



A wealth of riches: A comprehensive revision of diamond frogs, genus *Rhombophryne* Boettger, 1880 (Microhylidae: Cophylinae), with the description of seven new species

Mark D. Scherz¹, Frank Glaw², Alice Petzold^{3,4}, Franco Andreone⁵, Jörn Köhler⁶, Achille P. Raselimanana^{7,8}, Carl Hutter⁹, Francesco Belluaro^{10,11}, Andolalao Rakotoarison^{12,13}, Michael Hofreiter³, Miguel Vences¹⁴, Angelica Crottini¹⁵

1 Natural History Museum Denmark, University of Copenhagen, Universitetsparken 15, 2100, Copenhagen Ø, Denmark

2 Zoologische Staatssammlung München (ZSM-SNSB), Münchhausenstr. 21, 81247 München, Germany

3 Institute of Biochemistry and Biology, University of Potsdam, Karl-Liebknecht-Str. 24–25, 14476 Potsdam, Germany

4 Museum für Naturkunde—Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, Germany

5 Museo Regionale di Scienze Naturali, Via G. Giolitti 36, Torino, 10123, Italy

6 Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany

7 Mention Zoologie et Biodiversité Animale, Université d'Antananarivo, BP 906, Antananarivo, 101 Madagascar

8 Association Vahatra, lot VA 38 LB Ter A, Ambohidempona-Tsiadana, Antananarivo, 101, Madagascar

9 Museum of Natural Sciences and Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

10 EnviXLab, Department of Biosciences and Territory, University of Molise, Contrada Fonte Lappone s.n.c., 86090 Pesche, Italy

11 CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Campus de Vairão, Vairão, 4485-661, Portugal

12 School for International Training, VN 41A Bis Ankazolava Ambohitsoa, Antananarivo, 101 Madagascar

13 Mention Environnement, Institut d'Enseignement Supérieur de Soavinandriana Itasy, Faliarivo, Soavinandriana Itasy 118, Madagascar

14 Institute for Cell- and Neurobiology, Technische Universität Braunschweig, Mendelssohnstraße 4, 38106 Braunschweig, Germany

15 Department of Biology, University of Florence, Via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy

<https://zoobank.org/72D3AFA4-D4DA-4EF8-9734-B592172E6095>

Corresponding author: Mark D. Scherz (mark.scherz@gmail.com)

Academic editor Deepak Veerappan | Received 3 October 2025 | Accepted 29 May 2026 | Published 22 July 2026

Citation: Scherz MD, Glaw F, Petzold A, Andreone F, Köhler J, Raselimanana AP, Hutter C, Belluaro F, Rakotoarison A, Hofreiter M, Vences M, Crottini A (2026) A wealth of riches: A comprehensive revision of diamond frogs, genus *Rhombophryne* Boettger, 1880 (Microhylidae: Cophylinae), with the description of seven new species. *Vertebrate Zoology* 76: 485–610. <https://doi.org/10.3897/vz.76.e172567>

Abstract

The diamond frogs of the genus *Rhombophryne* are a poorly understood clade of morphologically diverse frogs native to the humid forests of Madagascar. We here present a monographic revision of the taxonomy and natural history of these frogs. We first provide morphological diagnoses and contents of the established species groups in *Rhombophryne*. We then integrate molecular phylogenetic data from mitochondrial and nuclear genetic markers, with morphometrics, bioacoustics, and micro-CT-based osteology, to describe seven new species from across Madagascar. This brings the number of species in the genus to 27. We have obtained DNA sequences from name-bearing specimens of 23 of these species, plus topotypical specimens of two further species; we used museomics methods to sequence name-bearing types of three species collected before 1976, as well as several other specimens of interest, allowing us to clarify taxonomic assignment of those individuals. In our treatments of all existing and new species, we provide new insights into their anatomy, diet, ecology, and distribution. We provide the first published key to the genus, which we hope will make their identification more straightforward. Finally, we suggest a revised conservation assessment in light of the data that we present. We estimate 24 of the 27 species to be threatened, with two species (*R. kilonjy* sp. nov. and *R. matavy*) probably worthy of being classified as

‘Critically Endangered’. Several candidate species remain taxonomically unaddressed, due to the poor representation of specimens in museum collections. We therefore emphasise the need for increased survey efforts to fill knowledge gaps in both the taxonomy and the natural history of these frogs.

Keywords

Amphibia, Anura, bioacoustics, integrative taxonomy, micro-CT, museomics, natural history, osteology, species delimitation

Introduction

Madagascar is a world hotspot of frog diversity, with an estimated 700+ species, all but two of which are endemic to the island (Glaw and Vences 2007; Vieites et al. 2009; Perl et al. 2014; Antonelli et al. 2022; Carné and Vieites 2024). As of June 2026, there are 446 described frog species from Madagascar (Frost 2026). Thus, a substantial taxonomic gap remains, which, however, is rapidly being addressed, often in monographic treatments yielding numerous new species at once (e.g., Glaw et al. 2010a; Rakotoarison et al. 2017; Scherz et al. 2022a).

Madagascar’s anuran diversity is divided across five families, with the greatest species richness in the Microhylidae Günther, 1858 and Mantellidae Laurent, 1946, which account for around 30% and 67%, respectively, of the 446 species described so far (Frost 2026). The Malagasy microhylids belong to three endemic subfamilies, but their diversity is mostly concentrated in one of them: the Cophylinae (Scherz et al. 2022b). This subfamily currently contains 118 of the world’s 771 described microhylid species (Frost 2026) in nine genera: *Anilany* Scherz et al., 2016 (2 spp.), *Anodonthyla* Müller, 1892 (12 spp.), *Cophyla* Boettger, 1880 (7 spp.), *Madecassophryne* Guibé, 1973 (1 sp.), *Mini* Scherz et al., 2019 (3 spp.), *Platypelis* Boulenger, 1882 (18 spp.), *Plethodontohyla* Boulenger, 1882 (11 spp.), *Rhombophryne* Boettger, 1880 (20 spp.), and *Stumpffia* Boettger, 1881 (44 sp.).

As a whole, the subfamily Cophylinae is ecologically and morphologically very diverse, containing arboreal, terrestrial, fossorial, and scansorial species, ranging from the largest microhylids known (>100 mm), to some of the smallest vertebrates on Earth (<9 mm; Scherz et al. 2022b). Within the subfamily, the diamond frogs, genus *Rhombophryne*, are remarkable in consisting of species that span from highly fossorial to leaping, potentially scansorial, species, and ranging from large frogs reaching nearly 60 mm in snout–vent length, down to a highly miniaturised species reaching just 12 mm. Despite substantial recent taxonomic work that brought this genus from eight species in 2007 (Glaw and Vences 2007) to the present 20 species (Frost 2026), several candidate species remain to be scientifically named and described. Additionally, a good deal of new information has been assembled on some of the nominal species. With the aim of synthesising the state-of-the-art knowledge on this remarkable genus and providing a foundation for future reference, we here present a detailed monographic treatment of the genus.

Genus-level taxonomy of *Rhombophryne* species

The genus *Rhombophryne* was established by Oskar Böttger, based on the single species *R. testudo* Boettger, 1880. As a specialised burrowing frog, this species is distinctive in many respects, notably in its round habitus, small eyes, ‘barbels’ (spine-like dermal projections) on the lower lip, short limbs, and short and wide head. Indeed, so unusual is *R. testudo* that it was maintained as a monotypic genus for over a century, even receiving its own subfamily at one point (Noble 1931) that was maintained only for a few years before being synonymised with Cophylinae by Parker (1934). It came as a great surprise when, in 2005, genetic results revealed that several species that had previously been ascribed to *Plethodontohyla* Boulenger, 1882 were more closely related to *R. testudo* than to other members of the genus *Plethodontohyla* (Andreone et al. 2005). As a result, Frost et al. (2006) transferred three species [*Plethodontohyla alluaudi* (Mocquard, 1901), *P. coudreaui* Angel, 1938, and *P. laevipes* (Mocquard, 1895)], to *Rhombophryne*. Glaw and Vences (2007) then transferred four more species to *Rhombophryne* [*Plethodontohyla coronata* Vences & Glaw, 2003, *Plethodontohyla serratopalpebrosa* (Guibé, 1975), *P. guentherpetersi* (Guibé, 1973), and *P. minuta* (Guibé, 1975)] in anticipation of the genetic results of Wollenberg et al. (2008). This was a fairly sudden and major change to our understanding of the diversity and evolution of the Cophylinae but not the first such event; 15 years earlier, the six species in the genus *Mantipus* Peters, 1883, had been merged with the seven in the genus *Plethodontohyla* when Blommers-Schlösser and Blanc (1991) synonymised those genera.

Since 2007, only two small taxonomic transfers have occurred between *Rhombophryne* and *Plethodontohyla*: Firstly, Peloso et al. (2016) erroneously transferred *R. matavy* D’Cruze, Köhler, Vences & Glaw, 2010 to *Plethodontohyla* based on a mislabelled sample of *Plethodontohyla fonetana*; this mistake was identified, clarified, and reversed by Scherz et al. (2016b). Secondly, Bellati et al. (2018) transferred *Rhombophryne alluaudi* to *Plethodontohyla* because it was discovered that the nomen *Dyscophus alluaudi* Mocquard, 1901 had been misapplied to a well-known but as yet unnamed species of *Rhombophryne*; *Plethodontohyla alluaudi* is a poorly

known frog from the southeast of Madagascar (Bellati et al. 2018). The taxonomic issues between *Rhombophryne* and *Plethodontohyla* are now resolved, and we do not anticipate that there will be any further transfers of available names among these genera. Scherz et al. (2016b) provided a key in their supplementary files to aid in the assignment of specimens to these two genera (and *Stumpffia* and *Anilany*), which relies heavily on osteological characters.

The genus *Stumpffia* Boettger, 1881 was also synonymised with *Rhombophryne* by Peloso et al. (2016), because they found *Stumpffia* and *Rhombophryne* samples to be intermixed in their multi-gene phylogenies. However, a re-analysis of their data and results in the context of a new multi-gene phylogeny with near-complete taxon sampling of cophylines by Scherz et al. (2016b) found that numerous specimens or tissue samples had been mislabelled and/or misidentified by Peloso et al. (2016), and concluded that this synonymisation was unjustified—partly as a result of these mislabellings—and reversed them; *Rhombophryne* and *Stumpffia* are not just genetically distinct, but also ecomorphologically and osteologically distinct. However, one lineage of ‘*Stumpffia*’ incontrovertibly split from a node basal to that demarcating the *Stumpffia*+*Rhombophryne* clade, and morphological and osteological investigation of that lineage revealed such strong differences that a new genus, *Anilany*, was erected for it (Scherz et al. 2016b). Peloso et al. (2017) challenged this conclusion when they re-analysed the data of Scherz et al. (2016b) with more extensive outgroup sampling and more genetic data, even though they found almost the same topology as Scherz et al. (2016b). They advocated for their former synonymies, but Scherz et al. (2017b) rejected their decisions and again advocated for the continued use of *Rhombophryne*, *Stumpffia*, and *Anilany*, because they are each monophyletic, diagnosable taxa. Molecular results from Tu et al. (2018) further supported the genus-level distinction of *Rhombophryne* and *Stumpffia* and the validity of *Anilany*. Scherz et al. (2017b) also emphasised the need for clarification of the phylogenetic relationships of several undescribed candidate taxa and *Stumpffia tridactyla* relative to these genera. *Stumpffia* was subsequently revised thoroughly by Rakotoarison et al. (2017), who described 26 new species in this genus. The description of a second *Anilany* species, which also contained a detailed osteological treatment of the genus, has further solidified the stability of this generic taxonomy (Petzold et al. 2025).

Species diversity in *Rhombophryne*

Between 1880 and 2007, seven *Rhombophryne* species were scientifically named (Boettger 1880a; Mocquard 1895; Angel 1938; Guibé 1973, 1975; Vences and Glaw 2003), at an average rate of roughly one species every 18 years. However, since 2007, research on the genus has intensified, and 13 new species have been named (D’Cruze et al. 2010; Glaw et al. 2010b; Scherz et al. 2014, 2015a, 2015b, 2016a, 2017a, 2019b; Lambert et al. 2017; Scherz 2020). Today, *Rhombophryne* thus contains 20 nominal species. Recently, Belluaro et al. (2022) provided a

phylogenetic revision of *Rhombophryne*, proposing six species groups. They also identified 10 candidate species awaiting taxonomic assessment and description, and they provided maps of the known distribution of all nominal species and unnamed lineages or candidate species.

Here, we embark on a taxonomic revision of *Rhombophryne*. We provide accounts for all six species groups and detailed taxonomic accounts of all species. We describe and name seven new species, one of which has not been previously identified as a candidate species. We also provide a key to the genus to enable field identification of these sometimes difficult to distinguish frogs. Finally, we provide preliminary conservation assessments of all species.

Materials and Methods

Specimens were collected in the field using standard procedures for amphibian collection. After euthanasia using MS-222, chlorobutanol, or lidocaine, specimens were fixed in either ~90% ethanol or 4% formalin solution and subsequently transferred to 70% ethanol for long-term storage. Specimens were almost always preserved with mouths closed. Field numbers refer to the zoological collections of **ACZCV** Angelica Crottini, **APR** Achille P. Raselimanana, **CRH** Carl R. Hutter, **DLR** Dina Lydie Ramamonjisoa, **DRV** David R. Vieites, **FGMV** Miguel Vences and Frank Glaw, **FGZC** Frank Glaw, **FN**, **FAZC** Franco Andreone, **MSZC**, **MSTIS** Mark D. Scherz, **RJS** Jasmin E. Randrianirina, **THC** Thio Rosin Fulgence, and **ZCMV** Miguel Vences. Institutional abbreviations refer to **AMNH** American Museum of Natural History, New York, NY USA; **BMNH** Natural History Museum, London, UK; **EHT-HMS** University of Illinois Museum of Natural History; **FMNH** Field Museum of Natural History, Chicago IL, USA; **KU** Zoological Collections of Kansas University, Lawrence KS, USA; **MCZ** Museum of Comparative Zoology, Harvard MA, USA; **MNCN** Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN** Muséum National d’Histoire Naturelle, Paris, France; **MRSN** Museo Regionale di Scienze Naturali, Turin, Italy; **SMF** Senckenberg Naturmuseum Frankfurt, Frankfurt am Main, Germany; **UADBA-(A)** the (amphibian) collections of the Université d’Antananarivo Département de Biologie Animale; **ZFMK** Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; **ZMB** Museum für Naturkunde, Berlin, Germany; and **ZSM** Zoologische Staatssammlung München, Munich, Germany. All geographical coordinates are given in datum WGS84.

Morphological measurements

Morphological measurements were taken by MDS using a digital calliper to the nearest 0.01 mm and rounded to 0.1 mm. Ratios were calculated prior to rounding to avoid compound rounding errors.

The measurement scheme (Fig. 1) generally follows that used on this genus previously (e.g., Scherz et al. 2015a): **SVL** snout–vent length, **HW** maximum head width, **HL** head length, from the maxillary commissure to the anterior-most point of the mouth, **ED** horizontal eye diameter, **END** eye–nostril distance, **NSD** nostril–snout tip distance, **NMD** nostril–premaxillary symphysis distance, **NND** inter-narial distance, **TDH** horizontal tympanum diameter, **TDV** vertical tympanum diameter, **HAL** hand length, from the metacarpal–radioulnar articulation to the tip of the longest finger, **LAL** lower arm length, from the carpal–radioulnar articulation to the centre of the radioulna–humeral articulation, **UAL** upper arm length, from the centre of the radioulna–humeral articulation to the trunk, measured along the posterior aspect of the arm, **FORL** forelimb length, given by the sum of HAL, LAL, and UAL, **FOL** foot length, from the tarsal–metatarsal articulation to the tip of the longest toe, **TARL** tarsal length, from the tarsal–metatarsal articulation to the tarsal–tibio-

fibular articulation, **FOTL** foot length including tarsus, from the tibiotarsal articulation to the tip of the longest toe, given by the sum of FOL and TARL, **TIBL** tibiofibula length, **TIBW** tibiofibula width at thickest point, measured in dorsal aspect, **THIL** thigh length, from the vent to the femoral–tibiofibular articulation, **THIW** thigh width at thickest point, measured in supine position, **HIL** hindlimb length, given by the sum FOL, TARL, TIBL, and THIL, **IMCL** maximum length of inner metacarpal tubercle, **OMCL** maximum length of outer metacarpal tubercle, **IMTL** maximum length of the inner metatarsal tubercle, **OMTL** maximum length of outer metatarsal tubercle. We add the measurement **FARL** forearm length, given by the sum of LAL and HAL, as a more reliable measure than FORL, as UAL is highly variable depending on fixation quality, and its proximal point is ambiguous. With very few exceptions, all examined specimens were measured, and thus for a nearly exhaustive list of examined material for each species, the reader is referred

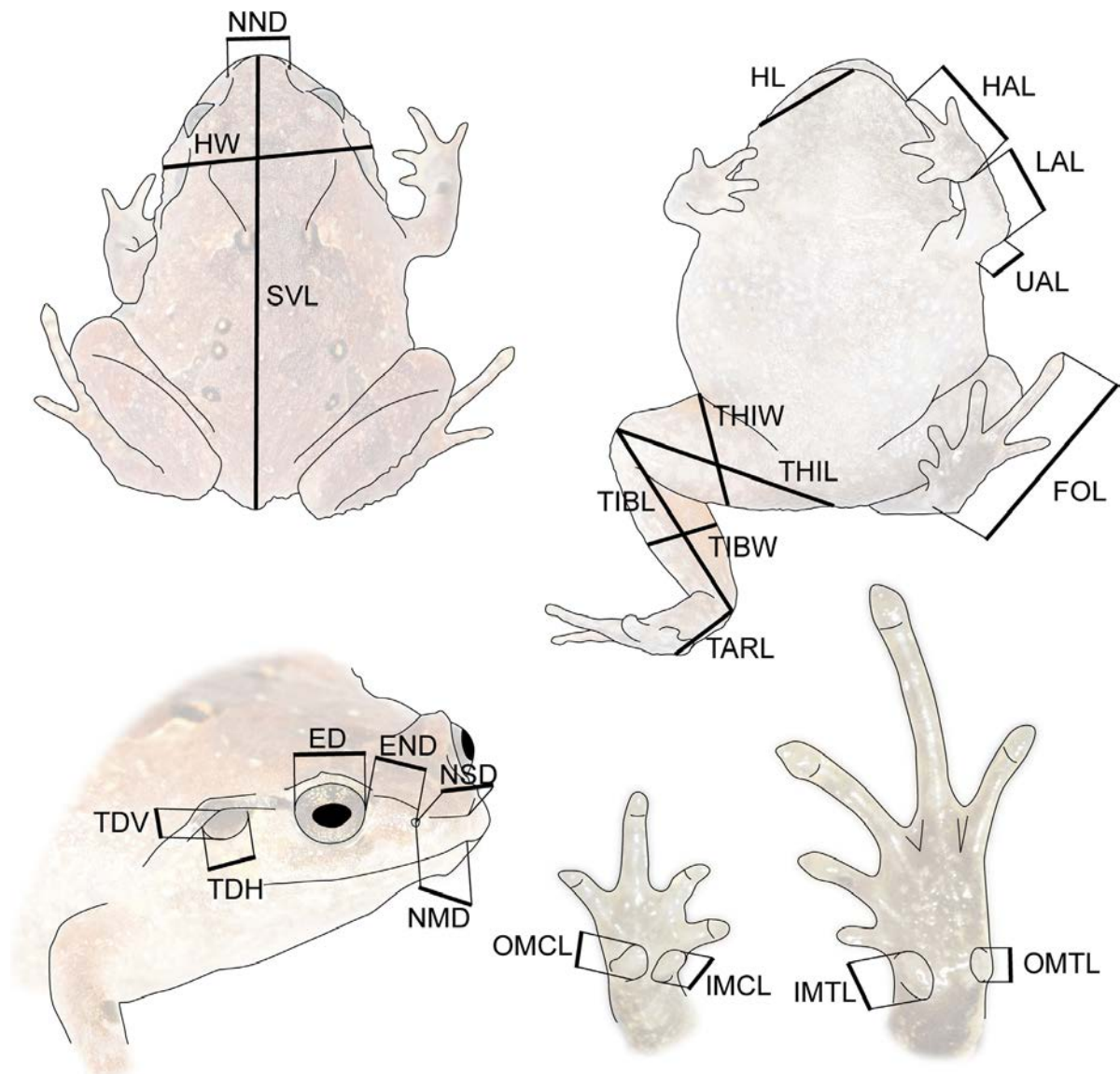


Figure 1. The morphometric scheme used herein. See Morphological measurements section of Materials and Methods for explanation of abbreviations. Not shown: **FARL** (=LAL+HAL), **FORL** (=UAL+FARL), **HIL** (=THIL+TIBL+TARL+FOL), **FOTL** (=TARL+FOL).

to the tables of morphometric measurements presented as Electronic Supplement (Tables S5–S11) to this article for each species group treatment, rather than producing redundant lists of examined material for each species account.

Specimens were sexed based on one of up to four different assessment methods: (1) field notes documenting an individual as having emitted advertisement calls, confirming it to be an adult male; (2) dissection, wherein a slit is made starting from the inguinal region along the flank, and the gonads are physically examined; (3) identification of vocal slits, indicating the male sex (note: this is the first study on cophylines to seek vocal slits and confirms that they are present, but they are extremely difficult to find in most specimens because the tongue is very broad and the mouth tissue soft, rendering them hidden); (4) identification of oocytes in micro-CT scans, confirming the female sex and sexual maturity. Although we made a major effort to sex as many individuals as possible, many remained unsexed, either because we did not have permission to perform dissection or because none of the above approaches yielded definitive results.

Morphometric differences among species groups were explored and plotted with Principal Component Analysis (PCA) in R 4.4.1 (2024-06-14) (R Core Team 2024) in RStudio 2024.09.0.375 (Posit team 2024), using tidyverse (Wickham et al. 2019) and ggplot2 (Wickham 2016) packages; and Linear Discriminant Analysis (LDA) using MASS (Venables and Ripley 2002), FactoMineR (Lê et al. 2008), tidyverse (Wickham et al. 2019), and ggplot2 (Wickham 2016) packages. We first filtered data to include only adults or presumed adults, and we removed all individuals with missing data. Input data were corrected for allometry by taking residuals against SVL, except SVL itself, which was ln-transformed. PCA was performed using the `prcomp()` function with `centre = TRUE` and `scale = TRUE`. Performance of LDA was assessed by examining the confusion matrix following leave-one-out cross validation (`lda()` call with `CV=T`). Boxplots of morphometrics (divided by SVL for ease of computation in the field) were generated using ggplot2 (Wickham 2016). The full morphometric dataset is included in our Zenodo repository (<https://doi.org/10.5281/zenodo.17247222>).

Micro-computed tomography

Micro-CT scans were made with a phoenix|x nanotom m (GE Measurement & Control, Wunstorf, Germany), using a diamond, molybdenum, or tungsten target and a 0.1 mm Cu filter. Specimens were sealed inside polyethylene containers mounted and secured at an oblique angle using polystyrene such that no extremities were in contact with the plastic container. A small volume of 70–80% ethanol was added to the vessel to maintain air saturation and prevent desiccation. Scan times ranged from 20 to 30 minutes and consisted of 1440 or 2440 projections, with a timing of 500 or 750 ms. Scanning parameters were adjusted according to the target type and specimen, and are listed in Table S12.

Scan files were assembled using phoenix|x reconstruct (GE Measurement & Control), set for low noise, ROI-CT filter, and in-line median. Reconstructed volumes were imported at 8-bit into VG Studio Max 2.2 (Volume Graphics GmbH, Heidelberg, Germany). Models were visualised using the Phong settings, with thresholds adjusted manually, and a standard colour palette applied and manually adjusted. Figures used herein were produced using the built-in image capture function and are based on volumes and not surfaces (see discussion by Scherz et al. 2017a). Volumes were exported as DICOM stacks, which have been deposited on Morphosource.org (see Table S1 for individual Media ID's).

Abbreviations used in figures are as follows: **asp**, angulosplenic; **cp**, coronoid process of angulosplenic; **asp.lf**, lateral facet of angulosplenic; **asp.pp**, posterior process of angulosplenic; **asp.vf**, ventral foramen of angulosplenic; **cl**, cleithrum; **col.pip**, pars interna plectri of columella; **col.pmp**, pars media plectri of columella; **cpl(s)**, carpal(s); **dn**, dentary; **exc**, exoccipital; **exc.oc**, occipital condyle of exoccipital; **fp**, frontoparietal; **fp.dp**, dorsal process of frontoparietal; **hy.mp**, medial process of hyoid; **mmk**, mentomeckelian; **mx**, maxilla; **mx.pf**, pars facialis of maxilla; **mx.pp**, pars palatina of the maxilla; **n**, nasal; **n.mp**, maxillary process of nasal; **npl**, neopalatine; **pmx**, premaxilla; **pmx.ap**, alary process of premaxilla; **pmx.lp**, lateral process of the pars palatina of the premaxilla; **pmx.pp**, palatine process of the pars palatina of the premaxilla; **povm**, post-choanal portion of vomer; **pvt**, prootic; **prvm**, pre-choanal portion of vomer; **psp**, parasphenoid; **psp.ap**, alary process of parasphenoid; **psp.pp**, posterior process of parasphenoid; **pt.ar**, anterior ramus of pterygoid; **pt.mr**, medial ramus of pterygoid; **pt.pr**, posterior ramus of pterygoid; **qj**, quadratojugal; **smx**, septomaxilla; **spt**, sphenethmoid; **sq.or**, otic ramus of squamosal; **sq.vr**, ventral ramus of squamosal; **sq.zr**, zygomatic ramus of squamosal; **tsl(s)**, tarsal(s). Terminology follows Trueb (1968, 1973, 1993) and Scherz et al. (2017a).

Bioacoustics

We recorded anuran vocalization in the field using various digital or analogue devices such as Sony WM-D6C and Tensai RCR-3222 tape recorders with external microphones (Sennheiser Me-80, Vivanco EM 238), and Tascam DR07, DR05, Marantz PMD 660 or Roland Edirol R-09 digital recorders, with built-in microphones (Tascam) or accessorized with semi-directional microphones (Marantz and Roland). We obtained digital recordings at a sampling rate of 44.1 kHz and 24-bit resolution and saved them as uncompressed files. Recordings were digitized or resampled at 22.05 kHz and 32-bit resolution (except for *R. coronata*, digitized at 44.1 kHz) and computer-analysed using the software CoolEdit Pro 2.0. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points) at Hanning window function; audiospectrograms were drawn at Blackman window function with 256 bands resolution. Temporal characters

were measured from oscillograms. Measured numerical call parameters were provided as range followed by mean $\pm$ standard deviation in parentheses. Terminology of call descriptions and methods for call analyses follow those recommended by Köhler et al. (2017), using the call-centred terminological scheme. In several cases, filtering was applied to recordings containing background sounds. In all cases of filtering, frequency sectors to be filtered were carefully chosen to avoid any effects on the bandwidth of the focal frog calls. All advertisement calls described herein were analysed using the same methodology. Even in cases where call parameters were formerly published from the same recordings, we analysed and describe these calls again, applying the methodological and terminological approach described above to ensure greatest possible comparability across species. However, in some cases this procedure may result in slight differences in parameter values when compared to already published data.

For the purpose of easy and immediate comparability, audiospectrograms and the corresponding oscillograms of advertisement calls of all species are shown at a standardized time scale of 1000 ms. To provide an impression of patterns of call repetition, in most cases we provide additional oscillograms at variable time scale among species, figuring either an entire call series or a general pattern of call repetition.

Molecular relationships and divergences

For this study, we analysed two fragments of the mitochondrial 16S rRNA gene (the 3' and 5' termini, 16S3' and 16S5', respectively) for preliminary species identification; and a fragment of the nuclear-encoded recombination activating gene 1 (RAG1) to assess the potential absence of haplotype sharing in this nuclear DNA fragment that could be indicative of cessation or limitation of gene flow; concordance between the mitochondrial and nuclear signal was also implicitly used to exclude misassignment of specimens that might occur if there had been mitochondrial introgression. Neither of these sets of analyses, however, has sufficient resolution to give a robust or well-resolved representation of phylogenetic relationships within the genus *Rhombophryne*; for that purpose, a multigene phylogeny is needed. To avoid unnecessary repetition, we refer to the recent multigene phylogeny of Belluaro et al. (2022), which was based on analyses of most of the specimens analysed here. Their multigene analysis was based on a concatenated alignment of 9844 bp, comprising fragments of the mitochondrial genes for 12S (12S) and 16S3' and 16S5' rRNA, cytochrome oxidase subunit I (COI), and cytochrome b (COB), and the protein-coding nuclear-encoded genes for brain-derived neurotrophic factor (BDNF), pro-opiomelanocortin (POMC), RAG1, recombination activating gene 2 (RAG2), two non-overlapping portions of sacsin (SACS-A and SACS-B), leucine-rich repeat and WD repeat-containing protein (KIAA1239), and titin (TTN). Most nodes in that tree are fully resolved, and only few

lineages are present in the analyses of our study that were not present in theirs.

For our 16S analysis, we compiled a dataset including 100 individuals assigned to the genus *Rhombophryne* (see Table S13 for details), covering two adjacent fragments of the 16S rRNA gene (the 16S3' and 16S5' terminus, respectively), a marker commonly used for preliminary molecular species delimitation in Malagasy and other anurans (e.g., Fouquet et al. 2007; Vieites et al. 2009; Rakotoarison et al. 2012, 2015, 2017; Scherz et al. 2017a). For this dataset, sequences available on GenBank (<https://www.ncbi.nlm.nih.gov>) from previous studies (Andreone et al. 2005; Vieites et al. 2009; Scherz et al. 2014, 2015a, 2015b, 2016b, 2017a; Lambert et al. 2017; Scherz 2020; Belluaro et al. 2022) were complemented with a total of 37 newly generated sequences from 27 individuals with either (i) data obtained from modern samples using a Sanger sequencing approach ($n = 12$ sequences from 12 individuals) or sequences ($n = 10$ sequences for 6 individuals) extracted from raw Illumina reads from a target-enrichment dataset (Hutter et al. 2021) generated for a different project (Petzold et al. in prep.), or (ii) data obtained from museum samples ($n = 15$ sequences from 9 individuals) using a museomics approach (see Table S13 for a list of all samples).

(i) For the Sanger sequencing approach, genomic DNA was extracted from muscle tissue samples preserved in 99% ethanol using the SPRI Bead DNA Extraction Protocol (<http://phyletica.org/lab-protocols/extraction-spri.html>; under 6.1 Laboratory Protocols). The obtained DNA was quantified with an Agilent Genomic DNA Screen Tape assay in conjunction with the Agilent 2200 TapeStation system (Agilent Technologies) and subsequently PCR-amplified, using the primer 16SL3 (5'-AGCAAAGAHYWACCTCGTACCTTTTGCAT-3') and 16SAH (5'-ATGTTTTTGATAAACAGGCG-3') (Vences et al. 2003a) for the 16S5' terminus, and 16Sar-L (5'-CGCCTGTTTATCAAAAACAT-3') and 16SBr-H (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi et al. 1991) for the 16S3' terminus. PCR amplifications were performed in a total volume of 25 μ l using 12.5 μ l nuclease-free water, 5 μ l 5 $\times$ Green GoTaq Flexi Buffer (Promega), 4 μ l 25 mM MgCl₂ (Promega), 0.4 μ l dNTPs (10 mM) (Invitrogen), 1 μ l of forward and reverse primers (10 pM) (Thermo Fisher Scientific), 0.1 μ l 5 U/ μ l GoTaq Flexi DNA Polymerase (Promega) and 1 μ l of the extracted DNA. The protocol and conditions were used as described in Belluaro et al. (2022), but always used a final extension step at 72 °C of 10 min. The amplification products were subsequently purified using the MinElute PCR Purification Kit (Qiagen), and the amplicon size was checked with gel electrophoresis on a 2% agarose gel. Sequencing reactions for each fragment were performed in a total volume of 10 μ l, including 2 μ l 5 $\times$ Sequencing Buffer, 0.5 μ l BigDye v.3.1, 0.5 μ l forward or reverse primer, 6 μ l HPLC-water and 1 μ l purified PCR product. All components are from the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific) and were used with the following temperature profile: 96 °C for 90 s,

followed by 30 cycles of 96 °C for 20 s, 55 °C for 15 s and 60 °C for 4 min using a Biometra T3000 or T1 Cycler. Reaction products were purified using gel filtration (Sephadex G-50 Superfine; Sigma-Aldrich via Merck KGaA) on a MultiScreen-HTS-HV plate and subsequently analysed on a 3500 Genetic Analyzer. Sequencing of samples was done in both forward and reverse directions.

The modern dataset was subsequently complemented with sequences extracted from the Illumina reads generated for a separate project by A. Petzold and colleagues, which included six recently collected individuals of the genus *Rhombophryne*: *R. diadema* FGZC 3604; *R. laevipes* MSZC 648; *R. matavy* ZSM 1628/2008; *R. minuta* FGZC 2898; *R. savaka* ZSM 468/2005; and *R. vaventy* FGZC 2876. These samples underwent hybrid-enrichment sequence capture (HybSeq) using a universal bait set for anuran species called FrogCap (Hutter et al. 2021) that targets ~20,000 nuclear markers and also recovers mitochondrial data as bycatch. For the retrieval of 16S sequences, raw reads were first assessed for quality using FastQC (<https://www.bioinformatics.babraham.ac.uk>) twice, both before and after trimming of Illumina adapter sequences. Quality filtered and trimmed reads were subsequently mapped with Geneious Prime v.2023.2.1 (Biomatters Ltd., Auckland, New Zealand) using the 16S sequence of a conspecific or a closely related species as a reference. Individual mapping was run for 25 iterations using a mapping quality filter of 30 and medium-low sensitivity options with an identity threshold of 0.9. The obtained contigs derived from unique reads were assembled into a consensus sequence of either 16S3' or 16S5', with missing sites between contigs denoted as Ns.

(ii) To obtain new sequences from museum specimens ('museomics'), i.e., material from which no tissue samples were freshly taken in the field, either liver or thigh muscle tissue was taken in a minimally invasive manner under clean conditions and subsequently processed in a dedicated laboratory, which meets all requirements to work with historical samples (see Fulton and Shapiro 2019). We sampled the holotype (MNHN 1975.24) and another specimen (UADBA 18258, APR 04222) of *Rhombophryne serratopalpebrosa*, the holotype (SMF 4241) and another specimen (BMNH 1895.10.29.30) of *R. testudo*, a specimen of *R. laevipes* (ZSM 853/2003), a paratype of *R. anatalia* **sp. nov.** (MRSN A4600) described herein, several specimens of *Rhombophryne* sp. 'Ivohibe' (UADBA 17430, UADBA 17419, UADBA 17420, UADBA 17422, UADBA 17424), the holotype of *R. minuta* (MNHN 1975.15), the holotype of *R. kilonjy* **sp. nov.** (MRSN A4627) described herein, and the holotype of *R. coudreaui* (MNHN 1937.19). Not all of these efforts were successful (see Results, below).

For the extraction of genomic DNA for museomics, each tissue sample was weighed prior to being incubated in 1 ml of guanidinium thiocyanate buffer (5 M GuSCN, 50 mM Tris pH 8.0, 25 mM NaCl, 20 mM EDTA, 1% Tween-20, 1% 2-mercaptoethanol), adapted from Rohland et al. (2004), at 37 °C for 18 h overnight. The next day, the lysate was centrifuged, and processed following

the consecutive steps described in Dabney et al. (2013), starting with adding 1 ml of the supernatant to 13 ml of binding buffer (5 M guanidine hydrochloride, 40% isopropanol, 0.05% Tween-20, 90 mM sodium acetate). DNA was purified on MinElute silica spin columns (Qiagen) and eluted twice with TET buffer (10 mM Tris-HCl, 1 mM EDTA, 0.05% Tween-20) for a total amount of 25 µl DNA extract; see also Straube et al. (2021). Subsequently, the yield of DNA was quantified using the Qubit dsDNA HS Assay Kit 0.2–100 ng/µl (Life Technologies, Carlsbad, California, US) according to the instructions of the manufacturer. For single-stranded library preparation, a maximum of 13 ng from each DNA extract was used following the protocol of Gansauge et al. (2017). Final library concentrations and fragment length distributions were assessed using a 2200 TapeStation (Agilent Technologies) assay. Finished libraries were shotgun-sequenced either once or twice (in case the first approach did not provide usable sequence data) for approximately one million 75 bp single-end reads using an Illumina Nextseq 500/550 sequencing platform at the University of Potsdam, following the procedure described in Paijmans et al. (2017). The treatment of the obtained reads followed the same procedure described above for sequences derived from the target-enrichment approach.

Separate 16S3' and 16S5' alignments were generated using the MAFFT local pair algorithm implemented in AliView v1.26 (Larsson 2014) and manually adjusted if necessary. We then combined both alignments, 16S3' (527 bp) and 16S5' (670 bp), using Concatenator v0.2.1 from the iTaxoTools toolkit 0.1 (Vences et al. 2021). The dataset of the combined fragments, hereafter called 16S (1274 bp), was used to make phylogenetic inferences in IQtree v1.6.12 (Nguyen et al. 2015) under 1000 replicates and the best suited substitution model inferred using the command `-m TEST` in the implemented program ModelFinder (Kalyaanamoorthy et al. 2017). The tree was rooted using publicly available sequences from *Scaphiophryne brevis* (ZCMV 12812) and *S. boribory* (AMNH A16739) as outgroups, and visualised in FigTree version 1.4.4 (<https://github.com/rambaut/figtree>).

Uncorrected pairwise distances (p distances) for 16S3' and 16S5' were calculated for modern samples in Taxi2 (Vences et al. 2024a), which is part of the iTaxoTools toolkit (Vences et al. 2021). Lineages were identified guided by thresholds of 3% for 16S fragments following Fouquet et al. (2007) and Vieites et al. (2009). This approach is in line with the one used in Belluardo et al. (2022) who also based lineage identification on a similar point of reference in mitochondrial distances, i.e., 6% for COI following Perl et al. (2014). The 16S3' alignment was also used as input for statistical ASAP species delimitation (Puillandre et al. 2021), using the iTaxoTools distribution with default settings (Vences et al. 2021). Non-summarised distance tables with museomics samples included are given as Tables S14, S15; non-summarised distance tables without museomics samples included are given as Tables S16, S17.

