (e) additional specimen from near Antsohihy (catalogue number uncertain); (f–g) UADBA-A 60288 (ZCMV 12160) from Ankarafantsika.

(4955 ± 520 Hz, N = 11). Calls from Benavony recorded in 1992 generally agree in all temporal and spectral characters.

***Stumpffia analamaina* KLAGES, GLAW, KÖHLER, MÜLLER, HIPSLEY & VENCES, 2013**

(Figures 21 and S92)

Name-bearing type. Holotype ZSM 542/2009 (ZCMV 11428), collected “at a bridge located at km 27 on the national road from Antsohihy to Mandritsara” according to the original description.

Identity and diagnosis. *Stumpffia analamaina* was described from a locality near Antsohihy in north-western Madagascar, and genetically slightly divergent specimens assignable to this species are also known from a second north-western locality (Ankarafantsika National Park). (1) Small-sized species (SVL 11.2–13.4 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.20–0.24, FOTL/SVL 0.57–0.76; (5) dorsum smooth or slightly tubercular; (6) grayish or brownish coloration with variable but typically indistinct pattern and without contrasted ventral coloration, red color elements on ventral side, or sharp color border between dorsum and flanks; (7) regularly repeated short single-note chirp call.

Distinguished from *S. psoglossa* by a shorter unpulsed call (Fig. 22), and in most specimens by a different color pattern, different skin texture, and slightly stronger reduction of first toe.

Specimens examined. Holotype ZSM 542/2009 (ZCMV 11428) collected on 18 June 2009 by M. Vences, D.R. Vieites, F.M. Ratsoavina, R.D. Randrianaiaina, E. Rajeriarison, T. Rajoafiarison, and J.L. Patton, at km 27 on the national road from Antsohihy to Mandritsara (S15.0532, E48.2064, 140 m a.s.l.). Paratypes ZSM 2829/2010 (ZCMV 10034), ZSM 2830/2010 (ZCMV 10036), ZSM 2831/2010 (ZCMV 10037), all collected on 29 June 2010 at the type locality by M. Vences, E. Rajeriarison, T. Rajoafiarison, A. Rakotoarison, S. Rasamison, F. Randrianasolo, R.D. Randrianaiaina, F.M. Ratsoavina, and D.R. Vieites. Referred specimens: ZSM 3224/2012 (ZCMV 12159) and UADBA-A 60288 (ZCMV 12160), collected on 7 January 2012 at Ankarafantsika National Park by A. Rakotoarison. KUZA 0001 (2010-F002), collected on 2 December 2010 at Ampijoroa in Ankarafantsika National Park (S16.3132, E46.8172, 274 m a.s.l.) by R. Ito; KUZA 0002 (2010-F003), collected on 2 December 2010 at Ampijoroa by T. Jono; KUZA 0003 (2010-F004), collected on 5 December 2010 at Ampijoroa by R. Ito; KUZA 0004 (2010-F005), collected on 6 December 2010 at Ampijoroa by T. Jono; KUZA 0005 (2011-Ad-049), collected on 25 February 2011 at Ampondrabe (S16.3166, E46.9) by A. Mori; KUZA 0006 (2011-Ad-050), collected on 25 February 2011 at Ampondrabe by U. Kawai; KUZA 0007 (2011-Ad-059), collected on 25 February 2011 at Ampondrabe by A. Mori; KUZA 0008–0009 (2012-089–2012-090), collected on 19 January 2013 by pitfall trap at Ampijoroa by T. Jono; KUZA 0010 (2013-NoCode), collected on 12 March 2013 at Ampijoroa by R. Ito; KUZA 0011 (2010-F001), collected on 25 November 2010 at Ampijoroa by T. Jono.

Distribution. This species is known from two localities, (1) its type locality (27 km northeast of Antsohihy) and (2) Ankarafantsika National Park. Populations of the latter locality are here allocated to *S. analamaina* based on morphology and molecular genetics with Ankarafantsika specimens being only slightly differentiated genetically from topotypic ones (Fig. 3).

Natural history. Frogs stay on or under leaves on the forest floor when they call. The habitat consists of dense shrub and leaf litter in the relatively humid parcels of

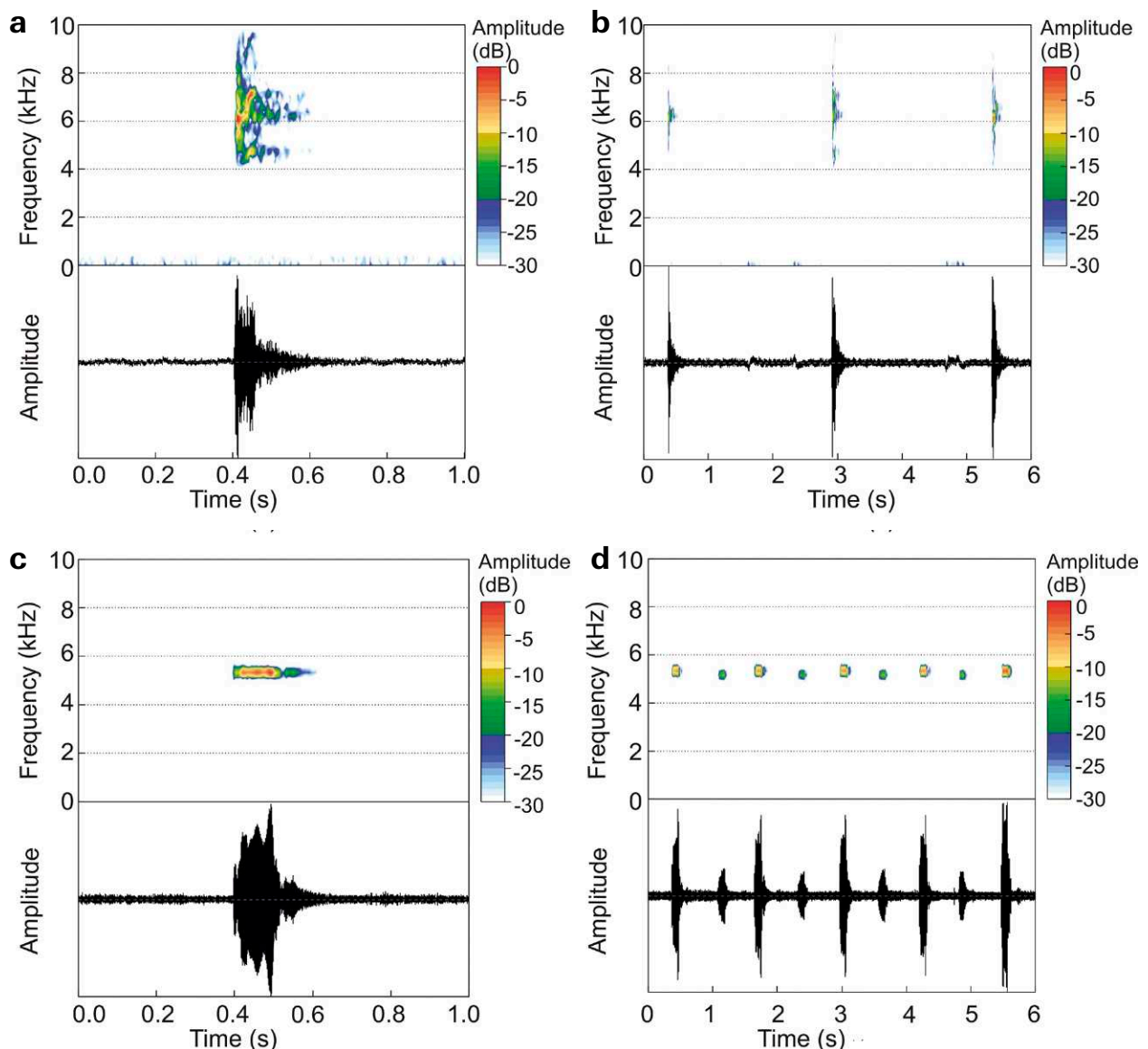


Fig. 22. Spectrograms (above) and oscillograms (below) of the advertisement calls of *Stumpffia analamaina* (1 s and 6 s duration sections each). (a–b) Calls recorded in captivity from topotypes at 23°C air temperature; (c–d) call recorded in natural habitat by T. Jono at Ampijoroa at 28.5°C air temperature. Note that d shows the sounds produced by two individuals intermittently calling, of which one is louder (i.e., closer to the microphone).

dry deciduous forests. During field surveys at Ankarafantsika (2010–2013; data in Fig. 23), *S. analamaina* called throughout the study period, from early December to mid February. Calling activity appeared to be rather independent from rainfall intensity and from air temperature (Fig. 23), although calling activity decreased for a few weeks in early January 2013 when rainfall ceased. Although this species usually called in the evening and at night, they also emitted calls on several rainy mornings. In the observation times, calls peaked around 17:00.

Call. The advertisement call of *S. analamaina* consists of a single short note repeated in series at regular intervals. Calls of a topotypic male recorded by J. Klages in captivity (KLAGES *et al.*, 2013) at 23°C air temperature had the following call parameters (Fig. 22): call duration (= note duration) 228–286 ms (260 ± 23.6 ms; $N=5$), inter-call

intervals 1974–2260 ms (2242 ± 136 ms; $N=4$), and dominant frequency at 6130–6330 Hz (6210 ± 80.4 Hz, $N=5$). Calls recorded by T. Jono on 5 December 2010, at Ampijoroa, Ankarafantsika National Park, had the following parameters (air temperature 28.5°C): call duration 134–175 ms (153 ± 13.5 ms; $N=10$), inter-call intervals 1055–1160 ms (1120 ± 30 ms; $N=9$), and a dominant frequency at 5343–5531 Hz (5399 ± 91 Hz, $N=10$). Generally, characteristics of calls from both localities are in agreement, but slight differences are obvious, with the Ampijoroa calls being more tonal in character, whereas calls from the topotype are more pulsatile. However, the latter could likely represent an artifact, because recordings were obtained from individuals kept in terraria (see KLAGES *et al.*, 2013). Call repetition rate is more dramatically different, with calls recorded from Ankarafantsika being almost twice as frequently repeated as those record-

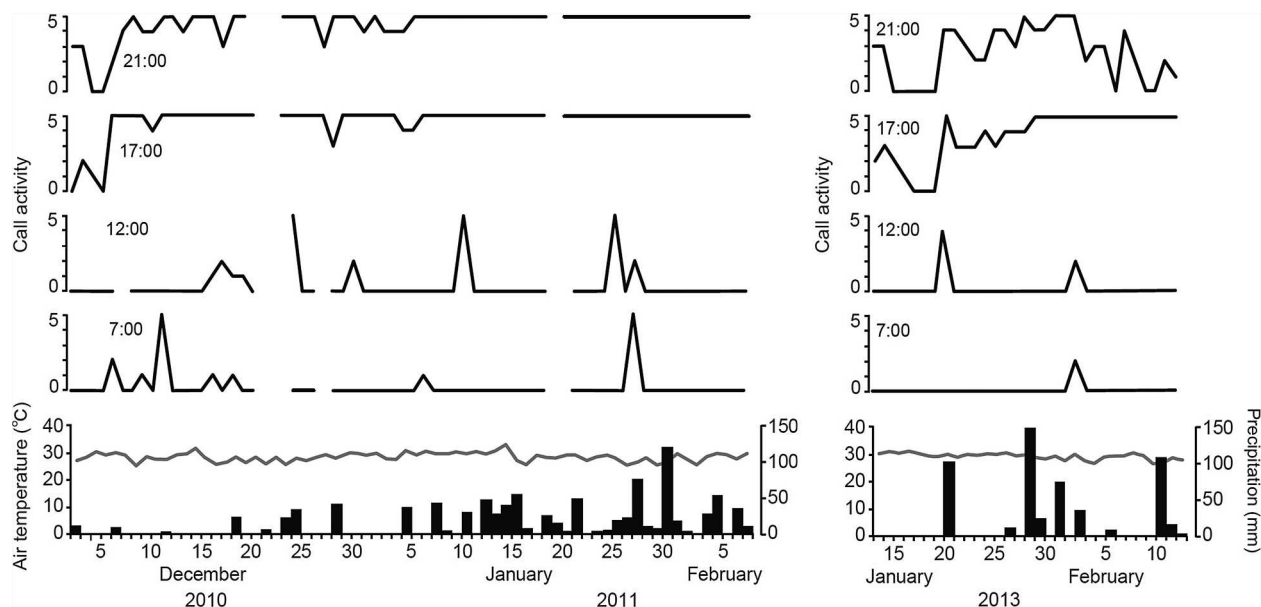


Fig. 23. Graphic scheme showing calling activity of *Stumpffia analamaina* at Ankarafantsika National Park, recorded in 2010–2013 by T. Jono. The level of call activity 0 indicates no vocalizations were heard; level 1: single or a few calls were heard, but did not make a chorus; level 2: calls or choruses were heard intermittently, but in most of the time no vocalizations occurred; level 3: calls or choruses were frequently heard, but silent intervals were still obvious; level 4: intensive choruses were heard during most of the census, but several occasional cessation of the chorus was recognized; level 5: choruses were intensive and never ceased. Air temperature is given as a line graph and precipitation as a bar chart.

ed from a terrarium (inter-call intervals 1055–1160 ms vs. 1974–2260 ms). This might be explained by differences in air temperature (5.5°C warmer in Ankarafantsika than in the terrarium), or individual motivation.

Stumpffia gimmeli GLAW & VENCES, 1992

(Figures 24 and S93)

Name-bearing type. Holotype ZFMK 53780 from “a primary forest near Benavony (environments of Ambanja, NW-Madagascar)” according to the original description.

Identity and diagnosis. As currently defined, *S. gimmeli* is a species from the Sambirano Region in northern Madagascar. It is known from various localities and includes a substantial amount of genetic variation. Because at present, insufficient data are available about the various populations, we follow KLAGES *et al.* (2013) and consider them as deep conspecific lineages in a preliminary way. This implies that *S. gimmeli* as defined here includes *Stumpffia* sp. 3 and sp. 4 in VIEITES *et al.* (2009) (not included in GLAW & VENCES, 2007; WOLLENBERG *et al.*, 2008; KÖHLER *et al.*, 2010; KLAGES *et al.*, 2013; only *Stumpffia* sp. 4 included in SCHERZ *et al.*, 2016). (1) Small- to moderately-sized (up to 18.1 mm; adult male SVL 14.5 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe almost not reduced in length); (3) terminal phalanges of fingers and toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.19–0.23, FOTL/SVL 0.65–0.67; (5) dorsum

slightly to moderately tubercular; (6) grayish or brownish coloration with variable but typically indistinct pattern and without contrasted ventral coloration, red color elements on ventral side, or sharp color border between dorsum and flanks, typically with a hint of yellow on the abdomen; (7) regularly repeated short single-note chirp call.

Distinguished from *S. psologglossa* by shorter and unpulsed advertisement call, larger size, and color pattern and skin texture in most specimens; and from *S. analamaina* by distinctly larger size and lower degree of reduction of first toe.

Specimens examined. Holotype ZFMK 53780 from Benavony, collected by F. Glaw and J. Müller on 16 February 1992; paratypes ZFMK 52536–52540, collected by F. Glaw and M. Vences on 27 March 1991 at Ambanja (ZFMK 52537 cleared and stained); paratypes ZFMK 53776–53778, collected on 17 February 1992 by F. Glaw & J. Müller at Ambanja; paratype ZFMK 53779 and 53781–53785, collection data as holotype. Referred specimens: ZSM 412/2000, collected on 18 February 2000 in Berara (Anabohazo) by M. Vences, F. Andreone, and J.E. Randrianirina; ZSM 597/2001 (MV 2001.36), collected on 30 January 2001 at Antsirahira by F. Andreone, F. Mattioli, J.E. Randrianirina & M. Vences; ZSM 833/2003 (FG/MV 2002.784), collected on 2 January 2003 in Manongarivo, Camp 0 (S13.9755, E48.4266, 688 m a.s.l.) by F. Glaw, R.D. Randrianiana & M. Vences; ZSM 3231/2012 (ZCMV 13538), collected on 31 January 2012 at 27 km from Ambanja by A. Rakotoarison and A. Razafimanantsoa; ZSM 3240/2012 (ZCMV 13552), UADBA-A 60286 (ZCMV 13550) and UADBA-A 60287 (ZCMV 13551), all collected on 4 February 2012 in Antsirahira by A. Rakotoarison and A. Razafimanantsoa; ZSM 631/2014 (DRV 6450), collected on 30 June 2010 in Angorony forest fragment near Maromandia (S14.2211, E48.14211, 115 m a.s.l.); ZSM 614/2014 (DRV 6475) and ZSM 615/2014 (DRV 6481), collected on 30 June 2010 in Maromandia forest fragment near Ankaramy (S13.99653, E48.21770, 283 m a.s.l.) by F.M. Ratsoavina, S. Rasamison, T. Rajoariason, and F. Randrianasolo.



Fig. 24. *Stumpffia gimmel*: (a) ZSM 412/2000 from Berara; (b) Specimen from Ambanja (photo not assignable to collected voucher specimens); (c–d) UADBA-A 60286 (ZCMV 13550) from Antsirasira; (e–f) UADBA-A 60287 (ZCMV 13551) from Antsirasira; (g–h) ZSM 3240/2012 (ZCMV 13552) and (i–j) ZSM 3231/2012 (ZCMV 13538) collected at 27 km from Ambanja.

Distribution. This species is known from eight localities in northeastern Madagascar, including (1) Benavony (type locality), (2) Antsirasira, (3) Ambanja and vicinity, (4) Angorony, (5) Manongarivo, (6) Maromiandra, (7) Berara, and (8) Tsaratanana (molecular data only; Manarikoba Forest, Andampy campsite). All these populations were allocated to *S. gimmel* mainly based on their molecular phylogenetic relationships, although a substantial degree of genetic differentiation among populations is present (see Fig. 3).

Natural history. Typically found in the leaf litter of rain-forest and transitional forest, as well as cacao plantations. Specimens call in the evening and at night (GLAW & VENCES, 1992; 1994). The karyotype of specimen ZMA 19572 (FG/MV 2002.2216) from Manongarivo has been described by APREA *et al.* (2007).

Call. The advertisement call of *S. gimmel* consists of a single short note repeated in series at regular intervals. Recordings are available from two populations that are here assigned to this species (Fig. 25): (1) Calls recorded by F. Glaw on 16 February 1992 at Benavony (26°C air temperature; VENCES *et al.*, 2006: CD3, track 40), with

the following parameters: call duration (= note duration) 96–116 ms (103.5 ± 6 ms; $N=10$), inter-call intervals 1367–3084 ms (1892 ± 106 ms; $N=9$), and a dominant frequency at 4521–4608 Hz (4584 ± 31.5 Hz, $N=10$). (2) Calls recorded by M. Vences on 2 February 2001 at Andampy Campsite, Manarikoba forest, Tsaratanana (25°C air temperature), and here tentatively assigned to this species, with the following parameters: call duration 143–185 ms (160 ± 16 ms; $N=7$), inter-call intervals 2469–4204 ms (2990 ± 616 ms; $N=6$), and a dominant frequency at 5124–5211 Hz (5167 ± 25 Hz, $N=7$). Although detailed parameters vary slightly among populations, these differences are likely explained by differences in motivation, temperature and body size of the males recorded (frequency). The calls reported here all sound very similar to the human ear.

Stumpffia madagascariensis MOCQUARD, 1895

(Figures 26, S94–S95)

Name-bearing type. Holotype MNHN 1893.286 collected “sur la montagne d’Ambre” according to the original description.

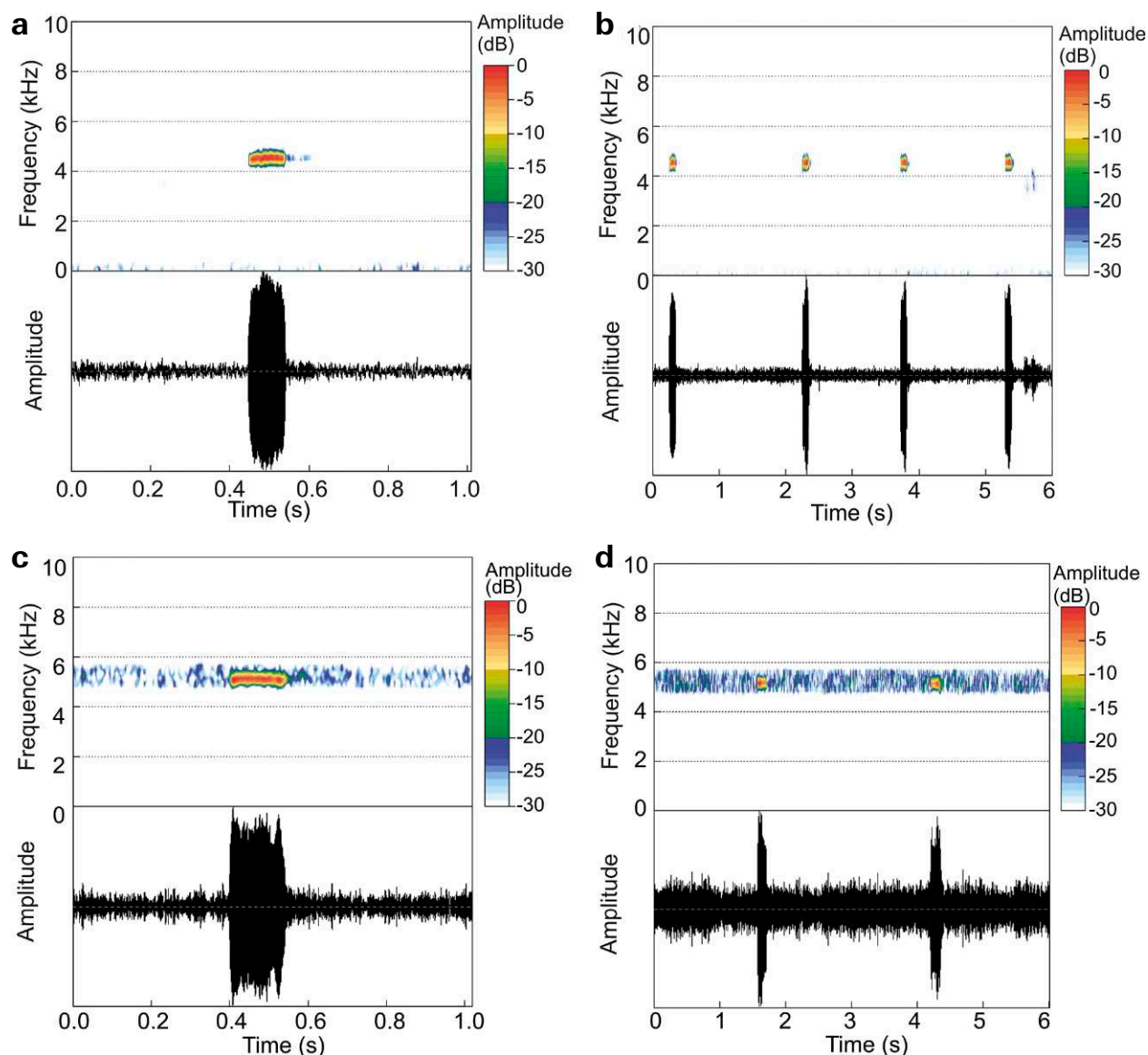


Fig. 25. Spectrograms (above) and oscillograms (below) of the advertisement calls of *Stumpffia gimmel* from two localities (1 s and 6 s duration section each): (a–b) call from Benavony; (c–d) call from Manarikoba forest, Tsaratanana (bandpass filter applied).

Identity and diagnosis. The identity of *S. madagascariensis* has been difficult to ascertain due to the very poor state of preservation of the holotype. However, based on the type locality (Montagne d'Ambre), color patterns as available from the original description, as well as body size and digital reduction, KÖHLER *et al.* (2010) assigned this nomen to one of the several species occurring on Montagne d'Ambre. (1) Miniature to small-sized (SVL 10.0–13.6 mm); (2) manus with four fingers (first finger moderately reduced in length) and pes with five toes (first toe strongly reduced in length); (3) terminal phalanges of fingers not enlarged, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.15–0.18, FOTL/SVL 0.54–0.63; (5) dorsum slightly tubercular; (6) grayish or brownish dorsally, often with a darker central patch covering most of the posterior dorsum, this patch either distinct or faintly recognizable only. Typically with a sharp color border between lighter dorsum and darker flanks. No contrasted ventral coloration and no red color elements on ventral side; (7) regularly repeated short single-note chirp call.

Distinguished from *S. psologlossa* by shorter unpulsed advertisement call, and by color pattern and skin texture in most specimens; from *S. analamaina* by color pattern, possibly by longer inter-call interval, and possibly by proportionally longer hand and feet; and from *S. gimmel* by smaller body size, color pattern, and longer inter-call interval.

Specimens examined. Holotype MNHN 1893.286, collected between May and July 1893 on Montagne d'Ambre by C. Alluaud & Mr. Belly. Referred specimens: ZSM 201/2004 (FGZC 389) and ZSM 202/2004 (FGZC 390), collected on 19 February 2004 on Montagne d'Ambre (S12.5200, E49.1755, 1052 m a.s.l.) by F. Glaw, M. Puente, R.D. Randrianiana & A. Razafimanantsoa; ZSM 2168/2007 (FGZC 1241), collected on 12 March 2007 on Montagne d'Ambre (S12.5166 E49.1766, 1050 m a.s.l.) by F. Glaw, P. Bora, H. Enting, J. Köhler, A. Knoll; ZSM 3242/2012 (ZCMV 12185), collected on 16 January 2012 on Montagne d'Ambre by A. Rakotoarison and A. Razafimanantsoa.

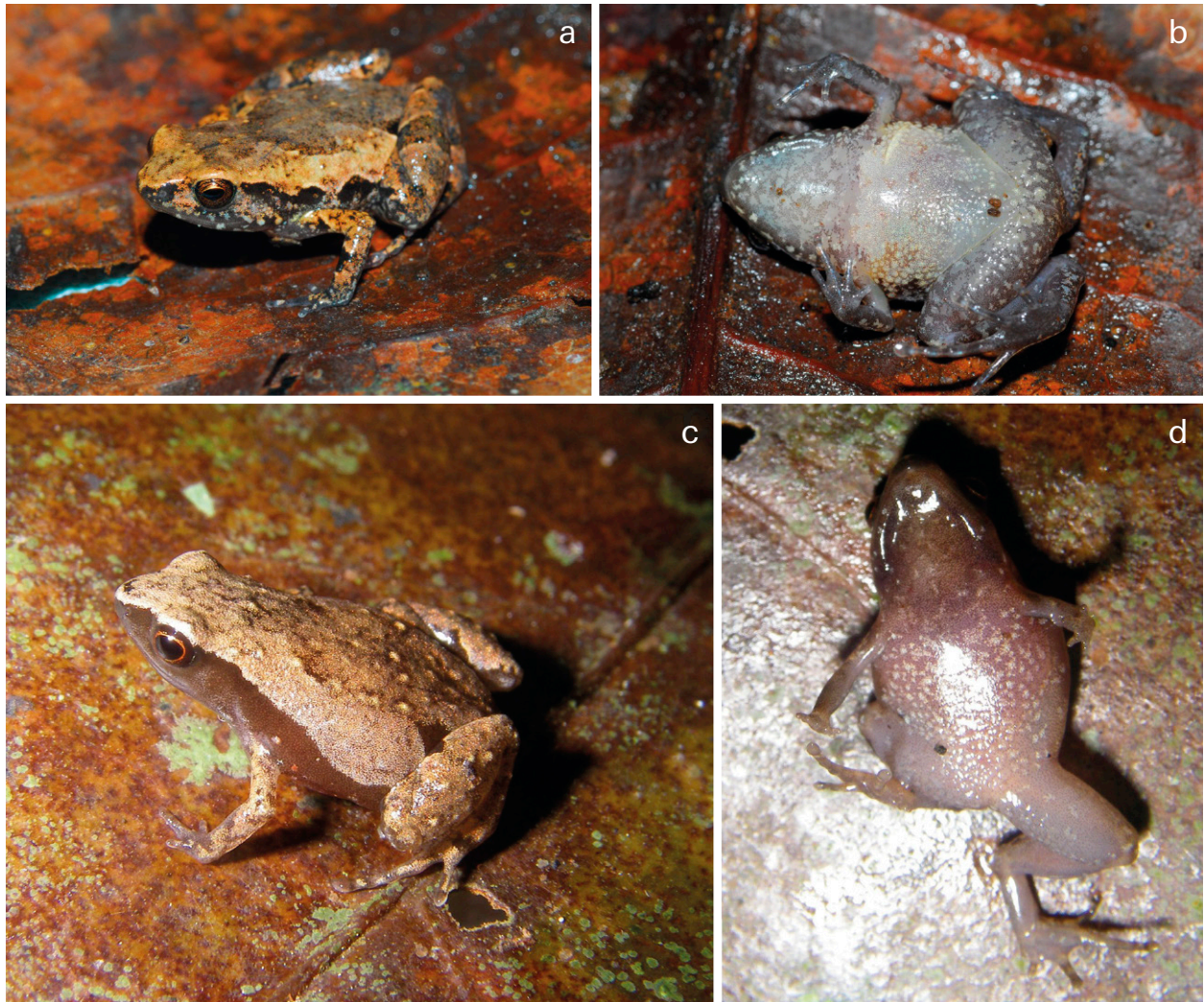


Fig. 26. *Stumpffia madagascariensis* in life: (a–b) Specimen from Forêt d'Ambre Special Reserve (not sequenced; identification tentative); (c–d) ZSM 3242/2012 (ZCMV 12185) from Montagne d'Ambre National Park.

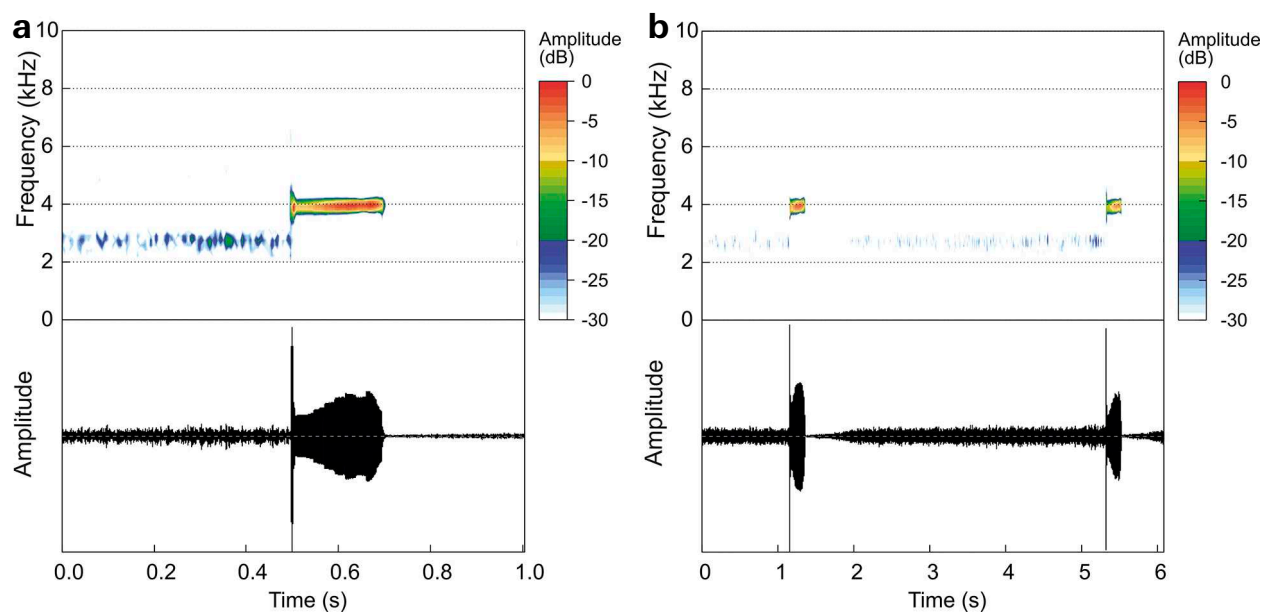


Fig. 27. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia madagascariensis* from Montagne d'Ambre National Park, recorded from specimen ZSM 3242/2012 (ZCMV 12185). (a) 1 s duration section; (b) 6 s duration section. Note that the initial peak in amplitude at beginning of each note is the result of an artifact produced by a damaged recording device.

Distribution. Only known from Montagne d'Ambre National Park, although probably also occurring in Forêt d'Ambre Special Reserve (specimens tentatively identified from photos by color pattern; Fig. 26). Specimens from Montagne des Français are considered to represent a closely related candidate species (*S. cf. madagascariensis* Ca25; see remark below).

Natural history. Specimens were observed calling from the leaf litter of rainforest in the evening.

Call. Advertisement calls were recorded by A. Rakotoarison on 16 February 2012 in Montagne d'Ambre National Park from specimen ZSM 3242/2012 (ZCMV 12185) and consist of single short note repeated in series at regular intervals (Fig. 27). Numerical parameters are as follows: call duration (= note duration) 187–198 ms (195 ± 5 ms; $N=5$), inter-call intervals 4060–4427 ms (4224 ± 153 ms; $N=4$), and a dominant frequency at 3980–4579 Hz (4231 ± 197 Hz, $N=5$). It is important to mention that recordings contain artifacts such as initial peaks of amplitude at beginning of each note, which were produced by a damaged recording device. Therefore the call data presented herein must be treated with caution.

Remark. We here discuss along with *S. madagascariensis* a genetically divergent form found at Montagne des Français and named *Stumpffia* sp. Ca25 according to VIEITES *et al.* (2009), KÖHLER *et al.* (2010), Klages *et al.* (2013), and SCHERZ *et al.* (2016). This lineage is resolved with high support as sister to *S. madagascariensis* from Montagne d'Ambre based on genetic information from several specimens. Despite a substantial genetic divergence (5.8–6.3% in the 16S gene) the available data do not allow a clear conclusion as to whether this lineage is better considered a deep conspecific lineage of *S. madagascariensis*, or a distinct species. No information on call and natural history are available. Referred specimens of *S. sp. Ca25*: ZSM 2108/2007 (FGZC 1103), ZSM 2109/2007 (FGZC 1105) collected on 27 February 2007 on Montagne des Français (S12.3258, E49.3380) by F. Glaw, P. Bora, H. Enting, J. Köhler and A. Knoll.

Stumpffia pygmaea VENCES & GLAW, 1991

(Figures 28 and S96)

Name-bearing type. Holotype ZFMK 52541 from “am Straßenrand, ca. 1 km nördlich von Andoany, Nosy Be, Nordwest-Madagaskar,” translated: “at the edge of the road, ca. 1 km north of Andoany (= Hellville), Nosy Be, northwest Madagascar,” from the original description.

Identity and diagnosis. *Stumpffia pygmaea* is a small-sized species of the north-western lineage, without strong digital reduction, that so far has only been found on the offshore island Nosy Be and Nosy Komba. (1) Miniaturized species (SVL 8.3–12.5 mm); (2) manus with four fingers (first finger slightly reduced in length)

and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.13–0.19, FOTL/SVL 0.48–0.77; (5) dorsum smooth or very slightly tubercular; (6) light brownish coloration with typically indistinct or absent pattern and without contrasted ventral coloration, red color elements on ventral side, or sharp color border between dorsum and flanks; (7) regularly repeated short single-note chirp call.

Distinguished from *S. psologlossa* by shorter unpulsed advertisement call, and by color pattern and skin texture in most specimens; from *S. analamaina* by longer inter-call intervals, and possibly by proportionally longer hand and feet; from *S. gimmerli* by smaller body size, and higher dominant frequency of calls; and from *S. madagascariensis* by lack of sharp color border between dorsum and flanks. Morphologically similar to *S. analamaina* but phylogenetically not closely related to that species. Sister group to *S. madagascariensis*, which also is morphologically similar but differs in color pattern, call, and concordant nuclear and mitochondrial DNA divergence.

Specimens examined. Holotype ZFMK 52541, collected on 28–29 March 1991 near Andoany, Nosy Be by F. Glaw and M. Vences; paratypes ZFMK 52542, ZFMK 52544 and ZSM 557/1999 (formerly ZFMK 52543), same collection data as holotype. Referred specimens: ZFMK 53762–53769, 53772, 53773, all collected in January–February 1992 on Nosy Be by F. Glaw and J. Müller; ZSM 430/2010 and ZSM 431/2010, collected on 13 February 2010 from a forest near Ampasipohy, Nosy Be (S13.3933, E48.3411, 39 m a.s.l.) by F. Glaw.

Distribution. This species is known from several different localities on Nosy Be, and the nearby island of Nosy Komba (ANDREONE *et al.*, 2003; HYDE ROBERTS & DALY, 2014; BLUMGART *et al.*, 2017).

Natural history. A locally quite common species in Nosy Be, in leaf litter of secondary forest and ylang-ylang plantations. Calling activity mostly observed 1–2 hours before dusk, from the leaf litter, with rain also during the day (VENCES & GLAW, 1991).

Call. Advertisement calls were recorded by F. Glaw and M. Vences in 1991 at the type locality Nosy Be (VENCES *et al.*, 2006: CD3, track 36) and consists of a single high-pitched, tonal note (Fig. 29). Numerical parameters are as follows: call duration (= note duration) 185–210 ms (196 ± 10 ms; $N=5$), inter-call intervals 2900–3882 ms (3447 ± 419 ms; $N=4$), and a dominant frequency at 5986–6115 Hz (6054 ± 49 Hz, $N=5$).

Stumpffia angeluci sp. nov.

(Figures 30 and S97)

Holotype. ZSM 3241/2012 (ZCMV 12184) (Figs. 12 a, 30 d–e), an adult male, collected on 16 January 2012, at the park entrance to Montagne d'Ambre National Park (S12.5134, E49.1835, ca. 975 m above sea level), Antsiranana Province, Madagascar, by A. Rakotoarison and A. Razafimanantsoa.



Fig. 28. *Stumpffia pygmaea*. Specimens in life from Nosy Be (photos not assignable to voucher specimens). (a) neometamorph specimen on matchstick; (b–c) adults; (d) foam nest with embryos and endotrophic tadpoles.

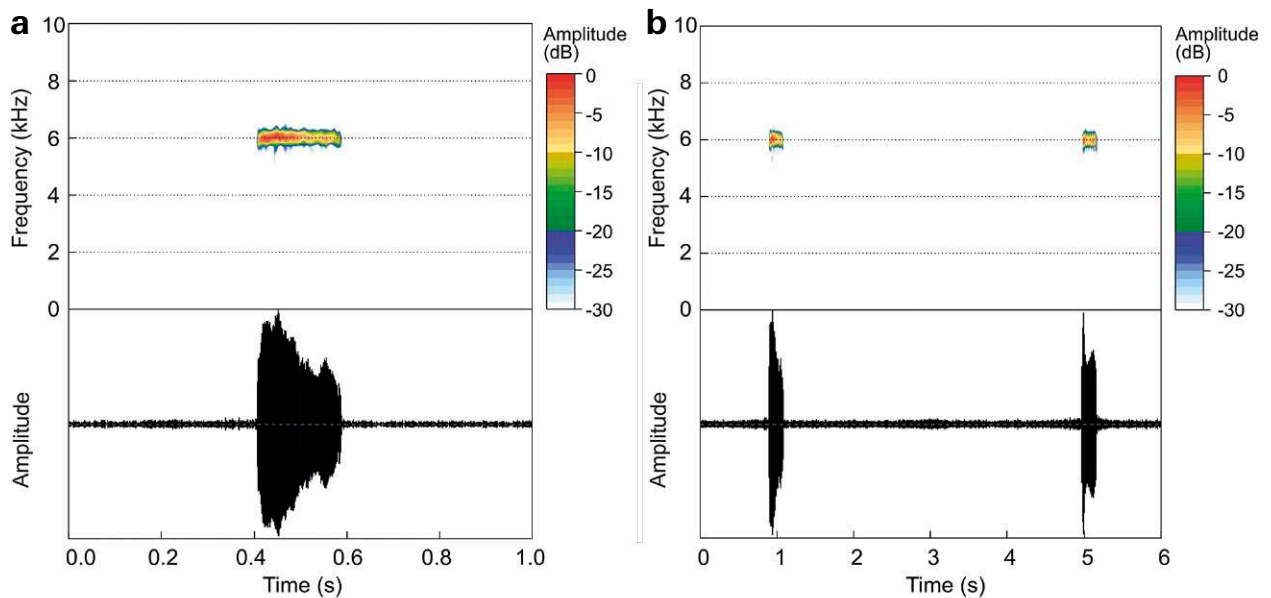


Fig. 29. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia pygmaea* from Nosy Be: (a) 1 s duration section; (b) 6 s duration section.

Paratypes. ZSM 219/2004 (FGZC 428), ZSM 223/2004 (FGZC 433), ZSM 224/2004 (FGZC 434), UADBA-A 24159 (FGZC 436) and UADBA-A 24108 (FGZC 435), collected on 20–21 February 2004 in Montagne d’Ambre National Park by F. Glaw, M. Puente, R.D. Randrianiana and A. Razafimanantsoa; ZSM 303/2004 (FGZC 586), ZSM 300/2004 (FGZC 580), ZSM 301/2004, (FGZC 581), ZSM 302/2004 (FGZC 583), UADBA-A 24765 (FGZC 582)

and UADBA-A 24163 (FGZC 585), collected on 28 February 2004 in Montagne des Français (S12.333, E49.35, 80–200 m a.s.l.) by F. Glaw, M. Puente, R.D. Randrianiana and the employees of Kings Lodge; ZSM 1671/2008 (FGZC 1901), collected on 2 March 2008 in Montagne des Français (S12.3308, E49.3557, 140 m a.s.l.) by F. Glaw; ZSM 1639/2012 (FGZC 4915), collected on 10 December 2012 in Forêt d’Ambre Special Reserve, ca. 5 km SW Sakaramy

(S12.4714, E49.2204, 487 m a.s.l.), by F. Glaw, O. Hawlitschek, T. Rajaofiarison, A. Rakotoarison, FM. Ratsavina, A. Razafimanantsoa; ZSM 3243/2012 (ZCMV 12197), collected on 17 January 2012 around the park entrance to Montagne d'Ambre National Park (S12.5134S, E49.1835, ca. 975 m a.s.l.) by A. Rakotoarison and A. Razafimanantsoa; ZSM 229/2016 (ZCMV 13608), collected in Joffreville between 2011–2013 by A. Rakotoarison and A. Razafimanantsoa; UADBA-A 60281 (ZCMV 13612), collected in Montagne d'Ambre National Park between 2011–2013 by A. Rakotoarison and A. Razafimanantsoa.

Diagnosis. One of several morphologically similar but partly sympatric *Stumpffia* species from northern Madagascar. This species has been previously listed as *Stumpffia* sp. 27 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), KLAGES *et al.* (2013), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Small- to moderately-sized species (adult male SVL 13.7–16.1 mm); (2) manus with four fingers (first finger not obviously reduced in length) and pes with five toes (first toe slightly to moderately reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.20–0.25, FOTL/SVL 0.64–0.73; (5) dorsum slightly tubercular; (6) dorsally uniformly apricot with some small, indistinct and poorly contrasted dark pattern, that can be more intense. Ventrally translucent peach with some indistinct dark and light mottling especially on the chest, and sometimes dark color on throat. No red color ventrally, no sharp border between dorsal and lateral color; (7) regularly repeated single-note tonal call.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. gimmeli* by a longer call duration in advertisement call and less expressed length reduction of fingers; from *S. tetradactyla* by less expressed length reduction of first finger and especially first toe; from *S. psiloglossa* by slightly more enlarged toe discs, coloration, and a shorter, unpulsed advertisement call; from *S. pygmaea*, *S. madagascariensis*, and *S. analamaina* by larger body size. Phylogenetically in clade A1, which contains only two nominal species (*S. psiloglossa* and *S. gimmeli*), which are distinguished by bioacoustic characters.

Description of the holotype. Specimen in good state of preservation, piece of left thigh removed as a tissue sample for DNA extraction. Body round; head slightly wider than long, narrower than body; snout slightly pointed in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, straight; loreal region straight, slightly oblique; tympanum distinct, about 62% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle distinct, single, oval; palmar tubercle distinct, single, round, equal in size to outer metacarpal tubercle; prepollex either small or inner metacarpal

tubercle, about the same size as other carpal tubercles; fingers without webbing; no fingers reduced; relative length of fingers $1 < 2 = 4 < 3$, fourth finger subequal in length to second; finger tips not expanded into discs. Hind limbs slender; TIBL 48% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle distinct, small, and oval; outer metatarsal tubercle absent; no webbing between toes; toes not reduced; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe slightly shorter than third. Skin on dorsum smooth, without distinct dorsolateral folds; ventral skin smooth; in life, dorsal skin was granular.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is pinkish with cream flanks. Two darker dots are present over the anterior of the scapular region, forming the anterior ends of a faint X-like marking above the scapulae. A brown spot is present above the insertion of each arm, and in the inguinal region. A brown M-like line runs between the posteriors of the eyes. Nostril surrounded by brown; dark supratympanic stripe ending just beyond the tympanum; lateral head below this stripe is beige. Ventrally beige flecked with cream, slightly translucent anterior to the legs; ventral surface of thigh as trunk but slightly browner, shank dark beige; sole of foot brown; vent region brown. Dorsal thigh pinkish as dorsum, with faint brown crossband; posterodorsal surface of thigh brown towards knee. Dorsal shank pinkish, with a perpendicular brown crossband midway along its length. Foot dorsally pinkish, with a dark spot on its outer edge; toes mottled brown. Arms dorsally pinkish; lower arm with a single brown crossband; hands speckled.

Color in life (holotype and variation). Dorsum apricot with subtle markings made of dense speckles of ebony, with one forming a concave interocular bar, a weak anterior chevron around the suprascapular region, and another weak anterior chevron from the inguinal region to the mid-back. These markings can be more intense (Fig. 30). The flank becomes increasingly cream ventrally. A large ebony spot is present above the insertion of the arm (can be weaker, cf. Fig 29d, or stronger with more spots on the flank, cf. Fig. 30). Another ebony marking runs from the posterior margin of the eye, curving toward the anterior insertion of the arm over the tympanum. The dorsal forelimb is as the back, with an ebony crossband on the forearm. The fingers are mottled gray and apricot with a whitish annulus before the terminal phalange of each finger. The dorsal legs are as the back, with one weak crossband at the mid-thigh and one on the mid-shank. The toes are mottled ebony and tan, with a white annulus before the terminal phalange of each toe. The ventral skin is translucent peach across the whole body, with cream flecks in a fairly dense band at and just posterior to the pectoral girdle. The iris of the holotype is dark copper reticulated with black, but it can also be gold with black reticulations.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens



Fig. 30. *Stumpffia angeluci* **sp. nov.** from Montagne d'Ambre National Park in life: (a–c) ZSM 3243/2012 (ZCMV 12197); (d–e) holotype ZSM 3241/2012 (ZCMV 12184); (f–g) ZSM 3243/2012 (ZCMV 13608).

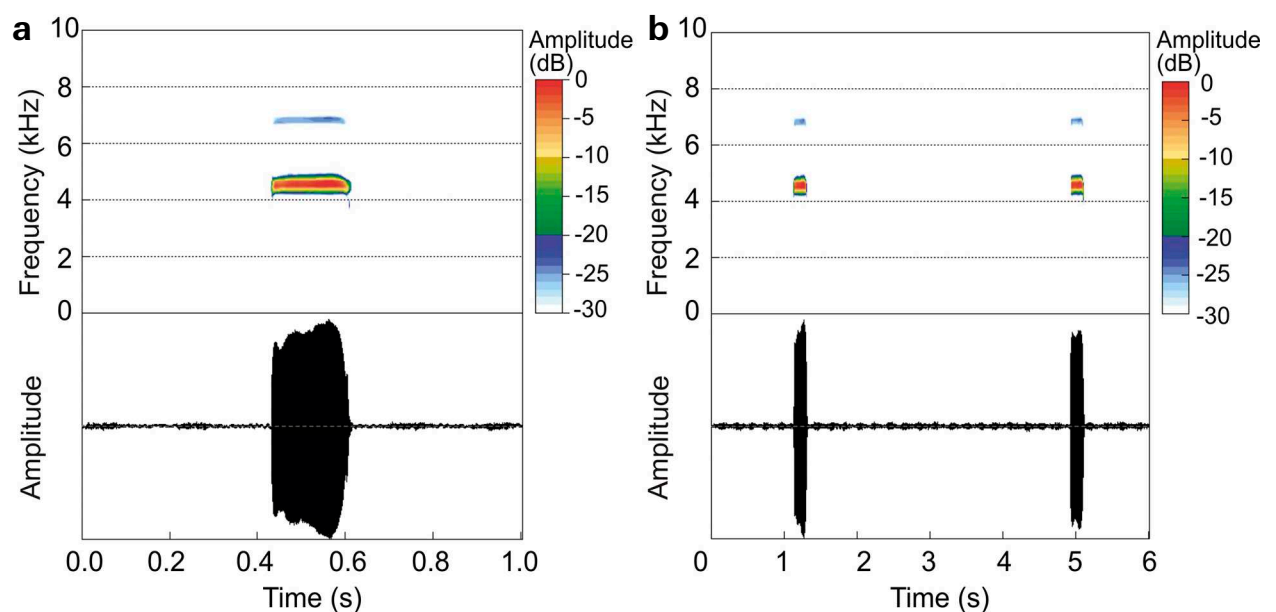


Fig. 31. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia angeluci* **sp. nov.** from Joffreville recorded on 17 January 2016 from paratype UADBA-A 60281 (ZCMV 13612): (a) 1 s duration section, (b) 6 s duration section.

agree strongly with the holotype in morphology. Tubercles of the hand vary from the condition of the holotype by palmar and outer metacarpal tubercles being fused. An intermediate degree of variability was noted in the coloration of specimens; the M- and X-like markings of the holotype are lacking from all other specimens. The dark dots above the insertion of the arm are weakly present in ZSM 3243/2012 and absent in all other paratypes. In one specimen (ZSM 300/2004), two pairs of white dots are present on the dorsum, one behind the scapular region, and one in front of the inguinal region. However, the inguinal spots, supratympanic stripe, brown cloacal region, and brown nostril are present in all specimens (degree of visibility varies). The degree of visibility of leg crossbands varies strongly, but they are present to some degree in all specimens.

Etymology. The species name is a patronym honoring Angeluc Razafimanantsoa, in recognition of his invaluable help in herpetological exploration of Montagne d'Ambre and neighbouring regions.

Distribution. This species is known from northern Madagascar and occurs in and around Montagne d'Ambre National Park, at Joffreville, in Forêt d'Ambre Special Reserve as well as Montagne des Français. The range encompasses elevations from 80–975 m above sea level.

Natural history. The calling male was observed hiding between tree roots on the forest floor, and other active individuals were observed sitting on plants, about 5 cm above the ground.

Call. Advertisement calls were recorded at Montagne d'Ambre National Park by A. Rakotoarison on 17 January 2016 from paratype UADBA-A 60281 (ZCMV 13612) and consist of a single, short, tonal note repeated in series at regular intervals (Fig. 31). Numerical parameters are as follows: call duration (= note duration) 179–187 ms (182 ± 2.7 ms; $N=6$), inter-call intervals 3174–3801 ms (3596 ± 254 ms; $N=5$), and a dominant frequency at 4565–4694 Hz (4651 ± 47 Hz; $N=6$).

Stumpffia huwei sp. nov.

(Figures 32 and S98)

Holotype. ZSM 221/2016 (ZCMV 13618) (Figs. 12 b, 32 a and S98 a–b), an adult male, collected between 2011–2013 in Montagne d'Ambre National Park (S12.51483, E49.17617, 1018 m above sea level), Antsiranana Province, Madagascar by A. Rakotoarison and A. Razafimanantsoa.

Paratypes. ZSM 3245/2012 (ZCMV 13514) and UADBA-A 60281 (ZCMV 13515), UADBA-A 60282 (ZCMV 13619), ZSM 222/2016 (ZCMV 13620), UADBA-A 60283 (ZCMV 13621) and ZSM 223/2016 (ZCMV 13622), all collected between 2011–2013 in Montagne d'Ambre National Park, by A. Rakotoarison and A. Razafimanantsoa; ZSM 224/2016 (ZCMV 13611), collected in December 2011 in Montagne d'Ambre National Park, by A. Rakotoarison and A. Razafimanantsoa; ZSM 904/2003 (FG/MV 2002.920), collected on 18 February 2003 in Montagne

d'Ambre by F. Glaw, R.D. Randrianiaiana and A. Razafimanantsoa.

Diagnosis. One of the several morphologically similar but partly sympatric *Stumpffia* species from northern Madagascar. This species has not been previously listed as candidate species in any publication. (1) Small-sized species (male SVL 12.5–14.8 mm); (2) manus with four fingers (first finger not or very weakly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.16–0.22, FOTL/SVL 0.57–0.69; (5) dorsum smooth; (6) dorsally grayish to reddish brown, sometimes with a large central dark teddybear shaped patch bordered with lemon on the dorsal flanks. Ventrally some specimens uniformly grayish with some yellowish color on belly, other specimens with more intensive yellowish color on belly and especially on throat. No red color ventrally, no sharp border between dorsal and lateral color; (7) regularly repeated single-note tonal call with call duration > 100 ms.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by a lower frequency range of advertisement calls, and less expressed length reduction of fingers; from *S. tetradactyla* by less expressed length reduction of first finger and especially first toe; from *S. psologlossa* by slightly less reduced first finger, skin texture, coloration, and shorter, unpulsed advertisement call; from *S. gimmeli* by shorter call duration; from *S. madagascariensis* by the lack of a sharp border between dorsal and lateral color and a slightly larger body size; from *S. pygmaea* and *S. analamaina* by larger body size; from *S. angeluci* by distinctly shorter call duration. The species is included in clade A1 but is not the direct sister group of any of the nominal species described so far (see below for its distinction from its sister species, *S. mamitika* sp. nov.).

Description of the holotype. Specimen in good state of preservation, left thigh muscle removed as a tissue sample. Body elongate; head slightly longer than width, narrower than body; snout rounded in dorsal view, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis slightly distinct, straight; loreal region concave, oblique; tympanum slightly distinct, about 60% of eye diameter; supratympanic fold not recognizable; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle not recognizable; inner metacarpal tubercle small, oval; fingers without webbing; relative length of fingers $1 < 4 < 2 < 3$, fourth finger slightly shorter than second; finger tips not expanded into discs. Hind limbs slender; TIBL 47% of SVL; lateral metatarsalia strongly connected; inner metatarsal



Fig. 32. *Stumpffia huwei* sp. nov. specimen from Montagne d'Ambre National Park in life: (a) Holotype ZSM 221/2016 (ZCMV 13618); (b–c) ZSM 3245/2012 (ZCMV 13514); (d–e) UADBA-A 60283 (ZCMV 13621); (f–g) ZSM 223/2016 (ZCMV 13622).

tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After four years in 70% ethanol, the dorsum is light beige, banded with brown from the middle of the eyes to the inguinal region. The dorsal surface of the head is light beige flecked with brown. The nostril is beige surrounded with brown. The lateral surface of the head is as the dorsal surface of the head. The flanks are laterally and ventrally beige flecked with brown. The flank coloration merges with the ventral coloration. The ventral trunk is uniformly beige. The chin is beige vermiculated with brown. The ventral thigh is beige spotted with brown. The shank is ventrally beige vermiculated with light brown. The tarsus is ventrally beige spotted with brown. The sole of the foot is as the tarsus but darker. Dorsally, the thigh is beige spotted with brown and with one brown crossband. The posterodorsal surface of the thigh is beige mottled with dark brown. The shank is as the thigh but without crossbands. The tarsus, foot, and toes are as the shank. The cloacal region

is dark brown. The arms are beige spotted with brown. The dorsomedial surface of the hand is beige. The fingers are as the arms. The underside of the arm is as the chin.

Color in life (holotype and variation). Dorsal color mottled copper and burnt umber, bordered by lemon yellow on the dorsolateral head, spreading down to the flanks (Fig. 32). The lateral head to behind the insertion of the forelimb is as the dorsum. The forelimb is also as the back, with weak lighter bands before each terminal phalange of the hand. The dorsal leg is as the back, with one burnt umber crossband on the mid-thigh and mid-shank, and distinct whitish bands before the terminal phalange of each toe. The venter of the holotype was not photographed in life, but the venters of paratypes vary from yellowish cream dappled with whitish spots, to lemon yellow with whitish dappling in the posterior body and burnt umber reticulations under the chin (Fig. 32 d, e, g). The ventral legs are taupe. The iris is brown to copper.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology, with the exception of ZSM 224/2016 (ZCMV 13611), which is the largest known specimen. A high degree of variability

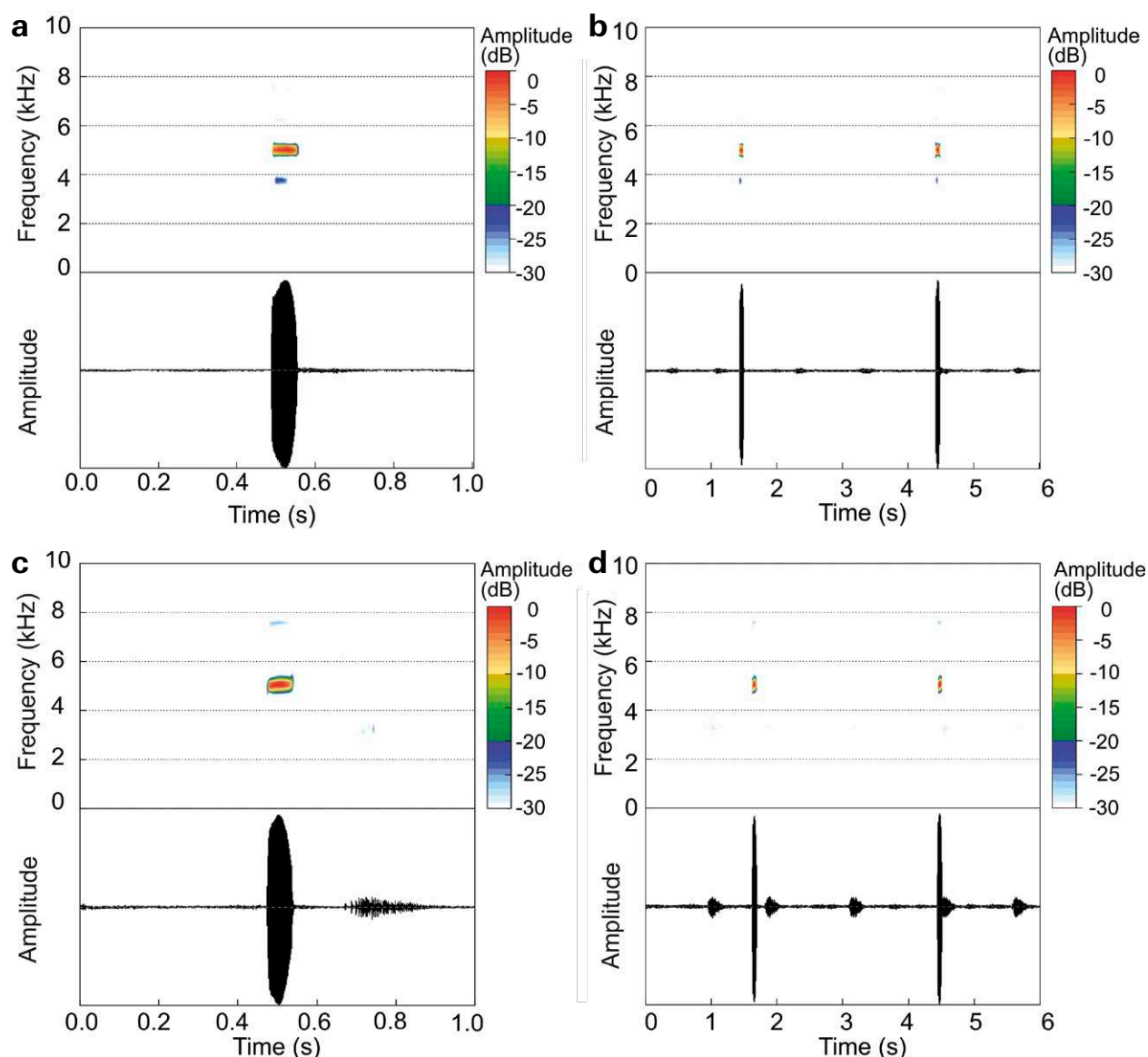


Fig. 33. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia huwei* sp. nov. from Montagne d’Ambre National Park, from (a–b) holotype ZSM 221/2016 (ZCMV 13618) and (c–d) paratype UADBA-A 60282 (ZCMV 13621), recorded between 2011–2013: (a, c) 1 s duration section; (b, d) 6 s duration section.

was noted in the coloration of specimens in preservative: UADBA-A 60283 (ZCMV 13621) is dorsally pinkish with brown X-shaped marking starting from the eyes to the scapular region and a brown spot in the inguinal region; ZSM 223/2016 (ZCMV 13622) is uniformly dark brown with some metallic spots on dorsum; UADBA-A 60282 (ZCMV 13619) is beige with a brown X-shaped marking from the eyes to the inguinal area, and shank and tarsus with brown crossband; ZSM 904/2003 (FG/MV 2002.920) is dorsally light brown with a brown V-shaped marking in the scapular region.

Etymology. The name is a patronym honoring Reinhard Huwe, dedicated naturalist and ornithologist in Braunschweig and technician at the Zoological Institute of the Technical University of Braunschweig, in recognition of his immense and creative contributions to research and teaching in zoology.

Distribution. The species is known only from Montagne d’Ambre National Park. The range encompasses elevations from 997–1066 m above sea level.

Natural history. The species occurs in rainforest in Montagne d’Ambre National Park. Active individuals were found in dense leaf litter, however the calling males were found at dusk at sites with less dense leaf litter cover as well.

Call. The advertisement call consists of a single, very short note emitted in series at regular intervals (Fig. 33). Two recordings are available from Montagne d’Ambre National Park: (1) Calls recorded by A. Rakotoarison between 2011–2013 from specimen ZCMV 13618 had the following numerical parameters: call duration (= note duration) 67–74 ms (70 ± 2.4 ms; $N=6$), inter-call intervals 2340–3117 ms (2687.5 ± 267 ms; $N=6$), and a dominant

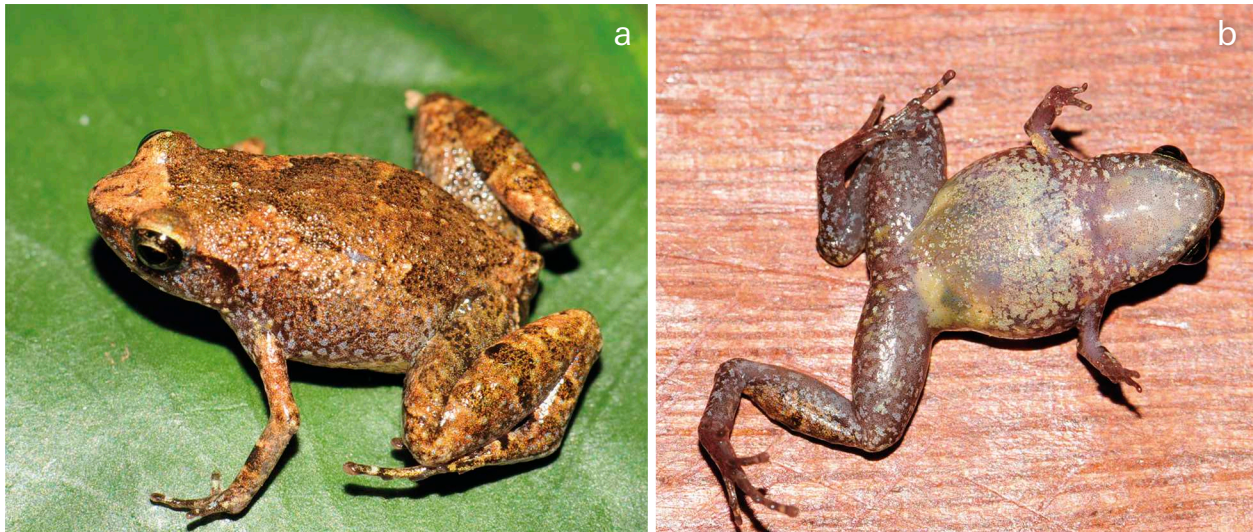


Fig. 34. *Stumpffia iharana* sp. nov. from Fanambana forest in life. Paratype, ZSM 1652/2012 (FGZC 3927) in (a) dorsolateral and (b) ventral view.

frequency at 4952–5061 Hz (5020 ± 39 Hz, $N=6$). (2). Calls recorded by A. Rakotoarison between 2011–2013 from specimen ZCMV 13621: call duration 61–69 ms (66.7 ± 2.75 ms; $N=7$), duration of inter-call intervals 2470–3643 ms (2845.8 ± 424 ms; $N=6$), and a dominant frequency at 5038–5167 Hz (5081 ± 60.8 Hz, $N=7$).

Stumpffia iharana sp. nov.

(Figures 34 and S99)

Holotype. ZSM 1651/2012 (FGZC 3895) (Figs. 12 c, S99 c–d), collected on 4 December 2012 in gallery forest southeast of Andra-faikona (S13.7139, E49.4966, 820 m above sea level), Antsiranana Province, Madagascar, by F. Glaw, O. Hawlitschek, F.M. Ratsoavina, A. Rakotoarison, T. Rajoafiarison, and A. Razafimanantsoa.

Paratypes. ZSM 1650/2012 (FGZC 3893) and UADBA-A 60276 (FGZC 3894), with same collecting data as holotype; ZSM 1642/2012 (FGZC 3800) collected on 3 December 2012 near Ambodimandresy (ca. S13.7133, E49.4911, 778 m a.s.l.) by F. Glaw, O. Hawlitschek, F.M. Ratsoavina, A. Rakotoarison, T. Rajoafiarison, and A. Razafimanantsoa; ZSM 1652/2012 (FGZC 3927) and UADBA-A 60277 (FGZC 3926), collected on 6 December 2012 in Fanambana forest (S13.6138, E50.0019, 53 m a.s.l.) by F. Glaw, O. Hawlitschek, F.M. Ratsoavina, A. Rakotoarison, T. Rajoafiarison, and A. Razafimanantsoa.