The protein-coding nuclear RAG1 gene was analysed using a haplotype-network approach so as to gather ev-

idence for lineage distinction from a locus unlinked to the mitochondrial sequences used to identify candidate lineages (Belluardo et al. 2022). Nuclear sequences were either obtained by (i) extraction from FrogCap datasets generated for different projects (Hutter et al. 2021, Petzold et al. in prep) using the above-mentioned mapping approach ($n = 12$) or (ii) newly generated from tissue samples taken from 28 individuals (Table S13). For the latter, total genomic DNA was extracted using proteinase K digestion (10 mg/ml concentration) followed by a standard salt-extraction protocol (Bruford et al. 1992). A fragment of RAG1 was successfully amplified for 28 specimens with primers RAG1_Coph_F1 5'-CGT-GATCGGGTAAAAGGTGT-3' and RAG1_Coph_R1 5'-TCGATGATCTCTGGAACGTG-3' using the following amplification conditions: 94 °C for 120 s, 35 cycles of 94 °C for 20 s, 53 °C for 50 s, 72 °C for 180 s, followed by a final extension at 72 °C for 600 s (Rakotoarison et al. 2019). PCR reactions were performed in a final volume of 25 µl using 0.75 µl each of 10 pmol primer, 0.4 µl of total dNTP 10 mM (Promega), 0.1 µl of 5 U/mL GoTaq, 5 µl 5X Green GoTaq Reaction Buffer (Promega) and 4 µl of MgCl₂ 25mM (Promega). Successfully amplified PCR products underwent post-purification prior to sequencing using a Sanger sequencing approach on a 3730xl sequencer (Applied Biosciences) at MacroGen Inc. Newly generated sequences were checked by eye, edited and aligned in BioEdit (version 7.0.5.3; Hall 1999).

We compiled a RAG1 alignment by combining seven sequences available on Genbank with the 40 sequences newly obtained in this study, which account for 18 described species of *Rhombophryne* and eight candidate species (Table S13). The following species and candidate species are missing from this analysis: *R. regalis*, *R. sp. Ca16*, *R. sp. 'Ivohibe'*, *R. mavokely* **sp. nov.** (Ca17), and *R. kilonjy* **sp. nov.** (the latter two described herein, with *R. kilonjy* **sp. nov.** not previously sequenced). We assessed the diversity in the protein-coding nuclear gene RAG1 (315 bp) using a haplotype-network approach in the program Hapsolutely (Vences et al. 2024b) from the iTaxoTools toolkit (Vences et al. 2021). Nuclear haplotypes (alleles) were initially inferred using the PHASE algorithm (Stephens et al. 2001) implemented in Hapsolutely, using a phase (-p) and allele (-q) threshold of 0.5 with 1000 MCMC iterations. Subsequently, the network was inferred from the phased alignment based on the TCS algorithm (Clement et al. 2000) and graphically edited in Adobe Illustrator (Adobe Inc.).

Table S13 includes a table of GenBank accession numbers for all mitochondrial and nuclear sequences used in and produced by this study ($n = 204$). Newly generated sequences ($n = 77$) from this study belong to the following GenBank series: PZ405231–PZ405243, PZ418412–PZ418427, and PZ376996–PZ377035. Some sequences were too short or too fragmentary to be accepted by NCBI, so these are only available from our alignments. Alignment files and other input files used in this study are available from the Zenodo repository (<https://doi.org/10.5281/zenodo.17247222>).

Taxonomic methodology

Our approach to the description and redescription of species is intended to be thorough and yet concise, optimising for consistency across species by preparing descriptions in a standardised, formulaic order. In species for which the original description was brief, a redescription of the holotype is given, as well as a description of variation based on additional examined specimens. In redescrptions, we have explicitly tried to remain true to the original description of the species, and as such we use either the same terminology or direct translations of that terminology when it was not originally published in English, with modifications to fit the overall scheme of the descriptions used as standard here.

We also follow Rakotoarison et al. (2017) in treating species in species groups, in each case first treating the available nominal species in chronological order of their description (not alphabetically), then describing our new species. Diagnoses are given from all hitherto described species, and from all new species presented preceding the current taxon (i.e., species 1 is diagnosed against only all hitherto described species, species 2 against all hitherto described species and species 1, species 3 against all hitherto described species and species 1 and 2, etc.), with occasional deviations where mentions of species described further down are warranted. To avoid redundancy, each pairwise comparison is given only once (with few exceptions), and subsequently referred back to (e.g., *R. testudo* is distinguished from *R. coudreaui*, but in the account of *R. coudreaui* we refer the reader to the diagnosis of *R. testudo*). To further shorten diagnoses, where possible comparisons are made to whole groups rather than individual species (e.g., '*R. testudo* can be distinguished from the *R. serratopalpebrosa* group by the absence of superciliary spines'). In these instances, the full known diversity of that species group is meant, including the taxa newly described herein, but we do not explicitly state which species the group contains each time, as this information is given repeatedly elsewhere in the text.

For the sake of brevity, diagnoses also do not include a justification for the inclusion of the species within the genus *Rhombophryne*; all simply conform with the diagnosis of the genus, given below. For all species, inclusion in this genus is supported on the basis of molecular phylogenetic data and morphology (Scherz et al. 2016b; Belluardo et al. 2022). As all species have been sequenced, and species groups have been established based on phylogenetic relationships (Belluardo et al. 2022), assignment to species group is not included in the diagnosis beyond a statement of affinity.

Osteological descriptions are not intended to be fully comprehensive but instead focus specifically on those characters that appear to have diagnostic value within this genus and subfamily. For more exhaustive descriptions of the skeleton of some *Rhombophryne* species, the reader is referred to Scherz et al. (2015a, 2017a).

We implement an integrative taxonomic approach (Padial et al. 2010), using multiple lines of evidence to support the hypothesis of species as evolutionarily inde-

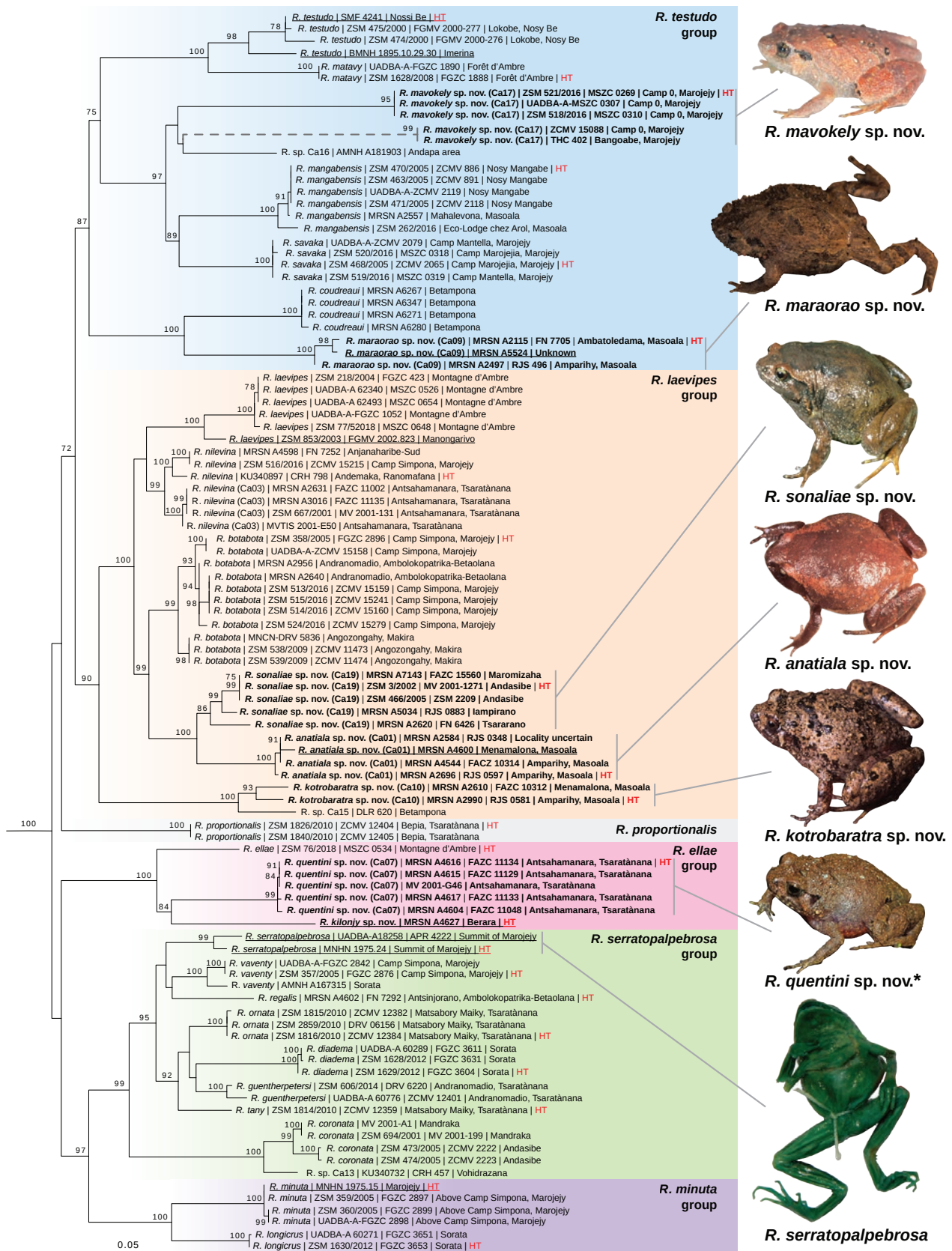


Figure 2. Maximum likelihood phylogeny inferred from the mitochondrial 16S rRNA gene, showing genetic relationships among all members of the genus *Rhombophryne*. The outgroups [*Scaphiophryne brevis* (ZCMV 12812) and *S. boribory* (AMNH A16739)] have been removed post-analysis for graphical purposes. The paraphyletic placement of *R. mavokely* sp. nov. (grey dotted line) is probably an artifact resulting from non-overlapping fragments (either 16S3' or 16S5') among sequenced individuals. Bootstrap support values are shown at corresponding nodes, and values below 70 are not displayed. Species newly described herein are in boldface. Specimens sequenced using museumics approaches are underlined. Photos show the newly described species, as well as the holotype of *R. serratopalpebrosa* (*=photograph mirrored). Photographs are not to scale. Museumics-derived sequence data of *Rhombophryne* sp. 'Ivohibe' was too poor to include. HT = Holotype. For field and collection abbreviations, see Materials and Methods.

pendent units, in the framework of the general lineage concept (de Queiroz 1998, 2007). Lines of evidence include (1) mitochondrial differentiation exceeding 3% in a fragment of the 16S rRNA mitochondrial gene, used to establish candidate species in previous studies (Vieites et al. 2009; Scherz et al. 2016b; Belluardo et al. 2022); (2) absence of haplotype sharing in the nuclear RAG1 gene, frequently used as an independent nuclear marker in other studies on Malagasy amphibians and reptiles (e.g., Rakotoarison et al. 2017; Scherz et al. 2022a; Vences et al. 2022); (3) morphological differentiation (including features of colouration, external anatomy, osteology); and (4) bioacoustic differentiation in advertisement calls. In some cases, the situation remains ambiguous, and in these cases, we present treatments of the lineages but have not described them as new species until new data are collected that give convincing evidence for or against species status of the lineages. For greater clarity, we use the names of the new taxa in the Results section already before the taxonomic section, in anticipation of our taxonomic treatments.

We determined molecular diagnostic sites differentiating all *Rhombophryne* lineages for the mitochondrial markers 16S3' and 16S5' using MolD (Fedosov et al. 2022), as implemented in iTaxoTools (Vences et al. 2021), using only the data obtained from recently collected specimens (i.e., excluding museum samples, for which assemblies are often fragmentary or too short). For this purpose, the full length 16S sequence of *Anilany helena* (MZ751042) served as indexing reference, which was extracted from the complete mitochondrial genome available on GenBank (<https://www.ncbi.nlm.nih.gov>). To avoid biased results, ambiguous sites and sequences with >50% missing data were removed from the analysis. Gaps were considered as non-diagnostic sites (Gaps_as_chars=no), NumberN was adjusted to the amount of missing bases at the beginning and end of the alignment,

caused by the insertion of the reference covering the full length of the gene, and a percent difference of 1% was used for the inference of redundant diagnostic nucleotide combinations (rDNCs; Pdiff=1) with 20,000 iterations. The alignment used for calculation of diagnostic sites is available from Zenodo (<https://doi.org/10.5281/zenodo.17247222>).

Results

Molecular phylogenetic relationships and species delimitation

Our 16S phylogeny (100 individuals plus two outgroups; total alignment length 1196 nucleotides; Fig. 2) corresponds well to that recovered by Belluardo et al. (2022), with moderate to high support (87–100% bootstrap support [BS]) for all six species groups established by those authors. Because this analysis is based on a single mitochondrial gene, it does not constitute a reliable hypothesis of higher-level relationships among clades and is primarily used to heuristically propose distinct species-level units; for a much more robust, multi-gene tree, the reader is referred to Belluardo et al. (2022).

The ASAP analysis on 16S3' with the best partition (ASAP score 3.0) consists of 28 subsets (putative species), corresponding well to currently described species (19 included) and established candidate species (nine). Two exceptions are *R. sp. Ca03*, which is suggested to be conspecific with *R. nilevina* and is not treated here as a distinct species; and AMNH A167315, referred to by Belluardo et al. (2022) as '*R. cf. vaventy*', which is suggested to be conspecific with *R. vaventy*, supporting the results of Carné and Vieites (2024) and expanding the distribu-

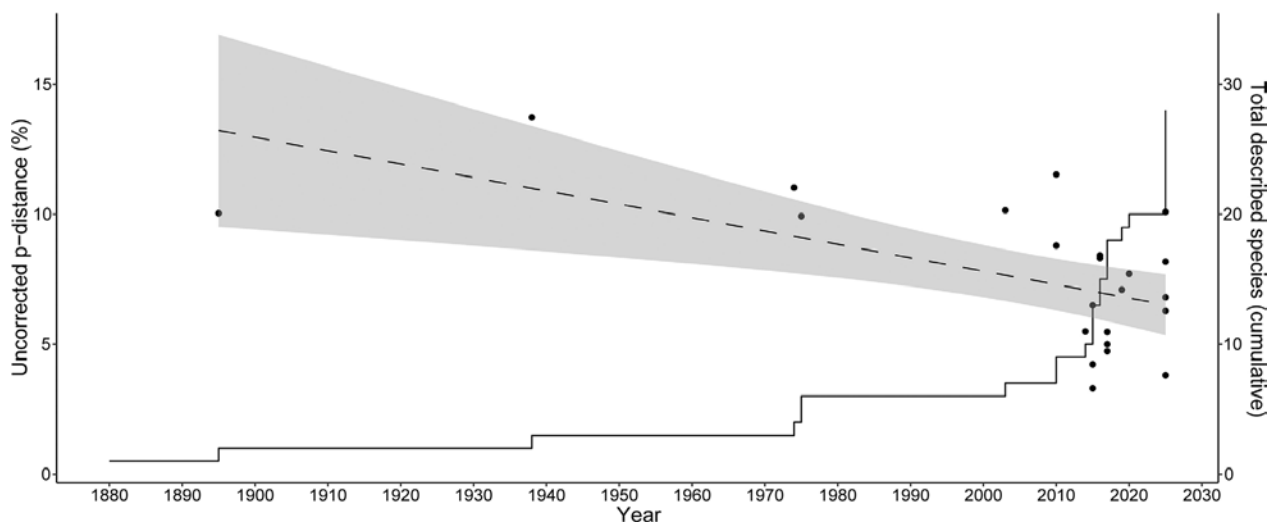


Figure 3. Number and genetic distinctiveness of newly described *Rhombophryne* species over time. Points show the smallest uncorrected p-distance for each new species among all species described before it (including those published simultaneously). The dashed line indicates the overall distance among described species over time, based on a Pearson correlation, and around it is shown the standard error of the model. The solid line is an accumulation curve of total species over time. Plot generated using ggplot2 (Wickham 2016) in the R environment (R Core Team 2024).

tion of that species to Sorata (see the account of the species below). Uncorrected p distances in our 16S3' dataset (Table S2) revealed *R. sp. Ca03* and *R. nilevina* to be separated by just 1.39–2.05% (mean 1.75%, in line with the findings of Belluardo et al. 2022). Additionally, *R. ornata* and *R. guentherpetersi* were separated by comparatively low uncorrected p distances of 2.27–3.83%, as was also found by Scherz et al. (2015b); in this case, morphological differences among these lineages strongly support their distinction. The highest intraspecific distance in the 3' fragment was 3.61% in *R. botabota*, suggesting a potentially significant lineage differentiation in this species that may warrant further investigation in the future (i.e., the division between populations from southwestern Makira and the rest of the distribution range). However, ASAP partitions splitting these clusters into different hypothesised species involved over-splitting across the entire genus, so the present data and approach does not appear to support treating these populations of *R. botabota* as distinct units.

The ASAP analysis on 16S5' with the best partition (ASAP score 1.5) also consists of 28 subsets, but the input taxon set is not completely overlapping with the 16S3' dataset, and this analysis involves further splitting, in line with the overall higher uncorrected p distances recovered by 16S5' than 16S3' (compare Tables S2, S3; see also our museomics findings for ZSM 853/2003, below). Here, *R. sonaliae* **sp. nov.** (= *R. sp. Ca19*) is divided into two lineages. Likewise, *R. kotrobaratra* **sp. nov.** (= *R. sp. Ca10*) is divided into two lineages, as found by Carné and Vieites (2024), who referred to them as 'UCS "Sp. 10"' and 'UCS "Sp. 20"'. All partitions that are more conservative resulted in over-lumping of the *R. serratopalpebroso* species group in unrealistic ways, based on detailed taxonomic work that has been published on that group (Scherz et al. 2017a). Consequently, it is possible that these two candidate species (*sp. Ca10* and *sp. Ca19*) harbour further cryptic diversity; both have intraspecific uncorrected p distances ranging beyond 3% (4.33% in *R. sp. Ca10* and 2.20–5.70% in *R. sp. Ca19*). However, to remain conservative in our taxonomic treatment, we here treat both *R. sp. Ca19* and *R. sp. Ca10* as single species, but flag that they may harbour further cryptic diversity needing investigation. In this partition, *R. nilevina* and *R. sp. Ca03* are again recovered as conspecific; although they are 3.06% divergent, the overall greater divergence in this marker suggests that the point of reference of 3% set by Vieites et al. (2009) for the 16S3' would be too low to use as an indicator of species-level divergence.

All of these lineages except one were recovered as monophyletic in our phylogenetic analysis (Fig. 2): two specimens belonging to *R. mavokely* **sp. nov.** (= *R. sp. Ca17*), ZCMV 15088 and THC 402, were recovered as sister to *R. sp. Ca16*, rendering *R. mavokely* **sp. nov.** paraphyletic. This is likely an artefact due to incomplete overlap between sequenced markers (16S3' for ZCMV 15088 and THC 402 vs. 16S5' for ZSM 518/2016, ZSM 521/2016 and UADBA-A-MSZC 0307) and not a reflection of the real phylogenetic relationships between these two lineages, as the genetic distances between these lin-

eages were high (9.11% in 16S3', and 13.58–13.88% in 16S5'), whereas sequences in *R. mavokely* **sp. nov.** were all identical in 16S5'.

To examine the pattern of genetic distance among described taxa over time, we calculated the smallest uncorrected p distance for each new species among all species described before and simultaneous with it. The overall trend in genetic distances is significantly negative (linear model, $F_{1,22}=11.22$, $p = 0.0029$, $R^2 = 0.31$, slope = -0.22; Fig. 3), in accordance with the expectation for random sampling within a monophyletic group (probability to sample the deepest split in the tree equals $n-1/n+1$, where n is the number of terminals). All species with p distances <10% have been described since 2000, but species described herein and in recent years remain well spread, and all are substantially over 3% divergent. Several of the most recently described species are amongst the most distinct *Rhombophryne* species ever found.

RAG1 haplotype network

The RAG1 haplotype network (315 bp; Fig. 4) based on the analyses of 47 specimens from 25 lineages presented a comparatively high amount of variation with a total of 45 haplotypes, including several singletons, i.e., haplotypes present only in one heterozygous individual (Fig. 4). There is very limited haplotype sharing among the analysed taxa in this marker. Only three instances of haplotype sharing among species-level lineages are observed: one haplotype is shared between *R. coronata* and *R. sp. Ca13*; another is shared between *R. nilevina*, *R. botabota*, and *R. quentini* **sp. nov.**; and a third is shared between *R. ornata* and *R. tany* (Fig. 4). Species groups form loose haplogroups.

Museomics

Using museomics methods (described above), we successfully recovered DNA from nine key samples pertinent to the phylogeny and taxonomy of *Rhombophryne* (details of recovered data are provided in the Zenodo repository, <https://doi.org/10.5281/zenodo.17247222>), but we mostly recovered only extremely fragmentary sequences at low coverage, which we tentatively interpret as follows:

- (1) MNHN 1975.24, the holotype of *Rhombophryne serratopalpebroso* from Marojejy. For 16S3' (total length 505 bp), only four reads mapped, but for 16S5' (total length 613 bp), 18 reads mapped for a mean depth of $1.2\times$ (389 bp recovered). Consequently, we are able to include this species in a phylogenetic analysis of the genus for the first time. As expected on biogeographic grounds, the species falls sister to other species occurring on Marojejy in northeastern Madagascar, namely *R. regalis* and *R. vaventy* (Fig. 2).
- (2) UADBA 18258 (APR 4222), a specimen from Marojejy NP (Camp Simpona) that is morphologically

referable to *R. serratopalpebrosa* that was not tissue-sampled when it was collected. For 16S3', only two reads mapped, but for 16S5', ten reads mapped for a mean depth of 0.6× (229 bp recovered). This was, however, sufficient for phylogenetic analyses to place it alongside the holotype of *R. serratopalpebrosa* (Fig. 2), confirming that it is the second specimen ever to be found of that species. We provide a description of this new specimen in the species account, below.

- (3) SMF 4241, the holotype of *R. testudo* from the island Nosy Be off the northwest coast of Madagascar. For both 16S3' and 16S5' only one read of 35 bp and 46 bp mapped, respectively, which was however sufficient to tentatively assign the specimen to the clade comprising all other specimens assigned to *R. testudo* (Fig. 2), based on a shared unique combination of sites in the 16S5' alignment (see Fig. S1).
- (4) BMNH 1895.10.29.30, a specimen of *R. testudo* allegedly from 'Imerina' in central Madagascar. For 16S3', 45 reads mapped for a mean depth of 4.9× (410 bp); for 16S5', 51 reads mapped for a mean depth of 2.9× (527 bp). In our phylogenetic analysis, this specimen is recovered as sister to specimens of *R. testudo* from the type locality Nosy Be (Fig. 2), and they are separated by an uncorrected p distance of 2.63–4.00% in the 16S3' marker, and 5.55% in the 16S5' marker (distance tables includ-

ing museomics samples are given as Tables S14, S15, and deposited in the Zenodo repository, <https://doi.org/10.5281/zenodo.17247222>). This confirms that this specimen requires further examination, and it could indeed represent a divergent lineage.

- (5) ZSM 853/2003 (FGMV 2002.823), a specimen of the *R. laevipes* species complex from Manongarivo. For 16S3', 26 reads mapped for a mean coverage of 3.4× (494 bp); for 16S5', 53 reads mapped for a mean coverage of 5.5× (609 bp). Phylogenetic analysis places it sister to *R. laevipes* (Fig. 2), and it is separated by an uncorrected p distance of 1.40–2.72% from other specimens of that species in the 16S3' marker, and 5.05–5.65% in the 16S5' marker (Tables S14, S15 and Zenodo repository, <https://doi.org/10.5281/zenodo.17247222>). We tentatively refer it to *R. laevipes* here, but emphasise that further work is needed in Manongarivo and other appropriate humid forests between Manongarivo and Montagne d'Ambre, to provide more samples and clarify the identity of this lineage.
- (6) MRSN A4600, a specimen from Menamalona, Masoala assignable to the *R. laevipes* species group based on its external morphology. For 16S3', 16 reads mapped for a mean coverage of 2.0× (253 bp); for 16S5' three reads mapped for a mean coverage of 0.2× (153 bp), which was however sufficient to confirm the specimen to be genetically identical to other specimens *R. sp.* Ca01 (Fig. 2), herein de-

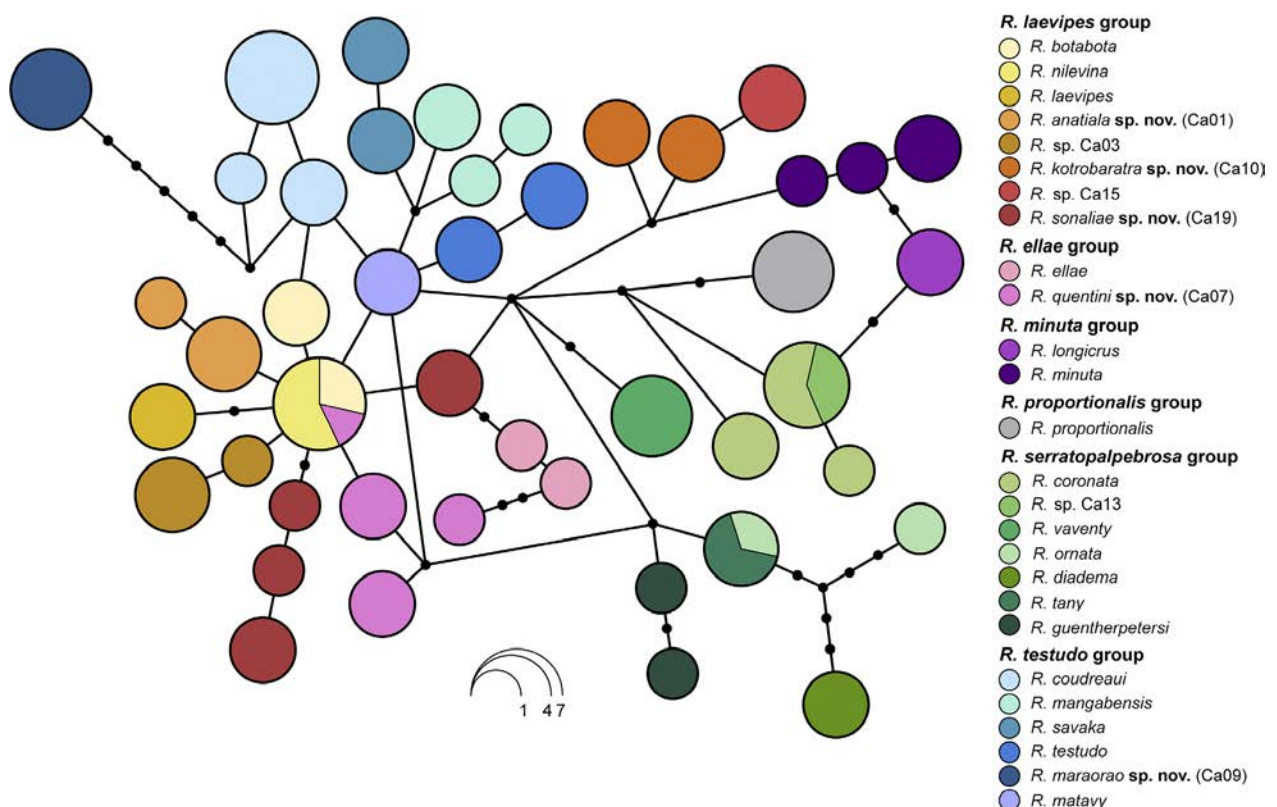


Figure 4. Haplotype network reconstruction (based on 315 bp, haplotypes inferred using the PHASE algorithm); all available RAG1 sequences for the nominal and candidate species of the genus *Rhombophryne* were used. Small black dots represent unsampled inferred intermediate haplotypes between those sampled, and lines between haplotypes indicate a single mutational step. Overlapping RAG1 fragments of *R. regalis*, *R. mavokely* sp. nov. (Ca17), *R. kilonjy* sp. nov., and *R. sp.* Ca16 were not available.

scribed as *R. anatalia* **sp. nov.** (Tables S14, S15 and Zenodo repository, <https://doi.org/10.5281/zenodo.17247222>). It is therefore included as a paratype of that species here.

- (7) UADBA 17419, UADBA 17420, UADBA 17422, UADBA 17424, UADBA 17430, five specimens from Ivohibe in the southeast region of Madagascar, assignable to the *R. serratopalpebrosa* species group based on its external morphology. From all of these individuals, mapping was extremely poor, if at all successful, even after attempts using hot alkaline lysis extraction (Hahn et al. 2024). The cause of this failure is unclear, given that the specimens are not especially old, and we have had good success from other specimens even stored >30 years in formalin solution. Additional specimens are needed to assess the phylogenetic placement of this population, which appears to be morphologically distinct from all known *R. serratopalpebrosa* species group members (circumscribed below). We refer to it throughout this manuscript as *R. sp. 'Ivohibe'*.
- (8) MNHN 1975.15, the holotype of *R. minuta* from Marojejy. For 16S3', eight reads mapped for a mean coverage of 0.6× (239 bp); for 16S5', six reads mapped for a mean coverage of 0.3× (140 bp). Phylogenetic analysis placed it together with the other specimens referred to *R. minuta*, which is sister to *R. longicrus* (Fig. 2).
- (9) MRSN A4627, a specimen of previously uncertain affiliation from Sahamalaza in northwestern Madagascar described below as *R. kilonjy* **sp. nov.** For 16S3', three reads mapped for a mean cover-

age of 0.4× (117 bp); for 16S5', 11 reads mapped for a mean coverage of 0.9× (272 bp). Genetically, the specimen was assigned to the *R. ellae* species group, being the sister lineage to *R. quentini* **sp. nov.** (Fig. 2).

- (10) MNHN 1937.19, the holotype of *R. coudreaui* from the Betampona Reserve in eastern Madagascar. No reads mapped to 16S3' or 16S5', so it could not be included in our analyses. Using a target-enrichment approach in a future study may overcome the shortage of molecular data for this specimen.

Diagnosis of species groups

Each of the six species groups in *Rhombophryne* proposed by Belluardo et al. (2022)—the *Rhombophryne testudo* species group, *R. laevipes* species group, *R. ellae* species group, *R. proportionalis* species group, *R. minuta* species group, and *R. serratopalpebrosa* species group (Fig. 5)—presents apomorphic features or character state combinations that support their recognition (Appendix 1), and projection of the first two principal components of a PCA (Fig. 5A) also reveals that some of these species groups occupy distinct areas of morphospace (e.g., the *R. testudo* group and *R. proportionalis* are distinct from the *R. minuta*, *R. serratopalpebrosa*, and most members of the *R. ellae* and *R. laevipes* species groups, but not from each other; the *R. minuta* group is furthermore distinct from the *R. ellae* group and *R. proportionalis* species group). LDA (Fig. 5B) performed well at distinguishing species groups (accuracy = 89.2%, $\kappa = 0.8595$, $P < 2.2 \times 10^{-16}$),

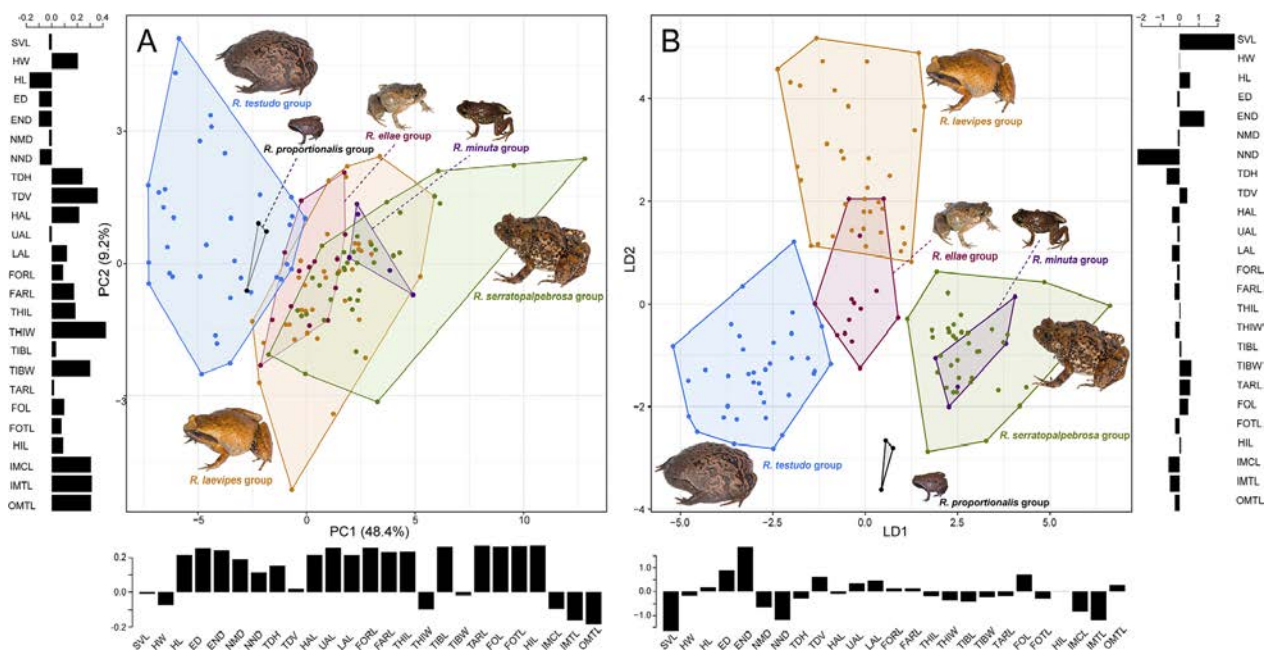


Figure 5. Dimensionality reduction ordinations of *Rhombophryne* morphometrics, coloured by species group. **A** Principal Component Analysis (PCA) with weightings of the two shown principal components (PCs) given as bar plots beside the axes. **B** Linear Discriminant Analysis (LDA) with scaling weights of the two shown Linear Discriminants (LDs) given as bar plots beside the axes. For morphometric abbreviations, see Materials and Methods. Data were filtered to include only adults and remove all individuals with missing data. All described species are included. See Zenodo repository (<https://doi.org/10.5281/zenodo.17247222>), for the morphometric input data.

with the most common misassignments in a leave-one-out cross validation being between the *R. ellae* and *R. laevipes* species groups (five misclassifications), and between the *R. testudo* species group and the *R. ellae* and

R. laevipes species groups (five misclassifications); in a plot of LD1 (weighted most strongly by SVL and END) vs LD2 (weighted most strongly by SVL and NND), most species groups are distinct, but there is partial over-



Figure 6. Morphometric summary of *Rhombophryne* in the form of Tukey's box and whisker plots, coloured by species group. The box represents the first and third quartiles, and the line indicates the median. All measurements are given relative to SVL, except SVL itself (given in mm), and a ratio capturing tympanum shape, TDH/TDV. For abbreviations, see Materials and Methods. Full data are provided in our Zenodo repository (<https://doi.org/10.5281/zenodo.17247222>).

lap between the *R. ellae* and *R. laevipes* species groups, and total overlap between the *R. minuta* and *R. serratopalpebrosa* species groups (but these groups are easily morphologically distinguishable based on the absence vs. presence of superciliary spines).

Extensive work has already been done to characterise the *Rhombophryne serratopalpebrosa* group (Scherz et al. 2015b, 2017a), and we here complement that work by characterising the other species groups with the aim that these units will help us to work on the taxonomy of the genus and especially aid in field identification. A summary of morphometrics among species is shown in Figure 6. A full key to the genus is also provided below.

Rhombophryne testudo species group

Rhombophryne coudreaui, *R. mangabensis*, *R. maraorao* **sp. nov.** (sp. Ca09), *R. matavy*, *R. mavokely* **sp. nov.** (sp. Ca17), *R. savaka*, *R. sp.* Ca16, *R. testudo*

Summary of morphology. A group of small to large (SVL 18.7–45.1 mm), detriticolous to truly fossorial *Rhombophryne* species. All have relatively short limbs and a rather flat and round habitus. Fossorial species (*R. testudo*, *R. matavy*, *R. coudreaui*, and *R. maraorao* **sp. nov.**) lack clavicles entirely. The remaining species are detriticolous and retain clavicles (though reduced in *R. mangabensis*). Skin texture ranges from smooth (*R. mangabensis*) to rugose and tubercular (*R. coudreaui*). Maxillary, premaxillary, and vomerine teeth are present or absent.

Calls. Calls known from all species except *R. coudreaui* and *R. maraorao* **sp. nov.** The call of *R. testudo* is a rather long, deep, pulsed note. That of *R. matavy* is a shorter tonal call, emitted in a series. The calls of *R. mangabensis*, *R. savaka*, and *R. mavokely* **sp. nov.** consist of high-pitched whistles, emitted in series.

Distribution. This group is widely distributed (Fig. 7; Table S4), with members in the north (*R. matavy* and *R. testudo*), northeast (*R. mangabensis*, *R. maraorao* **sp. nov.**, *R. mavokely* **sp. nov.**, *R. savaka*, *R. sp.* Ca16), and east (*R. coudreaui*) of Madagascar.

Ecology. Species found in humid and subhumid tropical forest. Some present on both mainland and off-shore islands.

Rhombophryne laevipes species group

Contents. *Rhombophryne anatalia* **sp. nov.** (sp. Ca01), *R. botabota*, *R. kotrobaratra* **sp. nov.** (sp. Ca10), *R. laevipes*, *R. nilevina* (including sp. Ca03), *R. sonaliae* **sp. nov.** (sp. Ca19), *R. sp.* Ca15

Summary of morphology. A group of large-bodied, detriticolous to terrestrial *Rhombophryne* species. All have

a rotund habitus but less flattened than members of the *R. testudo* species group. This group has the largest body size in the genus (SVL 24.1–57.2 mm). Almost all species have whitish spots on the legs and inguinal region (absent in *R. botabota*, *R. kotrobaratra* **sp. nov.**, and some specimens of *R. nilevina*). Teeth are present on the maxilla, premaxilla, and postchoanal vomer. Clavicles are present. Skin texture is smooth to granular.

Calls. Calls are known from *R. nilevina*, *R. laevipes*, *R. botabota* and *R. sonaliae* **sp. nov.** They consist of single low frequency, pulsed or tonal notes emitted at long intervals.

Distribution. This group is widely distributed (Fig. 7; Table S4), with members in the north (*R. laevipes*, *R. nilevina*), northeast (*R. botabota*, *R. nilevina*, *R. anatalia* **sp. nov.**, and *R. kotrobaratra* **sp. nov.**), and east (*R. nilevina*, *R. sonaliae* **sp. nov.**, *R. sp.* Ca15) of Madagascar.

Ecology. Species found in humid and subhumid tropical forest.

Rhombophryne ellae species group

Rhombophryne ellae, *R. kilonjy* **sp. nov.**, *R. quantini* **sp. nov.** (sp. Ca07)

Summary of morphology. A group of medium-sized (SVL 22.1–30.1 mm), terrestrial or detriticolous *Rhombophryne* species. All have a rotund habitus, very similar to the *R. laevipes* species group. They have bright-orange colouration on the posterior side of the limbs in life, and *R. ellae* and *R. quantini* **sp. nov.** have black inguinal ocelli outlined in white (absent in *R. kilonjy* **sp. nov.**). Teeth are present on the maxilla, premaxilla, and postchoanal vomer. Clavicles are present. Skin texture is granular.

Calls. Unknown.

Distribution. This group is restricted to the north of Madagascar (Fig. 7; Table S4), in Montagne d’Ambre (*R. ellae*), Tsaratànana (*R. quantini* **sp. nov.**), and the Sahamalaza Peninsula (*R. kilonjy* **sp. nov.**).

Ecology. Species found in humid and subhumid tropical forest.

Rhombophryne proportionalis species group

Contents. *Rhombophryne proportionalis*

Summary of morphology. A highly divergent, proportionally miniaturised species (SVL 11.0–12.3 mm), characterised by its small body size, paedomorphic skull with anteriorly displaced mandibular articulation and verticalized lateral elements, and the absence of ossified clavicles. Teeth are present on the maxilla, premaxilla, and

postchoanal vomer; those on the vomer are diminutive. Skin is fairly smooth.

Calls. A trill-like call, consisting of high-pitched tonal notes of short duration emitted in regular call series at regular and fast succession, unlike that of any other known *Rhombophryne* species.

Distribution. This group is currently only known from Tsaratànana (Fig. 7; Table S4).

Ecology. Known only from humid tropical forest in northern Madagascar.

Rhombophryne minuta species group

Contents. *Rhombophryne longicrus*, *R. minuta*

Summary of morphology. A group of small to medium-sized (SVL 16.9–28.0 mm) terrestrial, and likely scansorial, *Rhombophryne* species. Both species have a gracile habitus, long, slender limbs, and lack inguinal markings. Teeth are present on the maxilla, premaxilla,

and postchoanal vomer. Clavicles are present. Skin texture is rather smooth.

Calls. Calls are only known from *R. minuta*. It emits a high-pitched two-pulsed call at regular, long intervals.

Distribution. This group is found only in the northeast (Marojejy, *R. minuta*) and north (Sorata, *R. longicrus*) of Madagascar (Fig. 7; Table S4).

Ecology. Species found in humid high-elevation tropical forest.

Rhombophryne serratopalpebrosa species group

Contents. *Rhombophryne coronata*, *R. diadema*, *R. guentherpetersi*, *R. ornata*, *R. regalis*, *R. serratopalpebrosa*, *R. tany*, *R. sp. Ca13*, *R. sp. 'Ivohibe'*, *R. vaventy*.

Summary of morphology. A group of small to large-sized (SVL 19.4–58.6 mm), mostly terrestrial, possibly semi-detriticolous or even semi-fossorial frogs. They

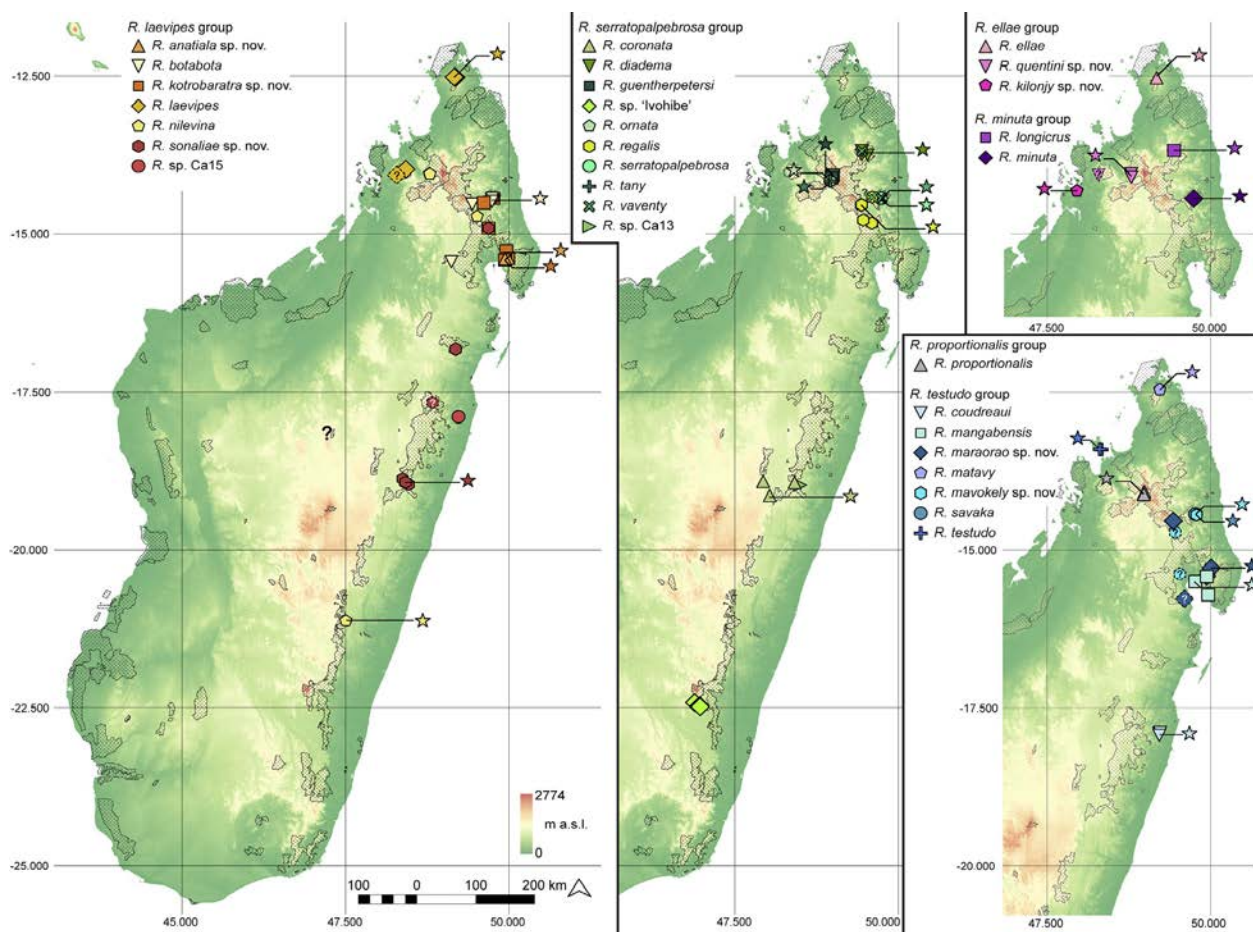


Figure 7. Distribution of *Rhombophryne* species, arranged by species group. Shapes with dotted outlines and question-marks inside them indicate records of referred but unconfirmed specimens. The questionmark beside Ambohitantely Special Reserve (ca 18.17°S, 47.28°E) in the *R. laevipes* species group map refers to an unvouchered photographic record of uncertain species identity requiring further study, included here because it is the only record from Madagascar's central highlands. Basemap is USGS 1-arc second SRTM data. Shaded polygons are outlines of protected areas. Stars represent type localities. For a gazetteer, see Table S4.

have a gracile to rotund habitus. The group is characterised by the possession of superciliary spines (otherwise only present on a few members of the *R. testudo* species group, which however differ strongly in other aspects of morphology, making confusion impossible). Most lack inguinal markings. Teeth are present on the maxilla, premaxilla, and postchoanal vomer. Clavicles are present. Skin texture varies from smooth to rugose.

Calls. Calls are only known from *R. coronata*. It makes a high-pitched short tonal note emitted in regular call series of variable duration. Most calls are composed of two recognizable pulses. Its frequency modulation—containing upward and downward frequency sweeps within each note—is unique among all known *Rhombophryne* calls.

Distribution. This group is widely distributed, with members in the north (*R. guentherpetersi*, *R. ornata*, *R. tany*, *R. diadema*), northeast (*R. serratopalpebrosa*, *R. vaventy*, *R. regalis*), and east (*R. coronata*, *R. sp.* ‘Ivohibe’, *R. sp.* Ca13) (Fig. 7; Table S4) of Madagascar. See Scherz et al. (2017a) for detailed discussion of the biogeography of this clade.

Ecology. Species found in humid and subhumid tropical forest.

Taxonomic treatments

Rhombophryne Boettger, 1880

Type species. *Rhombophryne testudo* Boettger, 1880

Synonymy. *Mantiphrys* Mocquard, 1895. Type species: *Mantiphrys laevipes* Mocquard, 1895.

Definition. A cophyline microhylid frog genus characterised by the following suite of characters: (1) a procoelous vertebral column, (2) knobbed or unornamented terminal phalanges (i.e., not Y- or T-shaped), (3) unexpanded or weakly expanded terminal discs of fingers and toes, (4) presence (very occasional absence) of a curved clavicle, and (5) divided vomer usually bearing teeth on the postchoanal portion.

Diagnosis. Within Madagascar, only *Scaphiophryne*, *Stumpffia*, and *Plethodontohyla* can be confused with *Rhombophryne*. *Scaphiophryne* are stouter and rounder in general, often with expanded terminal discs (vs knobbed or unornamented in *Rhombophryne*), and have an undivided vomer (vs divided into pre- and postchoanal portions). *Stumpffia* have straight or absent clavicles (vs curved or absent), typically lack teeth on the maxillae (vs generally present), lack teeth on the postchoanal vomers (vs generally present). Several members of the genus *Plethodontohyla* are arboreal and can easily be distinguished by presence of Y- or T-shaped terminal phalanges on fingers and toes; terrestrial *Plethodontohyla* can be

distinguished by the combination of absence of clavicles and absence of frontoparietal-nasal contact (vs frontoparietal-nasal contact present in all *Rhombophryne* lacking clavicles) (see also the key provided in the appendices of Scherz et al. 2016b).

Distribution. Limited primarily to the northern half of Madagascar, with the southern-most occurrence in Ivohibe in South Central Eastern Madagascar (*R. sp.* ‘Ivohibe’). Apparently absent from western and southern Madagascar.

Rhombophryne testudo species group

Rhombophryne testudo Boettger, 1880

Figures 2, 4–12

Holotype. SMF 4241 (formerly 1177.2a), an adult female, collected on an unknown date on ‘insula Nossi Bé’ (Nosy Be; approx. coordinates 13.2–13.4°S, 48.2–48.4°E), Diana Region, Madagascar, by Carl Ebenau (erroneously later designated as a lectotype by Mertens 1967) (Figs 8, 9, 11).

Paratypes. None. Boettger (1880a) states explicitly that the species is based on a single specimen.

Referred specimens. Numerous specimens claimed to be syntypes/paralectotypes exist as a result of the erroneous designation of SMF 4241 as lectotype by Mertens (1967). We are not aware of an exhaustive list, but Barbour and Loveridge (1929) stated there were seven in the Museum of Comparative Zoology of Harvard, namely MCZ 2163 (one specimen), 2236 (one), 2731 (three), plus 9317 and 9318 (two). At least one of the specimens in MCZ 2731 was exchanged to the Field Museum of Natural History, where it is archived as FMNH 73363 and incorrectly listed as a ‘co-type’. A further specimen (EHT-HMS 44690, ex-SMF 4267) is listed as present in the type collection of the University of Illinois Museum of Natural History (Phillips 2015). This is also not a type. Four specimens formerly under catalogue number ZMB 10059 (now divided into ZMB 10059 [one specimen] and 51041–51043) were also originally incorrectly included in the catalogue of the Museum für Naturkunde, Berlin as types of *R. testudo*, but this was corrected in the digital catalogue.

We here examined SMF 4247–4263 (16 specimens), which Mertens (1967) incorrectly considered paralectotypes—none of these specimens in fact has type status. Additionally, we examined ZSM 474/2000 (FGMV 2000.276) and ZSM 475/2000 (FGMV 2000.277), two adult specimens of uncertain sex, collected on 11 March 2000 on the east coast of Lokobe National Park (13.4133°S, 48.3342°E, 110 m a.s.l.), Nosy Be, Diana Region, northern Madagascar, by F. Glaw, K. Schmidt, and M. Vences; UADBA-A-FGZC 5620, an adult male, collected on 29 April 2019 on the Kindro trail, Ampa-

sindava (13.4099°S, 48.3051°E, ca 80 m a.s.l.), Lokobe National Park, Nosy Be, Diana Region, northern Madagascar, by F. Glaw, M.D. Scherz, and A. Razafindraibe

(Fig. 10); and ZMB 51041, an adult female, collected in 1887 on Nosy Be (no precise collection data), Diana Region, northern Madagascar, by C. Reuter (originally part



Figure 8. Name-bearing type specimens of species in the *Rhombophryne testudo* species group in dorsal (left) and ventral (right) views. Scale bars = 10 mm.

of ZMB 10059). We further examined photographs of the false ‘syntypes’, MCZ 2163, MCZ 9317, and MCZ 9318, to confirm their identity and morphological agreement with the holotype.

Assignment of specimens. All referred specimens are unambiguously assigned to the species based on their overall morphology (the rotund body, short limbs, and chin barbels are unmistakable) and collection around the type locality. ZSM 475/2000 is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ EU341110/AY594125; 16S5’ EU341110/AY594087; Vieites et al. 2009); a sample from either this specimen or ZSM 474/2000, with the tissue number MV 2000-B59, was used as the reference for COI barcoding (COI KF611596/MH940140; Perl et al. 2014). These specimens cluster in our mitochondrial phylogeny (Fig. 2). Both specimens are included in the RAG1 haplotype network (Fig. 4).

Definition. Type species of the genus *Rhombophryne*. Within the *R. testudo* group, this species is sister to *R. matavy* (Fig. 2; Belluardo et al. 2022). It is characterised by having the following unique suite of characters: (1) medium to large body size, adult SVL 33.0–43.1

mm; (2) head much wider than long (HW/HL 2.00–2.60); (3) small eyes (ED/HL 0.23–0.39); (4) short hindlimbs (HIL/SVL 1.18–1.41); (5) large inner metatarsal tubercle (IMTL/FOL 0.15–0.24); (6) generally pronounced outer metatarsal tubercle; (7) second finger slightly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin rough with converging paravertebral ridges; (10) presence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) highly robust skull with very broad squamosal, maxilla, and posterior process of angulosplenial; (15) clavicles absent; and (16) advertisement call (based on 4 analysed calls by one individual) highly pulsed (162–177 pulses per call), with (17) call duration 823–894 ms, (18) inter-call interval 6071–10186 ms, and (19) dominant frequency 508–524 Hz.

Rhombophryne testudo is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘T’ at site 456, ‘T’ at site 651 and ‘C’ at site 734; in 16S3’, ‘C’ at site 1099, ‘C’ at site 1179, and ‘G’ at site 1216.



Figure 9. Ventral views of hands and feet, and lateral views of head of name-bearing type specimens of members of the *Rhombophryne testudo* species group. Not to scale. * = mirrored for conformity.

Diagnosis. Within the genus *Rhombophryne*, *R. testudo* can easily be distinguished from all other species by the presence of several distinct chin barbels and its fortified skull, and from all species except *R. coudreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** described below by its rotund body. From *R. matavy* it can further be distinguished by its pulsed (vs tonal) advertisement call that is much longer (call duration 823–894 ms vs 161–209 ms), and with a lower dominant frequency (508–524 Hz vs 1588–1688 Hz).

Redescription of the holotype. A specimen in a good state of preservation, quite stiff and hard, somewhat desiccated (Figs 8, 9). Developing eggs evident in a micro-CT scan of the specimen.

Body robust, rhomboid. Head very wide and short, much wider than long (HW/HL 2.45). Eyes small, pupils small, round. Snout obtuse, slightly protruding and rounded in dorsal view, angular in lateral view, with five barbels on it, two slightly above and between the nostrils, two directly below these, and a central one below these over the commissure of the jaws. Canthus rostralis distinct, convex. Loreal region concave, slightly oblique. Nostril openings small, angled anterolaterally, equidistant between tip of snout and eye, slightly protuberant. Tympanum indistinct, vertically oval. TDH/ED 0.827. Supratympanic fold distinct, weakly raised but tubercular and

so uneven in height, forming a gentle curve from the line of the top of the eye over the tympanum, sloping down to the posterior of the top of the arm. Superciliary spines are absent but there is a small light-coloured spot centrally above each eye, with several small tubercles on the dorsal surface of the eye.

The jaw is firmly shut, such that it is impossible to open without damaging the specimen irreparably. The original description described the specimen as lacking maxillary teeth, having small and weak palatal bones (interpreted as the neopalatines), a simple unfringed ‘fold’ on the palate, which is interpreted as being the vomerine ridge, as the species lacks proper vomerine teeth (see Variation below), and having a large tongue that is wider than it is long, attached anteriorly and posteriorly free with a longitudinal furrow but without lateral emargination. Given that the jaw is so tightly shut, it is not clear how this information was obtained.

Forelimbs relatively short and thick, the upper arm hardly distinguishable from the trunk (FARL/SVL 0.397). Fingers without webbing, all short, relative lengths $1 < 2 = 4 < 3$ (Fig. 9). Finger subarticular tubercles indistinct, single, round; inner metacarpal tubercle large, slightly shorter than first finger (IMCL/HAL 0.278); outer metacarpal/palmar tubercle indistinct, single. Hind limb thick, tibiotarsal articulation extent when adpressed anteriorly along the body cannot be assessed due to strong fixa-



Figure 10. *Rhombophryne testudo* in life. Photographed in low-elevation rainforest in Lokobe National Park, Nosy Be. **A–D** adult male UADBA-A-FGZC 5620 in **A** lateral, **B** anterolateral, **C** dorsal, and **D** ventral views.

tion. TIBL/SVL 0.259. Inner metatarsal tubercle present, large, longer than first toe, roughly as long as second toe (IMTL/FOL 0.193). Outer metatarsal tubercle faint. Toes not webbed; first toe distinctly reduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; sub-articular tubercles indistinct, single and round; toe tips not enlarged. Finger and toe tips without circum-marginal grooves (Fig. 9).

Dorsal skin smooth, with numerous tubercles on the flanks and limbs and along the jaw, and especially a number of barbels on the bottom lip. The ventral skin is wrinkled but smooth. Symmetrical converging ridges are present from behind the exoccipital region of the head running toward the cloaca, with a pair of less distinct, less extensive ridges between them from the posterior head to roughly the level of the suprascapulae.

After at least 137 years in preservative, the colouration of the specimen is still brown and does not appear to have faded except perhaps in a blemished area on the right side of the dorsum at roughly the level of the ilia. The brown base colour has darker-brown symmetrical markings, which consist of a chevron running from the medial inguinal region to the centre of the dorsum and two dark irregular patches posterior to the suprascapular region. The tubercles and digits of the hands and feet are cream, and there is a fine cream line defining the fold between the dorsal and ventral posterior thigh. A single dark brown crossband is present on the shank, one on the tarsus, and one on the lateral foot that matches with that of the shank when the leg is fully folded. The ventral colour is as the dorsum, but lighter brown over the chin and with a curious translucent spot on the

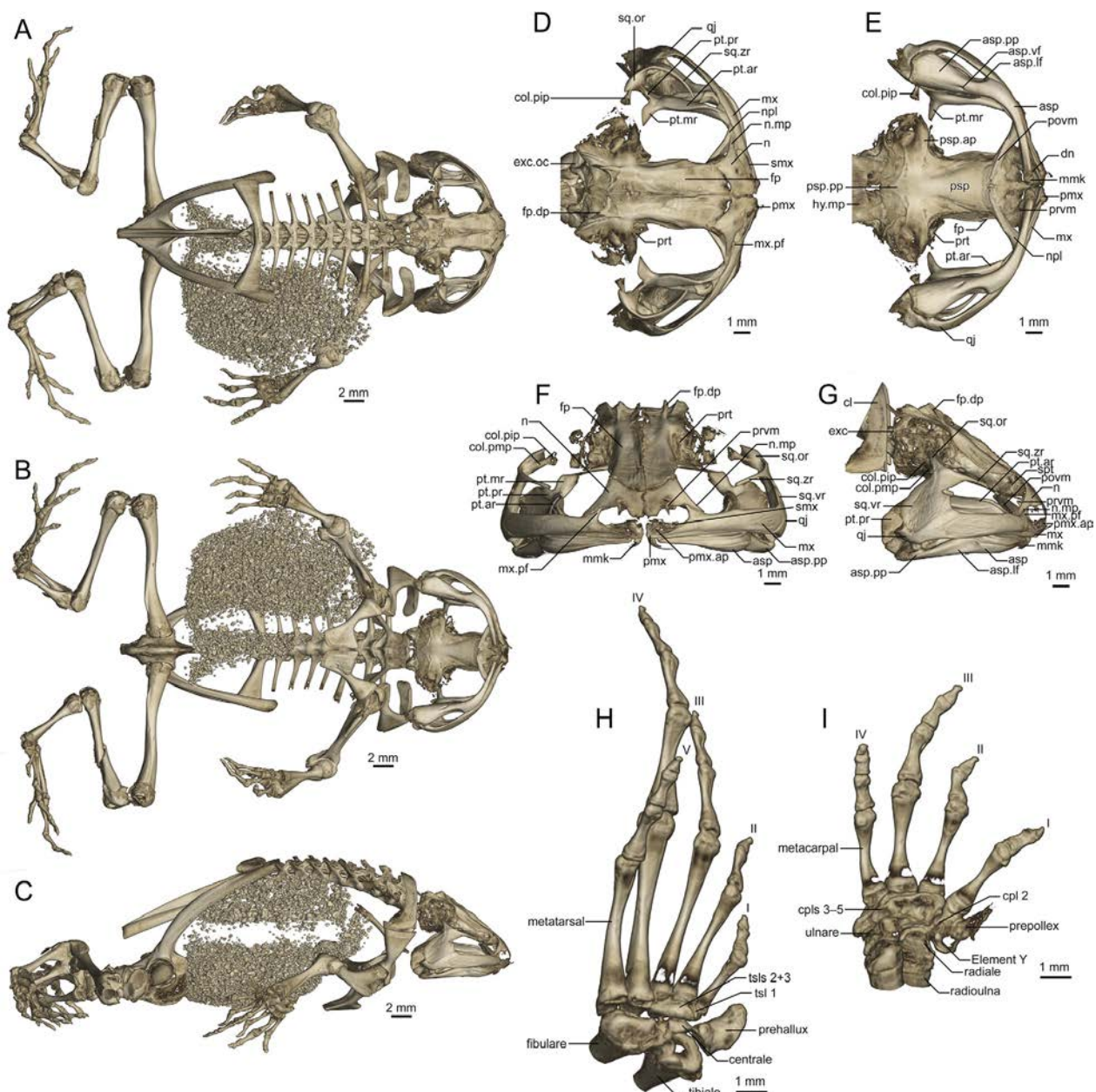


Figure 11. Skeleton of *Rhombophryne testudo* holotype SMF 4241. **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** are apparently dense soil, sand, and stones. Abbreviations are given under Materials and Methods.

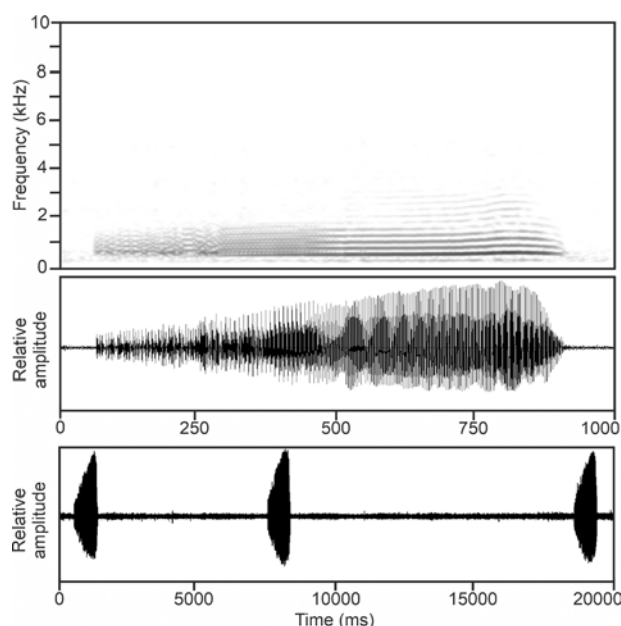


Figure 12. Advertisement calls of *Rhombophryne testudo*, recorded on Nosy Be in 1992. Top: audiospectrogram and corresponding oscillogram of one advertisement call at 1000 ms time scale. Bottom: oscillogram at 20000 ms time scale showing pattern of call repetition (three calls). Recording high-pass filtered at 175 Hz.

ventral abdomen. The colour of the specimen in life is unknown.

Variation. SVL 33.0–43.1 mm ($n = 18$); full measurements are presented in Table S5. Most specimens could not be sexed because we did not have permission to dissect them, and the jaws of most specimens were so firmly fixed shut that we could not open the mouth and search for traces of vocal slits. Overall morphology is highly consistent. The tongue is broad and disc-like, posteriorly free. Maxillary teeth are absent. The vomerine teeth ridges form two straight transversal rows posterior to the rounded choanae, not meeting medially. The second and fourth fingers can vary in which is longer. There is a little variation in colouration, with some individuals uniformly brown in dorsal colour and others with dark-brown markings (e.g., Fig. 10).

Call. The advertisement call recorded in January or February 1992 at Nosy Be (air temperature unknown) consists of a long, pulsed note emitted at irregular intervals (Fig. 12); calls are not arranged in call series. Pulses within calls are generally narrowly spaced and partly fused, but pulse repetition is distinctly faster in the second half of each call and results in respective parallel frequency bands reflecting pulse rate. Amplitude within calls is constantly increasing from the beginning towards the end where it drops to zero quickly. Numerical parameters of 4 analysed calls are as follows: call duration (= note duration) 823–894 ms (854 ± 30 ms); inter-call intervals 6071–10,186 ms (8370 ± 2100 ms); pulses per call 162–177 (169 ± 7); pulse repetition rate within first half of call approximately 135 pulses/second, within second half

approximately 280 pulses/second; dominant frequency 508–524 Hz (519 ± 7 Hz); prevalent bandwidth 500–3200 Hz. Calls from the same recording (Vences et al. 2006, CD 3, track 33) have been described by Glaw and Vences (1992), D’Cruze et al. (2010), and Lambert et al. (2017) using slightly different terminological schemes.

Etymology. Feminine nominative Latin noun meaning ‘turtle’ or ‘tortoise’, presumably in reference to the short limbs and rotund body shape of this species.

Distribution. Confirmed from (1) Nosy Be (type locality), and (2) Nosy Komba (Glaw and Vences 1992; Andreone et al. 2003; Hyde Roberts and Daly 2014). Elevation: 0–450 m a.s.l. (the peak of Mt Lokobe on Nosy Be).

Records from Réunion (Guibé 1978) resulted from a clerical error when information were being copied from one catalogue to another, and were corrected by Glaw and Vences (2002). A record from ‘Imerina’ by Parker (1934) is based on BMNH 1895.10.29.30, collected by Richard Baron. The location Imerina could refer to anywhere across the high plateau of central Madagascar (the area where Baron served as a reverend; Laurence 1987). Baron was one of the most widely travelled explorers of that time, and the lack of precise collection date means that refinement of locality is challenging. However, it should be noted that Baron undertook an enormous journey from central-eastern Madagascar, along the coast north to Antsiranana, and then down the west coast to Nosy Be (a journey of almost 2000 km), collecting plants along the way (JSTOR Global Plants correspondence KADC2664 from Library and Archives at Royal Botanic Gardens, Kew). It is therefore conceivable that the location is an error; that Baron collected the specimen in Nosy Be at the end of his journey and sent it along with the consignment of plants to London. Examination of this specimen revealed it to be an adult male. It does not have any evident morphological differences from other *R. testudo* specimens. However, as stated above, a museumic sample of this specimen confirmed it to have moderately strong genetic differentiation from other *R. testudo* specimens. A BLASTn search of every contig in NCBI, however, consistently identified *Rhombophryne testudo* ZSM 475/2000 as closest match, and with a sequence coverage of 4.9× and 2.9× for 16S3 and 16S5, respectively, it remains possible that a genetically divergent lineage is present in Imerina (or at some other location along Baron’s travel routes), which would be in need of re-discovery to verify. Records from Marojejy and Andapa-Sambava (Guibé 1978; Blommers-Schlösser and Blanc 1991; probably deriving from the same specimen, see Glaw and Vences 2002) referred to *R. coudreaui* by Andreone and Randrianirina (2008), but are here referred to *R. maraorao* sp. nov., described below.

Natural history. *Rhombophryne testudo* is a fossorial species found in primary and secondary low-elevation humid forest, where it inhabits burrows 5–10 cm deep beneath the leaf litter (Glaw and Vences 1994). Calls are emitted from January to April, at highest intensity before

and during heavy rain, irrespective of the time of day (Glaw and Vences 1994). Calling can occur without rain, but a series of two or three calls is then followed by a long pause of several minutes (Glaw and Vences 1994). Köhler et al. (1997) reported finding a 10 cm wide, 15 cm deep nest beneath a rock beside a small creek, containing two adults and 18 juveniles measuring 9–11 mm in SVL, in December 1995. This suggests development occurs in subterranean burrows with parental care, perhaps by both parents (Köhler et al. 1997). No tadpoles or eggs of the species have yet been observed.

A defensive behaviour is known wherein specimens stretch their hindlimbs to prevent them being turned onto their backs (Glaw and Vences 1994). We have also observed individuals puff themselves up significantly when caught, presumably to make them more difficult to swallow—common behaviours in burrowing microhylid frogs.

Keefe and Blackburn (2020) compared the humerus of *Rhombophryne testudo* to other burrowing frogs. They noted its similarity to forward-burrowers, suggesting that it may also be able to burrow forwards, but highlighting the need for behavioural observations of this species.

The gut of the holotype contains a great deal of soil, as evident from our micro-CT scans (Fig. 11). We examined the contents of the digestive system of an adult female specimen (with well-developed eggs), ZMB 51041. The stomach contained mostly detritus, especially tiny fragments of wood and leaves. Fragments of two insects were present in this detritus: the 4.7 mm abdomen of a small rove beetle (Staphylinidae), and the thorax and partial abdomen of an ant. The intestines contained mostly a fine mud with tiny fragments of wood and leaf, the head of an ant, and the thorax and head of the same rove beetle. By volume, the vast majority of gut contents was non-animal material. This suggests that most of the ingested matter of these frogs might be substrate, not insects. Although unlikely, more ecological research is needed to understand if these animals may be partly detritivorous or geophagous. However, it is more likely that insect larvae, annelid worms, or other soft-bodied organisms are the primary prey of these frogs, and are digested quickly and thus absent from the digestive system of preserved frogs.

Karyotype. The karyotype of this species was described by Aprea et al. (2007), with $2n = 26$ largely metacentric chromosomes (second and third pairs submetacentric, fourth pair subtelocentric/telocentric). Nucleolar organiser regions were in a pericentromeric position on the short arm of the second chromosome pair. Heterochromatin was indistinct, and Chromomycin A₃ (CMA₃) and 4',6-diamidino-2-phenylindole (DAPI) negative, i.e., lacking particularly GC- or AT-rich regions.

Rhombophryne coudreaui (Angel, 1938)

Figures 2, 4–9, 13, 14

Plethodontohyla coudreaui Angel, 1938

Rhombophryne coudreaui — Frost et al. (2006)

Holotype. MNHN 1937.19, an adult female, collected in January 1937 from ‘Réserve de Betampona (forêt orientale, près de Moramanga, à mi-chemin, entre Tamatave et Tananarive)’ (Angel 1938: 261), today the Réserve Naturelle Intégrale de Betampona, Antsinanana Region, eastern Madagascar (approx. coordinates 17.9°S, 49.2°E), by M. Coudreau (Figs 8, 9, 14).

Paratypes. None.

Referred specimens. MRSN A6280 (FAZC 13600), an unsexed adult, collected on 12 February 2007 at Sahambendrana (17.8984°S, 49.2154°E, 458 m a.s.l.), Betampona Strict Nature Reserve, Antsinanana Region, eastern Madagascar, by G. de Sousa Miranda Rosa and F. Andreone (Fig. 13A–C); MRSN A6347 (FAZC 13887), an adult male, collected on 17 November 2007 at Maintimbato (17.8940°S, 49.2283°E, 255 m a.s.l.), Betampona Strict Nature Reserve, Antsinanana Region, eastern Madagascar, by G. de Sousa Miranda Rosa, F. Andreone, and J. Noel; MRSN A6267 (FAZC 13624) and MRSN A6271 (FAZC 13653; Fig. 13D–G), two unsexed individuals, collected on 19 February 2007 at Maintimbato (17.8940°S, 49.2283°E, 255 m a.s.l.), Betampona Strict Nature Reserve, Antsinanana Region, eastern Madagascar, by G. de Sousa Miranda Rosa.

Assignment of specimens. The specimen MRSN A6347 is used as the reference specimen for this species in 16S rRNA barcoding (16S3' FJ559299/HM364772; Vieites et al. 2009). All referred material agrees morphologically with the holotype, and is topotypical. Assignment of MRSN A6271, MRSN A6267 and MRSN A6280 is further confirmed by molecular taxonomic identification (Fig. 2). An additional tissue sample from a topotypical individual (not collected), DLR 550 (tissue number ACZC 7731) is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. testudo* group, this species is sister to *R. maraorao* **sp. nov.** (described below) based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small to medium body size, adult SVL 21.5–26.4 mm; (2) head much wider than long (HW/HL 1.65–1.85); (3) small eyes (ED/HL 0.29–0.31); (4) short hindlimbs (HIL/SVL 1.17–1.30); (5) large inner metatarsal tubercle (IMTL/FOL 0.15–0.18); (6) generally indistinct outer metatarsal tubercle; (7) second finger equal in length to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin rough to rugose with converging longitudinal rows of tubercles; (10) presence of few, small chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) broad but not fortified skull, without expansion of squamosal, maxilla, or posterior process of angulosplenial; and (15) clavicles absent.

Rhombophryne coudreaui is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the

mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'C' at site 259, and 'T' at site 329 and 'T' at site 348. No diagnostic sites were identified for 16S3'.

Diagnosis. Within the genus *Rhombophryne*, *R. coudreaui* can easily be distinguished from all other species except *R. testudo*, *R. matavy*, and *R. maraorao* **sp. nov.** described below by its flattened, rotund body and short, broad head. Among these species, see the account of *R. testudo* above for distinction from that species; it can be distinguished from *R. matavy* by smaller body size (SVL 21.5–26.4 mm vs 40–50 mm), rougher dorsal skin, and less fortified skull; for distinction from *R. maraorao* **sp. nov.**, see the description of that species, below. *Rhombophryne coudreaui* may also differ from all other *Rhom-*

bophryne species by the absence of carpal 2 in the hand (vs presence); see the 'Osteology of the *Rhombophryne testudo* species group' below for discussion.

Redescription of the holotype. A specimen in a mediocre state of preservation, with its arms and legs stretched straight and several broken bones (Figs 8, 9, 14; see osteology, below). An incision made along the left flank makes ova visible and has torn the stomach, which evidently contains the remains of some arthropods, but which we have not emptied.

Body robust and rotund, stout. Head very wide and short, much wider than long (HW/HL 1.72). Eyes small, pupils round. Snout rounded in dorsal view, rounded in lateral view. A few small chin barbels. Canthus rostralis distinct, concave. Loreal region concave, slightly

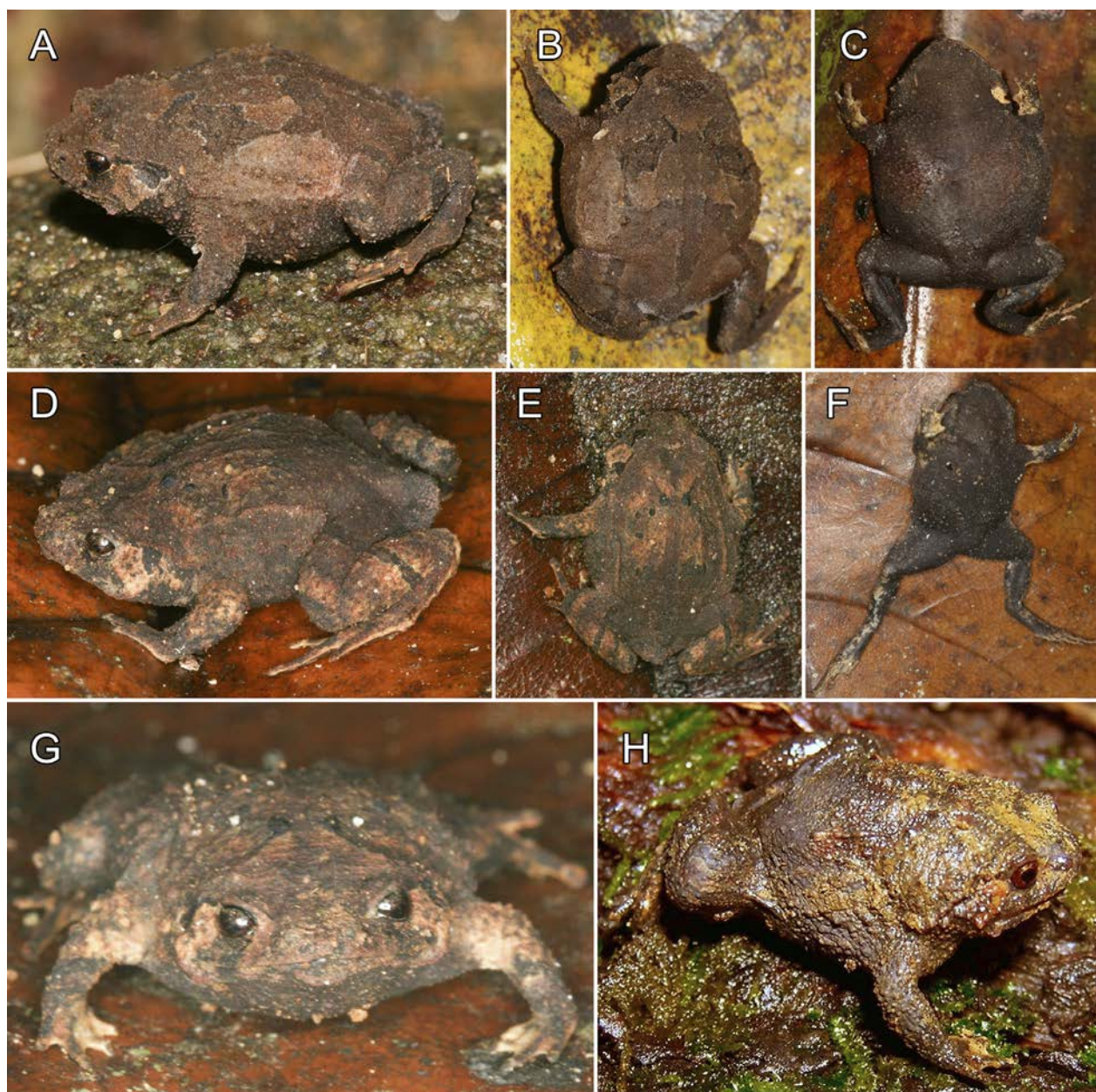


Figure 13. *Rhombophryne coudreaui* in life, all photographed in Betampona. **A–C** unsexed adult MRSN A6280 (FAZC 13600) in **A** dorsolateral, **B** dorsal, and **C** ventral view. **D–F** unsexed adult MRSN A6271 (FAZC 13653) in **D** dorsolateral, **E** dorsal, **F** ventral, and **G** anterior view. **H** unsexed individual (assignment to a specimen uncertain) in dorsolateral view.

oblique. Nostril openings small, angled laterally, closer to tip of snout than to eye, slightly protuberant. Tympanum indistinct, round. TDH/ED 0.824. Supratympanic fold distinct, raised, from posterior corner of eye straight over tympanum, then slightly curving downward. There are a few tiny bumps above each eye, which do not form distinct superciliary spines. Maxillary and vomerine teeth present, vomerine teeth distinct, each straight row bearing a diastema in its middle, separated from the contralateral at the midline by a small gap. Choanae oblong. Tongue very broad, round, attached anteriorly, posteriorly free.