Diagnosis. One of several morphologically similar but partly sympatric *Stumpffia* species from northern Madagascar. This species has not been previously listed as candidate species in any publication. (1) Small-sized species (adult SVL 14.0–15.5 mm; female SVL 14.7 mm); (2) manus with four fingers (first finger not or very weakly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly to moderately enlarged discs; (4) relative hand and foot length, HAL/SVL 0.19–0.22, FOTL/SVL 0.57–0.75; (5) dorsum smooth with a few scattered tubercles; (6) dorsally sand brown with poorly defined darker markings. Ventral

skin translucent with dense cream flecks over the pectoral girdle, becoming fine speckling posteriorly. No red color ventrally, no sharp border between dorsal and lateral color.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by less expressed length reduction of fingers; from *S. tetradactyla* by less expressed length reduction of first finger and especially first toe; from *S. psologlossa*, *S. analamaina*, *S. madagascariensis*, and *S. pygmaea* by larger body size; from *S. madagascariensis* also by the lack of a sharp border between dorsal and lateral color and a slightly larger body size. Most similar to *S. gimmeli*, *S. angeluci*, and *S. huwei*. These three species are all included with *S. iharana* in clade A1. The new species can be distinguished from *S. angeluci* and *S. huwei* because these do not constitute its direct phylogenetic sister groups, and do not share mitochondrial DNA or Rag-1 haplotypes. Phylogenetically the new species is sister to *S. gimmeli*. As discussed above, *S. gimmeli* contains numerous deep genetic lineages and might represent a species complex; we here consider and describe as distinct species *S. iharana* the most divergent of these lineages which differs concordantly in mtDNA and by not sharing Rag-1 haplotypes, and by a substantial geographic distance from its known distribution area. This species hypothesis requires future confirmation by a thorough revision of the *S. gimmeli* complex with the inclusion of bioacoustic data and fine-scale geographic sampling.

Description of the holotype. Specimen in good state of preservation, tongue removed as a tissue sample for DNA extraction. Body round; head longer than wide, wider than body; snout rounded in dorsal view, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis slightly distinct,

concave; loreal region straight, oblique; tympanum distinct, about 60% of eye diameter; supratympanic fold not distinct; tongue absent, maxillary teeth and vomerine teeth absent, choanae oval. Forelimbs slender; subarticular tubercles distinct, single, rounded; outer metacarpal tubercle small, elongate; inner metacarpal tubercle distinct; fingers without webbing; first finger slightly reduced; relative length of fingers $1 < 4 < 2 < 3$, fourth finger shorter than second; finger tips slightly expanded into discs. Hind limbs slender; TIBL 47% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle practically indistinguishable; outer metatarsal tubercle absent; no webbing between toes; toe tips not expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After four years in 70% ethanol, the dorsum is slightly pinkish beige with broad brown vertebral band. The dorsal surface of the head is as the back. The nostril is brown. The lateral surface of the head is beige mottled with brown. The flanks are cream mottled with beige. The flank coloration merges with the ventral coloration. The ventral trunk is as the flank. The chin is as the trunk. The ventral thigh is as the belly. The shank is ventrally as the thigh. The tarsus is ventrally as the shank. The sole of the foot is beige mottled with cream. Dorsally, the thigh is as the back with a brown crossband. The posterodorsal surface of the thigh is as the inguinal region. The shank, tarsus, and feet are as the thigh. The toes are as the feet with cream crossbands. The cloacal region is not dark brown. The arms are as the dorsum, a brown crossband present on the lower arm. The dorsomedial surface of the hand is cream. The fingers have small cream crossbands. The underside of the arm is as the ventral trunk.

Color in life (paratypes). Dorsum sandy brown with subtle, granular coffee-brown markings and patternings. The dorsal head is clean tan anterior to the level of the mid-eye. The flanks are as the dorsum, becoming increasingly flecked with cream and decreasingly brown ventrally. The lateral head is as the dorsum, though the nostril is surrounded by dark brown, as is the posterodorsal edge of the tympanum. The dorsal forelimb is as the trunk, with a sooty crossband on the forearm. The fingers are mottled with brown, with a light annulus before each terminal phalange. The dorsal hindlimb is as the dorsum, with one granular coffee-brown crossband on the thigh, one on the shank, and one on the tarsus. The toes are mottled as the dorsum, with a light annulus before each terminal phalange. The ventral skin is translucent cream, immaculate on the central chin but with cream speckles below the lower jaw. Dense cream flecks cover the pectoral girdle and decrease in density posteriorly, becoming fine speckles that cover the posterior abdomen and ventral legs. The iris is golden with black reticulations.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology, except: in ZSM 1642/2012 (FGZC 3800) snout slightly pointed dorsally and laterally, big elongate inner metacarpal tubercle, small elongate outer metacarpal tubercle, small elongate inner metatarsal tubercle, dorsally browner than the holotype, brown spot beyond the arm; in ZSM 1650/2012 (FGZC 3893) outer metacarpal tubercle indistinguishable, dorsal coloration grayish, brown X shape in the scapular region, reversed V in the inguinal region; in ZSM 1652/2012 (FGZC 3927) small elongate outer metacarpal tubercle, small inner metatarsal tubercle, dorsal coloration as the holotype, except for the presence of a beige triangle on the head.

Etymology. The species name is a noun in apposition to the genus name, and refers to the distribution of the new species, near Iharana (Vohemar in French), in north-eastern Madagascar.

Distribution. Currently known from four localities: (1) south-east of Andrafaikona (type locality), (2) Fanambana forest, (3) near Ambodimandresy, and (4) Bezavona. The latter locality Bezavona is assigned to this species based on a DNA sequence deposited in GenBank (accession number DQ283411) corresponding to the specimen AMNH A167359 (not examined by us). This species occurs in a remarkably broad altitudinal range (53–820 m a.s.l.).

Natural history. This species inhabits the leaf litter of coastal and mid-altitude rainforest.

Call. Unknown.

Stumpffia larinki sp. nov.

(Figures 35 and S100)

Holotype. ZSM 3236/2012 (ZCMV 13525) (Fig. 12 d, 35), collected on 26 January 2012 at ‘Campement des Princes’ (app. S12.9575, E49.1183, 90 m above sea level), Ankarana National Park, Antsiranana Province, Madagascar, by A. Rakotoarison and A. Razafimanantsoa.

Paratypes. UADBA (FG/MV 2002.593), UADBA (FG/MV 2002.595), ZSM 779/2003 (FG/MV 2002.594), and ZSM 861/2003 (FG/MV 2002.834), all collected on 11 February 2003 in Ankarana National Park by F. Glaw, R.D. Randrianiana, and A. Razafimanantsoa; ZSM 1669/2008 (FGZC 1620), collected on 13 February 2008 in Ankarana National Park, Petit Tsingy (= locality Campement des Princes; S12.9575, E49.1183, 90 m a.s.l.), by F. Glaw, M. Franzen, J. Köhler, N. D’Cruze; ZSM 205/2016 (ZCMV 13617), calling male, collected at the type locality by A. Rakotoarison and A. Razafimanantsoa.

Diagnosis. One of several morphologically similar and partly sympatric *Stumpffia* species from northern Madagascar. This species has been previously listed as *Stumpffia* sp. 26 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), KLAGES *et al.* (2013), SCHERZ *et al.* (2016) and



Fig. 35. *Stumpffia larinki* sp. nov. from Ankarana National Park in life: (a–c) Holotype ZSM 3236/2012 (ZCMV 13525).

PELOSO *et al.* (2017). (1) Small-sized species (SVL 12.5–12.8 mm); (2) manus with four fingers (first finger not or very weakly reduced in length) and pes with five toes (first toe very slightly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly to moderately enlarged discs; (4) relative hand and foot length, HAL/SVL 0.22–0.24, FOTL/SVL 0.51–0.70; (5) dorsum smooth; (6) dorsally iridescent copper with a faint burnt umber patch from the eyes to the mid-dorsum or vent. Ventrally translucent gray or light plum. No red color ventrally, no sharp border between dorsal and lateral color; (7) regularly repeated pulsatile single-note call with call duration > 100 ms.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi*

by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by a longer call duration and less expressed length reduction of fingers; from *S. tetradactyla* by less expressed length reduction of first finger and especially first toe; from *S. psologlossa* by a pulsatile but not clearly pulsed call; from *S. gim-meli* by lower dominant frequency in calls and slightly smaller body size; from *S. madagascariensis* by the lack of a sharp border between dorsal and lateral color and a slightly larger body size. Morphologically most similar to *S. angeluci*, *S. iharana*, *S. pygmaea*, and *S. analamaina*, but not the direct sister group of any of those species, strongly divergent in mitochondrial and nuclear DNA, and distinguished from *S. pygmaea* and *S. analamaina* by slightly larger body size, from *S. angeluci* by slightly

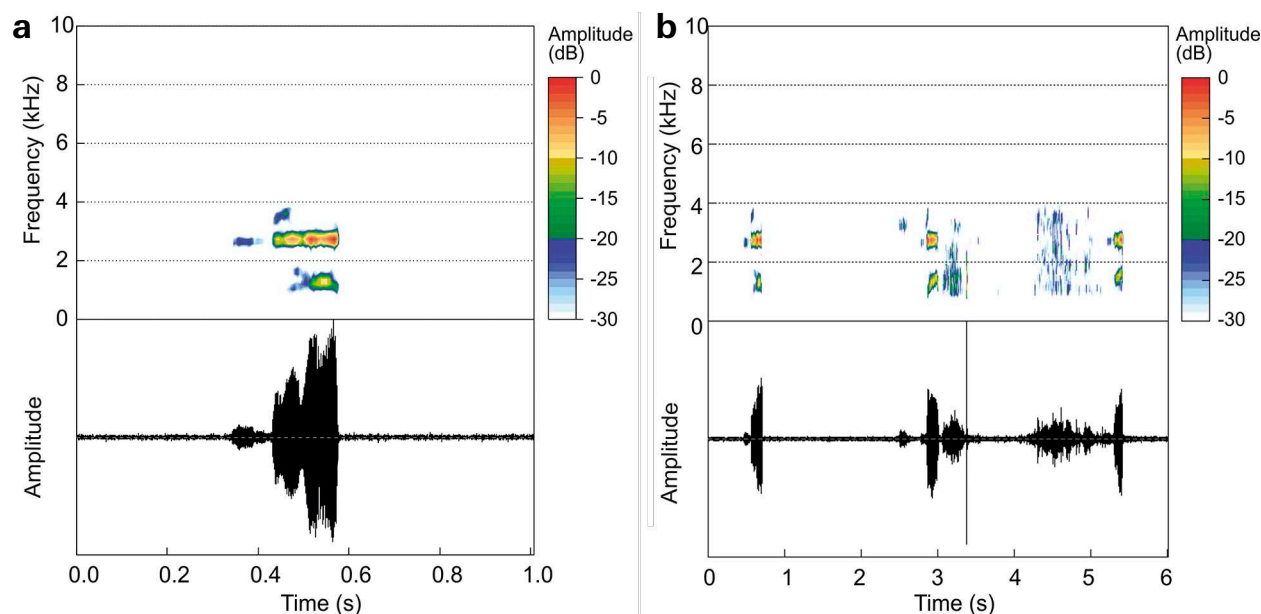


Fig. 36. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia larinki* **sp. nov.** from Ankarana National Park, recorded from paratype ZSM 205/2016 (ZCMV 13617): (a) 1 s duration section; (b) 6 s duration section (including some microphone noise).

shorter call duration, and from *S. huwei* by a longer call duration. The species is included in clade A1 but is not the direct sister group of any nominal species, and is characterized by a comparatively long branch separating it from its closest relatives.

Description of the holotype. Specimen in good state of preservation, left leg partially removed as tissue sample, skin of the right leg slightly damaged. Body round; head wider than long, narrower than body; snout rounded in dorsal view, somewhat truncate in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis straight or slightly concave; loreal region concave, oblique; tympanum visible, about 55% of eye diameter; supratympanic fold not visible; tongue long, slightly broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; sub-articular tubercles not visible; outer metacarpal tubercle distinct, elongate; palmar metacarpal distinct, triangular, prepollex visible, elongate; fingers without webbing; first finger reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly longer than second; finger tips not expanded into discs. Hind limbs slender, TIBL 47% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; no toes reduced; toe tips slightly expanded into discs; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe slightly shorter than third; sub-articular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is beige in the lateral regions with a broad light brown band from the head to the anterior

inguinal region. No inguinal spots. The dorsal surface of the head is as the back with a black oval spot in the scapular region. The nostril is light brown. The lateral surface of the head and the flanks are beige spotted with brown. The flank coloration merges with the ventral coloration. The ventral body is uniformly cream on the abdomen and spotted with brown laterally. The chin is as the ventral abdomen, with cream patches. The ventral thigh is as the belly. The shank and tarsus are ventrally as the thigh. The sole of the foot is brown mottled with cream. Dorsally, the thigh is beige spotted with brown. The posterodorsal surface of the thigh is as the dorsal surface. The shank is as the thigh with weakly distinct crossband. The tarsus and foot are as the thigh, without crossbands. The toes are mottled with dark brown. The cloacal region is brown. The arms are as the dorsum. A weakly contrasted brown crossband is present on the lower arm. The dorsomedial surface of the hand and the fingers are beige spotted with brown. The underside of the arm is as the ventral trunk.

In life, dorsum iridescent copper with a faint burnt umber patch running from between the eyes to the mid-dorsum. A weak lateral color border divides the dorsal coloration from the burnt umber flank. Whitish flecks are present on the flank. The dorsal arm is as the back, with the fingers being burnt umber with a light annulus before each terminal phalange. The dorsal hindlimb is as the back with burnt umber flecks. The toes have a light annulus before each terminal phalange. The ventral skin is translucent, light gray over the vocal sac, a light plum over the pectoral region, and taupe on the posterior trunk and hindlimbs. The iris is golden reticulated with black.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology, ex-

cept: ZSM 779/2003 (FG/MV 2002.0594), inguinal spot present, a broad indistinct dark patch beginning in the middle of the eyes region and running over most of the dorsum; in ZSM 861/2003 (FG/MV 2002.0834), dorsum with a brown X-shaped marking starting in the scapular region and ending in the middle of the body.

Etymology. The species name is a patronym honoring Otto Larink, Professor Emeritus at Technical University of Braunschweig, in recognition to his achievements in zoology and his continued assistance for specialized research on the Malagasy fauna.

Distribution. This species is only known from Ankarana National Park.

Natural history. The species occurs in dry forest in Ankarana National Park. One calling male was found at night, calling from a limestone rock and a second calling male was found during the day hiding in a small limestone cave.

Call. Advertisement calls were recorded by A. Rakotoarison on 8 January 2016 in Ankarana National Park from paratype ZSM 205/2016 (ZCMV 13617). The call consists of a single pulsatile note repeated in series at regular intervals (Fig. 36). Numerical call parameters are as follows: call duration (= note duration) 114–155 ms (138 ± 21 ms; $N=3$), inter-call intervals 2143–2289 ms (2216 ± 103 ms; $N=2$), and a dominant frequency at 2842–3057 Hz (2914 ± 124 Hz, $N=3$). The pulsatile nature of notes is evident from expanded oscillograms as well as recognizable by the human ear. However, pulses are not clearly separated or countable.

Stumpffia maledicta sp. nov.

(Figures 37 and S101)

Holotype. ZSM 2079/2007 (FGZC 1049) (Figs. 12 e, S101 a–b), an adult, collected on 25 February 2007 near the “Gîte d’etape” campsite (S12.5268, E48.1721, ca. 1050 m above sea level), Montagne d’Ambre National Park, Antsiranana Province, Madagascar by F. Glaw, P. Bora, H. Enting, J. Köhler, and A. Knoll.

Paratypes. ZSM 2169/2007 (FGZC 1244) and UADBA (FGZC 1243), collected on 12 March 2007 at Voie des Milles Arbres (S12.51667 E, 049.17667, 1050 m a.s.l.) in Montagne d’Ambre National Park by F. Glaw, P. Bora, H. Enting, J. Köhler, and A. Knoll; ZSM 3244/2012 (ZCMV 13504), collected on 22 January 2012 at Lac Maudit, Montagne d’Ambre National Park by A. Rakotoarison and A. Razafimanantsoa.

Diagnosis. One of several morphologically similar but partly sympatric *Stumpffia* species from northern Madagascar, with probably very long inter-call interval duration. This species has been previously listed as *Stumpffia* sp. 28 in KÖHLER *et al.* (2010), KLAGES *et al.* (2013), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Small-to moderately-sized species (SVL up to 16.8 mm; one adult male SVL 13.8 mm); (2) manus with four fingers

(first finger weakly reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.18–0.20, FOTL/SVL 0.60–0.71; (5) dorsum slightly to moderately tubercular; (6) dorsally uniformly sand brown with some small, indistinct and poorly contrasted dark pattern. Ventrally translucent lemon yellow with a gray lip and anterior chin, with off-white speckles posterior to the pectoral region. No red color ventrally, no sharp border between dorsal and lateral color; (7) regularly repeated single-note tonal call of ca. 100 ms duration; if available call recordings refer to adequately motivated specimens, this species has the longest inter-call interval duration of all known *Stumpffia* species (5167–5637 ms).

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. huwei* by a longer call duration and less expressed length reduction of fingers; from *S. tetradactyla*, by less expressed length reduction of first finger and especially first toe; from *S. psologlossa* by a tonal call (vs pulsed); from *S. pygmaea*, *S. madagascariensis*, and *S. analamaina*, by larger body size; from *S. angeluci* by shorter call duration and longer inter-call intervals; from *S. iharana* by a separate phylogenetic position and lack of haplotype sharing in Rag-1.

The species is recovered in clade A1. It is the sister group of *S. angeluci* and occurs syntopically with its sister species. However, the two species are concordantly differentiated in mitochondrial and nuclear genes despite sympatry, and appear to differ bioacoustically, thus confirming their species status.

Description of the holotype. Specimen in a good state of preservation, its right arm removed as a tissue sample. Body round; head wider than long, narrower than body; snout pointed in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer to the tip of snout than to eye; canthus rostralis distinct, concave; loreal region straight, slightly oblique; tympanum distinct, about 80% of eye diameter; supratympanic fold not visible; tongue damaged, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle large, oval; palmar tubercle round, abutting outer tubercle; inner metacarpal tubercle distinct, oval; fingers without webbing; first finger reduced; relative length of fingers $1 < 2 = 4 < 3$, fourth finger subequal in length to second; finger tips not expanded into discs. Hind limbs robust; TIBL 49% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle indistinct, small, oval; outer metatarsal tubercle absent; no webbing between toes; first toe reduced; toe tips slightly enlarged; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third; subarticular tubercles distinct, single. Skin on

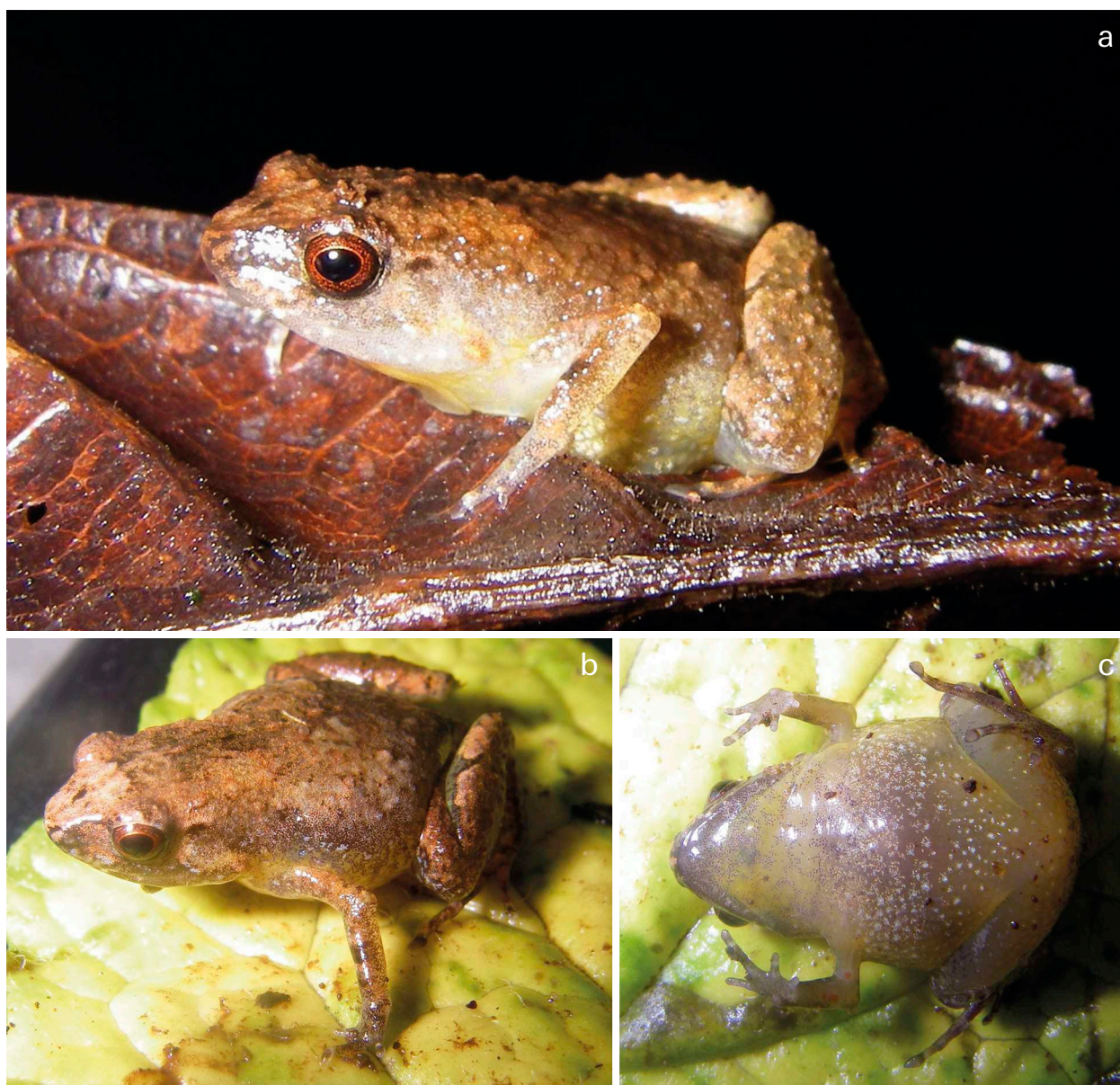


Fig. 37. *Stumpffia maledicta* sp. nov. in life: (a–c) paratype ZSM 3244/2012 (ZCMV 13504) from Lac Maudit, Montagne d’Ambre National Park.

dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After eight years in 70% ethanol, the dorsum is beige, with no pattern. No spots are present in the inguinal region. The dorsal surface of the head is as the back. The color of the nostril is not distinct from the lateral head coloration. The lateral surface of the head is granular brown, with irregular cream dots. A cream stripe runs from the tympanum toward the insertion of the arm. The color of flanks is a continuation of the lateral head coloration, forming a distinct color border with the dorsum. The flank coloration is distinct from the ventral coloration. The ventral abdomen is cream with traces of brown speckling. The chin has more intense brown flecking than the abdomen. The ventral thigh is cream. The shank is ventrally cream mottled with light

brown. The tarsus is ventrally as the shank. The sole of the foot is beige. Dorsally, the thigh is beige as the back. The anterodorsal thigh is brown with irregular cream dots, like the flank. The posterodorsal surface of the thigh is as the anterodorsal side. The shank is dorsally beige. The tarsus is as the shank. The foot is laterally beige and medially cream at its base, fading to become cream distally. The toes are mottled cream and beige. The cloacal region is not darker than the rest of the thighs. The arms are dorsally and laterally as the dorsum and flank, and ventrally clean cream. The dorsomedial surface of the hand is cream. The fingers are brown with cream flecks.

Color in life (holotype and paratypes). Dorsum sand brown with a slightly darker midregion. The flank fades from the dorsal coloration to a lemon yellow. The dorsal forelimb is as the back, with a sooty crossband on the

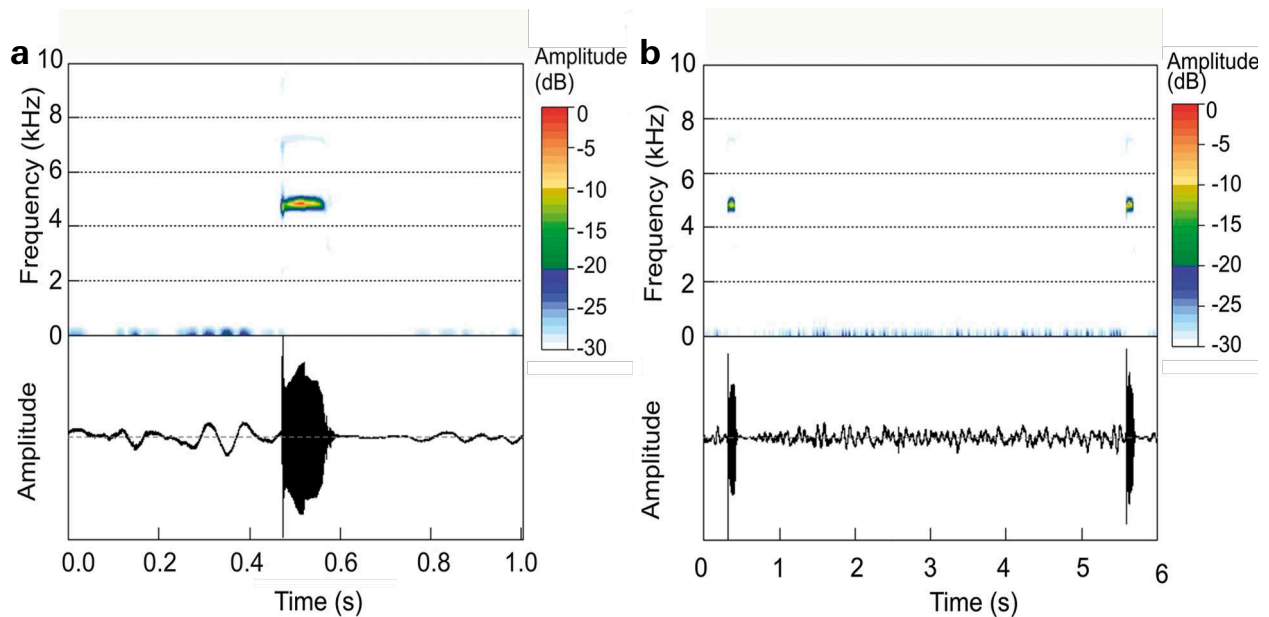


Fig. 38. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia maledicta* sp. nov. from Montagne d'Ambre National Park, recorded from paratype ZSM 3244/2012: (a) 1 s duration section; (b) 6 s duration section. The initial peak in amplitude at the beginning of each note most probably represents an artifact produced by a damaged recorder.

forearm. The fingers are mottled sand brown and gray, with a whitish annulus before each terminal phalange. The dorsal hindlimbs are as the back, with the toes as the fingers. The ventral coloration of the holotype in life is not known, but one paratype had a translucent lemon yellow ventral skin with a gray lip and anterior chin, and off-white speckles from the pectoral region decreasing in density to the legs (Fig. 37c). The iris is russet.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. ZSM 3244/2012 is overfixed, resulting in artefactual supratympanic folds and a transverse head fold. This specimen has a more boxy snout than the holotype and paratype ZSM 2169/2007. A relatively low degree of variability was noted in the coloration of specimens in preservative: in ZSM 3244/2012 and ZSM 2169/2007 the dorsum is lightly flecked with brown, and the distinction of the dorsum and flank is less strong than in the holotype; in ZSM 2169/2007, an hour-glass shaped marking is present on the anterior dorsum. In this specimen the dorsal surface of the thigh is also reticulated with brown; ZSM 3244/2012 has a brown interocular bar.

Etymology. The species name is the feminine nominative single form of the Latin adjective *maledictus* = cursed, referring both to one of the collecting localities (Lac Maudit) and to the difficulty in finding this species.

Distribution. This species is only known from Montagne d'Ambre National Park.

Natural history. The species occurs in rainforest. The calling male was found at night, hiding between roots on the forest floor.

Call. Advertisement calls were recorded by A. Rakotoarison on 16 February 2012 in Montagne d'Ambre National Park, near Lac Maudit, from the specimen ZSM 3244/2012. The call consists of a single short tonal note repeated in series at regular intervals (Fig. 38). Numerical parameters are as follows: call duration (= note duration) 98–104 ms (102 ± 2.8 ms; $N=4$), inter-call intervals 5167–5637 ms (5927 ± 735 ms; $N=3$), and a dominant frequency at 4823–4866 Hz (4833 ± 21.5 Hz, $N=4$). It is important to mention that call recordings of this species may suffer from certain artifacts produced by a damaged recording device. Results thus must be treated with caution.

Stumpffia mamitika sp. nov.

(Figures 39 and S102)

Holotype. ZSM 3237/2012 (ZCMV 13524) (Figs. 12 f, 39 e, j, k), an adult male, collected on 26 January 2012 near the 'Campement des Princes' (ca. S12.9575, E49.1183, 90 m above sea level), Ankarana National Park, Antsiranana Province, Madagascar by A. Rakotoarison and A. Razafimanantsoa.

Paratypes. ZSM 862/2003 (FG/MV 2002.838), collected on 15 February 2003 around Mahamasina in Ankarana National Park by F. Glaw, R.D. Randrianiaina, and A. Razafimanantsoa; ZSM 307/2004 (FGZC 592) collected on 27 February 2004 in Ankarana National Park, pitfall site (S12.9619, E49.1208, 121 m a.s.l.) by F. Glaw, M. Puente and R. Randrianiaina; ZSM 375/2005 (FGZC 2725), collected on 13 February 2005 between Andrakata and Andapa by F. Glaw, M. Vences, and R.D. Randrianiaina; ZSM 3232/2012 (ZCMV 13528), UADBA-A 60278 (orig. ZSM 3233/2012, ZCMV 13529), UADBA-A 60284 (orig. ZSM 3234/2012, ZCMV 13530), and UADBA-A 60285 (orig. ZSM 3235/2012, ZCMV 13531), all collected on 29 January 2012 from a site 4 km from Vohemar by A. Rakotoarison and A. Razafimanantsoa; ZSM 228/2016 (ZCMV 13616), collected between 2011–2013 in Ankarana National Park (S12.96448, E49.12995) by A. Rakotoarison and A. Razafimanantsoa.

Diagnosis. One of several morphologically similar but partly sympatric *Stumpffia* species from northern Madagascar. This species has been previously listed as *Stumpffia* sp. 5 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), KLAGES *et al.* (2013), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Small-sized species (male SVL 12.7–15.0 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.16–0.24, FOTL/SVL 0.62–0.75; (5) dorsum smooth with few scattered tubercles or slightly tubercular; (6) dorsally russet to sand brown, often with a large central dark teddybear shaped patch which can however be indistinct. Ventrally translucent gray to plum with flecks of iridescent cream scattered across the abdomen and/or chest. No red color ventrally, no sharp border between dorsal and lateral color; (7) regularly repeated single-note tonal call.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by a longer call duration and less expressed length reduction of fingers; from *S. psologlossa* by an unpulsed call structure; from *S. tetradactyla* by less expressed length reduction of first finger and especially first toe; from *S. pygmaea*, *S. mada-gascariensis*, and *S. analamaina* by slightly larger body size and shorter duration of calls.

The species is placed in clade A1 and within this clade it is distinguished from *S. angeluci* by shorter duration of calls and of inter-call intervals; from *S. maledicta* by shorter duration of inter-call intervals; from *S. larinki* by shorter inter-call intervals. Most similar morphologically and bioacoustically to *S. gimmeli* and *S. iharana* but not the direct sister group of these species, strongly divergent in mitochondrial and nuclear DNA, and possibly differing from *S. gimmeli* by a slightly shorter duration of inter-call intervals. Direct sister taxon of *S. huwei*, but distinguished from this species by longer call duration and shorter inter-call interval duration.

Description of the holotype. Specimen in a good state of preservation, a piece of its inner thigh removed as a tissue sample. Body round; head wider than long, narrower than body; snout slightly pointed in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, straight; loreal region slightly concave, slightly oblique; tympanum indistinct, about 70% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles distinct, single; outer metacarpal tubercle distinct, oval; inner metacarpal tubercle distinct, oval; fingers without webbing; first finger slightly reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly longer than second; finger tips not expanded into discs. Hind limbs slender; TIBL 44% of

SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, round; outer metatarsal tubercle absent; no webbing between toes; first toe reduced; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe slightly shorter than third; subarticular tubercles distinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is light brown. The back is flecked with dark brown, forming a faint X-shaped marking over the scapular region. Dorsolateral regions are gray. Dark spots are present in the inguinal region. The dorsal surface of the head is as the back. The nostril is dark brown. The lateral surface of the head is mottled dark brown, with cream spots behind the angle of the jaw. An almost black supratympanic stripe is present, extending toward the insertion of the arm. The flanks are mottled gray and dark brown with cream speckling. A dark brown spot is present above the insertion of the arm. The flank coloration fades rapidly to the cream of the trunk. The ventral abdomen is cream with brown flecks. The chin is browner, with some cream spots. The ventral thigh is as the trunk. The shank is ventrally brown with cream spots. The tarsus is ventrally as the shank. The sole of the foot is brown. Dorsally, the thigh is lighter brown than the dorsum, with large brown flecks. The posterodorsal and anterior surfaces of the thigh are brown flecked with cream. The shank, tarsus, and foot are as the thigh. The toes are flecked with light and dark brown. The cloacal region is dark brown. The arms are as the legs, without crossbands. The dorsomedial surface of the hand is mottled cream and brown. The fingers are brown with small cream stripes. The underside of the arm is as the ventral abdomen.

Color in life (holotype and variation). Dorsum russet medially, fading through copper to sand brown laterally, and over the flanks darkening to ebony. Lateral head ebony with a few copper flecks, including on the tympanum and anterior to the eye. A faint burnt umber chevron is present in the suprascapular region. A series of ebony spots are present on the flanks, with one above the insertion of the forelimb, and two on the mid-flank at different heights. The flank has also numerous bluish flecks, decreasing in density dorsally. The dorsal forelimb is proximally russet, becoming increasingly mottled with darker brown distally. The fingers are mottled sand brown and burnt umber, with a light annulus before each terminal phalange. The hindlimbs are as the dorsum with flecks of ebony, the toes are as the fingers. The ventral skin is translucent, light gray over the chin, plum over the anterior trunk with flecks of iridescent cream, becoming taupe over the posterior body and legs. The soles of the feet are burnt umber. The iris is dorsally copper, anteriorly and posteriorly rust red.

The paratypes have rather a different color pattern, with a sand brown dorsum and a central burnt-umber-demarcated teddybear-shaped marking of varying intensity, tan to taupe lateral coloration, and a creamy venter.



Fig. 39. *Stumpffia mamitika* sp. nov. from Ankarana National Park and Vohemar in life: (a–b) UADBA-A 60284 (ZCMV 13530); (c–d) UADBA-A 60285 (ZCMV 13531); (f–g) ZSM 3232/2012 (ZCMV 13528); (h–i) UABA-A 60278 (ZCMV 13529) from Vohemar; (e, j–k) holotype ZSM 3237/2012 (ZCMV 13524) from Ankarana National Park.

Variation. For variation in measurements among specimens see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. In some specimens the canthus rostralis is slightly concave, and the snout can be slightly rounded in lateral view. A high degree of variability was noted in the coloration of specimens in preservative; in the oldest specimen, ZSM 862/2003, the color is largely obscured and the whole dorsum is homogeneous brown; the flanks are still lighter; the lateral head is as the dorsum; cream flecks are absent from the posterior thigh. It also lacks dark spots above the tympanum, arms, and in the inguinal region. This discoloration may be associated with strong fixation

or age. In the other paratypes, ventral coloration is generally consistent with the holotype, although in some cases it has more or less brown. The dark dorsal markings of the holotype are more pronounced in several specimens. In these, a border is formed between the lighter brown head anterior to the eyes and the darker brown dorsal coloration. In a few specimens, the body is gray instead of brown. The inguinal spots are absent in two specimens (ZSM 862/2003 and ZSM 207/2004) but present in all others. The supratympanic marking and the spot above the insertion of the arm are absent from these specimens as well, and also from ZSM 3754/2005, but are present in all other specimens. In addition, a dark flank spot is

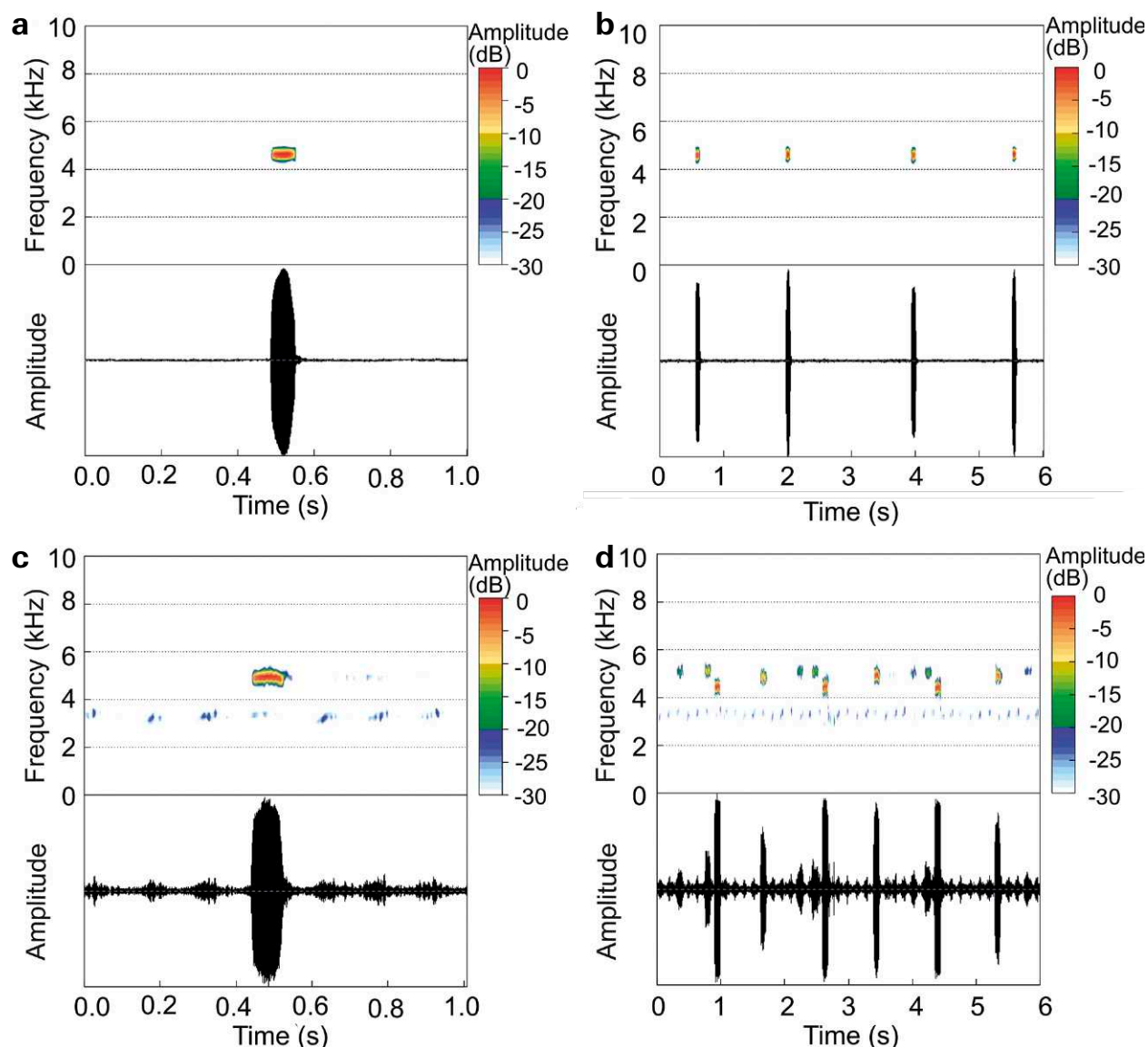


Fig. 40. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia mamitika* sp. nov. (1 s and 6 s duration section each): (a–b) Calls from Ankarana National Park recorded in 2016 from paratype ZSM 228/2016 (ZCMV 13616); (c–d) calls from near Andapa recorded in 1995 and tentatively assigned to this species.

present in ZSM 3234/2012 and ZSM 3235/2012, which is lacking from the holotype. A light vertebral stripe is present in ZSM 3235/2012. The forearm has a crossband in ZSM 3232–3235/2012. A crossband is present on the mid-shank of some specimens.

Etymology. The species name is a noun in apposition to the genus name, derived from the Malagasy word *mamitika*=sting, because the first author got stung several times by a wasp whilst she collected the specimens in Vohemar.

Distribution. This species is known from three localities: (1) Ankarana National Park (type locality), (2) Andrakata-Andapa, and (3) Vohemar. Specimens from Ankarana National Park are genetically slightly divergent from those originating from Vohemar and Andrakata-Andapa. The range encompasses elevations from 90–121 m above sea level.

Natural history. The species occurs in dry forest in Ankarana NP as well as in a mango plantation in Vohemar. In Ankarana NP, one calling male was found calling from a bush about 5 cm above the ground, and a second one was found hiding between branches. The specimens collected in Vohemar were found in dense leaf litter. All specimens were collected at night.

Call. The advertisement call of *S. mamitika* consists of a single short tonal note repeated in series at regular intervals (Fig. 40). Recordings are available for two different localities: (1) Recorded by A. Rakotoarison in January 2016 at the type locality, Ankarana National Park, from paratype ZSM 228/2016 (ZCMV 13616), with the following numerical parameters: call duration (= note duration) 68–84 ms (79 ± 7.3 ms; $N=4$), inter-call intervals 1335–1881 ms (1569 ± 281 ms; $N=3$), and a dominant frequency at 4565–4694 Hz (4619 ± 54 Hz, $N=4$). (2)



Fig. 41. *Stumpffia sorata* sp. nov. from Sorata forest in life: (a–b) specimen not assignable to a voucher; (c–d) ZSM 1643/2012 (FGZC 3618).

Recorded by F. Glaw on 19 February 1995 near Andapa (VENCES *et al.*, 2006: CD3, track 44, as *Stumpffia* sp.) and tentatively assigned to this species, with the following numerical parameters: call duration 90–124 ms (103 ± 9 ms; $N=20$), inter-call intervals 612–1510 ms (955 ± 264 ms; $N=19$), and a dominant frequency at 4435–5081 Hz (4749 ± 257 Hz, $N=20$). Call recordings obtained at Vohemar in 2012 suffer from several artifacts but are in principal identifiable as belonging to this species.

Stumpffia sorata sp. nov.

(Figures 41 and S103)

Holotype. ZSM 1644/2012 (FGZC 3621) (Figs. 12 g, S103 c–d), collected on 26 November 2012 on the Sorata Massif (S13.6817, E49.4411, 1339 m above sea level), Antsiranana Province, Madagascar by F. Glaw, O. Hawlitschek, F.M. Ratsoavina, A. Rakotoarison, T. Rajoafiarison, and A. Razafimanantsoa.

Paratypes. ZSM 1643/2012 (FGZC 3618), ZSM 1645/2012 (FGZC 3622), UADBA-A 60272 (FGZC 3617), UADBA-A 60273 (FGZC

3619), UADBA-A 60274 (FGZC 3620), and UADBA-A 60275 (FGZC 3623), all with same collecting data as holotype.

Diagnosis. One of several morphologically similar but partly sympatric *Stumpffia* species from northern Madagascar. This species has not been listed as candidate species in previous publications. (1) Small-sized species (SVL 15.6–16 mm); (2) manus with four fingers (first finger very slightly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.18–0.23, FOTL/SVL 0.63–0.65; (5) dorsum slightly to moderately granular; (6) dorsally taupe, occasionally with horizontal bands of tan or gray-brown, with numerous light spots. Several ebony markings on the flank, including one in the inguinal region. Ventral skin translucent with a dense pattern of flecks of cream on and posterior to the chest; the throat occasionally sooty or simply translucent. No red color ventrally, no sharp border between dorsal and lateral color.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by a longer call duration and less expressed length reduction of fingers; from *S. tetradactyla* by less expressed length reduction of first finger and especially first toe; from *S. analamaina*, *S. madagascariensis*, *S. pygmaea*, and *S. psologlossa* by larger body size.

The species is placed in clade A1 and within this clade it is morphologically rather similar to the majority of species, but is placed phylogenetically apart from most of them. It is part of a clade containing *S. larinki*, and is the direct sister taxon to a candidate species (*S. sp.* Ca7) from Marojejy. Although we lack bioacoustic data for this taxon, we here suggest its status as new species *S. sorata* due to its high genetic differentiation from its closest relative (pairwise 16S distance from *S. larinki*: 9.8%), as well as its granular dorsal skin (smooth in *S. larinki*) and ventral cream flecks and occasionally dark throat (more uniform in *S. larinki*). We are aware that this species hypothesis requires further testing in the future.

Description of the holotype. Specimen in a good state of preservation, left thigh muscle removed as a tissue sample. Body round; head slightly wider than long, narrower than body; snout rounded in dorsal view, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region slightly concave, slightly oblique; tympanum indistinct, about 55% of eye diameter; supratympanic fold not visible; tongue long, expanding slightly posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, indistinct; outer metacarpal tubercle small, oval; palmar tubercle round; inner metacarpal tubercle small, oval; fingers without webbing; first finger slightly reduced; relative length of fingers $1 < 2 = 4 < 3$, fourth finger subequal in length to second; finger tips not or weakly expanded into discs. Hind limbs slender; TIBL 44% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, round; outer metatarsal tubercle absent; no webbing between toes; first toe reduced; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third; subarticular tubercles indistinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is metallic silver. Darker silver areas are present at the posterior end the dorsum, just behind the scapular region, and behind the eyes. Circular diffuse black markings are present behind the scapular region. An oblong dark brown marking is present in the inguinal region. The dorsal surface of the head is as the back. The nostril is surrounded by brown. The lateral surface of the head is as the dorsum. A dark brown supratympanic marking is present, not exceeding the tympanum poste-

riorly. The flanks are as the dorsum. A large dark brown spot is present dorsally and posteriorly to the insertion of the arm. This is followed by a series of smaller dark brown spots. These form a border between the dorsal and ventral coloration. The ventral trunk is cream flecked with brown, most intensely over the pectoral girdle. The chin is as the ventral trunk. The ventral thigh is brown spotted with cream. The shank is ventrally brown with a few cream flecks. The tarsus is ventrally as the shank. The sole of the foot is brown. Dorsally, the thigh is dark silver like the posterior dorsum. The posterodorsal surface of the thigh is brown with cream spots. The shank is as the thigh, with a dark crossband midway along its length. The tarsus is as the shank but lacks crossbands. The exterior of the foot is as the tarsus, with a single dark spot; the medial foot is brown with cream flecks. The toes are mottled gray and cream. The cloacal region is dark brown. The arms are as the dorsum. A dark crossband is present on the lower arm. The dorsomedial surface of the hand is mottled gray and cream. The fingers have small gray and cream stripes. The underside of the arm is as the ventral trunk.

Color in life (paratype). Dorsal base color taupe, with numerous cream to tan spots over the whole dorsum. Wide horizontal bands of tan and gray-brown can be present on the dorsum. A large ebony marking bordered with a thin line of cream can be present in the inguinal region. Further cream-bordered ebony markings are present around the nostril, below the eye, in the posterodorsal part of the tympanum, and in two spots of varying shape on the flanks, which are continuous with the dorsum. The dorsal forelimb is bisque, with a sooty crossband on the forearm. The toes are bisque with a whitish annulus before each terminal phalange. The dorsal hindlimb is as the dorsum, without crossbands. An ebony marking can be present on top of the foot. The throat skin can be translucent and mottled with lighter flecks, or sooty with weak lemon flecks. The ventral trunk's skin is translucent, with cream flecks or speckles mostly concentrated on and posterior to the pectoral girdle. The ventral legs have faint cream mottling.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology, although two paratypes (ZSM 1643/2012 and 1645/2012) have pointed snouts in dorsal and lateral view. An intermediate degree of variability was noted in the coloration of specimens; ZSM 1643/2012 is similar to the holotype in pattern, but brown colors prevail instead of silver, with slightly fewer dark brown markings; ZSM 1645/2012 is dorsally pinkish, with the inguinal and lateral spots and brown cloacal region and shank crossband of the other two specimens, more black spots on the dorsum, one on the lower back, another almost chevron shaped over the scapular region, and a few spots on the posterior head. The legs of this specimen have more dark brown spots than the holotype, and are also pinkish in color.

Etymology. The species name is a noun in apposition to the genus name, and refers to the type locality of the new species, the Sorata forest in north-eastern Madagascar.

Distribution. This species is known only from its type locality in the Sorata Massif.

Call. Unknown.

***Stumpffia yanniki* sp. nov.**

(Figures 42 and S104)

Holotype. ZSM 629/2014 (DRV 6413) (Fig. 12), collected on 29 June 2010 in a forest fragment beside Route Nationale 31, near the border between the Bealanana and Antsohihy Districts (S14.72145, E48.56272, 1187 m above sea level), Mahajanga Province, Madagascar by M. Vences, D.R. Vieites, R.D. Randrianiana, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, F. Randrianasolo, and T. Rajoafiarison.

Paratypes. ZSM 1825/2010 (ZCMV 12600), UADBA-A 60888 (ZCMV 12601), UADBA 60887 (ZCMV 12599), and UADBA (DRV 6412), all with same collecting data as holotype.

Diagnosis. A poorly known species from north-western Madagascar, previously listed as *Stumpffia* sp. 31 in Klages *et al.* (2013). (1) Small-sized species (SVL 9.8–10.6 mm); (2) manus with four fingers (first finger moderately reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.18–0.19, FOTL/SVL 0.62–0.65; (5) dorsum smooth; (6) dorsally with a large and well-contrasted central dark teddybear shaped mid-dorsal marking, bordered on the head and dorsolateral body by lighter coloration. Ventrally grayish with very little light mottling in preservation. No red color ventrally, no sharp border between dorsal and lateral color.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by distinctly smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by less expressed length reduction of fingers; from *S. tetradactyla* by somewhat lower degree of length reduction of first toe.

The new species is phylogenetically placed in clade A2, and differs from all species in clade A1 (*S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. mamitika*, *S. maledicta*, *S. sorata*) by slightly smaller body size. Within clade A2 *S. yanniki* is distinguished from *S. madagascariensis* by the lack of a sharp border between dorsal and lateral color, and from *S. psologlossa* by a completely smooth dorsal skin. It is morphologically most similar to *S. pygmaea* and *S. analamaina*, but strongly divergent in mitochondrial and nuclear DNA from these species. *Stumpffia yanniki* is phylogenetically sister to *S. analamaina*, but appears to differ slightly by having relatively shorter hands and feet (KLAGES *et al.*, 2013) and, despite geographical proximity of their ranges, these two species are genetically highly divergent.



Fig. 42. *Stumpffia yanniki* sp. nov. from a forest fragment beside Route Nationale 31, near the border between the Bealanana and Antsohihy Districts in life; paratype ZSM 1825/2010 (ZCMV 12600).

Description of the holotype. Specimen in a good state of preservation, left thigh muscle removed as a tissue sample. Jaw broken. Body stocky; head wider than long, narrower than body; snout rounded in dorsal view, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct, straight; loreal region concave, oblique; tympanum indistinct, about 80% of eye diameter; supratympanic fold absent; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slender; subarticular tubercles indistinct, single; outer metacarpal tubercle not recognizable; inner metacarpal tubercle small, round; fingers without webbing; first finger reduced, second and fourth fingers slightly reduced; relative length of fingers $1 < 2 = 4 < 3$, fourth finger subequal in length to second; finger tips not expanded into discs. Hindlimbs slender; TIBL 43% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, round; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced; toe tips not expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe slightly shorter than third; subarticular tubercles distinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After five years in 70% ethanol, the dorsum is light brown, with a dark brown broad central stripe, and a cream vertebral stripe. A dark spot is present in the inguinal region. The dorsal surface of the head is as the back. The nostril is dark brown. The lateral surface of the head is dark brown. A dark stripe divides dorsal and flank coloration, running forward to the eye. Below it, the flanks are cream reticulated with brown. Flank coloration extends onto the ventral trunk. The chin is plain cream. The ventral thigh is as the chin. The shank is ventrally as the thigh. The tarsus is ventrally as the shank. The sole of the foot is dark brown. Dor-

sally, the thigh is light brown with a dark brown oblique crossband. The posterodorsal surface of the thigh has a white line running its length, below which it is brown with white dots. The shank is light brown with an oblique crossband. The tarsus is as the shank with an oblique crossband. The foot is as the shank, with a dark spot on its external face. The toes are brown with light brown flecks. The cloacal region is dark brown. The arms are as the legs. A dark crossband is present on the forearm. The whole hand is light brown. The underside of the arm is as the chin.

Color in life (paratype). The only existing photo of a specimen of this species in life (Fig. 42) has a distinct purple tinge to it. This may be a result of chromatic aberration, and therefore colors are not named here in detail, but rather the overall pattern of the specimen is described: A central, dark, teddybear-like patch is present on the mid-dorsum, bordered on the anterior head and dorsolateral body by lighter coloration. The lateral head and flank are continuous, darker coloration, with a black marking posterior to the insertion of the forelimb. The dorsal forelimb is brownish mottled with black and gray, as is the hand. The dorsal hindlimb is continuous with the mid-dorsal coloration, but more mottled. The ventral color in life is not known.

Variation. For variation in measurements among specimens, see Table 3. The paratype ZSM 1825/2010 is more or less identical to the holotype in morphology, but differs strongly in coloration from the holotype. The dorsal color of this specimen is light brown, laterally gray; the dorsum is flecked with dark brown; inguinal spots are present as in the holotype; the lateral surface of the body is as in the holotype, but more solidly brown than reticulated; the whole venter is more cream than the holotype; the thighs lack the white stripe, but otherwise the leg coloration is similar, albeit lighter; the arm is also similar.

Etymology. The species name is a patronym, dedicated by the first author to her “honorary nephew” Yannik Hill, to introduce him to the herpetofauna of Madagascar.

Distribution. The species is known only from its type locality, a forest fragment beside Route Nationale 31, near the border between the Bealanana and Antsohihy Districts.

Natural history. Specimens were collected during the day, from the leaf litter in a rainforest fragment, relatively close to a stream.

Call. Unknown.

2. Large-sized species of clade A

This section contains a clade of four *Stumpffia* endemic to small ranges in the North of Madagascar that form

a monophyletic group (subclade A3), sister to all other species in clade A. Three of the species in subclade A3 are the largest known species of the genus. These large-sized *Stumpffia* species have no digital reduction and have distinctly enlarged discs on terminal phalanges of fingers and toes, and they appear to be specialized to live in karstic environments, particularly in crevices and caves. They may be superficially confused with some species of *Rhombophryne*, but can be distinguished from all morphologically similar species of that genus (e.g. *R. minuta*) by the absence of vomerine teeth (vs. presence in *Rhombophryne*).

Stumpffia be KÖHLER, VENCES, D’CRUZE & GLAW, 2010

(Figure 43)

Name-bearing type. Holotype ZSM 1668/2008 (FGZC 1612) (Fig. 43 a–b), from “the edge of the river below the ‘Point de Vue Petit Tsingy’, S 2.95, E 49.116, c. 90 m a.s.l., Ankarana Special Reserve, Antsiranana Province, northern Madagascar” according to the original description.

Identity and diagnosis. This species has been listed as *Stumpffia* sp. 23 in VIEITES *et al.* (2009) (not included in GLAW & VENCES, 2007 and WOLLENBERG *et al.*, 2008). A large species of *Stumpffia* known only from the karstic Ankarana Massif. (1) Large-sized species (female SVL 25.2 mm); (2) manus with four fingers (none of them reduced in length) and pes with five toes (none of them reduced in length); (3) terminal phalanges of fingers and toes with enlarged discs; (4) relative hand and foot length, HAL/SVL 0.3, FOTL/SVL 0.6; (5) dorsum smooth; (6) light brown with indistinct pattern. Concealed surfaces of hindlimbs with orange-red color. Ventrally uniformly grayish. Juveniles apparently with different coloration, blackish with many small white dots and brown patches on dorsum; (7) tonal single-note call of 170–179 ms duration, emitted in regular series (inter-call intervals 784–1053 ms).

Distinguished from *S. psologlossa*, *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. grandis*, *S. huwei*, *S. iharana*, *S. larinki*, *S. madagascariensis*, *S. maledicta*, *S. mami-tika*, *S. miery*, *S. pygmaea*, *S. sorata*, *S. tetradactyla*, *S. tridactyla*, and *S. yanniki* by distinct red color on concealed parts of hindlimbs. From the species listed, and from *S. kibomena* and *S. roseifemoralis* by larger discs on fingers, and lack of digital length reduction. From all these species except for *S. grandis*, *S. kibomena*, and *S. roseifemoralis* by larger body size.

Specimens examined. Holotype ZSM 1668/2008 (FGZC 1612), collected on 12 February 2008 from the edge of the river below the ‘Point de Vue Petit Tsingy’ in Ankarana National Park (S12.95 E49.1166, 90 m a.s.l.) by Jacques, N. D’Cruze, M. Franzen, F. Glaw, and J. Köhler; paratype ZSM 1664/2008 (FGZC 1643), juvenile, collected on 13 February 2008, 20 m west of holotype locality by N. D’Cruze, M. Franzen, F. Glaw, and J. Köhler.

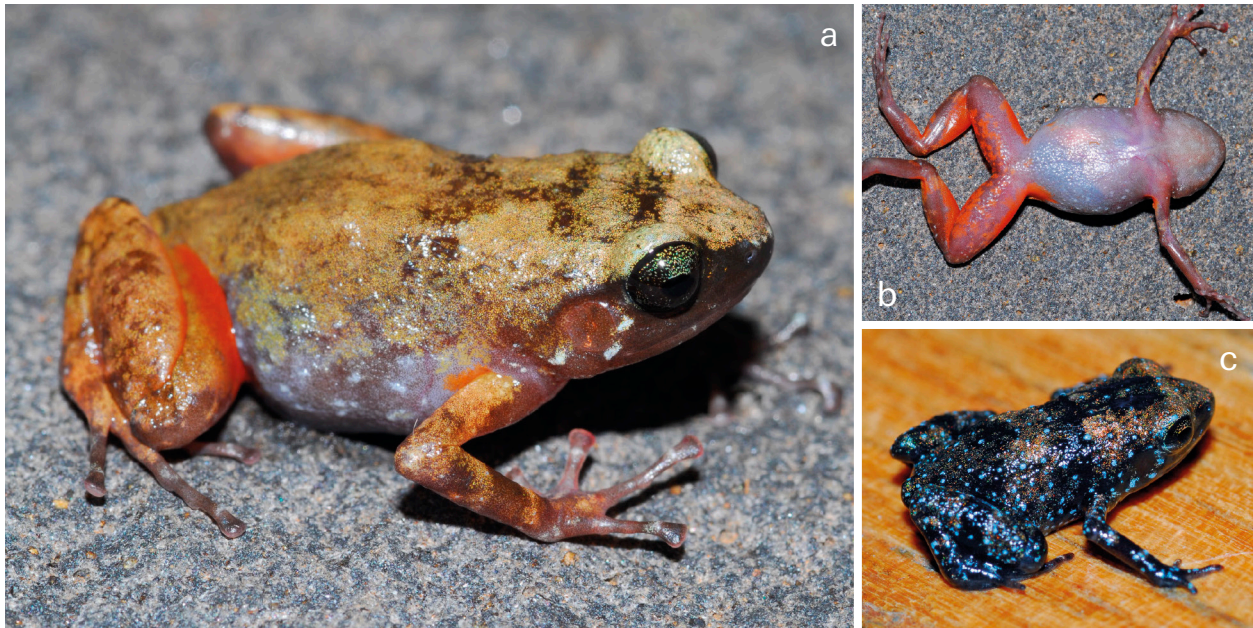


Fig. 43. *Stumpffia be* from Ankarana National Park in life: (a–b) holotype ZSM 1668/2008 (FGZC 1612); (c) juvenile paratype, ZSM 1664/2008 (FGZC 1643).

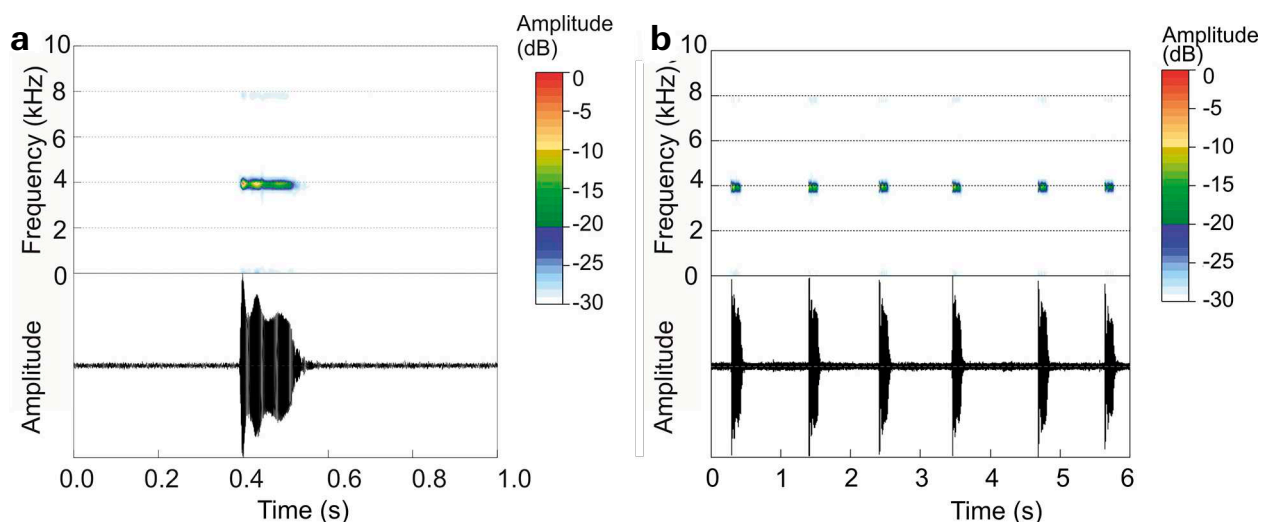


Fig. 44. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia be*, based on the recording of LATTENKAMP *et al.* (2016). (a) 1 s duration section; (b) 6 s duration section.

Distribution. This species is known from its type locality at the eastern side of Ankarana National Park.

Natural history. Specimens were found on rocks and vegetation 50 cm above the ground in karstic limestone areas; one specimen contained remains of large black ants in its stomach (KÖHLER *et al.*, 2010). A male was observed calling from a crack in a limestone rock in a riverbed (LATTENKAMP *et al.*, 2016).

Call. The advertisement call has been described by LATTENKAMP *et al.* (2016). It consists of a single short tonal note repeated in series at regular intervals (Fig. 44). Call parameters as taken from this publication were as follows: call duration (= note duration) 170–179 ms

(174 ± 3 ms; $N = 7$), inter-call interval 784–1053 ms (919 ± 84 ms; $N = 6$), dominant frequency 3899–3928 Hz (3912 ± 11 Hz; $N = 7$).

Stumpffia hara KÖHLER, VENCES, D’CRUZE & GLAW, 2010

(Figure 45)

Name-bearing type. Holotype ZSM 1666/2008 (FGZC 1813) (Fig. 45 a–b), from “a small creek on the western flank of Nosy Hara, $12^{\circ}14'40''$ S, $49^{\circ}00'30''$ E [S12.24444, E49.00833], 20 m a.s.l., Antsiranana Province, northern Madagascar” according to the original description.



Fig. 45. *Stumpffia hara* from Nosy Hara in life: (a–b) holotype ZSM 1666/2008 (FGZC 1813); (c–d) paratype ZSM 2195/2007 (FGZC 1293).

Identity and diagnosis. This species has been listed as *Stumpffia* sp. 22 in VIEITES *et al.* (2009) (not included in GLAW & VENCES, 2007 and WOLLENBERG *et al.*, 2008). A large-sized species of *Stumpffia* known only from the island Nosy Hara. (1) Large-sized species (female SVL 22.4–25.6 mm); (2) manus with four fingers (none of them reduced in length) and pes with five toes (none of them reduced in length); (3) terminal phalanges of fingers and toes with enlarged discs; (4) relative hand and foot length, HAL/SVL 0.2–0.3, FOTL/SVL 0.5–0.6; (5) dorsum smooth; (6) light brown with indistinct pattern. Ventrally grayish with numerous small whitish dots.

Distinguished from *S. psologlossa*, *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. grandis*, *S. huwei*, *S. iharana*, *S. kibomena*, *S. larinki*, *S. madagascariensis*, *S. maledicta*, *S. mamitika*, *S. miery*, *S. pygmaea*, *S. roseifemoralis*, *S. sorata*, *S. tetradactyla*, *S. tridactyla*, and *S. yanniki* by larger discs on fingers, and lack of digital length reduction; and from all these species except for *S. grandis*, *S. kibomena* and *S. roseifemoralis* by larger body size. The species is included in clade A3, and therefore not closely related to any of the previously mentioned species. Distinguished from *S. be* by the lack of red color on concealed surfaces of hindlimbs.

Specimens examined. Holotype ZSM 1666/2008 (FGZC 1813), collected on 22 February 2008 from a small creek on the west-

ern flank of Nosy Hara, Antsiranana (S12.2444, E49.175, 20 m a.s.l.), by F. Glaw and J. Köhler; paratype ZSM 1665/2008 (FGZC 1801), same collecting data as holotype; paratypes ZSM 2195/2007 (FGZC 1293), ZSM 2196/2007 (FGZC 1296), and UADBA-A (FGZC 1294–1295) collected on 7 March 2007 from a cave entrance on the western flank of Nosy Hara, Antsiranana (S12.2425, E49.0088, 9 m a.s.l., by H. Enting, F. Glaw, and J. Köhler.