Forelimbs relatively short and thick, the upper arm hardly distinguishable from the body cavity (FARL/SVL 0.321). Fingers without webbing, all short, relative lengths $1 < 2 = 4 < 3$. Finger subarticular tubercles distinct, large and flat; inner metacarpal tubercle large (IMCL/HAL 0.289); outer metacarpal/palmar tubercle paired. Hind limb thick, tibiotarsal articulation extent when addressed

anteriorly along the body cannot be assessed due to the many broken bones in the legs. TIBL/SVL 0.302. Inner metatarsal tubercle present, large (IMTL/FOL 0.178). Outer metatarsal tubercle absent. Toes not webbed; first toe strongly reduced, second toe moderately reduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles indistinct, single and round; toe tips not enlarged.

The dorsal skin is rather rough, with notable tubercles outlined in dark brown above the suprascapular and sacral regions. The ventral skin is as rough as the dorsal. Along the lower lip there are a series of small barbels, especially two on either side of the medial symphysis a little behind the line of the jaw.

After at least 83 years in preservative, the colouration of the specimen is pale creamy brown, with darker areas on the forearms and the areas of the body that are covered in the fixed specimen, such as the axillae. The ventral sur-

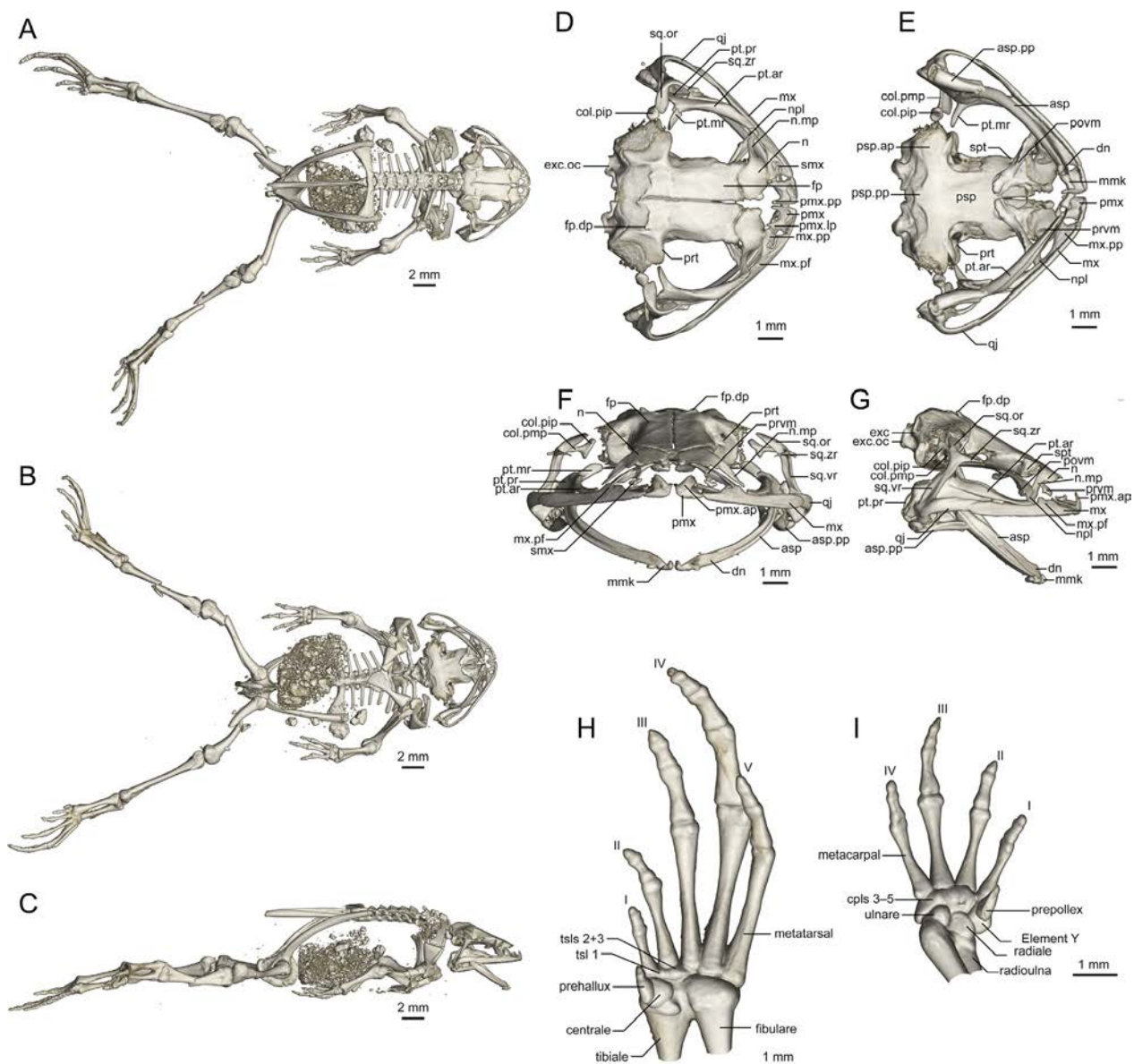


Figure 14. Skeleton of *Rhombophryneoudreaui* holotype MNHN 1937.19. **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** left foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** are apparently dense soil and stones. Abbreviations are given under Materials and Methods.

face is a more homogeneous light brown. Distinctive dark brown markings surround the tubercles on the suprascapular and sacral regions, but otherwise the dorsum is rather homogeneous in colour. The hindlimbs have lost most colouration, but a distinctive cream tubercle surrounded in brown is present on each shank. The forelimbs are ventrally dark brown on the lower arm, with a brown cross-band anteriorly; pale and indistinctly patterned on the upper arm. The colour of the specimen in life is unknown.

Variation. SVL 21.5–26.4 mm ($n = 5$); full measurements are presented in Table S5. The base colouration of all recently collected specimens is a dark chocolatey brown (see Fig. 13 for an idea of colour variation in life). Much of the body patterning is consistent, especially the dark suprascapular spots which define the short edge of a trapezium where the eyes mark the long edge. MRSN A6271 has a chin marbled with cream and also has cream spots on its anterior thigh and interior shank; no other examined specimen shares these patterns.

Call. The call of this species is not known.

Etymology. Eponym for Mr. Coudreau, ‘Conservateur des Réserves naturelles de Madagascar’ (Angel 1938).

Distribution. This species is confined to low-elevation forests in eastern Madagascar, and is with certainty known only from (1) Réserve Naturelle Intégrale de Betampona (type locality), where it has been found at Sahambendrana, Maintimbato and Sahaindrana (Rosa et al. 2012) as well as at Sahabefoza (17.9142°S, 49.2078°E, 353 m a.s.l.). However, S. Andrianarivo provided MDS photographs clearly assignable to this species from (2) Ampasina, a highly degraded forest just 8 km east of Betampona (17.918°S, 49.323°E, ca 80 m a.s.l.), taken on 2 October 2022. This indicates that the species is present and may be able to persist in strongly anthropogenically altered forest. Elevation: ca 80–200 m a.s.l.

The record from Ambolokopatrika-Betaolana (Andreone 2003) unambiguously refers to *R. maraorao* **sp. nov.** (described below), as it is based on the type material of that species. The specimen MNHN 1973.576 from Marojejy in the northeast of Madagascar was assigned to *R. coudreaui* by Andreone and Randrianirina (2008), but the material used for comparison to *R. coudreaui* was also from the northeast and is described as a new species, *R. maraorao* **sp. nov.**, below. Based on the locality of this specimen and its apparent affinity with *R. maraorao* **sp. nov.**, we consider it likely that MNHN 1973.576 is referable to that species, and therefore remove Marojejy from the locality record of *R. coudreaui*. The same applies also to other records from Marojejy (Raselimanana et al. 2000) and Maroantsetra (IUCN SSC Amphibian Specialist Group 2016d).

Natural history. *Rhombophryne coudreaui* is a fossorial species restricted to low-elevation humid forest that is seldom encountered and poorly known. This species exhibits a death-feigning behaviour beyond normal ton-

ic immobility wherein it straightens and stiffens all four limbs (Fig. 13F). One specimen was found at Sahaindrana campsite (Betampona Strict Nature Reserve) walking on the leaf litter in the early hours of the morning (around 6 am). Two individuals were found underneath wet leaf litter and rotten logs in almost-closed-canopy humid forest on the ridge at 460 m at 10:40 am in Sahabefoza.

Rhombophryne matavy D’Cruze, Köhler, Vences & Glaw, 2010

Figures 2, 4–9, 15–17

Plethodontohyla matavy — Peloso et al. (2016), ex-error due to sample confusion

Rhombophryne matavy — Scherz et al. (2016b)

Remark. This species is only known from the type series.

Informal names. This species was listed as ‘*Rhombophryne* **sp. nov.**’ by D’Cruze et al. (2008), and ‘*Rhombophryne* sp. 8’ by Vieites et al. (2009).

Holotype. ZSM 1628/2008 (FGZC 1888), an adult male, collected on 27 February 2008, in Forêt d’Ambre Special Reserve (now part of Montagne d’Ambre National Park) (12.4628°S, 49.2233°E, 482 m a.s.l.), Diana Region (part of former Antsiranana Province), northern Madagascar, by N. D’Cruze, F. Glaw, J. Köhler, and local guides (Figs 8, 9, 15, 16).

Paratypes. Three specimens: ZSM 1629/2008 (FGZC 1889), UADBA-A-FGZC 1890, and UADBA-A-FGZC 1891, three adult males with the same collection data as the holotype except that UADBA-A-FGZC 1891 was collected on 28 February 2008.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ FJ559298; Vieites et al. 2009) and COI barcoding (COI KF611589; Perl et al. 2014). All paratypes agree morphologically with the holotype, and are topotypical. Assignment of UADBA-A-FGZC 1890 is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 1628/2008 is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. testudo* group, this species is sister to *R. testudo* based on molecular phylogenetic data (Fig. 2; Belluaro et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) large body size, adult SVL 40–50 mm (see ‘Variation’ below for discussion of these values); (2) head much wider than long (HW/HL 1.88–2.05); (3) small eyes (ED/HL 0.24–0.28); (4) short hindlimbs (HIL/SVL 1.17–1.25); (5) large inner metatarsal tubercle (IMTL/FOL 0.21–0.26); (6) pronounced outer metatarsal tubercle; (7) second finger rough equal in length to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin with scattered



Figure 15. *Rhombophryne matavy* in life, all photographed in the Forêt d'Ambre parcel of Montagne d'Ambre National Park. **A**, **B** adult male holotype ZSM 1628/2008 (FGZC 1888) in **A** anterolateral view while calling, and **B** anterodorsolateral view; **C**, **D** an adult male, probably a paratype in the UADBA collection, in **C** anterodorsolateral and **D** ventral view. **E–G** an adult male, probably a paratype in the UADBA collection in **E** anterodorsolateral, **F** ventral, and **G** closeup anterior view. Notice the lack of distinct chin barbels.

warts and ridges; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) broad and slightly fortified skull, but without expansion of maxilla or posterior process of angulosphenial; and (15) clavicles absent; and (16) advertisement call (based on 15 analysed calls by one individual) tonal, with (17) call duration 161–209 ms, (18) inter-call interval 267–353 ms, and (19) dominant frequency 1588–1688 Hz.

Rhombophryne matavy is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'T' at site 474, 'T' at site 475, and 'C' at site 538;

in 16S3', 'A' at site 1018, 'C' at site 1072, and 'T' at site 1078.

Diagnosis. Within the genus *Rhombophryne*, *R. matavy* can easily be distinguished from all other species except *R. testudo*, *R. coudreaui*, and *R. maraorao* **sp. nov.** described below by its rotund body and short, broad head. Among these species, see the accounts of *R. testudo* (its sister species) and *R. coudreaui* above for distinction from those species; for distinction from *R. maraorao* **sp. nov.**, see the description of that species, below.

Variation. Adult male SVL 44.6–45.1 mm ($n = 2$); full measurements are presented in Table S5. D'Cruze et al. (2010) measured the same specimens and reported their SVLs to be substantially larger (46.7–47.6 mm).

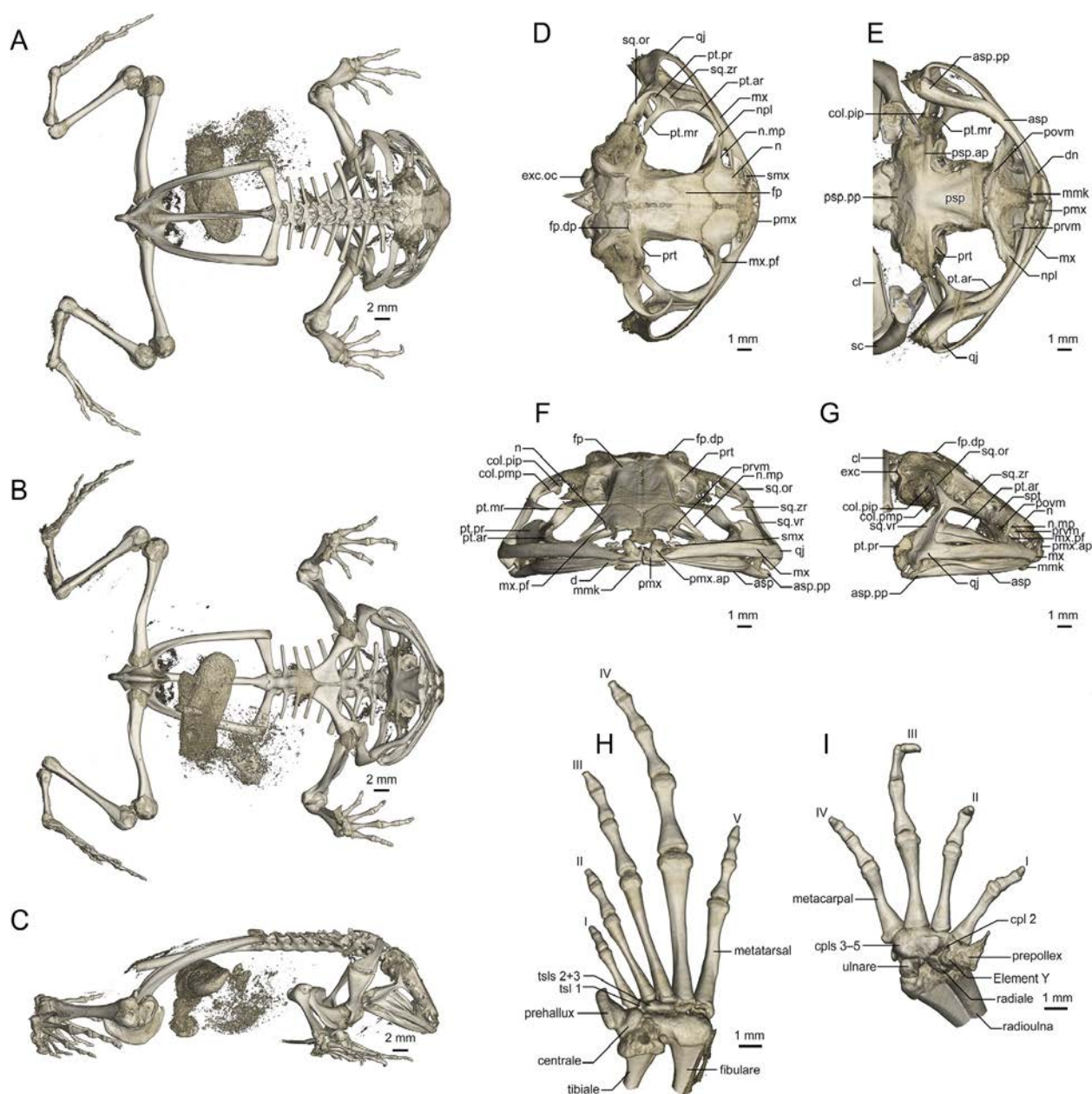


Figure 16. Skeleton of *Rhombophryne matavy* holotype ZSM 1628/2008 (FGZC 1888). A–C Whole skeleton in A dorsal, B ventral, and C lateral view; D–G skull in D dorsal, E ventral, F anterior, and G lateral view; H left foot in ventral view; I right hand in ventral view. Gut contents in A–C are apparently dense soil and stones. Abbreviations are given under Materials and Methods.

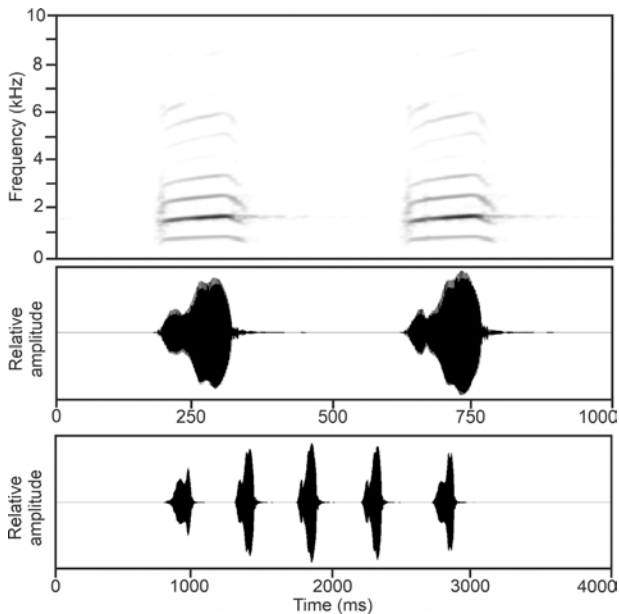


Figure 17. Advertisement calls of *Rhombophryne matavy* (ZSM 1628/2008, holotype), recorded in Forêt d'Ambre Special Reserve (now part of Montagne d'Ambre National Park) in 2008. Top: audiospectrogram and corresponding oscillogram of two advertisement calls from a regular call series at 1000 ms time scale. Bottom: oscillogram at 4000 ms time scale depicting a regular call series containing five calls.

The reason for the discrepancy in measured size is not clear. D'Cruze et al. (2010) also measured two paratypes, UADBA-A-FGZC 1890 and 1891, as 39.4 and 49.4 mm, respectively. For this reason, we have given the SVL in the diagnosis above as between 40 and 50 mm.

Call. The advertisement call of the holotype (ZSM 1628/2008), recorded on 27 February 2008 at Forêt d'Ambre Special Reserve (air temperature unknown), consists of a tonal note of moderate duration emitted in regular call series containing 5 calls repeated at regular succession ($n = 3$; Fig. 17). Each call exhibits considerable amplitude modulation, with highest energy present at approximately the last third of the call's duration. Slight upward frequency modulation is evident in each call, followed by a fast terminal drop in frequency. Numerical parameters of 15 analysed calls are as follows: call duration (= note duration) 161–209 ms (183 ± 14 ms); inter-call intervals within regular call series 267–353 ms (299 ± 22 ms); number of calls per call series 5 (5.0 ± 0.0); duration of regular call series 2091–2202 ms (2130 ± 48 ms); dominant frequency 1588–1688 Hz (1652 ± 16 Hz); prevalent bandwidth 750–6800 Hz; frequency bands recognizable at approximately 880, 2500, 3360, 4160, 5060, and 5840 Hz. Calls from the same recording have been described by D'Cruze et al. (2010) using a slightly different terminological scheme.

Etymology. The Malagasy adjective *matavy* meaning 'fat', in reference to the body shape of the species, especially when inflated (D'Cruze et al. 2010). Used as an invariable noun in apposition.

Distribution. This species is only known from (1) the low-elevation parcel of forest in Montagne d'Ambre National Park, formerly known as Forêt d'Ambre Special Reserve (type locality). Elevation: ca 482 m a.s.l.

Natural history. *Rhombophryne matavy* is a fossorial species found in low-elevation humid forest; its ecology is poorly known, but presumably much like its sister species, *R. testudo*. Highest calling activity (in choruses) was noticed during and just after rain, and the specimens were collected at night, mostly up to 5 cm deep in the leaf litter, though one was found active on top of it (D'Cruze et al. 2010). D'Cruze et al. (2010) noted a defensive behaviour involving the stretching of the limbs and arching the back, like *R. testudo*. They reported the faeces of one individual (ZSM 1628/2008) to include the remains of several insects, including beetles.

Rhombophryne mangabensis Glaw, Köhler & Vences, 2010

Figures 2, 4–9, 18–20

Rhombophryne minuta [partim] – Glaw and Vences (1992)

Remark. This species was referred to as *R. minuta* by Glaw and Vences (1992), where its call and morphology were first described.

One sequence belonging to this species, KU724182 in GenBank, is erroneously ascribed to collection number ZCMV 891 (corresponding to ZSM 463/2005, a *Platyplelis grandis*); the actual *R. mangabensis* specimen to which this sequence belongs is ZCMV 890.

Informal names. The call was published as '*Plethodon-tohyla* sp. (Nosy Mangabe)' by Vences et al. (2006). This species was listed as '*Rhombophryne* sp. aff. *minuta*' by Glaw and Vences (2007), as '*Rhombophryne* sp. 2 Nosy Mangabe' by Wollenberg et al. (2008), and as '*Rhombophryne* sp. 5' by Vieites et al. (2009).

Holotype. ZSM 470/2005 (ZCMV 886), an adult male, collected on 22 February 2005 on 'Nosy Mangabe island' (ca 15.50°S, 49.77°E, ca 50–100 m a.s.l.), Analanjirofo Region, northeastern Madagascar, by F. Glaw, R.D. Randrianaiaina, and M. Vences (Figs 8, 9, 19).

Paratypes. Eight specimens: ZSM 471/2005 (ZCMV 2118), ZSM 472/2005 (ZCMV 2154), UADBA-A-ZCMV 2119, and UADBA-A-ZCMV 890, three adult specimens (probably males) and one subadult, with the same collection data as the holotype (Fig. 18A–C); ZFMK 52769–52771, three adult males, and ZFMK 52772, one subadult specimen, all collected on 13 March 1991 at the type locality, by F. Glaw and M. Vences (ZFMK 52769 is shown in Fig. 18D).

Referred specimens. ZSM 1573/2009, a subadult, collected in May/June 2003 on Nosy Mangabe (15.4959°S,

49.7693°E), Analanjirofo Region, northeastern Madagascar, by N. Lutzmann; ZSM 262/2016 (FGZC 5417), an unsexed adult, collected on 10 August 2016 near the ‘Eco-Lodge chez Arol’ (ca 15.712°S, 49.964°E, 21 m a.s.l.), Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by F. Glaw, D. Prötzel, J. Forster,

K. Glaw, and T. Glaw; MRSN A2557, an unsexed adult, collected on 8 February 2002 at ‘Camp 2’ Mahalevona (ca 15.4178°S, 49.9410°E, ca 669 m a.s.l.), Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by J.E. Randrianirina; UADBA-A-APR12051 (Fig. 18E), an unsexed specimen, collected on 25 November



Figure 18. *Rhombophryne mangabensis* in life. **A, B** probably paratype UADBA-A-ZCMV 890 from Nosy Mangabe in **A** dorsolateral and **B** ventral view. **C** paratype ZSM 471/2005 (ZCMV 2118), adult presumed male from Nosy Mangabe, in dorsolateral view. **D** paratype ZFMK 52769, adult male from Nosy Mangabe, in dorsolateral view. **E** UADBA-A-APR12051, unsexed adult from Ambohitsitondroina, Masoala National Park, in dorsolateral view, photographed on 25 November 2015.

2015 at Ambohitsitondroina (15.5694°S 50.0034°E, 609 m a.s.l.), Masoala National Park, Analanjirofo Region, northeastern Madagascar, by A. Raselimanana.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S3' EU341109/KU724181; 16S5' EU341109; Vieites et al. 2009) and COI barcoding (COI KF611588/KU937775; Perl et al. 2014). All paratypes and referred specimens conform well with the holotype in morphology. The paratypes are all topotypical. Assignment of specimens ZSM 471/2005, UADBA-A-ZCMV 2119, MRSN A2557, and ZSM 262/2016 is further confirmed by molecular taxonomic identification (Fig. 2). MRSN A2557 and ZSM 262/2016 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. testudo* group, this species is sister to *R. savaka* based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small body size, adult SVL 19.6–23.2 mm; (2) head wider than long (HW/HL 1.60–1.86); (3) moderately small eyes (ED/HL 0.34–0.38); (4) short hindlimbs (HIL/SVL 1.54–1.60); (5) small inner metatarsal tubercle (IMTL/FOL 0.09–0.12); (6) indistinct outer metatarsal tubercle; (7) second finger roughly equal in length to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular with a few scattered warts, especially a suprascapular pair outlined in black; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull

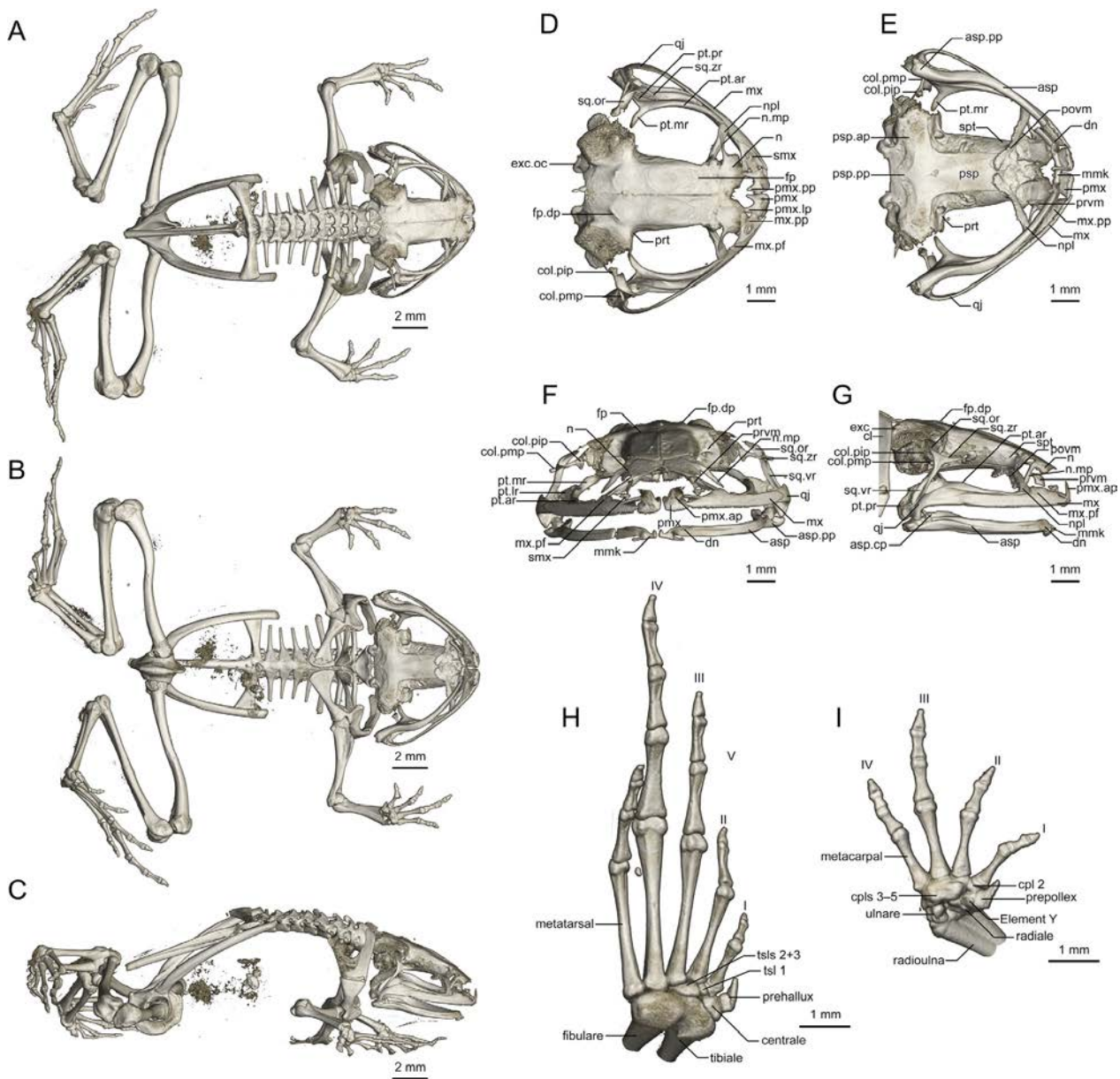


Figure 19. Skeleton of *Rhombophryne mangabensis* holotype ZSM 470/2005 (ZCMV 886). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** are apparently dense soil and small stones. Abbreviations are given under Materials and Methods.

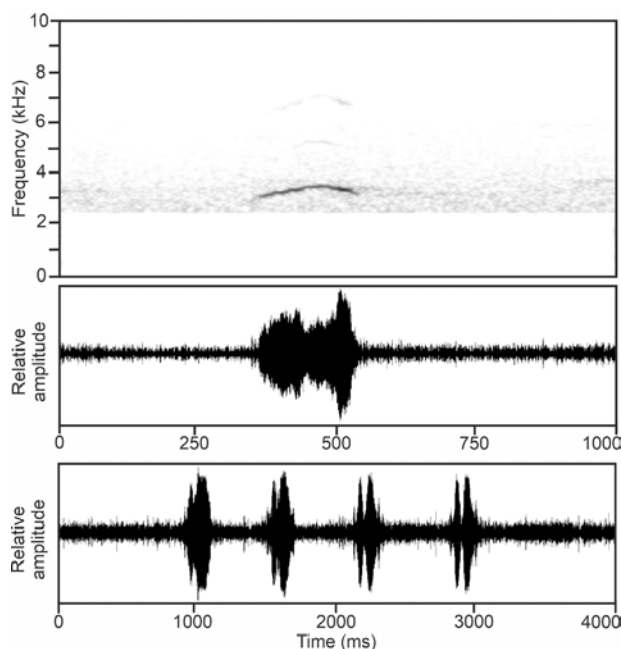


Figure 20. Advertisement calls of *Rhombophryne mangabensis*, recorded on Nosy Mangabe in 1991. Top: audiospectrogram and corresponding oscillogram of one advertisement call from a regular call series at 1000 ms time scale. Bottom: oscillogram at 4000 ms time scale depicting a regular call series containing four calls. Recording high-pass filtered at 2500 Hz.

without expansion of maxilla or posterior process of angulosphenial; (15) clavicles reduced, thin, curving; and (16) advertisement call (based on 20 analysed calls by one individual) tonal, with (17) call duration 180–237 ms, (18) inter-call interval 419–822 ms, and (19) dominant frequency 3300–3550 Hz.

Rhombophryne mangabensis is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'A' at site 383, 'G' at site 567 and 'C' at site 641; in 16S3', 'A' at site 917, 'A' at site 1088, 'G' at site 1090, and 'A' at site 1127.

Diagnosis. Within the genus *Rhombophryne*, *R. mangabensis* can easily be distinguished from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence); from members of the *R. minuta* species group by less gracile body and much shorter limbs; from *R. proportionalis* by its much larger body size (SVL 19.6–23.2 mm vs 11.0–12.3 mm); from members of the *R. ellae* species group by the absence of inguinal spots and reddish orange colouration on the hindlimbs (vs presence); from members of the *R. laevipes* species group by the absence of inguinal spots or ocelli (vs presence in most species), and smaller adult body size (SVL 19.6–23.2 mm vs 24.1–57.2 mm). Within the *R. testudo* species group, see accounts of *R. testudo*, *R. coudreaui*, and *R. matavy* above for distinction from those species. From its sister species, *R. savaka*, it can be distinguished by the less pronounced diastema in vomer-

ine teeth, slightly longer relative tibia length (TIBL/SVL 0.44–0.46 vs 0.37–0.42), absence of inguinal spots (vs presence), and by advertisement call with slightly longer call duration (180–237 ms vs 121–142 ms), generally longer inter-call interval (419–822 ms vs 302–451 ms), and lower dominant frequency (3300–3550 Hz vs 4144–4210 Hz). For distinction from newly described species, see accounts of those species, below.

Variation. SVL 19.6–23.2 mm ($n = 4$ adults; two presumed subadults measure 16.5 and 18.9 mm, respectively); full measurements are presented in Table S5. Measurements are largely consistent with those given in the original description by Glaw et al. (2010b). All specimens are consistent in morphology and colouration, including the newly referred specimens from mainland Madagascar (ZSM 262/2016 and MRSN A2557). Two raised black markings with small light brown points in the suprascapular region are consistently present as part of the variably complete anterior chevron marking; a posterior chevron running from the inguinal region anteriorly over the dorsum is sometimes incomplete at the midline but is usually indicated (Fig. 18A, C–E). Shanks often exhibit a broad middle stripe and two narrow stripes proximal and distal to this stripe (Fig. 18A, C–E).

Call. The advertisement call recorded on 13 March 1991 at Nosy Mangabe (air temperature unknown) consists of a tonal note of moderate duration emitted in regular call series containing a variable number of calls (2–5) repeated at rather regular succession (Fig. 20). Each call exhibits some irregular amplitude modulation, with 2 or 3 peaks recognizable within each call, with the terminal peak having the highest energy. Slight upward frequency modulation is evident in each call until the last third of the call's duration, followed by a terminal drop in frequency. Numerical parameters of 20 analysed calls are as follows: call duration (= note duration) 180–237 ms (198 ± 15 ms); inter-call intervals within regular call series 419–822 ms (484 ± 113 ms); duration of regular call series 820–2895 ms (1779 ± 925 ms); dominant frequency 3300–3550 Hz (3434 ± 85 Hz); prevalent bandwidth 2800–7500 Hz; weak frequency bands recognizable at approximately 5250 and 6760 Hz. Calls from the same recording (Vences et al. 2006, CD 3, track 31) have been described by Glaw et al. (2010b) using a slightly different terminological scheme.

Etymology. Toponym referring to Nosy Mangabe, the island where the species was originally discovered.

Distribution. This species was originally known only from (1) Nosy Mangabe (type locality), but its presence on the Masoala Peninsula was reported by Raherilalao et al. (2016) and confirmed by Belluardo et al. (2022). The extent of its range on the peninsula constitutes three further distinct sites: (2) Tampolo (under which we include the nearby 'Eco-Lodge chez Arol'), (3) Mahalevona, and (4) Ambohitsitondroina (15.5694°S 50.0034°E, 609 m a.s.l.; Fig. 18E). Elevation: ca 15–669 m a.s.l.

Natural history. *Rhombophryne mangabensis* is a semi-fossorial or detriticolous species found in low-elevation humid forest. Specimens were collected at night during heavy rain, during which many calls were heard in an intense chorus. Males called from concealed positions in the leaf litter of ‘apparently primary low-altitude rainforests’ (Glaw et al. 2010b: 240). Calling has not been directly observed, but the call described above certainly belongs to this species, as specimens caught while searching for the source of calling were inflated with air, typical for calling *Rhombophryne*. Active specimens were encountered on the forest floor during the day, in the evening, and at night. One individual was captured by pitfall traps set up in a valley with closed-canopy humid forest associated with thick leaf litter and many rotten logs.

Karyotype. Aprea et al. (2007) reported on the karyotype of ‘*Rhombophryne* sp. aff. *minuta*’ from Masoala, but the specimen number they reported, MRSN A3656, is from Manarikoba in Tsaratànana, and is therefore not referable to this species, but in fact belongs to *Rhombophryne quantini* **sp. nov.**, described below. The karyotype of *R. mangabensis* is therefore unknown.

Rhombophryne savaka Scherz et al., 2016

Figures 2, 4–9, 21–23

Informal names. This species was listed as ‘*Rhombophryne* sp. 4’ by Vieites et al. (2009) and Glaw et al.

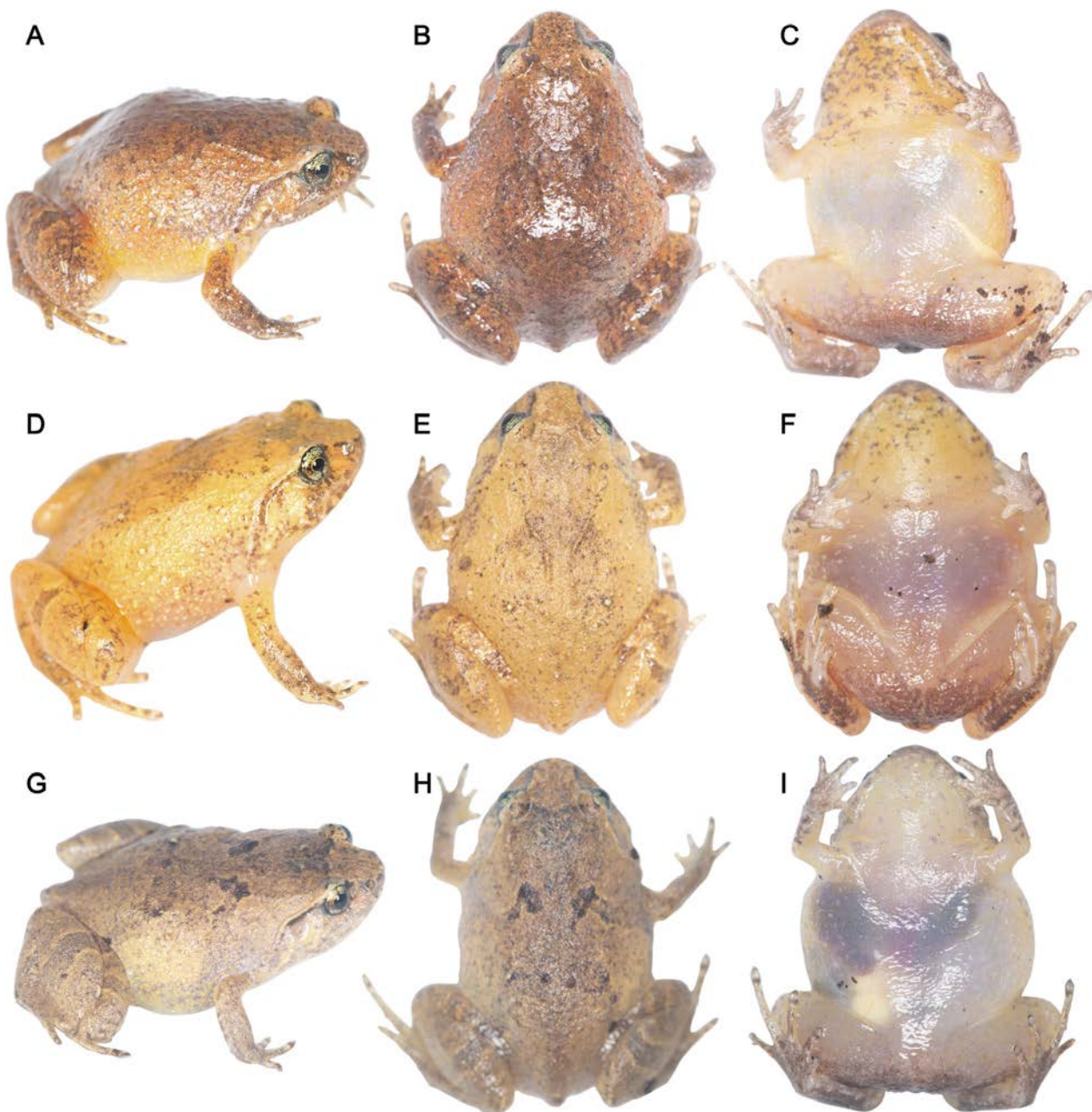


Figure 21. *Rhombophryne savaka* in life. Not to scale. All photographed in low elevation primary rainforest in Marojejy National Park. **A–C** adult male KU 347465 (CRH 1653), and **D–F** adult male ZSM 519/2016 (MSZC 0319), from near ‘Camp Mantella’; **G–I** adult female ZSM 520/2016 (MSZC 0318; notice large white eggs visible in ventral view) from near ‘Camp Marojejia’.

been sequenced with the FrogCap hybrid capture probe set; it is included in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. testudo* group, this species is sister to *R. mangabensis* based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small body size, adult SVL 18.8–20.9 mm; (2) head wider than long (HW/HL 1.66–1.80); (3) moderately small eyes (ED/HL 0.35–0.43); (4) short hindlimbs (HIL/SVL 1.37–1.55); (5) small inner metatarsal tubercle (IMTL/FOL 0.11–0.14); (6) moderately distinct outer metatarsal tubercle; (7) second finger roughly equal in length to fourth, except in one individual where it is much shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular with a few scattered warts, especially a suprascapular pair outlined in black; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) occasional presence of small black inguinal ocelli without light outline; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; (15) clavicles present, thin, curving; and (16) advertisement call (based on 28 analysed calls by one individual) tonal, with (17) call duration 121–142 ms, (18) inter-call interval 221–395 ms, and (19) dominant frequency 3714–3861 Hz.

Rhombophryne savaka is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'C' at site 355, 'G' at site 664 and 'T' at site 687; in 16S3', 'A' at site 937, 'T' at site 1094, and 'T' at site 1155.

Diagnosis. Within the genus *Rhombophryne*, *R. savaka* can easily be distinguished from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence); from members of the *R. minuta* species group by less gracile body and much shorter limbs; from *R. proportionalis* by its much larger body size (SVL 18.8–20.9 mm vs 11.0–12.3 mm); from members of the *R. ellae* species group by the absence of reddish orange colouration on the hindlimbs (vs presence); from members of the *R. laevipes* species group by the absence of white outline on inguinal spots or whitish inguinal spots (vs presence in most species), and smaller adult body size (SVL 18.8–20.9 mm vs 24.1–57.2 mm). Within the *R. testudo* species group, see accounts of *R. testudo*, *R. coudreaui*, *R. matavy*, and its sister species *R. mangabensis* above for distinction from those species. For distinction from newly described species, see accounts of those species, below.

Variation. SVL 18.7–20.9 mm (n = 3). For variation in other measurements, see Table S5.

A detailed description of the species is given in Scherz et al. (2016a), but it was based on just a single individual. Additional specimens collected in 2016 are very similar to the holotype (Fig. 21). The largest

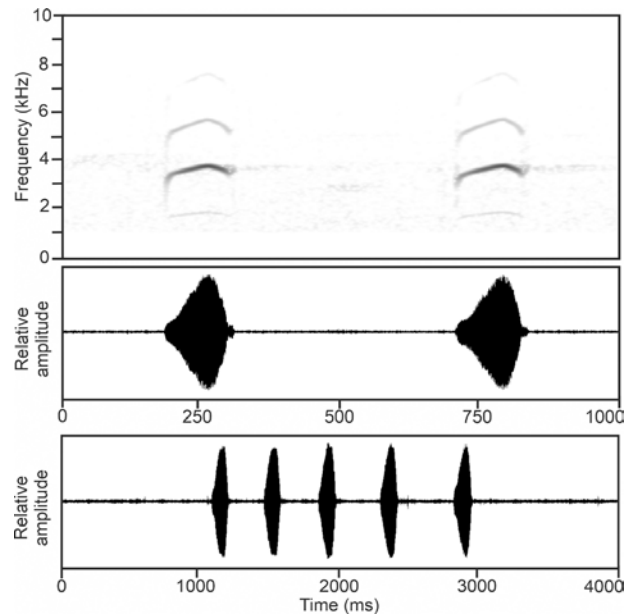


Figure 23. Advertisement calls of *Rhombophryne savaka* (ZSM 519/2016), recorded in Marojejy National Park in 2016. Top: audiospectrogram and corresponding oscillogram of two advertisement calls from a regular call series at 1000 ms time scale. Bottom: oscillogram at 4000 ms time scale depicting a regular call series containing five calls. Recording high-pass filtered at 1000 Hz.

specimen is an ovigerous female, ZSM 520/2016 (Fig. 21G–I), but this specimen is only 0.5 mm larger than the male holotype. The skin was consistently rather smooth in all individuals. ZSM 519/2016 shows a large diastema in its vomerine teeth, consistent with the holotype. All specimens are consistent in overall colouration, but differ in details of patterning. ZSM 520/2010 has an extensive near-black bar on its lower posterior thigh, where the other specimens have only a small trapezoid. This specimen also has blackish spots above its suprascapular region and faint crossbands on its hindlimbs, which are lacking from the other specimens. Inguinal spots were present only in the holotype; ZSM 520/2016 has a diminutive inguinal spot on the right side but not the left. The posterior thigh is solid cream in colour. The abdomen is also immaculate cream in all specimens, and very translucent in life (Fig. 21C, F, I). At least one specimen (ZSM 520/2016) has dark markings above the suprascapular region, but these are not as distinctive or dark as in *R. mangabensis* or in *R. mavokely* **sp. nov.** described below.

Call. The advertisement call recorded on 2 December 2016 at Camp 1, Marojejy National Park (call voucher ZSM 519/2016 [MSZC 0319]; air temperature 22.6 °C) during rainfall, consists of a tonal note of short duration emitted in short regular call series (Fig. 23). Inter-call intervals within call series tend to be slightly longer in duration towards the end of a series. Each call exhibits some slight amplitude modulation, with call energy moderately fast increasing towards the middle of the call, then keeping the same level of energy until the last quar-

ter of the call's duration when it quickly drops towards the call's end. Slight upward frequency modulation is evident in each call until two thirds of the call's duration, followed by a slight terminal drop in frequency. Numerical parameters of 28 analysed calls are as follows: call duration (= note duration) 121–142 ms (132 ± 5 ms); inter-call intervals within regular call series 221–395 ms (296 ± 45 ms); number of calls per call series 4–5 (4.3 ± 0.5); duration of regular call series 1342–1883 ms (1483 ± 187 ms); dominant frequency 3714–3861 Hz (3807 ± 47 Hz); prevalent bandwidth 1600–7800 Hz; frequency bands recognizable at approximately 1900, 5700, and 7680 Hz.

Additional calls recorded on 2 December 2016 at the same locality (voucher specimen KU 347465 [CRH 1653]) completely agree in general characteristics with the call described above, except for a slightly higher dominant frequency explainable by smaller body size of the calling male, and have the following numerical parameters (3 call series and 13 calls analysed): call duration (= note duration) 110–122 ms (115 ± 3 ms); inter-call intervals within regular call series 302–451 ms (340 ± 46 ms); number of calls per call series 4–5 (4.3 ± 0.6); duration of regular call series 1461–1932 ms (1631 ± 261 ms); dominant frequency 4144–4210 Hz (4175 ± 27 Hz); prevalent bandwidth 1800–8500 Hz.

Etymology. The Malagasy noun *savaka* meaning 'diastema', in reference to the diastema in the vomerine teeth that were thought to be diagnostic of this species. Used as an invariable noun in apposition.

Distribution. *Rhombophryne savaka* is known only from (1) Marojejy National Park (type locality). Elevation: 450–750 m a.s.l. (based on newly collected material). Records from 1300 ± 200 m a.s.l. by Rakotoarimalala and Raselimanana (2023) cannot be verified as we have not examined material and have no DNA sequences, so they are here not included.

Natural history. *Rhombophryne savaka* is a semi-fossorial or detriticolous species found in low- to mid-elevation humid forest. Calling activity was triggered by rain in November and December 2016, especially at night. Locally the species seemed rather common, though it was very difficult to localise calling individuals. Males emit advertisement calls from within or on the leaf litter; ZSM 519/2016 was observed calling with a leaf resting on its back. Females likewise live within the leaf-litter; ZSM 520/2016 was collected whilst attempting to find a calling male from within the same quadrat of leaf litter (the male could not be found).

Rhombophryne maraorao sp. nov.

<https://zoobank.org/0E6F8C26-9223-4075-89C7-C9CC9D8D6DD3>

Figures 2, 4–9, 24, 25

Remark. Specimens assignable to this species were attributed to *Rhombophryne testudo* by Blommers-Schlösser and Blanc (1991) and Guibé (1978), as *R. coudreaui* by Andreone (2003), as both *R. coudreaui* and *R. testudo* by Glaw and Vences (2007), and as *R. coudreaui* by Andreone and Randrianirina (2008).

Informal names. This species was listed as '*Rhombophryne* sp. 9' by Vieites et al. (2009), '*Rhombophryne* sp. Ca09' by Belluardo et al. (2022), and '*Rhombophryne* sp. 9' and 'CCS "Sp. 9"' by Carné and Vieites (2024).

Justification of the new species. According to current knowledge, this is the allopatric sister lineage of *R. coudreaui*, which it also closely resembles morphologically. However, it is genetically highly divergent (10% uncorrected p distance in the 16S3' fragment), there is no haplotype sharing with *R. coudreaui* or any other *Rhombophryne* species in the nuclear gene RAG1 (Fig. 4), and it has subtle but recognizable morphological differences (see Diagnosis below). We are therefore convinced that it represents an evolutionarily independent lineage.

Holotype. MRSN A2115 (FN 7705), an adult male, collected on 2 December 1998 in the Ambatoledama Corridor (Andasin'i Governera) (ca. 15.30°S , 50.02°E , 650 m a.s.l.), Masoala Peninsula, Sava Region, northeastern Madagascar, by F. Andreone and J.E. Randrianirina (Figs 8, 9, 24D, 25).

Paratypes. Three specimens: MRSN A2496 (no field number) and MRSN A2497 (RJS 0496), an adult female and a juvenile, respectively, collected on 8 February 2002 at 'Camp 7' Antsiranana Faritany (15.4177°S , 49.9403°E , ca. 800 m a.s.l.), Amparihy, Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by J.E. Randrianirina; MRSN A6929 (FN 7292), an adult male, collected on 13 December 1997 at 'Camp 3' Antsinjorano (14.5433°S , 49.4300°E , ca. 950 m a.s.l.), Ambolokopatrika-Betaolana Forest, Sava Region, northeastern Madagascar by F. Andreone, G. Aprea & J.E. Randrianirina (Fig. 24A–C). Note: MRSN A6929 formerly bore the collection number MRSN A2066 (Andreone 2003), but this number was apparently duplicated, so a new number was issued.

Referred specimens. MNHN 1973.576, an unsexed specimen, collected on 19 December 1972 at 'Sambava, km 17 route d'Andapa' near the Marojejy Massif, Sava Region, northeastern Madagascar, by C. Blanc. This specimen was assigned morphologically to '*R. coudreaui*' by Andreone and Randrianirina (2008), but the material used for comparison to *R. coudreaui* in that work constitutes the type series of *R. maraorao* sp. nov., and does not include any material of *R. coudreaui* sensu stricto. Although we were not able to re-examine this specimen, its assignment to *R. maraorao* sp. nov. is partly supported by the textual description from Andreone and Randrianirina (2008: 47), 'this specimen (likely a female 34.9 mm long) does not show an evident tympanum, lacks protruding jaw whiskers and shows the typical rhomboidal

drawing on the head, and has a rather dark belly'. This assignment remains tentative, however, and requires confirmation by either morphological inspection or museum sequencing.

MRSN A5524, originally reported by Andreone and Randrianirina (2008) as being from Tsingy de Bemaraha in western Madagascar, was found by Belluaro et al. (2022) to be genetically identical with *R. maraorao* **sp. nov.** Belluaro et al. (2022) showed that its locality was probably confused, and it is most likely from somewhere in northeastern Madagascar. It is referred to this species on genetic and morphological grounds, but its incorrect former locality is not considered as part of the distribution of the species. We also do not include it in the diagnosis of the species, but comment on how its morphology expands our knowledge of the species in the Variation section, below.

BMNH 1987.331, an unsexed possible subadult, collected on 31 August 1986 in Anandrivola Forest (15.775°S, 49.600°E, ca 580 m a.s.l.), Analanjirofo Region, northeastern Madagascar, by C.J. Raxworthy, is tentatively assigned to this species based on its small size, rotund body and short head, rough skin, and the second finger being slightly shorter than the fourth (the last character being the key feature distinguishing it from *R. coudreaui*; see Diagnosis, below).

Specimens previously attributed to *R. coudreaui* from Marojejy (Raselimanana et al. 2000) and Maroantsetra (IUCN SSC Amphibian Specialist Group 2016d) may be referable to *R. maraorao* **sp. nov.**, as these two species are only now being recognised as distinct, with *R. maraorao* **sp. nov.** apparently occurring north of *R. coudreaui*. However, these records may also refer to *R. mavokely* **sp. nov.** (described below), which may look similar in its flat body profile and broad head, so carefully scrutiny is warranted, and we do not include these locations in the distribution of this species.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S5' AY594072; Andreone et al. 2005; 16S3' AY594110; Vieites et al. 2009). All paratypes and referred specimens conform well with the holotype in morphology. Assignment of MRSN A2497 is further confirmed by molecular taxonomic identification. MRSN A2115 and MRSN A2497 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. testudo* group, this species is sister to *R. coudreaui* based on molecular phylogenetic data (Fig. 2; Belluaro et al. 2022). It is characterised by the possession of the following unique suite of characters:

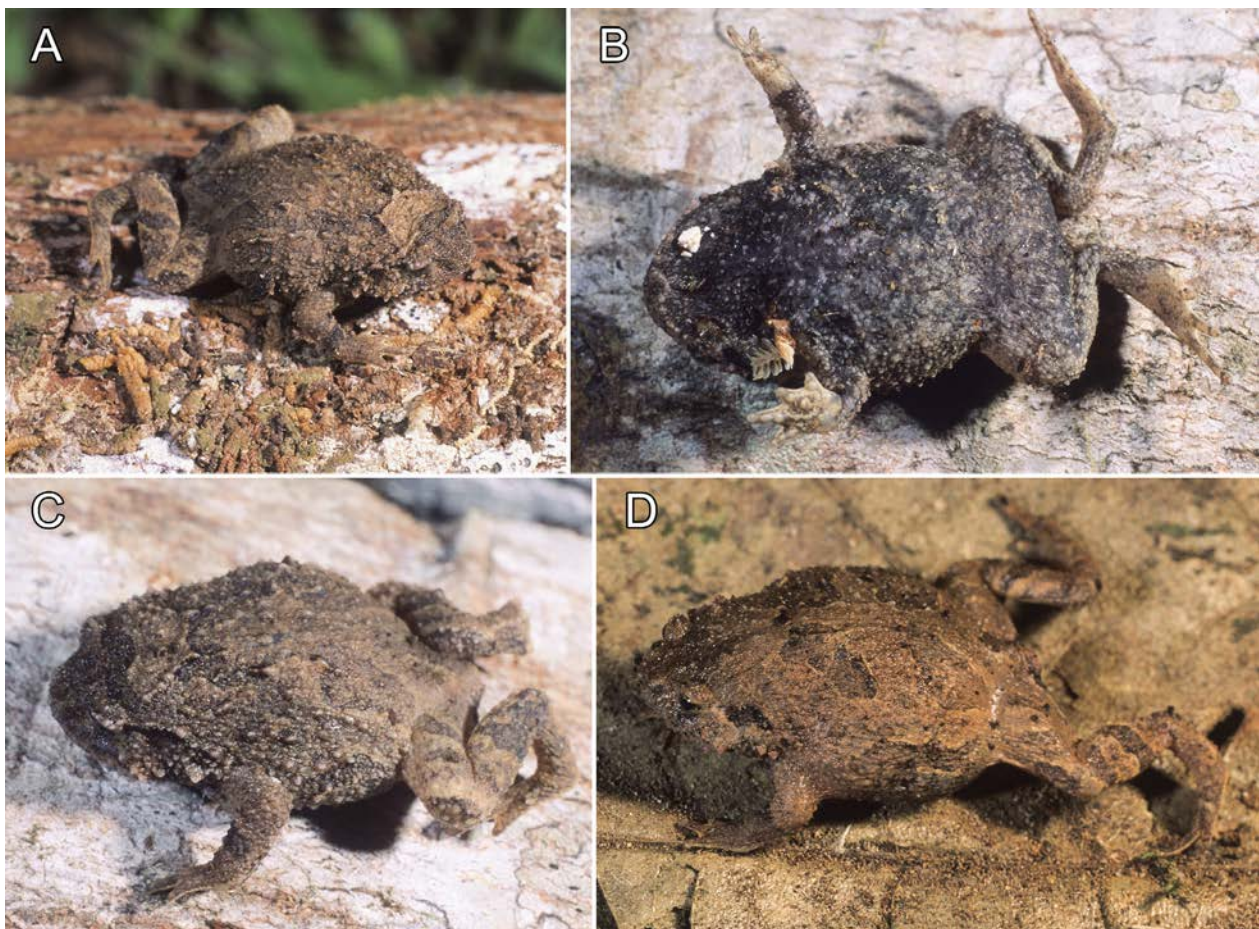


Figure 24. *Rhombophryne maraorao* **sp. nov.** in life. **A–C** adult male paratype MRSN A6929 (FN 7292) from Ambolokopatrika in **A** anterodorsolateral, **B** ventral, and **C** dorsolateral view. **D** adult male holotype MRSN A2115 (FN 7705) from Masoala Peninsula (Ambatoledama Corridor: Andasin'i Governera) in dorsolateral view.

(1) small to medium body size, adult SVL 22.5–28.9 mm; (2) head much wider than long (HW/HL 1.69–1.88); (3) small eyes (ED/HL 0.25–0.27); (4) short hindlimbs (HIL/SVL 1.10–1.28); (5) well-developed inner metatarsal tubercle (IMTL/FOL 0.13–0.19); (6) indistinct outer metatarsal tubercle; (7) second finger slightly to distinctly longer than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin rough to rugose with longitudinal rows of tubercles; (10) presence of pronounced, pointed chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) broad but not fortified skull, without expansion of squamosal, maxilla, or posterior process of angulosplenial; and (15) clavicles absent.

Rhombophryne maraorao **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide

combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'C' at site 406, 'T' at site 459, and 'T' at site 500; in 16S3', 'A' at site 1057, 'A' at site 1075, and 'A' at site 1092.

Diagnosis. Within the genus *Rhombophryne*, *R. maraorao* **sp. nov.** can easily be distinguished from all other species except *R. testudo*, *R. coudreaui*, and *R. matavy* by its rotund body and short, broad head. Among these species, it can be distinguished from *R. testudo* by smaller body size (SVL 22.5–28.9 mm vs 33.0–43.1 mm), longer head (HW/HL 1.69–1.88 vs 2.00–2.60), rougher skin, smaller chin barbels, and much less fortified skull; and from *R. matavy* by smaller body size (SVL 22.5–28.9 mm vs 40–50 mm), longer head (HW/HL 1.69–1.88 vs 1.88–2.05), presence of chin barbels (vs absence), and less fortified skull. *Rhombophryne maraorao* **sp. nov.** is

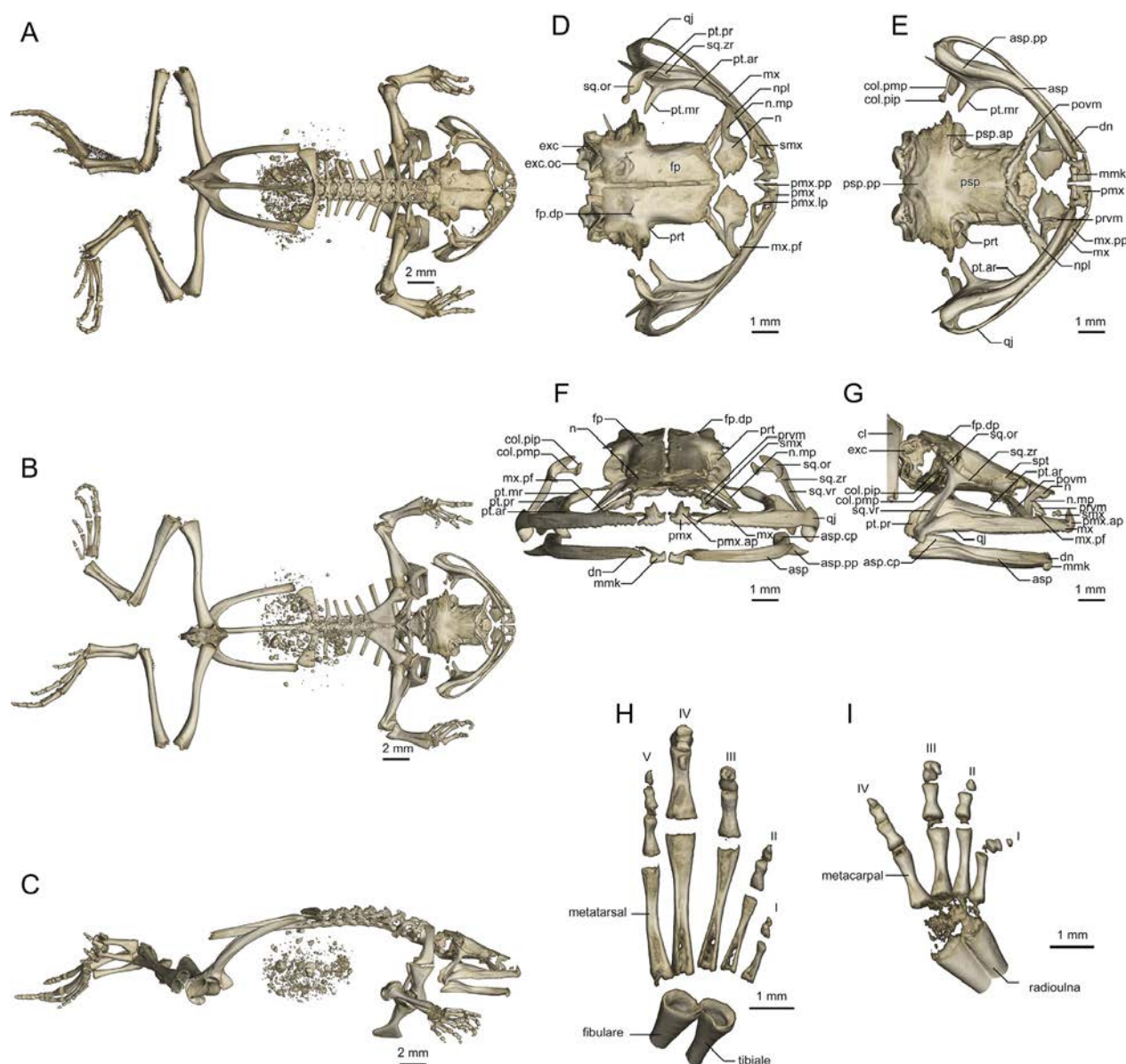


Figure 25. Skeleton of *Rhombophryne maraorao* **sp. nov.** holotype MRSN A2115 (FN 7705). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** are apparently small stones. Abbreviations are given under Materials and Methods.

most closely related to, and most similar to, *R. coudreaui*. These species are difficult to distinguish morphologically. The most reliable character for distinguishing these species is the presence of pronounced pointed barbels along the lower lip in *R. maraorao* **sp. nov.**, versus fewer, less pronounced barbels in *R. coudreaui*. They may also differ in eye size, with *R. coudreaui* having larger relative eye size (ED/HL 0.29–0.31) than *R. maraorao* **sp. nov.** (ED/HL 0.25–0.27); and in relative finger length, with the second finger at least slightly longer than the fourth in *R. maraorao* **sp. nov.**, vs equal in length in *R. coudreaui*.

Description of holotype. An adult male specimen in a moderately good state of preservation, though fairly soft (Figs 8, 9). An incision made along the right flank to check the sex. Testes distinct.

Body robust and rotund. Head wider than long (HW/HL 1.76). Eyes quite small (ED/HL 0.25), pupils large, round. Snout rounded in dorsal and lateral views. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril closer to tip of snout than to eye, slightly protuberant. Tympanum indistinct, round, TDH/ED 0.594. Supratympanic fold moderately distinct, raised but tubercular and so uneven in height, forming a sigmoid curve from the line of the top of the eye straight over the tympanum, curving down behind the tympanum, and then posteriorly to the top of the arm. A row of five (right) or three (left) small superciliary spines above each eye, as well as small granules distributed over the top of the eye and head. A row of pronounced tubercles (barbels) along the lower lip. Tongue partly removed as a tissue sample. It was attached anteriorly, broad, and unlobed. Maxillary and vomerine teeth present, vomerine teeth present in two curving rows separated at the midline by a small gap. Choanae round, placed laterally in the roof of the mouth.

Forelimbs relatively short and thick, the upper arm hardly distinguishable from the body cavity (FARL/SVL 0.323). Fingers without webbing, all short, relative lengths $1 < 2 = 4 < 3$ (Fig. 9). Finger subarticular tubercles distinct, round, whitish; inner metacarpal tubercle broad and flat, outer metacarpal/palmar tubercle distinct and round. Hind limb thick, tibiotarsal articulation reaching insertion of arm when addressed anteriorly along the body. TIBL/SVL 0.304. Inner metatarsal tubercle present, large. Outer metatarsal tubercle faint. Toes not webbed; first toe distinctly reduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles distinct, broad and round; toe tips not enlarged (Fig. 9).

After 25 years in preservative, the colouration of the specimen is largely faded. It is beige in base colour, with light brownish symmetrical markings. These border the back of the head region, the scapular region, and from the inguinal region to the posterior third of the back, forming a beige cross-like shape over the central dorsum. The legs too are beige above with faint light brown crossbands on the thigh, more distinct crossbands on the shank, and a dark posterior tarsus. The hidden surfaces of the thighs are whitish, but there is a trapezoidal brown

marking around the vent. The dorsal and lateral foot are beige with very fine brown specks. The ventral body has a beige base-colour, intensely speckled with brown (more distinct than above), especially over the chin and pectoral girdle. This pattern extends onto the ventral arms and legs. Colouration in life (Fig. 24D) was much browner than the specimen is in preservative. The outline of the markings on the dorsum in beige-cream was particularly distinctive.

Variation. SVL 22.5–28.9 mm ($n = 3$; a putative subadult, MRSN A2497, measures 20.9 mm, and the referred specimen with uncertain collection locality, MRSN A5524, measures 29.8 mm). For variation in measurements, see Table S5. All specimens have pronounced tubercles along the lower lip. Most individuals are a brownish cream colour dorsally in preservative, much lighter in colour than most *R. coudreaui*, but MRSN A5524 is much browner and more mottled, and the colour of this species in life is also dark brown (Fig. 24); differences in colour of the specimens may be due to preservation fluids or other factors, and are not taken to be diagnostic. The referred specimen BMNH 1987.331 is rather dark, but has also been stained to have blue-green bones, which may have altered its skin colour as well. Much of the body patterning is consistent, especially the dark suprascapular spots which define the short edge of a trapezoid where the eyes form the ends of the long edge. The sacral region also has dark markings, though less consistently than in *R. coudreaui*. In four of the five specimens (not MRSN 2497) the chin is marbled brown and cream. The first toe of MRSN A2496 is less distinctly reduced than other specimens, and is connected to the second toe with distinct webbing on the left side but not on the right. MRSN A5524 has a substantially larger relative inner metatarsal tubercle than the other individuals (IMTL/FOL 0.23 vs 0.13–0.19).

Call. The call of this species is not known.

Etymology. The Malagasy adjective *marao* meaning ‘rough to the touch’, in reference to the rugose skin of this species in life and in preservative. Used as an invariable noun in apposition.

Distribution. Currently known from (1) Ambatolédama Corridor (Andasin’i Governera); (2) Amparihy, (3) Ambolokopatrika-Betaolana, and possibly (4) Anandrivola. Referral of material from Marojejy to this species remains too uncertain to include in its distribution at present. Elevation: ca 650–950 m a.s.l.

Natural history. *Rhombophryne maraorao* **sp. nov.** is a fossorial species found in low- to mid-elevation humid forest; its ecology is poorly known, but presumably much like *R. coudreaui*. All of the individuals from Masoala and Ambolokopatrika-Betaolana were unearthed and collected whilst digging in the soil to install pitfall traps. The gut of MRSN A6929 contained a beetle, an amphipod, a small ant, pieces of an arthropod, and detritus (several leaf and bark fragments).

***Rhombophryne mavokely* sp. nov.**

<https://zoobank.org/EDDD599C-C5B4-45F6-91B0-051D68C-9C91D>

Figures 2, 5–9, 26–29

Informal names. This species was listed as ‘*Rhombophryne* sp. Ca17’ by Belluaro et al. (2022), and ‘*Rhombophryne* sp. 17’ and ‘CCS “Sp. 17”’ by Carné and Vieites (2024).

Justification of the new species. The new species is placed in a clade containing *R. mangabensis*, *R. savaka*,

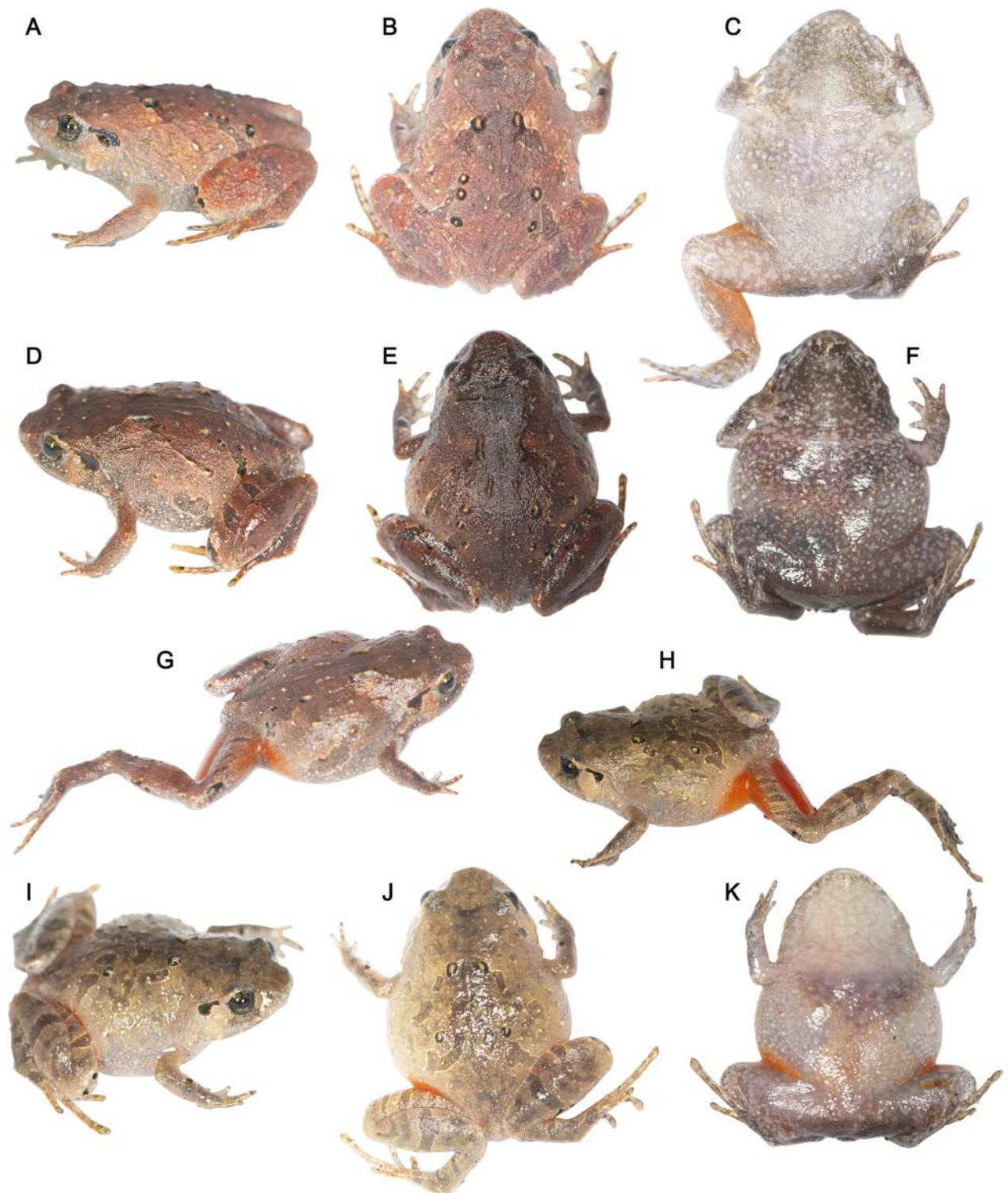


Figure 26. *Rhombophryne mavokely* sp. nov. in life. Not to scale. All photographed in low elevation primary rainforest within Marojejy National Park in 2016. **A–C** adult male holotype ZSM 521/2016 (MSZC 0269) in **A** lateral, **B** dorsal, and **C** ventral view; **D–G** unsexed adult paratype ZSM 517/2016 (ZCMV 15088) in **D** lateral, **E** dorsal, **F** ventral view, and **G** with its right hindlimb stretched to reveal the orange flash colouration; and **H–K** unsexed adult paratype UADBA-A-MSZC 0307 **H** with its left hindlimb stretched to reveal the orange flash colouration, and in **I** lateral, **J** dorsal, and **K** ventral view.

and an undescribed candidate species (*R. sp.* Ca16) from the Andapa area for which only genetic data are known. It differs, however, from all nominal species of *Rhombophryne* by very high genetic divergences: 10.3% and 10.9% uncorrected p distance in the 16S3' fragment from *R. mangabensis* and *R. savaka*, respectively; and >11% from all other species (Belluardo et al. 2022). It furthermore differs from *R. mangabensis* and *R. savaka* by the presence of reddish-orange colouration on the posterior thigh, and from the syntopic *R. savaka* by bioacoustic and further morphological characters (see Diagnosis below). In addition, it is phylogenetically sister to the *R. mangabensis* / *R. savaka* subclade (Belluardo et al. 2022) and thus cannot be considered conspecific with either of these species. Its status as distinct species is therefore beyond doubt.

Holotype. ZSM 521/2016 (MSZC 0269), an adult male (call voucher), collected on 22 November 2016 in low elevation primary rainforest within Marojejy National Park (14.4400°S, 49.7782°E, 402 m a.s.l.), Sava Region,

northeastern Madagascar, by M.D. Scherz, J.H. Razafindraibe, and A. Razafimanantsoa (Figs 8, 9, 26A–C, 28).