Distribution. This species is known only from its type locality at the western slope of Nosy Hara.

Natural History. Found in forest along a small creek and inside and at the entrance of a cave. A large number of arthropods of considerable size were found in the stomach of one specimen (KÖHLER *et al.*, 2010).

Call. Unknown.

Stumpffia megsoni KÖHLER, VENCES, D'CRUZE & GLAW, 2010

(Figure 46)

Name-bearing type. Holotype ZSM 1663/2008 (FGZC 1951) (Fig. 46), from “Ampombofofo, from a small cave, 12°05'58”S, 49°20'20”E, 20 m a.s.l., Antsiranana Province, northern Madagascar” according to the original description.

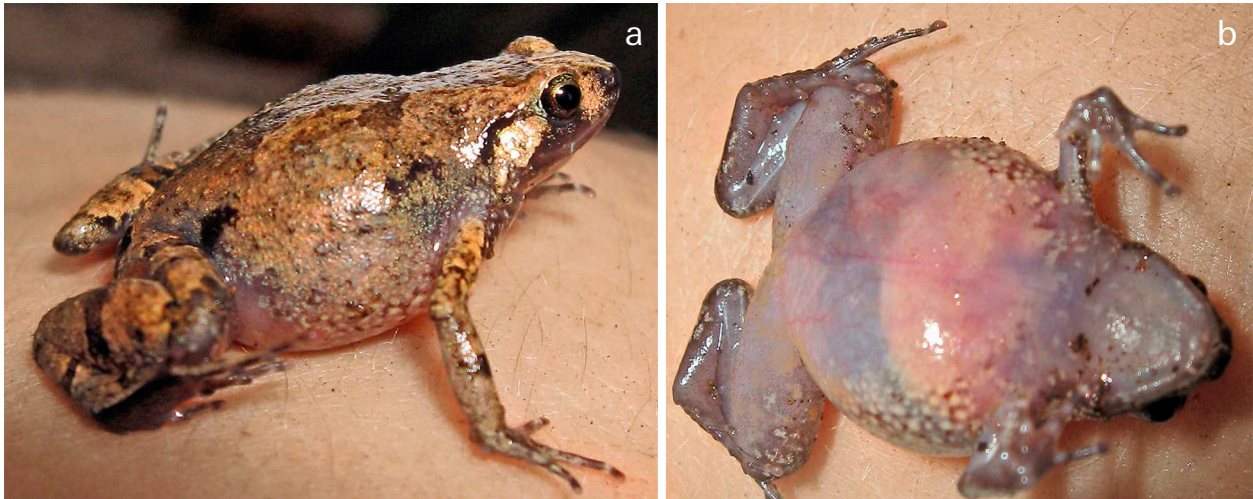


Fig. 46. *Stumpffia megsoni* holotype ZSM 1663/2008 (FGZC 1951) from Ampombofofo in life: (a) dorsolateral and (b) ventral view.

Identity and diagnosis. This species has been listed as *Stumpffia* sp. 21 in VIEITES *et al.* (2009) (not included in GLAW & VENCES, 2007 and WOLLENBERG *et al.*, 2008). A moderately large-sized species of *Stumpffia*, possibly less specialized to karstic environments and caves than the other three species in this subclade. (1) Moderately large-sized species (female SVL 21.0–22.7 mm); (2) manus with four fingers (none of them reduced in length) and pes with five toes (none of them reduced in length); (3) terminal phalanges of fingers and toes with only very slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.2–3, FOTL/SVL 0.7; (5) dorsum smooth with small tubercles; (6) light brown with indistinct pattern. Ventrally uniformly grayish without pattern.

Distinguished from *S. psologlossa*, *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. madagascariensis*, *S. maledicta*, *S. mamitika*, *S. miery*, *S. pygmaea*, *S. sorata*, *S. tetradactyla*, *S. tridactyla*, and *S. yanniki* by larger body size, and from many of these species by a lower degree of digital length reduction; from *S. kibomena*, and *S. roseifemoralis* by the lack of red color on ventral surfaces; from *S. grandis* by lack of distinct black-light gray/blue marbling ventrally. The species is included in clade A3, and therefore not closely related to any of the previously mentioned species. Distinguished from *S. be* by the lack of red color on concealed surfaces of hindlimbs; and from *S. hara* and *S. be* by smaller terminal discs on fingers and toes.

Specimens examined. Holotype ZSM 1663/2008 (FGZC 1951), collected on 23 February 2007 at Ampombofofo from a small cave (S12.0994, E49.3388, 20 m a.s.l.) by S. Megson; paratype ZSM 1662/2008 (FGZC 1951), collected on 21 November 2006 at the same locality as holotype, by S. Megson.

Distribution. This species is known from its type locality Ampombofofo in northernmost Madagascar.

Natural history. Specimens were found on walls in a small limestone cave on a steep slope, close to primary forest and a stream, but also in secondary habitat. Body

inflation and death-feigning were observed as probable antipredator mechanisms (KÖHLER *et al.*, 2010).

Call. Unknown.

***Stumpffia staffordi* KÖHLER, VENCES, D'CRUZE & GLAW, 2010**

(Figure 47)

Name-bearing type. Holotype ZSM 1667/2008 (FGZC 1674) (Fig. 47 a, b, c), from a “large cave, 12°19'S, 49°20', c. 260 m a.s.l., Montagne des Français, Antsiranana Province, northern Madagascar” according to the original description.

Identity and diagnosis. This species has been listed as *Stumpffia* sp. 24 in VIEITES *et al.* (2009) (not included in GLAW & VENCES, 2007 and WOLLENBERG *et al.*, 2008). The largest of all *Stumpffia*, known only from the karstic massif of Montagne des Français. (1) Large-sized species (male SVL 27.0–27.9 mm); (2) manus with four fingers (none of them reduced in length) and pes with five toes (none of them reduced in length); (3) terminal phalanges of fingers and toes with enlarged discs; (4) relative hand and foot length, HAL/SVL 0.3, FOTL/SVL 0.6; (5) dorsum smooth with a few weakly expressed tubercles; (6) reddish brown or grayish brown with indistinct pattern. Ventrally grayish with some dark mottling particularly on the throat.

Distinguished from *S. psologlossa*, *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. madagascariensis*, *S. maledicta*, *S. mamitika*, *S. miery*, *S. pygmaea*, *S. sorata*, *S. tetradactyla*, *S. tridactyla*, and *S. yanniki* by larger body size, larger discs on fingers, and from most of these species by the lack of digital length reduction. The species is included in clade A3, and thus not closely related to any of the previously mentioned species. Distinguished from *S. be* by the lack of red color on concealed surfaces of hindlimbs, from *S. megsoni* by

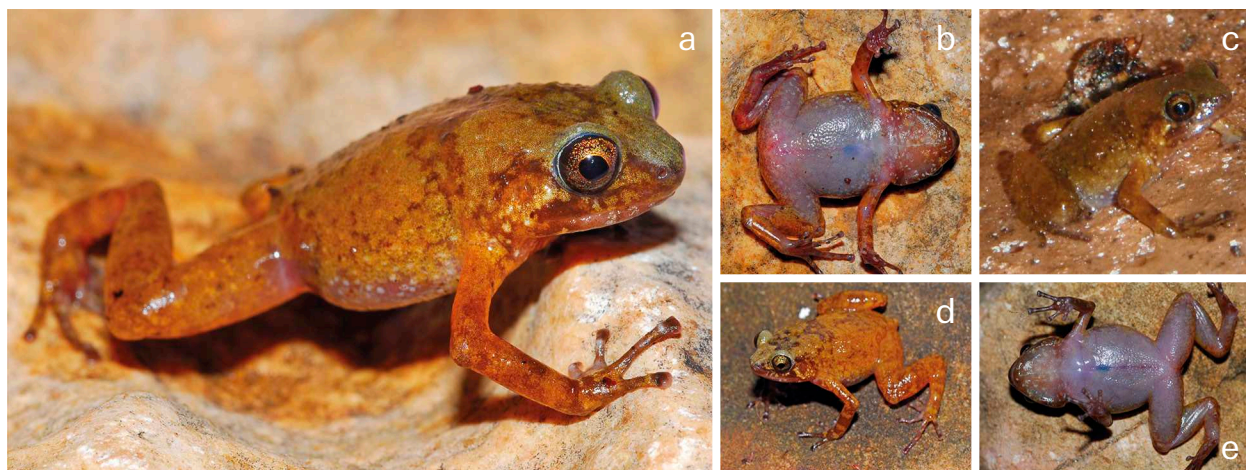


Fig. 47. *Stumpffia staffordi* from Montagne des Français in life: (a–c) holotype, ZSM 1667/2008 (FGZC 1674); (d–e) paratype UADBA (FGZC 1601).

larger body size, and from *S. hara* by the lack of whitish spotting on venter.

Specimens examined. Holotype ZSM 1667/2008 (FGZC 1674), collected on 16 February 2008 on Montagne des Français (S12.3166, E49.333, 260 m a.s.l.) by N. D’Cruze, M. Franzen, F. Glaw, J. Köhler, and Z. Nagy; paratype UADBA (FGZC 1601), collected on 11 February 2008 at same locality as holotype by N. D’Cruze.

Distribution. This species is known only from its type locality on Montagne des Français.

Natural history. Specimens were found deep inside a karstic cave, with the holotype specimen perching at the edge of a small puddle (Fig. 47c) (KÖHLER *et al.*, 2010).

Call. Advertisement call unknown. The distress call has been described by KÖHLER *et al.* (2010).

3. Small-sized or miniaturized species of clades B and D

For convenience, we include in this cluster several species of small-sized *Stumpffia* that belong to two distinct clades, B and D (Fig. 3). Most of these species are characterized by distinct digital reduction, yet clades B and D do not appear to be sister groups, and clade B also includes one large-sized species described in the next section.

Stumpffia miery NDRIANTSOA, RIEMANN, VENCES, KLAGES, RAMINOSOA, RÖDEL & GLOS, 2013

(Figure 48)

Name-bearing type. Holotype ZMB 77453 (#_611) (Fig. 48 a, d) from “Madagascar, Ranomafana region, Ambolo forest fragment, S 21.2625, E 47.5068’ (site name: FFst04), app. 660 m a.s.l., near a small stream” according to the original description.

Identity and diagnosis. *Stumpffia miery* is a small-sized species included in clade B. Its occurrence in the southern central east at comparatively low elevations is striking, as only one other species (*S. nigrorubra* **sp. nov.**) is known from this area. (1) Small-sized species (SVL 12.0–14.6 mm); (2) manus with four fingers (first finger very strongly reduced in length; also second and fourth fingers short) and pes with five toes (first toe strongly reduced in length, almost rudimentary); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.15, FOTL/SVL 0.5–0.6; (5) dorsum smooth or slightly granular; (6) light brown to reddish brown dorsal color, typically with a distinct dark brown teddybear shaped central marking, and often additional dark patches laterally. Ventrally gray with dark gray mottling but without contrasted ventral coloration, red color elements on ventral side, or sharp continuous color border between dorsum and flanks; (7) regularly repeated short single-note chirp call.

Distinguished from *S. be*, *S. grandis*, *S. hara*, *S. kibomena*, *S. megsoni*, *S. roseifemoralis*, and *S. staffordi* by distinctly smaller body size; from *S. tridactyla* by a lower degree of digital reduction; from *S. tetradactyla* by more expressed length reduction of first finger and somewhat less expressed length reduction of first toe. The stronger first toe reduction also distinguishes *S. miery* from all species in clade A, including the roughly similar-sized or smaller sized *S. psologlossa*, *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. madagascariensis*, *S. maledicta*, *S. mamitika*, *S. miery*, *S. pygmaea*, *S. sorata*, *S. tetradactyla*, *S. tridactyla*, and *S. yaniki*. Further distinguished from most of the species in clade A (all for which calls are known) by shorter call duration.

Specimens examined. Holotype ZMB 77453 (#_611) collected on 1 March 2011 at Ambolo forest fragment (S21.2625, E47.5068, 660 m a.s.l.) by J.C. Riemann and A. Telo; paratype ZMB 77454 (#_677), collected on 10 March 2011 at Andalangina, near Ifanadiana (S21.2970, E47.5995, 515 m a.s.l.) by J.C. Riemann and A. Telo; paratype ZMB 77455 (#_768) collected on 4 April 2011 at



Fig. 48. Dorsolateral and ventral views of *Stumpffia miery* from the Ranomafana region, southeastern Madagascar, in life: (a, d) male holotype ZMB 77453; (c) male paratype ZMB 77454; (e) male paratype ZSM 2447/2007.

Ambolo forest fragment (S21.2636, E47.509, 640 m a.s.l.) by J.C. Riemann and A. Telo; paratype ZSM 121/2011 (#_804) collected on 6 April 2011 in a coffee and banana plantation in Andalangina (S21.2993S, E47.5976, 450 m a.s.l.) by J.C. Riemann and A. Telo;

paratype ZMB 77456 (#_09) collected on 9 March 2010 at Ambolo forest fragment (S21.2635, E47.5092, 670 m a.s.l.) by S.H. Ndrisantsoa, J.C. Riemann, J. Solo, A. Telo, and M.-O. Rödel; paratype UADBA-A 62120 (#_621) collected on 2 March 2011 in forest ca.

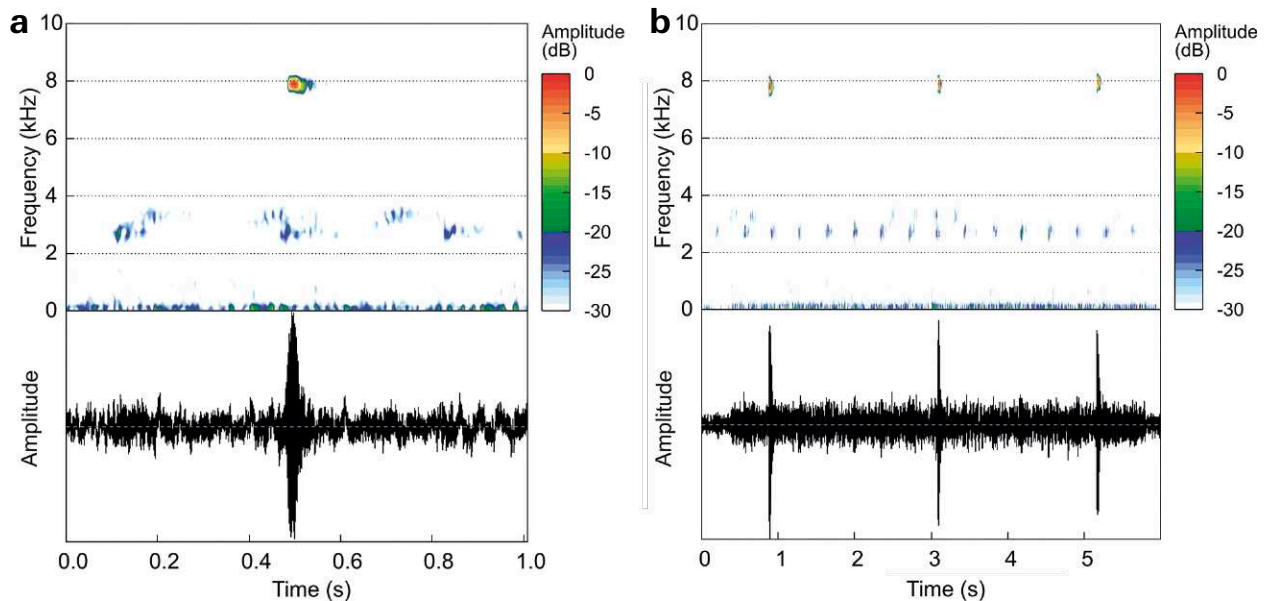


Fig. 49. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia miery* from Ambohitsara (paratype ZSM 244/2007), recorded in 2007. (a) 1 s duration section; (b) 6 s duration section.

150 m to next stream (S21.2624, E47.5074, 680 m a.s.l.) by J.C. Riemann and A. Telo; paratype ZSM 2447/2007 (ZCMV 5868) collected on 3 March 2007 at Ambohitsara (S21.3571 E47.8153, 294 m a.s.l.) by M. Vences; paratype UADBA-A 62121 (# 770) collected on 4 April 2011 at Ambolo forest fragment (S21.2639, E47.5092, 700 m a.s.l.) by J.C. Riemann and A. Telo; paratype UADBA-A 62122 (# 1393) collected on 2 February 2011 at Andalangina (S21.2984, E47.6033, 490 m a.s.l.) by S.H. Ndriantsoa and J. Solo; paratype UADBA-A 62124 (# 1738) collected on 10 March 2011 in a coffee and banana plantation in Andalangina (S21.2993, E47.5976, 450 m a.s.l.) by J.C. Riemann and A. Telo.

Variation. Although our 16S tree (Fig. 3) only contains a single specimen of *S. miery*, DNA sequences of another segment of the 16S gene are available from three additional specimens (see NDRIANTSOA *et al.*, 2013).

Distribution. This species is known from three localities in the Ranomafana region: (1) Ambolo forest fragment (type locality), (2) Andalangina, near Ifanadiana, and (3) Ambohitsara.

Natural history. Summarized from NDRIANTSOA *et al.* (2013). Calling males were found in the leaf litter of rainforest. Specimens were also collected in degraded forest fragments and a mixed coffee banana plantation. Calling males were heard in the afternoon but also at night, usually from rather hidden positions in the leaf litter.

Call. The advertisement call of *S. miery* consists of a very short single note repeated in series at regular intervals (Fig. 49). Numerical call parameters for the male holotype (ZMB 77453) recorded on 1 March 2011, at 20.5°C, in Ambolo forest fragment are as follows (according to NDRIANTSOA *et al.*, 2013): call duration (= note duration) 51–88 ms (73 ± 12 , $N=10$), inter-call intervals 2679–4247 ms (3102 ± 456 , $N=10$), and a dominant frequency at 7751–8225 Hz (8057 ± 136.9 , $N=10$). For

the paratype (ZSM 2447/2007) recorded on 3 March 2007 in the rainforest near Ambohitsara, at an estimated temperature of 25°C, parameters are as follows: call duration 40–53 ms (47 ± 5 , $N=10$), inter-call intervals 1850–2610 ms (2105 ± 243 , $N=10$), and a dominant frequency at 7708–8010 Hz (7877 ± 109 , $N=10$).

Stumpffia tridactyla GUIBÉ, 1975

(Figures 50 and S105)

Name-bearing type. Holotype MNHN 1975.25 from “Massif du Marojézy” according to the original description.

Identity and diagnosis. *Stumpffia tridactyla* is a highly miniaturized species with strong digital reduction, known only from the Marojezy Massif in north-eastern Madagascar, that forms with its sister species (described below as *S. contumelia* **sp. nov.**) clade D, which is phylogenetically placed sister to all other *Stumpffia*. (1) Miniaturized species (SVL 8.6–10.6 mm); (2) manus with one finger only (first finger not visible; second and fourth fingers reduced to small knobs; third finger broadened to a triangular shape) and pes with three toes (first toe not recognizable, second toe reduced to a small knob); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length HAL/SVL 0.14–0.16, FOTL/SVL 0.55–0.60; (5) dorsum smooth; (6) reddish brown dorsally, with distinct color border to the dark brown flanks. Ventrally without contrasted ventral coloration or red color elements; (7) regularly repeated short single-note frequency-modulated whistle call.

Distinguished from all nominal species of *Stumpffia* by stronger digital reduction with only one finger and three toes recognizable (shared with the new spe-



Fig. 50. *Stumpffia tridactyla* from Marojejy National Park in life: (a–b) ZSM 527/2016 (ZCMV 15282) from Marojejy, high altitude; (c–d) uncatalogued specimen from Marojejy, high altitude; (e) ZSM 382/2005 (FGZC 2844) from Marojejy, Camp Simpona; (f–g) female specimen ZSM 526/2016 (ZCMV 15284) from Marojejy, Camp Simpona.

cies *S. contumelia* **sp. nov.** and *S. obscoena* **sp. nov.** described below). Also distinguished from most other *Stumpffia* by its frequency-modulated call. Phylogenetically the species is sister to the new species *S. contumelia* **sp. nov.**, the only other known representative of clade D; for its differentiation from that species, see its description below.

Specimens examined. Holotype MNHN 1975.25, and paratypes MNHN 1975.26–29, all collected from the Marojejy Massif by C. Blanc. Referred specimens: ZSM 382/2005 (FGZC 2844) collected on 17 February 2005 from Camp Simpona, Marojejy National Park (S14.4886 E49.9002, 1326 m a.s.l.), by F. Glaw, R.D. Randrianiana and M. Vences; ZSM 526/2016 (ZCMV 15284) and ZCMV 15285 collected 17–20 November 2016 from Camp Simpona, Marojejy National Park (S14.4499, E49.7433, 1326 m a.s.l.) by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences. ZSM 528/2016 (ZCMV 15290) collected 19 November 2016 from a high-elevation site in Marojejy National Park (S14.44064, E49.73995, 1573 m a.s.l.) by M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences. ZCMV 15227, ZSM 527/2016 (ZCMV 15282), and ZSM 525/2016 (ZCMV 15283) collected 19 November 2016

from a high-elevation site in Marojejy National Park (S14.44755, E49.73365, 2026 m a.s.l.) by M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences.

Distribution. This species is known only from Marojejy National Park. Elevational range based on voucher specimens extends from 1326–2026 m a.s.l., but according to our observations in 2016, calls can be heard from distinctly lower and higher elevations, probably ranging at least from ca. 1000–2100 m a.s.l.

Natural history. At Marojejy, calling specimens were heard from the leaf litter in primary rainforest, during the day. The specimens were deeply hidden in the leaf litter and exceedingly difficult to find. In 2016, calls were heard from rainforest as well as from shrubs and vegetation mats including grasses above the treeline.

Call. The advertisement call very probably emitted by ZSM 382/2005 (specimen not seen calling) consists of a single, short, pulsatile, high-pitched, and frequency-

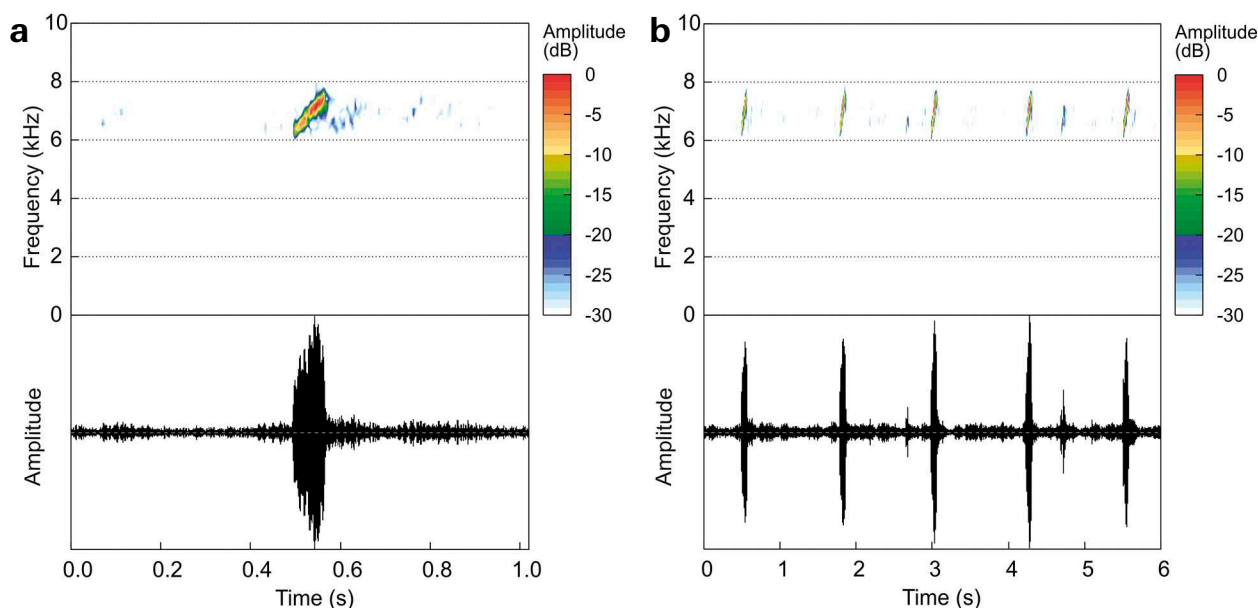


Fig. 51. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia tridactyla* (probably from ZSM 382/2005) from Marojejy National Park: (a) 1 s duration section; (b) 6 s duration section.

modulated note repeated in series at regular intervals (Fig. 51). Calls recorded by M. Vences and F. Glaw on 16 February 2005 at Marojejy National Park, near camp Simpona, at 21.5°C air temperature (VENCES *et al.*, 2006: CD3, track 38, cut 1) are as follows: call duration (= note duration) 101–198 ms (132 ± 23 ms; $N=18$), inter-call intervals 969–1121 ms (1012 ± 39 ms; $N=17$), and a dominant frequency at 6933–7835 Hz (7244 ± 200 Hz, $N=18$). Within notes, distinct frequency modulation is evident, with a steep increase in dominant frequency from the beginning to the end.

Stumpffia contumelia sp. nov.

(Figures 52 and S106)

Holotype. ZSM 443/2010 (FGZC 4258), an adult male, collected on 2 April 2010 in Ambodivoangy (S15.289944, E49.620278, 287 m above sea level), Toamasina Province, Madagascar, by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, and F.M. Ratsoavina.

Paratypes. ZSM 441/2010 (FGZC 4248) and ZSM 442/2010 (FGZC 4252) with the same collection data as the holotype.

Diagnosis. A very small species of *Stumpffia* with strong digital reduction in clade D, related and similar to *S. tridactyla*. Not included in previous studies. (1) Miniaturized species (adult male SVL 8.0–8.9 mm); (2) manus with one finger only (first finger not visible; second and fourth fingers reduced to small knobs; third finger broadened to a triangular shape) and pes with three toes (first toe not recognizable, second toe reduced to a small knob); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.18–0.16, FOTL/SVL 0.66–0.81; (5) dorsum smooth with a few scattered tubercles; (6) iridescent copper with irregular dark flecks, with a distinct color bor-

der to the dark flanks in at least some specimens and in the anterior half of the body. Ventrally slate gray with whitish flecks posterior to the throat. Without contrasted ventral coloration or red color elements on ventral side; (7) regularly repeated short single-note frequency-modulated whistle call.

Distinguished from all nominal species of *Stumpffia* except *S. tridactyla* (and *S. obscoena* sp. nov., described below) by stronger digital reduction with only one finger and three toes recognizable. Also distinguished from most other *Stumpffia* by its frequency-modulated call. The new species is placed in clade D as the sister species of *S. tridactyla*, but differs from that species by (1) a strong genetic divergence in both mitochondrial and nuclear genes, (2) a more granular dorsum, (3) probably a shorter call duration, higher frequency and steeper frequency modulation, although these traits are difficult to assess due to differences in recording conditions (especially temperature).

Description of the holotype. Specimen in a good state of preservation, right hindlimb removed as a tissue sample. The right forelimb is fractured. Body stocky; head slightly longer than wide, narrower than body; snout rounded in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis straight; loreal region straight, vertical; tympanum distinct, about 52% of eye diameter; supratympanic fold indistinct; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae small, rounded. Forelimbs slender; subarticular tubercles single, indistinct; outer metacarpal tubercle triangular, indistinct; inner metacarpal tubercle distinct, oblong; fingers without webbing; all fingers except third reduced; finger tips not expanded into discs. Hind limbs relatively thick; TIBL



Fig. 52. *Stumpffia contumelia* sp. nov. from Ambodivoangy in life: (a–c) paratype ZSM 441/2010 (FGZC 4248).

49% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle elongated, thin; outer metatarsal tubercle absent; no webbing between toes; first toe absent, second strongly reduced; relative length of toes $2 < 5 < 3 < 4$; fifth toe slightly shorter than third. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After five years in 70% ethanol, the dorsum is silver with irregular black markings, and occasional circular white spots; black spots in the inguinal region. The supraocular regions contain several small black spots. Dorsal surface of the head as the back. Nostril brown, the lateral surface of the head is brown mottled with cream. A stark color border is present between the silver dorsal coloration and the dark brown lateral coloration, running over the tympanum to the rostrum. White spots permeate the dark brown color along the lower lip. The ventral trunk is vermiculated white and dark brown. The chin has a cream base color spotted with tiny dark brown spots. Vermiculations extend onto the ventral surface of the thighs to become brown spotted with white. Interior surface of the shank cream. Dorsally, the thigh is bronze, with irregular dark markings. The shank has a strong dark crossband midway down its length. The feet also have a strong dark crossband, bordered either side by silver. The toes are striped silver and dark brown. The arms are bronze and silver flecked with dark markings. A crossband is present in the middle of the lower arm.

Color in life (based on paratype ZSM 441/2010). Dorsum iridescent copper with irregular dark flecks and lighter spots. Supraocular region with dark patches. Inguinal spots present, black. Stark lateral color border traversing the middle of the eye; flank black to gray with small irregular iridescent light flecks, at high concentration pos-

terior to the insertion of the forelimb. Forelimbs dorsally as the dorsum, with a single black crossband on the distal half of the forearm. Hands mottled gray. Hindlimbs as the dorsum, with one dark crossband on the shank, and one on the dorsal surface of the foot. Fourth toe dorsally gray with a light golden spot just posterior to the terminal phalange. Ventral body slate gray in base color. Dense concentration of iridescent whitish flecks directly posterior to the pectoral girdle, decreasing in density posteriorly. Light gray spots present on the posteroventral thighs. Iris rust red around the pupil, darkening externally (Fig. 52a).

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens strongly agree with the holotype in morphology. A high degree of variability was noted in the coloration of specimens: ZSM 441/2010 agrees well with the holotype, except in lacking a shank crossband, having weaker inguinal spots, and lacking superocular black spots; ZSM 442/2010 differs strongly, with the ventral coloration of trunk extending onto the chin, the ventral coloration being less vermiculated than spotted, dorsally with an X-like marking in the scapular region, and a faint brown chevron extending anteriorly to the mid-dorsum from the large dark inguinal spots. These chevron and inguinal spots extend onto the thigh as an oblique crossband. The shank has a thick dark crossband. The dorsal surface of the eye also lacks black spots.

Etymology. The species name is a noun in apposition to the generic name, derived from Latin *contumēlia* = insult. It is in reference to the offensive shape of the hand caused by digital reduction.

Distribution. Known only from its type locality Ambodivoangy.

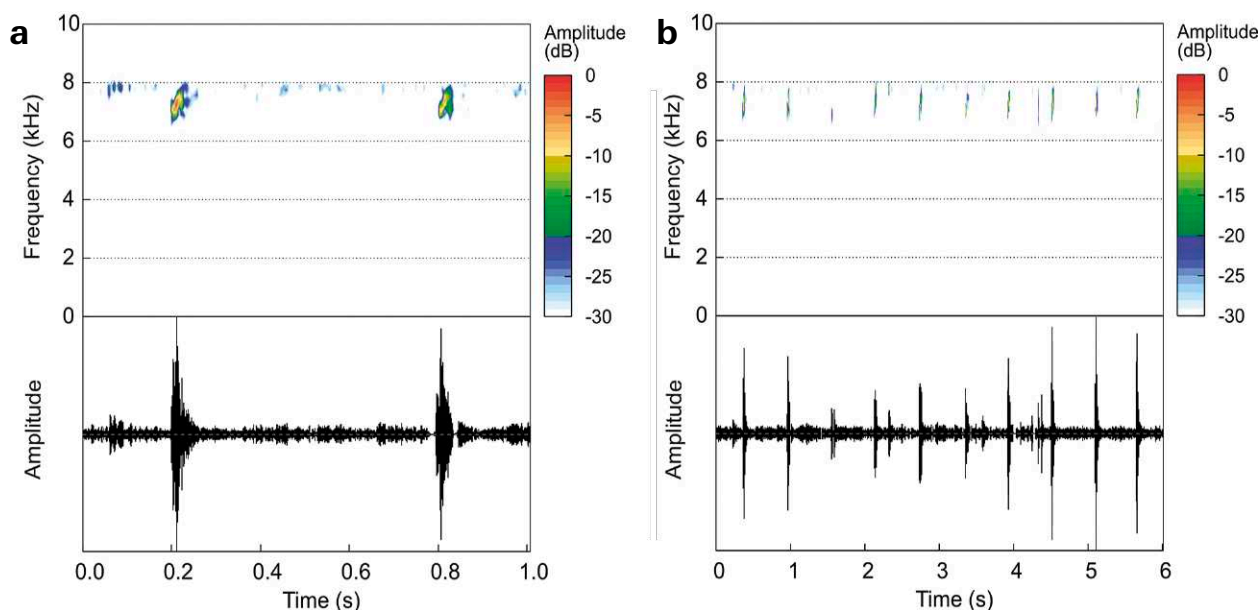


Fig. 53. Spectrograms (above) and oscillograms (below) of advertisement calls attributed to *Stumpffia contumelia* **sp. nov.** from Ambodivoangy: (a) 1 s duration section; (b) 6 s duration section.

Natural history. At Ambodivoangy, males called from the forest floor from hidden positions under leaf litter during the day and at dawn.

Call. The advertisement call of *S. contumelia* consists of a single, very short, high-pitched and pulsatile note repeated in series at regular intervals (Fig. 53). Calls recorded by J. Köhler on 2 April 2010 at Ambodivoangy very likely corresponding to this species (males not observed calling, but found in leaf litter from where calls were emitted) had the following numerical parameters: call duration (= note duration) 38–50 ms (42 ± 4 ms; $N=7$), inter-call intervals 508–580 ms (543 ± 27 ms; $N=6$), and a dominant frequency at 7450–7493 Hz (7493 ± 50 Hz, $N=7$). Within notes, distinct frequency modulation is evident, with an increase in dominant frequency from the beginning to the end.



Fig. 54. *Stumpffia obscoena* **sp. nov.** from Andasibe in life, photographed 1991 (not assignable to a voucher specimen).

Stumpffia obscoena **sp. nov.**

(Figures 54 and S107)

Holotype. ZSM 381/2005 (FGZC 2666), sex undetermined, collected on 9 February 2005 around Andasibe (S18.9333, E48.4166, 900 m above sea level), Toamasina Province, Madagascar, by F. Glaw, R.D. Randrianiaina, and R. Dolch.

Paratypes. ZSM 380/2005 (FGZC 2664), UADBA (FGZC 2663), and UADBA (FGZC 2665), same collecting data as holotype; ZFMK 52550–52552 collected in February 1991 around Andasibe by F. Glaw and M. Vences; ZFMK 53748–53749 collected on 11 and 13 January 1992 around Andasibe by F. Glaw and J. Müller; ZFMK 59875 collected in January or February 1994 in Andasibe by F. Glaw and M. Vences.

Diagnosis. A very small species of *Stumpffia* with strong digital reduction, phenotypically similar to *S. tridactyla* but placed in clade B. This species has previously been

listed as *Stumpffia* sp. 6 (VIEITES *et al.*, 2009; KÖHLER *et al.*, 2010; PELOSO *et al.* 2017 and SCHERZ *et al.*, 2016), as *Stumpffia* sp. 7 in WOLLENBERG *et al.* (2008), and as part of *Stumpffia tridactyla* in BLOMMERS-SCHLÖSSER & BLANC (1991) and GLAW & VENCES (2007:126–127). (1) Miniaturized species (SVL 9.7–11.1 mm); (2) manus with one finger only (first, second and fourth finger not visible; third finger broadened to a triangular shape by extended lateral fringes) and pes with three toes (first toe not recognizable, second toe reduced to a vestigial knob); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.13–0.16, FOTL/SVL 0.53–0.64; (5) dorsum smooth with a few scattered tubercles; (6) chocolate dorsally, with distinct color border to the ebony flanks in at least some specimens and in the anterior half of the body. Ventrally grayish with dark mottling, throat dark. With-

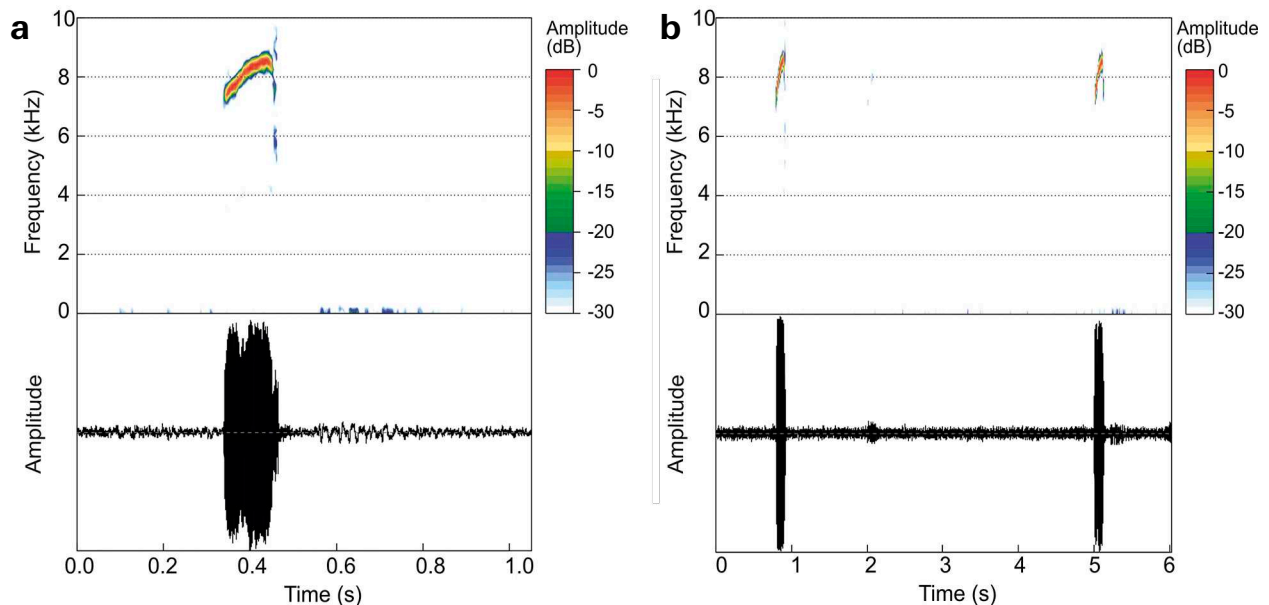


Fig. 55. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia obscoena* sp. nov. from Andasibe: (a) 1 s duration section; (b) 6 s duration section.

out contrasted ventral coloration or red color elements on ventral side; (7) regularly repeated short single-note frequency-modulated whistle call.

Distinguished from all nominal species of *Stumpffia* except *S. tridactyla* and *S. contumelia* by stronger digital reduction with only one finger and three toes recognizable. Also distinguished from most other *Stumpffia* by its frequency-modulated call. The new species is very similar at first glance to *S. tridactyla* and *S. contumelia*, but according to the molecular phylogeny is not closely related to those species, being placed in clade B rather than in clade D. It differs from *S. tridactyla* and *S. obscoena* by (1) a strong genetic divergence in both mitochondrial and nuclear genes and distant phylogenetic position, (3) a distinctly longer inter-call interval, and (3) a different external morphology of the hand, with the enlargement of the third finger made up by lateral fringes rather than by a more uniform broadening of the entire finger into a conical shape.

Description of the holotype. Specimen in a good state of preservation, its left forelimb removed as a tissue sample. Body oval; head slightly wider than long, narrower than body width; snout slightly pointed in dorsal view, somewhat truncate in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct, straight; loreal region straight, vertical; tympanum distinct, about 70% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle distinct, broad, flat, and round; inner metacarpal tubercle distinct, oblong; fingers without webbing, all fingers except third reduced, finger tips not expanded into discs. Hind limbs relatively thick;

TIBL 46% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle elongated, thin; outer metatarsal tubercle absent; no webbing between toes; first toe practically absent, second toe strongly reduced; relative length of toes $2 < 5 < 3 < 4$; fifth toe distinctly shorter than third. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After 10 years in 70% ethanol, the dorsum is brown with two oblong beige patches over the hip region, and a further two spots of beige over the scapular region. A dark brown oblique fleck is present in the inguinal region. The nostril is beige surrounded with brown. The lateral sides of the head are darker brown than the dorsum. The ventral surface is brown speckled with beige; speckling extends up lateral sides of body; chin slightly darker than trunk. Ventral surface of thighs speckled as trunk, becoming lighter on ventral surfaces of shanks and feet. Anterodorsal surface of thigh also speckled with beige, posterodorsal region beige without speckling; proximal half of shank brown, distal half beige, with beige and brown halves separated by a dark crossband. Tarsus beige. Feet dorsally beige medially, dark brown laterally. Cloacal region dark brown. Upper arm dorsally beige, ventrally brown, elbow brown, lower arm brown; hand brown dorsolaterally, beige dorsomedially, ventrally beige.

In life, dorsum chocolate with irregular black or dark brown flecks. Superocular region with dark patches. Inguinal spots present, black. Stark lateral color border traversing the middle of the eye; flank ebony with small irregular iridescent light flecks, at high concentration posterior to the insertion of the forelimb. Forelimbs dorsally as the dorsum, without crossbands. Hands dorsally brown. Hindlimbs as the dorsum, with one dark crossband on the proximal thigh, and one on the distal

shank, which line up when the leg is bent. Foot without crossbands. Fourth toe dorsally brown with light iridescent flecks. Ventral color in life not known. Iris rust red around the pupil, darkening externally (Fig. 54).

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens strongly agree with the holotype in morphology. A high degree of variability was noted in the coloration of specimens: The dorsum of FGZC 2664 is light brown (lighter than the holotype), with beige regions on the dorsum as in the holotype but more faint, but between hip and shoulder spots an almost triangular dark brown marking is present. Inguinal spots are present as in the holotype. A strong color border is present between the light brown dorsum and the dark brown lateral region extending to the lateral side of the head. Vent region is dark as in the holotype. The dorsal surface of the whole leg is beige instead of brown with beige flecks; a dark crossband is present on the dorsal surface of the proximal end of the thigh. A discontinuous crossband is also present in the middle of the tibia as in the holotype. The foot is dorsolaterally dark surrounded by light beige areas, and dorsomedially beige. The ventral surface is as in the holotype except that speckling of beige is absent from the chin. ZFMK 53748 and ZFMK 53749 are strongly discolored (orangish), but the former clearly agrees with the holotype, while the latter agrees with FGZC 2664 in coloration. In all specimens, the dark vent region, inguinal spots, leg crossbands, and ventral flecking are distinct. The specimens ZFMK 52550–52552 and 59875 agree with holotype in color and morphology.

Etymology. The species name is the feminine nominative singular form of the Latin adjective *obscoena*/obscoena=obscene. As for *S. contumelia* above, it is in reference to the offensive shape of the hand caused by digital reduction.

Distribution. Known from forests around Andasibe.

Natural history. Specimens typically call during the day from the leaf litter in primary rainforest but also from secondary (mature eucalypt) forest, from hidden positions. Sometimes many calling males can be heard, suggesting that these frogs occur all over the forest.

Call. The advertisement call of *S. obscoena* consists of a single pulsatile note repeated in series at regular intervals (Fig. 55). Calls recorded by F. Glaw on 9 January 1992 at Andasibe (VENCES *et al.*, 2006: CD3, track 38, cut 2) had the following numerical parameters: call duration (= note duration) 137–154 ms (144 ± 8 ms; $N=8$), inter-call intervals 3948–6322 ms (4619 ± 990 ms; $N=5$), and a dominant frequency at 8225–8397 Hz (8361 ± 68 Hz, $N=6$). Within notes, distinct frequency modulation is evident, with an increase in dominant frequency from the beginning to the end.

Stumpffia davidattenboroughi sp. nov.

(Figures 56 and S123)

Holotype. ZSM 204/2016 (ACZCV 0106), Figs. 56 and S123, adult male, collected on 6 November 2013 in Sahambendrana (S17.9013, E49.2109, 558 m above sea level), Betampona Strict Nature Reserve, Toamasina Province, Madagascar, by G.M. Rosa, D.J. Harris, M.Randriamialisoa, and H. Lava.

Diagnosis. A small species of *Stumpffia* with digital reduction. This species has not been listed as candidate species in previous publications. (1) Miniaturized species (adult male SVL 11.72 mm); (2) manus with four fingers (first finger very strongly reduced in length; also second and fourth finger short) and pes with four toes (first toe absent, second and fifth toes reduced in length); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.17, FOTL/SVL 0.55; (5) dorsum smooth; (6) dorsally mocha bordered around the lateral edges with champagne, forming a teddybear shape. Flanks mocha, with sharp continuous color border between dorsum and flanks.

Distinguished from all nominal species of *Stumpffia* by the pattern of digital reduction, with completely reduced first toe and length-reduced second toe (otherwise only found in *S. tetradactyla*, but with different degree of finger reduction), and strongly length-reduced first finger (only found in *S. miery*). Phylogenetically placed in clade B, forming the sister taxon of *S. obscoena*, which presents much stronger digital reduction.

Description of the holotype. Specimen in good state of preservation, left foot removed as a tissue sample. Body slender; head longer than width, slightly narrower than body; snout slightly pointed in dorsal view, rounded in lateral view; nostrils directed laterally, not protuberant, slightly nearer to tip of snout than to eye; canthus rostralis not distinct; loreal region concave, oblique; tympanum distinct, about 80% of eye diameter; supratympanic fold not distinct; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle not recognizable; inner metacarpal tubercle distinct, oval, fused with the prepollical tubercle; fingers without webbing; first finger very strongly reduced, second and fourth fingers short; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly longer than second; finger tips not expanded into discs. Hind limbs slender; TIBL 30% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, round; outer metatarsal tubercle absent; no webbing between toes; toe tips slightly expanded; first toe absent, second and fifth toes reduced in length; relative length of toes $2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is metallic brown with a brown ted-



Fig. 56. *Stumpffia davidattenboroughi* sp. nov. from Betampona Strict Nature Reserve in life: (a–b) holotype ZSM 204/2016 (ACZCV 0106); (c) egg clutch found close to the specimen; note that assignment of the clutch to this species is tentative and requires confirmation by further field observation.

dybear shape starting from the middle of the eyes to the inguinal region. A dark brown spot, bordered with a light brown line is present in the inguinal region. The dorsal surface of the head is metallic and brown in color with a beige line connecting the eyes and defining the teddy-bear shape along the dorsum. The nostril is surrounded with beige. The lateral surface is homogeneously dark brown flecked with small beige dots. The flank coloration merges with the ventral coloration. The ventral trunk is brown flecked with beige. The chin is brown spotted with beige but with less and smaller flecks than the other ventral parts. The ventral thigh is as the belly. The shank, tarsus, and foot are ventrally as the thigh. Dorsally, the thigh is beige spotted with brown with a dark crossband bordered by a whitish line. The posterodorsal surface of the thigh is beige spotted with brown and with dark brown oval shape bordered with a whitish line close the cloacal region. The shank is beige spotted with brown with a dark crossband bordered by a whitish line and in the distal portion is pinkish. The coloration of the distal portion of the shank merges with the coloration of the tarsus. The foot including the toes is as the tarsus but darker. The arms are beige with pinkish color. The dorsomedial surface of the hand is beige. The underside of the arm is as the ventral trunk.

In life, dorsally dichromatic: internally mocha in a teddybear shape, bordered around the lateral edges and the anterior head by a stripe of champagne. The flank is darker, with small iridescent light flecks. Dorsal forelimbs dark brown proximally, becoming copper before the elbow, fading again to brown distally. Small iridescent light flecks are present on the hand. The hindlimbs are trichromatic: from the hip to the mid-shank is mocha. At the mid-shank, a dark crossband bordered with a champagne line is present. Beyond this point, the leg becomes coppery orange. A weak dark crossband is pre-

sent on the tarsus. The dorsal foot has irregular light iridescent flecks. The ventral coloration in life is unknown (Fig. 56).

Etymology. We dedicate this species to Sir David Attenborough, who celebrated his 91st birthday on the 8th of May 2017, in recognition of his services to science communication and natural history broadcasting with the BBC for the last 65 years. Sir David first visited Madagascar in the 1960s, and has been an ambassador for the island's wildlife, and for threatened wildlife around the globe, throughout his long career.

Distribution. This species is so far known only from its type locality in the Betampona Strict Nature Reserve.

Natural history. This specimen was found during the day in the leaf litter in close proximity with a jelly nest. The individual seemed to be guarding the egg clutch inside this curled dry leaf forming a sort of half pipe. This leaf had yet another leaf on top providing a safer microhabitat, both by keeping higher level of humidity and away from potential predators. Unfortunately, the developing embryos were not sampled and it is therefore not possible to unequivocally assign these eggs to this species. However, if they were indeed the eggs of this species, they would represent the first evidence of jelly- instead of foam-nests in *Stumpffia*, more similar to those of *Rhombophryne* and other cophylines (see also other observations on *S. achillei* sp. nov. below). This species appears to be uncommon, or have extremely elusive habits. At least four amphibian surveys coupled with molecular taxonomic identification were carried out in the reserve (from 27 February to 23 March 2004; from 3 February to 2 April 2007, from 25 October to 16 December 2007, and from 3 to 25 November 2013) and only

one of the many collected *Stumpffia* individuals has been assigned to this new species.

Call. Unknown.

4. Large-sized species of clade B

Clade B contains three small-sized to miniaturized species (*S. davidattenboroughi*, *S. miery*, *S. obscoena*, discussed above), all with at least a certain degree of digital reduction. Surprisingly, this clade contains with high support also one undescribed, geographically disparate large-sized species without obvious digital reduction, which we describe in this section.

Stumpffia meikeae sp. nov.

(Figures 57 and S108)

Holotype. ZSM 1823/2010 (ZCMV 12374) (Fig. 57 d–e), an adult male, collected on 13 June 2010 at Matsabory Maiky Campsite, Tsaratanana Strict Nature Reserve (S14.15256, E48.95728, 2021 m above sea level), Antsiranana/Mahajanga Province, Madagascar, by M. Vences, D.R. Vieites, R.D. Randrianaiaina, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, F. Randrianasolo, and T. Rajoafiarison.

Paratypes. UADBA-A 60773 (DRV 6178), UADBA-A 60774 (DRV 6172), UADBA-A 60767 (DRV 6169), UADBA-A 60770 (DRV 6176), UADBA-A 60771 (DRV06173), UADBA-A 60772 (DRV06174), UADBA-A 60833 (ZCMV 12378), UADBA-A 60842 (ZCMV 12375), ZSM 1821/2010 (ZCMV 12372), ZSM 1822/2010 (ZCMV 12373), ZSM 617/2014 (DRV 6163), ZSM 618/2014 (DRV 6170), ZSM 619/2014 (DRV 6171), ZSM 620/2014 (DRV 6175), ZSM 621/2014 (DRV 6177), ZSM 622/2014 (DRV 6179), ZSM 623/2014 (DRV 6184), ZSM 624/2014 (DRV 6185), ZSM 625/2014 (DRV 6188), and ZSM 626/2014 (DRV 6189), all with the same collecting data as the holotype.

Diagnosis. A fairly large, conspicuously colored species from high elevations on the Tsaratanana Massif. Previously listed as *S. sp. Ca33* in SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Moderately large-sized species (SVL 19.2–23.4 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers and toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.21–0.24, FOTL/SVL 0.65–0.81; (5) dorsum smooth; (6) dorsally gray to chocolate brown, with darker patterns that are highly variable among specimens but generally consist of an interocular-anterior dorsal triangle, and several smaller patches bordered with cream. Ventrally, the chin and abdomen is champagne to salmon colored, while the hindlimbs are a more intense salmon or orange coloration.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. madagascariensis*, *S. mamitika*, *S. maledicta*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tetradactyla*, *S. tridactyla*, and *S. yanniki* by larger

body size; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi* by stronger length reduction of first toe; from *S. grandis*, *S. hara*, *S. megsoni*, and *S. staffordi* by a champagne to salmon-colored belly and ventral salmon to orange color on hindlimbs (vs. no or very little reddish ventral color); from *S. kibomena* by a different dorsal pattern, and by lack of dense blackish pigmentation of the throat. Morphologically most similar to *S. roseifemoralis*, which has a similar ventral and dorsal color pattern and also occurs at comparatively high elevations, but occupies a very distant position in the *Stumpffia* phylogeny, and is concordantly differentiated in mitochondrial and nuclear genes. A probable morphological difference between these two species is relative toe length, with the third toe being distinctly longer than the fifth toe in *S. roseifemoralis*, but only slightly longer than the fifth toe in the new species.

Description of the holotype. Specimen in good state of preservation, thigh muscle on right leg partly removed as a tissue sample. Body pear shaped; head slightly longer than wide, narrower than body; snout pointed in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct concave; loreal region concave, oblique; tympanum distinct, about 59% of eye diameter; supratympanic fold not distinct; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slightly thick; subarticular tubercles single, round; outer metacarpal tubercle distinct, small, palmar metacarpal visible, close to the outer metacarpal, round; prepollex present, oval; fingers without webbing; first finger reduced, second finger reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger distinctly longer than second; finger tips expanded into discs. Hind limbs slender, 52% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third; subarticular tubercles distinct, single, elongate. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After five years in 70% ethanol, the dorsum is brown with dark brown patches. Dark brown reversed V in the inguinal region. The dorsal surface of the head is as the back, with a reversed triangular dark brown patch starting in the middle of the eye to the forelimb, dark brown patches in the lateral side close to the forelimb. The nostril is beige. The lateral surface of the head is brown mottled with beige. The flanks are beige spotted with brown. The flank coloration merges with the ventral coloration. The ventral abdomen is as the flanks. The chin is beige flecked with brown. The ventral thigh is as the belly. The shank and tarsus are ventrally as the thigh. The sole of the foot is dark brown mottled



Fig. 57. *Stumpffia meikeae* sp. nov. from Matsabory Maiky campsite, Tsaratanana Strict Nature Reserve, in life: (a) paratype ZSM 1821/2010 (ZCMV 12372); (b–c) paratype ZSM 1822/2010 (ZCMV 12373); (d–e) holotype ZSM 1823/2010 (ZCMV 12374).

with beige. Dorsally, the thigh is dark brown with perpendicular brown crossband. The posterodorsal surface of the thigh is beige flecked with brown. The shank is as the thigh with an oblique dark brown crossband. The tarsus is lighter than the thigh with a perpendicular crossband. The foot is as the thigh without a crossband. The toes are striped with beige patches. The cloacal region is dark brown. The arms are dark brown. A dark crossband is present on the lower arm. The dorsomedial surface of the hand is beige. The fingers have a small white annulus before each terminal phalange. The underside of the arm is as the trunk.

Color in life (holotype and variation). Dorsum with a distinctive pattern formed of dark brown markings bordered by cream: an isosceles triangular marking starts between the eyes and narrows to a point around the suprascapular region (can be irregular in some specimens, compare Fig. 57b with 57a and 57d). A second marking converges anteromedially from the inguinal region to form a second semi-triangular marking. A further two dark markings are present behind the suprascapular region. These together with the second semi-triangular marking can form an asymmetrical X-like marking; compare Fig. 57d with 57b and 57a. A further small marking can be present on the snout. Dorsal base color burnt umber (lighter in some paratypes, even ranging to gray; Fig. 57). No dorsolateral color border is present. The flanks are mostly as the dorsum, fading to the ventral champagne, with small irregular whitish flecks. A cream marking runs from the tympanum to the insertion of the arm. The dorsal forelimb is as the back. A crossband is present on the forearm. The hand is dorsomedially cream, dorsolaterally as the dorsum, with irregular whitish flecks, including one before each terminal phalange. Dorsal hindlimb as the back, with a cream-bordered dark brown crossband at the mid-thigh, mid-shank, and on the foot. The dorsal foot and toes have several whitish flecks, including one before each terminal phalange. The ventral trunk is champagne to salmon. The chin is champagne with brown flecks,

decreasing in density posteriorly (mostly absent in some paratypes, Fig. 57). The ventral legs and inguinal region are salmon. Ventral hands and feet rosy brown. The iris is russet (lighter browns in some paratypes, Fig. 57).

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology, except ZSM 1822/2010 (ZCMV 12373): first toe slightly bigger than in the holotype, inner metacarpal smaller, coloration uniformly brown; ZSM 624/2014 (DRV 06185): snout dorsally slightly round, tongue broadening posteriorly, inner metatarsal small oval, coloration in dorsal view is as the holotype but with white spots across all parts of the body; ZSM 619/2014 (DRV 6171): dorsally on the head present, dark brown spot in the choanae region; ZSM 622/2014 (DRV 6179) and 626/2014 (DRV 6189): outer metacarpal present and oval, coloration as ZSM 624/2014; ZSM 621/2014 (DRV 6177): outer metacarpal small, oval, coloration dorsally lighter than the holotype with cream spot; ZSM 620/2014 (DRV 6175): palmar metacarpal close to the outer metacarpal, brown broad mid-dorsal stripe on the back starting between the eyes and running to the inguinal region; ZSM 618/2014 (DRV 6170): large, elongate inner metacarpal tubercle, palmar metacarpal close to the outer metacarpal, both elongate. Coloration in dorsal view similar to the holotype except for the presence of cream spots across the whole body. In ZSM 617/2014 (DRV 6163) coloration uniformly brown, outer metacarpal large, elongate, palmar metacarpal small elongate. In ZSM 1821/2010 (ZCMV 12372) the thigh and tarsus lack crossbands, and the palmar metacarpal is small.

For five paratypes, no molecular data are available: ZSM 617/2014 (DRV 6163), ZSM 623/2014 (DRV 6184), ZSM 624/2014 (DRV 6185); ZSM 625/2014 (DRV 6188), ZSM 626/2014 (DRV 6189). However, since these specimens were collected at exactly the same site as the rest of the type series, and they agree with the holotype in morphology, we here assign them to *S. meikeae*.



Fig. 58. *Stumpffia grandis* from above Camp Simpona, Marojejy National Park, in life (not assignable to voucher specimen): (a) dorsolateral view; (b) ventral view.

Etymology. The species name is a matronym honoring Meike Kondermann, to whom we are pleased to dedicate this attractively colored species in recognition for the invaluable help, supervision and friendship she provided to the first author and many other students during molecular labwork at TU Braunschweig.

Distribution. Known only from its type locality, Matsabory Maiky, Tsaratanana Strict Nature Reserve, 2021 m above sea level.

Natural history. Specimens were found after the main rainy season (in June), inactive under stones, boulders and roots in the dry bed of a tiny stream. Multiple individuals were found under the same stones, suggesting they might have been estivating at this place.

Call. Unknown.

5. Moderate- to large-sized species of clade C

Three nominal species of *Stumpffia* are comparatively large-sized, distributed in eastern and north-eastern Madagascar, and belong to clade C (Fig. 3). These three species plus the small-sized *S. tetradactyla* are the only described species in this clade. A large number of additional clade members exist and will be described as new species in the following. In this section, we review and describe first the species of moderate to large size, and in the subsequent section we focus on the small-sized species of clade C.

Stumpffia grandis GUIBÉ, 1974

(Figure 58)

Name-bearing type. Holotype MNHN 1973.715 from “Massif du Marojezy (1300 m)” according to the original description.

Identity and diagnosis. A comparatively large-sized species only known from the Marojejy Massif in north-eastern Madagascar, distinguished from all other species of the genus by its highly contrasted black-bluish ventral color pattern. (1) Moderately large-sized species (SVL 19.3–23.7 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length not measured HAL/SVL 0.19–0.25, FOTL/SVL 0.69–0.75; (5) dorsum smooth; (6) reddish brown dorsally, with distinct dark brown to black patches. Ventrally light bluish with distinct and strongly contrasted black pattern, especially in the throat, which can be entirely black, without red color elements on ventral side.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by distinctly larger body size. From all these species and *S. be*, *S. hara*, *S. meikeae*, *S. megsoni* and *S. staffordi* by distinct and contrasted ventral color pattern and larger body size, furthermore from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction.

Specimens examined. Holotype MNHN 1973.715 collected in July 1972 from Marojejy (1300 m a.s.l.) by C.P. Blanc; paratypes MNHN 1973.716–719 with same collection data as holotype. Referred specimens: ZSM 372/2005 (FGZC 2820) collected on 16 February 2005 from above camp Simpona, Marojejy National Park (coordinates not taken) by F. Glaw, M. Vences, and R.D. Randrianaina (note: this animal unfortunately disintegrated in preservative).

Distribution. Known only from Marojejy National Park at around 1300–1400 m a.s.l.

Call and natural history. – Unknown.



Fig. 59. *Stumpffia kibomena* in life: (a–b) specimen from Andasibe (not collected); (c–d) female specimen from An'Ala; (e–f) male paratype NMBE 1034211 from near Andasibe. Plate from GLAW *et al.* (2015).

***Stumpffia kibomena* GLAW, VALLAN, ANDREONE, EDMONDS, DOLCH & VENCES, 2015**

(Figures 59 and S109)

Name-bearing type. Holotype ZFMK 60007 (Fig. S109) from “near Andasibe (S18.9333, E48.4166), ca. 900 m elevation, central-eastern Madagascar” according to the original description.

Identity and diagnosis. A recently described moderately large-sized species of *Stumpffia* from the northern central east of Madagascar, with distinct red color on belly and limbs. (1) Moderately large-sized (adult male SVL

17–21 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe slightly reduced in length); (3) Terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.2, FOTL/SVL 0.7 (according to the original description); (5) dorsum smooth, sometimes with a few scattered tubercles; (6) reddish brown dorsally, with distinct dark brown patches usually forming longitudinal bands, and one triangular path between the eyes and running along the anterior third of the dorsum. Ventrally light reddish to deep red on belly; throat with dense black pattern, often almost completely black; (7) regularly repeated short single-note tonal call.

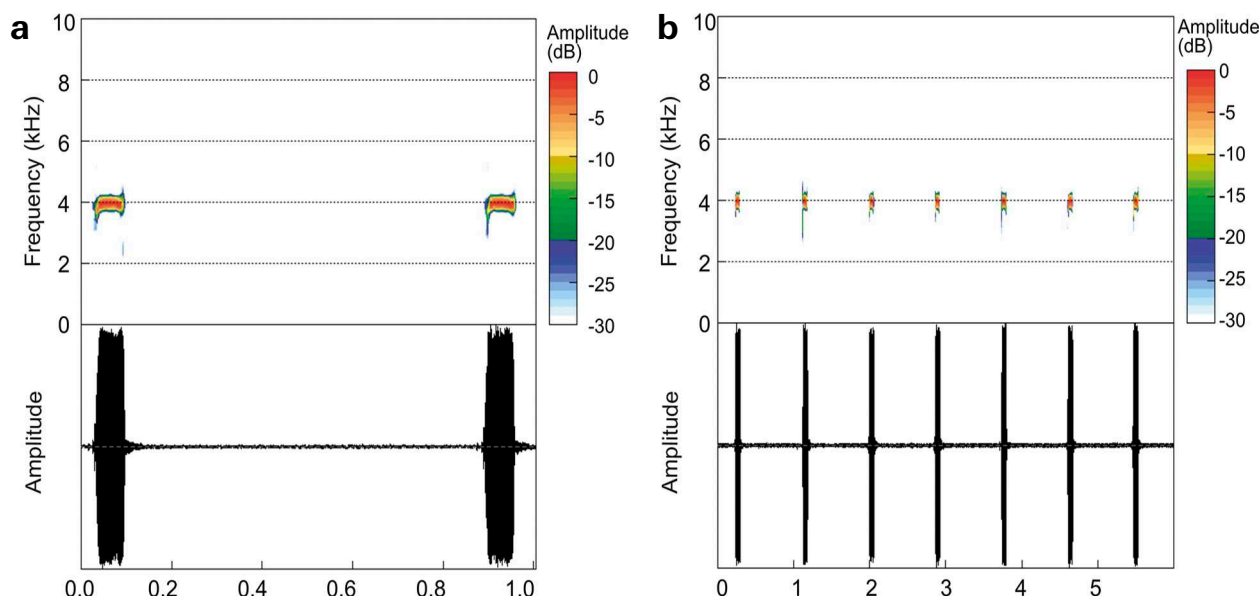


Fig. 60. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia kibomena* recorded near Andasibe: (a) 1 s duration section; (b) 6 s duration section.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by distinctly larger body size. From all these species and *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi*, distinguished by distinct red color on belly (vs. red color absent from ventral surface, or restricted to limbs in *S. be*). Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction. *Stumpffia meikeae* has reddish color on belly similar to *S. kibomena*, but in *S. meikeae* this color is typically more faint (champagne to salmon), the throat has less expressed black pattern, the dorsal pattern is different, and the species belongs to a completely different major clade of *Stumpffia* (clade B rather than clade C).

Specimens examined. Holotype ZFMK 60007 collected on 17 January 1995 near Andasibe (S18.9333, E48.4166, ca. 900 m a.s.l.) by F. Glaw; paratype NMBe 1044940 collected on 14 February 1997 in An'Ala forest (S18.9166, E48.4833, ca. 850 m a.s.l.) by D. Vallan; paratype NMBe 1034211 collected on 13 February 1995 near Andasibe (S18.9166, E48.4166, ca. 950 m a.s.l.) by D. Vallan.

Distribution. Known from eastern rainforests at Andasibe and An'Ala.

Natural history. Specimens were found during the day in leaf litter of primary rainforest, eucalypt forest, and fern scrub. Calls were heard in the morning and afternoon (GLAW *et al.*, 2015).

Call. The advertisement call of *S. kibomena* consists of a single short and slightly pulsatile note repeated in series at regular intervals (Fig. 60). Calls recorded on 20

March 1995 at 15:15 h near Andasibe and at 24°C air temperature had the following numerical parameters (according to GLAW *et al.*, 2015): call duration (= note duration) 70–76 ms (73 ± 2 ms, N=9), inter-call intervals 770–813 ms (797 ± 15 ms, N=9), and a dominant frequency at 3900–4300 Hz. Within notes, distinct frequency modulation is evident, with an increase in dominant frequency from the beginning to the end.