Paratypes. Three specimens: ZSM 517/2016 (ZCMV 15088), an unsexed adult, collected on the morning of 16 November 2016 at ‘Camp 0’ (ca 14.446°S, ca 49.785°E, ca 310 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by M.D. Scherz, M. Vences, A. Rakotoarison, M.C. Bletz, J.H. Razafindraibe, and A. Razafimanantsoa (Fig. 26D–G); ZSM 518/2016 (MSZC 0310), a juvenile, and UADBA-A-MSZC 0307 (Fig. 26H–K), an unsexed adult, both collected in the evening of the 26 November 2016 from the same locality as ZSM 517/2016, by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, and C.R. Hutter.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S5' OL780607; Belluardo et al. 2022). All paratypes conform well with the holotype in morphology, and are from near the type locality. Assignment of specimens ZSM 518/2016, ZSM 517/2016, and UADBA-A-MSZC



Figure 27. Uncollected specimens tentatively referred to *Rhombophryne mavokely* **sp. nov.** based on dark suprascapular spot with a light middle, a dark marking in the supratympanic region, absence of chin barbels, and presence of dorsal ridges. **A–C** a specimen from Anjanaharibe-Sud Special Reserve in **A** dorsolateral, **B** dorsal, and **C** anterior view, photographed by Éric Matthieu; **D** a probable juvenile specimen from Simpona Lodge in Makira Natural Park in dorsolateral view, photographed by Lucas Pastor. Used with permission.

0307 is further confirmed by molecular taxonomic identification (Fig. 2). RAG1 sequence of this species is so far not available.

Definition. Within the *R. testudo* group, this species is most closely related to *R. mangabensis*, *R. savaka*, and its possible sister lineage *R. sp.* Ca16 based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small body size, adult SVL 21.2–21.3 mm; (2) head wider than long (HW/HL 1.60–1.68); (3) moderately small eyes (ED/HL 0.36–0.38); (4) short hindlimbs (HIL/SVL 1.50–1.61); (5) small inner metatarsal tubercle (IMTL/FOL 0.12–0.13); (6) outer metatarsal tubercle absent; (7) second finger distinctly longer than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular with a few scattered warts, especially a suprascapular pair outlined in black; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) presence of reddish orange in the inguinal region and on the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; (15) clavicles present, thin, curving; and (16) advertisement call (based on 16 analysed calls by one individual) tonal, with (17) call duration 231–262 ms, (18) inter-call interval 623–808 ms, and (19) dominant frequency 3178–3265 Hz.

Rhombophryne mavokely **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5, 'A' at site 315, 'C' at site 326, and 'T' at site 331; in 16S3, 'G' at site 937, 'G' at site 938, and 'A' at site 956.

Diagnosis. Within the genus *Rhombophryne*, *R. mavokely* **sp. nov.** can easily be distinguished from all species except *R. ellae*, *R. ornata*, and two other species described below (*R. quentini* **sp. nov.** and *R. kotrobaratra* **sp. nov.**), by the presence of reddish orange colouration on the posterior thigh. Among these species, it can be distinguished from *R. ellae* by a more dorsoventrally compressed habitus, smaller body size (SVL 21.2–21.3 mm vs 24.9 mm), wider head (HW/HL 1.60–1.68 vs 1.47), and shorter hindlimbs (HIL/SVL 1.50–1.61 vs 1.71); and from *R. ornata* by the absence of superciliary spines (vs presence). For distinction from *R. quentini* **sp. nov.** and *R. kotrobaratra* **sp. nov.**, see the descriptions of those species, below. When the orange of the limbs is not visible there is also some resemblance to *R. coudreaui* and *R. maraorao*, which however differ by generally larger adult body size (SVL 21.5–28.9 vs 21.2–21.3 mm), much shorter hindlimbs (HIL/SVL 1.10–1.30 vs 1.50–1.61), and presence of chin barbels (vs absence).

Rhombophryne mavokely **sp. nov.** occurs syntopically or in near sympatry with the closely related *R. savaka*. Aside from colouration, *R. mavokely* **sp. nov.** can be distinguished from *R. savaka* by its rougher dorsal skin with more ridges (vs relatively smooth), and by the longer ad-

vertisement call duration (231–262 ms vs 121–142 ms), longer inter-call interval (623–808 ms vs 221–395 ms), and slightly lower dominant frequency (3178–3265 Hz vs 3714–3861 Hz).

Description of holotype. A specimen in a good state of preservation (Fig. 8). A tissue sample was taken from its left thigh for genetic analysis.

Body rotund. Head wider than long (HW/HL 1.68). Eyes quite small (ED/HL 0.36), pupils small, round. Snout rounded in dorsal view, truncate in lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril closer to tip of snout than to eye, slightly protuberant. Tympanum indistinct, round, TDH/ED 0.62. Supratympanic fold indistinct, demarcated at its anterior end by a dark comma-shaped marking. In life it was more distinct, curving from the posterior corner of the eye over the tympanum and towards the insertion of the arm (Fig. 26A). Superciliary spines absent, but two white dots above each eye. Small granules and ridges distributed over the body in life are largely flat in preservative but mostly still marked by a lighter colouration. Most prominent of these are a pair of markings in the suprascapular region, and a series of three (left) and two (right) bumps along the ilia and in the sacral region. Tongue broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth present in two curving rows separated at the midline by a small gap. Choanae round, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.417), fairly slender. Fingers without webbing, all short, relative lengths $1 < 4 < 2 < 3$, second finger slightly longer than fourth (Fig. 9). Finger tips not expanded, slightly pointed. Finger subarticular tubercles indistinct, whitish; inner metacarpal tubercle broad and flat, outer metacarpal/palmar tubercle indistinct, greyish. Hind limb thick, tibiotarsal articulation reaching the eye when adpressed anteriorly along the body. TIBL/SVL 0.461. Inner metatarsal tubercle present, oblong, whitish. Outer metatarsal tubercle visible only as a slightly lightened area of the outer metatarsus. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles distinct, greyish, rather flat; toe tips slightly enlarged, slightly pointed (Fig. 9).

After seven years in preservative, the colouration of the specimen is quite vibrant, though lighter than in life (Fig. 8). The base colour is a soft pink, becoming more reddish posteriorly and mauve anteriorly, especially over the head. The dorsal surfaces of the eyes are dark mauve. There are several dark brown markings on the body, particularly the comma-shaped markings in the supratympanic region, the black spots with mauve centres on the suprascapular region and iliac/sacral region, and crossbands on the forelimbs. Additionally, the ventral surfaces of the feet, and especially the ventral portion of the posterior thigh are almost black. The darkened area of the thigh is not trapezoidal as in some other *Rhombophryne* species, but really extends over the entire length of the posterior thigh. It is separated from the dorsal coloura-

tion by areas that are cream in preservative. The dorsal surfaces of the legs have faint brown crossbands, two on the thigh, two on the shank, and two or three on the feet. The dorsal surface of the foot is laterally pinkish, but over most of its surface is mottled brown, with a light annulus before each toe tip. The dorsal surfaces of the hands are similar. The flank colouration merges seamlessly with the venter (i.e., there is no dorsolateral colour border, nor indeed a lateral head colour border). The ventral colouration is largely cream mottled with a greyish brown. The chin is darkest, with the posterior extent of the vocal sac clearly demarcated. The ventral arms are a light cream, less yellow than over the hind limbs. Colouration in life was like in preservative but generally more orange.

Variation. SVL 21.2–21.3 mm ($n = 2$). For variation in other measurements, see Table S5. Morphology is highly consistent. All specimens collected were characterised by highly similar colouration and patterning, except that in ZSM 517/2016 the posterior thigh is bright pink where it is cream in ZSM 521/2016, the thigh is more clearly striated, and the dark colouration around the cloaca is more restricted in distribution. All known specimens possess a dark suprascapular spot with a light middle, and a dark, almost comma-shaped marking in the supratympanic region (Figs 26, 27), similar to *R. mangabensis* (Fig. 18), and distinct from *R. savaka* (Fig. 21).

Call. The holotype (ZSM 521/2016) was collected after recording a call in primary low-altitude rainforest, under

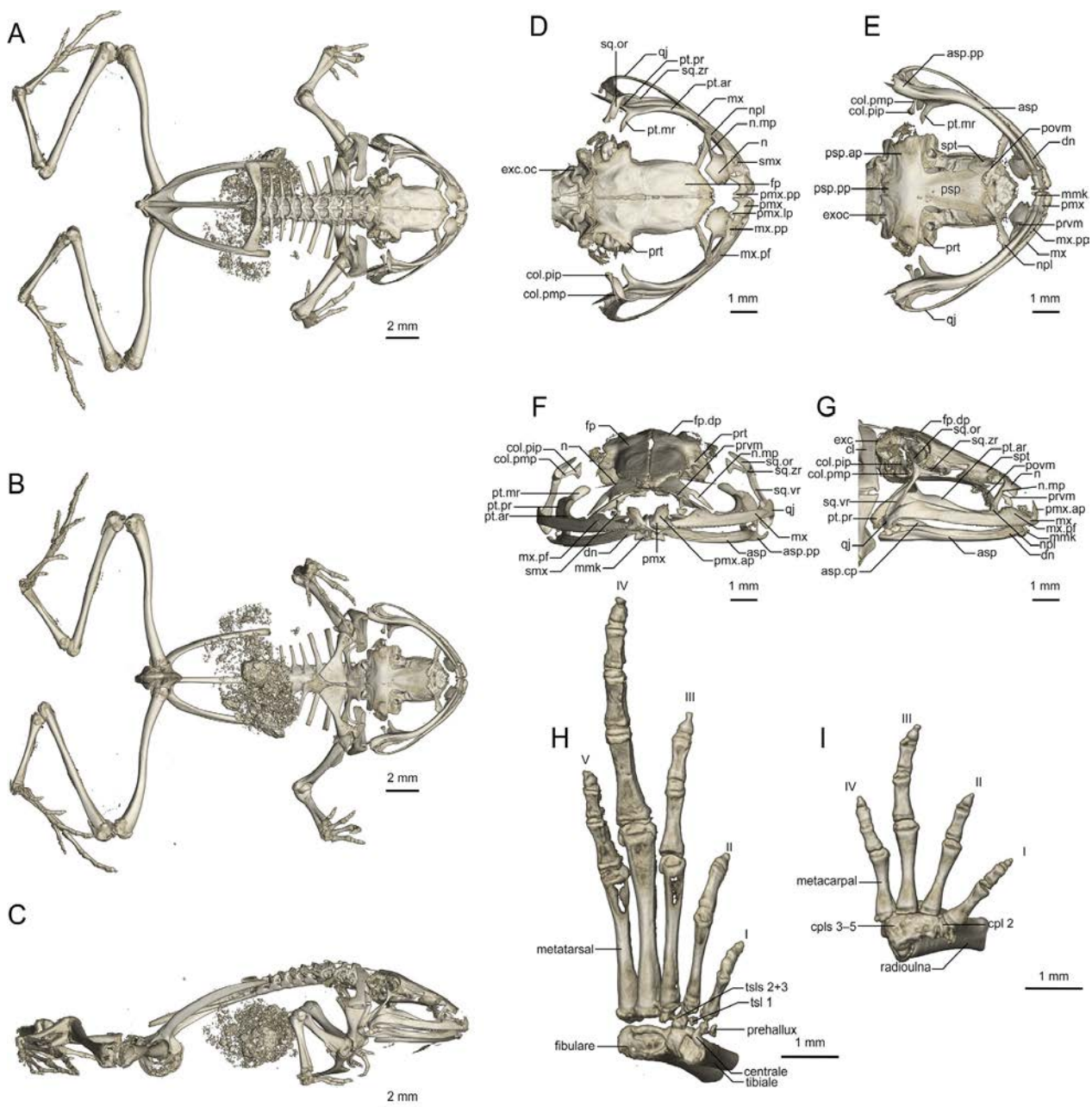


Figure 28. Skeleton of *Rhombophryne mavokely* sp. nov. paratype ZSM 517/2016 (ZCMV 15088). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** include dense soil and stones. Abbreviations are given under Materials and Methods.

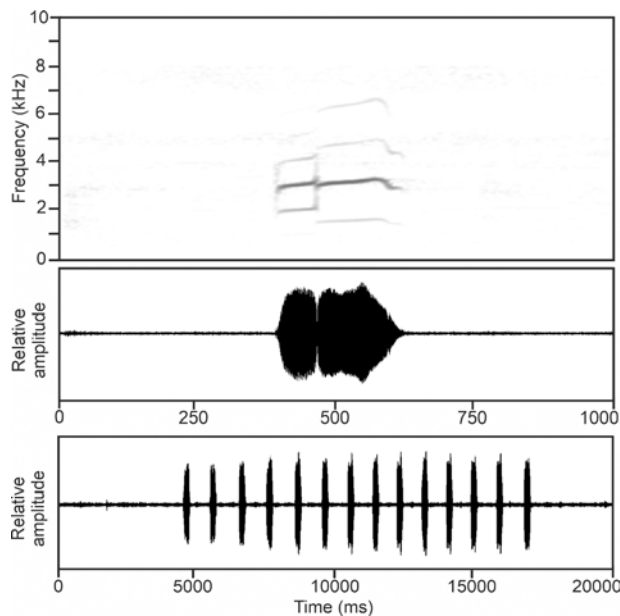


Figure 29. Advertisement calls of *Rhombophryne mavokely* sp. nov. (ZSM 521/2016), recorded in Marojejy National Park in 2016. Top: audiospectrogram and corresponding oscillogram of one advertisement call from a regular call series at 1000 ms time scale. Bottom: oscillogram at 20,000 ms time scale depicting a regular call series containing fourteen calls. Recording band-pass filtered at 500–8500 Hz.

leaf litter, during dry weather. It was not seen calling, but was collected from the location of the call emission, and the call is similar to but distinctly different from that of *R. savaka*, and we are therefore confident that it is assignable to this species and this individual. The advertisement call, recorded on 23 November 2016 (20:20 h) at an unknown air temperature, consists of a tonal note of moderate duration emitted in regular call series (Fig. 29). Each call exhibits some amplitude modulation with a very short intermittent drop in energy occurring after about one third of the call's duration. This drop in energy is also visible in the audiospectrogram, with frequencies slightly being shifted in the last two thirds of the call's duration when compared to the first third and showing a somewhat different structure of harmonics. Overall, slight upward frequency modulation is evident within each call, with a short terminal drop. Numerical parameters of one complete call series and 16 analysed calls are as follows: call duration (= note duration) 231–262 ms (245 ± 8 ms); inter-call intervals within regular call series 623–808 ms (701 ± 59 ms); number of calls per call series 14; duration of regular call series 12,583 ms; dominant frequency 3178–3265 Hz (3219 ± 28 Hz); prevalent bandwidth 1500–8400 Hz; frequency bands in the first third of the call recognizable at approximately 2050, 3100, 4200, 5200 and 6140 Hz, in the last two thirds of the call at approximately 1650, 3250, 4800, 6400, and 8100 Hz.

Etymology. The Malagasy adjective *mavokely* meaning 'pink', in reference to the pinkish colouration of this species in life and in preservative, especially on the legs. 'Mavokely' is also a linguistic quirk of the Malagasy lan-

guage, as it is derived from the juxtaposition of the components *mavo* meaning 'yellow, and *kely* meaning 'small'. This name thus forms a double entendre, by referring also to the small stature and yellowish colouration of some individuals in life. Used as an invariable noun in apposition.

Distribution. This species is currently definitively known only from (1) Marojejy National Park (type locality). However, photographs of specimens tentatively referable to this species from (2) Anjanaharibe-Sud (14.72°S, 49.46°E, ca 1430 m a.s.l.) and (3) Simpona Lodge in Makira Natural Park (near 15.1992°S, 49.6208°E, ca 410 m a.s.l.) have been sent to us by Éric Mathieu and Lucas Pasteur, respectively (Fig. 27), suggesting that it may have a somewhat larger distribution in the rainforests of northeastern Madagascar. Elevation: ca 310–402 m a.s.l., but the record from Anjanaharibe-Sud would add ca 1000 m elevation to ca 1430 m a.s.l., if verified.

Natural history. *Rhombophryne mavokely* is a semi-fossorial or detriticolous species found in low- to mid-elevation humid forest. All specimens were found in the leaf litter, and this species probably spends most of its life in the interstitial layer between the surface of the leaf litter and the soil. ZSM 517/2016 was collected less than a metre from a curled-up snake, *Alluaudina bellyi*, which is likely to prey upon this and other leaf-litter dwelling frog species (Hutter et al. 2018). We found *Rhombophryne mavokely* sp. nov. at consistently lower elevation than *R. savaka*, but it is not clear if there is a contact zone between the two species at around 400–450 m a.s.l., and records from higher elevations mentioned above remain to be verified.

Rhombophryne sp. Ca16

Remark. This candidate species was identified by Belluardo et al. (2022) based exclusively on GenBank sequences of the specimen AMNH A181903 (RAX 10368), a specimen registered as '*Rhombophryne* cf. *minuta*' on the AMNH online database portal (<https://emu-prod.amnh.org>, accessed 25 January 2023). It was referred to as '*Rhombophryne* sp. 16' by Belluardo et al. (2022) and 'UCS "Sp. CA16"' by Carné and Vieites (2024). It has been sequenced for mitochondrial markers 16S3' and 16S5' (KM509192), COI (KM509860), and nuclear genes BDNF (KM509332), TYR (KM509984), SIAH1 (KM509728), and C-MYC (KM509466). It was collected in the Andapa area (given as a county in the AMNH online database, without precise coordinates) of the Sava Region, northeastern Madagascar by C.J. Raxworthy. Based on its phylogenetic position (Fig. 2; Belluardo et al. 2022), it appears to be a member of the *R. mangabensis* species complex, but we have not been able to examine this specimen, and therefore are not able to assess it taxonomically. Genetically, it differs by >7.95% uncorrected p distance in the 16S3' fragment from all other *Rhombophryne* species (Table S2). It is distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in

the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'A' at site 293, 'G' at site 483, and 'A' at site 539. No diagnostic sites were identified for 16S3'.

Osteology of the *Rhombophryne testudo* species group

Material examined. This description is based on the following specimens: *R. coudreaui* (MNHN 1937.19; Fig. 14), *R. mangabensis* (ZSM 470/2005; Fig. 19), *R. maraorao* **sp. nov.** (MRSN A2115; Fig. 25), *R. matavy* (ZSM 1628/2008; Fig. 16), *R. mavokely* **sp. nov.** (ZSM 517/2016; Fig. 28), *R. savaka* (ZSM 519/2016; Fig. 22), *R. testudo* (SMF 4241; Fig. 11). The right mandible of ZSM 470/2005, left tibiofibula of SMF 4241, and numerous bones of MNHN 1937.19 are broken.

The *Rhombophryne testudo* species group exhibits remarkably high levels of osteological variation. Especially *R. testudo* itself has highly derived skeletal morphology, only a few elements of which have been described previously (Howes and Ridewood 1888; Parker 1934). Here, we provide a description of the osteology of the group that highlights particularly diagnostic features of each species.

The skeleton of members of this group is generally robust and dorsoventrally compressed. The skull is broader than long, extremely so in *R. testudo* and *R. matavy*. In *R. testudo* and, to a slightly lesser extent in *R. matavy*, there are obvious osteological adaptations to a fossorial lifestyle, with hyperossification of the skull and extreme broadening of several bones of the skull. Remarkably, the skull of *R. coudreaui* and *R. maraorao* **sp. nov.** is not so strongly adapted, despite their externally similar, highly fossorial morphology. The more terrestrial *R. mangabensis*, *R. savaka*, and *R. mavokely* **sp. nov.** do not show obvious adaptations for fossoriality.

Dorsal investing bones. Nasals closely abutting the frontals in most species (exceptions: *R. maraorao* **sp. nov.**, *R. mavokely* **sp. nov.**), in contact with the sphenethmoid in *R. testudo*, *R. mangabensis*, *R. savaka*, *R. coudreaui*, and *R. matavy*. The maxillary process of the nasal reaches the maxilla in *R. testudo* and nearly in *R. matavy*. The anterior edge of the maxillary process is hollowed out to be concave in *R. maraorao* **sp. nov.** and *R. coudreaui* (a feature unique to these two species).

The frontoparietals are hyperossified in *R. testudo*, with a substantial medial ridge at their suture; to a lesser degree and without the median ridge in *R. matavy*. The lateral ventrally descending flange of the frontoparietal extends almost the full length in *R. testudo*, *R. maraorao* **sp. nov.**, and *R. matavy*. The dorsal processes of the frontoparietals range from small bumps in *R. mavokely* **sp. nov.** to almost horn-like projections in *R. testudo*, with a further accessory structure that is flared dorsally on top of the lateral flange of the frontoparietal in that species.

Neurocranium. The sphenethmoid varies from fully ossified and covering the entire wall of the braincase

(*R. testudo*, *R. matavy*, *R. maraorao* **sp. nov.**), to strongly ossified and covering most of the wall of the braincase (*R. coudreaui*, *R. mangabensis*, *R. savaka*), to strongly ossified but only covering the anterior half of the wall of the braincase (*R. mavokely* **sp. nov.**).

The exoccipital is surprisingly weakly ossified in the otherwise hyperossified skull of *R. testudo*. It is ossified in *R. savaka*, *R. mangabensis*, and *R. matavy*, but not the other species (but this is not a diagnostic feature, as ossification in this bone varies within species). The occipital condyles are enlarged in *R. testudo* and *R. matavy*. The exoccipitals do not meet medially. The prootic is well ossified in all species.

The septomaxilla is strongly reduced in *R. testudo* to a diminutive element lacking the medial ramus (and apparently unossified on the right side, see Fig. 11D). The medial ramus is apparently also missing from *R. maraorao* **sp. nov.**, *R. mangabensis*, and *R. coudreaui*, but it is present in *R. matavy*; however, see our previous comments on the septomaxilla and its ossification, and why it should not be relied upon as a diagnostic feature in micro-CT scans (Scherz et al. 2017a).

The columella is rather similar in shape and structure among species. It nearly touches the otic ramus of the squamosal in *R. testudo*.

Ventral investing and palatal bones. The cultriform process of the parasphenoid is extremely broad in *R. testudo* and *R. matavy*, broad in *R. coudreaui* and *R. maraorao* **sp. nov.**, and not expanded in *R. mavokely* **sp. nov.**, *R. mangabensis*, and *R. savaka*.

The anterior portion of the vomer is triradiate, nearly crescentic in some species. The posterior portion is generally sigmoid, but rather straight in *R. testudo* and *R. matavy*. It bears distinct teeth in all species except *R. testudo*, where there are strong, bumpy ventral ridges. There is a distinct diastema in the vomerine teeth of *R. savaka*, *R. mavokely* **sp. nov.**, and *R. coudreaui*, and a small gap that may be a diastema in *R. mangabensis*. The neopalatine, which lies dorsally on top of the vomer, is distally expanded in *R. testudo* and *R. matavy*.

Maxillary arcade. Maxillary teeth are present in all species except *R. testudo*. The premaxilla is small in *R. testudo*. The maxilla itself is extremely deep in *R. testudo*, much more so than any other species. The facial process of maxilla is bluntly (*R. coudreaui*, *R. mangabensis*, *R. maraorao* **sp. nov.**, *R. mavokely* **sp. nov.**, *R. savaka*, *R. mangabensis*), or sharply and triangularly (*R. matavy*, *R. testudo*) raised, in *R. testudo* in broad dorsal contact with the maxillary process of the nasal (closely approaching in *R. matavy*, not in contact in any other species). The contact with the quadratojugal is extremely fortified in *R. testudo*, and is strong in all other species.

Suspensorium. The anterior ramus of the quadratojugal in *R. savaka* and *R. mavokely* **sp. nov.** has a concave ventral edge in lateral view; it is rather straight in the other species, except *R. testudo*, where it is highly unusual in shape, curving ventrally, in the opposite direction to its normal curve in lateral perspective (Fig. 11G). The quadratoju-

gal-squamosal contact in *R. testudo* is nearly the full length of the bone; in the other species, it is brief and posterior.

The squamosal is ventrally hugely fortified in *R. testudo* and to a lesser degree in *R. matavy*, with a strongly expanded ventral ramus. The otic and zygomatic rami form a scooped structure in dorsal view in all species of this group. The zygomatic ramus is longer than the otic in *R. testudo*, but they are more or less the same length in the other taxa. In all species, the otic ramus ascends and flattens dorsoventrally. It is flat ended in *R. testudo*, but bluntly rounded in all other species.

The pterygoid is likewise extraordinary in *R. testudo*, with a massively expanded posterior ramus and expanded medial ramus. The medial ramus is exceptionally long in *R. matavy*.

Mandible. The mentomeckelians of *R. testudo* are at an almost right-angle to their normal position, forming essentially blunt caps for the angulosplenials. They are ‘normal’, hourglass-shaped small elements forming the mandibular symphysis medially in all other species. The dentary is either totally reduced or short and thin in *R. testudo*. It is poorly ossified in *R. maraorao* **sp. nov.** and *R. matavy*.

The angulosplenial is posteriorly strongly expanded in *R. testudo*, with a deep posterolateral facet that gives it a rather unusual shape. The coronoid process is strongly raised in that species. The coronoid process of *R. mavokely* **sp. nov.** is more strongly raised than that of *R. savaka* or *R. mangabensis*. The posterior process (articular facet) is moderately expanded in all species except *R. testudo*, where it is strongly expanded.

Pectoral girdle. The coracoids of *R. testudo* and *R. matavy* have a long medial contact facet (unossified), much longer than other members of the species group. Clavicles are present and curved in *R. mavokely* **sp. nov.** and *R. savaka*, reduced (or poorly ossified) in *R. mangabensis*, but absent in all other species. The scapula and cleithra do not differ sufficiently for further comment.

The humeral crests are strongly developed in all species, though to the greatest extent in *R. testudo*. The crista ventralis is strong, extending one third (*R. mavokely* **sp. nov.**), around half (*R. savaka*, *R. maraorao* **sp. nov.**, *R. mangabensis*), or over half (*R. testudo*, *R. coudreaui*, *R. matavy*) the length of the bone. The crista lateralis is particularly strong in *R. testudo* and *R. matavy*. The radioulna varies in dimensions, but not substantially in structure among species.

Carpals 2, 3–5, element Y, radiale and ulnare present. Howes and Ridewood (1888) asserted that the carpus of *Rhombophryne testudo* has carpal 2 fused into the joint 3–5 element of most other frogs, but we do not find this to be the case. However, *R. coudreaui* does not seem to have a carpal 2 (Fig. 14I), so it may be that Howes and Ridewood (1888) were examining bones of that species. The carpal elements of the examined specimen of *R. maraorao* **sp. nov.** were not sufficiently ossified to study the bones of the hands (Fig. 25I). The prepollex of *R. savaka*, *R. mangabensis*, *R. testudo*, *R. matavy*, and *R. coudreaui* is large and subtriangular. The digital formula of all spe-

cies is the same (2-2-3-3), and terminal phalanges consistently end with small knobs.

Vertebral column. Transverse processes of V2 perpendicular to body axis in all species except *R. savaka*, where they are angled anteriorly. All transverse processes long, much longer than the centra are wide in all species except *R. mangabensis*, *R. savaka*, and *R. maraorao* **sp. nov.**, where the posterior four presacrals have transverse processes slightly shorter than the centrum is wide. The sacrum is as wide as V4 in all species, its anterior edge straight, angled either slightly anteriorly (*R. savaka*) or posteriorly (all other species). The diapophyses are not strongly flared, and the posterior edge is at most slightly curved. The urostyle has a dorsal ridge along its entire length in *R. testudo* and *R. maraorao* **sp. nov.**, but the posterior quarter is free in all other species.

Pelvic girdle. Iliac shafts with strong dorsal crests in all species except *R. mavokely* **sp. nov.** and *R. savaka*. The oblique groove is practically absent and dorsal prominence absent in all species except *R. matavy*, where there is a distinct dorsal prominence and corresponding oblique groove, and *R. mangabensis*, where an oblique groove is recognisable, but there is no dorsal prominence. The femur has a slight posterior ridge in all species except *R. savaka*, *R. mavokely* **sp. nov.**, and *R. mangabensis*. The tibiofibula and tarsus do not bear further comment. The toe formula is standard (2-2-3-4-3). The prehallux of *R. testudo* and *R. matavy* is a dramatically expanded single element. In *R. savaka*, *R. mangabensis*, and *R. coudreaui* it is comprised of two elements. The state in *R. maraorao* **sp. nov.** and *R. mavokely* **sp. nov.** cannot be commented upon because of the low ossification. Terminal phalanges of all toes short and knobbed.

Rhombophryne laevipes species group

Rhombophryne laevipes (Mocquard, 1895)

Figures 2, 4–7, 30–35

Mantiphrys laevipes Mocquard, 1895

Mantophrys laevipes — Mocquard (1909), subsequent incorrect spelling

Mantipus laevipes — Guibé (1946)

Plethodontohyla laevipes — Blommers-Schlösser and Blanc (1991)

Rhombophryne laevipes — Frost et al. (2006)

Remarks. Type species of *Mantiphrys* Mocquard, 1895. Parker (1934) considered *R. laevipes* to be a synonym of *Mantipus hildebrandti* Peters, 1883, and it was, in essence, described as such by Mocquard; the description given is of a specimen assigned to *M. hildebrandti*, but in a footnote Mocquard notes the numerous points of difference from Peters’ description, and states that, if Peters’ description is found to be accurate, then he would propose to name the new form *Mantiphrys laevipes*

(Mocquard 1895). The name was resurrected by Guibé (1946). Today, *Mantipus hildebrandti* is considered a junior synonym of *Plethodontohyla inguinalis* Boulenger, 1882. We have verified this based on re-examination of the holotype of *M. hildebrandti*, ZMB 10440, which was reported lost by Glaw and Vences (1992) but was rediscovered by Bauer et al. (1996).

Some specimens formerly thought to be juveniles of this species have been reidentified in this study as *R. ellae*.

Holotype. MNHN 1893.285, an adult male, collected on an unknown date on ‘Montagne d’Ambre’, Diana Region, northern Madagascar by Mr Alluaud and Mr Belly (Figs 30, 31, 34).

Paratypes. None.

Referred specimens. ZSM 902/2003 (FGMV 2002.0916), a juvenile specimen, collected on 19 Feb-

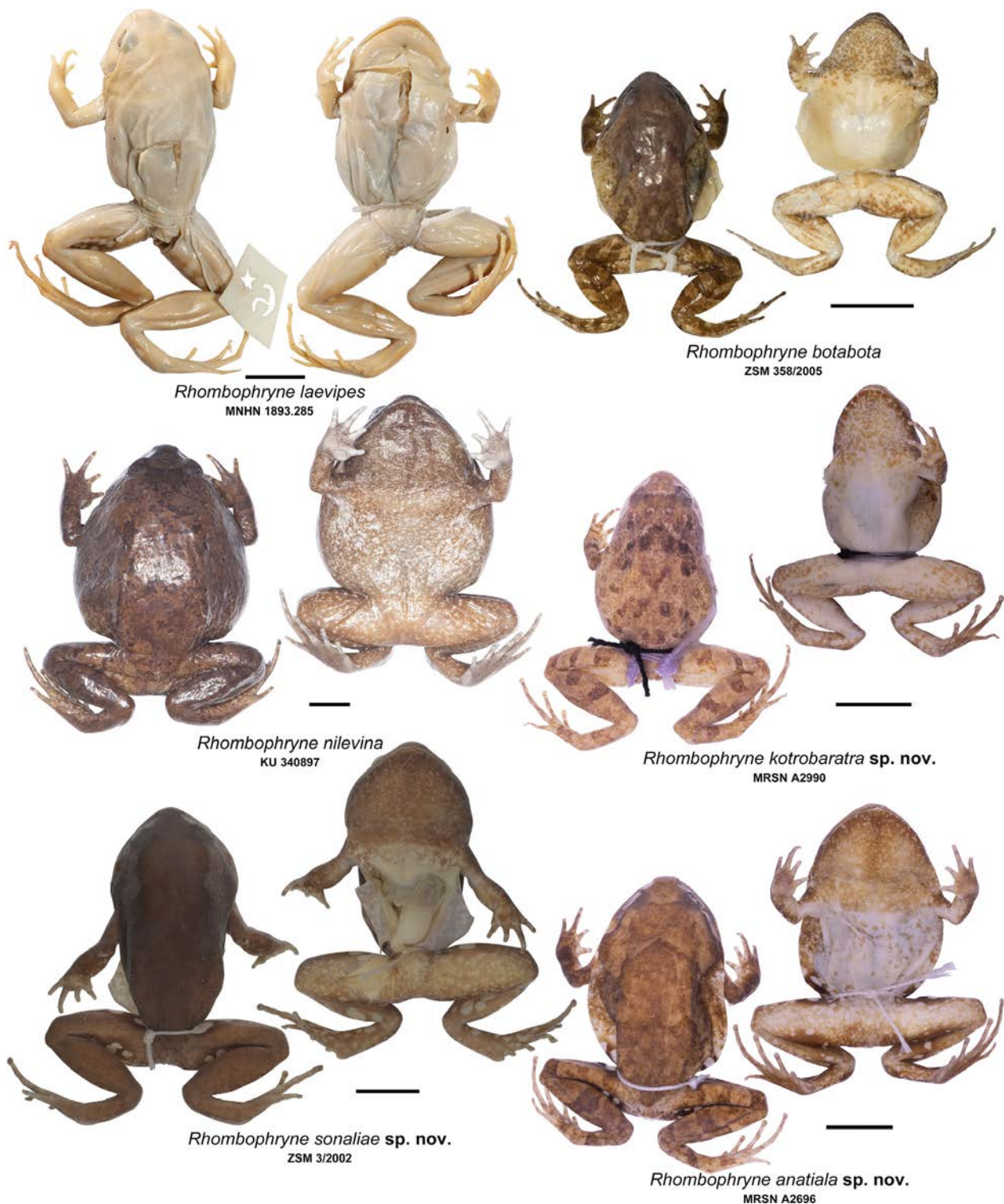


Figure 30. Name-bearing type specimens of species in the *Rhombophryne laevipes* species group in dorsal (left) and ventral (right) views. Scale bars = 10 mm.

ruary 2003, and ZSM 925/2003 (FGMV 2002.0998), an adult female, collected on 19–20 February 2003 on Montagne d'Ambre (no precise coordinates), Diana Region, northern Madagascar, by F. Glaw, R.D. Randrianaina, and A. Razafimanantsoa; ZSM 200/2004 (FGZC 387) and ZSM 218/2004 (FGZC 423), a juvenile and an unsexed individual, collected on 19 February 2004 on the Voie des Milles Arbres (12.5200°S, 49.1756°E, 1052 m a.s.l.), Montagne d'Ambre National Park, Diana Region, northern Madagascar, by F. Glaw, M. Puente, R. Randrianaina, A. Razafimanantsoa; ZSM 2188/2007 (FGZC 1283), a juvenile, collected on 13 March 2007 near the Cascade Antakarana (ca 12.52°S, 49.17°E, ca 1030 m a.s.l.), Montagne d'Ambre National Park, Diana Region, northern Madagascar, by P. Bora; ZSM 77/2018 (MSZC 0648), adult male (call voucher), collected at 14:56 h on 19 November 2017 near the Gîte d'Étape (12.5204°S, 49.1718°E, 1066 m a.s.l.), Montagne d'Ambre National Park, Diana Region, northern Madagascar, by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, and A. Rakotoarison (Fig. 32A–C, 33A–C); UADBA-A 62340 (MSZC 0526), a subadult, collected at night on 25 December 2017 at 12.5205°S, 49.1890°E, 1028 m a.s.l. in Montagne d'Ambre National Park, Diana Region, northern Madagascar, by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, and A. Rakotoarison (Fig. 32D–F); UAD-

BA-A 62493 (MSZC 0654), a juvenile, collected on 19 November 2017 at 12.5206°S, 49.1862°E, 1008 m a.s.l. in Montagne d'Ambre National Park, Diana Region, northern Madagascar, by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, and A. Rakotoarison (Fig. 32G–I); UADBA-A-FGZC 1052, individual of unknown sex or maturity, collected on 25 February 2007 on Montagne d'Ambre in a pitfall trap (precise coordinates not available), Diana Region, northern Madagascar, by F. Glaw, P. Bora, H. Enting, J. Köhler, and I. Knoll.

The specimen ZSM 853/2003 (FGMV 2002.823), an adult female, collected on 3 February 2003 at 'Camp 1' (13.9770°S, 48.4220°E, 751 m a.s.l.), Manongarivo Massif, Diana Region, northern Madagascar, by F. Glaw, R.D. Randrianaina, and M. Vences (Fig. 33H–I), is phylogenetically sister to all other specimens collected so far (Fig. 2), and differs genetically from all other specimens of *R. laevipes* by 1.24–2.46% in the 16S3' marker, and 4.90–5.45% in the 16S5' marker, but is consistently recovered as conspecific in species delimitation, and is therefore assigned to this species. A second specimen from the other side of this mountain, BMNH 1987.2300, an unsexed adult, collected on 25 February 1988 at 'Camp B' (14.067°S, 48.283°E, 350 m a.s.l.), Manongarivo Massif, Sofia Region, northern Madagascar, by C.J. Raxworthy, agrees morphologically, and is consequently also assigned to this species.