Remark. We here list along with *S. kibomena* two lineages corresponding to the candidate species here named *S. sp. Ca11* and *S. sp. Ca34* (note: the candidate species Ca34 as used in SCHERZ *et al.* 2016 did not refer to this species). These are resolved in a clade with *S. kibomena* but separated by a substantial genetic divergence. Each is known from a single individual not available to us for morphological examination in the framework of the present study, and based on these deficient data, their status must remain unresolved. *Stumpffia sp. Ca11* is known from the specimen MRSN A2583 from Ambolokopatrika, whereas *S. sp. Ca34* is represented by UADBA (ZCMV 3319) from Ranomena forest in Ranomafana National Park, collected by M. Vences and collaborators. According to field notes, this specimen is a juvenile with red belly in life.

Stumpffia roseifemoralis GUIBÉ, 1974

(Figures 61 and S110)

Name-bearing type. Holotype MNHN 1973.712 from “Massif du Marojezy (1300 m)” according to the original description.

Identity and diagnosis. A moderately large-sized species of *Stumpffia* described from the Marojezy Massif in



Fig. 61. *Stumpffia roseifemoralis* from Marojejy National Park in life: (a–b) ZSM 374/2005 (FGZC 2883); (c) ZSM 487/2005 (FGZC 2047); (d–e) ZSM 529/2016 (ZCMV 15172).

the north east of Madagascar, characterized by distinct reddish color ventrally on limbs. (1) Moderately large-sized species (SVL 16.2–18.4 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.21–0.26, FOTL/SVL 0.68–0.70; (5) Dorsum smooth; (6) grayish brown to reddish brown dorsally, with a poorly contrasted dark brown teddybear shaped marking centrally on dorsum, without sharp color border between color of dorsum and flanks. Ventrally with reddish-orange color on belly and chest, and more intense reddish color on ventral surface on hindlimbs, without obvious dark pattern on ventral surface; (7) regularly repeated long tonal single-note advertisement call.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*,

S. pygmaea, *S. sorata*, *S. tridactyla*, and *S. yanniki* by distinctly larger body size. From all these species and *S. hara*, *S. megsoni*, and *S. staffordi*, distinguished by the distinct red color on belly. Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction. Among species with red ventral color, distinguished from *S. be* by smaller body size and smaller terminal discs on fingers; from *S. kibomena* by less expressed black pattern on throat and a different dorsal pattern. Most similar to *S. meikeae* but this species belongs to a completely different major clade of *Stumpffia* (clade B rather than clade C).

Specimens examined. Holotype MNHN 1973.712 collected in July 1972 from the Marojejy Massif by C.P. Blanc; paratypes MNHN 1973.713–714 with same collection data as holotype. Referred specimens: ZSM 373/2005 (FGZC 2808) collected on 14 February 2005 from Marojejy National Park, probably Camp Mantella (S14.421 E49.4376, 481 m a.s.l.) by F. Glaw, R.D. Randrianaiaina, and M. Vences; ZSM 374/2005 (FGZC 2883), and ZSM

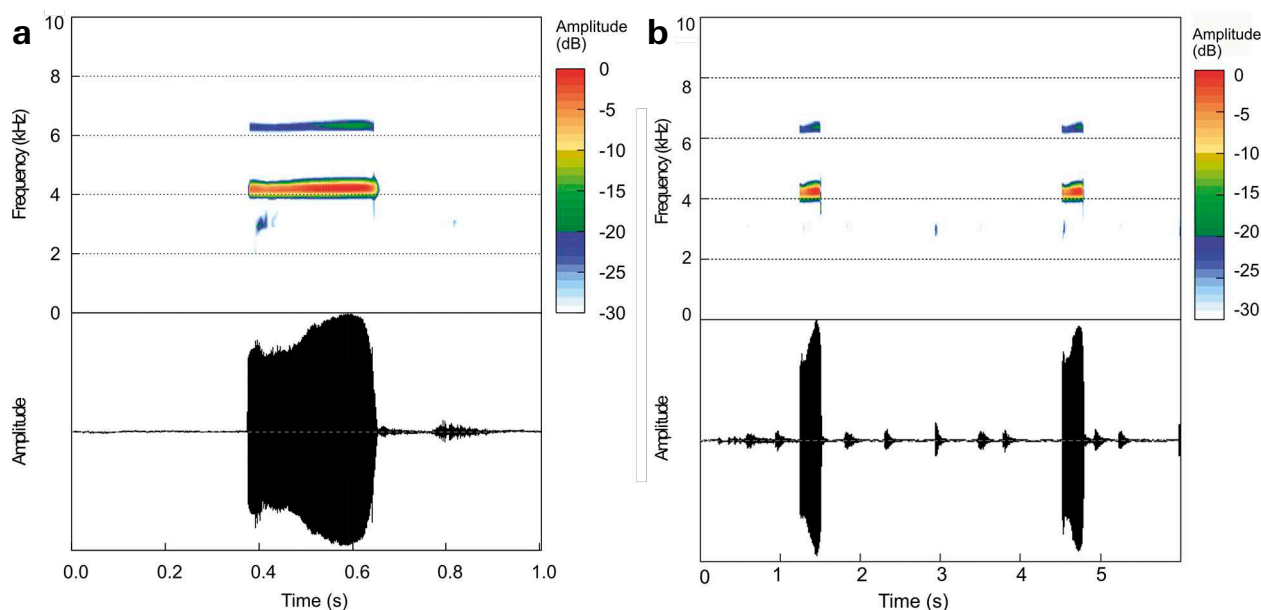


Fig. 62. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia roseifemoralis* from Marojejy National Park (call recorded from ZSM 529/2016, ZCMV 15172): (a) 1 s duration section; (b) 6 s duration section.

487/2005 (ZCMV 2047), collected on 16 and 17 February 2005 at Camp Simpona, Marojejy National Park (S14.4886 E49.9002, 1326 m a.s.l.) by F. Glaw, R.D. Randrianaiaina, and M. Vences. ZCMV 15163–15164, ZSM 529/2016 (ZCMV 15172, ZSM 530/2016 (ZCMV 15206), ZCMV 15207, ZCMV 15209, ZSM 531/2016 (ZCMV 15274), ZSM 532/2016 (ZCMV 15277), ZCMV 15299–15300, all collected 17–20 November 2016 from Camp Simpona, Marojejy National Park (S14.4499, E49.7433, 1326 m a.s.l.) by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences.

Distribution. Known from Marojejy National Park between 480–1350 m a.s.l. (occurrence at low elevation at Camp Mantella indicated by a single voucher specimen only and in need of confirmation).

Natural history. In November 2016, specimens were very common in the leaf litter around Camp Simpona in Marojejy National Park, in particular in moist and dense leaf litter along small streams. However, calls putatively belonging to this species were rarely heard, from only a limited number of specimens, in the evening and at night.

Call. The advertisement call here preliminarily assigned to *S. roseifemoralis* consists of a single, moderately long note emitted in series at regular intervals (Fig. 62). Calls were recorded by M. Vences on 18 November 2016 (21:00) in Marojejy National Park, probably from specimen ZSM 529/2016 (ZCMV 15172; not seen calling, but found at the spot of call emission with partly extended vocal sac; air temperature estimated at 17°C), and had the following parameters: call duration (= note duration) 276–280 ms (278 ± 1.6 ms; $N=6$), inter-call intervals 2891–3304 ms (3073.8 ± 152 ms; $N=6$), and a dominant frequency at 4220–4306 Hz (4234.3 ± 35.1 Hz, $N=6$).

Remark. Genetically divergent specimens that phylogenetically are sister to *S. roseifemoralis* were recorded

from the lowland locality of Ambodivoangy (specimens FGZC 4238 and 4250; both deposited in the UADBA collection and not available for morphological examination in this study). They are here referred to as a new unconfirmed candidate species, *Stumpffia* sp. Ca57, with strong genetic divergence (9.6% in the 16S rRNA) to *S. roseifemoralis*.

Stumpffia achillei sp. nov.

(Figures 63 and S111)

Holotype. ZSM 536/2016 (ZCMV 15149), an adult male, collected on 16 November 2016 near Camp Mantella, Marojejy National Park (ca. S14.438, E49.776, 450 m above sea level), Antsiranana Province, Madagascar, by M.D. Scherz, A. Rakotoarison, M. Vences, M. Bletz, J.H. Razafindraibe, and A. Razafimanantsoa.

Paratypes. ZSM 493/2005 (ZCMV 860) and 494/2005 (ZCMV 861) collected on 19 February 2005, and UADBA (FGZC 2729), UADBA (FGZC 2765), and ZSM 377/2005 (FGZC 2750), collected on 14 February 2005, in Camp Mantella, Marojejy National Park (S14.421, E49.4376, 481 m above sea level), Antsiranana Province, Madagascar, by F. Glaw, M. Vences, and R.D. Randrianaiaina. UADBA (ZCMV 2095) collected on 19 February 2005 from a site below Camp Mantella (coordinates not taken), by F. Glaw, M. Vences, and R.D. Randrianaiaina. UADBA (ZCMV 866) collected on 19 February 2005 in Camp Marojejia, Marojejy National Park by F. Glaw, M. Vences and R.D. Randrianaiaina; ZFMK 57460 and ZFMK 57461 (Fig. 63) collected on 27–31 March 1994 from Marojejy National Park below 500 m a.s.l. by F. Glaw, N. Rabibisoa, and O. Ramilison; ZFMK 59893 collected between 25 February to 1 March 1995 from Marojejy National Park (coordinates not taken) by F. Glaw and O. Ramilison. ZSM 534/2016 (ZCMV 15141) and ZSM 535/2016 (ZCMV 15143), collected on 16 November 2016, and ZSM 533/2016 (ZCMV 15308), male, and ZCMV 15307, eggs collected along with ZSM 533/2016, collected on 21 November 2016, all from Camp Mantella, Marojejy National Park (S14.43766, E49.77557, 456 m a.s.l.) by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences.



Fig. 63. *Stumpffia achillei* sp. nov. from Marojejy National Park in life: (a) paratype ZFMK 57461; (b) male, ZSM 535/2016 (ZCMV 15143); (c) ZCMV 15307, egg clutch of *S. achillei*; (d) calling holotype.

Diagnosis. A species from the north-east of Madagascar characterized by the fastest call repetition rate among those species with known advertisement calls. It has been previously listed as *Stumpffia* sp. 10 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017), as *Stumpffia* sp. 4 in WOLLENBERG *et al.* (2008), as *Stumpffia* sp. ‘Marojejy 2’ in GLAW & VENCES (2007), and as *Stumpffia* sp. b in GLAW & VENCES (1994). (1) Moderately large-sized species (SVL 14.6–19.1 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers and toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.24–0.26, FOTL/SVL 0.71–0.77; (5) dorsum smooth with weak dorsolateral ridges or rows of tubercles; (6) dorsally typically with a sand brown mid-dorsal stripe bordered by various darker and lighter brown markings over the flanks. Ventrally with some dark pattern especially on the throat, without contrasted ventral coloration or red color elements on ventral side; (7) regularly repeated short single-note tonal call with fast repetition rate.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by distinctly larger body size; from *S. be*, *S. kibomena*, *S. meikeae*, and *S. roseifemoralis* by the lack of red color

ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern. Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction; from *S. hara*, *S. megsoni*, and *S. staffordi* by smaller body size and stronger length reduction of first toe; from all other species by the presence, in many individuals, of a broad light patch or band covering most of the dorsum; and from all *Stumpffia* for which advertisement calls are known by shorter inter-call intervals.

Description of the holotype. Specimen in good state of preservation, left thigh muscle removed as a tissue sample. Body slightly rounded; head slightly longer than wide, narrower than body; snout rounded in dorsal view, rounded in lateral view; nostrils directed laterally, not protuberant, nearer to the tip of snout than to the eye; canthus rostralis distinct, concave; loreal region slightly concave, vertical; tympanum distinct, about 53% of eye diameter; supratympanic fold not distinct; tongue long, straight, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slender; subarticular tubercles single, weakly visible; outer metacarpal tubercle visible, single; inner metacarpal tubercle visible, oval; fingers without webbing; no reduced fingers; relative length of fingers $1 < 2 < 4 < 3$, fourth finger longer than second; finger tips expanded into small discs. Hind limbs slender; TIBL 57% of SVL;

lateral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; first toes slightly reduced; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After one year in 70% ethanol, the dorsum is gray with broad light gray dorsal stripe covering the whole head, narrowing to the suprascapular region, and then running to the vent, with a small darker gray heart-shaped marking over the posterior head, and a light dorsal snout. The gray dorsal stripe is bordered by fine blackish irregular lines, and then darker gray patches on the flanks; further, rounded light gray areas are present in the inguinal region. Black spots are present above the tympanum and over the suprascapular region, the insertion of the eye, and anterior to the inguinal region. Inguinal spots are present, small and irregular and black. Tympanum white, supratympanic stripe ending behind the tympanum. The nostril is blackish. The lateral surface of the head is dark gray with black spots, especially a large blackish area below the eye. The flank coloration merges with the ventral coloration. The ventral trunk is immaculate cream, with brown mottling in the lateral region and on the chin. The ventral thigh is brown with cream mottling. The shank is ventrally cream. The tarsus is ventrally brown. The sole of the foot is brown. Dorsally, the thigh is beige with one perpendicular brown crossband. The posterodorsal surface of the thigh is beige. The shank is beige with one crossband. The tarsus is as the shank but with two crossbands. The foot is cream speckled with beige with one crossband. The toes are speckled with beige. The cloacal region is dark brown. The arms are as the dorsum. A dark crossband is present on the forearm. The dorsomedial surface of the hand is cream. The fingers have small dark crossband. The underside of the arm is as the ventral trunk.

Color in life (holotype and variation). A dorsal stripe of sand brown to light rust brown covers the whole head, narrows to the suprascapular region, and then runs to the vent. The lateral body is gray-brown or sand-brown in base color with light rust markings arising from the inguinal region running to contact the dorsal stripe, which can be bordered with cream. Dark markings are present posterodorsal to the tympanum, below the eye, and around the nostril, above the insertion of the arm, sometimes on the middle of the flank, on the suprascapular region, and in the inguinal region. The dorsal forelimb is light peach to beige, with a dark crossband on the forearm. The hand is internally cream, laterally as the rest of the forelimb, with a small whitish annulus before each terminal phalange. The cloacal region is black. The legs are

sand brown to light peach to beige in dorsal coloration, with one gray-brown to dark brown crossband on the thigh, two on the shank, and one each on the tibiofibular and metatarsal regions of the foot. The toes are mottled cream and dark brown. Ventrally mauve in base color, fading to peach over the chin, with light lemon flecks on the abdomen. The ventral thighs and feet smoke colored, translucent over the anterior portion of the thigh. The iris is golden with black reticulations.

Variation. For variation in measurements among specimens, see Table 3. All examined specimens agree strongly with the holotype in morphology, and have highly similar coloration, except ZSM 494/2005, which has no distinct dorsal stripe, and has a dark spot centrally over the pectoral region and lacks inguinal spots. A dark spot is always present above the insertion for the arm and over the tympanum. The legs are as the holotype. Ventral coloration in preservative can be mottled with beige, brown, or gray, except in ZSM 493/2005, where the venter is flecked with brown anteriorly and under the chin.

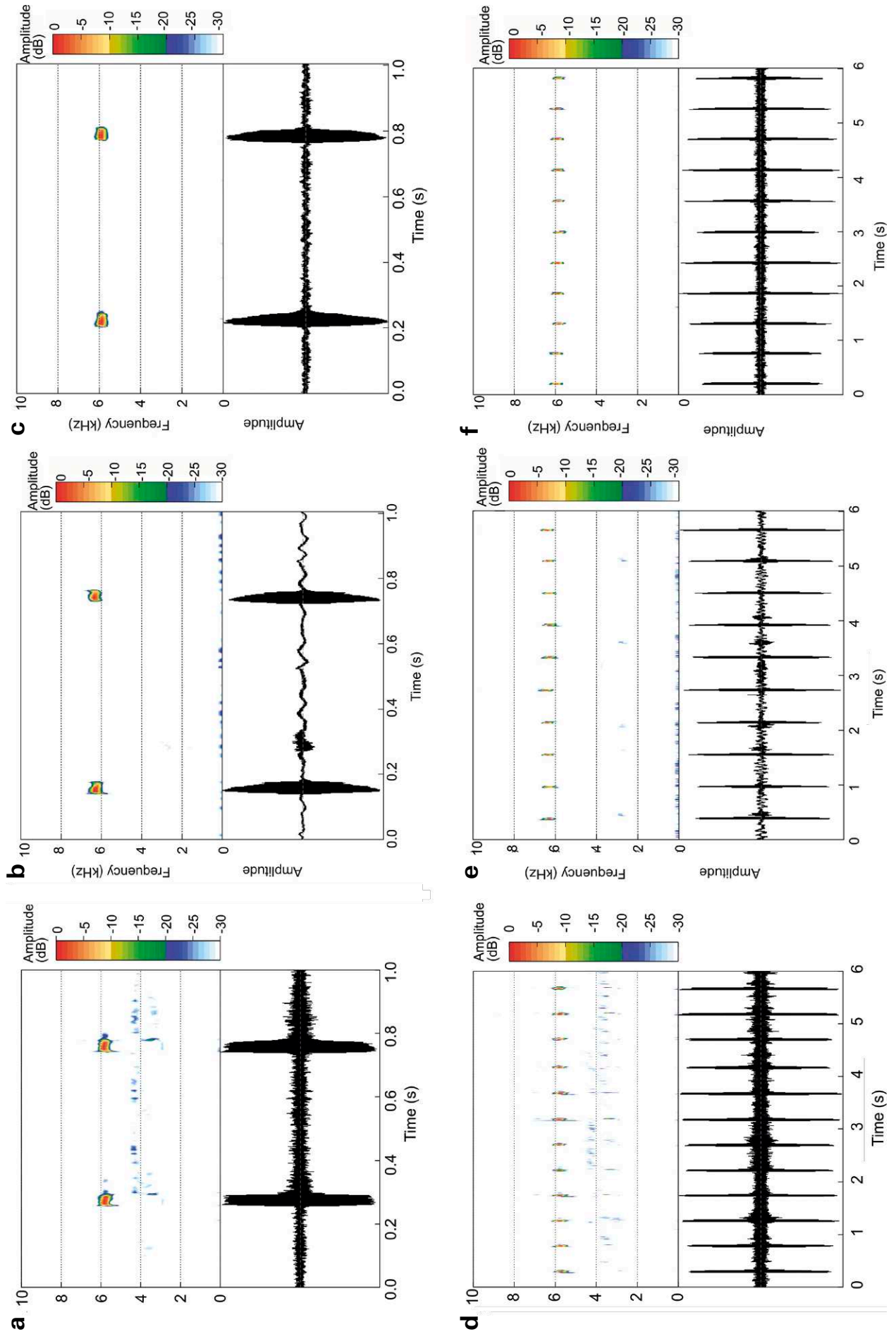
Etymology. The species name is a patronym honoring Achille P. Raselimanana, in recognition for his substantial contributions to the study and conservation of the herpetofauna of Madagascar.

Distribution. The species is known only from Marojejy National Park, between 450–581 m above sea level.

Natural history. Calling specimens were heard during the day from leaf litter in primary rainforest, in the late afternoon and in the night shortly after dusk. In November, one male specimen (ZSM 533/2016) was found in a water-filled empty snail shell along with 86 unpigmented (white) early embryos of 2.5 mm in diameter, surrounded by a jelly capsule of 5.1 mm in diameter (average values). The embryos were identified as *S. achillei* by DNA barcoding. They were in different embryonal stages (75 eggs in stage 11, and 11 eggs in stage 13, according to GOSNER, 1960); therefore, and because of their high number, it is probable that they originated from different females. This discovery constitutes further evidence that foam nest building is not the rule among *Stumpffia* species, and their reproductive habits are more diverse than previously thought.

Call. The advertisement call of *S. achillei* consists of a single, short and high-pitched note repeated in series at fast succession. Recordings are available from three different calling male that are here assigned to this species (Fig. 64): (1) Calls recorded by F. Glaw on 29 March 1994 (18:00 h) in Marojejy National Park at an air temperature of 23.4°C (VENCES *et al.*, 2006: CD3, track 46)

→ **Fig. 64.** Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia achillei* **sp. nov.** from Marojejy (1 s and 6 s duration section each): (a–d) call recorded from specimen ZFMK 59893; (b–e) call recorded from holotype ZSM 536/2016 (ZCMV 15149); (c–f) call recorded from specimen ZSM 535/2016 (ZCMV 15143).



had the following numerical parameters: call duration (= note duration) 45–79 ms (60 ± 10 ms; $N=13$), inter-call intervals 401–480 ms (422 ± 21 ms; $N=12$), and a dominant frequency at 5770–5986 Hz (5873 ± 60 Hz, $N=13$). (2) Calls recorded by M. Vences on 16 November 2016 (19:00 h; ca. 22°C air temperature) from specimen ZSM 535/2016 (ZCMV 15143) in Marojejy National Park with following parameters: call duration (= note duration) 40–52 ms (44.3 ± 3.4 ms; $N=10$), inter-call intervals 518–582 ms (545 ± 16 ms; $N=10$), and a dominant frequency at 5813–6072 Hz (5917 ± 95.7 Hz, $N=10$). (3) Calls recorded by M. D. Scherz on 16 November 2016 (ca. 22°C air temperature) from holotype ZSM 536/2016 (ZCMV 15149) in Marojejy National Park with following parameters: call duration (= note duration) 36–46 ms (41.8 ± 3.1 ms; $N=10$), inter-call intervals 507–527 ms (515.8 ± 7.9 ms; $N=10$), and a dominant frequency at 6287–6459 Hz (6351.5 ± 58.2 Hz, $N=10$).

Stumpffia analanjirofo sp. nov.

(Figures 65 and S112)

Holotype. ZSM 489/2005 (ZCMV 873) (Fig. 65 a–b), adult female, collected on 22 February 2005 in Nosy Mangabe Special Reserve (ca. S15.500, E49.766, ca. 50–100 m above sea level), Toamasina Province, Madagascar, by F. Glaw, M. Vences, and R.D. Randrianaiaina.

Paratypes. ZSM 492/2005 (ZCMV 2178), ZSM 491/2005 (ZCMV 2104), UADBA (ZCMV 2161), UADBA (ZCMV 2105), and UADBA (ZCMV 2142), all with same collecting data as holotype; UADBA (ZCMV 7232), collected on an unknown date in Ambatoroma by J.E. Randrianirina; ZSM 225/2016 (ACZCV 0121), collected on 8 November 2013 at Sahambendrana (S17.89917, E49.21651, 447 m a.s.l.), Betampona Strict Nature Reserve by G.M. Rosa, D.J. Harris, M. Randriamialisoa, and H. Lava; ZSM 226/2016 (ACZCV 0224) and ZSM 227/2016 (ACZCV 0225), collected on 16 November 2013 at Vohitsivalana (S17.88473, E49.20378, 487 m a.s.l.), Betampona Strict Nature Reserve by A. Crottini, D. Salvi, E. Scanarini, and George.

Referred specimen. ZSM 490/2005 (ZCMV 889), with same collecting data as holotype, is not included in the type series due to the lack of reliable molecular data.

Diagnosis. A species from north eastern lowlands of Madagascar which has not previously been included in any study as a separate candidate species; listed under *Stumpffia tetradactyla* in GLAW & VENCES (2007), WOLLENBERG *et al.* (2008), and VIEITES *et al.* (2009). (1) Moderately large-sized species (female SVL 20.3–20.4 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers with very slightly enlarged discs, those of toes with moderately enlarged discs; (4) relative hand and foot length, HAL/SVL 0.24–0.25, FOTL/SVL 0.64–0.75; (5) dorsum moderately tubercular, with numerous distinct scattered tubercles which sometimes are large and even form small ridges; (6) dorsally tan, with large indistinct symmetrical dark markings. Ventral skin transparent to translucent in life, with a few cream and dark gray flecks behind the

pectoral girdle, on the chin, and on the ventral legs, without any red color elements.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by distinctly larger body size; from *S. be*, *S. kibomena*, *S. meikeae*, and *S. roseifemoralis* by the lack of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern. Furthermore, distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction; from *S. be*, *S. hara*, and *S. staffordi* by smaller body size, and from them and *S. megsoni* also by stronger length reduction of first toe. Within clade C2 the species is the direct sister group to *S. achillei*, which also occurs in the eastern lowlands and which is rather closely related (16S divergence 3.0%). A bioacoustic comparison of the two species is currently impossible due to the lack of call recordings of *S. analanjirofo*; however, due to concordant differentiation in mitochondrial and nuclear genes, the absence of a clear broad dorsal light brown stripe, and the strikingly tubercular dorsum of *S. analanjirofo*, we here describe it as distinct species, a hypothesis that requires confirmation from future studies.

Description of the holotype. Specimen in good state of preservation, a part of right thigh removed as a tissue sample. Body elongate; head slightly wider than long, narrower than body width, snout slightly pointed in dorsal view, slightly pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis not distinct, concave; loreal region concave, oblique; tympanum distinct, about 68% of eye diameter; supratympanic fold not visible; tongue long, slightly broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, round; outer metacarpal tubercle distinct, small, oval; inner metacarpal tubercle distinct, elongate; fingers without webbing; no reduction of fingers; relative length of fingers $1 < 2 < 4 < 3$, fourth finger longer than second; finger tips expanded into discs. Hind limbs slender; TIBL 49% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced; toe tips expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles indistinct. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After 10 years in 70% ethanol, the dorsum is beige mottled with brown. A brown chevron rises anteriorly from the inguinal region. Inguinal spots are present. The dorsal surface of the head is beige mottled with brown. A brown heart shape is present

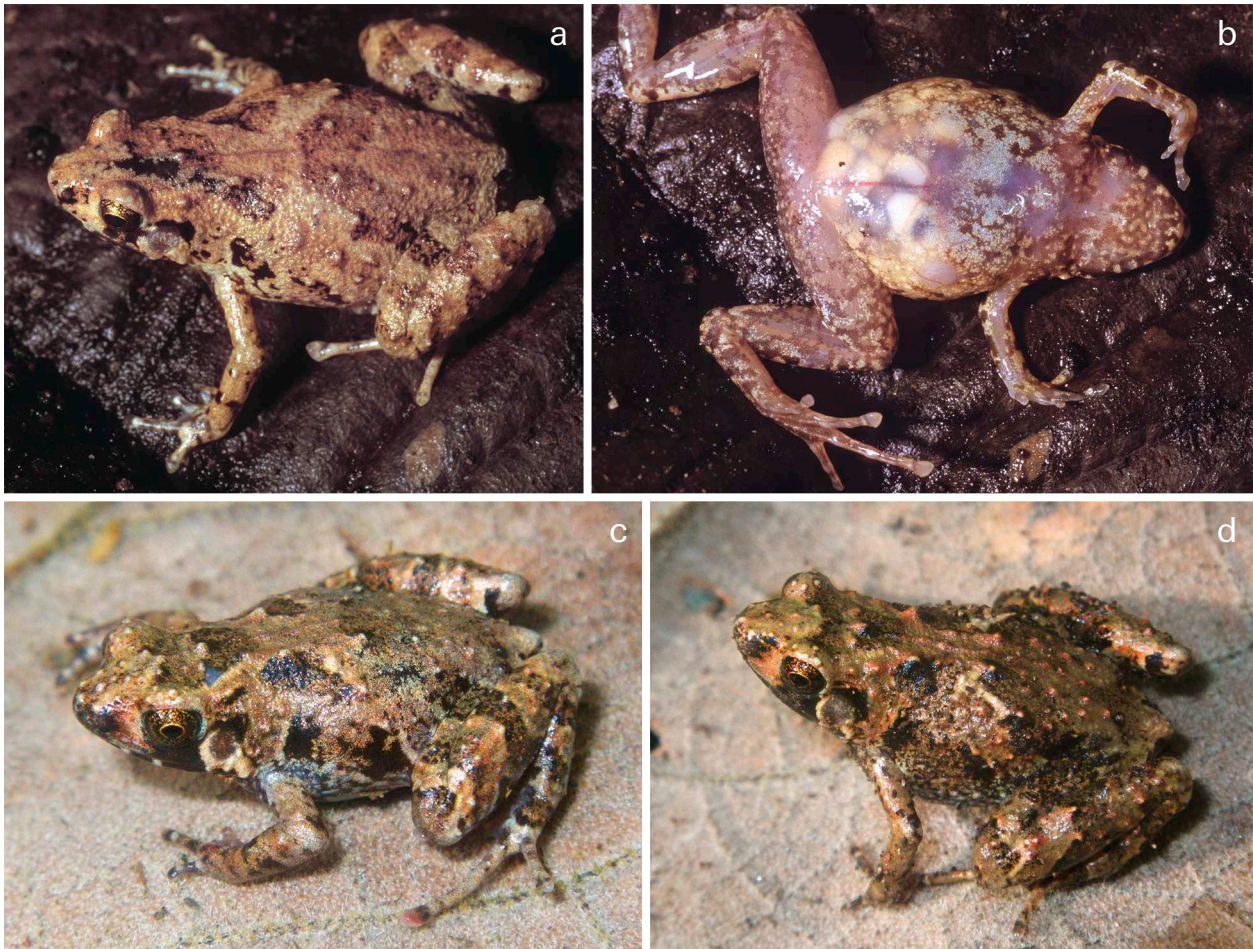


Fig. 65. *Stumpffia analanjirofo* sp. nov. in life: (a–b) holotype ZSM 489/2005 (ZCMV 873) from Nosy Mangabe; (c) ZSM 226/2016 (ACZCV 0224) from Betampona; (d) ZSM 227/2016 (ACZCV 00225) from Betampona.

in the scapular region. The nostril is light brown. The lateral surface of the head is beige mottled with brown. The flanks are as the lateral surface of the head. The flank coloration merges with the ventral coloration. The ventral trunk is uniformly beige in the middle and laterally beige mottled with brown. The chin is more mottled with brown than the trunk. The ventral thigh is as the chin. The shank ventrally is more mottled with brown than the thigh. The tarsus and foot are ventrally as the shank. Dorsally, the thigh is beige mottled with brown, with a dark brown crossband. The posterodorsal surface of the thigh is beige mottled with brown. The shank is as the tarsus with two fine dark brown crossband. The tarsus is as the shank without crossbands. The foot and toes are as the shank. The cloacal region is brown. The arms are beige mottled with brown. A dark brown crossband is present on the forearm. The dorsomedial surface of the hand is beige mottled with brown. The fingers have small white crossbands. The underside of the arm is as the lateral part of the ventral trunk.

Color in life (holotype and variation). Dorsal base color tan. Chocolate markings are present over the suprascapular region (common also to all of the paratypes) and in a chevron from the inguinal region to the mid-back (more

or less complete in all paratypes). A dark spot is present on the dorsal head between the eyes of the holotype (possibly a scar). The flank is flecked with irregular ebony markings, including one around the nostril, one over the tympanum (present in all paratypes), one over the insertion of the forelimb (present in all paratypes), and one on the midbody (present in all specimens). The dorsal forelimb is as the back, with one incomplete ebony crossband on the forearm. The hand is mottled tan and ebony. A light annulus is present on each finger before the terminal phalange. The dorsal hindlimb is as the back, with two chocolate crossbands on the thigh and three on the shank. Three crossbands are present on the feet of the paratypes, and presumably also present on the holotype, but not visible from images. The toes are tan, with a white annulus before each terminal phalange. The ventral skin is mostly transparent. Mottled cream and brown pigment is present on the abdomen, chin, and legs. The iris is golden reticulated with black.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. In the paratypes, a brown interocular bar is present. Paratypes from Betampona Strict Nature Reserve have tubercles on

the back, which can be particularly numerous, such as in ZSM 227/2016 (ACZCV 0225). ZSM 226/2016 (ACZCV 0224), and ZSM 227/2016 (ACZCV 0225) present a shade of copper coloration on top of the overall tanned color. The tan/ebony pattern in some specimens is strongly contrasted as in ZSM 225/2016 (ACZCV 0121), but in others quite muted.

Etymology. The species name is a noun in apposition to the genus name and refers to the known range of the new species with localities in the so-called Analanjirofo region in eastern Madagascar.

Distribution. Known from three localities in eastern Madagascar: (1) Nosy Mangabe Special Reserve (type locality), (2) Betampona Strict Nature Reserve, and (3) Ambatoroma. In Betampona this species has thus far been found only around Sahambendrana and Vohitsivalana campsites, which are located in the center and north-west of the Reserve, respectively.

Natural history. In Betampona this species seems to be uncommon (or have secretive habits) and so far restricted to intermediate elevations within the protected area (records are thus far available from 447–487 m a.s.l.).

Call. Unknown.

Stumpffia diutissima sp. nov.

(Figures 66 and S113)

Holotype. ZSM 378/2005 (FGZC 2751), an adult male, collected on 14 February 2005 in Camp Mantella, Marojejy National Park, (S14.421, E49.4376, 481 m above sea level), Antsiranana Province, Madagascar by F. Glaw, M. Vences, and R.D. Randrianiaina.

Paratypes. ZSM 376/2005 (FGZC 2742) and UADBA (FGZC 2730) collected on 14 and 15 February 2005 in Camp Mantella, Marojejy National Park (S14.421, E49.4376, 481 m a.s.l.) by F. Glaw, M. Vences, and R.D. Randrianiaina; ZSM 495/2005 (ZCMV 2067) collected on 18 February 2005 in Camp Marojejy National Park, (S14.4333, E49.4977, 746 m a.s.l.) by F. Glaw, M. Vences, and R.D. Randrianiaina; ZSM 496/2005 (ZCMV 2082) collected on 19 February 2005 in Marojejy National Park between Camp Marojejy and Camp Mantella by F. Glaw, M. Vences, and R.D. Randrianiaina; UADBA-ZCMV 15057, ZSM 546/2016 (ZCMV 15064), ZSM 548/2016 (ZCMV 15077), UADBA-ZCMV 15078, UADBA-ZCMV 15116, and ZSM 547/2016 (ZCMV 15117), all collected on 15 November 2016 at a campsite called ‘Camp 0’ in Marojejy National Park (S14.44633, E49.78523, 310 m a.s.l.) by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences; ZSM 549/2016 (ZCMV 15144) and ZSM 553/2016 (ZCMV 15153) collected on 16 November 2016 in Camp Mantella, Marojejy National Park (S14.43766, E49.77557 456 m a.s.l.) by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences.

Diagnosis. A moderately large-sized species from the north-east of Madagascar. It has been previously listed as *Stumpffia* sp. 13 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017), as *Stumpffia* sp. 3 in WOLLENBERG *et al.* (2008), as *Stumpffia*

sp. ‘Marojejy 1’ in GLAW & VENCES (2007). It might also correspond to the species listed and figured as *Stumpffia* sp. c in GLAW & VENCES (1994). (1) Moderately large-sized species (SVL up to 20.0 mm; adult male SVL 13.6–15.9 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers with very slightly, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.21–0.22, FOTL/SVL 0.70–0.73; (5) dorsum smooth; (6) dorsally highly variable in coloration, brownish to reddish to yellowish with dark brown to black pattern or mottling, with a distinctly lighter patch on the postero-dorsal shank. Ventrally light with or without dark mottling, especially in the throat region; (7) regularly repeated single-note tonal call with short note duration.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by larger body size of most specimens; from *S. be*, *S. kibomena*, *S. meikeae*, and *S. roseifemoralis* by the lack of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern. Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction; from *S. hara*, *S. megsoni*, and *S. staffordi* by smaller body size and stronger length reduction of first toe; from *S. analanjirofo* by a less tubercular dorsum; from *S. psologlossa* by an unpulsed call; from *S. analamaina*, *S. gimmeli*, *S. madagascariensis*, *S. pygmaea*, *S. angeluci*, *S. larinki*, *S. maledicta*, *S. mamitika*, *S. be*, *S. tridactyla*, *S. obscoena*, and probably also *S. huwei* and *S. kibomena*, by a shorter advertisement call duration; and from the sympatric *S. achillei* by a much longer inter-note interval duration.

Description of the holotype. Specimen in a good state of preservation, right thigh muscle removed as a tissue sample. Body elongate; head slightly wider than long, narrower than body; snout pointed in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, straight; loreal region straight, slightly oblique; tympanum distinct, about 67% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, indistinct; outer metacarpal tubercle indistinct, rounded; prepollex present, large, oval; fingers without webbing; first finger reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger distinctly longer than second; finger tips not expanded into discs. Hind limbs slender; tibiotarsal articulation reaching anterior eye corner; TIBL 52% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, thin, oval; outer metatarsal tubercle absent; no

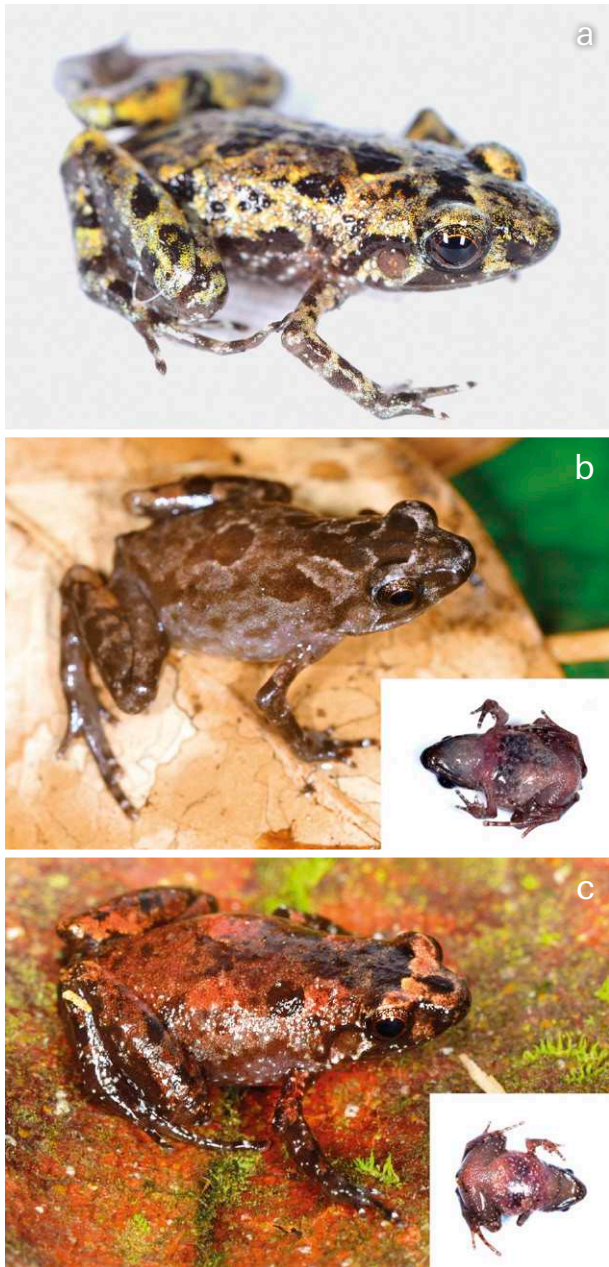


Fig. 66. *Stumpffia diutissima* sp. nov. from Marojejy National Park in life: (a) ZSM 546/2016 (ZCMV 15064); (b) ZSM 549/2016 (ZCMV 15144); (c) ZSM 547/2016 (ZCMV 15117). Small inset photos showing ventral surfaces.

webbing between toes; first toe strongly reduced; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After 10 years in 70% ethanol, the dorsum is brown. Dark irregular mottling is present on the back. No distinct spot is present in the inguinal region. The dorsal surface of the head is as the back. A dark horizontal interocular bar is present. The nostril is surrounded by brown. The lateral surface of the head is brown, with a few cream flecks below the tympanic region. The flanks fade to a lighter brown ventrally, and

become increasingly spotted with cream. The flank coloration merges with the ventral coloration; the ventral trunk is light brown mottled with cream. The chin is as the ventral trunk but with less cream. The ventral thigh is light brown with a few cream dots. The shank and tarsus are ventrally as the thigh. The sole of the foot is light brown. Dorsally, the thigh is as the dorsum. The posterodorsal surface of the thigh is light brown like the ventral surface. The shank is dorsally also as the thigh, except for a light area from the heel to the mid-shank on the internal surface. The tarsus and foot are dorsally as the shank; the foot is dorsomedially cream. The toes are light brown with cream flecks. The cloacal region is dark brown. The arms are as the dorsum. The dorsomedial surface of the hand is cream. The fingers have small white flecks. The underside of the arm is as the ventral trunk.

Color in life (variation). Coloration is highly variable in life. Dorsally can be mostly patternless brown with head a dark sooty orange, lightening through burnt umber to brown posteriorly (unidentified specimen Fig. 66a), or can be yellowish, reddish, or brownish in base color with a series of black to russet markings on the back (Fig. 66b). Whatever the dorsal pattern, the legs and arms match it, such that the plain brown specimen has plain brown arms and legs, whereas ZSM 546/2016 has yellow and black arms and legs to match its dorsum, and ZSM 549/2016 has light brown arms with dark brown spots to match its dorsum, etc. In all specimens, the posterior shank is a lighter color than the rest of the legs, ranging from coppery to lemon yellow to clay (Fig. 66). In some specimens, there are hints of pattern elements that might give rise to a teddybear shape if connected, such as a heart-shaped marking over the posterior head in ZSM 549/2016. A white annulus is always present on each toe before the terminal phalange. The ventral skin is translucent and consequently plum to flesh in color, flecked with white over the abdomen and ventral legs (Fig. 66). Iris copper around the pupil, darkening externally.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree with the holotype in morphology. In all paratypes, the canthus rostralis is concave and distinct, the first toe is less reduced than in the holotype, and toes 2–5 have slightly expanded terminal discs. Several specimens lack prepollices, and have small, oval inner metatarsal tubercles. A high degree of variability was noted in the coloration of specimens in preservative, that reflects also their variability in life. In all specimens, a lighter area is present between the mid-shank and heel. This is most strongly visible in ZSM 495/2005, and weakest in the holotype. Wholly brown chin was noted only in the holotype and ZSM 495/2005, which are also the only specimens with distinct prepollices.

Etymology. The species name is derived from the Latin adverb “diutissime” meaning “for a long time” and refer-

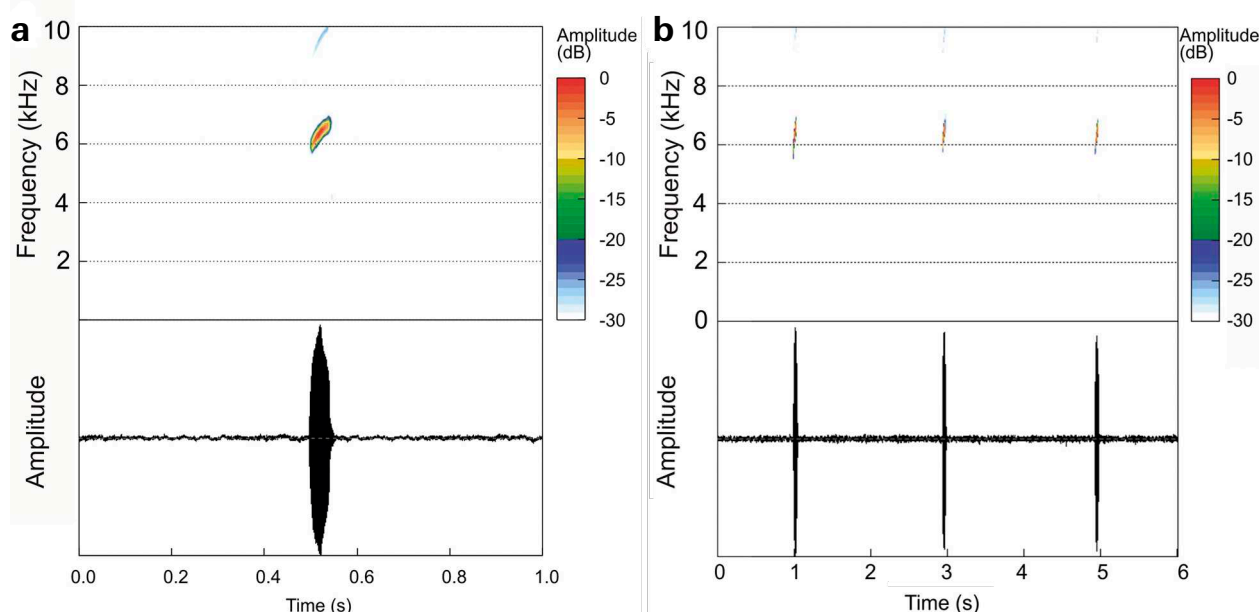


Fig. 67. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia diutissima* sp. nov. from Marojejy National Park (call recorded from ZSM 549/2016, ZCMV 15144): (a) 1 s duration section; (b) 6 s duration section.

ring to the considerable amount of time it took to describe this species after its initial collection and identification as new species in 1994. The species name is used as an adjective in the feminine nominative singular as also done previously by some Latin authors.

Distribution. The species is known only from Marojejy National Park at elevations between 310–750 m a.s.l.

Natural history. Calling males were found in the leaf litter of primary rainforest in the afternoon and in the evening.

Call. The advertisement call of *S. diutissima* consists of a single, short, tonal note emitted in series at regular intervals (Fig. 67). Calls recorded by A. Rakotoarison on 16 November 2016 from specimen ZSM 549/2016 (ZCMV 15144) in Marojejy National Park at an air temperature estimated around 22°C had the following parameters: call duration (= note duration) 53–56 ms (54.6 ± 1 ms; $N=10$), inter-call intervals 1775–2200 ms (1924.1 ± 126.8 ms; $N=10$), and a dominant frequency at 6459–6632 Hz (6498.3 ± 51.8 Hz, $N=10$).

Stumpffia edmondsi sp. nov.

(Figures 68 and S114)

Holotype. ZSM 371/2005 (FGZC 2677), collected on 9 February 2005 from Vohidrazana (S18.95, E48.5, ca. 700–800 m above sea level), Toamasina Province, Madagascar by F. Glaw, R.D. Randrianiana, and R. Dolch.

Paratype. ZSM 1731/2012 (RDR 1065), collected on 6 November 2011 in the Andasibe region at the entrance to the Analamazaotra Forest Station (sometimes called the Mitsinjo Reserve), near the road leading to Andasibe, by M. Vences, D. Edmonds, R.D. Randrianiana, and A. Rakotoarison.

Diagnosis. A rather inconspicuous species from the northern central east which has been previously listed as *Stumpffia* sp. 8 in VIEITES *et al.* (2009), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017), and as *Stumpffia* sp. 2 in WOLLENBERG *et al.* (2008). (1) Moderately-sized species (adult male SVL 17.4 mm); (2) manus with four fingers (first finger moderately reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers without, those of toes with very slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.25, FOTL/SVL 0.61–0.72; (5) dorsum smooth; (6) dorsally ebony, with irregular and poorly contrasted black patches and speckled with a few small iridescent whitish flecks. Posterodorsal shank can be burnt orange. Ventrally translucent skin, apricot on the posterior belly and ventral inguinal region; (7) regularly repeated single-note tonal call (heard in the wild but not recorded).

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by larger body size; from *S. be*, *S. kibomena*, *S. meikeae*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on limbs (except for a limited amount of burnt orange on posterodorsal shank); from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi* by smaller body size and stronger length reduction of first toe; from *S. achillei* by dorsal color pattern; from *S. analanjirofo* by a less tubercular dorsum. Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by distinctly lower degree of digital length reduction. *Stumpffia diutissima* has a somewhat



Fig. 68. *Stumpffia edmondsi* sp. nov. from Andasibe in life: (a–b) dorsal and ventral view of paratype ZSM 1731/2012 (RDR 1065).

similar color pattern but belongs to a different subclade of C1, and, though variable in coloration, seems to have more transparent ventral skin.

Description of the holotype. Specimen in good state of preservation, right thigh muscle removed as a tissue sample for DNA extraction. Body elongate; head slightly longer than wide, narrower than body width; snout pointed in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct, concave, loreal region concave, oblique; tympanum distinct, about 42% of eye diameter; supratympanic fold not visible; tongue long, slightly broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs thick; subarticular tubercles single, slightly distinct; outer metacarpal tubercle small, oval; prepollex distinct, thick, elongate; fingers without webbing; first finger reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger longer than second; finger tips slightly expanded into discs. Hind limbs slender; TIBL 53% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, elongate; outer metatarsal tubercle absent; no webbing between toes; first toes reduced; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After 10 years in 70% ethanol, the dorsum is beige with a broad brown band running from the scapular region to the inguinal region. Elongate brown patches are present in the inguinal region. The dorsal surface of the head is dark brown. The nostril is brown. The lateral surface of the head is beige mottled with brown. The flanks are beige mottled with brown spots, which continues ventrally onto the ventral abdomen and legs. The sole of the foot is brown mottled with beige. Dorsally, the thigh is brown mottled with beige,

including its posterodorsal surface. The shank, tarsus, and foot are as the thigh, seemingly without a distinctly different color to the posterodorsal shank. The cloacal region is brown. The arms are dorsally and ventrally as the dorsum. The dorsomedial surface of the hand is as the lower arm. The fingers are cream mottled with brown.

Color in life (paratype ZSM 1731/2012). Dorsal base coloration ebony. Irregular, asymmetrical black markings are present, most notably forming oblong spots in the inguinal region, and an interocular bar on the posterior half of the eye. This bar is anteriorly bordered by a lighter brown. The dorsum is sparsely interspersed with iridescent whitish flecks. The dorsal forelimb is as the dorsum. The hand is internally rosy brown, laterally as the rest of the forelimb, with a small whitish annulus before each terminal phalange. The hindlimbs are as the dorsum except that the posterior shank is burnt orange. The foot is dorsally as the shank, with a small whitish annulus before each terminal phalange. The ventral skin is translucent. Whitish flecks are present on the lower jaw. Silvery flecks are present at and behind the pectoral gridle, becoming decreasingly dense posteriorly. The lateral abdomen is apricot. The ventral legs are taupe. The iris is dark.

Variation. For measurements of the holotype and paratype, see Table 3. In general, the paratype specimen agrees strongly with the holotype in morphology, except that the tongue broadens more strongly posteriorly; small palmar metacarpal tubercle distinct, round; several small differences in color pattern exist, the most notable of which is the presence of a distinct, burnt orange posterodorsal shank in life (beige in preservative), which is absent from the holotype.

Etymology. The species name is a patronym honoring Devin Edmonds to whom we are glad to dedicate this species in recognition for his efforts in amphibian conservation in Madagascar, and for his help in collecting the paratype specimen of this new species.

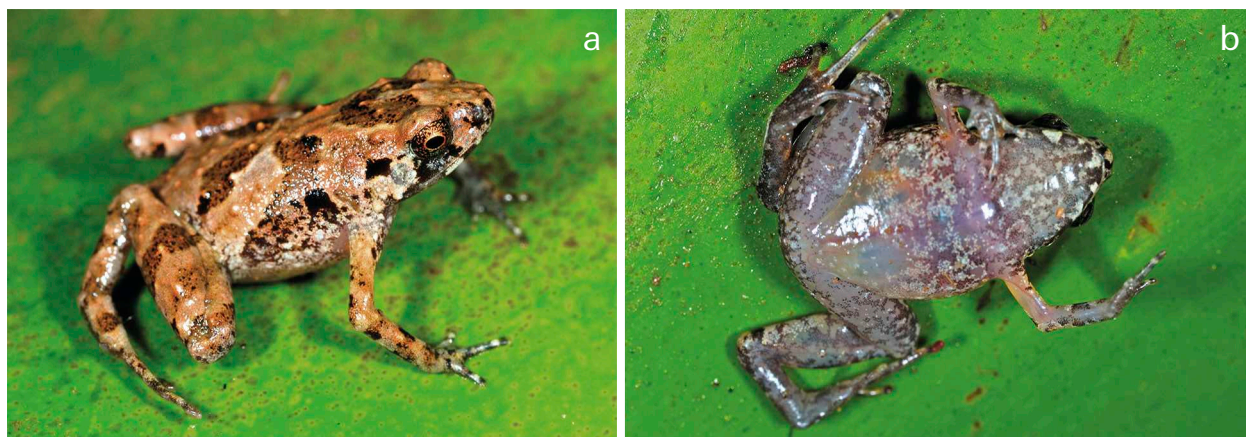


Fig. 69. *Stumpffia fusca* sp. nov. from Ambodivoangy in life: (a–b) dorsolateral and ventral view of paratype ZSM 436/2010 (FGZC 4253).

Distribution. The species is known from forests at Vo-hidrazana and near Andasibe, around 700–800 m above sea level.

Natural history. One calling male was found in dense leaf litter along the trail in Analamazaotra forest near Andasibe.

Call. Unknown.

Stumpffia fusca sp. nov.

(Figures 69 and S115)

Holotype. ZSM 437/2010 (FGZC 4254), an adult ovigerous female, collected on 2 April 2010 in Ambodivoangy (S15.2899, E49.6202, ca. 100 m above sea level), Toamasina Province, Madagascar by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, and F.M. Ratsoavina.

Paratype. ZSM 436/2010 (FGZC 4253) with same collecting data as holotype.

Referred specimens. UADBA (FGZC 4207) collected on 31 March 2010 in Ambodivoangy (S15.2899, E49.6202, ca. 287 m a.s.l.) by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, and F.M. Ratsoavina (not included as paratype because no DNA sequence data is available for this specimen).

Diagnosis. A rather inconspicuous species from north-eastern lowlands of Madagascar which has been previously listed as *Stumpffia* sp. 33 in PERL *et al.* (2014) whereas the species was not included in SCHERZ *et al.* (2016); in that study, *Stumpffia* sp. Ca33 corresponds to *S. meikeae*, described above. (1) Moderately-sized species (female SVL 17.7 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe very strongly reduced in length); (3) terminal phalanges of fingers without, those of toes with moderately enlarged discs; (4) relative hand and foot length, HAL/SVL 0.23–0.26, FOTL/SVL 0.72–0.78; (5) dorsum smooth with numerous small, distinct regularly scattered tubercles; (6) dorsally tawny, with large symmetrical black copper-infused markings covering much or

most of the dorsum. Ventral skin translucent with many large cream flecks, and without any red color elements.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by larger body size in unambiguously adult specimens; from *S. be*, *S. kibomena*, *S. meikeae*, and *S. roseifemoralis* by lack of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi* by smaller body size. From *S. achillei*, *S. diutissima*, and *S. edmondsi*, and in general from most other large-sized *Stumpffia*, by the more expressed length reduction of first toe. Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by lower degree of digital length reduction (especially on fingers). By color pattern reminiscent of the closely related *S. achillei* and *S. analanjirofo*, but these species differ strongly in mitochondrial and nuclear DNA sequences, and the specimens examined have a less expressed length reduction of first toe; *S. analanjirofo* may also have a somewhat more tubercular dorsum.

Description of the holotype. Specimen in a good state of preservation, the right foot removed as a tissue sample for DNA extraction. An incision was made in the right flank to check the sex. Body elongated; head slightly wider than long, narrower than body; snout pointed in dorsal view, slightly pointed in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region concave, slightly oblique; tympanum distinct, about 69% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, indistinct; outer metacarpal tubercle subtriangular; palmar tubercle round; inner metacarpal tuber-

cle oblong, distinct; fingers without webbing; first finger slightly reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly shorter than second; finger tips not expanded into discs. Hind limbs slender; TIBL 51% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle oval, distinct; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced; toe tips expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third; subarticular tubercles distinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After five years in 70% ethanol, the dorsum is brown. A dark brown heart-like marking is present on the head, extending to the shoulder region. This is followed posteriorly by two blackish spots either side of the midline. These are followed by large, oblique, light brown markings extending down the flanks. A black spot is present in the inguinal region (two small spots on the right). Finally, a triangular light brown patch is present from between the inguinal regions to the vent. The nostril is surrounded by dark brown. The lateral surface of the head is beige speckled with black. Dark flecks are present under the eye and over the tympanum. The flanks fade from the dorsal markings to the cream of the venter. The ventral trunk is cream. The chin is flecked with light brown. The ventral thigh is light brown flecked with cream. The shank is ventrally light brown with few cream flecks. The tarsus is ventrally as the shank. The sole of the foot is brown. Dorsally, the thigh is beige with two oblique brown crossbands. The posterodorsal surface of the thigh is cream with brown flecks. The shank is light brown with three oblique crossbands. The tarsus is as the shank with one crossband. The foot is light brown with dark brown flecks. The toes are cream speckled with brown. The cloacal region is dark brown. The arms are beige speckled with dark brown. A dark crossband is present on the lower arm. The dorsomedial surface of the hand is cream. The fingers have small brown speckles. The underside of the arm is as the ventral trunk.

Color in life (paratype ZSM 436/2010). Dorsal base coloration is tawny, with semi-symmetrical black markings with iridescent copper infusions: a pair of broad lines converging on the midline from the inguinal region, a pair of broad markings running from behind the suprascapular region to the flank, and a sub-triangular marking starting between the eyes and narrowing to a point between the suprascapulae. The flank fades to a cream mottled with taupe, and possesses two black spots, one posterodorsal to the insertion of the arm, and one posterodorsal to the tympanum. The lateral head has two further black spots, one broad beneath the eye, and one on the nostril. The dorsal arm is as the dorsum, interspersed with black flecks. A whitish annulus is present before the terminal phalange of each finger. The dorsal leg is as the back, with one black crossband with copper infusions on the mid-thigh, one on the mid-shank, and two on the foot. The toes are mottled, with a light band present before

each terminal phalange. The ventral skin is translucent and thus plum, densely flecked with cream markings on the chin and posterior to the pectoral gridle, fading posteriorly. Two off-white markings are present on the bottom lip on either side of the head, one beneath the eye, one beneath the nostril. The anterior point of the mandible is also off-white. The ventral legs are plum flecked with dark gray. The iris is copper.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. A low degree of variability was noted in the coloration of specimens; ZSM 436/2010 is almost identical to the holotype in dorsal coloration, but overall lighter. Ventrally it is clean cream.

Etymology. The species name is the feminine nominative singular form of the Latin adjective *fusca*=brown. It refers to the various brown markings of the dorsum of this species.

Distribution. The species is known only from its type locality Ambodivoangy, at ca. 100 m above sea level.

Natural history. At the type locality, specimens were collected from the leaf litter on the forest floor during daytime. Nothing else is known of the species' habits.

Call. Unknown.

Stumpffia jeannoeli sp. nov.

(Figures 70 and S116)

Holotype. ZSM 206/2016 (ACZCV 0056), adult male, collected on 8 November 2013, at Sahaindrana (S17.8968, E49.1995, 344 m above sea level), Betampona Strict Nature Reserve, Toamasina Province, Madagascar by A. Crottini, D. Salvi, E. Scanarini, and J.H. Velo.

Paratypes. MRSN A6283 (FAZC 13682), collected on 28 February 2007 at Vohitsivalana (S17.8862 E49.2024, 517 m a.s.l.) by G.M. Rosa; MRSN A6386 (FAZC 13903), adult male, collected on 19 November 2007 along Piste Principale (S17.902250, E49.215270, 514 m a.s.l.) by G.M. Rosa, F. Andreone, and J. Noël; MRSN A6281 (FAZC 13599), MRSN A6284 (FAZC 13587), MRSN A6245 (FAZC 13556) and MRSN A6284 (FAZC 13587), all collected between 7 and 11 February 2007 at Sahambendrana (S17.8983, E49.2153, 458 m a.s.l.) by G.M. Rosa and F. Andreone; MRSN A6261 (FAZC 13711) and MRSN A6287 (FAZC 13729) collected on 6 and 8 March 2007 at Sahabefoza (S17.9142, E49.2076, 349 m a.s.l.) by G.M. Rosa; MRSN A6307 (FAZC 13622), MRSN A6318 (FAZC 13656), and MRSN A6277 (FAZC 13651) collected between 19 and 22 February 2007 at Maintimbato (S17.894 E49.2282, 255 m a.s.l.) by G.M. Rosa; MRSN A6346 (FAZC 13900) collected on 18 November 2007 at Maintimbato (S17.8952, E49.2266, 277 m a.s.l.) by G.M. Rosa, F. Andreone and J. Noël; ZSM 208/2016 (ACZCV 0218) collected on 15 November 2013 at Vohitsivalana (S17.88501, E49.20339, 481 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, and George; ZSM 207/2016 (ACZCV 0167) collected on 22 November 2013 at Maintimbato (S17.8938, E49.2250, 274 m a.s.l.) by G.M. Rosa, D.J. Harris, M. Randriamialisoa, and H. Lava; ZSM 209/2016 (ACZCV 0118)



Fig. 70. *Stumpffia jeannoeli* sp. nov. paratype specimens from Betampona Strict Nature Reserve in life: (a–b) ZSM 208/2016 (ACZCV 0218); (c) ZSM 211/2016 (ACZCV 0062); (d) ZSM 210/2016 (ACZCV 0070); (e) ZSM 209/2016 (ACZCV 0118); (f) ZSM 207/2016 (ACZCV 0167); (g) MRSN A6245; (h–i) MRSN A6307; (j) MRSN A6346; (k–l) MRSN A6386.

collected on 07 November 2013 at Sahambendrana (S17.8990, E49.2163, 455 m a.s.l.) by G.M. Rosa, D.J. Harris, M. Randriamialisoa, and J.H. Lava; ZSM 210/2016 (ACZCV 0070) collected on 11 November 2013 at Rendrirendry (Piste Fotsimavo) (S17.9230, E49.2086, 204 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, George, G.M. Rosa, D.J. Harris, M. Randriamialisoa, and H. Lava; ZSM 211/2016 (ACZCV 0062) and ZSM 212/2016 (ACZCV 0063) collected on 7 and 8 November 2013 at Sahaindrana (S17.8968, E49.1995, 344 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, and J.H. Velo; ZSM 213/2016 (ACZCV 0247) collected on 7 and 8 November 2013 at Sahabefoza (S17.9127, E49.2106, 478 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, J.H. Velo, F. Andreone, J. Noël, and S. Faravelli. All these localities refer to sites within Betampona Strict Nature Reserve, Toamasina Province, East Madagascar.

Diagnosis. A moderately sized species from the northern central east which has been previously listed as *Stumpffia* sp. 20 in VIEITES *et al.* (2009), SCHERZ *et al.* (2016) and

PELOSO *et al.* (2017) and as *Stumpffia* sp. [Ca FJ559315] and as *Stumpffia* sp. aff. *grandis* [Ca HM364799] in ROSA *et al.* (2011, 2012). (1) Moderately-sized species (SVL 16–20 mm, adult male SVL 17 mm); (2) manus with four fingers (first finger moderately reduced in length, especially in males) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers without, those of toes with very slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.17–0.22, FOTL/SVL 0.55–0.73; (5) dorsum smooth with a few scattered tubercles; (6) dorsally mocha to tan, with variably intense darker patches of variable size and number. Ventrally variable, but always with a pattern of light spots. The heel is often distinctly different in color to the rest of the leg. No red color ventrally; (7) regularly repeated single-note tonal call.

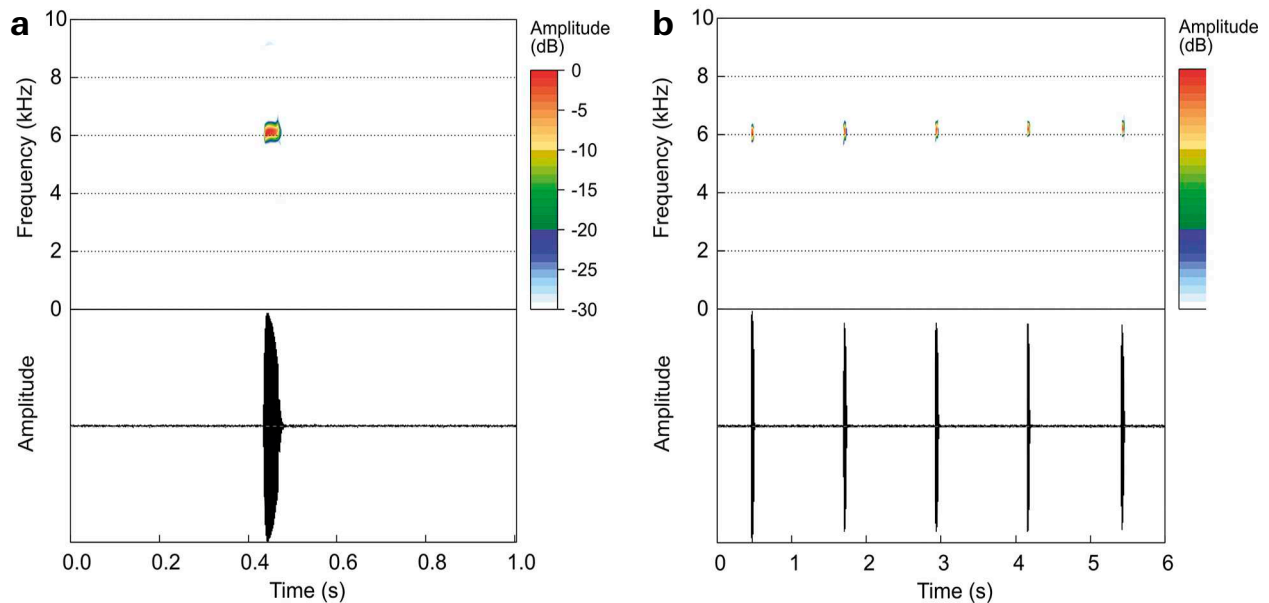


Fig. 71. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia jeannoeli* **sp. nov.** from Betampona, MRSN A6386 (FJ559315): (a) 1 s duration section; (b) 6 s duration section.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by larger body size; from *S. be*, *S. kibomena*, *S. meikeae*, and *S. roseifemoralis* by lack of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi* by smaller body size; from *S. achillei* by distinctly longer inter-call intervals; from *S. analanjirofo* and *S. fusca* by a less tubercular dorsum and different dorsal and ventral pattern; from *S. diutissima* by slightly shorter call duration and shorter inter-call intervals; from *S. edmondsi* by the brownish rather than reddish color on dorsal part of shank around tibiotarsal articulation. Furthermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetractyla*, and *S. tridactyla* by lower degree of digital length reduction (especially on fingers). Phylogenetically, the species is placed in a subclade of clade C1 of unresolved internal nodes; within this subclade, morphologically similar species are only *S. edmondsi* and *S. nigrorubra* **sp. nov.** (described below) but both of these species have at least some reddish color on hindlimbs and at least *S. nigrorubra* also differs bioacoustically (see below).

Description of the holotype. Specimen in a good state of preservation, tongue removed as a tissue sample for DNA analysis. Body elongate; head slightly wider than long, narrower than body width; snout rounded in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to the tip of snout than to eye; canthus rostralis slightly visible, concave; loreal region concave, oblique; tympanum distinct, about 76% of eye diameter;

supratympanic fold not distinct; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle slightly visible, rounded; inner metacarpal tubercle visible, oval, fused with the prepollical tubercle; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, fourth finger longer than second; finger tips not expanded into discs. Hind limbs slender; TIBL 50% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle not visible; outer metatarsal tubercle absent; no webbing between toes; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe slightly shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is uniformly pinkish beige. A brown heart shape bordered with a champagne line is present in the scapular region. A brown oval is present in the inguinal region. The dorsal surface of the head is as the back with irregular brown spots. The nostril is surrounded with beige. The lateral surface of the head is dark brown spotted with beige. The flanks are laterally beige flecked with brown, ventrally beige with white flecks. The lower flank coloration merges with the ventral coloration. The ventral trunk is beige with white flecks bordered with a brown line. The chin is as the abdomen. The ventral thigh is as the abdomen. The shank is ventrally beige spotted with dark brown. The tarsus and foot are ventrally as the shank but darker. Dorsally, the thigh is pink-reddish and beige with brown crossband. The posterodorsal surface of the thigh is beige spotted with brown. The shank and tarsus are as the back, with reddish color on the posterodorsal shank. The foot is beige with brown crossband. The toes are speckled with brown. The cloacal region is dark

brown. The arms are as the dorsum. A dark crossband is present on the lower arm. The dorsomedial surface of the hand is beige. The fingers are beige spotted with brown. The underside of the arm is as the ventral trunk.

Color in life (variation among paratypes; see Fig 70). Dorsal base coloration ranges from mocha to tan. Darker markings, oftenly bordered by a thin light line, are present, which range from faintly darker than the base color (e.g. Fig. 70k) to black and strongly contrasting (e.g. Fig. 70j). The markings follow a fairly consistent pattern: a dark bar is present posterior to the mid-ocular line and is generally delimited in front with a thin champagne line; a small fleck is present on the snout; on the dorsum there can be an X-like marking between the suprascapulae and a second X-like marking on the mid-dorsum (Fig. 70a, c, h, k). The cloacal region also has a trapezoidal dark marking (weakly visible in Fig. 70a, c, d, j, k). The lateral face is continuous with the dorsal head, except for the dark nostril. Posterior to the eye, a discontinuous, irregular band of dark markings runs along the flank, always incorporating the tympanum. The dorsal forelimb is as the dorsum, with several dark markings, including a crossband on the forearm. The hand is internally as the dorsum, and laterally dark, with a white annulus before the terminal phalange of each finger. The dorsal leg is as the dorsum, with one dark crossband at the mid-thigh, one on the shank, and up to four on the foot. The posterodorsal shank tends to have a unique color, which can be almost yellow (Fig. 70d, f) or russet (Fig. 70g, j) the anterior forelimb usually has the same color as this shank region, but slightly weaker (Fig. 70g). The dorsal foot is as the rest of the leg, the toes being mottled, with a white annulus before each terminal phalange. The ventral coloration is highly variable, and can be almost ebony brown with numerous whitish flecks (Fig. 70i), dark mocha with white flecks and with translucent beige chin and posterior trunk (Fig. 70l), or a beige with larger white flecks bordered with a brown line (Fig. 70b). Density, size, and position of whitish flecks are not consistent. The iris is golden.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. A low variability was noted in the coloration of specimens in preservative; ACZCV 0218 has a pinkish coloration in the arm and in the legs; in MRSN A6386 the dorsal pattern is less contrasted, resulting in an almost uniform brown coloration.

Etymology. The species name is a patronym honoring Jean Noël, a talented research guide and passionate her-

petologist working at Betampona Strict Nature Reserve, on behalf of Madagascar Fauna and Flora Group in recognition of his assistance and friendship. His interest has contributed boosting herpetological research in Betampona and led to the identification of numerous new species of amphibians and reptiles inhabiting this remnant forest fragment of the east coast.

Distribution. This species is so far known only from Betampona Strict Nature Reserve, where it is thought to have a broad distribution, being found in most of the surveyed areas (Rosa *et al.* 2012), from around 200–517 m above sea level.

Natural history. The holotype was found, together with other individuals of the same species during the day in the leaf litter. Several individuals were calling simultaneously from hidden positions on the ground. However, the species is most often heard calling at dusk and at night, particularly when it is drizzling or lightly raining. This species appears to be quite abundant across the Reserve.

Call. The advertisement call consists of a single, short tonal note emitted in series at regular intervals (Fig. 71). Calls recorded by G.M. Rosa (ROSA *et al.*, 2011: track 51) on 6 November 2007 at Betampona (21:45 h, air temperature 21°C) had the following numerical parameters: call duration (= note duration) 43–45 ms (44.2 ± 0.8 ms; $N=6$), inter-call intervals 1183–1220 ms (1195.2 ± 17 ms; $N=5$), and a dominant frequency at 6072–6244 Hz (6166.6 ± 76.9 Hz, $N=6$).

Stumpffia nigrorubra sp. nov.

(Figures 72 and S124)

Holotype. ZSM 2448/2007 (ZCMV 5967) (Fig. S124), collected in February–March 2007 from a locality along the road between Ifanadiana and Tolongoïna, Fianarantsoa Province, Madagascar (approximately at S21.35, E47.62) by M. Vences.

Paratypes. ZSM 641/2003 (FG/MV 2002.163), an adult male, collected on 15 January 2003 in Ranomafana by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas, and D.R. Vieites; ZSM 640/2003 (FG/MV 2002.162), adult male, collected on 15 January 2003 in Ranomafana village by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas, and D.R. Vieites; ZMA 20201 (ZCMV 17) collected on 18 January 2004 at the type locality by M. Vences; ZMA 20202 (ZCMV 98) collected on 21 January 2004 in Ambohitsara (S21.4697 E48.0613, 294 m a.s.l.) by D.R. Vieites and I. de la Riva; ZMB 81994 (JCR 5), calling male, collected on 3 September 2010 in Ambolo forest fragment, Ranomafana (S21.26359, E47.50921, 643 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; UADBA-A 43170 (JCR 29) collected on 12 March 2010 in Ambatolahidimy forest, Ranomafana (S21.24831, E47.41987, 1006 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; ZMB 81996 (JCR 562), calling male, collected on 11 February 2011 in a banana plantation, Anan-

→ **Fig. 72.** Dorsolateral and ventral views of life specimens of *Stumpffia nigrorubra* sp. nov.: (a, h) UADBA-A 43170 (JCR 29), male from Ambatolahidimy, Ranomafana; (b) calling male from Manombo Reserve; (c) ZMB 81998 (NSH 2599), male from Manombo village forest; (d, g) ZSM 640/2003 (FG/MV 2002.162) from Ranomafana village; (e, i) JCR 3154, male from Manombo village forest, see nuptial pads on right hand; (f) ZMB 81994 (JCR 5), male from Ambolo, Ranomafana, illustrating red coloration on heels and outer parts of thighs.



itehana, Ranomafana (S21.26549, E47.44296, 782 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; UADBA-A 62126 (JCR 678), calling male, collected on 10 March 2011 in a banana plantation, Andalangina, near Ifanadiana (S21.29712, E47.59951, 515 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; ZMB 81997 (JCR 855), calling male, collected on 16 April 2011 in Sahadikaina forest fragment, Ranomafana (S21.24658, E47.52178, 643 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; UADBA-A 62125 (NSH 1322), collected on 27 January 2011 in Ambolo forest fragment (S21.26307, E47.50696, 660 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; ZMB 81995 (NSH 1416), gravid female, collected on 3 February 2011 in Andalangina forest fragment (S21.29644, E47.59872, 551 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; UADBA-A 62127 (NSH 2197) collected on 24 May 2011 in a coffee and banana plantation, Andalangina, near Ifanadiana (S21.29862, E47.60222, 450 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; ZMB 81999 (JCR 3245), collected on 4 April 2012 in a banana plantation, Andalangina, near Ifanadiana (S21.29712, E47.59951, 515 m a.s.l.) by J.C. Riemann and S.H. Ndriantsoa; UADBA-A 64052 (JCR 3246), calling male, collected on 3 April 2012 in a gallery forest near Ambatolahy, Ranomafana (coordinates not taken) by J.C. Riemann and S.H. Ndriantsoa; ZMB 81998 (NSH 2599) and JCR 3154, calling males, collected on 29 March 2012 in forest near Manombo village (S23.02521, E47.72515, 46 m a.s.l.) by J.C. Riemann, S.H. Ndriantsoa, M.-O. Rödel, J. Glos, and A. Rakotoarison.

Diagnosis. A species from the southern central east of Madagascar that has previously been listed as *Stumpffia* sp. 1 in WOLLENBERG *et al.* (2008), as *Stumpffia* sp. 9 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017), and as *Stumpffia* sp. ‘Ranomafana’ in GLAW & VENCES (2007). (1) Moderately-sized species (adult male SVL 17.4–17.7 mm); (2) manus with four fingers (first finger distinctly reduced in length at least in males) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers with slightly enlarged discs, those of toes with very slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.23–0.24, FOTL/SVL 0.52–0.72; (5) dorsum smooth to slightly granular; (6) dorsally mottled black and dark iridescent dirty golden with irregular and indistinct pattern of lighter and darker elements, and without sharp color border between color of dorsum and flanks. Posterodorsal part of shank with rust red color. Ventrally with rust red color on posterior belly and hindlimbs, gray-brownish with white dotting on anterior belly, chest and throat; (7) regularly repeated short single-note tonal call.

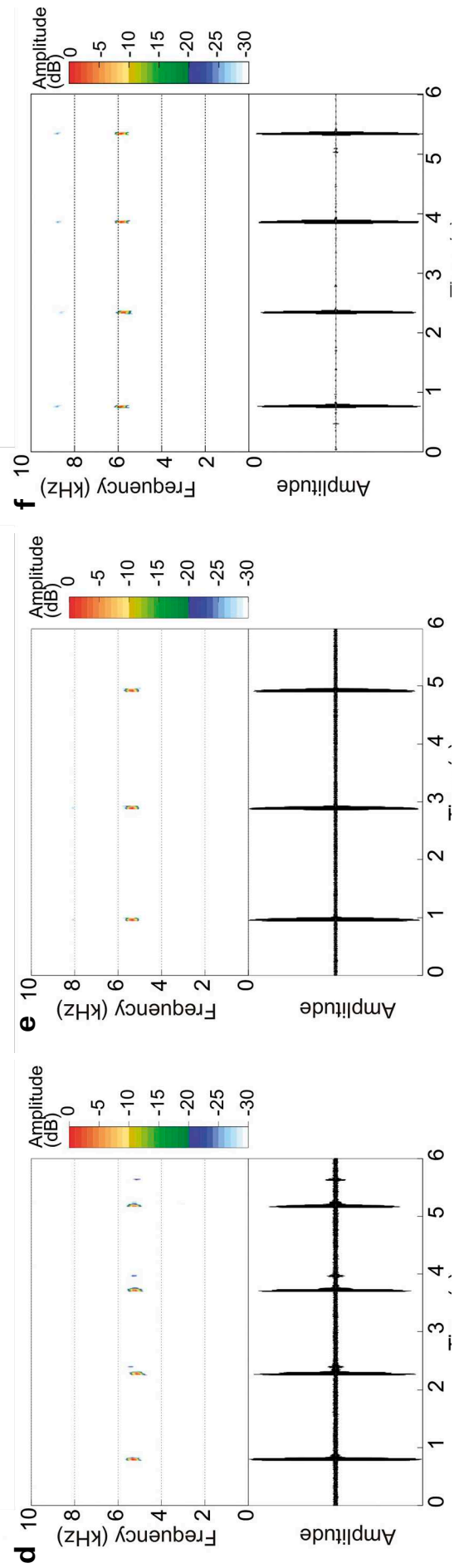
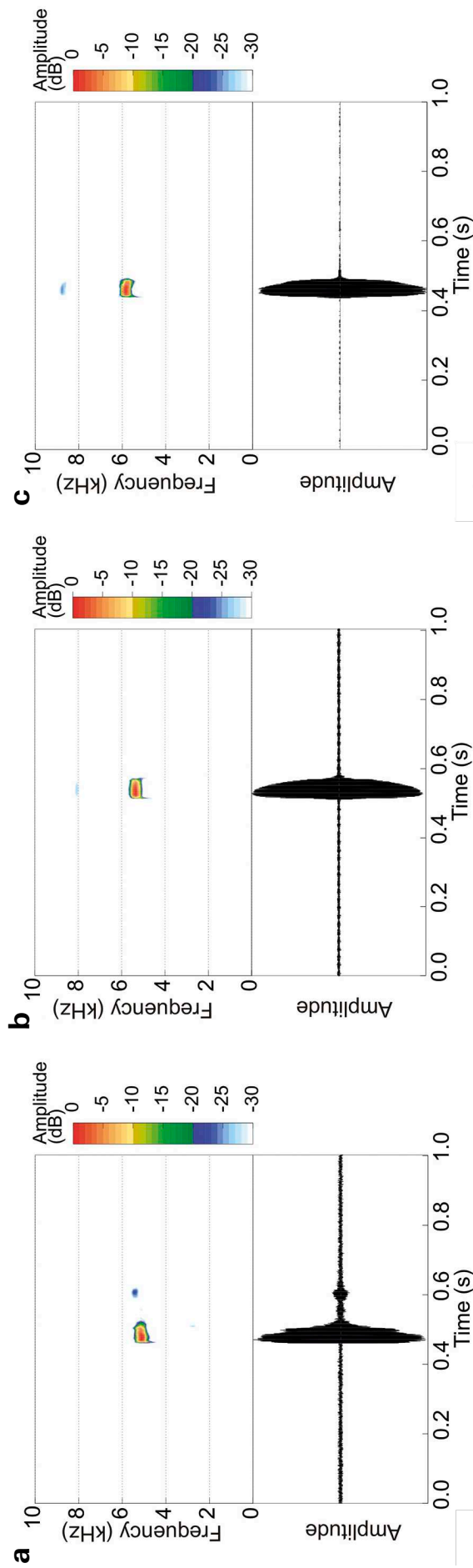
Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by larger body size; from all these species and *S. achillei*, *S. analanjirofo*, *S. diutissima*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. megsoni*, and *S. staffordi* by the presence of distinct rust red color ventrally on belly and hindlimbs, as well as posterodorsally on the shanks; fur-

thermore distinguished from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, *S. tetradactyla*, and *S. tridactyla* by lower degree of digital length reduction (especially on fingers); and from *S. analanjirofo* by a less tubercular dorsum. Distinguished from *S. be* by smaller body size and presence of red color on belly (vs. only on hindlimbs); from *S. kibomena* by indistinct dorsal pattern and longer inter-note intervals; from *S. roseifemoralis* and *S. meikeae* by darker dorsal color and presence of red color posterodorsally on shanks. Morphologically most similar to *S. edmondsi*, which is in the same phylogenetic subclade but does not seem to be the direct sister species of *S. nigrorubra*, has less red color on belly, and does not share haplotypes in Rag-1.

Description of the holotype. Specimen in good state of preservation, left thigh muscle removed as a tissue sample for DNA analysis. Body elongate; head slightly longer than wide, narrower than body; snout pointed in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region concave, oblique; tympanum distinct, about 61% of eye diameter; supratympanic fold not distinct; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, slightly distinct; outer metacarpal tubercle not recognizable; inner metacarpal tubercle distinct, oval; fingers without webbing; first finger reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger longer than second; finger tips slightly expanded into discs. Hind limbs slender; TIBL 56% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, slightly visible, oval; outer metatarsal tubercle absent; no webbing between toes; first toe reduced; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After eight years in 70% ethanol, the dorsum is beige vermiculated with brown. The dorsal surface of the head is as the back. The nostril is brown. The lateral surface of the head is beige with brown dots. The flanks are beige with a brown stripe. The flank coloration merges with the ventral coloration. The ventral trunk is cream mottled with brown. The chin is darker than the abdomen. The ventral thigh is cream speckled with brown. The shank is ventrally brown speckled with beige. The tarsus is ventrally beige with darker dots. The sole of the foot is beige. Dorsally, the thigh is beige with brown crossband. The posterodorsal surface of the thigh is brown. The shank and the tarsus are similar to the thigh. The foot is brown mottled with beige. The toes are brown mottled with beige. A cream

→ **Fig. 73.** Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia nigrorubra* sp. nov. from Ranomafana: (a, d) 1 s and 6 s duration sections of male FG/MV 2002.162; (b, e) 1 s and 6 s duration sections of male ZMB 81999; (c, f) 1 s and 6 s duration sections of male ZMB 81999.



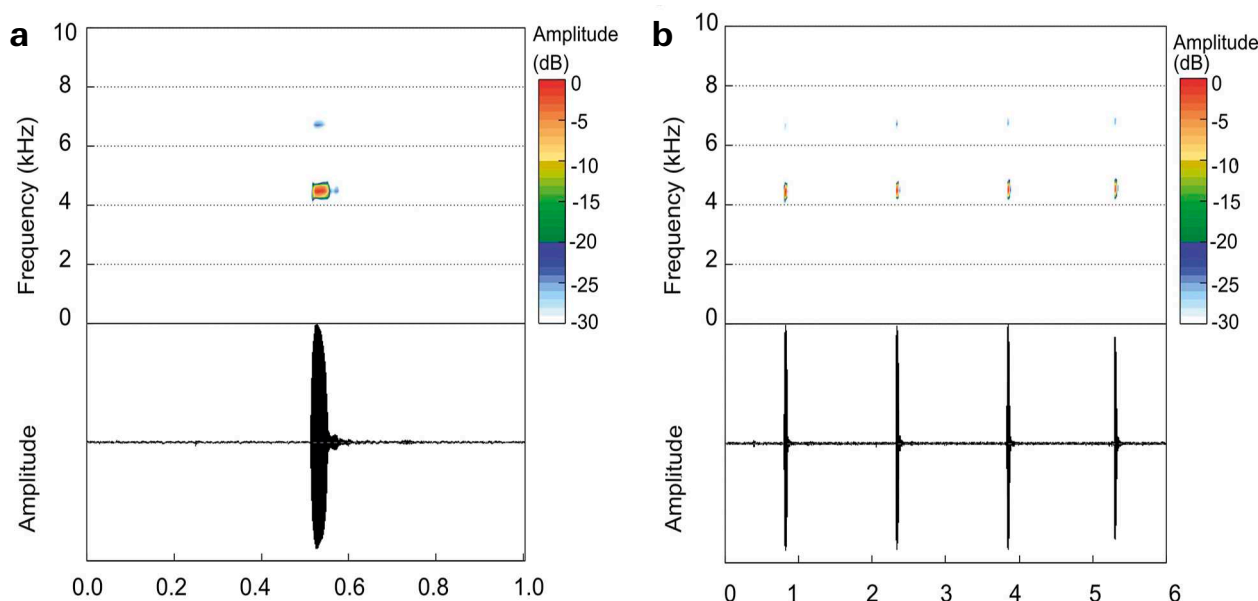


Fig. 74. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia nigrorubra* from Manombo (ZMB 81999): (a) 1 s duration section; (b) 6 s duration section.

marking is present on the posterodorsal face of the shank. The cloacal region is dark brown. The arms are dark brown. A beige crossband is present on the lower arm. The dorsomedial surface of the hand is dark brown. The fingers have beige crossbands. The underside of the arm is as the ventral trunk.

In life, dorsum mottled black and dark iridescent dirty gold. Flanks without color borders. A dark oblong marking is present on the flank, as well as fine irregularly sized whitish spots. Dorsal forelimb proximally rust red, fading to black distally. The hand is internally cream, laterally as the dorsum, with irregular whitish flecks, including an annulus before each terminal phalange. Hindlimb proximally black, becoming rust red dorsally by the mid-shank. The posterodorsal shank is strongly rust red. The foot is dorsally black, with irregular whitish flecks, including an annulus before each terminal phalange. The ventral chin is dark plum with small light flecks, becoming larger posteriorly. The plum of the anterior trunk merges into strong rust red over the abdomen, which covers the whole ventral legs. The ventral forelimbs are plum.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly the holotype in morphology. ZSM 640/2003 (FG/MV 2002.162) is strongly fixed; coloration pattern uniformly brown with dark brown dots. Advertisement calls of specimens from Manombo resemble those from Ranomafana in repetition rate, but differ in dominant frequency (4565–4608 Hz in Manombo vs. 5124–5857 Hz in Ranomafana; see below).

Etymology. The species name is a feminine nominative singular adjective derived from the Latin words *niger* = black and *ruber* = red, in reference to the black basal

coloration and red shank, abdomen, and ventral legs of this species.

Distribution. This species is known from various localities in the Ranomafana region, including: (1) road between Ifanadiana and Tolongoina (type locality), (2) Ambohitsara, (3) Ambolo forest fragment, (4) Ambatolahidimy forest, (5) Ananitehana, (6) Andalanagina, near Ifanadiana, (7) Sahadikaina forest fragment, (8) near Ambatolahy, and (9) Ranomafana village. Furthermore, it occurs (10) in a forest near Manombo village/Manombo Special Reserve, > 120 km south of Ranomafana, constituting the southernmost record for the genus *Stumpffia* (16S sequences show a 3.8% divergence to Ranomafana specimens; GenBank accession numbers MF768251–MF768252, not included in Fig. 3).

Natural history. The species occurs in rainforest habitat in Ranomafana National Park and is also common in forest fragments and banana plantations. Active individuals were observed in the leaf litter during the day and at night, however calling males were only found after dusk. Gravid females were found in the leaf litter in February 2011 in a forest fragment in Andalanagina. The species has a rather wide altitudinal range, from 46 m at Manombo up to over 1000 m a.s.l. in Ambatolahidimy forest. The karyotype has been described under the name *S. sp.* by APREA *et al.* (2007) for specimen ZMA 19420 (FG/MV 2002.449) from Ranomafana village.

Call. The advertisement call consists of a single short note emitted in series in slow regular succession (Figs. 73 and 74). Recordings are available from various localities in the Ranomafana region. (1) Calls recorded by M. Vences on 15 January 2003 at Ranomafana village from specimen ZSM 640/2003 (VENCES *et al.*, 2006: CD3, track

53) had the following numerical parameters: call duration (= note duration) 46–88 ms (67 ± 10 ms; $N=19$), inter-call intervals 1366–1720 ms (1472 ± 104 ms; $N=18$), and a dominant frequency at 5124–5426 Hz (5283 ± 70.5 Hz, $N=19$); (2) Calls recorded by J.C. Riemann and S.H. Ndriantsoa on 11 February 2011 at 20:25 h in a banana plantation near Ambatolahy, Ranomafana (air temperature 20.3°C) from specimen ZMB 81996 (JCR 562): call duration 69–75 ms (72 ± 3 ms; $N=3$), inter-call intervals 1421–1954 ms (1743 ± 283.5 ms; $N=3$), and a dominant frequency at 5426–5469 Hz (5440 ± 24.8 Hz, $N=3$); (3) Calls recorded by J.C. Riemann on 04 April 2012 at 21:15 h in a gallery forest near Ambatolahy (air temperature 21.5°C) from specimen ZMB 81999 (JCR 3245): call duration 56–63 ms (60 ± 3 ms; $N=4$), inter-call intervals 1421–1518 ms (1464 ± 49.4 ms; $N=3$), and a dominant frequency at 5727–5857 Hz (5813.5 ± 61 Hz, $N=4$); (4) Calls recorded by J.C. Riemann and S.H. Ndriantsoa on 29 March 2012 at night in a forest near Manombo village from specimen ZMB 81998 (NSH 2599): call duration 60–69 ms (65 ± 3 ms; $N=5$), inter-call intervals 1372–1453 ms (1416 ± 38 ms; $N=4$), and a dominant frequency at 4565–4608 Hz (4573 ± 19 Hz, $N=5$).

Stumpffia pardus sp. nov.

(Figures 75 and S117)

Holotype. ZSM 435/2010 (FGZC 4237) (Fig. 75 a), adult male, collected on 4 April 2010 at Ambodivoangy (S15.2899, E49.6202, ca. 100 m above sea level), Toamasina Province, Madagascar by F. Glaw, J. Köhler, P.-S. Gehring, M. Pabijan, and F.M. Ratsoavina.

Paratypes. Nine specimens collected at the same site and by the same collectors as holotype: ZSM 432/2010 (FGZC 4210), ZSM 433/2010 (FGZC 4213), ZSM 434/2010 (FGZC 4214), UADBA (FGZC 4216) and UADBA (FGZC 4217), all collected on 31 March 2010; ZSM 440/2010 (FGZC 4278) collected on 3 April 2010; ZSM 438/2010 (FGZC 4265), ZSM 439/2010 (FGZC 4268), and UADBA (FGZC 4239) collected on 2 April 2010; ZSM 230/2016 (ACZCV 0147) collected on 13 November 2013 at Betakonana (S17.91418, E49.21672, 356 m a.s.l.), Betampona Strict Nature Reserve, by G.M. Rosa, D.J. Harris, M. Randriamalisoa, and H. Lava; ZSM 770/2009 (ZCMV 11166) collected on 15 May 2009 from Melivinany-Manompana by J.E. Randrianirina; MRSN A2651 (FN 7021) collected on 2 December 1997 in Ambolokopatrika by F. Andreone and J.E. Randrianirina; MRSN A6204 collected on 17 March 2007 along the Piste Principale in Betampona Strict Nature Reserve (S17.9226, E49.1995, 438 m a.s.l.) by G.M. Rosa; MRSN A6276 (FAZC 13498) collected on 4 February 2007 in Rendriendry (S15.9316, E49.2034, 325 m a.s.l.), Betampona Strict Nature Reserve, by G.M. Rosa.

Diagnosis. A species from north-eastern lowland sites with a conspicuous and contrasted color pattern in many individuals, which has been previously listed as *Stumpffia* sp. 12 in VIEITES *et al.* (2009), as *Stumpffia* sp. aff. *tetradactyla* [Ca HM364800] by ROSA *et al.* (2012), and as *S.* sp. CaBetampona2 in SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Moderately large-sized species (adult male SVL 17.7–22.4 mm); (2) manus with four fingers (first finger slightly reduced in length) and pes with five toes (first toe slightly to distinctly reduced in length); (3)

terminal phalanges of fingers with slightly, those of toes with moderately enlarged discs; (4) relative hand and foot length, HAL/SVL 0.16–0.26, FOTL/SVL 0.67–0.88; (5) dorsum smooth to very slightly granular; (6) dorsally variable in color, most characteristically with reticulations of black spots with apricot borders on a background of copper, but can also be plum and brown, rosy brown, or silver with dark markings. Markings often forming a contrasted and symmetrical series of large patches on the central dorsum. The posterodorsal shank can be rust red to copper. Ventrally light, with or without a dark throat and light spots or vermiculations; (7) regularly repeated short single-note tonal call repeated after short intervals.

Distinguished from *S. analamaina*, *S. angeluci*, *S. contumelia*, *S. davidattenboroughi*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. miery*, *S. obscoena*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, *S. tridactyla*, and *S. yanniki* by larger body size; from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on limbs (only in some individuals, a limited amount of red on shank); from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. analanjirofo* and *S. fusca* by a less tubercular dorsum, and from these species and *S. achillei* by a different dorsal color pattern; from *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi* by smaller body size and stronger length reduction of first toe; from *S. diutissima* and *S. jeannoeli* by shorter inter-call intervals and lower dominant frequency; from *S. edmondsi* by a different dorsal color pattern in the majority of specimens. Phylogenetically the sister species of *S. diutissima*, a species that differs quite strongly in bioacoustics characters (longer inter-call interval, slightly longer call duration, higher dominant frequency) and is strongly divergent in mtDNA, despite sharing Rag-1 haplotypes.

Description of the holotype. Specimen in a good state of preservation, with its left arm removed as a tissue sample. Body elongate; head slightly longer than wide, narrower than body; snout pointed in dorsal and lateral view; nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct, concave; loreal region straight, almost vertical; tympanum indistinct, about 59% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimb thick; subarticular tubercles indistinguishable; outer metacarpal tubercle indistinct, oval; prepollex present; fingers without webbing; first finger reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly longer than second; finger tips not expanded into discs. Hind limbs slender; tibiotarsal articulation reaching center of eye; TIBL 49% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle indistinct, oblong; outer metatarsal tubercle absent; no webbing between toes; first toe reduced; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter



Fig. 75. *Stumpffia pardus* sp. nov. in life: (a) holotype ZSM 435/2010 (FGZC 4237); (b–e) paratype ZSM 439/2010 (FGZC 4268); (c–d) paratype ZSM 440/2010 (FGZC 4278), all from Ambodivoangy; (f–g) paratype ZSM 230/2016 (ACZCV 0147); (h–i) paratype MRSN A6204, both from Betampona Strict Nature Reserve.

than third; subarticular tubercles indistinguishable. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth. The skin of the flank and especially the anterior and posterior thigh is perforated with holes, ranging in size from 0.1 to 0.7 mm diameter. The cause of these holes is unknown, but we suppose that they may be caused by parasites.

Coloration of the holotype. After five years in 70% ethanol, the dorsum is dark brown. A few cream spots are present, but whether or not these are caused by parasites is unclear (see holotype description). No markings are present in the inguinal region. The dorsal surface of the head is as the back but more gray. The nostril is surrounded by brown. The lateral surface of the head is brown as the dorsum, the lip being more cream. A light cream marking extends from the posterior of the eye to the corner of the mouth in front of the tympanum, with a cream spot directly below the tympanum. The flanks fade from the brown of the dorsum to the cream of the ventral trunk, but are spotted with cream markings that may be caused by parasites. The ventral trunk is dark cream with light cream spots. The chin is as the ventral trunk. The

ventral thigh is as the ventral trunk. The shank and tarsus are ventrally beige. The sole of the foot is dark brown. Dorsally, the thigh is mottled dark and light brown. The posterodorsal surface of the thigh is light brown, with cream circular spots where skin is missing. The anterior surface of the thigh is dark brown with many of these spots where skin is missing. The shank is light brown with a dark brown oblique crossband and other flecks of dark brown. The tarsus is mottled light and dark brown. The foot is externally mottled light and dark brown, fading to cream internally. The toes are irregularly striped light and dark brown. The cloacal region is dark brown. The arm is mottled light and dark brown, without crossbands. The dorsomedial surface of the hand is cream. The fingers have small dark and light stripes. The underside of the arm is as the ventral trunk.

Color in life (total variation). Coloration extremely variable. Most characteristic coloration is a reticulated pattern of black spots with apricot borders on a background of reddish-copper (Fig. 75b), but dorsal coloration can also be fairly plain plum and brown (Fig. 75a) a rosy brown with X-shaped ebony markings (Fig. 75c), or reddish with

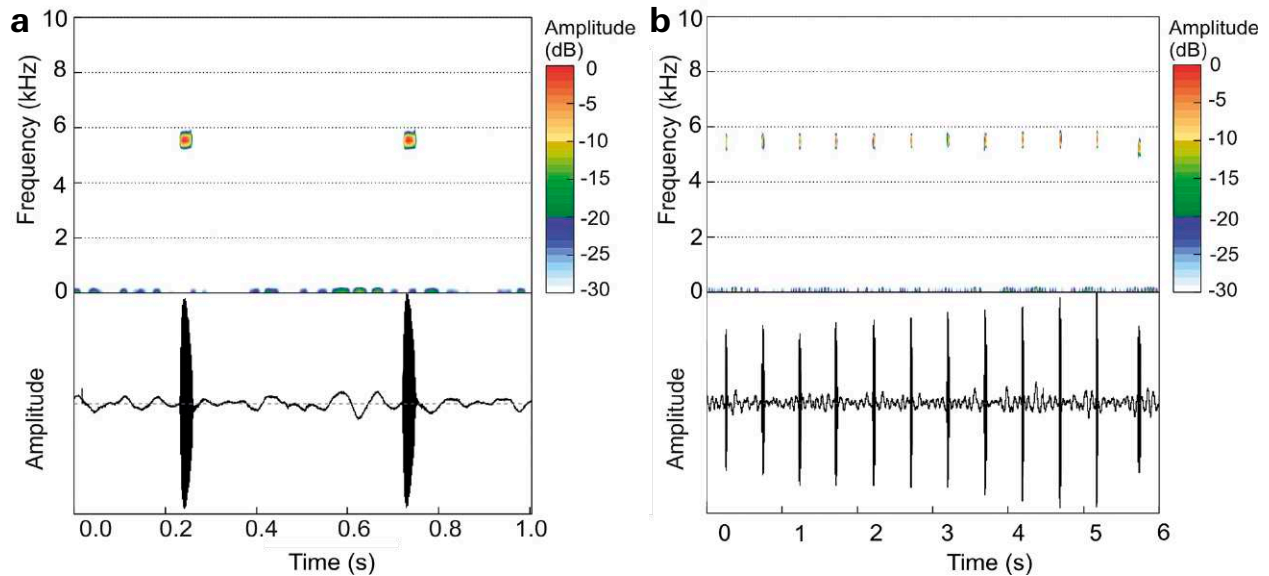


Fig. 76. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia pardus* sp. nov. recorded at Ambodivoangy from the holotype (ZSM 435/2010): (a) 1 s duration section; (b) 6 s duration section.

black to burnt umber irregular markings. Ventral coloration is similarly variable, and can be translucent plum (Fig. 75d), burnt umber with plum and white spots (Fig. 75e), or brown with cream to white spots or vermiculations (Figs. 75g, i). Most specimens seem to have a rusty red to copper posterior shank. All specimens have a white annulus before each terminal phalange of their fingers and toes. The iris ranges from dark brown to copper to gold.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. In almost all paratypes, the canthus rostralis is more distinct than in the holotype. All specimens except the holotype have slightly expanded finger tips, and most also have a distinctly longer fourth finger than second. In specimens without a prepollex, the first finger is still reduced. A high degree of variability was noted in the coloration of specimens in preservative. Four distinct color morphs were noticeable in our eight type specimens. The first is that of the holotype (N=1). The second (N=4; ZSM 440/2010, 439/2010, 770/2009, and 438/2010) is figured in Fig. 75b-e. In preservative, these specimens have a light base color ranging from light brown to fuchsia with dark markings. These markings generally consist of a cross-like diffuse blotch on the back surrounded by smaller dark markings, but these range from strong to weak. In some specimens, a dark dot is present on the rostrum. Dark flecks continue onto the legs and arms, forming a shank crossband in some specimens. All of these specimens have a pink to fuchsia marking on the posterodorsal shank. The third (N=1; ZSM 433/2010) is like the second, but the dorsal patterning is more irregular and reminds of a leopard's spots. This also has a pink marking on the posterodorsal shank. The fourth (N=2; ZSM 432/2010 and 434/2010) consists of a gray base-color with the whole dorsum flecked with irregular dark

gray markings. The posterodorsal shank lacks the distinct lighter area. Ventral coloration of these four groups is inconsistent; ventral coloration ranges from cream like the holotype to dark brown in ZSM 438/2010. The bottom lip of all specimens is brown with irregular cream spots.

Etymology. The species name is a noun in apposition to the generic name, derived from Greek *πάρδος* (*párdos*)=male leopard, in reference to the leopard-like pattern of some specimens of this species.

Distribution. This species has a wide distribution along the north-eastern Madagascan coast including four confirmed localities: (1) Ambodivoangy (type locality), (2) Ambolokopatrika, (3) Melivinany-Manompana, and (4) Betampona Strict Nature Reserve. In Betampona this species has thus far been found only around the Rendriren-dry and Betakonana campsites, which are located in the southern part of the Reserve. The specimens from Ambodivoangy and Ambolokopatrika are slightly differentiated genetically from those occurring at Betampona and Melivinany. The altitude ranges from 320–440 m a.s.l.

Natural history. At both, Betampona and Ambodivoangy, specimens were found in leaf litter at night. Males called during light rain from the ground not hiding under litter (Fig. 75a).

Call. The advertisement call consists of a single, very short note emitted in series and fast succession (Fig. 76). Calls recorded by J. Köhler on 2 April 2010 at Ambodivoangy from the holotype ZSM 435/2010 (FGZC 4237) had the following numerical parameters: call duration (= note duration) 35–44 ms (38.3 ± 2.3 ms; N=12), duration of inter-call intervals 467–495 ms (479.3 ± 7.6 ms; N=12), and a dominant frequency at 5124–5383 Hz (5264.5 ± 73.3 Hz, N=12).

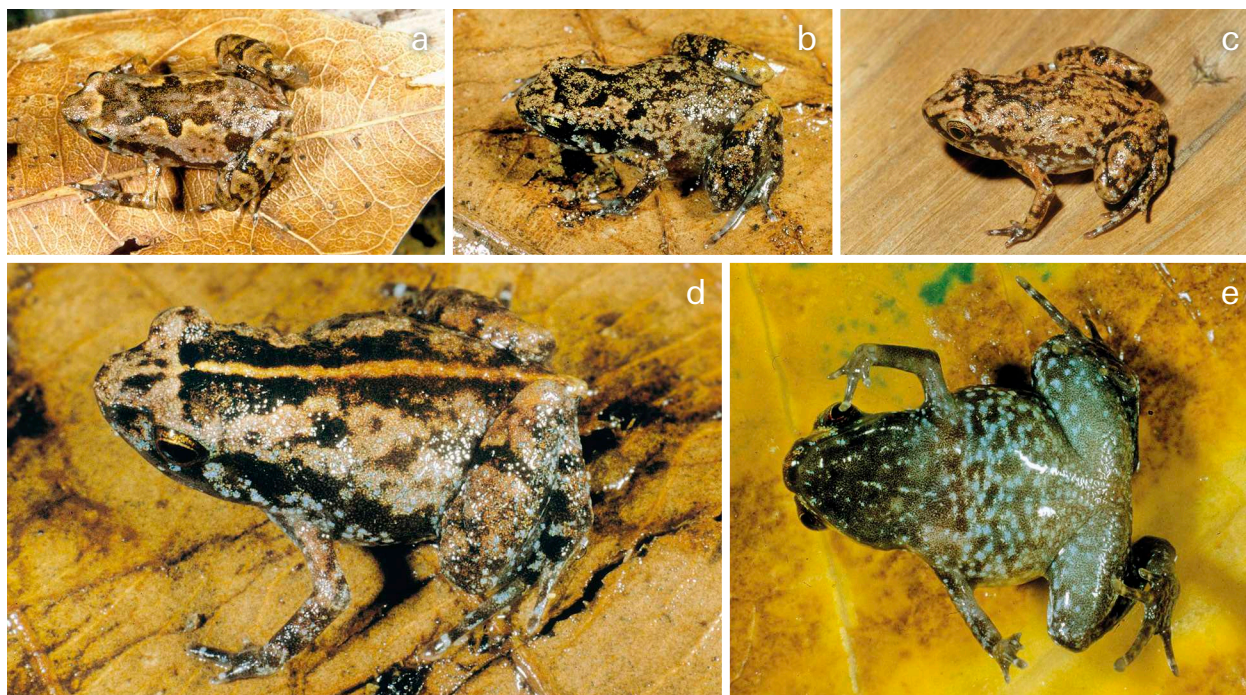


Fig. 77. *Stumpffia tetradactyla* from Nosy Boraha in life: (a) ZSM 593/2006 (ZCMV 3395); (d) ZSM 594/2006 (ZCMV 3396); the remaining photos (b, c, e) cannot be reliably assigned to voucher specimens.

6. Small-sized species of clade C

While only a single nominal species of small-sized *Stumpffia* fell into clade C (*S. tetradactyla*), the molecular data suggest a large diversity of new species in this clade, most of which are described in the following.

Stumpffia tetradactyla VENCES & GLAW, 1991

(Figures 77 and S118)

Name-bearing type. Holotype ZFMK 52547 from “Straßenrand, ca. 1 km südlich von Maromandia an der Westküste der Insel Nosy Boraha (= Sainte Marie), Ost-Madagaskar”; translated: “at the edge of the road, ca. 1 km south of Maromandia on the west coast of the island Nosy Boraha (= Île Sainte Marie), eastern Madagascar.”

Identity and diagnosis. *Stumpffia tetradactyla* is a small-sized species phylogenetically embedded in clade C, and so far known only from the offshore island Nosy Boraha. (1) Small-sized species (SVL 13.9–14.1 mm); (2) manus with four fingers (first finger moderately to strongly reduced in length) and pes with four toes (first toe reduced to a small rudiment); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.19–0.21, FOTL/SVL 0.58–0.69; (5) dorsum smooth; (6) light brown to grayish dorsal color, with variable dark dorsal markings, often with a dark central teddybear shaped patch (e.g. Fig. 77a), and one individual known with a light vertebral line (Fig. 77d). Ventrally gray with dark gray mottling and

sometimes a dark throat, but without contrasted ventral coloration, red color elements on ventral side, or sharp continuous color border between dorsum and flanks; (7) regularly repeated short single-note chirp call.

Distinguished from *S. achillei*, *S. analanjirofo*, *S. be*, *S. diutissima*, *S. edmonsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from the similar-sized species *S. analainaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, and *S. yaniki* by a more expressed digital reduction (almost complete reduction of first toe); from *S. contumelia*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. davidattenboroughi* by a less expressed digital reduction on hand. Furthermore distinguished from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; and from many species by advertisement call. *Stumpffia tetradactyla* is currently the only small-sized nominal species of *Stumpffia* in clade C (numerous additional species will be described below). It belongs to a highly supported subclade of clade C1 in which the only other small-sized species are *S. garraffoi* **sp. nov.** and *S. spandei* **sp. nov.** (described below).

Specimens examined. Holotype ZFMK 52547 collected on 4 March 1991 from Nosy Boraha by F. Glaw and M. Vences; paratype ZFMK 52545 with same collecting data as holotype; paratype ZSM 558/1999 (previously ZFMK 52546) collected on 6–7 March 1991 from Ambohidena forest, Nosy Boraha, near the

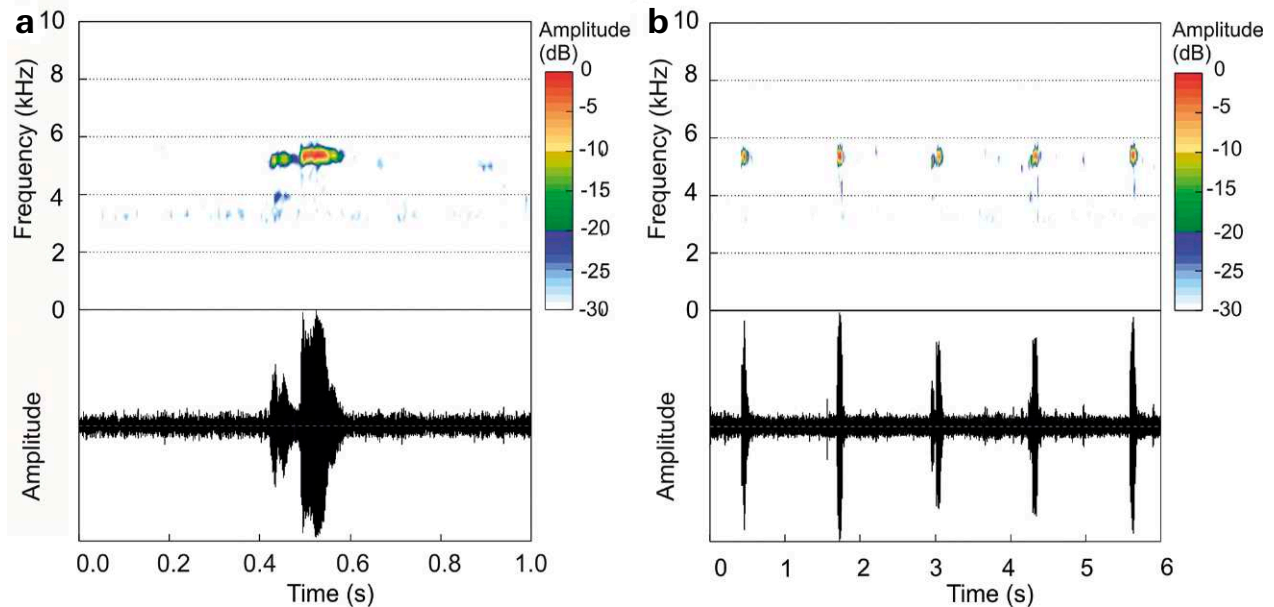


Fig. 78. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia tetradactyla* from Nosy Boraha (not associated with a specimen): (a) 1 s duration section; (b) 6 s duration section.

village Ambohidena, by F. Glaw and M. Vences. ZSM 593/2006 (ZCMV 3395) and ZSM 594/2006 (ZCMV 3396) collected on 7–8 March 2006 in Nosy Boraha, Maromandia village (S16.9089, E49.8678, 20 m a.s.l.) by M. Vences and J. Randrianirina.

Distribution. The species is known from several localities on Nosy Boraha.

Natural history. Specimens were observed both in primary rainforest and in degraded, secondary vegetation and plantations, calling from the leaf litter in the late afternoon and at night. At night, males might call from rather exposed positions (VENCES & GLAW, 1991).

Call. The advertisement call consists of a single short note emitted in series at regular intervals (Fig. 78). Calls recorded by M. Vences and F. Glaw on 4–9 March 1991 at the type locality Nosy Boraha (VENCES *et al.*, 2006: CD3, track 37, cut 1) had the following numerical parameters: call duration (= note duration) 77–109 ms (92 ± 9 ms; $N=11$), inter-call intervals 741–1566 ms (959 ± 244 ms; $N=10$), and a dominant frequency at 5081–5555 Hz (5355 ± 138 Hz, $N=11$).

Stumpffia betampona sp. nov.

(Figures 79 and S119)

Holotype. ZSM 214/2016 (ACZCV 0210) (Figs. 79 a–b), adult female, collected on 14 November 2013 at Vohitsivalana (S17.88501, E49.20339, 481 m above sea level), Betampona Strict Nature Reserve, Toamasina Province, Madagascar by A. Crottini, D. Salvi, E. Scanarini, and George.

Paratypes. MRSN A6315 and MRSN A6300, collected on 2 March 2007 at Vohitsivalana (S17.8862, E49.2024, 517 m a.s.l.) by G.M. Rosa; MRSN A6317, MRSN A6327, and MRSN A6246, all collected between 8 and 11 February 2007 at Sahambendrana (S17.8983 E49.4375, 458 m a.s.l.) by G.M. Rosa and F. Andreone; MRSN

A6313 (FAZC 13618), MRSN A6253, MRSN A6233, and MRSN A6273, all collected between 19 and 22 February 2007 at Maintimbato (S17.894, E49.2282, 255 m a.s.l.) by G.M. Rosa; MRSN A6387 collected on 14 November 2007 at Sahaindrana (S17.8972, E49.2002, 341 m a.s.l.) by G.M. Rosa and J. Noël; MRSN A6255 collected on 8 March 2007 at Sahabefoza (S17.9142, E49.2076, 349 m a.s.l.) by G.M. Rosa; UADBA (ACZCV 0203) collected on 15 November 2013 at Vohitsivalana (S17.88523, E49.2039542, 514 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, and George; ZSM 215/2016 (ACZCV 0039), UADBA (ACZCV 0040), and ZSM 216/2016 (ACZCV 0041), all collected on 7 November 2013 at Sahaindrana (S17.89481, E49.20081, 269 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, and J.H. Velo; ZSM 217/2016 (ACZCV 0046) and ZSM 218/2016 (ACZCV 0047) collected on 5 November 2013 at Sahaindrana (S17.898632, E49.200566, 360 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, and J.H. Velo; ZSM 219/2016 (ACZCV 0103) collected on 5 November 2013 at Sahambendrana (S17.89848201, E49.21470397, 476 m a.s.l.) by G.M. Rosa, D.J. Harris, M. Randriamialisoa, and J.H. Lava. All these localities refer to sites within Betampona Strict Nature Reserve, Toamasina Province, East Madagascar.

Diagnosis. A small sized species from the northern central east of Madagascar, which has been previously listed as *Stumpffia* sp. 17 in VIEITES *et al.* (2009), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017), and as *Stumpffia* sp. [Ca FJ559312] in ROSA *et al.* (2012). (1) Miniaturized to small-sized species (SVL 11.4–13.8 mm); (2) manus with four fingers (first finger moderately to strongly reduced in length, especially in males) and pes with five toes (first toe very strongly reduced in length, rudimentary); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.17–0.21, FOTL/SVL 0.65–0.76; (5) dorsum smooth with a moderate number of scattered tubercles; (6) dorsally gray to sandy brown. Can have an intricate but indistinct pattern of small dark brown patches, but can also have a series of broad longitudinal stripes of color. Ventrally with large cream flecks or reticulations, especially on the chest. No red color ventrally.



Fig. 79. *Stumpffia betampona* sp. nov. from Betampona Strict Nature Reserve in life: (a–b) holotype ZSM 214/2016 (ACZCV 0210); (c–d) ZSM 217/2016 (ACZCV 0046); (e–f) ZSM 218/2016 (ACZCV 0047); (g) ZSM 219/2016 (ACZCV 0103); (h) FAZC 13962 (voucher not collected); (i) MRSN A6313; (j) MRSN A6315.

Distinguished from *S. achillei*, *S. analanjirofo*, *S. be*, *S. diutissima*, *S. edmondsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from the similar-sized species *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, and *S. yanniki* by a more expressed digital reduction (almost complete reduction of first toe); from *S. contumelia*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. davidattenboroughi* by a less expressed digital reduction on hand. Furthermore, distinguished from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern. Along with *S. tetradactyla* and several other new species described below the species belongs to clade C; here it is placed sister to all other clade C lineages, albeit without support, suggesting it is not closely related to any other known species. It differs from *S. tetradactyla* and many of the other small-sized new species described below by the comparatively tubercular dorsum.

Description of the holotype. Specimen in a good state of preservation, fourth toe removed as a tissue sample.

Body rounded; head wider than long, narrower than body; snout rounded in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis slightly distinct, concave; loreal region distinct, concave, oblique; tympanum distinct, about 80% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, distinct; outer metacarpal tubercle not recognizable; inner metacarpal tubercle distinct, oval; fingers without webbing; relative length of fingers $1 < 4 < 2 < 3$, fourth finger slightly shorter than second; finger tips not expanded into discs. Hindlimbs slender; TIBL 48% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle not visible; outer metatarsal tubercle absent; no webbing between toes; toe tips not expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is pinkish gray. Two brown spots are present over the scapular region. Rounded dark brown spots are present in the inguinal region. The dorsal surface of the head is as the back. Dark brown flecks pre-

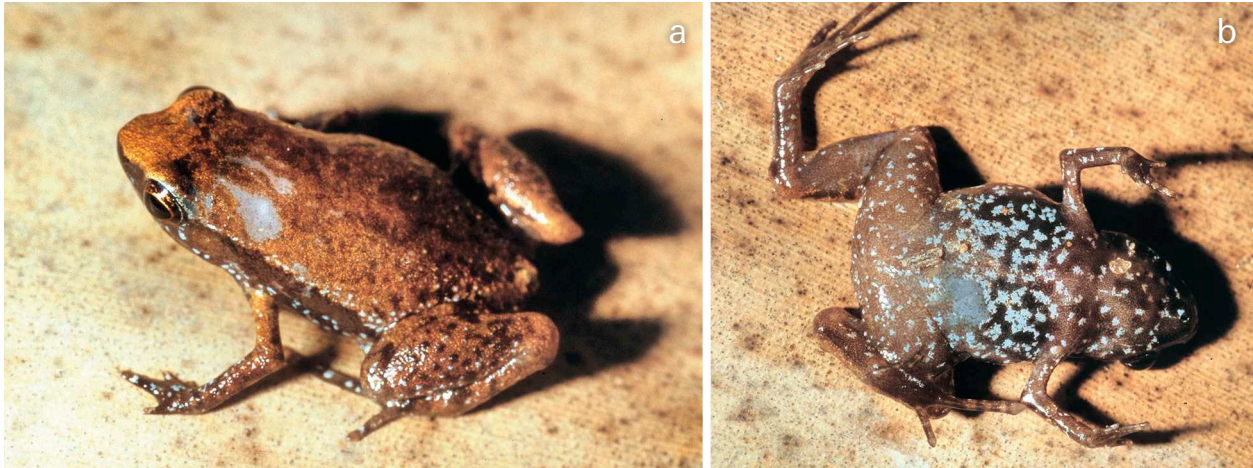


Fig. 80. *Stumpffia dolchi* sp. nov. from Nosy Mangabe in life: (a–b) dorsolateral and ventral view of holotype ZSM 488/2005 (ZCMV 2143).

sent above the eyes. The nostril is surrounded by beige. The lateral surface of the head is dark brown striped with beige. The flanks are ventrally beige mottled with brown and laterally beige. The flank coloration merges with the ventral coloration. The chin is brown with beige flecks. The ventral trunk is beige mottled with brown. The ventral thigh is brown with beige flecks. The shank and tarsus are ventrally as the thigh. The sole of the foot is as the thigh but darker. Dorsally, the thigh is pinkish spotted and mottled with brown and with a brown crossband. The posterodorsal surface of the thigh is as the dorsum. The shank, tarsus, and foot are as the thigh. The toes are dark brown mottled with beige. The cloacal region is dark brown. The arms are pinkish spotted with brown, mottled with dark brown on the lower arm. The dorsomedial surface of the hand is beige flecked with brown. The fingers are dark brown spotted with beige. The underside of the arm is as the ventral trunk.

Color in life (holotype and variation). The dorsum is dominated by a broad medial stripe of light-brown running from the snout to the vent, and irregularly defined by a beige lateral border. Along this broad band there are several pinkish-beige tubercles. A thin beige line starts from the snout and fades behind the scapular region. A stripe of dappled ebony and gray runs from the lateral face to the posterior trunk. The tympanum is gray. The dorsal forelimb is rosy tan, with two coppery-ebony crossbands on the forearm. The hand is mottled rosy tan and ebony, with a light annulus before the terminal phalange of the third finger. The dorsal leg is rosy tan speckled with ebony, with two light brown crossbands on the thigh and shank. The foot and toes are light salmon flecked with ebony. The chin is brown with cream reticulations. The ventral skin of the trunk is translucent in base color, and thus plum over the pectoral girdle becoming increasingly yellow toward the posterior abdomen, reticulated with splotches of cream. The ventral legs are brown with cream spots. The iris is coppery with black reticulations.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in external morphology. Coloration in this species is quite variable. Most individuals are a sandy brown in dorsal coloration, sometimes mottled with brown flecks, and several do not have dorsal stripes, or have more intricate dorsal patterning. The ventral coloration generally has a dark brown background coloration with dense cream markings, but is less reticulated than the holotype. ACZCV 0103 is dorsally dark beige mottled with dark brown, the shank in dorsal view is beige with one brown crossband, and the lower arm has a brown crossband. ACZCV 0047 is dorsally beige marbled with brown, has a brown triangular shape from the middle of the eye until the scapular area, and a brown crossband on the thigh and shank. ACZCV 0046 is overall pinkish-beige and lacks a broad median band.

Etymology. The species name is a noun in apposition to the genus name, and refers to the type locality of the new species, the forest of Betampona Strict Nature Reserve in eastern Madagascar.

Distribution. This species is so far known only from Betampona Strict Nature Reserve, where it is found across the entire Reserve with, thus far, the exception of Betakonana, although the species is expected to be present there as well. Within the Betampona, it ranges from 250–517 m a.s.l.

Natural history. The holotype was found at night in the leaf litter. This species appears to be quite abundant and distributed across the Betampona Strict Nature Reserve, therefore in areas completely overlapping with the larger species *S. jeannoeli* described above.

Call. Unknown.

Stumpffia dolchi sp. nov.

(Figure 80)

Holotype. ZSM 488/2005 (ZCMV 2143) (Fig. 80) collected on 22 February 2005 in Nosy Mangabe Special Reserve, near Maroantsetra (S15.5, E49.8, ca. 50–100 m above sea level), Toamasina Province, Madagascar, by F. Glaw, M. Vences, and R.D. Randrianiaina.

Diagnosis. A small sized species from the north east of Madagascar, which has been previously listed as a deep conspecific lineage of *S. tetradactyla* in VIEITES *et al.* (2009), and as *S. sp.* Ca32 in SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Miniaturized species (SVL 11.6 mm); (2) manus with four fingers (first finger strongly reduced in length) and pes with four toes (first toe completely reduced); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.18, FOTL/SVL 0.75; (5) dorsum smooth; (6) dorsally chocolate brown with indistinct and poorly contrasted dark speckling, or with some larger dark symmetrical markings. Flanks dark brown, with a distinct color border between dorsal and lateral color. Ventrally ebony with a distinct pattern of bluish white flecks, especially on chest. No red color ventrally.

Distinguished from *S. achillei*, *S. analanjirofo*, *S. be*, *S. diutissima*, *S. edmondsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from the similar-sized species *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, and *S. yanniki* by a more expressed digital reduction (complete reduction of first toe); from *S. contumelia*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. davidattenboroughi* by a less expressed digital reduction on the hand, especially of the fourth finger. Furthermore, distinguished from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. betampona* by a smooth dorsum; very similar morphologically to *S. tetradactyla* but differs by a more strongly expressed color border between flanks and dorsum, and strongly in mitochondrial and nuclear DNA. Along with *S. tetradactyla* and several other new species described herein the species belongs into clade C; phylogenetically it is placed as sister species to *S. makira* sp. nov. (described below) which is morphologically similar but differs by a more stout body and a more expressed digital reduction on the hand, especially of the fourth finger, and by concordant differentiation in mitochondrial and nuclear DNA.

Description of the holotype. Specimen in a good state of preservation. The right thigh muscle removed as a tissue sample. Body elongate; head longer than width, narrower than body; snout pointed in dorsal view, pointed in lateral view; nostrils directed laterally, not protuberant, nearer

to tip of snout than to eye; canthus rostralis not distinct; loreal region slightly concave, oblique; tympanum distinct; about 40% of eye diameter; supratympanic fold not visible; tongue destroyed, attached anteriorly; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles not recognizable; outer metacarpal tubercle not distinct; inner metacarpal tubercle distinct, rounded; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly longer than second; finger tips not expanded into discs. Hind limbs slender; TIBL 48% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; toe tips not expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After 10 years in 70% ethanol, the dorsum is beige vermiculated with brown. The dorsal surface of the head is as the back. The nostril is beige. The lateral surface of the head is brown. The flanks are laterally brown spotted with beige; ventrally beige spotted with brown. The flank coloration merges with the ventral coloration. The ventral trunk is beige mottled with brown. The chin is as the trunk. The thigh, shank, tarsus, and foot are ventrally as the abdomen. Dorsally, the thigh is beige spotted with brown. The posterodorsal surface of the thigh is as the dorsal aspect. The shank is as the thigh. The tarsus is as the shank. The foot is as the tarsus. The toes are as the foot. The cloacal region is brown. The arms are beige spotted with brown. The dorsomedial surface of the hand is as the arm. The underside of the arm is as the ventral trunk.

In life, dorsum chocolate brown with darker brown speckles. A strong lateral color border is present between the chocolate dorsum and the ruddy brown flank. Iridescent bluish flecks are present along the ventral edge of the flank. The dorsal forelimb is as the back, with some bluish flecks on the hand, including an annulus before the terminal phalange of each finger. The dorsal hindlimb is as the back, without crossbands, but with small dark brown speckles. The toes are dark brown with small light blue flecks, including an annulus before the terminal phalange of each finger. The venter is ebony with fairly large bluish white flecks throughout, at their highest density at the mid-trunk, decreasing in density on the thigh and chin. The ventral thigh is lighter than the trunk. The iris is copper.

Etymology. The species name is a patronym honoring Rainer Dolch, in recognition of his extraordinary achievements in the study and conservation of Madagascar's biota.

Distribution. The species is known only from its type locality on Nosy Mangabe at ca. 50–100 m a.s.l.

Natural history. The holotype was collected in the leaf litter of low-altitude rainforest.

Call. Not reliably known.

Remark. Two specimens from Nosy Mangabe assigned to *S. tetradactyla* in VENCES & GLAW (1991) probably belong to *S. dolchi* but are here not included in the type series because of the lack of genetic data. These specimens (ZFMK 52548–52549) emitted calls differing from *S. tetradactyla* from the type locality by much longer inter-note intervals and a higher frequency of about 6000 Hz.

***Stumpffia garraffoi* sp. nov.**

(Figures 81 and S120)

Holotype. ZSM 1752/2008 (ZCMV 8803) (Figs. 81 a–b), adult specimen, collected on 14 February 2008 in Mahasoia Forest near Ambodisakoa village (S17.29769, E48.70199, 1032 m above sea level), NE Vohimana/Lake Alaotra, Toamasina Province, Madagascar, by D.R. Vieites, J.L. Patton, P. Bora, and M. Vences.

Paratypes. ZSM 631/2009 (ZCMV 8684), ZSM 632/2009 (ZCMV 8685), ZSM 633/2009 (ZCMV 8687), all collected August 2009 in Tampolo Forest by H. Rasolonjatovo and R.D. Randrianiana; MRSN A6278 (FAZC 13489) collected on 4 February 2007 at Rendryendry, Betampona Strict Nature Reserve (S17.9316, E49.2034, 325 m a.s.l.) by G.M. Rosa; ZSM 220/2016 (ACZCV 0006) and UADBA (ACZCV 0007) collected on 4 November 2013 along Piste Fotsimavo at Rendryendry, Betampona Strict Nature Reserve (S17.92682, E49.20777, 287 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, George, G.M. Rosa, D.J. Harris, M. Randriamialisoa, and H. Lava; UADBA (ACZCV 0071) collected on 11 November 2013 along Piste Fotsimavo at Rendryendry, Betampona Strict Nature Reserve (S17.91861, E49.21030, 239 m a.s.l.) by A. Crottini, D. Salvi, E. Scanarini, Claude, G.M. Rosa, D.J. Harris, M. Randriamialisoa, and H. Lava; DRV 5698, DRV 5628, DRV 5622, DRV 5621 (to be catalogued in MNCN) with same collection data as holotype.

Diagnosis. A small *Stumpffia* from various localities along the northern Malagasy east coast which has been previously listed as *Stumpffia* sp. 18 in VIEITES *et al.* (2009), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017) and *Stumpffia* sp. [Ca FJ559313] in ROSA *et al.* (2012). (1) Small-sized species (adult male SVL 12.1–14.5 mm); (2) manus with four fingers (first finger distinctly reduced in length) and pes with five toes (first toe very strongly reduced in length, externally recognizable as rudiment only); (3) terminal phalanges of fingers without, those of toes with slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.14–0.23, FOTL/SVL 0.60–0.75; (5) dorsum smooth; (6) dorsally with a broad medial stripe of burnt umber in a teddybear-like shape, laterally bordered by copper. A strong dorsolateral color border can be present. Ventrally rosy brown to plum with dark mottling on the throat, and large cream flecks on the chest; (7) regularly repeated single-note tonal call.