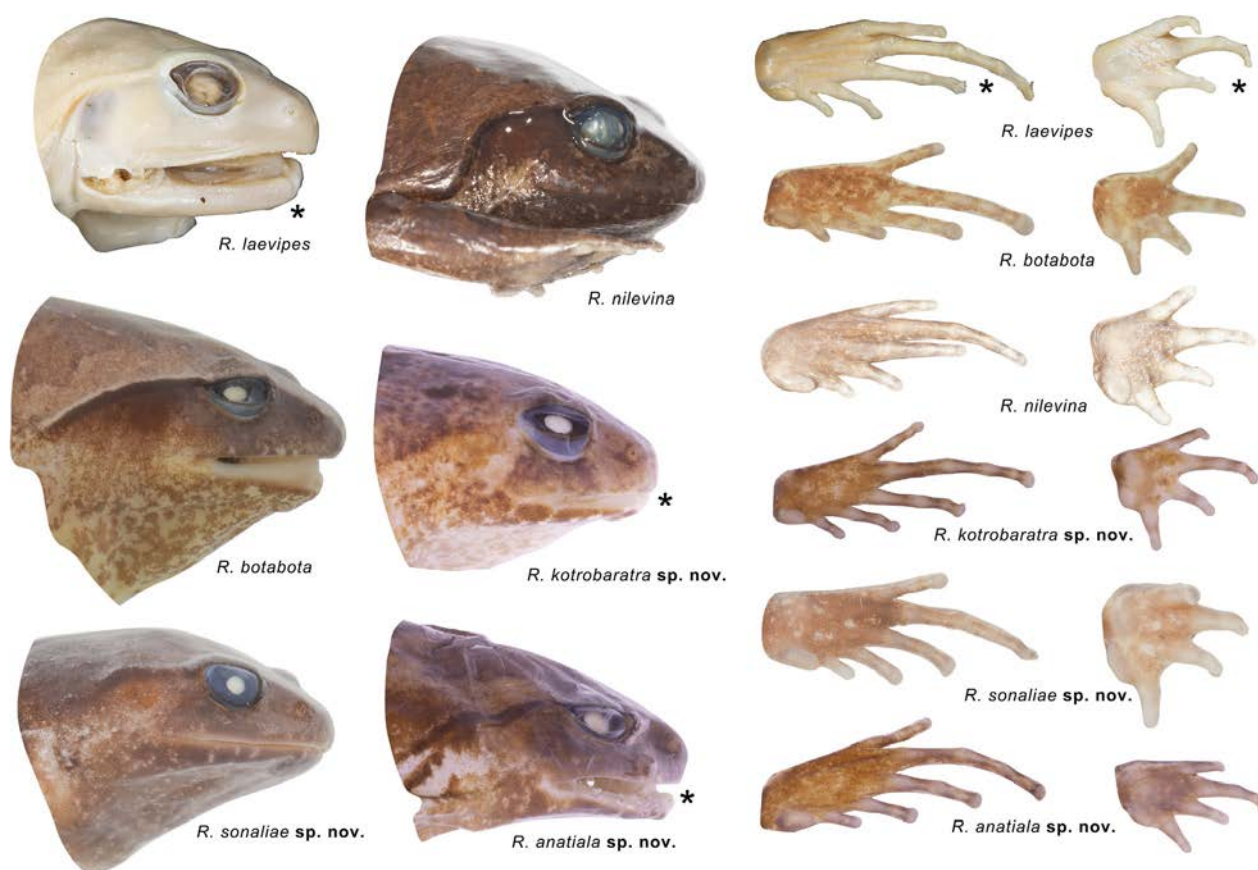


Figure 31. Ventral views of hands and feet, and lateral views of heads of name-bearing type specimens of members of the *Rhombophryne laevipes* species group. Not to scale. * = mirrored for conformity.

Assignment of specimens. ZSM 218/2004 is used as the reference specimen for this species in 16S rRNA barcoding (16S3' and 16S5' EU341104; Vieites et al. 2009) and COI barcoding (COI KF611587; Perl et al. 2014). All of the referred material except ZSM 853/2003 is collected at the general type locality. The adult specimens conform with the holotype in overall morphology, and especially in the presence of white spots on the hidden surfaces of the legs. Assignment of UADBA-A-FGZC 1052 (not examined morphologically), UADBA-A 62340 (MSZC 0526), UADBA-A 62493 (MSZC 0654), ZSM 77/2018, and ZSM 853/2003 is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 77/2018 has been

sequenced with the FrogCap hybrid capture probe set and is included in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. laevipes* group, this species has a rather isolated position, and is probably sister to a subclade containing various other species based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) large body size, adult SVL 42.8–50.8 mm; (2) head wider than long (HW/HL 1.57–1.84); (3) moderately small eyes (ED/HL 0.30–0.34); (4) relatively long hindlimbs (HIL/SVL 1.62–1.86); (5) small inner metatarsal tubercle (IMTL/FOL 0.08–0.11); (6)

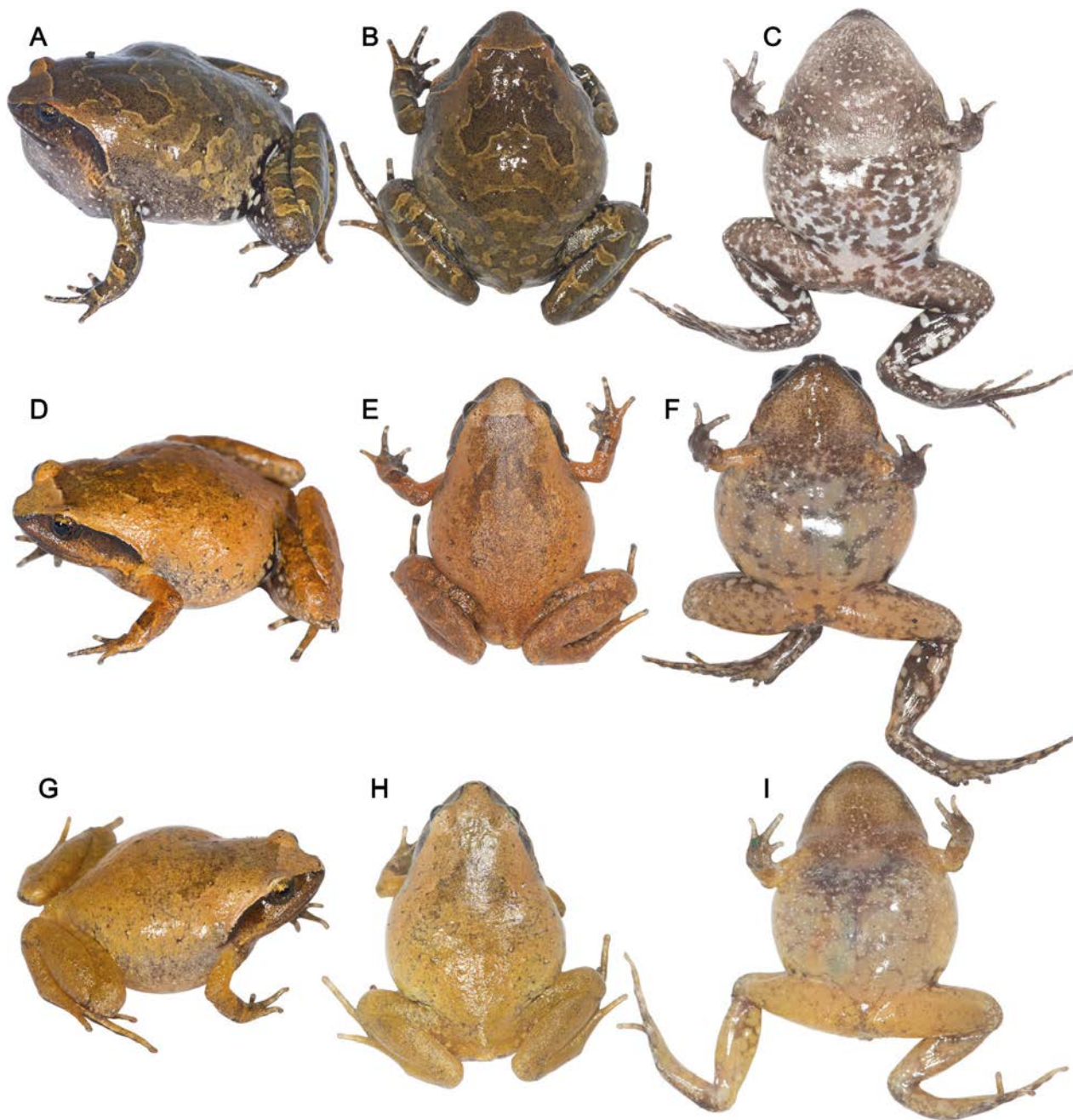


Figure 32. *Rhombophryne laevipes* in life. Not to scale. All photographed in Montagne d'Ambre National Park. **A–C** adult male ZSM 77/2018 (MSZC 0648) in **A** dorsolateral, **B** dorsal, and **C** ventral view; **D–F** subadult UADBA-A 62340 (MSZC 0526) in **D** dorsolateral, **E** dorsal, and **F** ventral view; **G–I** juvenile UADBA-A 62493 (MSZC 0654) in **G** dorsolateral, **H** dorsal, and **I** ventral view.

outer metatarsal tubercle absent; (7) second finger shorter than or equal in length to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin smooth with very few raised bumps in some individuals; (10) absence of chin

barbels; (11) absence of pronounced superciliary spines; (12) presence of white inguinal spots on a dark brown background; (13) presence of white spots on the posterior thigh and ventral surface of the shanks; (14) unfortified

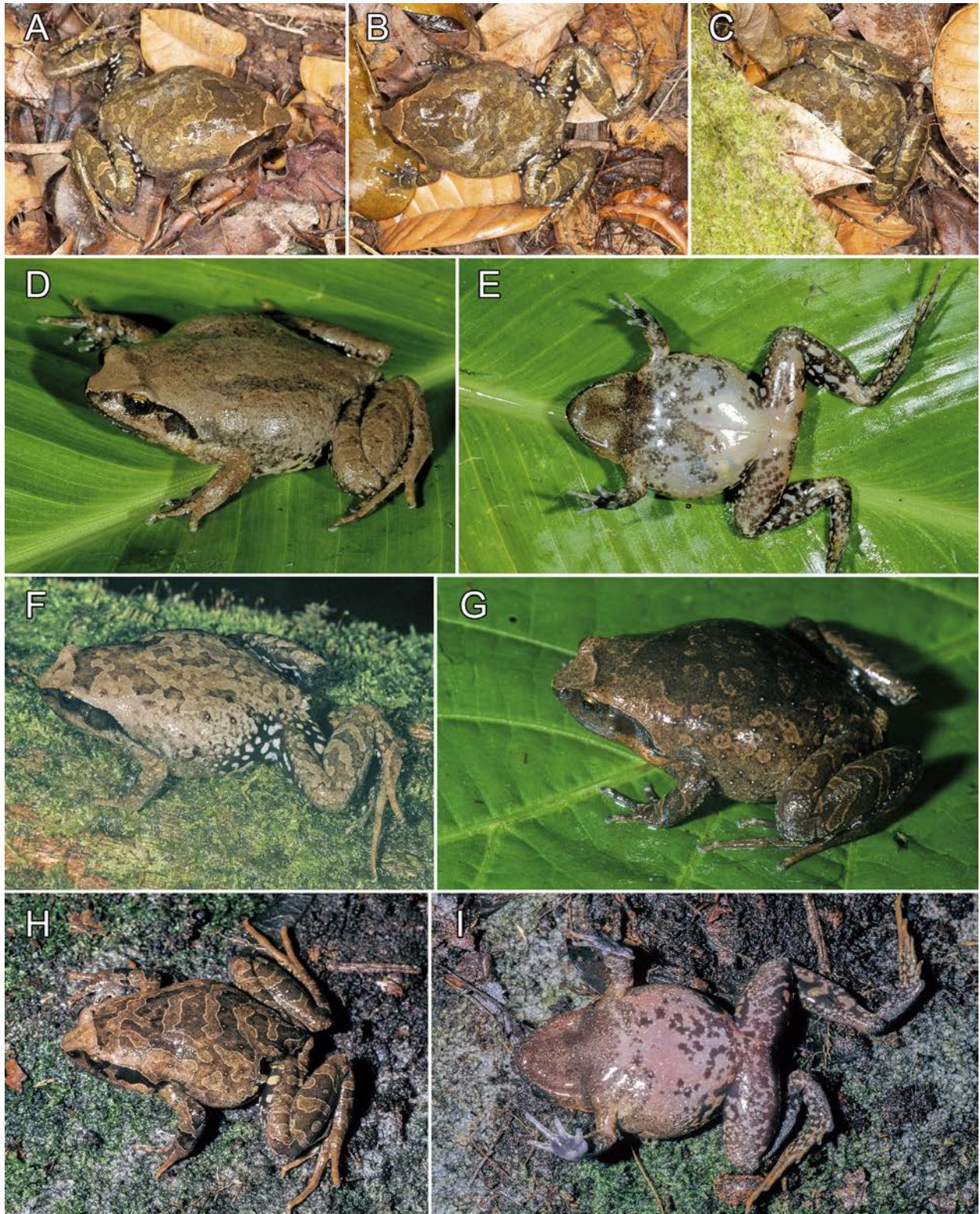


Figure 33. *Rhombophryne laevipes* in life. **A–C** adult male ZSM 77/2018 (MSZC 0648) from Montagne d'Ambre in **A** dorsolateral and **B** dorsal view, and **C** in the process of pushing its way beneath a mossy log; **D, E** adult putative female from Montagne d'Ambre, photographed in 2004, in **D** dorsolateral and **E** ventral view; **F** unsexed adult from Montagne d'Ambre, in dorsolateral view, photographed in 1994; **G** unsexed adult from Montagne d'Ambre, in dorsolateral view, photographed in 2003; **H, I** adult female ZSM 853/2003 (FGMV 2002.823) from Manongarivo in **H** dorsolateral and **I** ventral view.

skull without expansion of maxilla or posterior process of angulosplenial; (15) clavicles present, thin, curving, and (16) advertisement call (based on 12 analysed calls by one individual) highly pulsed, with (17) call duration 208–254 ms, (18) inter-call interval 1563–2186 ms, and (19) dominant frequency 612–631 Hz.

Rhombophryne laevipes is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* [MZ751042](#)): in 16S5', 'T' at site 354, 'G' at site 395, and 'C' at site 611; in 16S3', 'G' at site 1075, 'T' at site 1086, and 'G' at site 1165.

Diagnosis. Within the genus *Rhombophryne*, *R. laevipes* can easily be distinguished from *R. testudo*, *R. coudreaui*,

R. matavy, and *R. maraorao* **sp. nov.** by smooth skin (vs rough), absence of chin barbels (vs presence), much longer hindlimbs (HIL/SVL 1.62–1.86 vs 1.10–1.41), and presence of white spots in the inguinal region and on the ventral shank (vs absence); from *R. mangabensis*, *R. mavokely* **sp. nov.**, *R. savaka*, *R. proportionalis*, and members of the *R. ellae* and *R. minuta* species groups by much larger adult body size (SVL 42.8–50.8 mm vs 11.0–30.1 mm), and presence of white spots in the inguinal region and on the ventral shank (vs absence); and from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence), and presence of white spots in the inguinal region and on the ventral shank (vs absence).

Within the *R. laevipes* species group, *R. laevipes* may not be distinguishable from *R. nilevina* morphological-

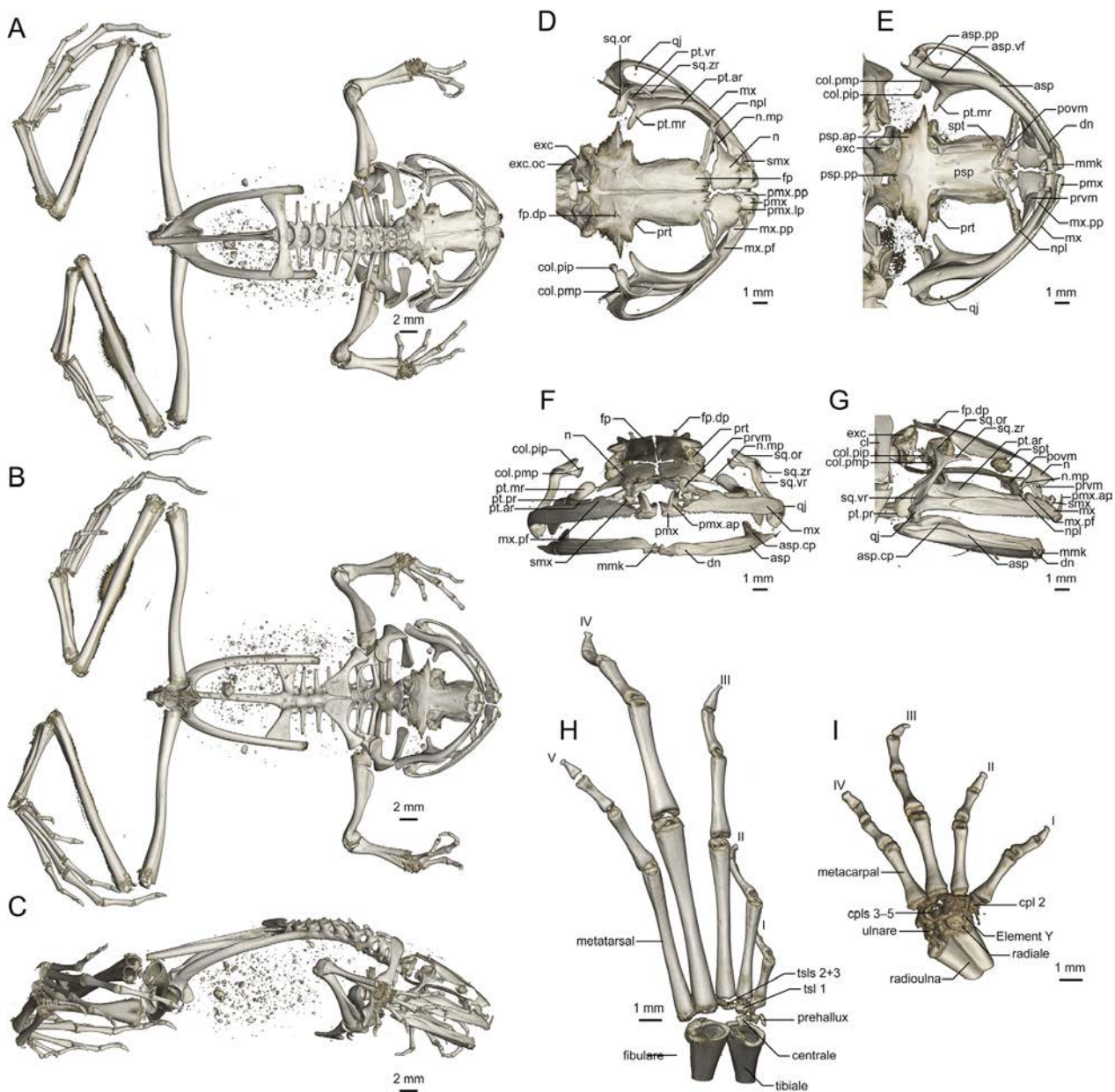


Figure 34. Skeleton of *Rhombophryne laevis* holotype MNHN 1893.285. **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** include soil and small stones. Abbreviations are given under Materials and Methods.

ly (traits formerly thought to be diagnostic of the latter species are now known to be variable and overlap with *R. laevipes*; see the account, below), but can be distinguished by its shorter advertisement call (call duration 208–254 ms vs 526–534 ms), much shorter inter-call interval (1.5–2.2 s vs 42–126 s), and higher dominant frequency (612–631 Hz vs 526–534 Hz). It can be distinguished from *R. botabota* by the presence of white spots on the inguinal region, posterior thigh, and ventral shank (vs black inguinal ocelli or absence of inguinal spots, and no remarkable colour on the hindlimbs), and pulsed (vs tonal) advertisement call that is longer (call duration 208–254 ms vs 161–201 ms) and lower in dominant frequency (612–631 Hz vs 1256–1291 Hz). For distinction from newly described members of this species group, see their respective descriptions below.

Redescription of the holotype. An adult male specimen in a good state of preservation, though strongly faded (Figs 30, 31). An L-shaped incision made in the dorsal skin, a further such incision made over the pectoral girdle to expose the pectoral girdle, and a straight incision along the right flank. The rictus is ripped on both sides, and a small pinhole through the middle of the chin.

Body robust. Head wider than long (HW/HL 1.62). Eyes quite large (ED/HL 0.31), pupils large, round. Snout rounded in dorsal and lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril closer to tip of snout than to eye, slightly protuberant. Tympanum distinct, oval, TDH/ED 0.57. Supratympanic fold distinct, strongly raised, running straight from posterior corner of eye over tympanum, curving ventrally posterior to the tympanum towards the insertion of the arm. Superciliary spines absent. Dorsal skin smooth. Ventral skin very finely granular. Tongue broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, varying in height, separated at the midline by a small gap. Choanae ovoid, placed laterally in the roof of the mouth.

Forelimbs relatively long (FARL/SVL 0.403), strongly built. Fingers without webbing, moderately long, relative lengths $1 < 2 < 4 < 3$, second finger slightly shorter than fourth. Finger tips not expanded, rounded. Finger subarticular tubercles distinct, whitish, flat; inner metacarpal tubercle broad and flat, outer metacarpal/palmar tubercle indistinct. Hind limb strong, tibiotarsal articulation reaching tympanum when adpressed anteriorly along the body. TIBL/SVL 0.524. Inner metatarsal tubercle present, oblong, somewhat bulging. Outer metatarsal tubercle absent. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles distinct, slightly raised; toe tips not enlarged, rounded.

After at least 128 years in preservative, the colouration of the specimen is largely lost and the skin rather translucent, especially ventrally. The only traces of colouration that remain are on the legs: The posterior thighs are dark brown with several large white spots on the ‘hidden’ areas (not symmetrical). The left shank and foot are dark brown dorsally, and ventrally the shanks are also dark brown with round whitish spots. Colouration in life unknown.

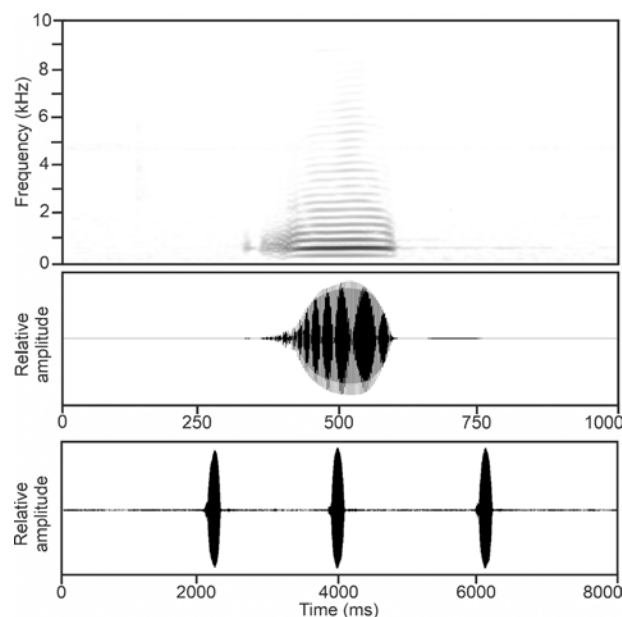


Figure 35. Advertisement calls of *Rhombophryne laevipes*, recorded on Montagne d’Ambre in 2017. Top: audiospectrogram and corresponding oscillogram of one advertisement call from a regular call series at 1000 ms time scale. Bottom: oscillogram at 8000 ms time scale depicting a regular call series containing three calls. Recording high-pass filtered at 110 Hz.

Variation. SVL 42.8–50.8 mm ($n = 5$). For variation in other measurements, see Table S6. A dark brown chevron is often present over the scapular region (Figs 32, 33), and the side of the head is usually dark brown below the supratympanic fold, but lighter brown ventrally along the mouth and rictus (Figs. 32A, D, G, 33A, D, F, H). The inguinal region is dark brown with white spots, and the posterior thigh (e.g., Fig. 33A, B, F, H) and ventral shank also have distinctive white or orange spots. These are present also in juveniles (e.g., Fig. 32I). The dorsal colouration can be highly reticulated dark patterns (e.g., Fig. 33G, H), or just scattered dark spots (e.g., Fig. 33F). The ventral abdomen is highly variable, usually with numerous dark spots, and large unpigmented areas (Figs 32C, F, I, 33E, I). The dorsal thigh and shank showed dark brown crossbands in all adult specimens we examined, but these were only very weakly visible in the juvenile UADBA-A 62493 (MSZC 0654) (Fig. 32G–I). Juveniles and subadults tend to be quite orange in colour (Fig. 32D–I, see also image captioned ‘*Rhombophryne* sp., Montagne d’Ambre’ on page 448 of Glaw and Vences 2007), often with an X-shaped marking (which can be indistinct, cf. Fig. 32I) on the dorsum. The areas that lack dark colouration appear to correspond to those that appear white in adults. Round spots on the ventral shank are less distinct in juveniles, and apparently become more distinct with age (Fig. 32). The dark colouration of the lateral head is always present.

Call. The advertisement call recorded on 19 November 2017 (14:30 h) near the Gîte d’Étape (air temperature 21.3 °C; voucher specimen ZSM 77/2018, MSZC 0648) consists of a low-pitched, pulsed note of moderate duration, usually emitted in short call series containing 2 or

3 calls, although one single call was also recorded (Fig. 35). Calls (= notes) exhibit distinct amplitude modulation, with call energy starting at low level, rapidly increasing after about a fifth of the call's duration, reaching its maximum at about half of the call's duration, followed by a decrease towards the call's end. Pulses are very narrowly spaced and very short in duration, with each pulse apparently shorter than 3 ms, but difficult to measure exactly. It is also not possible to count the number of pulses per note (= call), but pulse repetition rate can roughly be calculated in major parts of the note. Numerical parameters of 12 analysed calls are as follows: call duration (= note duration) 208–254 ms (228 ± 13 ms); inter-call intervals within regular call series 1563–2186 ms (1758 ± 231 ms); number of calls per call series 2 or 3 (2.1 ± 0.3); duration of regular call series 2008–4167 ms (2632 ± 899 ms); pulse repetition rate within calls about 310–320 pulses/second; dominant frequency 612–631 Hz (619 ± 6 Hz); prevalent bandwidth 320–3000 Hz; numerous parallel frequency bands recognizable with approximately 320 Hz spacing up to 9200 Hz, which represent a reflection of pulse rate (see Köhler et al. 2017).

Etymology. Latin feminine nominative singular adjective derived from the words 'laevis', meaning smooth or slippery, and 'pes' meaning 'foot'.

Distribution. This species is known from mid-elevation rainforests of (1) Montagne d'Ambre National Park (type locality). In an intensive survey on Montagne d'Ambre in 2017 and 2018, we did not find it above 1100 m a.s.l. on this mountain, nor did we find it below 900 m a.s.l. This matches observations by Raxworthy and Nussbaum (1994), who recorded this species to occur 900–1200 m a.s.l. Additionally, we here confirm its occurrence (2) on the Manongarivo Massif (at 350–751 m a.s.l.). Elevation: 350–1200 m a.s.l.

Natural history. *Rhombophryne laevipes* is a semi-fossorial or detriticolous species found in low- to mid-elevation humid forest. Males call during and shortly after rain, especially at night, from concealed positions within the leaf litter. Between November 2017 and January 2018, calling activity was greatest at the start of November, and diminished as rain frequency increased. This suggests that mating may take place at the start of the rainy season. When handled, captured males that had been calling struggled to deflate their vocal sacs, and emitted distress calls. Juvenile and subadult individuals were more commonly encountered than adults, usually active at night. After capture, we spent a short time observing the behaviour of ZSM 77/2018. Its initial escape attempts were long leaps. After calming down, when placed in leaf litter, it did not attempt to dig backwards, as is thought to be the dominant mode of digging in *Rhombophryne*. Instead, it attempted to hide by pushing itself under objects head-first, using its strong hindlimbs to push its body forward (Fig. 33C). Eudeline et al. (2015) reported on the predation of this species by *Compsophis albiventris*.

Rhombophryne botabota Scherz et al., 2016

Figures 2, 4–7, 30, 31, 36–38

Informal names. This species was listed as '*Rhombophryne* sp. 1' by Wollenberg et al. (2008), '*Rhombophryne* sp. 2' by Vieites et al. (2009), and '*Rhombophryne* sp. Ca2' by Perl et al. (2014). Carné and Vieites (2024) treated specimens from Makira as 'DCL "Makira"'.

Holotype. ZSM 358/2005 (FGZC 2896), an adult male, collected on 18 February 2005 at 'Camp Simpona' (14.4364°S, 49.7433°E, 1326 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by F. Glaw, M. Vences, and R.D. Randrianiana (Figs 30, 31, 37).

Paratypes. Six specimens: ZSM 538/2009 (ZCMV 11473), ZSM 539/2009 (ZCMV 11474), two presumably immature males, collected on 21 June 2009 at 'Camp 1' Angozongahy, (15.4370°S, 49.1186°E, 1009 m a.s.l.), western side of the Makira Plateau, Analanjirofo Region, northeastern Madagascar, by M. Vences, D.R. Vieites, F. Ratsoavina, R. Randrianiana, E. Rajeriarison, T. Rajofiarison, and J. Patton; MRSN A2956 (FN 7164), MRSN A2640 (FN 7238), MRSN A2954 (FN 7281), MRSN A2955 (FN 7300), two males and two females, collected on 9–15 December 1997 at 'Camp 2' Andranomadio (14.5304°S, 49.4383°E, 860 m a.s.l.), Ambolokopatrika-Betaolana Forest, Sava Region, northeastern Madagascar, by F. Andreone, G. Aprea, and J.E. Randrianirina.

Referred specimens. UADBA-A-ZCMV 15158 (Fig. 36L–N), ZSM 515/2016 (ZCMV 15241; Fig. 36J, K), and ZSM 513/2016 (ZCMV 15159; Fig. 36O–Q), three juveniles, and ZSM 514/2016 (ZCMV 15160; Fig. 36D–F), ZSM 523/2016 (ZCMV 15216; Fig. 36G–I), and ZSM 524/2016 (ZCMV 15279; Fig. 36A–C), three unsexed adults, all collected on 18–20 November 2016 in the vicinity of 'Camp Simpona' (ca 14.4366°S, 49.7434°E, 1325 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences, J. Razafindraibe, and A. Razafimanantsoa; MNCN-uncatalogued (DRV 5836), an unsexed individual, collected on 25 June 2009 at 'Camp 1' Angozongahy, (15.4370°S, 49.1186°E, 1009 m a.s.l.), western side of the Makira Plateau, Analanjirofo Region, northeastern Madagascar, by M. Vences, D.R. Vieites, F. Ratsoavina, R. Randrianiana, E. Rajeriarison, T. Rajofiarison, and J. Patton.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S3' EU341102/FJ559297; 16S 5' EU341102; Vieites et al. 2009) and COI barcoding (COI KF611585; Perl et al. 2014). All paratypes and referred specimens conform well with the holotype in morphology. MRSN A2640, MRSN A2956, ZSM 513/2016, ZSM 514/2016, ZSM 515/2016, ZSM 524/2016, ZSM 538/2009, ZSM 539/2009, MNCN-DRV 5836, and UADBA-A-ZCMV 15158 are further confirmed by molecular taxonomic

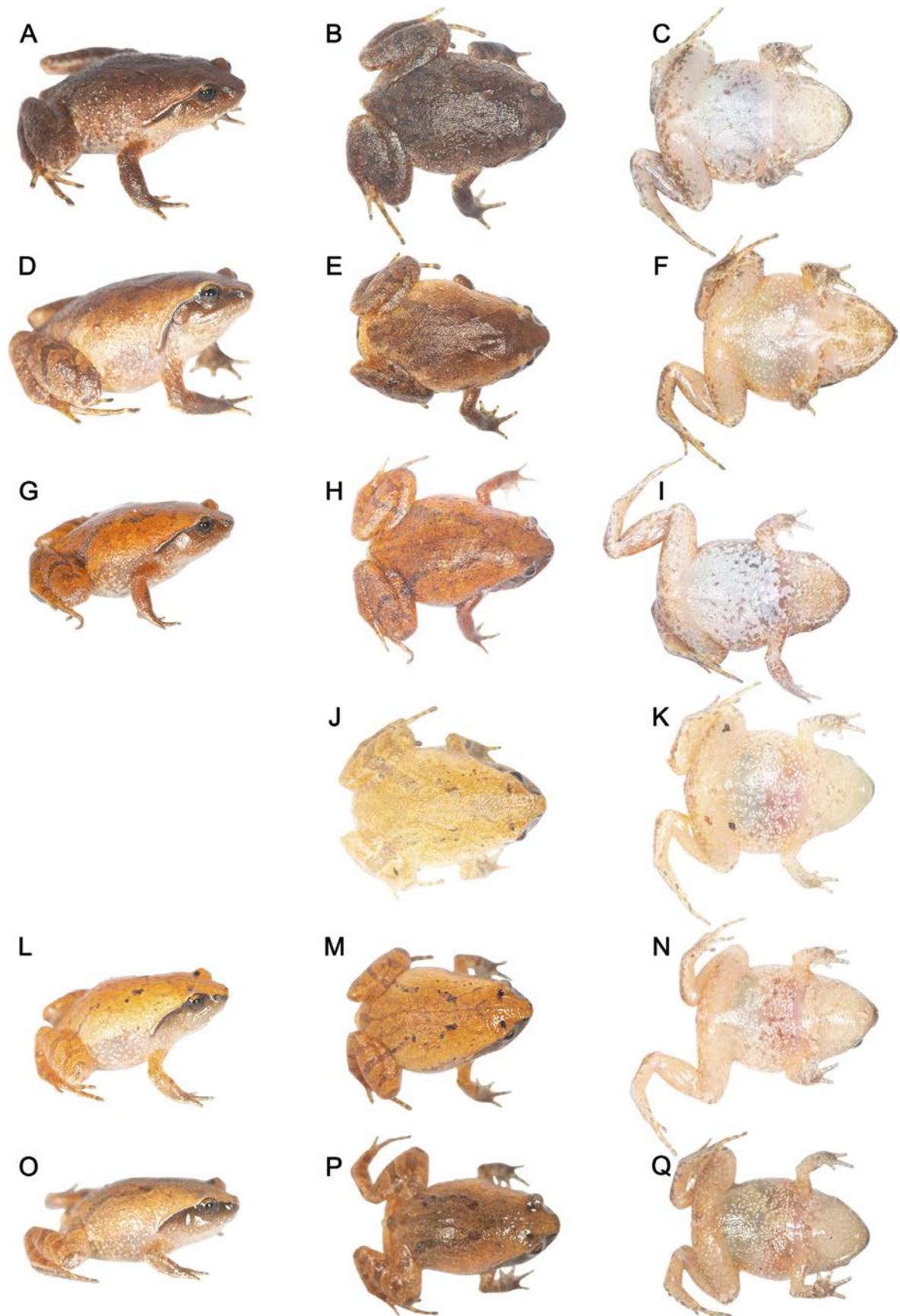


Figure 36. *Rhombophryne botabota* in life. Not to scale. All photographed in high elevation primary rainforest within Marojejy National Park. **A–C** adult ZSM 524/2016 (ZCMV 15279) in **A** dorsolateral, **B** dorsal, and **C** ventral view; **D–F** adult ZSM 514/2016 (ZCMV 15160) in **D** dorsolateral, **E** dorsal, and **F** ventral view; **G–I** adult ZSM 523/2016 (ZCMV 15216) in **G** dorsolateral, **H** dorsal, and **I** ventral view; **J, K** juvenile ZSM 515/2016 (ZCMV 15241) in **J** dorsal, and **K** ventral view; **L–N** juvenile UADBA-A-ZCMV 15158 in **L** dorsolateral, **M** dorsal, and **N** ventral view; **O–Q** juvenile ZSM 513/2016 (ZCMV 15159) in **O** dorsolateral, **P** dorsal, and **Q** ventral view.

identification (Fig. 2). MRSN A2956 is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. laevipes* group, this species appears to be sister to a clade consisting of *R. sonaliae* **sp. nov.** and *R. anatala* **sp. nov.** (described below) based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) medium body size, adult SVL 24.2–32.2 mm; (2) head wider than long (HW/HL 1.44–1.69); (3) moderately small eyes (ED/HL 0.33–0.38); (4) moderately long hindlimbs (HIL/SVL 1.41–1.75); (5) small inner metatarsal tubercle (IMTL/FOL 0.08–0.13); (6) outer metatarsal tubercle absent; (7) second finger shorter than or equal in length to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin

smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of distinct inguinal spots (sometimes dark brown lines converging anterodorsally); (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenic; (15) clavicles present, thin, curving; and (16) advertisement call (based on 4 analysed calls by one individual) tonal, with (17) call duration 161–201 ms, (18) inter-call interval 2529–2716 ms, and (19) dominant frequency 1256–1291 Hz.

Rhombophryne botabota is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* [MZ751042](#)): in

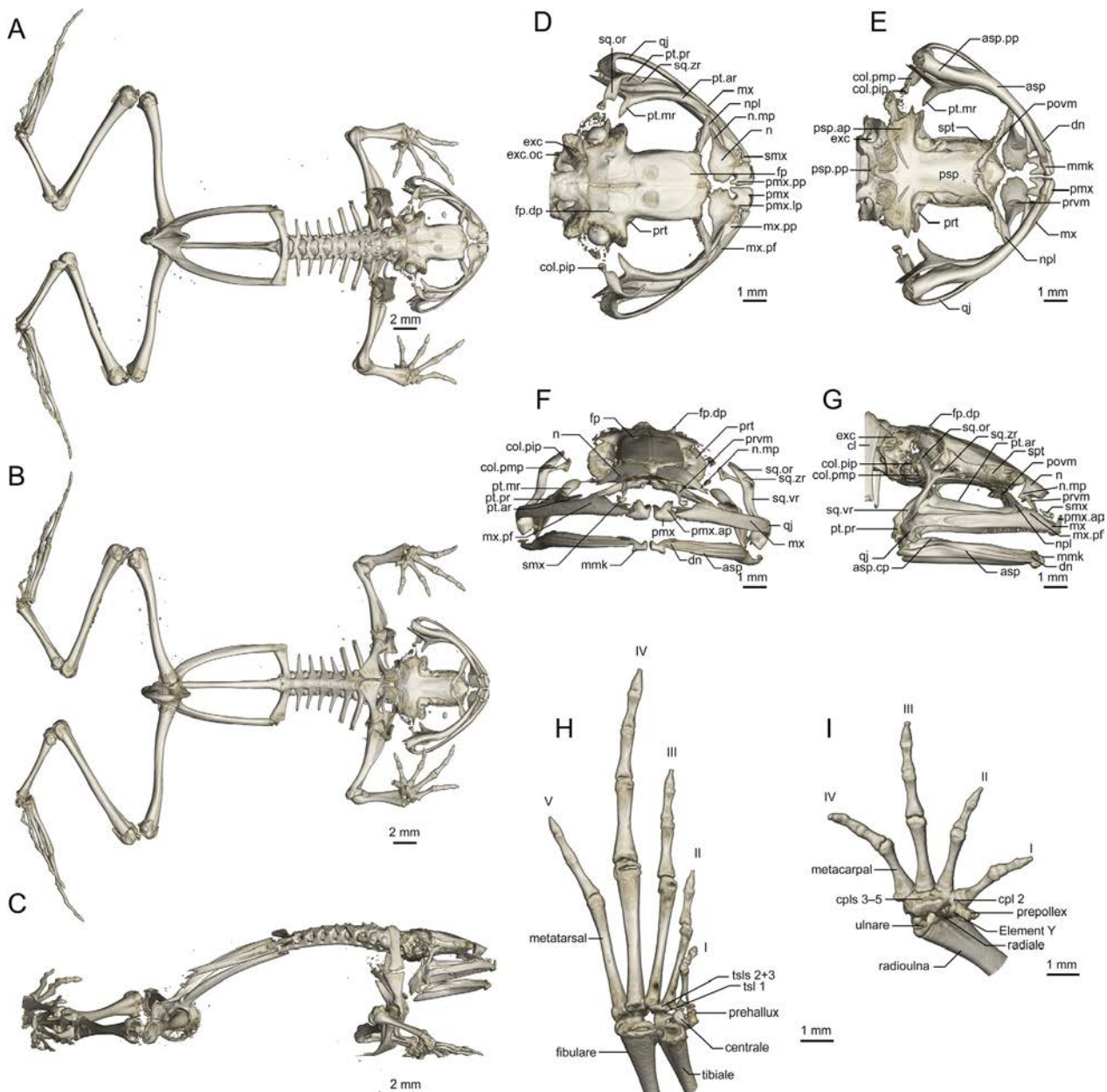


Figure 37. Skeleton of *Rhombophryne botabota* holotype ZSM 358/2005 (FGZC 2896). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

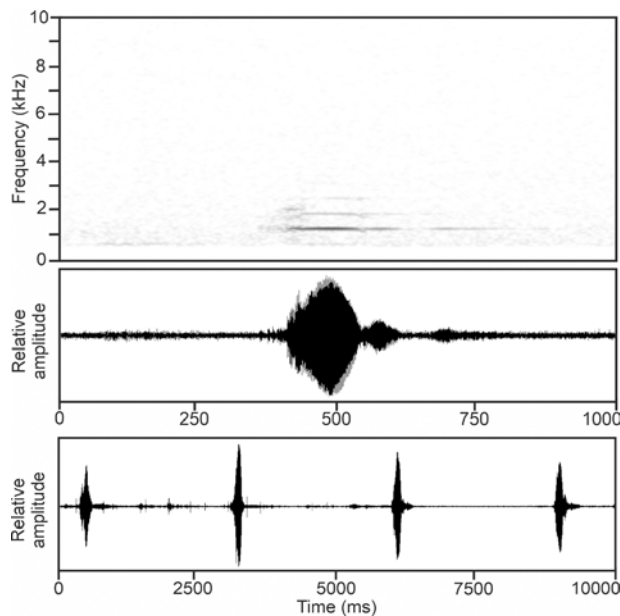


Figure 38. Advertisement calls assigned to *R. botabota*, recorded at Angozongahy, Makira, in 2009. Top: audiospectrogram and corresponding oscillogram of one advertisement call at 1000 ms time scale. Bottom: oscillogram at 10,000 ms time scale showing pattern of call repetition (four calls). Recording high-pass filtered at 550 Hz.