Distinguished from *S. achillei*, *S. analanjirofo*, *S. be*, *S. diutissima*, *S. edmondsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from the similar-sized species *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamiti-*

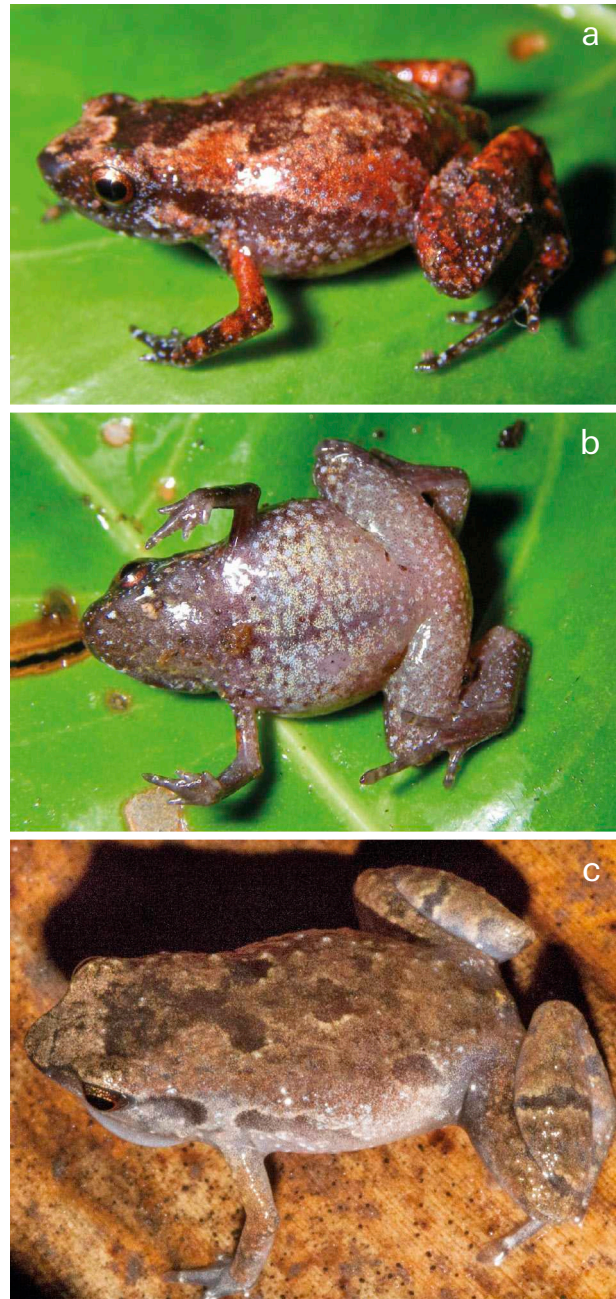


Fig. 81. *Stumpffia garraffoi* sp. nov. in life: (a–b) dorsolateral and ventral views of holotype, ZSM 1752/2008 (ZCMV 8803) from Mahasoia Forest; (c) MRSN A6278 from Betampona Strict Nature Reserve.

ka, *S. psologlossa*, *S. pygmaea*, *S. sorata*, and *S. yanniki* by a more expressed digital reduction (almost complete length reduction of first toe); from *S. contumelia*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. davidattenboroughi* by a less expressed digital reduction on hand, especially on fourth finger. Furthermore distinguished from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. betampona* by a smooth dorsum; from *S. dolchi* by lack of

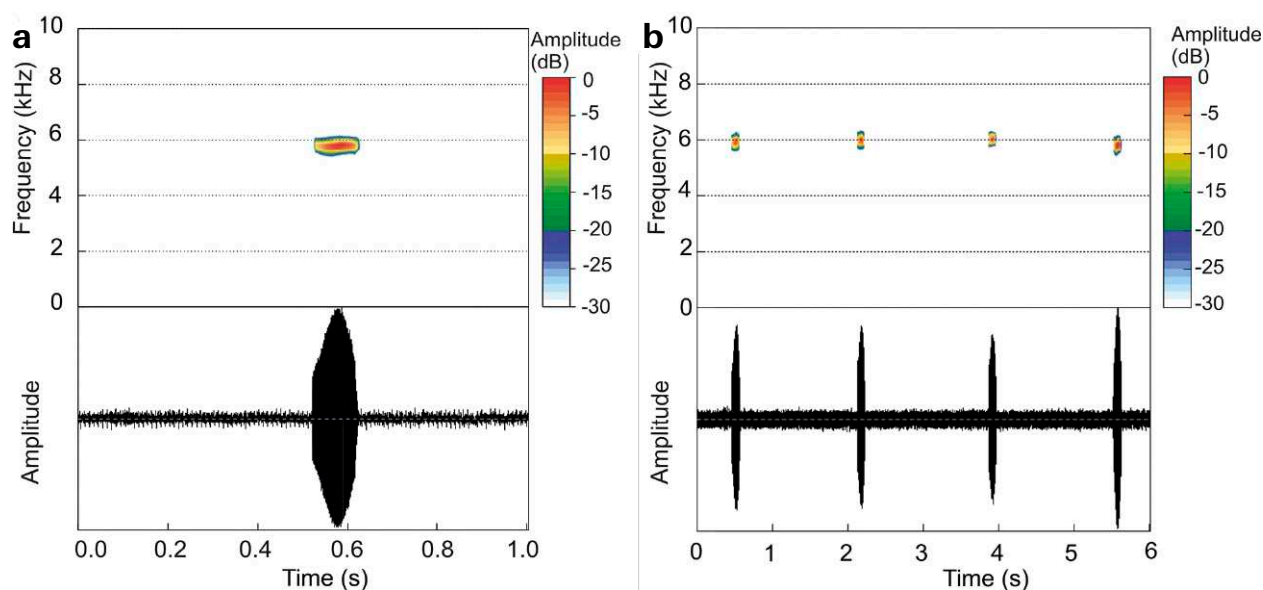


Fig. 82. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia garraffoi* sp. nov. from Mahaso Forest, recorded from holotype ZSM 1752/2008 (ZCMV 8803): (a) 1 s duration section; (b) 6 s duration section.

strongly expressed color border between flanks and dorsum; from *S. tetradactyla* by longer duration of inter-call intervals. Phylogenetically, placed within a subclade of clade C1 that otherwise contains only large-sized species, except for *S. tetradactyla* and *S. spandei* sp. nov. (described below) which both differ bioacoustically and in mitochondrial and nuclear DNA.

Description of the holotype. Specimen in fairly good state of preservation, right thigh muscle removed as a tissue sample. Body round; head slightly longer than wide, narrower than the body; snout pointed in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region straight, almost vertical; tympanum indistinct, about 41% of eye diameter; supratympanic fold not visible; tongue long, broadening slightly posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles distinct, single; outer metacarpal tubercle not recognizable; inner metacarpal tubercle distinct, oval; fingers without webbing; first finger strongly reduced, second and fourth fingers reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger slightly longer than second; tip of finger three expanded into a disc. Hind limbs slender; TIBL 55% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle oblong; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced, recognizable only as a rudiment, second toe reduced; toe tips expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third; subarticular tubercles indistinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After almost eight years in 70% ethanol, the dorsum is light gray. Almost symmetri-

cal dark brown and cream lines extend from the inguinal region to the back of the head on either side of the midline. A dark brown spot is present in the inguinal region. The dorsal surface of the head is gray with dark gray markings beside the eyes. The nostril is surrounded by brown. The lateral surface of the head is mottled gray and brown. A brown supratympanic marking is present. This is separated from a long dark marking on the flanks. Otherwise the flank is the color of the dorsum, fading ventrally to the color of the ventral trunk. The abdomen is cream with brown flecks, becoming increasingly brown anteriorly. The chin is brown with cream flecks. The ventral thigh is as as the chin. The shank and tarsus are ventrally as the thigh. The sole of the foot is dark brown. Dorsally, the thigh is as the dorsum. The posterodorsal surface of the thigh is dark brown with cream spots. The shank is as the thigh, with a brown perpendicular crossband. The tarsus is as the shank, with a similar crossband. The foot is externally gray with a brown spot on the exterior face, and brown interiorly. The toes are brown with cream flecks. The cloacal region is dark brown. The arms are as the dorsum. A dark crossband is present on the lower arm. The dorsomedial surface of the hand is brown. The underside of the arm is as the ventral trunk.

In life, dorsal body with an irregular broad medial stripe of burnt umber, with a wavy border to copper coloration of the dorsolateral body and head (making an almost teddybear-like shape). A lateral color border is present, the copper of the dorsolateral back has a straight border, to the umber flank, which fades ventrally to cream, merging with the venter. A high density of beige flecks is present on the flank, decreasing in density dorsally. The dorsal forelimb is copper, with a burnt umber crossband on the forearm. The hand is burnt umber with a high concentration of beige flecks. The dorsal leg is umber with some copper shading and has a high concen-

tration of beige flecks. The chin is rosy brown anteriorly, becoming increasingly plum posteriorly, with numerous small whitish flecks along the lips and over the throat. The ventral trunk is covered in large cream flecks between which the translucent skin is visible, which become smaller on the ventral legs. The iris is copper.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. A single exception is ZSM 631/2009, which has expanded terminal discs on its toes. A relatively low degree of variability was noted in the coloration of specimens in preservative; ZSM 632/2009 and ZSM 631/2009 are similar to the holotype in pattern, but dark brown with darker brown markings, instead of light gray with dark brown markings. The mid-dorsal marking is cross-shaped in these specimens. Ventrally, the abdomen is darker brown than the holotype, and the ventral legs are brown as well. ZSM 631/2009 is similar to these specimens, but lighter brown. It lacks the long dark marking on the flank present in the other specimens, and has more vermiculated dorsal markings. Specimens from Betampona Strict Nature Reserve: MRSN A6278 present mid-dorsal marking which is more cross-shaped than teddybear-shape, and presents a less evident copper coloration. In this specimen hindlimbs have two crossbands. ZSM 220/2016 (ACZCV 0006) has a poorly defined mid-dorsal marking resulting in a homogeneous dorsolateral coloration, which is copper in the background with irregular umber markings.

Etymology. The species name is a patronym honoring H. Martin Garraffo, in recognition of his substantial contributions to the study of anuran alkaloids, including numerous compounds of the Malagasy genus *Mantella*. We emphasize that Martin usually collaborated with Tom Spande, and it is thus no coincidence that *Stumpffia garraffoi* and *S. spandei* **sp. nov.** (described below) occur syntopically in the Mahasoia Forest.

Distribution. Known from three localities in eastern Madagascar including: (1) Mahasoia Forest (type locality), (2) Tampolo Forest, and (3) Betampona Strict Nature Reserve. In Betampona, although intensively sampled, the species is thus far known to occur only around the village of Rendrirendry (along Piste Fotsimavo). It occurs from 239–1032 m a.s.l.

Natural history. At the type locality, specimens were heard calling in the evening and at night, from the leaf litter in degraded rainforest, in mixed choruses with *S. spandei* **sp. nov.** (described below). The holotype was found calling from the leaf litter of Mahasoia Forest. In Betampona this species seems to be uncommon (or with quite secretive habits) and restricted to low elevations (239–325 m a.s.l.) in Rendrirendry and the surroundings, living on the edge of secondary forest with some level of disturbance.

Call. The advertisement call consists of a single, short and high-pitched note emitted in series at regular intervals (Fig. 82). Calls recorded on 14 February 2008 by M. Vences at Mahasoia forest had the following numerical parameters: call duration (= note duration) 101–107 ms (103.4 ± 2.5 ms; $N=7$), inter-call intervals 1553–1901 ms (1695.8 ± 150 ms; $N=6$), and a dominant frequency of 5813–6029 Hz (5936.7 ± 84.2 Hz, $N=7$). The wide range in inter-call interval duration is presumably caused by some calls being emitted after atypically long intervals due to disturbance.

Stumpffia makira **sp. nov.**

(Figures 83 and S119)

Holotype. ZSM 541/2009 (ZCMV 11257), adult male (Fig. 83), collected on 23–24 June 2009 on the Makira Plateau, within the Makira Natural Park, close to the source of the Fotsialanana River (S15.46675 E49.1288, 1067 m above sea level), Mahajanga Province, Madagascar, by M. Vences, D.R. Vieites, F.M. Ratsoavina, R.D. Randrianaina, E. Rajeriarison, T. Rajofiarison, and J.L. Patton.

Diagnosis. A small sized species from the north east of Madagascar, which has previously been listed as *S. sp.* Ca38 in SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Small-sized species (SVL 12.1 mm); (2) manus with four fingers (first finger strongly reduced in length, second and fourth finger moderately reduced in length) and pes with four toes (first toe externally completely reduced); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.16, FOTL/SVL 0.64; (5) dorsum smooth; (6) dorsally ebony bordered with gray-brown. Flanks ebony, with a distinct color border between dorsal and lateral color. Ventrally with translucent plum skin, ranging from ebony on the throat to the almost gray of the posterior abdomen, interspersed with increasingly dense cream flecks posteriorly. No red color ventrally.

Distinguished from *S. achillei*, *S. analanjirifo*, *S. be*, *S. diutissima*, *S. edmondsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from the similar-sized species *S. analainaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mami-tika*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, and *S. yan-niki* by a more expressed digital reduction (complete reduction of first toe); from *S. contumelia*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction; from *S. miery* and *S. davidattenboroughi* by a slightly lesser degree of digital reduction on hand, especially of the fourth finger. Furthermore distinguished from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, and *S. roseifemoralis* by the lack of large and distinct areas of red color ventrally or on the limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. betampona* by a smooth dorsum; from *S. dolchi* and *S. tetradactyla* by a stronger reduction of the fourth finger, and by a generally more stout body shape. Phylogenetically it

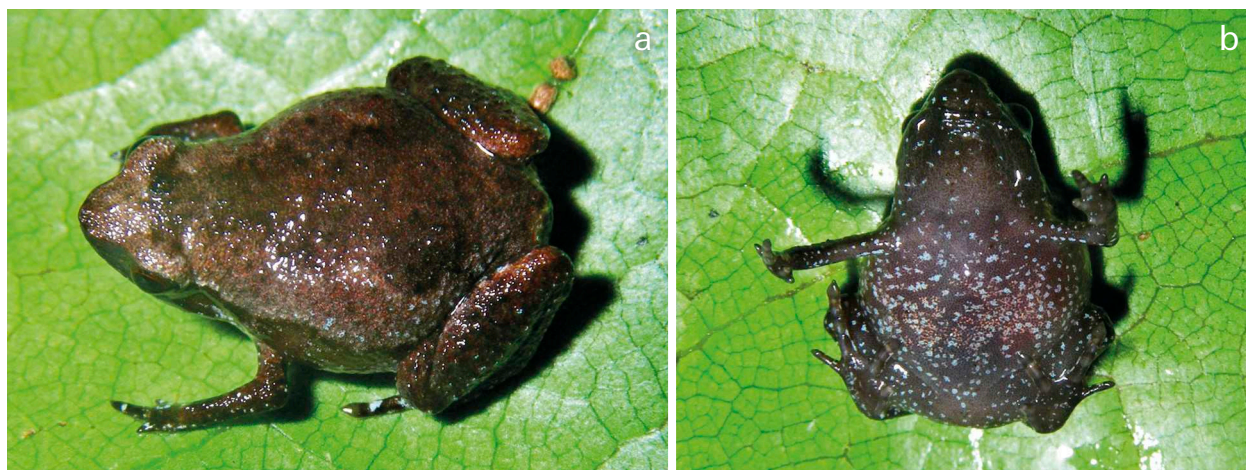


Fig. 83. *Stumpffia makira* sp. nov. in life: (a–b) dorsal and ventral views of holotype ZSM 541/2009 (ZCMV 11257) from the Makira Plateau.

is placed as sister species to *S. dolchi*, which is concordantly differentiated in mitochondrial and nuclear DNA.

Description of the holotype. Specimen in a good state of preservation, left thigh muscle removed as a tissue sample. Body rounded; head slightly wider than long, narrower than body width; snout rounded in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis concave; loreal region concave, oblique; tympanum slightly distinct, about 57% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles single, slightly distinct; outer metacarpal tubercle not recognizable; inner metacarpal tubercle distinct, oval, fused with tubercle prepollical; hand without webbing; first finger strongly reduced, second and fourth fingers moderately reduced; relative length of fingers $1 < 2 < 4 < 3$, fourth finger longer than second; finger tips not expanded into discs. Hind limbs slender; TIBL 45% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; toe tips not expanded; first toe totally reduced, relative length of toes $2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles distinct, single. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After seven years in 70% ethanol, the dorsum is beige mottled with brown. A brown band crosses the dorsum from the middle of the eye to the inguinal area. A beige spot is present in the inguinal region. The dorsal surface of the head is as the back. The nostril is beige. The lateral surface of the head is beige spotted with white dots. The flanks are as the lateral surface of the head. The flank coloration merges with the ventral coloration. The ventral trunk is uniformly beige spotted with brown and flecked with light beige. The chin is as the ventral trunk. The ventral thigh is as the abdo-

men. The shank is ventrally brown flecked with beige. The tarsus and foot are ventrally dark brown flecked with beige. Dorsally, the thigh is dark brown flecked with dark beige. The posterodorsal surface of the thigh is uniformly dark brown flecked with light beige. The shank, tarsus, and foot are as the thigh. The toes are light brown speckled with light beige. The cloacal region is dark brown. The arms are darker than the dorsum, speckled with light beige. The dorsomedial surface of the hand is light beige, mottled with beige and speckled with white. The fingers are uniformly beige. The underside of the arm is as the ventral trunk.

In life, dorsal base color ebony, bordered in the dorso-lateral regions and on the head by gray-brown. Numerous small bluish flecks are present on the flanks. The dorsal forelimb is as the back. The hand has several bluish flecks, including an annulus before the terminal phalange of each finger. The dorsal hindlimbs is as the back, without crossbands, with a slightly more orange brown on the posterodorsal shank. The toes have several bluish flecks, including an annulus before the terminal phalange of each toe. The ventral skin is translucent, a dark plum, especially dark (resembling ebony) in the chin region, lightening posteriorly; interspersed with dense cream flecks in the posterior trunk, decreasing in density anteriorly and posteriorly on the legs. The iris is dark copper.

Etymology. The species name is a noun in apposition to the genus name, and refers to the type locality of the new species, the Makira Nature Reserve in north-eastern Madagascar.

Distribution. The species is known only from its type locality on the Makira plateau.

Natural history. The single known specimen was collected during the day, active in the leaf litter of primary rainforest.

Call. Unknown.

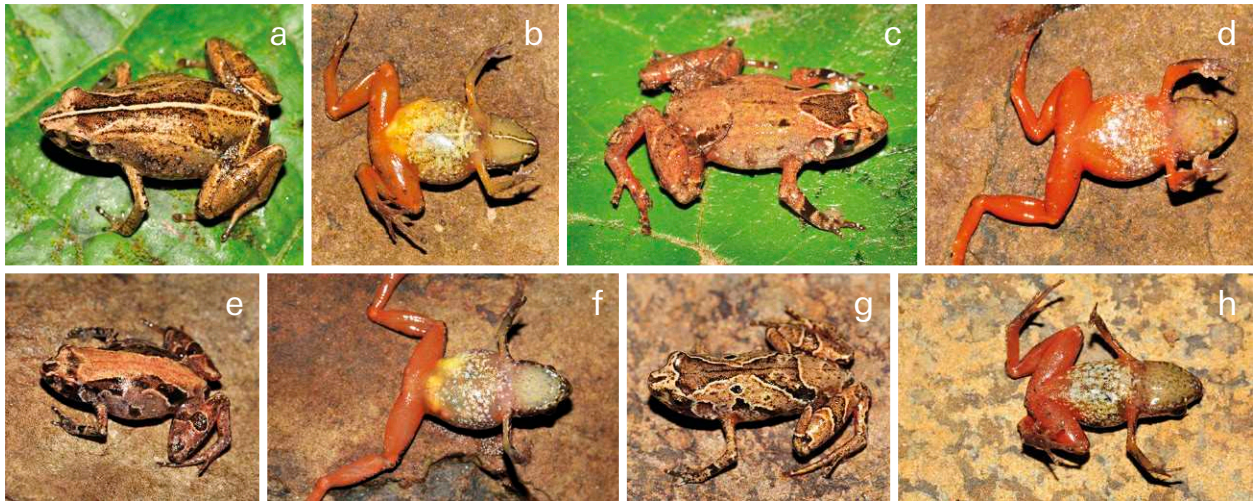


Fig. 84. *Stumpffia miovaova* sp. nov. from Sorata Forest in life: (a–b) holotype ZSM 1649/2012 (FGZC 3656); (c–d) paratype ZSM 1640/2012 (FGZC 3650); (e–f) paratype ZSM 1647/2012 (FGZC 3675); (g–h) paratype ZSM 1646/2012 (FGZC 3751).

Stumpffia miovaova sp. nov.

(Figures 84 and S121)

Holotype. ZSM 1649/2012 (FGZC 3656) (Figs. 84 a–b), adult male, collected on 28 November 2012 in Sorata forest (ca. S13.6811, E49.4455, 1398 m above sea level), Antsiranana Province, Madagascar, by F. Glaw, O. Hawlitschek, F.M. Ratsoavina, A. Rakotoarison, T. Rajoafiarison, and A. Razafimanantsoa.

Paratypes. ZSM 1640/2012 (FGZC 3650), ZSM 1646/2012 (FGZC 3751), ZSM 1647/2012 (FGZC 3675), UADBA-A 60280 (originally ZSM 1648/2012, FGZC 3676), UADBA-A 60279 (FGZC 3655) and UADBA (FGZC 3663), all collected between 28–30 November 2012 on the Sorata massif (approximately between S13.6811, E49.4455, 1398 m and S13.675, E49.4392, 1580 m a.s.l.) by F. Glaw, O. Hawlitschek, F.M. Ratsoavina, A. Rakotoarison, T. Rajoafiarison, and A. Razafimanantsoa.

Diagnosis. A moderately sized species with orange-red-dish ventral side from the north east of Madagascar, which has not been listed as a candidate species in previous publications. It is listed among the small-sized species of clade C, but it approaches the size of the larger species in the clade. (1) Small- to moderately-sized species (SVL 14.8–18.2 mm, adult male SVL 15.1 mm); (2) manus with four fingers (first finger strongly to moderately reduced in length) and pes with five toes (first toe distinctly reduced in length); (3) terminal phalanges of fingers and toes without enlarged discs; (4) relative hand and foot length, HAL/SVL 0.15–0.24, FOTL/SVL 0.64–0.76; (5) dorsum smooth with a number of distinct scattered tubercles; (6) dorsally copper, with copper-infused ebony markings. These markings and dorsal color can be variable, and can include stripes or isolated color elements. Ventral color with intense fiery orange on the trunk, ventral legs, and sometimes the ventral forelimbs. The ventral chin can have a light median stripe.

This species is easily distinguished from all species except *S. kibomena*, *S. be*, *S. roseifemoralis*, *S. edmondsi*, *S. nigrorubra*, and *S. meikeae* by orange to reddish ventral coloration. Among these, from *S. be* by fiery orange coloration on the ventral hindlimbs (vs. only on the

concealed portions of the hindlimbs); from *S. kibomena*, *S. roseifemoralis*, *S. meikeae*, *S. edmondsi*, and *S. nigrorubra* by more intense fiery orange ventral color, sometimes extending even onto the forelimbs (paler or more red in all other taxa). In addition, it can be distinguished from *S. achillei*, *S. analanjirofo*, *S. be*, *S. diutissima*, *S. edmondsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by slightly smaller body size; from numerous small-sized species in clades A, B, C and D by larger body size, i.e., from *S. analamaina*, *S. betampona*, *S. dolchi*, *S. garraffoi*, *S. madagascariensis*, *S. makira*, *S. psologlossa*, *S. pygmaea*, *S. tetradactyla*, and *S. yanniki*. Furthermore, from *S. contumelia*, *S. davidattenboroughi*, *S. miery*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction of the toes; and from *S. grandis* by the lack of a contrasted light blue-black ventral pattern. Phylogenetically, *S. miovaova* occupies a rather isolated position and possibly is the sister group of subclade C2 which exclusively contains *Stumpffia* species of relatively large body size.

Description of the holotype. Specimen in a good state of preservation, left thigh muscle removed as a tissue sample for DNA extraction. Body elongate; head as wide as long; snout rounded in dorsal view, boxy in lateral view; nostrils directed laterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region concave, vertical; tympanum distinct, about 52% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae rounded. Forelimbs slender; subarticular tubercles indistinguishable; outer metacarpal tubercle small, indistinct, oval; prepollex strong; fingers without webbing; first finger strongly reduced, second finger reduced; relative length of fingers $1 < 2 = 4 < 3$, fourth finger subequal in length to second; finger tips not expanded into discs. Hind limbs slender; TIBL 54% of SVL; lat-

eral metatarsalia strongly connected; inner metatarsal tubercle small, oval; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced, second toe reduced; toe tips slightly expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe distinctly shorter than third; subarticular tubercles distinct, single. Skin on dorsum smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After three years in 70% ethanol, the dorsum is pinkish gray. Two dark brown spots are present over the scapular region. Elongated dark brown markings are present in the inguinal region. The dorsal surface of the head has a large dark brown heart-shaped marking extending from the eyes to the back of the head. The tip of the rostrum has a dark brown spot as well. The nostril is surrounded by brown. The lateral surface of the head is as the dorsum. A dark brown marking is present beneath the eye, and a supratympanic marking is present as well. The flanks are gray, with a faint dark marking above the insertion of the arm. The flank fades to the cream of the ventral trunk. The ventral trunk is cream on the abdomen, anteriorly becoming flecked with increasing amounts of brown. The chin is speckled brown and cream. The ventral thigh, shank, and tarsus are also cream. The sole of the foot is light and dark brown. Dorsally, the thigh is light brown. A faint oblique crossband is present. The posterodorsal surface of the thigh is brown flecked with cream. The shank is as the thigh with an oblique crossband nearer to the knee than the heel. The tarsus is as the shank, without crossbands. The foot is externally as the shank, internally cream. The toes are flecked with cream and brown. The cloacal region is not different from the posterior thighs. The arms are as the dorsum. A dark crossband is present on the lower arm. The dorsomedial surface of the hand is cream. The fingers are brown with a few cream flecks. The underside of the arm is as the thigh.

Color in life (holotype and variation). Dorsal coloration copper, with a copper-infused ebony triangular marking between the eyes converging to a point between the suprascapulae bordered by champagne. A pair of symmetrical suprascapular ebony spots bordered with champagne behind the suprascapulae, and another pair of larger, oblong spots in the inguinal region. The flank is spotted with whitish flecks. The anterior half of the tympanum is champagne. An ebony marking is present below the eye and around the nostril. The dorsal forelimb is as the back, with an ebony crossband on the forearm. The medial hand is beige, the lateral hand burnt umber flecked with copper, with a whitish annulus before each terminal phalange. The dorsal hindlimb is a redder copper, with one ebony-copper crossband on the mid-thigh and mid-shank. The medial foot is fiery orange, the toes mottled fiery orange, burnt umber, and copper, with a whitish band before each terminal phalange. The chin is a gray-brown spotted with apricot. From the pectoral girdle pos-

teriorly the base-color is fiery orange, including the ventral arms and legs. Over the mid-trunk, whitish speckling and flecking is present. The iris is copper dorsally, rust red anteriorly and posteriorly.

The dorsal and ventral coloration is highly variable (Fig. 84). Dorsal patterns include a champagne to tan mid-dorsal stripe that can be broad or thin, an hourglass shaped dark marking, lateral dark spots, and strong to weak hindlimb crossbands. The chin spots can be yellow, and a mid-chin champagne stripe bordered in burnt umber can be present. The orange of the arms and legs can be more yellow or more red. The iris can be golden to copper, and can lack red coloration.

Variation. For variation in measurements among specimens, see Table 3. In general, all examined specimens agree strongly with the holotype in morphology. The loreal region varies from vertical to slightly oblique. The first finger appears less strongly reduced in specimens that lack a prepollex. A palmar tubercle is sometimes visible. A high degree of variability was noted in the coloration of specimens; ventral coloration in preservative was more or less consistent, with some specimens having a medial brown chin stripe ending at the pectoral girdle (ZSM 1648/2012 and 1640/2012), but most specimens having more or less pure cream venter, and immaculate cream ventral legs. Dorsal coloration can have a vertebral cream stripe (ZSM 1648/2012 and 1640/2012), and can vary from pink (ZSM 1647/2012 and 1648/2012) to gray (ZSM 1646/2012). A heart-shaped marking as in the holotype was noted only in ZSM 1646/2012, but this was posteriorly connected to a triangular dark gray marking. This specimen also has the same dorsal spots as the holotype. Thigh crossbands vary from absent (ZSM 1648/2012) to dark and strong (ZSM 1646/2012). The tip of the rostrum is dark in all specimens.

Etymology. The species epithet “miovaova” is a Malagasy word meaning “variable,” and refers to the variability of coloration in this species. It is used as a noun in apposition to the genus name.

Distribution. This species is known only from the Sorata Forest between ca. 1398–1580 m above sea level.

Natural history. The species was abundant at mid-elevations of the Sorata massif, and observed jumping on the ground along a trail within bamboo forest.

Call. Unknown.

Stumpffia spandei sp. nov.

(Figures 85 and S122)

Holotype. ZSM 1751/2008 (ZCMV 8802) (Figs. 85 and S122), a calling male, collected on 14 February 2008 in Mahasoa Forest near Ambodisakoa village (S17.29769, E48.70199, 1032 m above sea level), NE Vohimana/Lake Alaotra, Toamasina Province, Madagascar, by D.R. Vieites, J.L. Patton, P. Bora, and M. Vences.

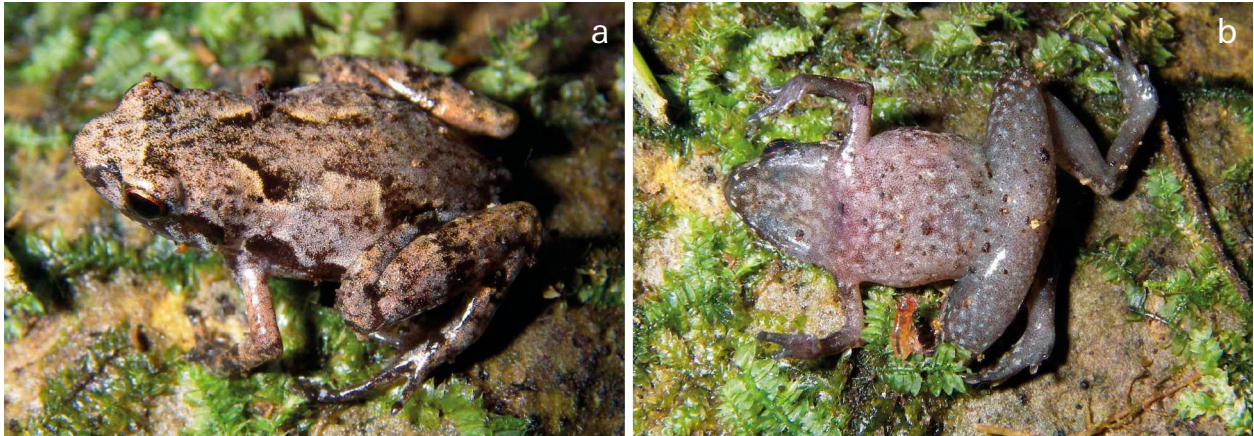


Fig. 85. *Stumpffia spandei* sp. nov. from Mahasoia Forest in life: (a–b) dorsolateral and ventral views of the holotype ZSM 1751/2008 (ZCMV 8802).

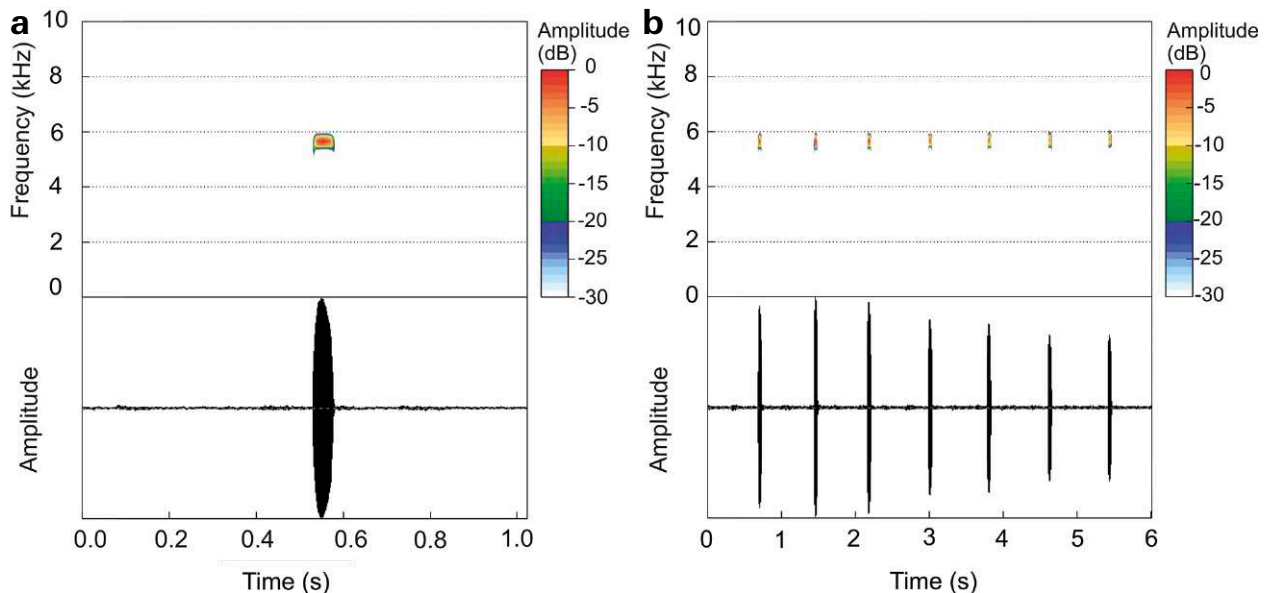


Fig. 86. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia spandei* sp. nov. from Mahasoia Forest (recorded from the holotype ZSM 1751/2008): (a) 1 s duration section; (b) 6 s duration section.

Diagnosis. A small *Stumpffia* from the northern central east, which has been previously listed as *Stumpffia* sp. 19 in VIEITES *et al.* (2009), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017). (1) Small-sized species (SVL 12.7 mm); (2) manus with four fingers (first finger distinctly reduced in length) and pes with five toes (first toe strongly reduced in length); (3) terminal phalanges of fingers without, those of toes with very slightly enlarged discs; (4) relative hand and foot length, HAL/SVL 0.21, FOTL/SVL 0.67; (5) dorsum smooth; (6) dorsally iridescent taupe with ebony to black irregular flecks, and two pairs of semi-symmetrical beige markings bordered in black. Ventrally light gray on the chin, rosy posteriorly, flecked with taupe; (7) regularly repeated single-note tonal call.

Distinguished from *S. achillei*, *S. analanjirofo*, *S. be*, *S. diutissima*, *S. edmondsi*, *S. fusca*, *S. grandis*, *S. hara*, *S. jeannoeli*, *S. kibomena*, *S. megsoni*, *S. meikeae*, *S. miovaova*, *S. nigrorubra*, *S. pardus*, *S. roseifemoralis*, and *S. staffordi* by smaller body size; from the similar-sized

species *S. analamaina*, *S. angeluci*, *S. gimmeli*, *S. huwei*, *S. iharana*, *S. larinki*, *S. maledicta*, *S. madagascariensis*, *S. mamitika*, *S. psologlossa*, *S. pygmaea*, *S. sorata*, and *S. yanniki* by a more expressed digital reduction (almost complete length reduction of first toe); from *S. contumelia*, *S. obscoena*, and *S. tridactyla* by a lower degree of digital reduction; from *S. miery* by a distinctly shorter inter-call interval length. Furthermore distinguished from *S. be*, *S. kibomena*, *S. meikeae*, *S. nigrorubra*, *S. roseifemoralis*, and *S. miovaova* by the lack of large and distinct areas of red or orange color ventrally or on limbs; from *S. grandis* by the lack of a contrasted light blue-black ventral pattern; from *S. betampona* by a smooth dorsum; from *S. davidattenboroughi*, *S. dolchi*, and *S. makira* by the lack of a strongly expressed color border between flanks and dorsum; from *S. tetradactyla* by slightly shorter call duration (without overlap of values), and concordant divergence in mitochondrial and nuclear genes. Phylogenetically, placed within a subclade of

clade C1 that contains only large-sized species, except for *S. tetradactyla* and *S. garraffoi* which both differ bioacoustically and in mitochondrial and nuclear DNA.

Description of the holotype. Specimen in a good state of preservation, left hindlimb removed as a tissue sample for DNA extraction. Body round; head slightly wider than long, narrower than body width; snout slightly pointed in dorsal and lateral view; nostrils directed laterally, not protuberant, nearer to the tip of the snout than to the eye; canthus rostralis distinct, slightly concave; loreal region slightly concave, oblique; tympanum slightly distinct, about 52% of eye diameter; supratympanic fold not visible; tongue long, broadening posteriorly, attached anteriorly, not notched; maxillary teeth and vomerine teeth absent; choanae oval. Forelimbs slender; subarticular tubercles single, slightly distinct; outer metacarpal tubercle slightly visible, rounded; prepollex visible, elongate. Fingers without webbing; first finger reduced; relative length of fingers $1 < 2 = 4 < 3$, fourth finger subequal to second; finger tips not expanded into discs. Hind limbs slender; TIBL 49% of SVL; lateral metatarsalia strongly connected; inner metatarsal tubercle indistinguishable from reduced first finger; outer metatarsal tubercle absent; no webbing between toes; first toe strongly reduced, second toe reduced; toe tips not expanded; relative length of toes $1 < 2 < 5 < 3 < 4$; fifth toe shorter than third; subarticular tubercles single, distinct. Skin on dorsum relatively smooth, without distinct dorsolateral folds. Ventral skin smooth.

Coloration of the holotype. After seven years in 70% ethanol, the dorsum is beige, with a broad brown band starting in the middle of the eyes and running to the inguinal region. Brown spots are present in the inguinal region. The dorsal surface of the head is as the back with a brown patch. The nostril is brown. The lateral surface of the head is beige flecked with brown. The flanks are beige flecked with brown. The flank coloration merges with the ventral coloration. The ventral trunk is beige mottled with brown. The chin is beige mottled with brown. The ventral thigh is as the abdomen. The shank is ventrally brown slightly flecked with cream. The tarsus is ventrally beige with brown flecks. The sole of the foot as the tarsus. Dorsally, the thigh is brown with a dark brown crossband. The posterodorsal surface of the thigh is brown flecked with cream. The shank is similar to the thigh. The tarsus is as the shank with a slightly brown crossband. The foot is beige flecked with brown. The toes are striped. The cloacal region is brown with cream flecks. The forelimb is beige, with a crossband on the forearm. The dorsomedial surface of the hand is beige spotted with brown. The fingers have small brown spots. The underside of the arm is as the ventral trunk.

In life, dorsally iridescent taupe in base coloration, interspersed with ebony to black irregular flecks. Two pairs of beige markings bordered in black are present, one in the suprascapular region (symmetrical), and one at the mid-back (asymmetrical). The head is beige. The flank has a row of large ebony spots, fusing posteriorly to

a colored band. A further ebony marking is present below the eye and around the nostril. The dorsal forelimb is as the back; an ebony crossband is present on the forearm. The fingers are mottled, with a light annulus before each terminal phalange. The dorsal hindlimb is as the back, with one ebony crossband with coppery inclusions on the midhigh, one on the midshank, and two on the foot. The posterodorsal shank is beige. The toes are mottled taupe and ebony, with a small whitish annulus before each terminal phalange. The ventral body is light gray on the chin, rosy posteriorly, flecked all over with taupe. The iris is copper.

Etymology. The species name is a patronym honoring Thomas F. Spande, in recognition of his substantial contributions to the study of anuran alkaloids, including numerous compounds of the Malagasy genus *Mantella*.

Distribution. The species is known only from its type locality in Mahaso Forest, ca. 1032 m above sea level.

Natural history. At the type locality, specimens were heard calling in the evening and at night, from the leaf litter in degraded rainforest in mixed choruses with *S. garraffoi*.

Call. The advertisement call consists of a single, very short and high-pitched note emitted in series at regular intervals (Fig. 86). Calls recorded by M. Vences on 14 February 2008 from the holotype at Mahaso forest had the following numerical parameters: call duration (= note duration) 43–49 ms (46 ± 1.8 ms; $N=11$), inter-call intervals 736–907 ms (801.8 ± 48.6 ms; $N=10$), and a dominant frequency at 5641–5857 Hz (5755 ± 69.8 Hz, $N=11$).

7. Candidate species not described herein

Stumpffia sp. Ca7

(Figure 87)

Remark. This species is listed as *Stumpffia* sp. 7 in VIEITES *et al.* (2009), KÖHLER *et al.* (2010), KLAGES *et al.* (2013), SCHERZ *et al.* (2016) and PELOSO *et al.* (2017), and as *Stumpffia* sp. 6 in WOLLENBERG *et al.* (2008). It is characterized by its very long call duration; however, the molecular phylogeny places it sister to *S. sorata* (Fig. 3), a species of which advertisement calls are unknown. Clarification of the status of *S. sp. Ca7* will be possible in the future by more detailed comparisons of advertisement calls and nuclear genes, once bioacoustic data for *S. sorata* become available.

Material examined. ZSM 379/2005 (FGZC 2826), FGZC 2827, and FGZC 2870, all collected on 16 February 2005 from Camp Simpona, Marojeje National Park (S14.4886, E49.9002, 1326 m a.s.l.) by F. Glaw, M. Vences, and R.D. Randrianiana; FGZC



Fig. 87. *Stumpffia* sp. Ca7 from Marojejy National Park in life: (a–b) adult male, ZSM 544/2016 (ZCMV 15181); (c) adult male, ZSM 555/2016 (ZCMV 15182); (d) uncatalogued specimen, ZCMV 15074.

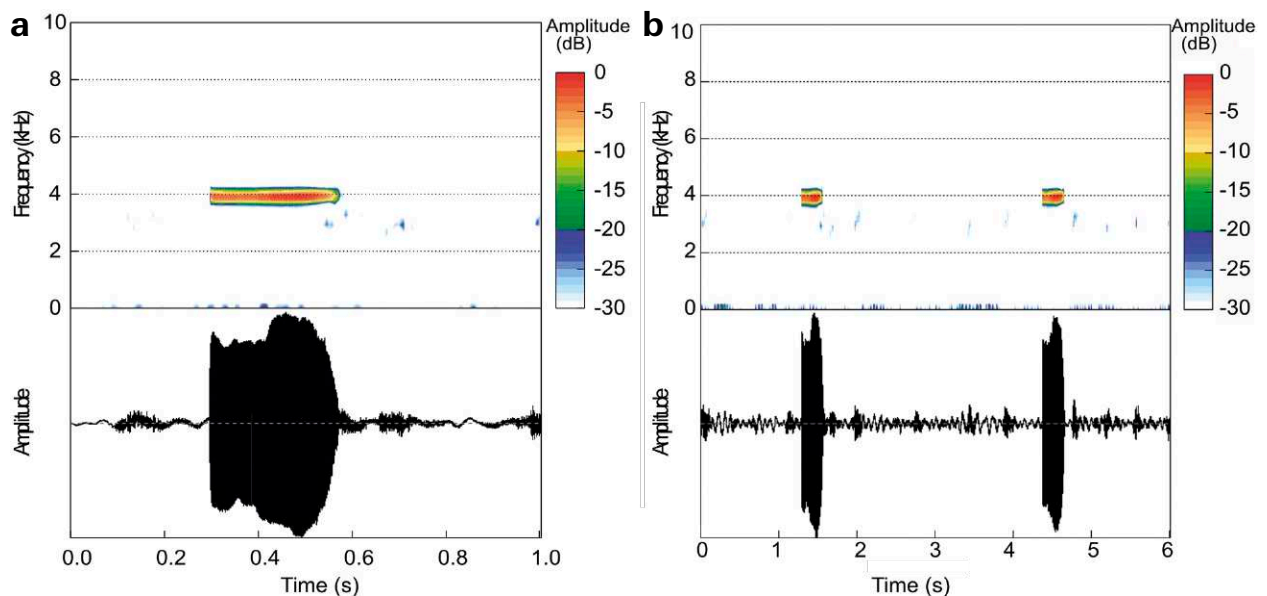


Fig. 88. Spectrograms (above) and oscillograms (below) of advertisement calls of *Stumpffia* sp. Ca7 from Marojejy (call recorded from specimen ZCMV 15181): (a) 1 s duration section; (b) 6 s duration section.

2728 collected on 14 February 2005 from Camp Mantella, Marojejy National Park (S14.5055 E, E49.9147, 481 m a.s.l.) by F. Glaw, M. Vences, and R.D. Randrianiaina; ZSM 537–540/2016 (ZCMV 15047–15050), ZCMV 15051–15054, 15056, 15061, ZSM 541/2016 (ZCMV 15069), ZSM 542/2016 (ZCMV 15070),

ZCMV 15074, ZCMV 15079, and ZCMV 15093, all collected on 15 November 2016 from a campsite called ‘Camp 0’ in Marojejy National Park (S14.44633, E49.78523, 310 m a.s.l.), by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences; ZCMV 15155, ZCMV 15166,

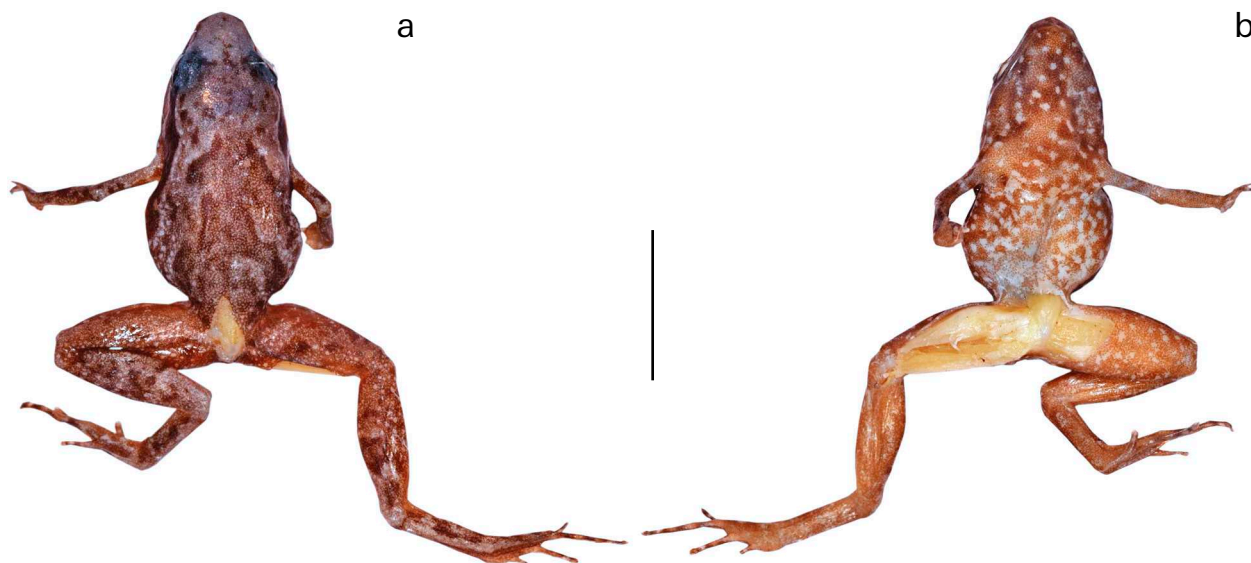


Fig. 89. Preserved specimen of *Stumpffia* sp. Ca7, ZSM 379/2005 (FGZC 2826), from Marojejy National Park; scale bar = 5 mm.

ZSM 543/2016 (ZCMV 15168), ZCMV 15169, ZCMV 15179, ZSM 544–545/2016 (ZCMV 15181–15182), ZSM 555/2016 (ZCMV 15187), ZSM 550/2016 (ZCMV 15212), ZCMV 15213, and ZSM 554/2016 (ZCMV 15281), all collected on 17–19 November 2016, from Camp Simpona, Marojejy National Park (S14.4499, E49.7433, 1326 m a.s.l.) by A. Rakotoarison, M.D. Scherz, M.C. Bletz, J.H. Razafindraibe, A. Razafimanantsoa, and M. Vences.

Call. The advertisement call of *S.* sp. Ca07 consists of a single, moderately long, tonal note emitted in series at regular intervals (Fig. 88). Calls were recorded by M.D. Scherz on 17 November 2017 from specimen ZCMV 15181 in Marojejy National Park, with the following parameters: call duration (= note duration) 290–299 ms (293.8 ± 2.9 ms; $N=10$), inter-call intervals 2764–3250 ms (2929.3 ± 182.9 ms; $N=10$), and a dominant frequency at 3919–3962 Hz (3931.9 ± 20.7 Hz, $N=10$).

Stumpffia sp. Ca11

Remark. This species is listed as *Stumpffia* sp. 11 in VIEITES *et al.* (2009).

Material examined. MRSN A2583, from Ambolokopatrika.

Stumpffia sp. Ca29

(Figs. 90, S125)

Remark. This species has been listed as *Stumpffia* sp. 29 in KLAGES *et al.* (2013).

Material examined. ZSM 1824/2010 (ZCMV 12387) collected on 13 June 2010 in Matsabory Maiky, Tsaratanana Strict Nature Reserve (S14.15256 E48.95728, 2021 m a.s.l.) by M. Vences, D.R. Vieites, R.D. Randrianiana, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, F. Randrianasolo, and T. Rajoafiarison; ZSM 627/2014 (DRV 6103) collected on 10 June 2010 in

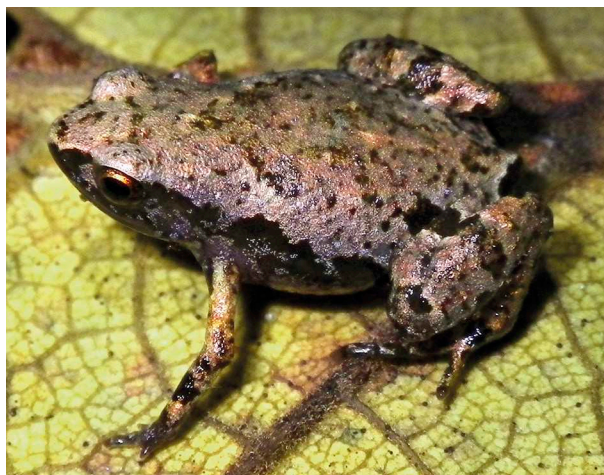


Fig. 90. *Stumpffia* sp. Ca29 (DRV 6103) from Antevialambazaha, Tsaratanana Strict Nature Reserve, in life.

Antevialambazaha, Tsaratanana Strict Nature Reserve (S14.17413, E48.94521, 1589 m a.s.l.) by M. Vences, D.R. Vieites, R.D. Randrianiana, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, F. Randrianasolo, and T. Rajoafiarison; MRSN A2653 collected in 2001 in the Tsaratanana Massif by F. Andreone, J.E. Randrianirina, and M. Vences.

Stumpffia sp. Ca30

Remark. This species has been listed as *Stumpffia* sp. 30 in KLAGES *et al.* (2013).

Material examined. UADBA-A 60690 (DRV 6459), UADBA-A 60689 (DRV 6458), UADBA-A 60680 (DRV 6457), UADBA-A 60677 (DRV 6456), UADBA-A 60681 (DRV 6455), ZSM 635/2014 (DRV 6454), ZSM 633/2014 (DRV 6452), ZSM 634/2014 (DRV 6453), ZSM 632/2014 (DRV 6451), and UADBA-A 60685 (DRV 6487), all collected on 30 June 2010 in Angorony forest fragment near Maromandia (S14.22111, E48.14211, 115 m a.s.l.) by F.M. Ratsoavina, S. Rasamison, T. Rajoafiarison, and F. Randrianasolo.

Stumpffia sp. Ca42

Material examined. ZMA 19327 (FG/MV 2002.2505), collected in February 2002 in Fierenana by M. Vences and D.R. Vieites.

Discussion

Fast track taxonomy

The inventory of Madagascar's amphibian fauna has seen steep progress over the past three decades (e.g., KÖHLER *et al.*, 2005; GLAW & VENCES, 2007; VIEITES *et al.*, 2009; GLAW *et al.* 2010; PERL *et al.*, 2014; SCHERZ *et al.*, 2016). Large numbers of new species have been described, hundreds of additional, still undescribed candidate species have been discovered, phylogenetic relationships among taxa have been revealed by extensive molecular data sets, and numerous field observations have considerably improved our understanding of the natural history of many of these frogs. While BLOMMERS-SCHLÖSSER & BLANC (1991) listed 133 described species of anurans in Madagascar, this number had risen to 244 species in VIEITES *et al.* (2009), 292 in PERL *et al.* (2014), and currently has climbed up to about 315 (AMPHIBIAWEB, 2017; FROST, 2017). Even more candidate species have already been identified but require taxonomic revisionary work before being confirmed, formally recognized, and named. While the discovery of new candidate species becomes ever more efficient by routine application of DNA barcoding pipelines in concert with more intense fieldwork in remote areas, the formal species descriptions remain as a major bottleneck in species inventory.

Recent efforts to overcome this “Linnean shortfall” (BROWN & LOMOLINO, 1998; WHITTAKER *et al.*, 2005; HORTAL *et al.*, 2015) include approaches of turbo-taxonomy (BUTCHER *et al.*, 2012) or fast-track taxonomy (RIEDEL *et al.*, 2013a) which chiefly combine DNA barcode sequences with concise morphological descriptions and high-resolution digital imaging to streamline the formal description of larger numbers of new species. This effort has proven to be of extraordinary efficiency, yielding descriptions of hundreds of new species (BUTCHER *et al.*, 2012; RIEDEL *et al.*, 2013b, 2014, 2016). Other authors (e.g., DIJKSTRA *et al.*, 2015) have also succeeded in describing large numbers of species by reducing the extent of morphological descriptions, and RENNER (2016) argues for an emphasis on DNA characters in the formal naming of species, complying with the essential focus of Linnaeus on diagnosis, not description.

Although such a simplified description pipeline is especially useful for hyperdiverse organisms poorly covered by current taxonomy, such as numerous groups of arthropods or nematodes, we realized the potential of an adapted and simplified description procedure also for vertebrates such as *Stumpffia*, in order to achieve a comprehensive revision of such species-rich and poorly known genera within a reasonable time frame.

Our taxonomic pipeline, compared to the standards followed in numerous species descriptions of Malagasy amphibians in the past, is simplified in that it relies on the following main components: (1) species delimitation is based on concordant differentiation in one mtDNA and one nucDNA marker, or one mtDNA marker and bioacoustics; (2) morphological diagnoses are abbreviated and simplified, only a selected number of morphometric measurements is taken, and not each species is diagnosed against each other species; diagnoses focus especially on differentiation from those species that were closely related to the new species in the molecular phylogeny, or that occur syntopically (see VIJAYAKUMAR *et al.*, 2014 for a distinction of lineage diagnosis and field diagnosis); (3) description of morphological variation is somewhat abbreviated, and instead, as many specimens as possible are documented by photographs in life and in preservative; and (4) most importantly, we deliberately accepted a number of inconsistencies and omissions in our pipeline, reflecting the lack of reliable data and preferences of researchers, as discussed in the following.

The foremost quality criterion for a species-level taxonomy is the robustness of the underlying species hypotheses. In general, the genetic divergences of *Stumpffia* proved extraordinary, with levels of mtDNA divergence in most cases much above the usually defined thresholds of 3% or 5% uncorrected pairwise distance in the 16S gene (e.g., VENCES *et al.*, 2005; FOUQUET *et al.*, 2007; VIEITES *et al.*, 2009). Allele sharing in Rag-1 is furthermore exceedingly rare despite using only a short fragment of this gene, with a correspondingly low number of informative sites. We are therefore convinced that the plethora of new species described herein are robustly supported as independent evolutionary lineages, even in cases where bioacoustic or morphological differences were faint or could not be assessed due to missing data.

Nevertheless, in a series of cases we opted not to describe species, even though these fulfilled at least the criterion of a very strong divergence in mtDNA. This applies especially for the *S. gimmeli* complex, in which we include two deep lineages. In this species, we refrained from further splitting because (1) we do not have clearly identified adult specimens and calls from all three lineages, (2) we do not have genetic data from the type locality of the species, Ambanja, and therefore cannot ascertain with certainty which of the lineages corresponds to *S. gimmeli* sensu stricto, and (3) the *S. gimmeli* complex is one of the rare cases of nuclear allele sharing, thus necessitating more extensive analyses of nucDNA markers. Two related lineages of *S. kibomena* are known from only a single juvenile specimen (*S.* sp. Ca34 from Ranomafana) or have no fresh tissue samples available to us (*S.* sp. Ca11 from Ambolokopatrika). We decided not to describe *S.* sp. Ca30 because we have no call recordings or photographs in life available, and because we observed one highly divergent lineage (specimen DRV 6487) suggesting that two distinct species might be involved. Since the available samples and specimens of *S.* sp. Ca30 were collected in the course of a rapid field

survey targeted at reptiles, we cannot fully ascertain all metadata accompanying the samples. For *S. obscoena*, we found a similar situation with a few specimens from the type locality Andasibe showing deeply divergent 16S sequences, but too little associated information (advertisement calls, nucDNA sequences) is available to taxonomically interpret these differences. The sister lineage of the highland species *S. roseifemoralis* is known from a lowland locality (*S. sp.* Ca57 from Ambodivoangy) and is therefore unlikely to represent the same species; yet, with only two samples available for molecular study, and no voucher specimen available for morphological comparison, we refrained from a taxonomic conclusion in this case.

In general, by not describing the lineages discussed above we follow the plea of MIRALLES *et al.* (2013) for conservativeness in erecting new species, given that under integrative taxonomic and species concepts (DAYRAT, 2005; DE QUEIROZ, 2007; PADIAL *et al.*, 2010) it is epistemologically difficult to decisively reject a two-species hypothesis and thus synonymize described species-level taxa. In only a few cases did we decide to describe lineages that are not fully supported by all evidence as full species. This applies to *S. angeluci* and *S. maledicta*, two species that are not separated by the 4% threshold in the 16S gene. In this case we consider their sympatric occurrence and lack of allele sharing in Rag-1 as sufficient for description, especially because we collected and observed the respective specimens for this study. Furthermore, the recognition of both *S. analanjirofo* and *S. achillei* as species requires confirmation, as they are sister species both occurring at lowland sites of the north-east. We decided to describe them as distinct species because the molecular species criteria did apply (> 4% 16S divergence; no allele sharing in Rag-1), and because we had a sufficient amount of well-preserved material to ascertain some faint morphological differences. Yet, we acknowledge that the status of *S. analanjirofo* requires confirmation as it might in the future be rather considered a DCL of *S. achillei*, once more data on the genetic contact zone of the two taxa become available.

To conclude, our somewhat relaxed application of the species criteria defined a priori largely depends on our interpretation of data quality. In cases where DNA sequences were available from sufficient specimens and could be assigned to the vouchers with full reliability, and other associated metadata were considered reliable as well, we decided for recognition and description of new species even if some species criteria were not or only barely fulfilled. On the other hand, wherever we had doubts as to the association of DNA sequences, voucher specimens, color photos, and collection metadata, we refrained from taxonomic conclusions. Given the massive amount of data analysed for this study, even in thoroughly compiled data sets some errors will persist, and it is important to carefully evaluate the possibility of sample confusion or other errors before changing the taxonomic classification of the organisms involved (SCHERZ *et al.*, 2016; 2017).

Deep genetic divergences within and between species

Besides the presence of deep *Stumpffia* lineages of still unclarified status, the surprisingly strong genetic divergence in these frogs warrants comment. Species in *Stumpffia* are in general differentiated by distinctly higher mitochondrial differences than other, co-distributed Malagasy frogs, and the almost complete lack of allele sharing in Rag-1 is exceptional as well. For instance, in species of the families Mantellidae and Hyperoliidae, nuclear allele sharing among closely related species has been regularly observed (e.g., *Guibemantis*: VENCES *et al.*, 2013; *Boophis*: VENCES *et al.*, 2012; *Heterixalus*: GEHRING *et al.*, 2012) despite the use of longer stretches of nuclear genes in the respective analyses.

Most species of *Stumpffia* are only known from single localities, or from very small geographic ranges. In cases where samples were available from more than one locality, these almost always had distinct mitochondrial haplotypes, e.g., *S. analamaina* from the type locality vs. Ankarafantsika, *S. gimmeli*, *S. mamitika*, and *S. psologlossa* from various sites, or *S. analanjirofo* from Betampona, Nosy Mangabe, and Ambatoroma. An exception is found in *S. angeluci* where specimens from Montagne d'Ambre and the nearby Montagne des Français have identical 16S sequences. In general, the strong genetic structuring in these frogs might be related to their small body size. Based on a multi-species analysis of mantellids, PABIJAN *et al.* (2012) found an inverse association between body size and nucleotide divergence between populations, and hypothesized that the lack of genetic cohesion among populations is exacerbated in small-sized species due to ecological and physiological constraints, thus leading to regional genetic fragmentation. In principle, this process has the potential to accelerate rates of allopatric speciation in small frogs relative to large species, and it might have led to the large number of microendemic species of *Stumpffia* uncovered in the current study. However, species diversification in Madagascar is driven by a multitude of factors (BROWN *et al.*, 2014; RODRÍGUEZ *et al.*, 2015). *Stumpffia* have their center of species richness in northern Madagascar where many complementary allopatric and sympatric processes might be influencing speciation (VENCES *et al.*, 2009; BROWN *et al.*, 2016), and more detailed biogeographic and phylogeographic analyses are therefore necessary to understand the processes driving their evolution.

Reproductive modes

Data on the reproductive modes of *Stumpffia* are only available for few species, i.e., *S. pygmaea*, *S. analamaina*, *S. achillei*, and possibly *S. gimmeli* and *S. davidattenboroughi* (pending confirmation). *Stumpffia pygmaea* and *S. analamaina* produce foam nests. In *S. pygmaea*, developing embryos and non-feeding tadpoles were found in these foam nests in the wild (GLAW & VENCES, 1994), with

a froglet measuring < 3 mm snout-vent length. In captivity, foam nests were found that contained no eggs, but were guarded by a male frog. A foam nest of *S. analamaina* produced in captivity contained no eggs but was guarded by an adult frog (KLAGES *et al.*, 2013). We also found comparatively large foam nests containing numerous eggs, embryos, and tadpoles in metamorphosis (ZFMK 81255–81256), possibly of *S. gimmeli*, attached to the inner wall of a hollow tree in Manongarivo Reserve in February 2003. Here we report that the only known specimen of *S. davidattenboroughi*, was observed to guard eggs in a jelly nest, although unfortunately those eggs were not collected and it was not possible to reliably ascertain species identity of the embryos. Furthermore, we observed a male and eggs of *S. achillei* in a water-filled snail shell, and verified the identity of these eggs by DNA barcoding. This confirms that the production of foam nests is not a general characteristic of breeding in *Stumpffia*.

In the closely related genus *Rhombophryne*, subterranean or terrestrial jelly nests are probably the norm (although in this genus breeding ecology is also poorly known). Other cophylines also lay jelly-bound eggs, often in water-filled tree holes or in burrows in the leaf litter (e.g. BLOMMERS-SCHLÖSSER, 1975). Given that foam nests are otherwise unknown in the family Microhylidae, it seems likely that they are a derived reproductive trait of *Stumpffia* that might characterize mainly or only the species in clade A, although more data are needed to test this hypothesis. Furthermore, parental care seems to be distributed across the majority of cophyline species (e.g., BLOMMERS-SCHLÖSSER, 1975; KÖHLER *et al.*, 1997). This subfamily, and the genus *Stumpffia* in particular, may therefore provide an excellent system for study of the evolution of breeding systems in anurans, especially in light of the resolution of their taxonomy and systematics.

Biogeographic patterns

Our phylogenetic analysis revealed that the two most species-rich clades of the genus (clades A and C) are predominantly distributed in two distinct areas of Madagascar, i.e., northern and north-western Madagascar vs. eastern and north-eastern Madagascar (Fig. 4). Within clade A, clade A1 and A3 contain species located only in northern Madagascar, and clade A2 contains species from northern and north-western Madagascar. In Clade C, both C1 and C2, are composed of species from eastern and north-eastern Madagascar.

WOLLENBERG *et al.* (2008) revealed a tendency to microendemism in cophyline microhylid frogs. Indeed, many *Stumpffia* are currently known only from small areas not larger than 50 to 100 km² (KÖHLER *et al.*, 2010; NDIANTSOA *et al.*, 2012). Range size in *Stumpffia* might be correlated to body size (KLAGES *et al.*, 2013), in agreement with a general pattern in Madagascar's amphibians and reptiles (BROWN *et al.*, 2016). Accordingly, one factor responsible for this microendemism might be the overall small size of *Stumpffia* species, as they are among the

smallest frogs in Madagascar, and some number among the smallest frogs in the world (GLAW & VENCES, 2007). However, there are exceptions that do not fit this pattern. Some species of clade A (i.e., small-sized or miniaturized frogs), *S. mamitika*, *S. psologlossa*, and *S. gimmeli*, have a relatively wide distribution, although more data is necessary to support this especially for *S. psologlossa* and *S. gimmeli*. Also, in clade C (i.e., small- to moderate-sized species), *S. garraffoi*, *S. pardus*, and *S. analanjirofo* have a relatively wide distribution, and the same is true for *S. nigrorubra* although the southernmost known specimens from Manombo are genetically strongly differentiated. In total, seven out of 41 nominal species have a wider distribution and are not microendemics according to current knowledge. We suspect that future research will lead to range extensions of many *Stumpffia* species but the general pattern in the genus, i.e., overall small ranges and existence of true microendemic species, is unlikely to change.

Only few *Stumpffia* were known to occur in the dry forests of Madagascar (KLAGES *et al.*, 2013). The results herein increase the number of these species occurring in dry forests. In addition to *S. staffordi*, *S. be*, *S. hara*, and *S. analamaina*, also *S. mamitika* and *S. larinki* occur in Ankarana National Park in northern Madagascar. This new dataset also revealed that *Stumpffia* collected in 2010 and 2012 by us from Ankarafantsika National Park are indeed *S. analamaina*, as previously hypothesized by KLAGES *et al.* (2013), and this probably also applies to earlier collected material from this area that previously was assigned to *S. psologlossa* by BLOMMERS-SCHLÖSSER & BLANC (1991).

Patterns of digital reduction

The loss of limbs is one of the most extreme morphological changes in the history of tetrapods (LANDE, 1978). A change in the number of digits is a process during the embryonic stage characterized by the process of construction followed by destruction (GALIS *et al.*, 2001). According to ALBERCH & GALE (1983, 1985), there is a well-defined pattern in terms of what elements are most likely to be reduced. In frogs, for example, the first toe is always reduced first.

Several digital reductions are seen in *Stumpffia*. The order in which their fingers are reduced is consistently first finger first, followed by the fourth, then second, with the third remaining as the only developed digit that becomes broadened in *S. tridactyla*, *S. contumelia*, and *S. obscoena*. Remarkably, toe reduction does not seem to follow the scheme of ALBERCH & GALE (1983, 1985). In most taxa, but especially in *S. tridactyla*, *S. contumelia*, and *S. obscoena*, the first and second toes are more strongly reduced than the fifth toe, at least externally (Figs. 9–11). If this trend is supported based on the phalangeal development, then it would be a significant deviation from what has been accepted as a typical trend among all frogs.

Several sister taxa are characterized by the same type of digital transformations: the first toes are reduced in *S. angeluci* and *S. maledicta*, the phalangeal discs are slightly enlarged in *S. gimmeli* and *S. iharana*, the first finger and toe are reduced in *S. yanniki* and *S. analamaina*, and in *S. madagascariensis* and *S. pygmaea* (all of which are small-sized or miniaturized species from clade A), and the first finger is very strongly reduced in length and first toe absent in *S. obscoena* and *S. davidattenboroughi* (small-sized or miniaturized species from clade B). In clade C, a trend is seen to reduce in length especially the first toe, even in some relatively large-sized species, and with a complete reduction in external view in some small-sized species (e.g., *S. tetradactyla*). In clade D, both *S. contumelia* and *S. tridactyla* have digital reductions, i.e., the first finger is not visible, the second and fourth fingers are reduced to small knobs, and the third finger is broadened to a triangular shape. Investigations into the osteological basis for these digital reductions are on-going (SCHERZ *et al.*, unpubl. data).

Body size patterns

The pattern of body size evolution is particularly expressed in Clade A. Clades A1 and A2 consist of only small-sized and miniaturized species (8.0–16.8 mm) distributed in the north and northwest of Madagascar, whereas A3 is composed of only large sized species (21–28 mm) from the north of Madagascar. Clade B, in contrast, is variable both in morphology and distribution. It is composed of both eastern (*S. miery*, *S. obscoena*, *S. davidattenboroughi*) and northwestern species (*S. meikeae*), and of small-sized or miniaturized species (*S. miery*, *S. obscoena*, *S. davidattenboroughi*) as well as larger species (*S. meikeae*). However, more data are needed on this group, as it is only moderately supported (0.94 BPP) in the consensus tree. Within clade C there is a considerable variation in body size. However, pairs of sister species in clade C, based on adult males, have comparable body sizes, such as *S. pardus* and *S. diutissima* (17–22 mm), *S. makira* and *S. dolchi* (12 mm), and *S. achillei* and *S. analanjirofo* (19–20 mm). Clade D is formed by the two miniaturized species *S. tridactyla* (10–11 mm) and *S. contumelia* (8–9 mm). The latter species is the smallest known frog species from Madagascar and among the smallest frogs in the world: RITTMAYER *et al.* (2012) identified 29 of the world's smallest frogs, among which 15 are microhylids. While this list would need to be adjusted to account for recent descriptions, at present *S. contumelia* (max. male SVL 8.9 mm) would compete with *Paedophryne amauensis* (max. male SVL 8 mm) and *P. swiftorum* (max. male SVL 8.9 mm) for the title of the smallest frog in the world. To our knowledge no other species described since 2012 might also be a candidate for this title.

The history of the body size evolution of this group is thus clearly confounded by repeated shrinkage and growth across different clades. However, there are several indica-

tions that the group may have had a very small common ancestor, in particular digital reduction in the majority of species, the absence of vomerine and maxillary teeth in even the largest species according to currently available data, and the basal relationship of the diminutive species of clade D with the rest of the genus. Further research into the evolution of the size of these frogs, including ancestral size reconstructions, may help us to understand not just the variety of sizes present in most clades, but also the dispersal and speciation history of the genus.

Color patterns

Three of the new species, *S. nigrorubra*, *S. miovaova*, and *S. meikeae*, show the red/orange color on the belly that was previously known only from *Stumpffia kibomana* and to some degree from *S. roseifemoralis* (GLAW *et al.*, 2015). While *S. meikeae* is a member of clade B, the other red-bellied species belong to clade C but do not form a monophyletic group (Fig. 4). The function of the red/orange ventral color is poorly known (GLAW *et al.*, 2015). Several other color elements repeat frequently across many unrelated taxa, including the teddybear shaped dorsal marking, dorsal chevrons, crossbands on the legs and arms, light annuli before the terminal phalanges of the fingers and toes, and lightened or bright areas on the posterodorsal shank. These may reflect some limitations or developmental consistencies in these frogs, especially as all of these elements are known also to some degree from other genera—indeed, most microhylids have light annuli before their terminal phalanges. At least among Malagasy frogs, the markings on the posterodorsal shank seem to be more or less restricted to *Stumpffia* (possibly also present in some species of *Anodonthyla*; GLAW & VENCES, 2007).

Call patterns

The calls of *Stumpffia* species are mostly composed of the repetition of single chirping notes, except for *S. psolloglossa* that emits a long note consisting of pulses (GLAW & VENCES, 1992). The calls of the newly described species are not fundamentally different to most of the formerly recognized nominal species of *Stumpffia*. Interestingly, our data reveals a similar pattern of call differences between species occurring in sympatry that indicates parallel processes in call evolution within *Stumpffia*:

Species from Montagne d'Ambre National Park, *S. angeluci*, *S. huwei*, and *S. maledicta*, differ in call duration, with *S. angeluci* emitting longer calls (179–187 ms) than *S. huwei* (61–74 ms), and *S. maledicta* emitting shorter calls (98–104 ms) than *S. angeluci* but longer than *S. huwei*. Similarly, this is the case for the species of the Marojejy Massif, with only some overlap in call duration between *S. achillei* (36–79 ms), *S. diutissima* (53–56 ms), *S. tridactyla* (101–198 ms), and *S. roseifemoralis* (276–280 ms).

Also the duration of inter-call intervals often differs among sympatric species, e.g. in Ankarana National Park, with *S. mamitika* (612–1510 ms; this is based on the longest call series available for the species) calling faster than *S. larinki* (2143–2289 ms). Similarly, this is the case for the species from Ranomafana (inter-call intervals for *S. nigrorubra* are 1366–1720 ms and for *S. miery* 2679–4247 ms). In Ambodivoangy, the dominant frequencies of calls differ between sympatric species with *S. contumelia* calls (7450–7579 Hz) having a higher frequency than those of *S. pardus* (5124–5383 Hz).

Conservation status and conservation significance of newly described species

Most species of *Stumpffia* were previously assessed as Data Deficient, except *S. analamaina*, which was considered Critically Endangered (KLAGES *et al.*, 2013), *S. gimmeli* (Least Concern; ANDREONE *et al.*, 2005a), and *S. pygmaea*, *S. be*, *S. hara*, *S. megsoni*, and *S. staffordi* (Vulnerable; ANDREONE *et al.*, 2005a, KÖHLER *et al.*, 2010). All members of the genus were again reassessed between 2014 and 2016 by the IUCN Species Survival Commission Amphibian Specialist Group for Madagascar (along with all other Malagasy amphibians). This reassessment found three species to be Data Deficient (*S. megsoni*, *S. tetradactyla*, and *S. tridactyla*), two Least Concern (*S. grandis* and *S. gimmeli*), one Vulnerable (*S. staffordi*), seven Endangered (*S. be*, *S. kibomena*, *S. madagascariensis*, *S. miery*, *S. psologlossa*, *S. pygmaea*, and *S. roseifemoralis*), and two Critically Endangered (*S. analamaina* and *S. hara*).

Our data reveals that *Stumpffia* species occur both in protected as well as in unprotected areas. Some of the species collected in unprotected areas like *S. mamitika* in Vohemar, *S. gimmeli* in Antsirasa and 27 km from Ambanja, and *S. iharana* in a gallery forest near Andrafainkona, were found in highly degraded areas (i.e. mango or vanilla plantations). Also, some species occurring in protected areas (*S. analamaina* in Ankarafantsika NP, *S. angeluci* in Montagne d'Ambre NP, *S. huwei* in Montagne d'Ambre NP, *S. garraffoi* in Betampona Strict Nature Reserve) were found in rather disturbed areas within these parks, i.e. either close to the park office or in dense leaf litter at the border of a trail.

We agree with the hypothesis of NDRIANTSOA *et al.* (2013) that most *Stumpffia* are able to dwell in secondary forest as long as a layer of leaf litter provides sufficient humidity and some shade exists. On the other hand, the strikingly distinct patterns of distribution observed in some of the six different species of *Stumpffia* occurring at Betampona Strict Nature Reserve might contradict this hypothesis and suggest a subtle underlying habitat specialization. However, studies from forest fragments in the Ranomafana region also confirm that *Stumpffia* spp. apparently persist in degraded habitat (RIEMANN *et al.*, 2015). Accordingly, even if most species within the genus have a very small range of distribution, we do not

consider all members of the genus to be under immediate threat of extinction. Nevertheless, strict application of the IUCN Red List criteria (IUCN 2001) yields 2 species as Least Concern, 6 species as Near Threatened, 5 species as Vulnerable, 17 species as Endangered, 8 species as Critically Endangered, and 3 species as Data Deficient (Table 6).

The IUCN Red List criteria are however inherently and intentionally subjective; explicitly they may take into account the suspicions and feelings of the assessors, however vague. This makes them practically impossible to apply consistently. To attempt to overcome this, we have made a concerted effort to keep these assessments consistent with those recently published—in which several of the authors were intensively involved—and in strict keeping with the criteria. Despite this, we wish to emphasise that (1) strict application of the criteria is often inappropriate; (2) even here there was some dissent among authors as to which criteria should be applied in which way to each species; and (3) the most commonly used criterion, B, which assesses the distribution of threat based on range size, occupancy, and on-going habitat and species trends within that range, is ill suited to handling small and/or microendemic taxa, but realistically only one other criterion (D2) can be applied to taxa from which no population size data are available.

The current Red List system results in inflation of risk, and emphasizes publication of high threat categories with totally inadequate data; the discovery of a single individual that expands a Critically Endangered species' range by 40 km would instantly result in its threat status being downgraded. This is a problem deeply nested within the IUCN's assessment strategy, and one that ought to be addressed due to the extreme value placed on Red List rankings by policy makers, conservation practitioners, and others. We therefore urge that more species be listed as Data Deficient instead of being given inflated statuses, as this is an honest, scientific statement of the current state of knowledge on them, which is largely inadequate. This includes not just species from which few individuals or few data are available, but also taxonomic species complexes, for which any assessment based on the full distribution of the complex will be a drastic overestimation of any individual member's range, and an underestimation of the threats each species is facing.

Final considerations

With this study, we have taken a first big step toward an integrative resolution of the taxonomy of the smaller cophylines, which have had an enormous taxonomic gap (VIEITES *et al.*, 2009; PERL *et al.*, 2014). We have increased the nominal diversity of *Stumpffia* from 15 to 41, and provided baseline information that will allow the description of a few more candidate species once additional specimen material becomes available. This brings us to approximately 100 named cophyline species. However, in other genera, numerous candidate species remain, and we expect

Table 6. Evaluation and proposal of the IUCN Red List status for nominal species in the genus *Stumpffia* (in alphabetical order) according to defined criteria (IUCN 2001). Please note that application of criteria partly remain subjective and not always identical rationale appears adequate (see column with comments). Abbreviations used: TDL = Threat-defined locality sensu IUCN 2001; AOO = Area of Occupancy; EOO = Extent of Occurrence; CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient.

Species	Applied IUCN Criteria	Comments	Current Red List Status	Proposed Red List Status
<i>S. achillei</i>	B1ab(iii)	One TDL, which is in a protected area. On-going habitat degradation due to illegal logging activity, especially at low altitudes. EOO and AOO probably > 10 km ² . In line with <i>Rhombophryne savaka</i> from same area.	Not yet evaluated	EN
<i>S. analamaina</i>	B1ab(iii), B2ab(iii)	Two TDLs, one in a protected area. Species proposed as CR in original description because of single known locality. Molecular studies now revealed a second locality within a protected area. New EOO still < 5000 km ² . Both known localities under heavy anthropogenic pressure.	CR	EN
<i>S. analanjirofo</i>	B1ab(iii)	Three TDLs including two protected areas. Probably relatively widespread in lowland rainforests along the northern east coast, but EOO still < 20,000 km ² , and population extremely fragmented. Lowland rainforest habitats are under severe human pressure.	Not yet evaluated	VU
<i>S. angeluci</i>	B1ab(iii)	Three TDLs in three protected areas (Joffreville is near to two of these protected areas and not considered its own TDL). EOO < 5000 km ² . Habitat degradation is ongoing at known localities.	Not yet evaluated	EN
<i>S. be</i>	B1ab(iii)	One TDL, which is a protected area. Does not qualify for CR under criterion B as its specialization to karstic habitat and caves means it is probably not experiencing decline in extent or quality of habitat. Could rapidly become CR if anthropogenic activity in the park increases drastically.	EN	EN
<i>S. betampona</i>	B1ab(iii), B2ab(iii)	One TDL, which is a protected area. EOO ~26km ² . Lowland rainforest habitat is under severe anthropogenic pressure. Probably also qualifies for CR under A2c.	Not yet evaluated	CR
<i>S. cotumelia</i>	B1ab(iii)	One TDL, which is in a protected area. Current knowledge is poor, and it may have a wider distribution, but all specimens were collected at exactly the same locality, and the habitat is under anthropogenic pressure.	Not yet evaluated	CR
<i>S. davidattenboroughi</i>	B1ab(iii), B2ab(iii)	See <i>S. betampona</i> .	Not yet evaluated	CR
<i>S. diutissima</i>	B1ab(iii)	See <i>S. achillei</i> .	Not yet evaluated	EN
<i>S. dolchi</i>	D2	One TDL, which is a protected area. AOO < 20 km ² . No on-going threats sensu criterion B. However, island population is vulnerable and could easily be driven to CR or EX quickly.	Not yet evaluated	VU
<i>S. edmondsi</i>	n/a	Currently one or two TDLs, in close proximity to several protected areas. Probably widespread in Andasibe-Mantadia area, and could extend north up to Zahamena through continuous forest; EOO is still certainly < 20,000 km ² . Apparently not immediately threatened by declines in habitat quality, but if this changes, will qualify for VU B1ab(iii).	Not yet evaluated	NT
<i>S. fusca</i>	B1ab(iii)	See <i>S. cotumelia</i> .	Not yet evaluated	CR
<i>S. garraffoi</i>	B2ab(iii)	Three TDLs, at least one in a protected area. Current EOO < 4000 km ² . Populations severely fragmented. On-going habitat decline, particularly of lowland rainforest.	Not yet evaluated	EN
<i>S. gimmeli</i>	None	Roughly nine TDLs currently known, at least two in protected areas. Although current EOO is less than 20,000 km ² , species is abundant, has apparently stable populations, occurs in secondary and disturbed habitats, and probably is not significantly affected by deforestation.	LC	LC
<i>S. grandis</i>	B1ab(iii)	See <i>S. achillei</i> , but found at higher elevation where threats are lower. EOO probably < 100 km ² . Assessed as EN in line with <i>Rhombophryne vaventy</i> and <i>R. serratopalebrosa</i> recently assessed from the same locality.	LC	EN
<i>S. hara</i>	B1ab(iii)	One TDL. AOO < 10 km ² . Known from several caves and around a small creek on Nosy Hara, the latter suffering from severe habitat modification (construction of concrete stairs for tourism).	CR	CR
<i>S. huwei</i>	n/a	One TDL, which is a protected area. Current EOO is small enough to qualify for CR, but currently there are no on-going declines or fluctuations in habitat, populations, or distribution at the relatively high altitude of the known localities.	Not yet evaluated	NT
<i>S. iharana</i>	B1a b(iii)	Three TDLs, none of which is protected. EOO < 5000 km ² . All localities under heavy anthropogenic pressure, severe degradation of habitat.	Not yet evaluated	EN
<i>S. jeannoeli</i>	B1ab(iii), B2ab(iii)	See <i>S. betampona</i> .	Not yet evaluated	CR
<i>S. kibomena</i>	n/a	See <i>S. edmondsi</i> .	EN	NT
<i>S. larinki</i>	D2	See <i>S. be</i> . Less specialized to karstic habitats than that species, but probably also not experiencing on-going declines in habitat, range, or population size.	Not yet evaluated	VU

Table 6 continued.

Species	Applied IUCN Criteria	Comments	Current Red List Status	Proposed Red List Status
<i>S. madagascariensis</i>	n/a	See <i>S. huwei</i> . Also found around Montagne des Français (<i>S.</i> sp. Ca25), increasing the spread of risk, but still could become EN or CR. Recently assessed as EN, but here shown to have wider distribution and is not known from edge areas most affected by deforestation.	EN	NT
<i>S. makira</i>	n/a	Known from only one specimen. Species could be found throughout Makira, or locally restricted (could be CR, EN, or VU). No known immediate threats in the center of Makira, but if found at the edges could be under significant threat. More information is needed.	Not yet evaluated	DD
<i>S. maledicta</i>	n/a	See <i>S. huwei</i> .	Not yet evaluated	NT
<i>S. mamitika</i>	n/a	Three known TDLs, one in a protected area. Current EOO < 20,000 km ² , but probably more widespread. Occurs in secondary habitats. No known on-going threats. Assessment of population trend is needed, but conservatively considered LC.	Not yet evaluated	LC
<i>S. megsoni</i>	n/a	One TDL, which is not protected and is threatened. Apparently tolerant to some degree of habitat modification, but certainly experiencing on-going decreases in quality of habitat. Difficult to assess, here classified as DD for consistency with current Red List.	DD	DD
<i>S. meikeae</i>	n/a	One confirmed TDL, but unpublished data suggest at least one more locality southwest of Bealanana (SCHERZ <i>et al.</i> , unpubl. data); currently in one protected area. EOO not currently calculable. Probably threatened by on-going habitat declines. Could qualify for CR, EN, or VU. More information is needed.	Not yet evaluated	DD
<i>S. miery</i>	B1ab(iii)	At last four TDLs, some inside a protected area. EOO < 5000 km ² . On-going decline in extent and quality of habitat, but apparently tolerant to some habitat degradation.	EN	EN
<i>S. miovaova</i>	B1ab(iii)	One TDL, which is not yet protected. EOO < 250 km ² . Continuing deforestation and habitat degradation; high anthropogenic pressure. In line with <i>Rhombophryne longicrus</i> from the same area.	Not yet evaluated	EN
<i>S. nigrorubra</i>	B1ab(iii)	At least six TDLs, some inside a protected area. EOO < 5000 km ² . On-going decline in extent and quality of habitat, but apparently tolerant to some habitat degradation.	Not yet evaluated	EN
<i>S. obscoena</i>	n/a	One TDL, which is in a protected area. Current EOO < 100 km ² , but probably more widespread. On-going decline in extent and quality of habitat outside of protected areas, but overall probably stable. Thus almost qualifies for CR B1ab(iii), but currently suspected to not satisfy any subcriterion of Bb.	Not yet evaluated	NT
<i>S. pardus</i>	B1ab(iii)	Three TDLs, one of which is protected. EOO < 20,000 km ² . Populations severely fragmented, and lowland forest is under heavy anthropogenic pressure.	Not yet evaluated	VU
<i>S. psologlossa</i>	B1ab(iii)	Four TDLs, at least one of which is protected. EOO < 5000 km ² , but probably more widespread than currently known. Anthropogenic pressure is high throughout range.	EN	EN
<i>S. pygmaea</i>	B1ab(iii)	One TDL, which is a protected area. EOO < 100 km ² . High anthropogenic pressure, but somewhat resilient to it. Could rapidly be driven to CR or EX by encroachment on its habitat, fire, or introduction of invasive species.	EN	EN
<i>S. roseifemoralis</i>	B1ab(iii)	See <i>S. achillei</i> .	EN	EN
<i>S. sorata</i>	B1ab(iii)	See <i>S. miovaova</i> .	Not yet evaluated	EN
<i>S. spandei</i>	B2ab(iii)	A single specimen is known. One TDL, which is not protected. Forest fragment where HT was found has an area of 6 km ² (approx. AOO), but species is probably more widely distributed. Nearby forest is highly fragmented.	Not yet evaluated	CR
<i>S. staffordi</i>	D2	AOO estimated to be < 10 km ² . Locality is suffering from on-going habitat degradation and high anthropogenic pressure.	VU	VU
<i>S. tetradactyla</i>	B1ab(iii)	One TDL, which is poorly protected. EOO < 300 km ² . Abundant in forest and secondary habitat, but suspected to be declining from anthropogenic activity.	DD	EN
<i>S. tridactyla</i>	B1ab(iii)	See <i>S. achillei</i> .	DD	EN
<i>S. yanniki</i>	B1ab(iii)	One TDL, which is in a new protected area. Known EOO is diminutive, but the species is probably found more widely in the Tsaratanana region. On-going declines in extent and quality of habitat throughout nearby areas. More research is likely to lower the threat status of this species.	Not yet evaluated	CR

to see similar approaches taken to resolving their taxonomy in the coming years. Yet, a complete and conclusive taxonomy of Madagascar's frogs is not on the horizon, and will require both the clarification of old names, and the collection of more material for taxonomic purposes.

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Appendix

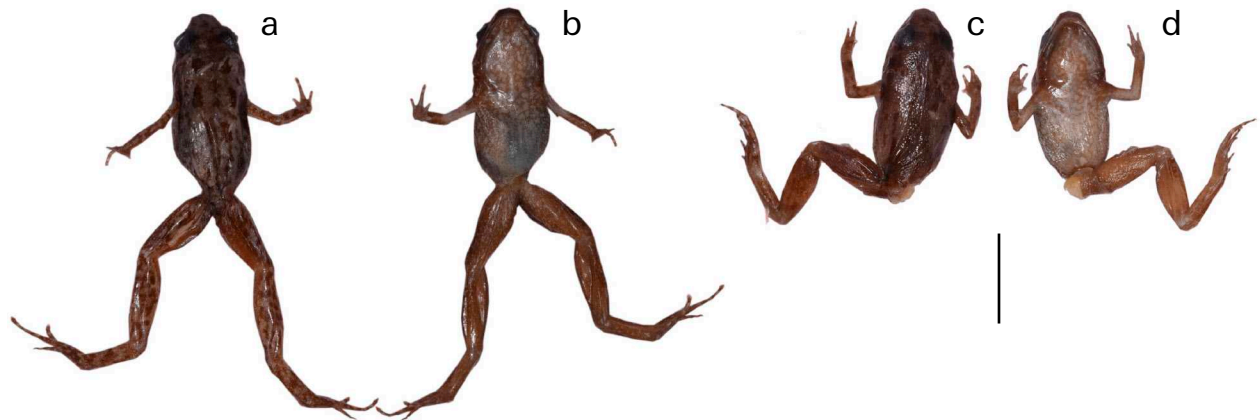


Fig. S91. *Stumpffia psologlossa*, preserved specimens from Nosy Be: (a–b) ZSM 479/2000 (FG/MV 2000.279); (c–d) ZSM 480/2000 (FG/MV 2000.837); Scale bar = 5 mm.

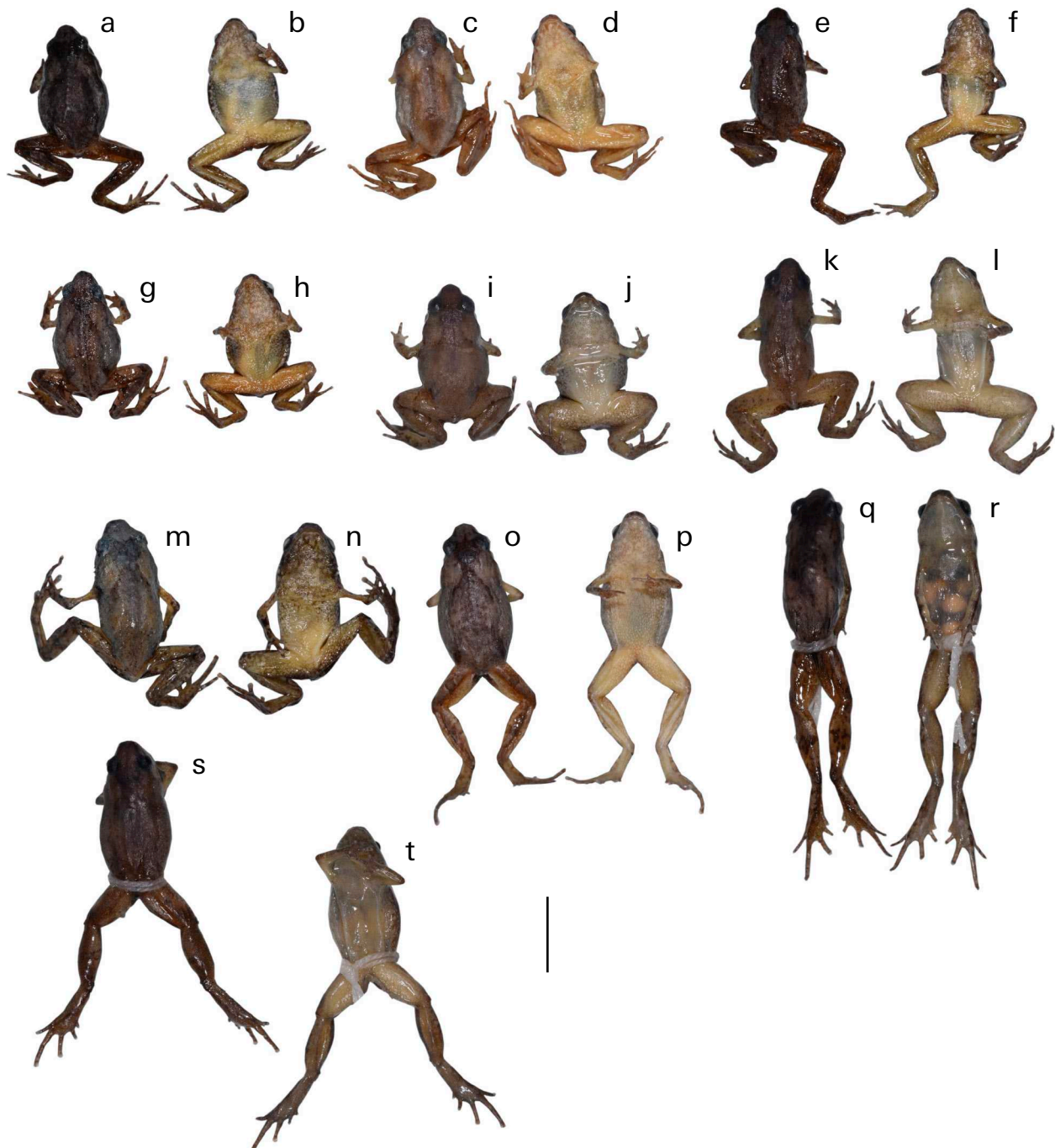


Fig. S92. *Stumpffia analamaina*, preserved specimens from Ankarafantsika National Park: (a–b) KUZA 0001 (2010-F002); (c–d) KUZA 0002 (2010-F003); (e–f) KUZA 0003 (2010-F004); (g–h) KUZA 0004 (2010-F005); (i–j) KUZA 0005 (2011-Ad-049), (k–l) KUZA 0006 (2011-Ad-050); (m–n) KUZA 0007 (2011-Ad-059); (o–p) KUZA 0010 (2013-NoCode); (q–r) KUZA 0008 (2012-089); (s–t) KUZA 0009 (2012-090); Scale bar = 5 mm.

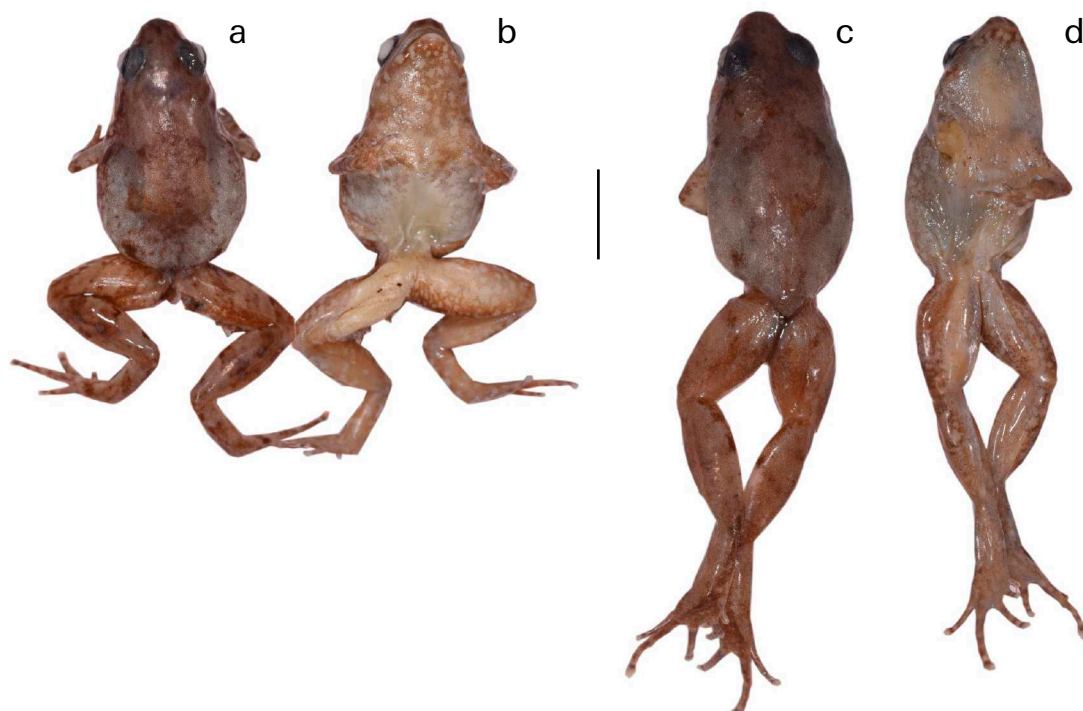


Fig. S93. *Stumpffia gimmeli*, preserved specimens: (a–b) ZSM 833/2003 (FG/MV 2002.784) from Manongarivo; (c–d) ZSM 597/2001 (MV 2001.36) from Antsirasilira; Scale bar = 5 mm.

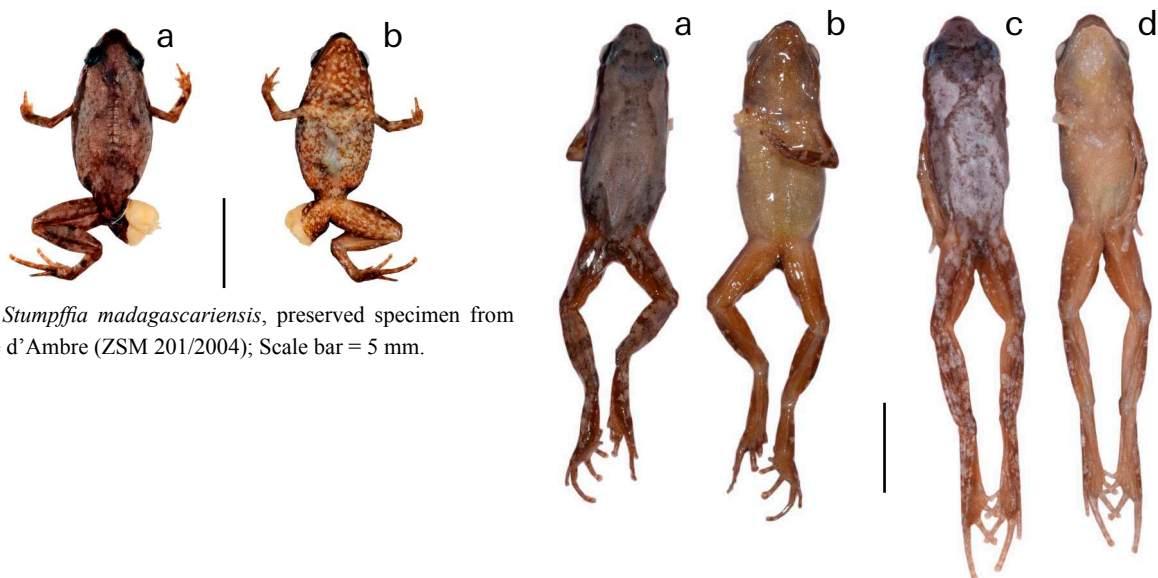


Fig. S94. *Stumpffia madagascariensis*, preserved specimen from Montagne d'Ambre (ZSM 201/2004); Scale bar = 5 mm.

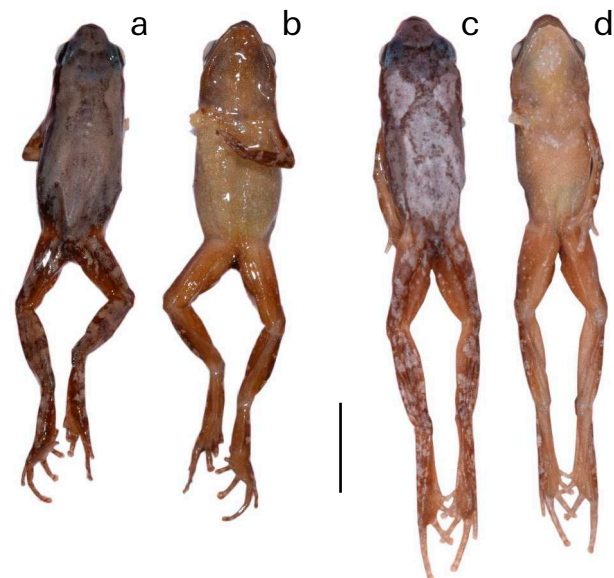


Fig. S95. *Stumpffia* cf. *madagascariensis* (= *S. sp. Ca25*), preserved specimens from Montagne des Français: (a–b) ZSM 2108/2007 (FGZC 1103); (c–d) ZSM 2109/2007 (FGZC 1105); Scale bar = 5 mm.

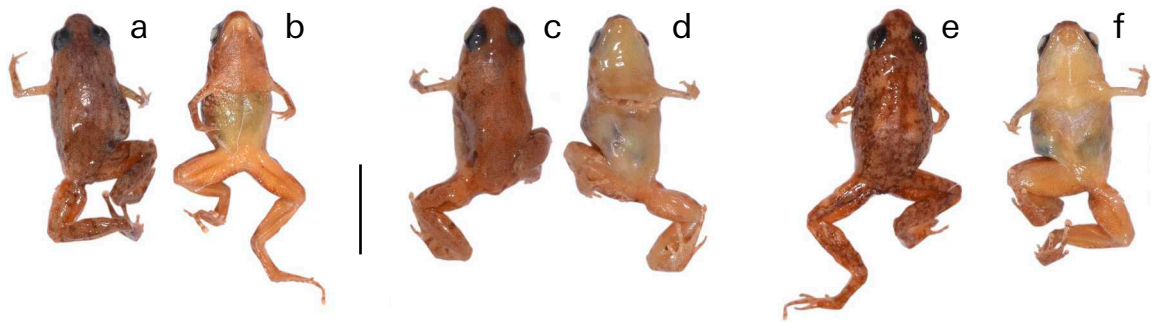


Fig. S96. *Stumpffia pygmaea*, preserved specimens from Nosy Be: (a–b) ZFMK 53769; (c–d) ZFMK 53772; (e–f) ZFMK 53773; Scale bar = 5 mm.

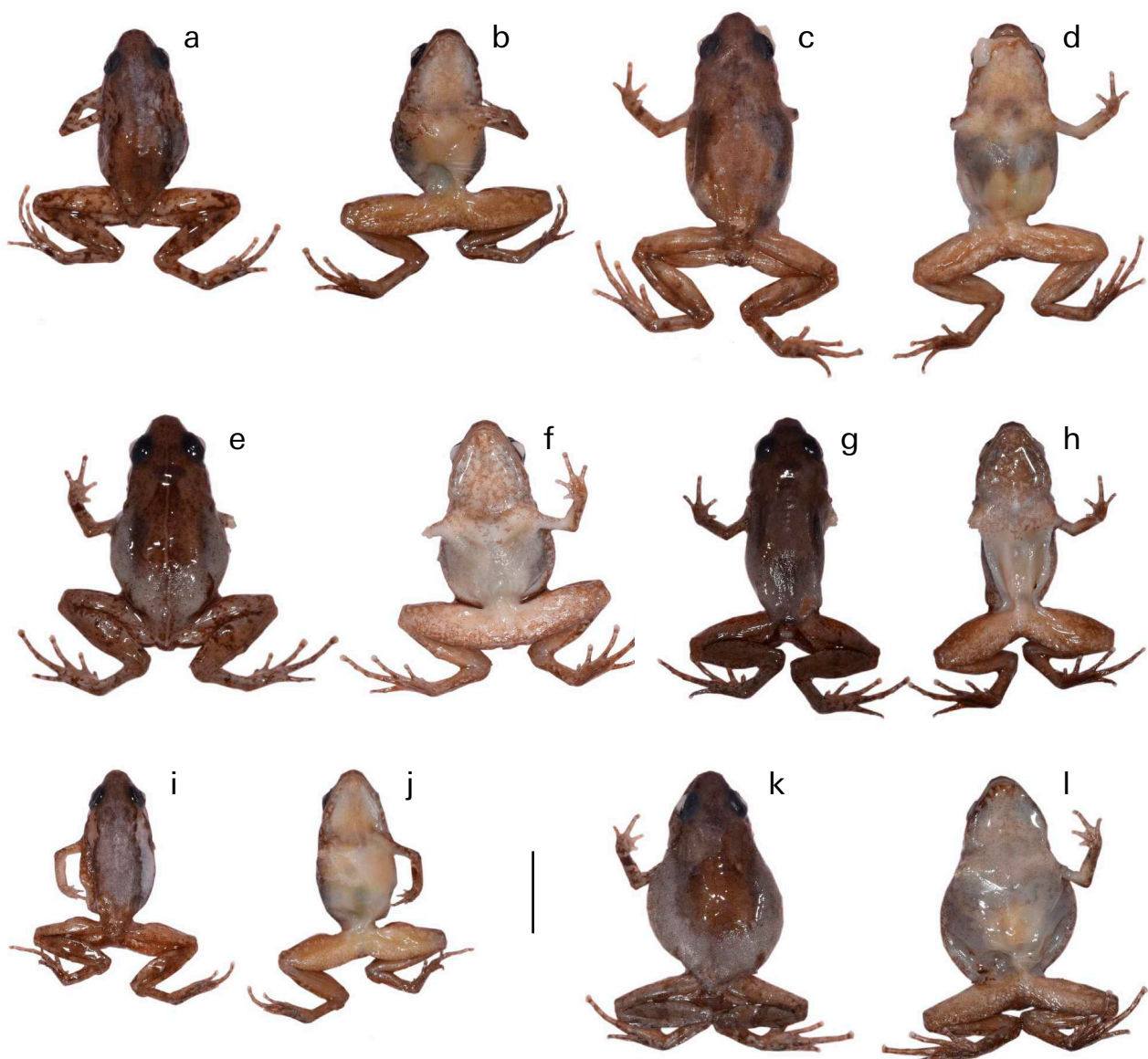


Fig. S97. *Stumpffia angeluci* **sp. nov.**, preserved paratype specimens from Montagne des Français: (a–b) ZSM 302/2004 (FGZC 583); (c–d) ZSM 301/2004 (FGZC 581); (e–f) ZSM 224/2004 (FGZC 434); (g–h) ZSM 223/2004 (FGZC 433); (i–j) ZSM 303/2004 (FGZC 586); (k–l) ZSM 300/2004 (FGZC 580); Scale bar = 5 mm.

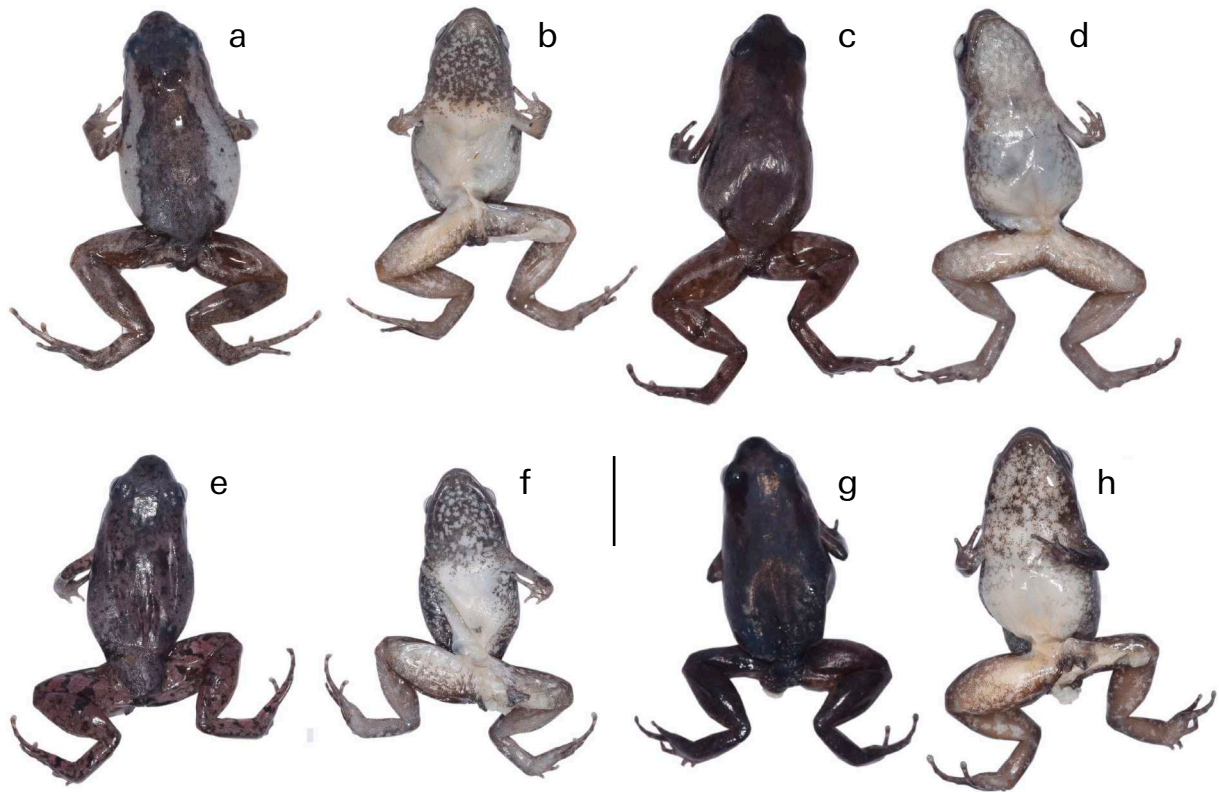


Fig. S98. *Stumpffia huwei* sp. nov., preserved specimens from Montagne d'Ambre National Park: (a–b) holotype ZSM 221/2016 (ZCMV 13618); (c–d) paratype ZSM 222/2016 (ZCMV 13620); (e–f) paratype UADBA-A 60282 (ZCMV 13621); (g–h) paratype ZSM 223/2016 (ZCMV 13622); Scale bar = 5 mm.

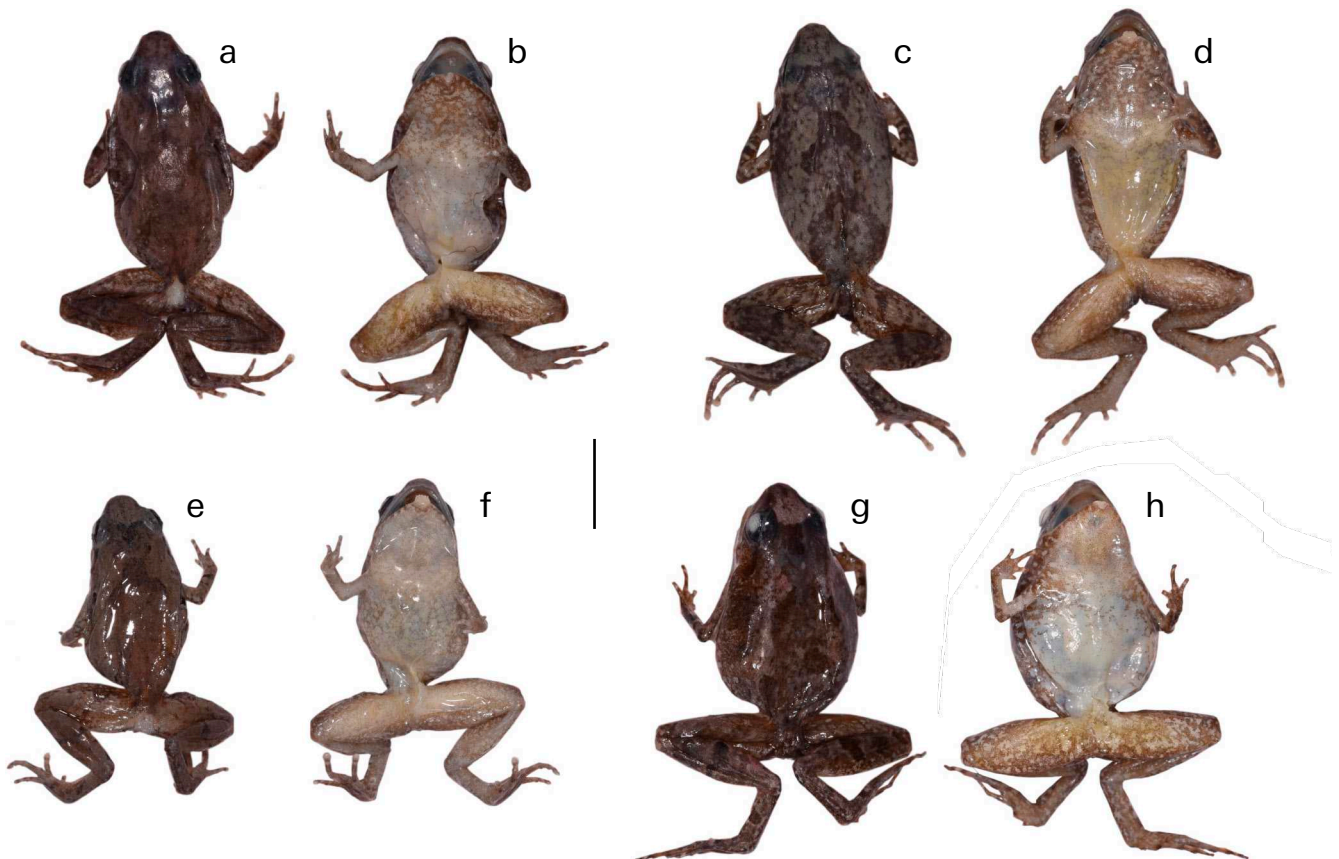


Fig. S99. *Stumpffia iharana* sp. nov., preserved specimens from Sorata: (a–b) paratype ZSM 1642/2012 (FGZC 3800); (c–d) paratype ZSM 1650/2012 (FGZC 3893); (e–f) holotype ZSM 1651/2012 (FGZC 3895); (g–h) paratype ZSM 1652/2012 (FGZC 3927); Scale bar = 5 mm.

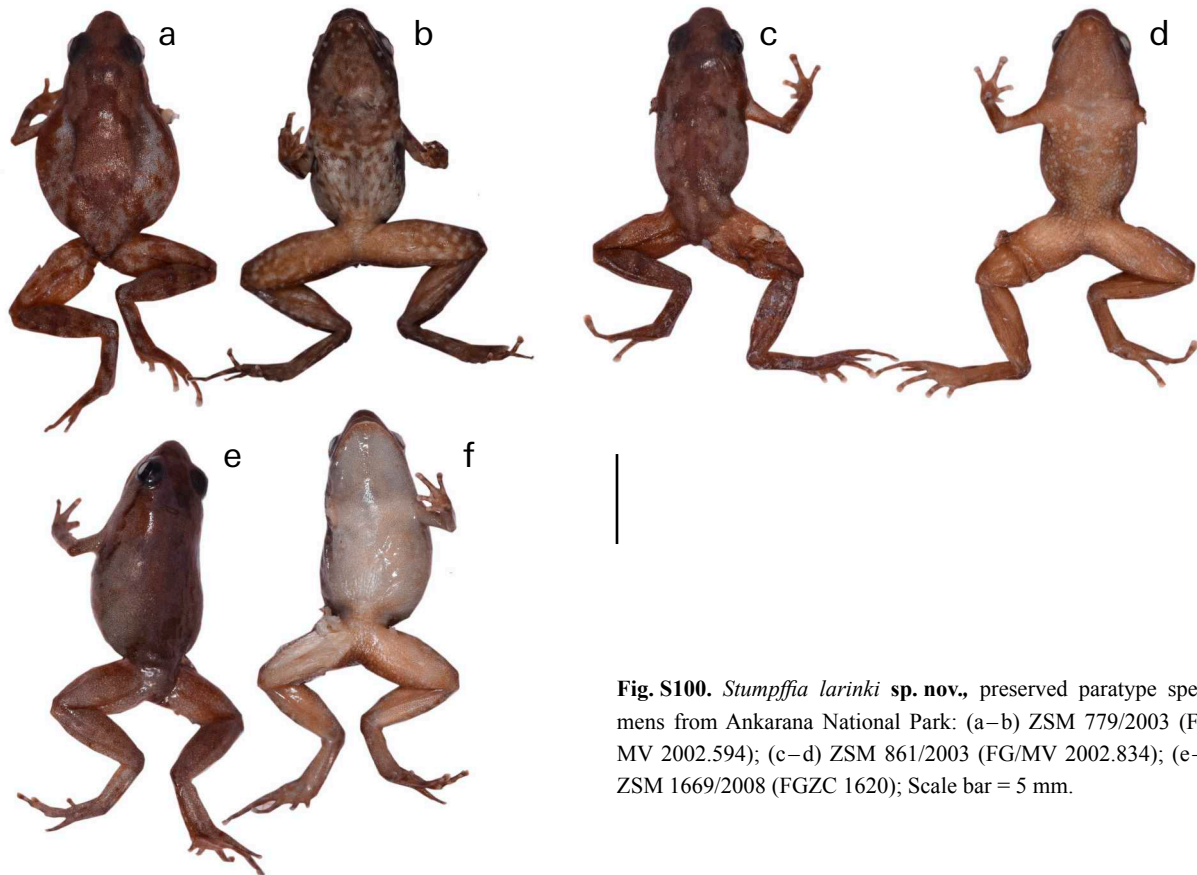


Fig. S100. *Stumpffia larinki* **sp. nov.**, preserved paratype specimens from Ankarana National Park: (a–b) ZSM 779/2003 (FG/MV 2002.594); (c–d) ZSM 861/2003 (FG/MV 2002.834); (e–f) ZSM 1669/2008 (FGZC 1620); Scale bar = 5 mm.

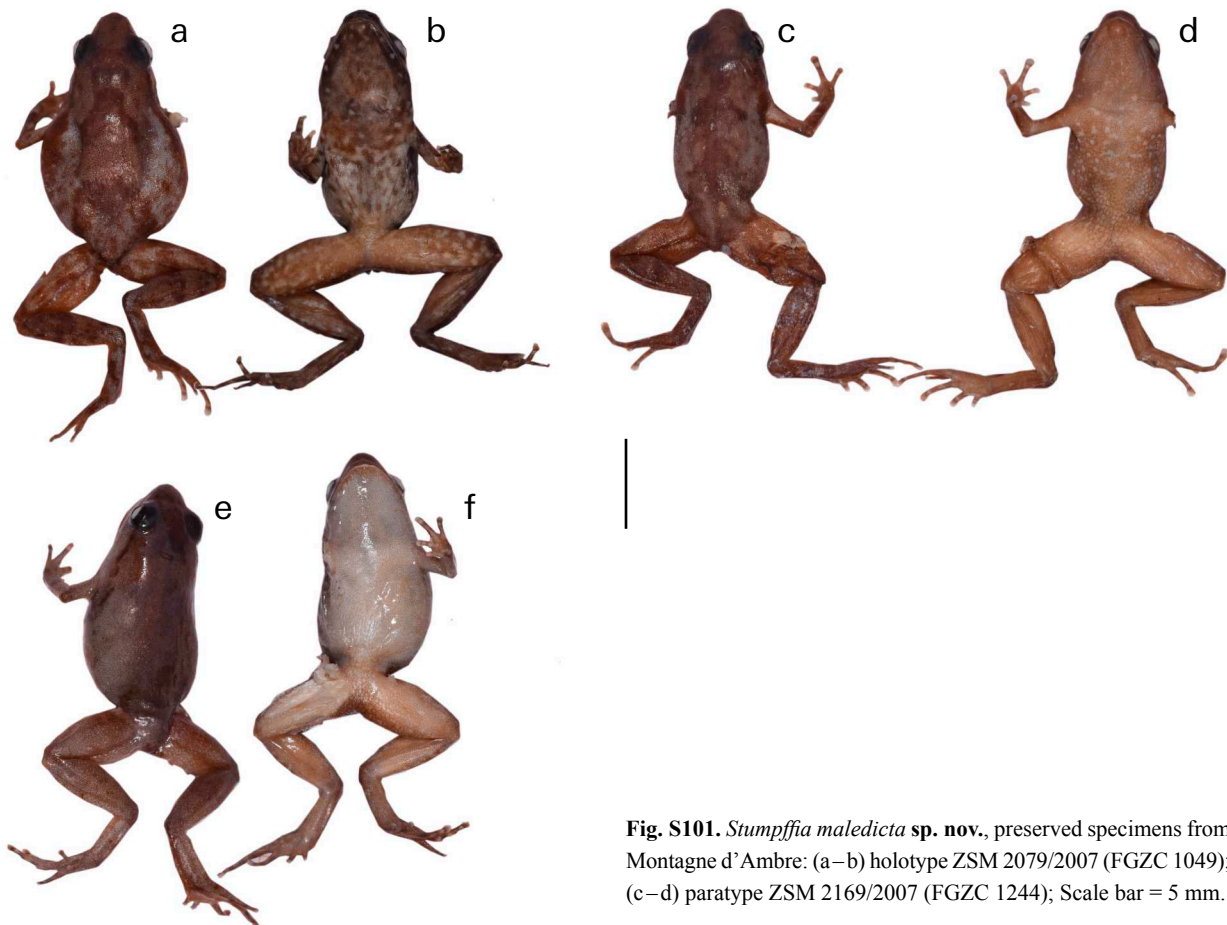


Fig. S101. *Stumpffia maledicta* **sp. nov.**, preserved specimens from Montagne d'Ambre: (a–b) holotype ZSM 2079/2007 (FGZC 1049); (c–d) paratype ZSM 2169/2007 (FGZC 1244); Scale bar = 5 mm.

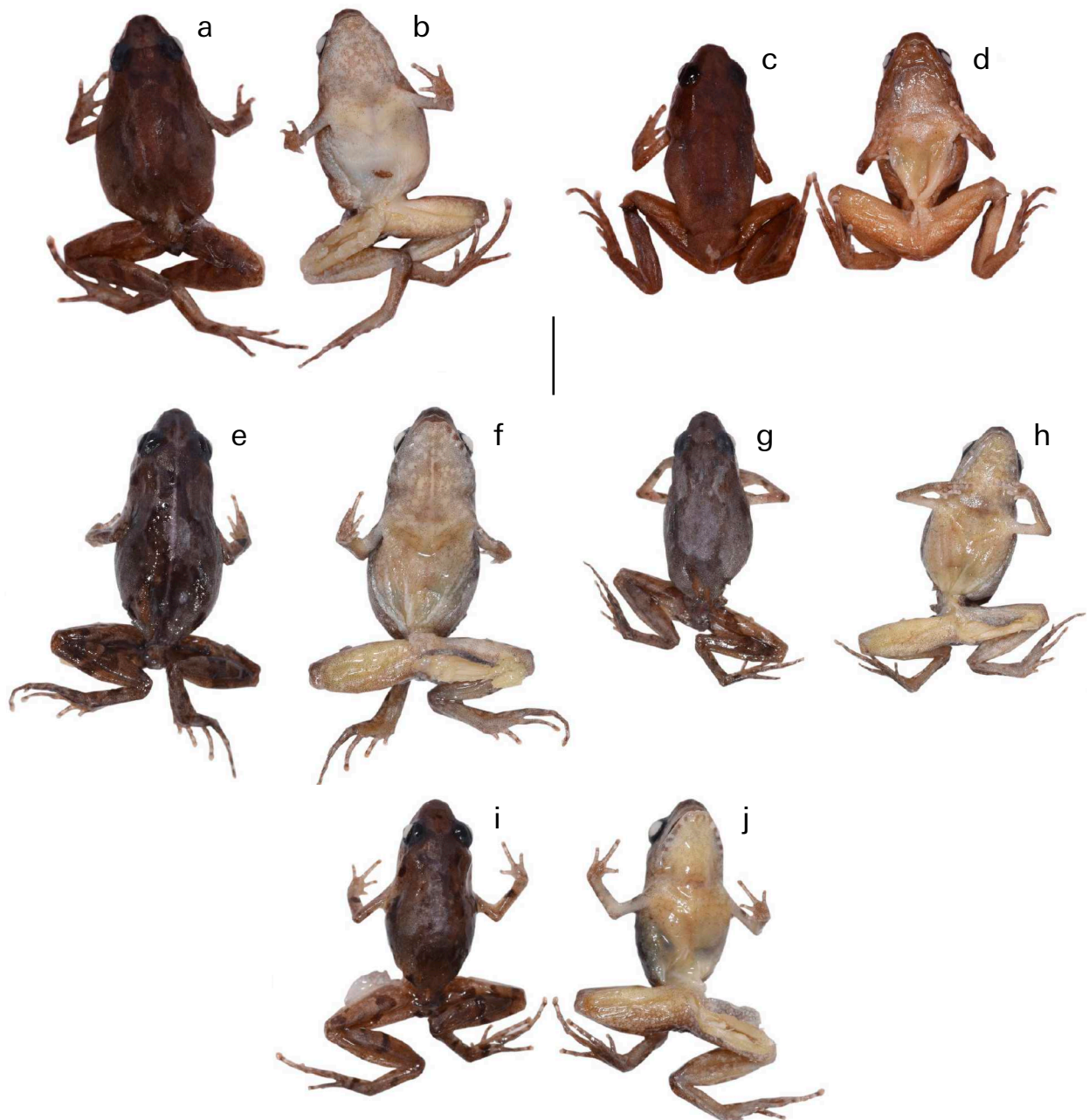


Fig. S102. *Stumpffia mamitika* **sp. nov.**, preserved paratype specimens: (a–b) ZSM 375/2005 (FGZC 2725) from Andapa; (c–d) ZSM 862/2003 (FG/MV 2002.838) from Ankarana National Park; (e–f) ZSM 3234/2012 (ZCMV 13531); (g–h) ZSM 3233/2012 (ZCMV 13529); (i–j) ZSM 3234/2012 (ZCMV 13530); Scale bar = 5 mm.

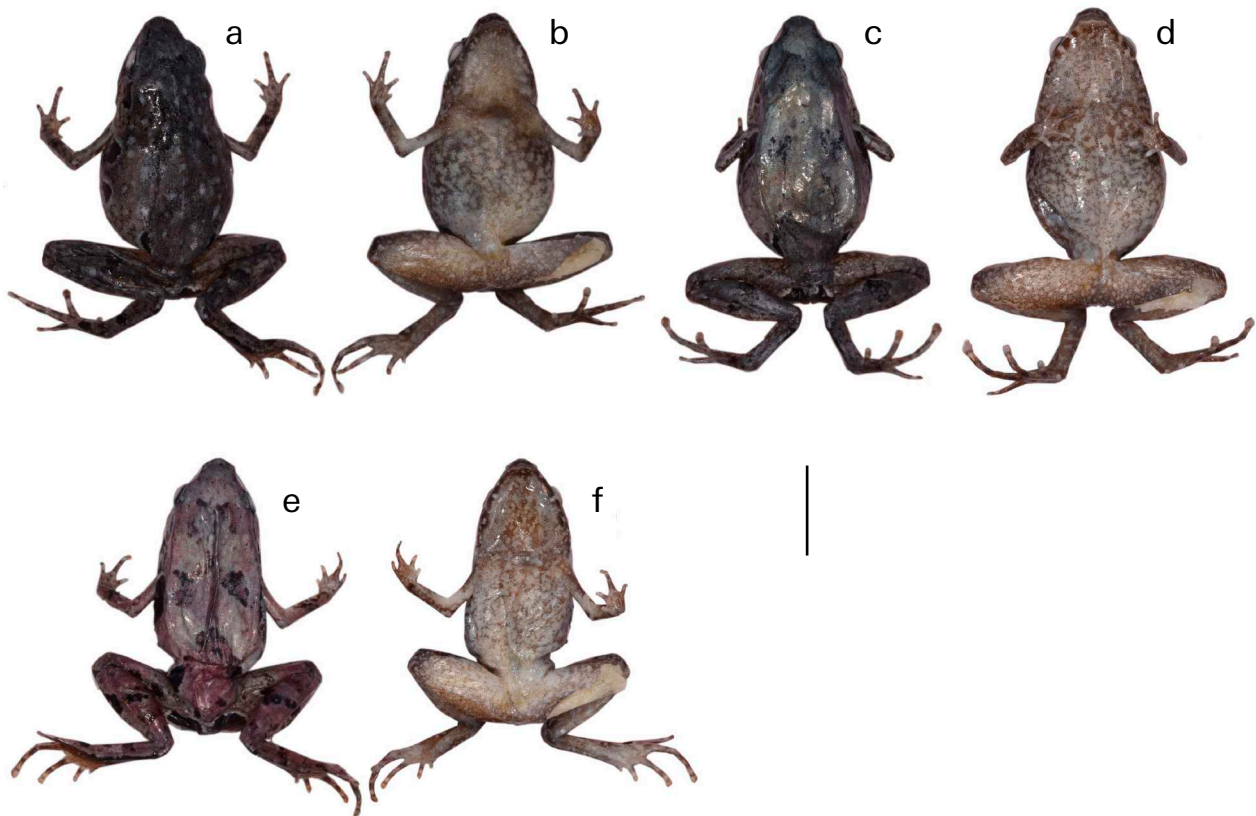


Fig. S103. *Stumpffia sorata* **sp. nov.**, preserved specimens from Sorata forest: (a–b) paratype ZSM 1643/2012 (FGZC 3618); (c–d) holotype ZSM 1644/2012 (FGZC 3621); (e–f) paratype ZSM 1645/2012 (FGZC 3622); Scale bar = 5 mm.

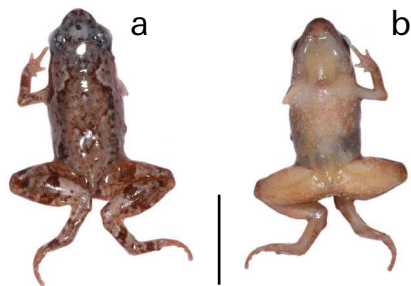


Fig. S104. *Stumpffia yanniki* **sp. nov.**, preserved paratype specimen collected in a forest fragment between Bealanana and Antsohihy, ZSM 1825/2010 (ZCMV 12600); Scale bar = 5 mm.

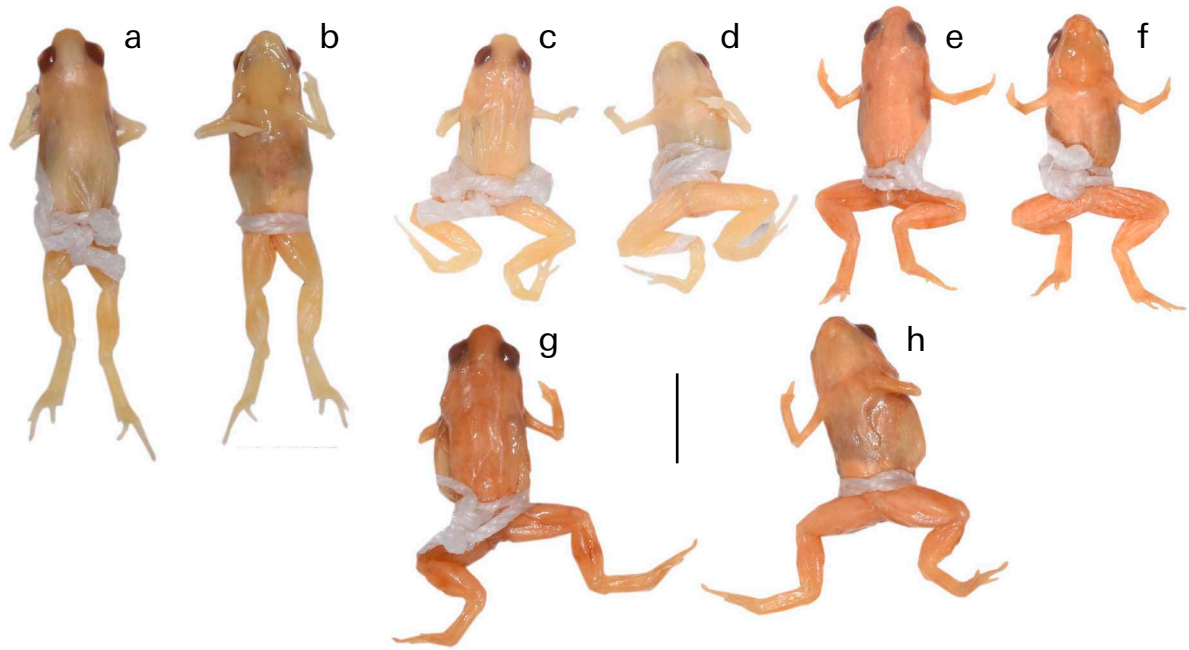


Fig. S105. *Stumpffia tridactyla*, preserved paratypes from Marojejy National Park: (a–b) MNHN 1975.26; (c–d) MNHN 1975.27; (e–f) MNHN 1975.29; (g–h) MNHN 1975.28; Scale bar = 5 mm.

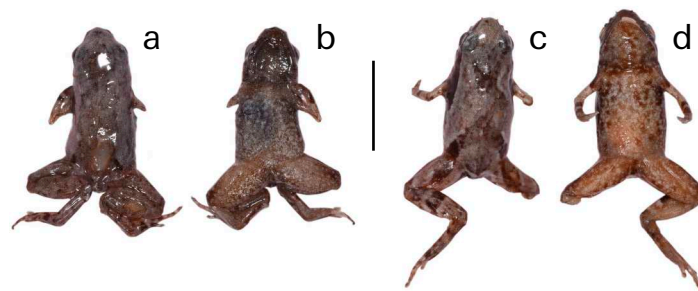


Fig. S106. *Stumpffia contumelia* **sp. nov.**, preserved paratype specimens: (a–b) ZSM 441/2010 (FGZC 4248) from Makira; (c–d) ZSM 442/2010 (FGZC 4252) from Makira; Scale bar = 5 mm.

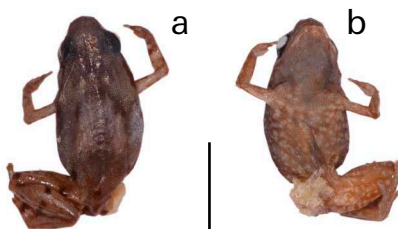


Fig. S107. *Stumpffia obscoena* **sp. nov.**, preserved paratype specimens in dorsal and ventral view from Andasibe: (a–b) ZSM 380/2005 (FGZC 2664); Scale bar = 5 mm.

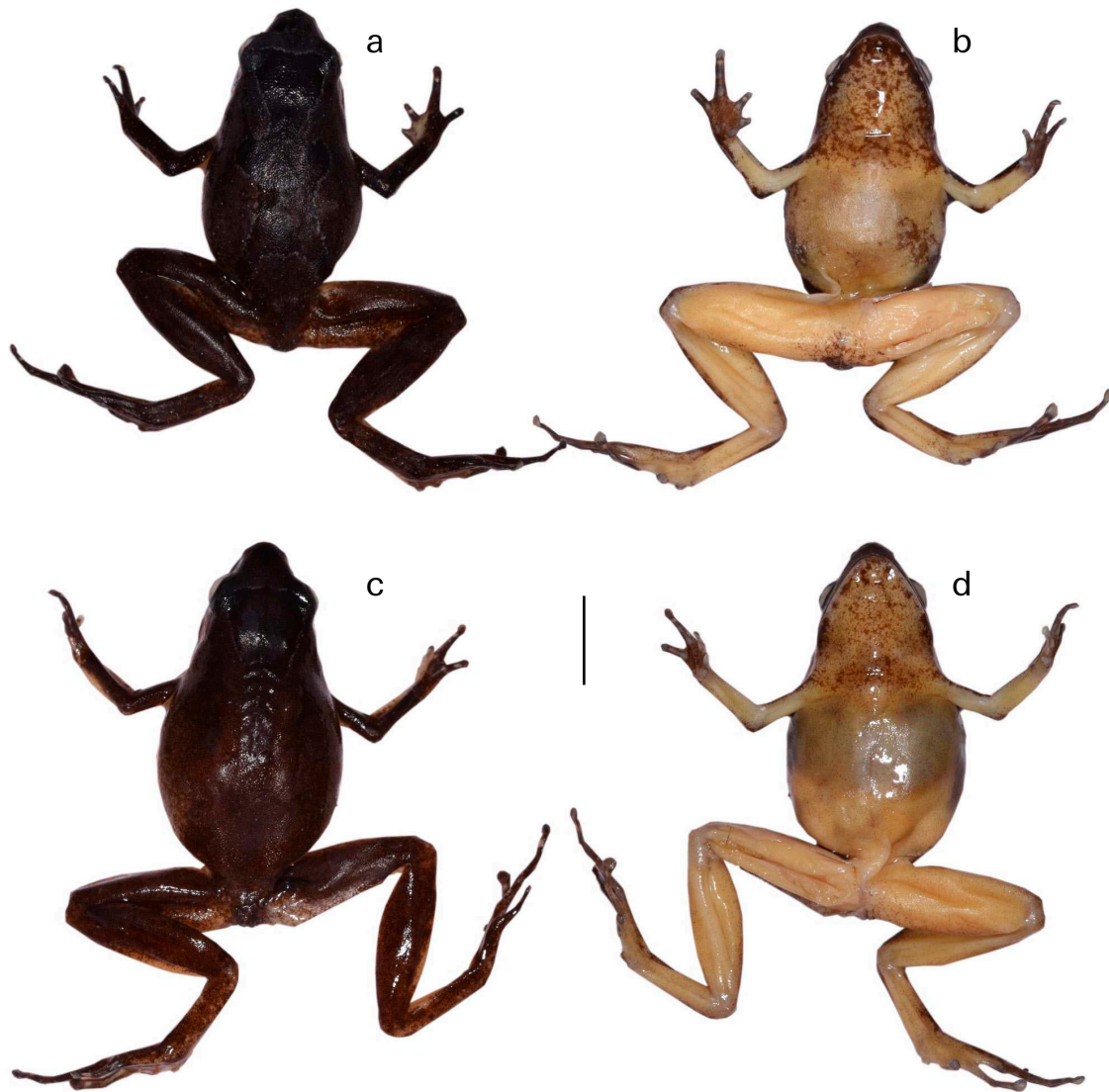


Fig. S108. *Stumpffia meikeae* sp. nov., preserved paratype specimens from Matsabory Maiky, Tsaratanana Strict Nature Reserve: (a–b) ZSM 1821/2010 (ZCMV 12372); (c–d) ZSM 1822/2010 (ZCMV 12373); Scale bar = 5 mm.



Fig. S109. *Stumpffia kibomena*, preserved holotype from near Andasibe (ZFMK 60007); Scale bar = 5 mm.

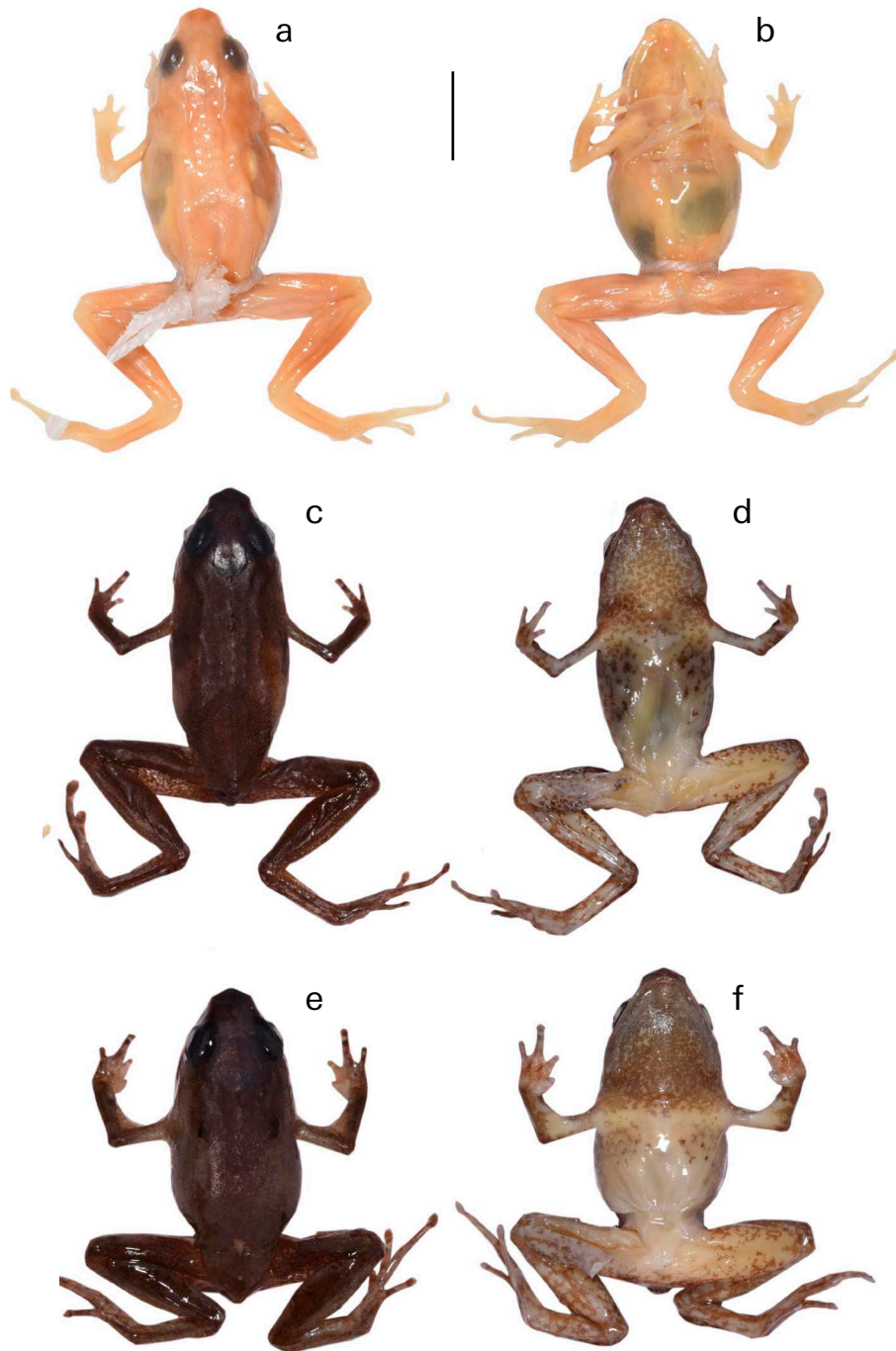


Fig. S110. *Stumpffia roseifemoralis*, preserved specimens from Marojejy National Park: (a–b) MNHN 1973.0714; (c–d) ZSM 373/2005 (FGZC 2808); (e–f) ZSM 374/2005 (FGZC 2883); (g–h) ZSM 487/2005 (ZCMV 2047); Scale bar = 5 mm.

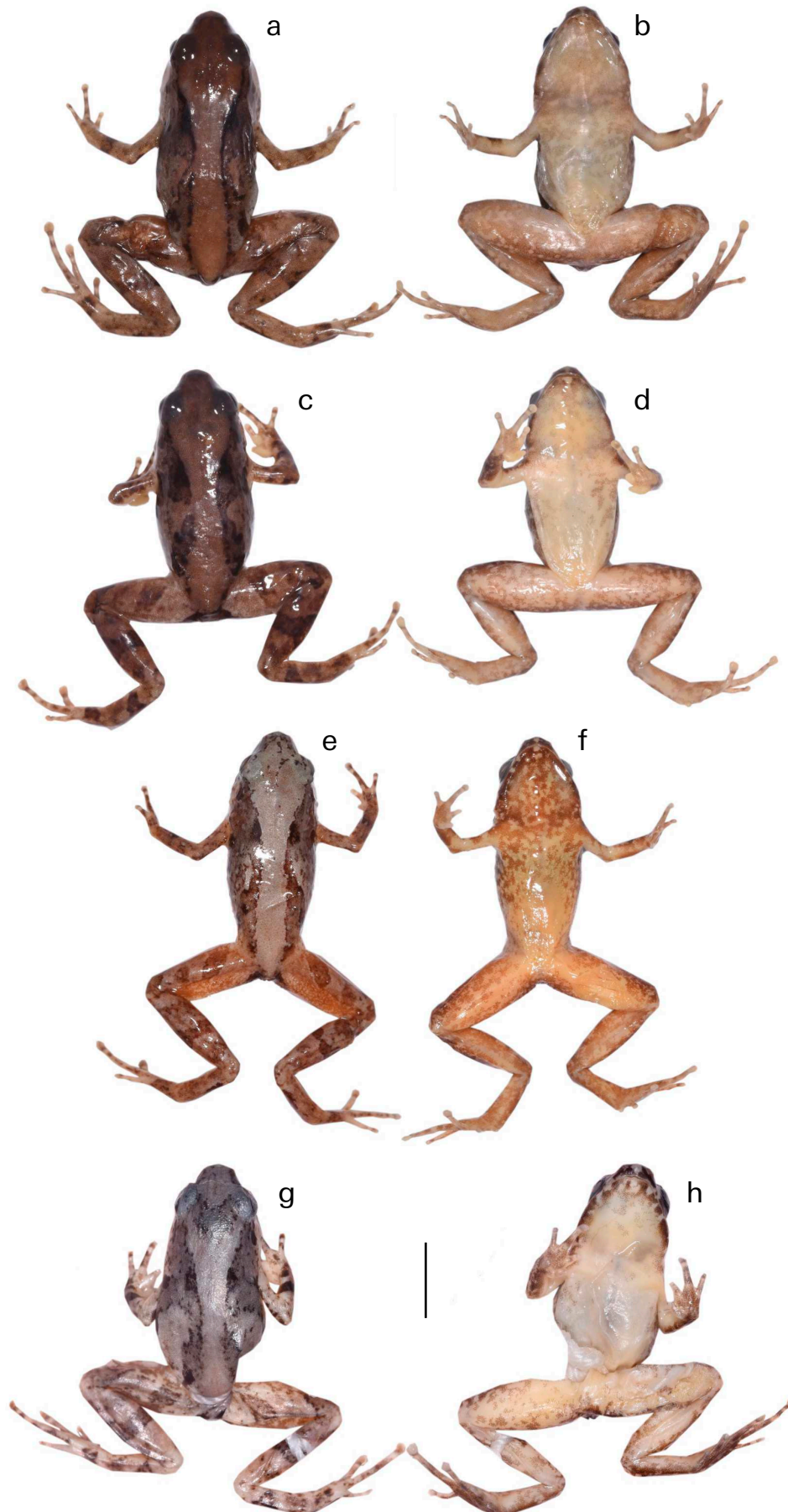


Fig. S111. *Stumpffia achillei* sp. nov., preserved specimens from Marojejy: (a–b) paratype ZFMK 57460; (c–d) paratype ZFMK 57461; (e–f) paratype ZFMK 59893; (g–h) holotype ZSM 536/2016 (ZCMV 15149); Scale bar = 5 mm.

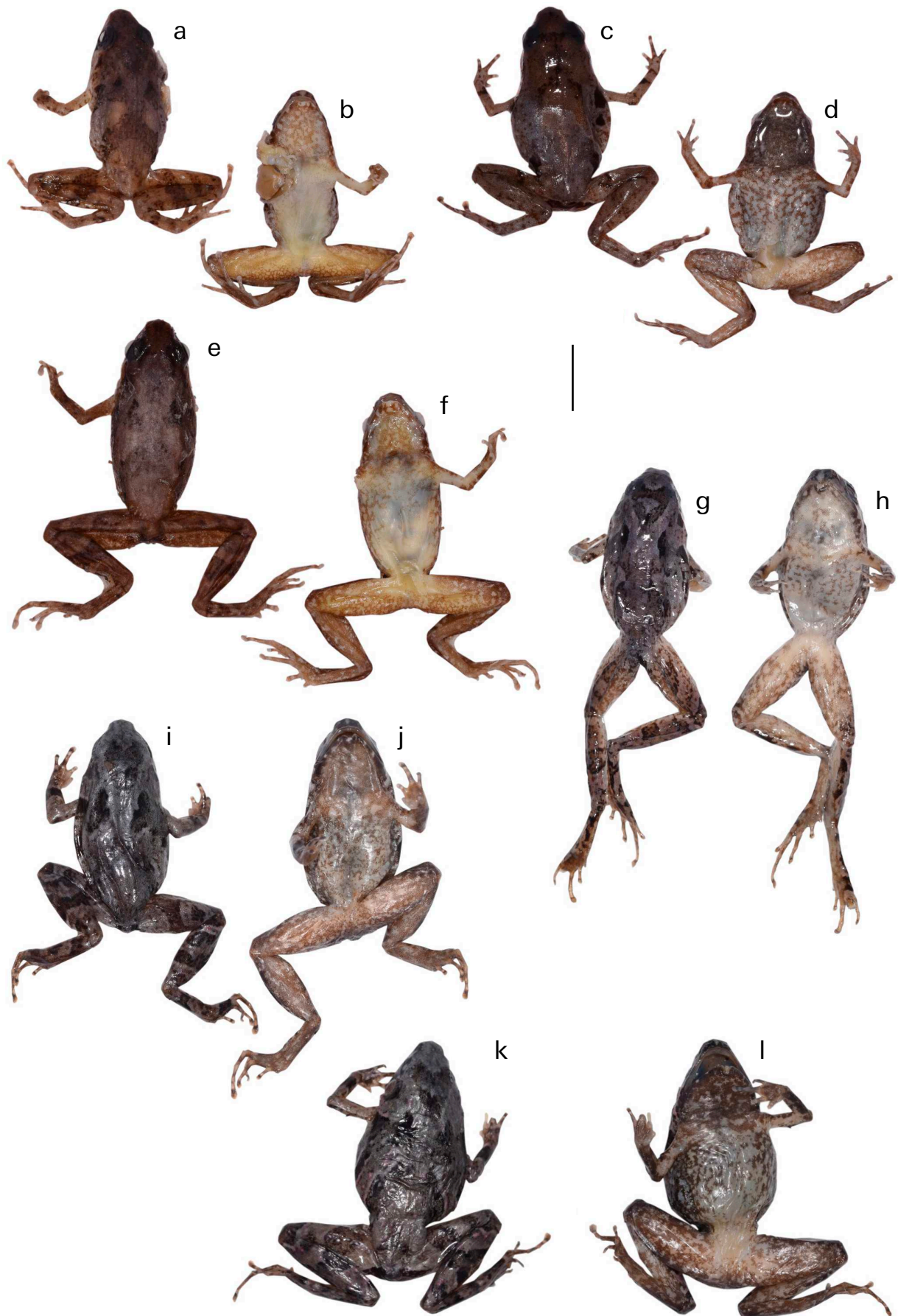


Fig. S112. *Stumpffia analanjirofo* sp. nov., preserved paratype specimens from Nosy Mangabe Special Reserve: a–b ZSM 491/2005 (ZCMV 2104); (c–d) ZSM 488/2005 (ZCMV 2143); (e–f) ZSM 492/2005 (ZCMV 2178); (g–h) ZSM 225/2016 (ACZCV 0121); (i–j) ZSM 226/2016 (ACZCV 0224); (k–l) ZSM 227/2016 (ACZCV 0225); Scale bar = 5 mm.

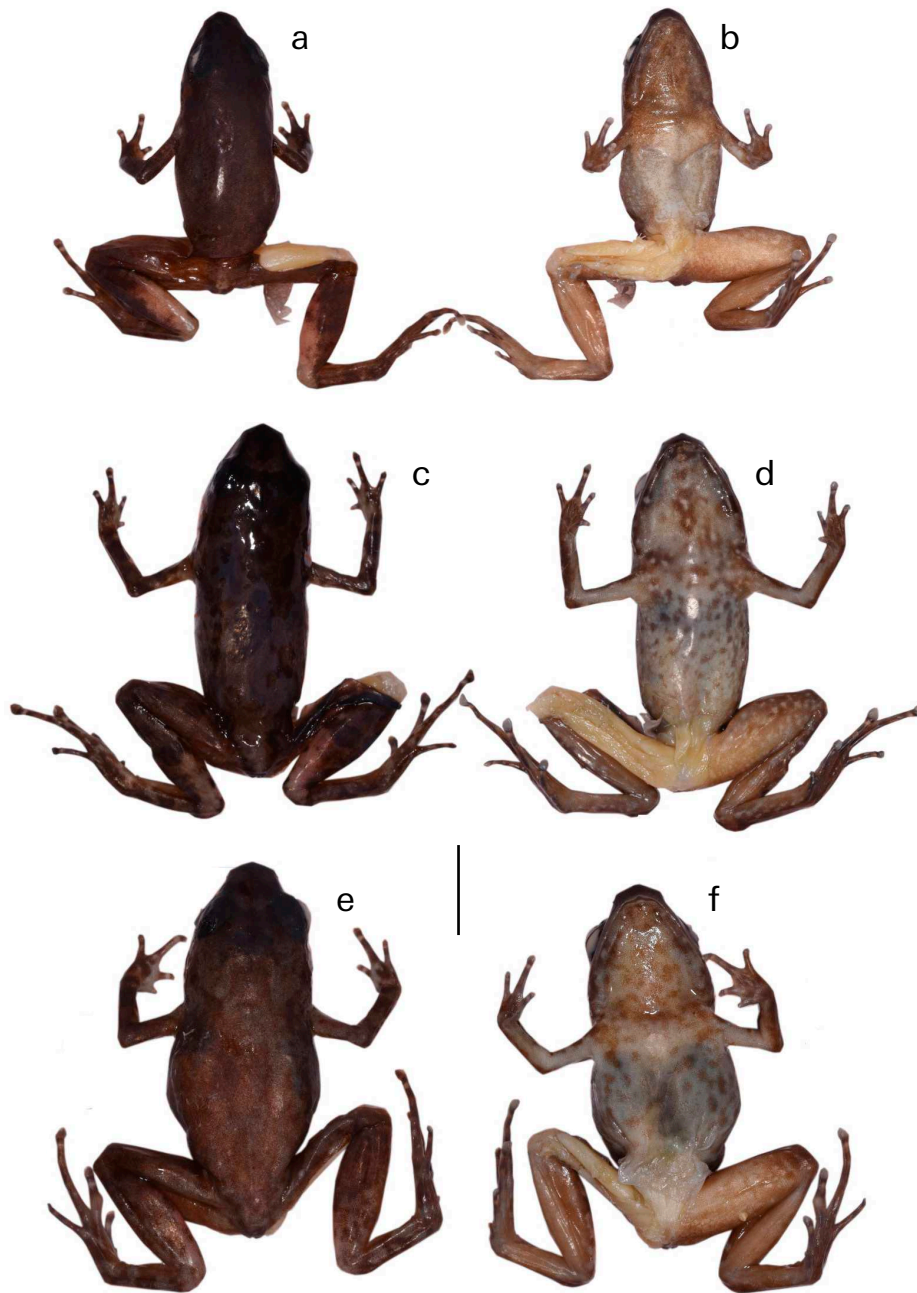


Fig. S113. *Stumpffia diutissima* **sp. nov.**, preserved paratype specimens from Marojejy National Park: (a–b) ZSM 496/2005 (ZCMV 2082); (c–d) ZSM 495/2005 (ZCMV 2067); (e–f) ZSM 376/2005 (FGZC 2742); Scale bar = 5 mm.

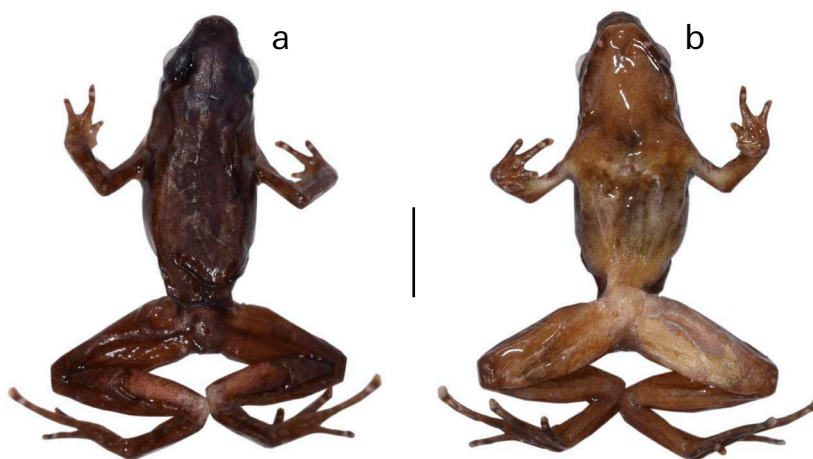


Fig. S114. *Stumpffia edmondsi* sp. nov., preserved paratype specimen : (a–b) ZSM 1731/2012 (RDR 1065) from Andasibe; Scale bar = 5 mm.

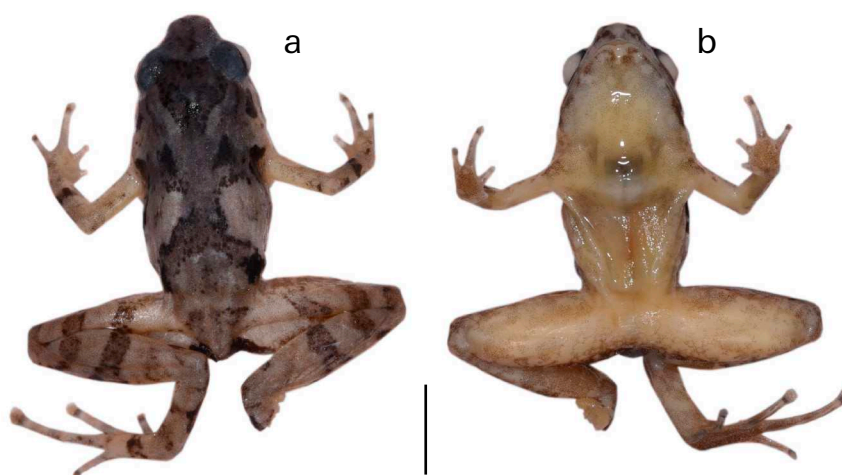


Fig. S115. *Stumpffia fusca* sp. nov., preserved paratype specimen from Ambodivoangy, Makira: (a–b) ZSM 436/2010 (FGZC 4253); Scale bar = 5 mm.



Fig. S116. *Stumpffia jeannoeli* **sp. nov.**, preserved paratype specimens from Betampona: (a–b) MRSN A6283; (c–d) MRSN A6386; (e–f) ZSM 207/2016 (ACZCV 0167); (g–h) ZSM 208/2016 (ACZCV 0218); Scale bar = 5 mm.

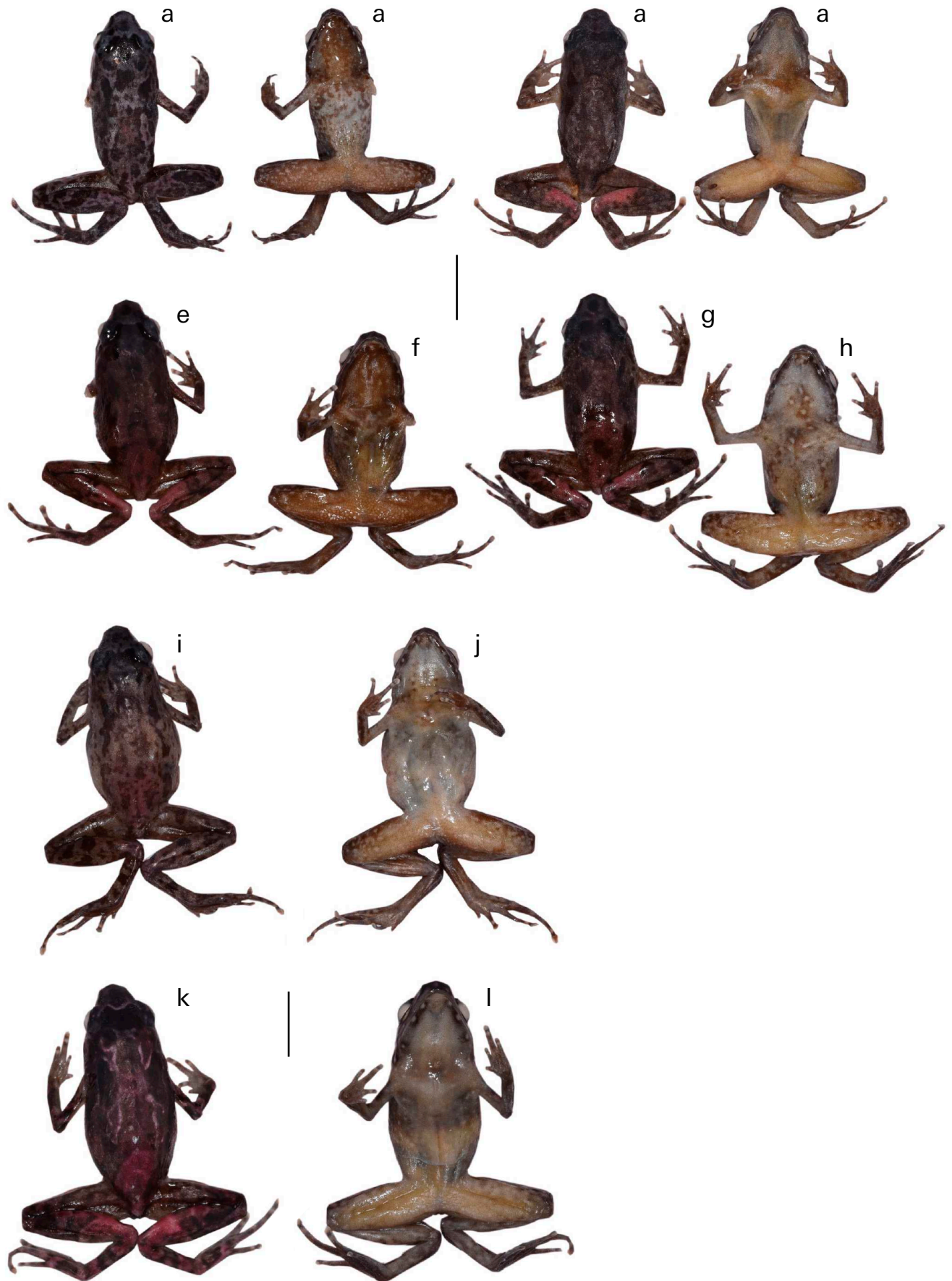


Fig. S117. *Stumpffia pardus* sp. nov., preserved paratype specimens from Makira: (a–b) ZSM 432/2010 (FGZC 4210); (c–d) ZSM 440/2010 (FGZC 4278); (e–f) ZSM 438/2010 (FGZC 4265); (g–h) ZSM 433/2010 (FGZC 4213); (i–j) ZSM 434/2010 (FGZC 4214); (k–l) ZSM 439/2010 (FGZC 4268); Scale bar = 5 mm.

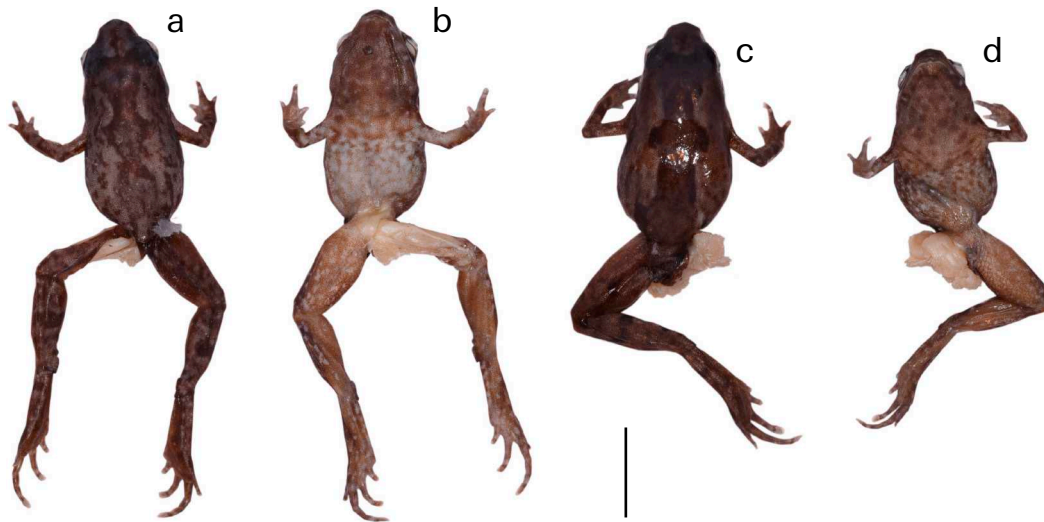


Fig. S118. *Stumpffia tetradactyla*, preserved specimens from Nosy Boraha: (a–b) ZSM 594/2006 (ZCMV 3396); (c–d) ZSM 593/2006 (ZCMV 3395); Scale bar = 5 mm.

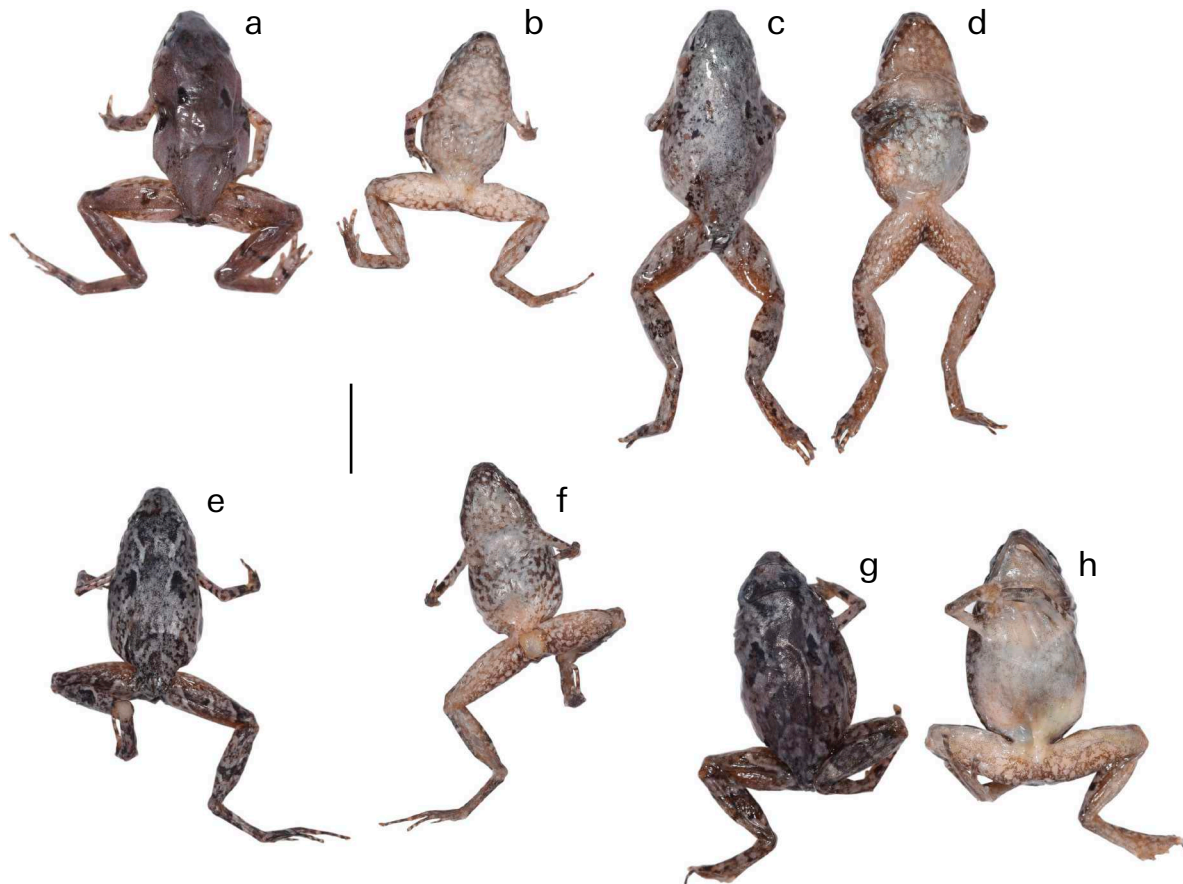


Fig. S119. *Stumpffia betampona* **sp. nov.**, preserved paratype specimens from Betampona: (a–b) ZSM 216/2016 (ACZCV 0041); (c–d) ZSM 217/2016 (ACZCV 0046); (e–f) ZSM 218/2016 (ACZCV 0047); (g–h) ZSM 219/2016 (ACZCV 0103); Scale bar = 5 mm.

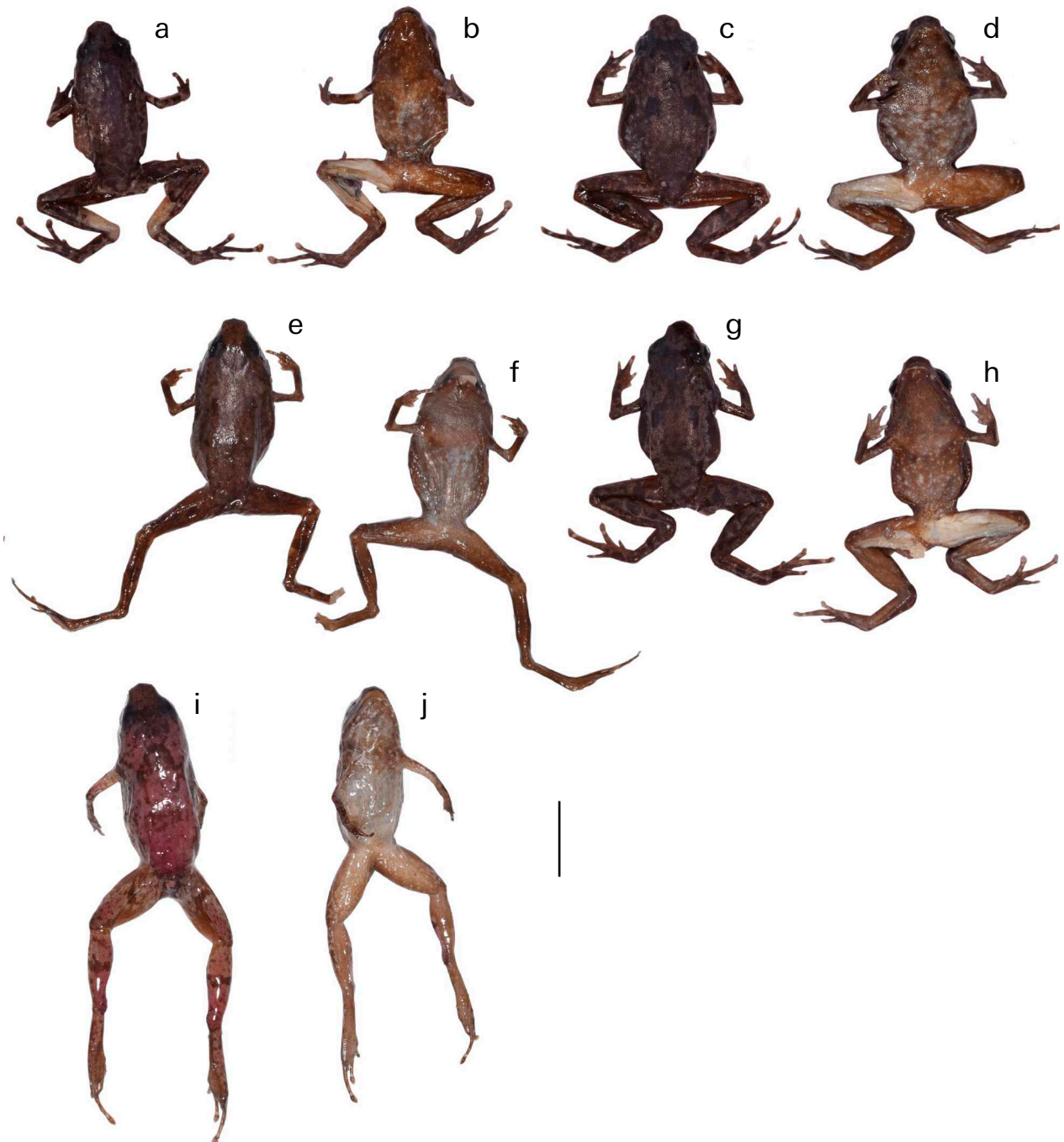


Fig. S120. *Stumpffia garraffoi* sp. nov., preserved paratype specimens from Mahasoia Forest: (a–b) ZSM 631/2009 (ZCMV 8684); (c–d) ZSM 632/2009 (ZCMV 8685); (e–f) ZSM 633/2009 (ZCMV 8687); (g–h) ZSM 220/2016 (ACZCV 0006); (i–j) MRSN A6278; Scale bar = 5 mm.

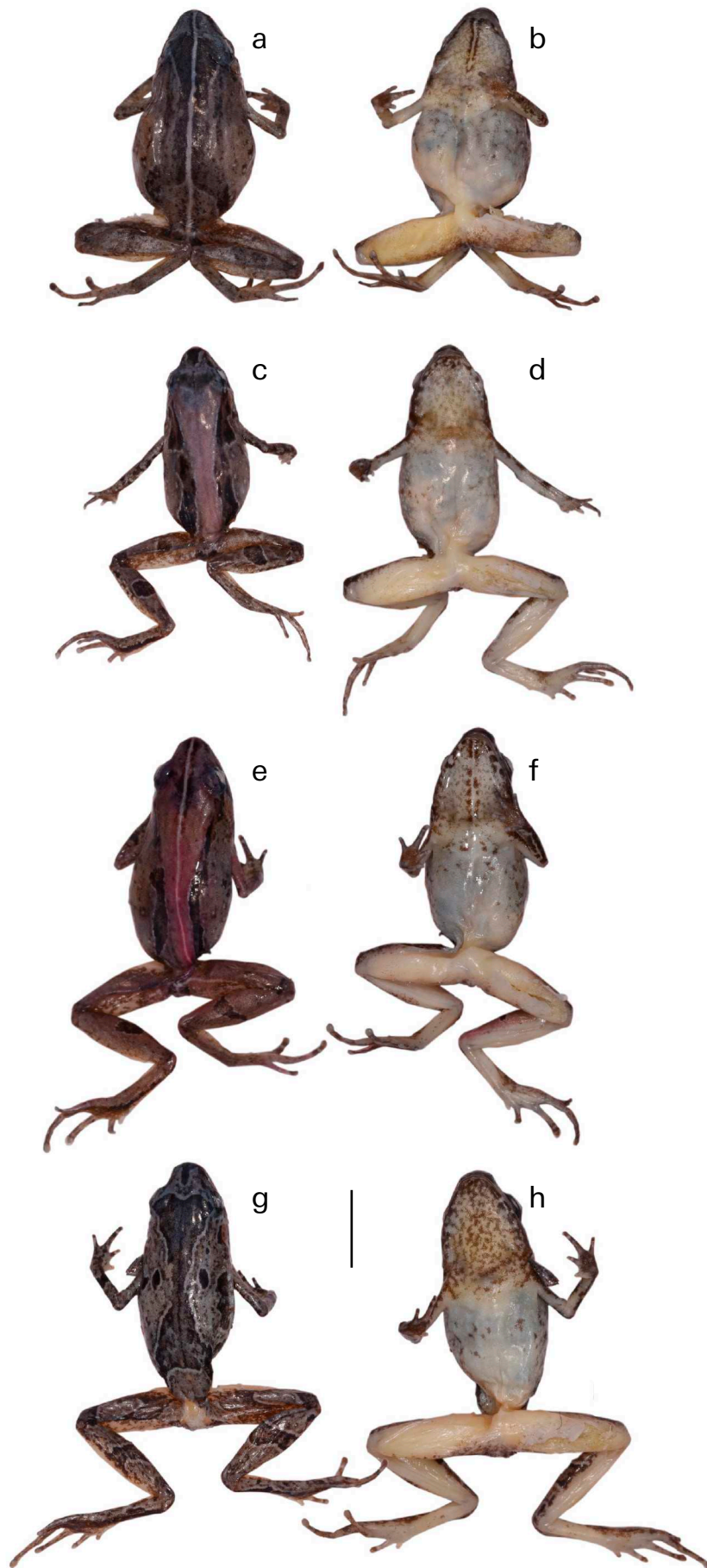


Fig. S121. *Stumpffia miovaova* **sp. nov.**, preserved paratype specimens from Sorata: (a–b) ZSM 1640/2012 (FGZC 3650); (c–d) ZSM 1647/2012 (FGZC 3675); (e–f) ZSM 1648/2012 (FGZC 3676); (g–h) ZSM 1646/2012 (FGZC 3751); Scale bar = 5 mm.

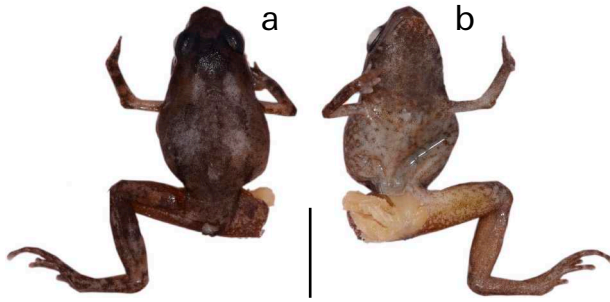


Fig. S122. *Stumpffia spandei* **sp. nov.**, preserved holotype from Mahasoia Forest: (a–b) ZSM 1751/2008 (ZCMV 8802); Scale bar = 5 mm.

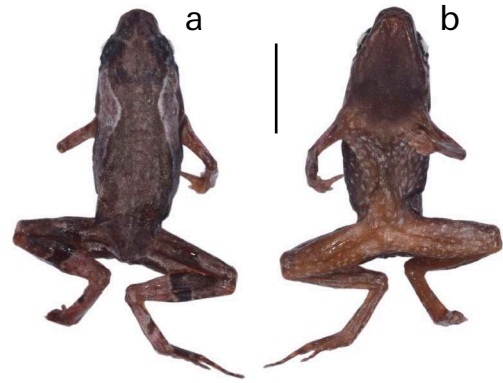


Fig. S123. *Stumpffia davidattenboroughi* **sp. nov.**, preserved holotype from Betampona Strict Nature Reserve: (a–b) ZSM 204/2016 (ACZCV 0106); Scale bar = 5 mm.

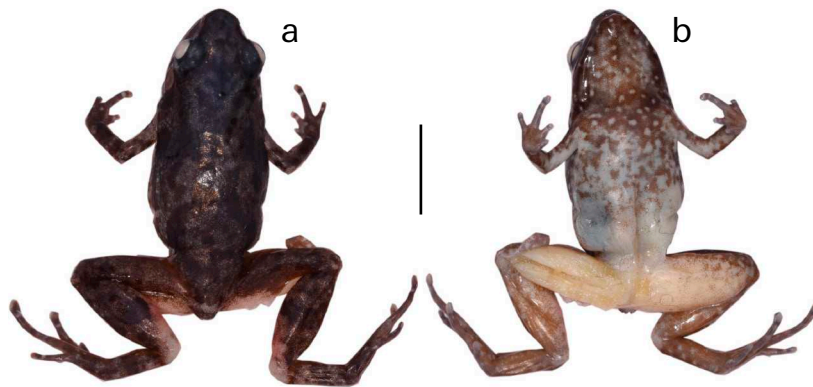


Fig. S124. *Stumpffia nigrorubra* **sp. nov.**, preserved holotype from along the road between Ifanadiana and Tolongoina: (a–b) ZSM 2448/2007 (ZCMV 5967); Scale bar = 5 mm.

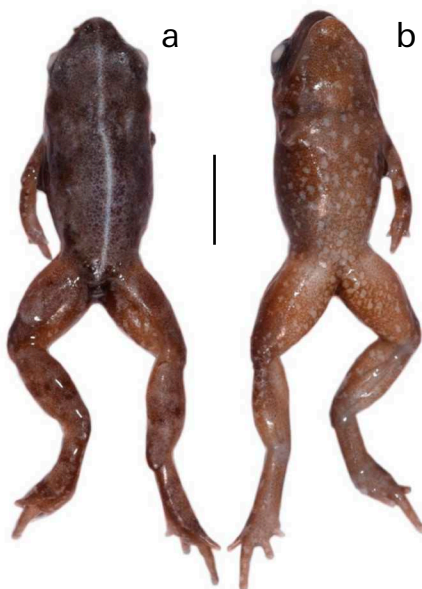


Fig. S125. *Stumpffia* sp. Ca29, preserved specimen from Matsabory Maiky, Tsaratanana Strict Nature Reserve: (a–b) ZSM 1824/2010 (ZCMV 12387); Scale bar = 5 mm.

Supplementary Table S1. Between-group mean distance in percent (number of base differences per site from averaging over all sequence pairs between *Stumpffia* groups, multiplied by 100) for species and candidate species of *Stumpffia*, based on 657 bp of the mitochondrial 16S rRNA gene (5' terminus of the gene). All ambiguous positions were removed for each sequence pair.

	<i>achil-</i> <i>lei</i>	<i>anala-</i> <i>maina</i>	<i>ana-</i> <i>lanji-</i> <i>rofo</i>	<i>ange-</i> <i>luci</i>	<i>be</i>	<i>betam-</i> <i>pona</i>	<i>contu-</i> <i>melia</i>	<i>diutis-</i> <i>sima</i>	<i>ed-</i> <i>mondsi</i>	<i>fusca</i>	<i>gar-</i> <i>raffoi</i>	<i>gim-</i> <i>meli</i>	<i>gran-</i> <i>dis</i>	<i>hara</i>	<i>hele-</i> <i>nae</i>	<i>ihara-</i> <i>na</i>	<i>jean-</i> <i>noeli</i>	<i>kibom-</i> <i>ena</i>	<i>larinki</i>	<i>mada-</i> <i>gasca-</i> <i>riensis</i>	<i>makira</i>				
<i>achillei</i>	—																								
<i>analamaina</i>	20.0	—																							
<i>analanjirofo</i>	4.7	19.0	—																						
<i>angeluci</i>	19.9	15.7	19.1	—																					
<i>be</i>	18.9	11.9	18.7	15.9	—																				
<i>betampona</i>	17.7	19.6	17.2	20.8	18.4	—																			
<i>contumelia</i>	20.6	22.1	20.7	21.2	20.3	20.2	—																		
<i>diutissima</i>	16.4	20.8	16.3	21.3	18.8	17.5	20.5	—																	
<i>edmondsi</i>	15.6	17.6	15.0	18.7	17.0	16.3	19.2	16.4	—																
<i>fusca</i>	8.0	17.5	8.0	18.7	18.1	16.0	18.1	15.4	13.5	—															
<i>garraffoi</i>	16.4	17.7	16.0	19.4	16.7	16.7	18.6	15.7	9.6	14.0	—														
<i>gimmeli</i>	19.9	14.2	19.3	11.7	14.4	17.8	21.4	21.2	18.6	18.6	18.1	—													
<i>grandis</i>	10.4	19.2	10.8	20.9	18.0	16.2	19.6	16.4	15.2	10.3	16.4	20.1	—												
<i>hara</i>	20.3	13.3	19.2	16.3	9.1	18.1	20.4	19.7	16.2	18.9	17.0	15.8	19.1	—											
<i>helenae</i>	26.0	26.0	24.8	24.7	22.4	23.7	23.4	24.9	23.3	25.8	23.7	25.6	25.4	22.8	—										
<i>iharana</i>	21.4	13.6	20.3	12.1	15.0	18.3	20.9	20.6	18.6	19.2	17.6	8.8	20.3	17.1	23.3	—									
<i>jeannoeli</i>	14.4	17.7	14.1	17.7	16.9	14.9	16.7	12.2	8.0	12.0	9.1	18.0	15.3	16.6	23.5	17.5	—								
<i>kibomena</i>	7.7	16.4	8.4	18.7	15.9	15.3	18.3	16.4	13.3	7.1	14.8	18.0	8.8	17.9	24.7	17.8	13.7	—							
<i>larinki</i>	19.1	15.1	18.9	11.4	14.1	19.1	21.1	20.3	17.5	16.0	17.9	11.8	18.5	17.8	24.9	11.4	16.9	15.5	—						
<i>madagascariensis</i>	20.1	16.1	20.2	17.5	13.7	19.8	22.2	22.0	19.6	20.4	21.1	16.1	20.8	16.5	23.9	16.0	20.0	18.8	15.1	—					
<i>makira</i>	17.3	19.2	16.8	20.0	18.0	16.0	19.8	15.3	14.5	14.9	13.9	19.3	18.2	20.0	23.4	19.0	12.7	15.5	17.2	20.1	—				
<i>maledicta</i>	20.0	15.2	19.4	3.3	14.9	20.3	21.2	21.4	18.3	18.4	18.5	10.7	20.3	16.4	23.6	11.2	17.5	18.7	10.8	16.7	19.6				
<i>megsoni</i>	20.4	15.8	19.3	16.7	11.0	18.0	20.4	19.5	16.0	18.3	17.9	15.3	18.5	6.7	23.7	16.7	16.2	17.7	16.8	17.7	20.4				
<i>meikeae</i>	17.4	15.2	17.2	17.8	15.2	15.5	19.7	17.6	14.7	16.6	15.3	15.4	17.9	16.3	23.6	15.0	13.6	14.3	15.2	15.6	16.1				
<i>miery</i>	18.9	18.2	18.9	18.9	16.2	17.9	20.2	17.8	16.6	17.8	17.3	18.1	18.4	17.4	23.3	18.9	14.4	16.9	16.3	19.0	18.0				
<i>nigrorubra</i>	16.8	17.3	16.6	18.5	17.9	16.8	18.7	14.5	10.1	13.5	8.9	18.8	16.7	17.9	24.7	17.6	7.8	14.6	18.2	21.8	14.6				
<i>obscoena</i>	18.3	19.2	18.5	21.2	18.6	17.3	22.0	19.1	18.2	16.9	19.4	19.7	19.0	17.8	26.5	20.1	16.7	17.0	19.3	20.5	18.5				
<i>pardus</i>	15.8	18.9	15.0	18.7	16.3	15.8	17.6	10.4	15.1	13.1	14.6	18.5	15.5	18.3	22.9	17.4	12.8	13.7	17.9	20.7	13.6				
<i>psologlossa</i>	19.4	14.3	19.2	13.3	14.4	18.7	21.0	18.9	16.5	16.7	16.6	11.9	18.9	14.4	23.4	12.6	14.9	17.0	12.6	15.6	18.5				
<i>pygmaea</i>	20.1	16.0	19.8	16.5	13.9	20.2	21.7	20.7	18.8	18.6	19.6	16.2	21.5	15.3	23.2	16.9	18.2	17.8	16.9	11.4	19.9				
<i>roseifemoralis</i>	17.7	19.5	16.8	18.3	18.2	15.5	17.6	18.5	14.9	15.0	16.0	18.3	17.0	18.9	22.4	17.5	14.5	14.5	15.6	18.7	15.0				
<i>miovaova</i>	12.9	16.6	12.6	18.5	15.9	12.0	16.3	13.0	11.2	10.5	12.7	15.5	10.1	14.3	19.1	16.5	12.8	9.8	16.2	17.2	13.9				
Ca11	9.7	14.5	9.4	18.4	14.1	15.0	15.2	15.1	13.3	7.8	10.8	15.9	10.2	16.2	19.1	14.5	12.4	5.5	15.8	17.8	13.9				
Ca29	19.8	10.7	18.3	15.3	12.5	18.9	21.0	20.5	15.9	17.8	16.7	16.0	19.9	14.8	24.1	15.1	16.7	16.3	15.4	16.1	18.5				
Ca30	19.4	18.5	19.5	17.6	16.3	19.0	20.8	19.9	19.0	18.3	18.1	18.1	19.5	17.4	22.8	18.0	17.1	18.2	17.0	15.8	18.1				
Ca42	15.7	17.0	15.4	18.9	17.3	16.1	18.9	15.3	6.9	13.6	9.4	18.8	14.7	17.3	24.6	17.0	7.4	12.7	17.9	20.8	15.0				
<i>sorata</i>	20.2	13.4	19.1	11.1	13.5	16.4	20.3	20.5	16.9	18.2	17.3	9.0	19.9	15.0	22.9	9.6	16.3	16.3	9.8	16.1	17.8				
<i>dolchi</i>	16.6	20.0	16.8	18.6	18.0	17.7	18.9	17.8	13.5	13.6	15.5	18.9	16.6	19.6	24.5	19.7	12.5	14.9	17.2	20.8	12.4				

Supplementary Table S1 continued.

	<i>achil-</i> <i>lei</i>	<i>anala-</i> <i>maina</i>	<i>ana-</i> <i>lanji-</i> <i>rofo</i>	<i>ange-</i> <i>luci</i>	<i>be</i>	<i>betam-</i> <i>pona</i>	<i>contu-</i> <i>melia</i>	<i>diutis-</i> <i>sima</i>	<i>ed-</i> <i>mondsi</i>	<i>fusca</i>	<i>gar-</i> <i>raffoi</i>	<i>gim-</i> <i>meli</i>	<i>gran-</i> <i>dis</i>	<i>hara</i>	<i>hele-</i> <i>nae</i>	<i>ihara-</i> <i>na</i>	<i>jean-</i> <i>noeli</i>	<i>kibom-</i> <i>ena</i>	<i>larinki</i>	<i>mada-</i> <i>gasca-</i> <i>riensis</i>	<i>makira</i>				
<i>huwei</i>	18.9	15.6	18.4	5.6	15.5	18.7	21.4	20.9	18.0	17.3	19.1	10.4	18.5	16.6	24.8	11.3	17.6	17.6	11.2	17.2	18.8				
<i>davidattenboroughi</i>	16.5	15.8	16.0	17.0	15.5	16.9	18.8	16.0	14.6	15.4	15.4	16.8	16.9	15.8	24.2	17.6	14.2	14.9	15.6	16.8	16.4				
<i>Ca7</i>	20.2	14.1	18.8	10.2	14.3	18.6	20.9	20.2	17.9	18.2	17.3	9.5	20.6	16.0	23.7	9.0	16.4	17.1	9.6	15.7	17.4				
<i>spandei</i>	16.8	17.7	15.5	18.5	16.9	16.0	16.7	15.6	10.1	14.1	9.6	18.7	16.8	17.4	22.0	19.0	8.1	14.6	18.4	21.3	14.2				
<i>staffordi</i>	19.7	14.3	18.6	18.1	11.2	18.6	21.4	20.5	16.2	18.4	15.7	16.4	20.0	11.0	21.7	15.9	18.7	17.5	16.7	16.0	17.3				
<i>mamitika</i>	20.0	15.2	19.4	5.9	15.1	19.2	21.9	21.4	19.4	18.4	20.0	11.7	19.6	17.1	24.3	12.3	18.4	18.1	11.9	17.6	18.8				
<i>tetradactyla</i>	15.0	16.3	14.7	18.9	16.9	16.4	18.3	14.3	8.2	12.9	10.9	17.5	15.9	18.0	24.2	17.6	8.4	13.2	17.4	20.9	13.8				
<i>tridactyla</i>	20.4	20.2	21.3	22.0	18.9	19.7	15.0	20.7	20.3	19.3	19.2	20.0	19.7	20.3	25.2	19.7	18.9	18.9	18.9	20.3	22.7				
<i>yanniki</i>	21.1	11.4	19.6	16.9	11.4	19.4	22.1	20.5	18.4	19.3	17.7	15.7	20.5	14.9	26.3	15.2	18.0	17.7	16.0	16.1	18.5				
	<i>mal-</i> <i>edicta</i>	<i>meg-</i> <i>soni</i>	<i>meike-</i> <i>ae</i>	<i>miery</i>	<i>ni-</i> <i>grorubra</i>	<i>ob-</i> <i>scoena</i>	<i>pardus</i>	<i>psolo-</i> <i>glossa</i>	<i>pyg-</i> <i>maea</i>	<i>roseif-</i> <i>emo-</i> <i>ralis</i>	<i>mio-</i> <i>vaova</i>	Ca11	Ca29	Ca30	Ca42	<i>sorata</i>	<i>dolchi</i>	<i>huwei</i>	<i>davi-</i> <i>datten-</i> <i>borou-</i> <i>ghi</i>	Ca7	<i>span-</i> <i>dei</i>	<i>staf-</i> <i>fordi</i>	<i>mami-</i> <i>tika</i>	<i>tetra-</i> <i>dac-</i> <i>tyla</i>	<i>tridac-</i> <i>tyla</i>
<i>maledicta</i>	—																								
<i>megsoni</i>	16.0	—																							
<i>meikeae</i>	16.6	15.5	—																						
<i>miery</i>	19.0	17.2	14.3	—																					
<i>nigrorubra</i>	18.6	17.9	16.5	15.9	—																				
<i>obscoena</i>	21.1	19.6	16.8	18.9	19.1	—																			
<i>pardus</i>	18.4	18.1	15.5	15.9	14.4	18.8	—																		
<i>psologlossa</i>	12.4	15.2	14.6	17.6	16.7	16.7	16.6	—																	
<i>pygmaea</i>	15.9	17.0	16.3	16.8	19.6	19.2	19.0	13.8	—																
<i>roseifemoralis</i>	18.1	19.0	15.9	16.1	15.3	17.7	15.0	17.9	18.9	—															
<i>miovaova</i>	18.8	14.2	13.7	14.9	12.8	14.7	13.1	13.4	16.2	13.0	—														
Ca11	18.4	16.9	13.5	14.8	12.1	15.3	10.9	13.8	14.8	14.8	11.1	—													
Ca29	15.0	16.0	15.0	16.8	17.7	18.5	17.3	14.4	15.6	16.7	15.5	13.0	—												
Ca30	18.0	17.7	17.1	17.6	18.6	18.8	18.9	16.6	16.3	19.2	16.3	16.4	18.6	—											
Ca42	18.7	16.5	14.4	15.9	8.4	18.6	14.5	17.0	18.9	16.5	12.3	10.8	17.0	18.4	—										
<i>sorata</i>	10.4	14.9	14.5	15.6	18.1	18.8	17.1	11.4	15.2	17.1	16.1	15.7	15.6	17.9	17.3	—									
<i>dolchi</i>	19.2	18.7	17.7	15.7	14.4	19.3	14.3	18.0	20.1	14.4	13.6	13.4	18.4	19.1	13.2	18.1	—								
<i>huwei</i>	5.3	16.3	16.4	19.0	19.1	20.8	18.0	13.0	16.7	18.2	17.2	17.4	15.5	18.1	18.3	10.7	17.8	—							
<i>davidattenboroughi</i>	16.1	15.8	12.9	14.6	16.6	14.4	16.9	14.6	16.3	15.2	13.1	13.6	15.0	17.2	14.7	15.7	16.8	17.2	—						
<i>Ca7</i>	10.0	15.6	15.4	17.4	17.7	19.0	16.7	11.5	15.5	17.9	16.3	15.3	16.5	17.3	18.0	5.1	19.2	10.3	16.3	—					
<i>spandei</i>	17.9	18.7	15.6	17.4	8.8	18.4	14.7	16.5	18.4	17.4	12.4	11.4	16.8	18.3	10.2	17.4	15.8	18.1	16.2	17.3	—				
<i>staffordi</i>	17.4	13.1	15.3	17.6	18.6	18.0	18.1	15.1	17.0	17.3	16.7	18.0	14.7	16.5	16.5	15.0	18.1	17.0	14.1	14.8	18.1	—			
<i>mamitika</i>	6.5	17.0	17.3	19.0	19.0	20.9	18.0	13.0	17.3	17.8	18.4	18.8	15.5	16.9	20.6	11.2	18.4	6.0	18.3	11.0	17.8	18.8	—		
<i>tetradactyla</i>	18.6	18.2	14.9	15.9	9.1	17.3	13.9	16.6	18.3	16.0	12.8	11.2	17.1	19.0	8.1	16.6	13.5	18.4	14.8	17.4	9.4	17.8	19.3	—	
<i>tridactyla</i>	21.7	20.4	17.2	19.8	20.7	22.7	19.1	20.0	22.3	19.5	16.7	16.0	19.3	21.2	19.7	19.2	21.3	21.7	19.2	19.9	20.4	21.8	21.9	20.3	—
<i>yanniki</i>	16.6	16.0	16.3	18.7	18.5	20.4	17.2	14.8	15.5	19.1	17.7	14.1	10.3	18.1	18.7	14.1	19.5	17.3	16.3	14.2	17.5	15.1	16.4	17.9	22.4

Supplementary Table 2. Zoobank registration numbers of new species described in this study. The article is registered under LSID: urn:lsid:zoobank.org:pub:9AC9A0D2-1F97-412D-A5A3-97458A137FEC.

Species	Zoobank registration number
<i>Stumpffia achillei</i> sp. nov.	urn:lsid:zoobank.org:act:44258244-EC05-4909-98BD-52605F800C42
<i>Stumpffia analanjirofo</i> sp. nov.	urn:lsid:zoobank.org:act:9F5B5620-4EE5-44B5-AC3A-C317EB1A9182
<i>Stumpffia angeluci</i> sp. nov.	urn:lsid:zoobank.org:act:DF961EC7-77B1-48F3-8AB1-141C83BA4966
<i>Stumpffia betampona</i> sp. nov.	urn:lsid:zoobank.org:act:9EBDCDE0-A0CE-40EB-8E4A-66606FDD2015
<i>Stumpffia contumelia</i> sp. nov.	urn:lsid:zoobank.org:act:9BE1DC6D-5FA6-429E-9ED6-971342D3CCC4
<i>Stumpffia davidattenboroughi</i> sp. nov.	urn:lsid:zoobank.org:act:1A2E8632-661C-43AC-8FC0-4BCA37CA37FB
<i>Stumpffia diutissima</i> sp. nov.	urn:lsid:zoobank.org:act:07FE3E8F-2408-4CB4-B8C3-A5EDDFE9561E
<i>Stumpffia dolchi</i> sp. nov.	urn:lsid:zoobank.org:act:E4D7BB04-45AD-44FE-A04A-307A1E5D59CA
<i>Stumpffia edmondsi</i> sp. nov.	urn:lsid:zoobank.org:act:DE0815F0-8F7D-464F-9F2D-9CB8AF36FE96
<i>Stumpffia fusca</i> sp. nov.	urn:lsid:zoobank.org:act:967BF2BD-89D9-4485-A2FF-B6F43FDD89A5
<i>Stumpffia garraffoi</i> sp. nov.	urn:lsid:zoobank.org:act:BB65A130-227F-481F-806B-FFD9CB049C09
<i>Stumpffia huwei</i> sp. nov.	urn:lsid:zoobank.org:act:D3B6C1DB-1A6F-4144-B610-82BD7237C281
<i>Stumpffia iharana</i> sp. nov.	urn:lsid:zoobank.org:act:61D2D8A9-0BE9-4CE0-B9F5-1845EDE61393
<i>Stumpffia jeannoeli</i> sp. nov.	urn:lsid:zoobank.org:act:2662B385-15EB-4D4A-BF19-DCB492E40B0A
<i>Stumpffia larinki</i> sp. nov.	urn:lsid:zoobank.org:act:8DFA4167-8E62-43F8-BE84-848018CA1EEB
<i>Stumpffia makira</i> sp. nov.	urn:lsid:zoobank.org:act:8DF67990-D8CD-40BD-93E2-9F7655EBD186
<i>Stumpffia maledicta</i> sp. nov.	urn:lsid:zoobank.org:act:74E46BB8-AD68-49AC-BBE1-121CA225111B
<i>Stumpffia mamitika</i> sp. nov.	urn:lsid:zoobank.org:act:57BA52EE-CDDF-466F-863E-5C642B4891FC
<i>Stumpffia meikeae</i> sp. nov.	urn:lsid:zoobank.org:act:3CFBD9FD-AB05-4C6C-852E-7C7D054BC3CA
<i>Stumpffia miovaova</i> sp. nov.	urn:lsid:zoobank.org:act:8B87250B-0EA4-4D00-A5E2-A51DE890C020
<i>Stumpffia nigrorubra</i> sp. nov.	urn:lsid:zoobank.org:act:E6CFA2C4-1D81-4495-A82D-573E4075D41C
<i>Stumpffia obscoena</i> sp. nov.	urn:lsid:zoobank.org:act:1E6F83FA-00BE-4D6B-A9DB-4513CAC5504B
<i>Stumpffia pardus</i> sp. nov.	urn:lsid:zoobank.org:act:8B7EB8FD-0BE4-4961-A09C-8EC179D2D15C
<i>Stumpffia sorata</i> sp. nov.	urn:lsid:zoobank.org:act:1436AA49-7545-403D-ACD4-BF3BCB578F69
<i>Stumpffia spandei</i> sp. nov.	urn:lsid:zoobank.org:act:BFBDD5FE7-A717-4C55-A97E-2E878F54AA1C
<i>Stumpffia yanniki</i> sp. nov.	urn:lsid:zoobank.org:act:114CE991-09BF-4B54-ABB4-9142C42649F4