16S5', 'G' at site 304, 'T' at site 568, and 'A' at site 682. No diagnostic sites were identified for 16S3'.

Diagnosis. Within the genus *Rhombophryne*, *R. botabota* can easily be distinguished from *R. testudo*, *R. coudreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** by smooth skin (vs rough), absence of chin barbels (vs general presence), longer hindlimbs (HIL/SVL 1.41–1.75 vs 1.10–1.41); from *R. mangabensis* by larger body size (SVL 24.2–32.2 mm vs 19.6–23.2 mm), and smooth skin (vs finely granular with scattered warts); from *R. savaka* by larger body size (SVL 24.2–32.2 mm vs 18.8–20.9 mm), absence of a diastema in the vomerine teeth (vs presence), and absence of inguinal spots (vs occasional presence); from *R. mavokely* **sp. nov.**, *R. ornata*, and members of the *R. ellae* species group by the absence of reddish orange colouration on the posterior thigh and in the inguinal region (vs presence); from members of the *R. minuta* species group by generally shorter hindlimb length (HIL/SVL 1.41–1.75 vs 1.73–1.84), and less gracile habitus; from *R. proportionalis* by much larger adult body size (SVL 24.2–32.2 mm vs 11.0–12.3 mm); and from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence).

Within the *R. laevipes* species group, see the account of *R. laevipes* above for distinction from that species. *Rhombophryne botabota* can be distinguished from *R. nivlevina* by smaller body size (SVL 24.2–32.2 mm vs 41.2–57.2 mm), absence of white spots in the inguinal region and on the posterior thigh and ventral shank (vs sometimes present), and tonal (vs pulsed) advertisement call that is shorter (call duration 161–201 ms vs 538–598 ms) and higher in dominant frequency (1256–1291 Hz vs 526–534

Hz). For distinction from newly described members of this species group, see their respective descriptions below.

Variation. SVL ranges from 24.2–32.2 mm; for variation in other measurements, see Table S6. Skin texture of the newly collected material was surprisingly variable in life, ranging from smooth to tubercular (Fig. 36). The supratympanic fold was consistently highly pronounced and always dark in colour. Colouration was noted to vary substantially in the type series by Scherz et al. (2016a), most importantly including the occasional presence of spots on the posterior thigh, and presence of a dark inguinal 'stripe' in almost all individuals. Many also possessed a pair of dark spots on top of the head behind the eyes (Fig. 36J, M, P).

Call. The allocation of the analysed recording to *R. botabota* is slightly tentative, as the recorded individual was not seen calling. However, *R. botabota* was the only *Rhombophryne* species found at the place of call emission (see Scherz et al. 2016a). The advertisement call recorded on 24 June 2009 (12:00 h) at Angozongahy site, Makira (estimated air temperature 22–24 °C), consists of a single tonal note of moderate duration repeated at regular intervals, but apparently not arranged in regular call series. Calls lack any frequency modulation, but exhibit moderate amplitude modulation, with call energy increasing from the beginning of the call and reaching its maximum at approximately half of the call's duration (Fig. 38). Numerical parameters of 4 analysed calls are as follows: call duration (= note duration) 161–201 ms (180 ± 19 ms); inter-call intervals 2529–2716 ms (2638 ± 97 ms); dominant frequency 1256–1291 Hz (1274 ± 16 Hz); prevalent bandwidth 1100–3200 Hz; harmonic frequency bands recognizable at about 630, 1910, 2580 and 3160 Hz. Calls from the same recording have been described by Scherz et al. (2016a) using a slightly different terminological scheme. Slight differences in temporal measurements when compared to Scherz et al. (2016a) result from different recognition of the 'tapering tail' in calls, which we here consider to likely represent an echo effect.

Etymology. The Malagasy adjective *botabota* meaning 'chubby', in reference to the body shape of this species. Used as an invariable noun in apposition.

Distribution. Known from (1) Marojejy National Park (type locality), (2) Ambolokopatrika-Betaolana, and (3) Makira in northeastern Madagascar (Scherz et al. 2016a). Elevation: 860–1326 m a.s.l. Records from 750±200 m a.s.l. by Rakotoarimalala and Raselimanana (2023) cannot be verified as we have not examined material and have no DNA sequences, so they are not included here.

Natural history. *Rhombophryne botabota* is a semi-fossorial or detriticolous species found in mid-elevation humid forest. In the vicinity of 'Camp Simpona' in November 2016, we found *R. botabota* to be moderately abundant during surveys. Specimens were routinely found by raking over quadrats of leaf litter, or collect-

ing the quadrats in rice bags and sorting through them by hand. Previously, most specimens had been collected using pitfall traps (Scherz et al. 2016a). Some calls were heard, but no individuals could be observed calling. Paratype ZSM 538/2009 was recorded by Scherz et al. (2016a) to have a subulinid snail in its gut, making it the only record of gastropod consumption by a *Rhombophryne* species.

***Rhombophryne nilevina* Lambert, Hutter & Scherz, 2017**

Figures 2, 4–7, 30, 31, 39–42

Remark. Lambert et al. (2017) mistakenly gave the holotype's collection number as KU 340893 in their tables 1 and 2 and figure 3. The correct number is KU 340897.

Informal names. The candidate species 'Rhombophryne sp. 3' of Vieites et al. (2009) and 'Rhombophryne sp.

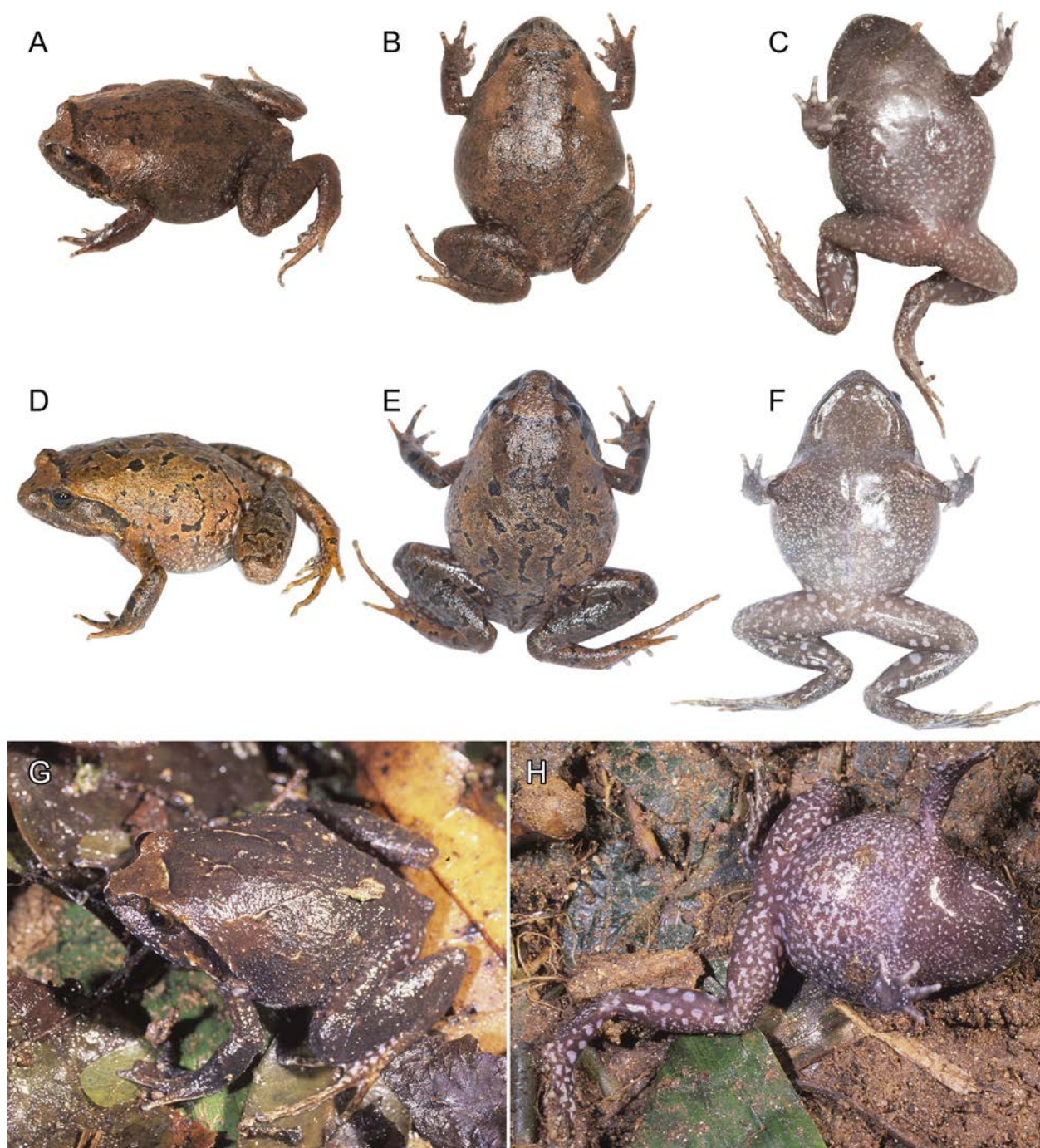


Figure 39. *Rhombophryne nilevina* in life. **A–C** adult male paratype UADBA-A-CRH 799 from near Andemaka, Ranomafana National Park in **A** dorsolateral, **B** dorsal, and **C** ventral view; **D–F** unsexed adult ZSM 516/2016 (ZCMV 15215) from Marojejy National Park in **D** dorsolateral, **E** dorsal, and **F** ventral view; **G–H** adult male MRSN A4598 from Ambolokopatrika-Betaolana in **G** dorsolateral and **H** ventral view.

Ca3' of Perl et al. (2014) and Belluardo et al. (2022) from Tsaratànana is here included in *R. nilevina* due to its small uncorrected p distances (Tables S2, S3) and the results of our species delimitation analysis.

Carné and Vieites (2024) treated specimens from Marojejy and Anjanaharibe-Sud as '*R. sp. cf. nilevina*' referring to them as 'DCL "North"', and treated *R. sp. Ca03* as an unconfirmed candidate species 'UCS "Sp. 3"'.

Holotype. KU 340897 (CRH 798), an adult male, collected at mid-day on 8 February 2015 from 'montane rainforest near the former village of Andemaka in Ranomafana National Park' (ca 21.1287°S, 47.5054°E, 1240 m a.s.l.), Vatovavy-Fitovinany Region, South Central East Madagascar, by S.M. Lambert, E. Rajeriarison, and R.J. Fulgence (Figs 30, 31, 40).

Paratypes. One specimen: UADBA-A-CRH 799, an adult male, collected on the morning of 7 February 2015 from the same locality as the holotype, by S.M. Lambert and R.J. Fulgence (Fig. 39A–C).

Referred specimens. ZSM 516/2016 (ZCMV 15215), an unsexed adult, collected on 18 November 2016 near 'Camp Simpona' (ca 14.4366°S, 49.7434°E, 1325 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences, J. Razafindraibe, and A. Razafimanantsoa; MRSN A4598 (FN 7252), an adult male, collected on 12 December 1997 near 'Camp 2' Andranomadio (ca 14.7180°S, 49.5124°E, 820 m a.s.l.), Ambolokopatrika-Betaolana corridor, Sava Region, northeastern Madagascar, by F. Andreone.

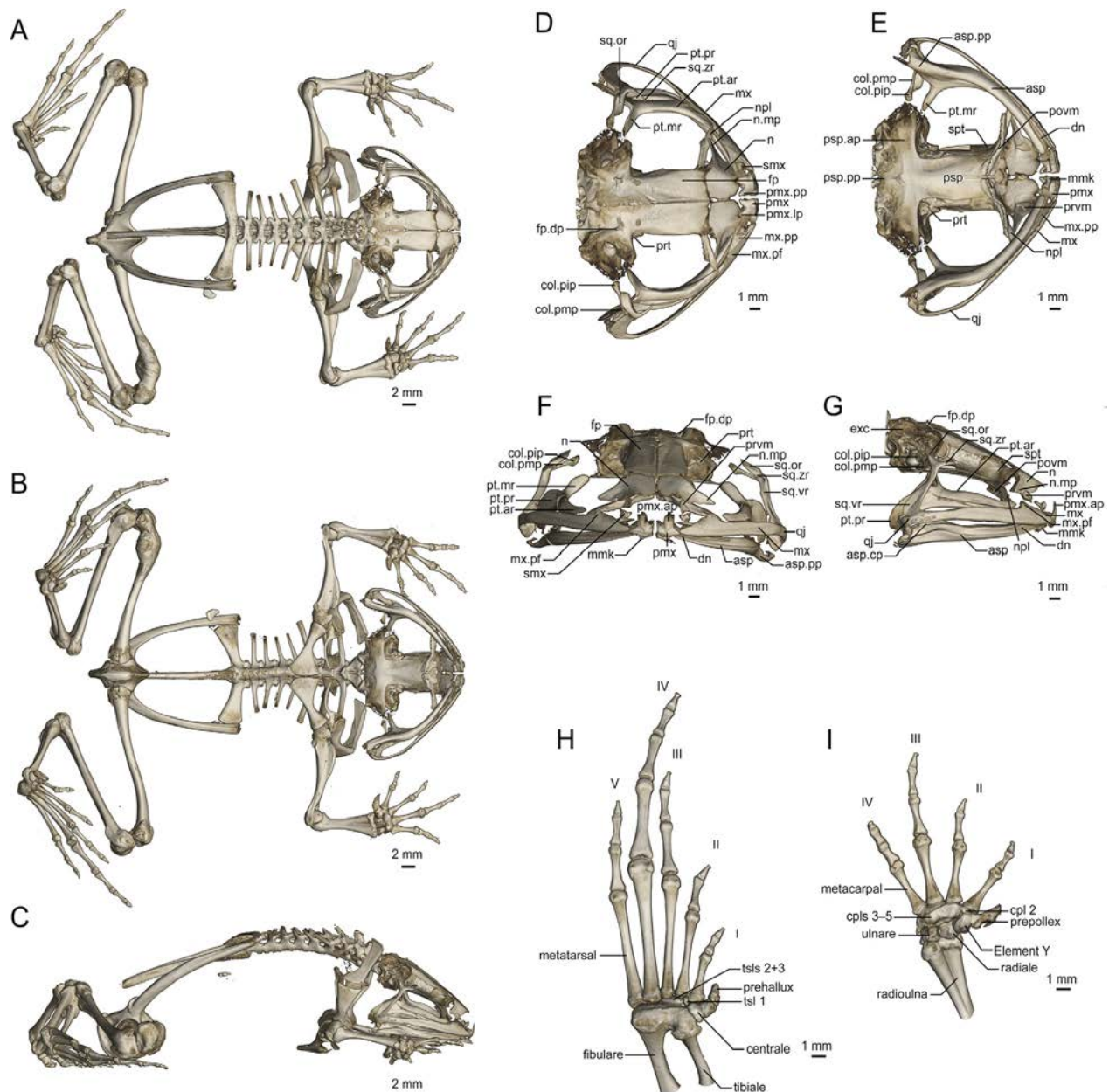


Figure 40. Skeleton of *Rhombophryne nilevina* holotype KU 340897 (CRH 798). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

According to our species delimitation, specimens formerly assigned to *R. sp. Ca03* are also included in *R. nilevina*: MRSN A2631 (FAZC 11002), an adult female, ZSM 664/2001 (FGMV 2001.124), a subadult, ZSM 667/2001 (FGMV 2001.131), a <10 mm juvenile (the original genetic reference specimen for the candidate species), MRSN A3016 (FAZC 11135), an adult male (sexed by incision), and MRSN A3249 (FAZC 11086), a juvenile, all collected between 4 and 9 February 2001 at Antsahamanara (ca 14.05°S, 48.79°E, ca 1000 m a.s.l.), Tsaratànana Massif, Diana Region, Madagascar, by F. Andreone, F. Mattioli, J.E. Randrianirina, and M. Vences.

Assignment of specimens. The holotype is to be used as the reference specimen for this species in 16S rRNA barcoding (16S3' KY288475; Lambert et al. 2017), but by inclusion of *R. sp. Ca03*, so too is ZSM 667/2001 (16S3' FJ559296; Vieites et al. 2009). ZSM 667/2001 (MV 2001. F5; KF611592) and MVTIS 2001.E50 (KF611593) (both originally *R. sp. Ca03*) are used as references for COI barcoding (Perl et al. 2014). The paratype and referred material conform well with the holotype in morphology, but see Variation section for comments on colour variation within the species. The paratype is topotypical. Assignment of specimens ZSM 516/2016, ZSM 667/2001, MRSN A2631, MRSN A4598, and MRSN A3016 (as well as tissue sample MV 2001-E50) is confirmed by molecular taxonomic identification (Fig. 2). KU 340897, MRSN A4598, MRSN A2631, and MVTIS 2001.E50 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. laevipes* group, this species forms a subclade with *R. botabota*, *R. sonaliae* **sp. nov.** and *R. anatalia* **sp. nov.** (described below) based on mo-

lecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) large body size, adult SVL 41.2–57.2 mm; (2) head wider than long (HW/HL 1.42–1.81); (3) moderately small eyes (ED/HL 0.31–0.34); (4) relatively long hindlimbs (HIL/SVL 1.52–1.83); (5) small inner metatarsal tubercle (IMTL/FOL 0.10–0.14); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence or absence of white inguinal spots on a blackish background; (13) presence or absence of white spots on the posterior thigh and ventral shank; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; (15) clavicles present, thin, curving; and (16) advertisement call (based on 7 analysed calls by one individual) pulsed, with (17) call duration 538–598 ms, (18) inter-call interval 42–126 s, and (19) dominant frequency 526–534 Hz.

Rhombophryne nilevina is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'G' at site 389, 'T' at site 401, and 'T' at site 555; in 16S3', 'T' at site 956, 'T' at site 1075, 'A' at site 1131, and 'A' at site 1157.

Diagnosis. Within the genus *Rhombophryne*, *R. nilevina* can easily be distinguished from *R. testudo*, *R. coudreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** by smooth skin (vs rough), absence of chin barbels (vs general presence), longer hindlimbs (HIL/SVL 1.52–1.83 vs 1.10–1.41);



Figure 41. *Rhombophryne nilevina* specimen MRSN A2631 (formerly referred to as *R. sp. Ca03*), from Antsahamanara on the Tsaratànana Massif, in life.

from *R. mangabensis* and *R. savaka* by much larger body size (SVL 41.2–57.2 mm vs 18.7–23.2 mm), longer relative forearm length (FARL/SVL 0.39–0.42 vs 0.33–0.38), well-ossified clavicles (vs poorly ossified), absence of black inguinal spots (vs presence in *R. savaka*); from *R. mavokely* **sp. nov.**, *R. ornata*, and members of the *R. ellae* species group by the absence of reddish orange colouration on the posterior thigh and in the inguinal region (vs presence); from members of the *R. minuta* species group by usually shorter relative hindlimb length (HIL/SVL 1.52–1.81 vs 1.73–1.84), and less gracile habitus; from *R. proportionalis* by much larger adult body size (SVL 41.2–57.2 mm vs 11.0–12.3 mm); and from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence).

Within the *R. laevipes* species group, see the accounts of *R. laevipes* and *R. botabota* above for distinction from those species. Note that several traits thought to distinguish *R. nilevina* from *R. laevipes* and *R. botabota* (e.g., absence of stark colour boundary between lateral head and dorsum, and absence of white spots in the inguinal region; Lambert et al. 2017) are now known to vary within the species (see Variation, below) and cannot be used as diagnostic traits anymore. For distinction from newly described members of this species group, see their respective descriptions below.

Description of MRSN A2631. (a specimen of *R. sp.* Ca03 now included in *R. nilevina*): An adult female specimen in a good state of preservation. The right half of the body cavity is opened with the organs exposed; a piece of liver tissue was taken for genetic analysis. A small number of well-developed eggs lies in the dorsal part of the body cavity, which is taken up mostly with the thick-walled stomach.

Body robust. Head wider than long (HW/HL 1.71). Eyes quite small (ED/HL 0.32), pupils large, round. Snout rounded in dorsal and lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril closer to tip of snout than to eye, slightly protuberant. Tympanum distinct, round, TDH/ED 0.75. Supratympanic fold distinct, slightly raised, running straight from posterior corner of eye over tympanum, curving gently ventrally posterior to the tympanum, demarcating the boundary of the dark brown lateral head colouration. Superciliary spines absent, but one white dot above each eye. Dorsal skin smooth in preservative, was slightly granular in life with a few larger granules (Fig. 41). Tongue broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth present, curved, with small lateral diastemata, separated at the midline by a small gap. Choanae round, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.443), strongly built. Fingers without webbing, moderately long, relative lengths $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth. Finger tips not expanded, rounded. Finger subarticular tubercles distinct, whitish, flat; inner metacarpal tubercle broad and flat, outer metacarpal/palmar tubercle indistinct, greyish. Hind limb strong, tibio-

tarsal articulation reaching between eye and nostril when adpressed anteriorly along the body. TIBL/SVL 0.537. Inner metatarsal tubercle present, oblong, whitish, somewhat bulging. Outer metatarsal tubercle absent. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles distinct, cream, slightly raised; toe tips not enlarged, rounded.

After 22 years in preservative, the colouration of the specimen remains quite vibrant, though less strongly contrasting than in life (Fig. 41). The base colour is a coffee brown across the dorsum, and venter except that it takes on a purplish tone over the abdomen, and a richer brown on the chin. On the dorsum, a broad pattern of darker brown is present, across which is strewn almost black markings, especially in an interocular line, a small trianguloid marking on the head, and a V-shaped area on the back. The lateral surface of the head is almost black, strongly separated from the dorsal body colouration. The inguinal region has a large blackish splotch and a series of small white spots. The dorsal surfaces of the hindlimbs have a series of dark brown crossbands; the posterior surfaces of the thighs are dark chocolate brown with a few light brown or cream spots. The cloaca marks the top of a blackish trapezoid, and above it there is a small blackish bar. The ventral thighs are coffee brown with small cream flecks, the ventral shanks are dark chocolate brown with cream spots. The dorsal foot is spotted with cream, its ventral surface dark brown. The ventral abdomen is cream and a purplish brown. Each finger and toe has a cream annulus before the distalmost phalange. The arm has blackish disjointed crossbands dorsally, but is coffee brown below, including on the palmar surface. Colouration in life was like in preservative but with a grey, rather than a brown, base colour (Fig. 41).

Variation. SVL ranges from 41.2–57.2 mm; for variation in other measurements, see Table S6. The newly examined material from northeastern Madagascar generally agrees well with the type series in morphology, despite extending the range of the species by well over 800 km. Unlike the types, northern specimens have distinct white spots in the inguinal region and on the posterior thigh and ventral shank. Many specimens have at least a spot, generally a bar, above the cloaca (absent from MRSN 4598), and all have a distinct colour border between their lateral head and dorsal head. MRSN A4598 has distinct vocal slits that confirm its sex as male.

Call. The advertisement call recorded on 8 February 2015 (12:00 h) near Andemaka, Ranomafana National Park (air temperature estimated to be around 20 °C; presumably emitted by the holotype KU 340897), consists of a pulsed note of moderate to long duration, emitted at irregular and long intervals. Calls (= notes) exhibit distinct amplitude modulation, with call energy starting at low level, moderately increasing to about one fourth of the call's duration, rapidly increasing after half of the call's duration, reaching its maximum in its last quarter, followed by a decrease towards the call's end.

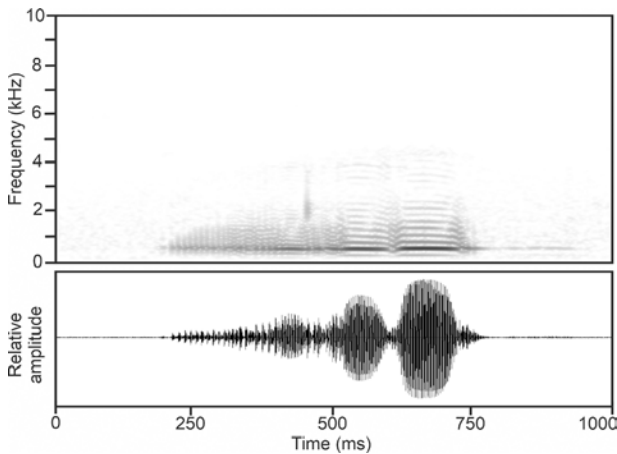


Figure 42. Advertisement call of *Rhombophryne nilevina*, recorded in Ranomafana National Park in 2015. Audiospectrogram and corresponding oscillogram of one advertisement call at 1000 ms time scale. Recording band-pass filtered at 110–6600 Hz.

The second half of the call is characterized by a short intermittent drop in call energy. Pulses are very narrowly spaced in the second half of the call and very short in duration, with each pulse being apparently shorter than 2 ms, but almost impossible to measure exactly. In the first half of the call, pulses are longer in duration (ca. 9 ms) and repeated less rapidly. It is not possible to count the number of pulses per note (= call), but pulse repetition rate can roughly be calculated for each section of the note. Numerical parameters of 7 analysed calls are as follows: call duration (= note duration) 538–598 ms (561 ± 21 ms); inter-call intervals rather long and irregular, varying from 42–126 s (81 ± 41 s); pulse repetition rate within first half of the call 100 pulses/second, within second half of the call approximately 260–270 pulses/second; dominant frequency 526–534 Hz (530 ± 3 Hz); prevalent bandwidth 250–4500 Hz; numerous parallel frequency bands recognizable within the second half of the call, representing a reflection of pulse rate (see Köhler et al. 2017). Calls from the same recording have been described by Lambert et al. (2017) using a different terminological scheme.

Etymology. The Malagasy adjective *nilevina* meaning ‘buried’, in reference to the habit of this species of calling from burrows that must be excavated to catch the frogs. Used as an invariable noun in apposition.

Distribution. Records from northern Madagascar (Belluardo et al. 2022) dramatically increased the range of *R. nilevina*. Currently known from (1) Andemaka in Ranomafana National Park (type locality), (2) Ambolokopatrika, (3) Marojejy, and (4) Antsahamanara on the Tsaratànana Massif. Elevation: 1000–1325 m a.s.l.

Natural history. *Rhombophryne nilevina* is a semi-fossorial or detriticolous species found in low- to mid-elevation humid forest. Lambert et al. (2017) reported that *R. nilevina* called during the day from burrows within the

soil, and its calling activity was heightened by inclement weather. The newly referred specimens from the north were collected active above the ground in largely undisturbed primary rainforest.

Karyotype. The karyotype of a specimen assignable to this candidate species (FAZC 11063 from Tsaratànana) was described by Aprea et al. (2007) under the name ‘*Plethodontohyla laevipes*’. Its karyotype was $2n = 26$, with a subtelocentric fourth chromosome pair. Nucleolar organiser regions were located in a peritelomeric position on the long arm of the second chromosome pair. Centromeric bands were CMA₃ and DAPI negative.

Rhombophryne sonaliae sp. nov.

<https://zoobank.org/CEEA0A07-BFC2-424F-A4D5-C15F95AA8C63>

Figures 2, 4–7, 30, 31, 43–45

Remarks. This species has been incorrectly assigned to *Plethodontohyla alluaudi* since at least 1975 (Blommers-Schlösser 1975, 1976; Blommers-Schlösser and Blanc 1991), but the identity of that nomen was recently clarified (Bellati et al. 2018), leaving this relatively well-known species in need of a new name.

The vast majority of mentions of ‘*Mantipus alluaudi*’, ‘*Plethodontohyla alluaudi*’, and ‘*Rhombophryne alluaudi*’ in publications between 1976 and 2018 in fact refer to this species, especially in all genetic analyses (Blommers-Schlösser 1976; Vences and Glaw 2003; Vences et al. 2003b, 2006; Vallan et al. 2004; Veith et al. 2004; Andreone et al. 2005; van der Meijden et al. 2005; Frost et al. 2006; Aprea et al. 2007; van der Meijden et al. 2007; Wollenberg et al. 2008; Vieites et al. 2009; D’Cruze et al. 2010; Glaw et al. 2010b; Raselimanana 2010; Perl et al. 2014; Scherz et al. 2014, 2015a, 2015b, 2016a, 2016b, 2017a, 2017b). The following exceptions are noted: records from the north of Madagascar, including Ambolokopatrika (Andreone et al. 2000), Manongarivo (Rakotomalala 2002), and Bemanevika (Rabearivony et al. 2010) probably refer to other species of *Rhombophryne*. Records from southeastern Madagascar likely refer to the true *Plethodontohyla alluaudi* (Ramanamanjato et al. 2002; Andrianarimisa et al. 2009; Ramanamanjato and Soanary 2011). Some records, e.g., that from Andringitra (Raxworthy and Nussbaum 1996) are uncertain, and are omitted from our treatment here, pending verification with voucher specimens.

Belluardo et al. (2022) mistakenly figured specimen MRSN A2610 of *R. sp.* Ca10 as specimen MRSN A2620 of *R. sp.* Ca19 in figure 1 of their paper.

Informal names. This species was referred to as ‘*Rhombophryne* sp.’ by Bellati et al. (2018), ‘*Rhombophryne* sp. ex-alluaudi’ by Scherz (2020), ‘*Rhombophryne* sp. Ca19’ by Belluardo et al. (2022), and ‘*Rhombophryne* sp. 19’ and ‘CCS “Sp. 19”’ by Carné and Vieites (2024).

Justification of the new species. The new species is placed in a clade containing *R. botabota*, *R. nilevina*, and a further new species, *R. anatalia* **sp. nov.** (described below), which was recovered as its sister species with high support (Belluardo et al. 2022). Genetic divergences among these lineages are less significant than those observed in the *R. testudo* group, but they all consistently differ among each other by >3.5% uncorrected p distance in the 16S3' fragment (3.8% between *R. sonaliae* **sp. nov.** and *R. anatalia* **sp. nov.**) and thus at a level typically indicative of species-level differentiation in Malagasy frogs (Vieites et al. 2009). Furthermore, the new species differs from *R. botabota* by larger body size, from *R. nilevina* by advertisement call differences, and from both these species by colour pattern (many individuals have a light brown dorsolateral stripe and large light spots in the inguinal region and posteroventrally on hindlimbs; see Diagnosis below). There is no detected haplotype sharing with any other *Rhombophryne* species in the nuclear gene RAG1 (Fig. 4). These differences are substantial and together with the molecular divergence strongly support the hypothesis of *R. sonaliae* **sp. nov.** constituting a new species. See also the Justification section for *R. anatalia* **sp. nov.** below.

Carné and Vieites (2024) recovered two deep conspecific lineages of this species, from Iampirano (misspelled 'Lampirano') and Tsararano. Our species delimitation based on 16S3' analyses also recovered these as conspecific.

Holotype. ZSM 3/2002 (FGMV 2001.1271) an adult male, collected on 3 December 2001 in Andasibe (no precise coordinates), Alaotra-Mangoro Region, North Central East Madagascar, by M. Vences (Figs 30, 31, 44).

Paratypes. Seven specimens: ZSM 467/2005 (ZCMV 2221), a juvenile, and ZSM 466/2005 (ZCMV 2209), an ovigerous adult female, collected in February 2005 in pitfall traps in Andasibe (ca 18.9361°S, 48.4122°E, 939 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar, by R. Dolch and Mitsinjo colleagues; MRSN A2620 (FN 6426), an adult male (sexed by incision), collected on 10 December 1996 in Tsararano (ca 14.907°S, 49.687°E, ca 700 m a.s.l.), Sava Region, northeastern Madagascar, by F. Andreone; MRSN A5034 (RJS 0883), an adult male, collected on 15 January 2005 in Iampirano (16.8218°S, 49.1843°E, ca 500 m a.s.l.), Analanjirofo Region, North Central East Madagascar, by J.E. Randrianirina; ZFMK 52765, an adult presumed male, collected on 16 February 1991 in Andasibe (ca 18.9245°S, 48.4149°E, ca 940 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar, by F. Glaw and M. Vences (Fig. 43A–D); UADBA 20308 (ZCMV 968), an adult male, collected on 21 February 2004 in Torotorofotsy (ca 18.874°S, 48.373°E, ca 960 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar, by M. Vences, E. Edwards, and C. Woodhead; MRSN A7143 (FAZC 15560), an adult male, collected on 6 March 2017 in Maromizaha (18.9653°S, 48.4652°E, ca 1000 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar, by E. Coppola (Fig. 43H, I).

Referred specimens. BMNH 1986.28, an unsexed adult, collected on 8 July 1985 by C.J. Raxworthy at 'Camp 5' in Zahamena Reserve (ca 17.67°S, ca 48.83°E, elevation unknown), Analanjirofo Region, North central east Madagascar, by C.J. Raxworthy. UADBA-A 62371 (MSZC 1480), collected on 13 March 2026 by Sandratra Rakotomanga, Alice Petzold, and Mark D. Scherz near Torotorofotsy (18.76965°S, 48.43532°E, 953 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar; this specimen has been partly dissected in order to sequence and annotate its genome.

Assignment of specimens. The paratype UADBA 20308 (ZCMV 968) is used as the reference specimen for this species in 16S rRNA barcoding (16S3' and 16S5' EU341105; Vieites et al. 2009) and COI barcoding (COI KF611584; Perl et al. 2014). The sequence of the holotype is identical to the sequence of this specimen in 16S3' (AY594112), and it differs by two mutations in 16S5' (99.7% identical; AY594074), and by five mutations in COI (99.1% identical; EF396063). All paratypes and referred specimens conform well with the holotype in morphology. Assignment of specimens ZSM 466/2005, MRSN A2620, MRSN A5034, and MRSN A7143 is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 3/2002, MRSN A2620, and MRSN A7143 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. laevipes* group, this species is sister to *R. anatalia* **sp. nov.** (described below) based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) medium to large body size, adult SVL 33.0–44.7 mm; (2) head wider than long (HW/HL 1.59–1.71); (3) moderately small eyes (ED/HL 0.28–0.36); (4) relatively long hindlimbs (HIL/SVL 1.44–1.53); (5) small inner metatarsal tubercle (IMTL/FOL 0.12–0.15); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth, reaching or barely surpassing the joint of the first and second phalange of the fourth toe; (9) dorsal skin smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence of large white or yellowish inguinal spots on a black background, and a light-brown dorsolateral stripe broadening from the eye towards the inguinal region; (13) presence of large white or yellowish spots on a black background on the posterior thigh and ventral surfaces of the shanks; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; (15) clavicles present, thin, curving; and (16) advertisement call (based on 4 analysed calls by one individual) pulsed, with (17) call duration 207–228 ms, (18) inter-call interval long (not measured), and (19) dominant frequency 785–828 Hz.

Rhombophryne sonaliae **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'T' at site 392, 'T' at site 445, and 'A' at site 740;

in 16S3', 'A' at site 1027, 'T' at site 1076, 'C' at site 1104, and 'T' at site 1172.

Diagnosis. Within the genus *Rhombophryne*, *R. sonaliae* **sp. nov.** can usually be distinguished from all species except *R. anatala* **sp. nov.** described below by the presence of a light brown dorsolateral stripe expanding from the

eyes towards the inguinal region. However, as this trait is not always present (Fig. 43E, F), additional traits are necessary for a reliable diagnosis.

Rhombophryne sonaliae **sp. nov.** can easily be distinguished from *R. testudo*, *R. coudreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** by smooth skin (vs rough), absence of chin barbels (vs general presence), longer hindlimbs



Figure 43. *Rhombophryne sonaliae* **sp. nov.** in life. **A–D** adult presumed male paratype ZFMK 52765 from Andasibe, in **A** dorso-lateral, **B** ventral, **C** oblique posterolateral, and **D** anterior view. **E, F** adult male paratype MRSN A7143 (FAZC 15560) from Maromizaha in **E** anterolateral, and **F** ventral view. **G–I** a specimen from Tsararano (could not be identified, but is not MRSN A2620), in **G** dorsolateral, **H** dorsal, and **I** ventral view. **J–L** adult male specimen UADBA-A 62371 (MSZC 1480) from near Torotorofotsy, in **J** lateral, **K** ventral, and **L** dorsal view. Note the distinctive spots on the limbs, and the light stripes along the dorsolateral flank.

ms vs 538–598 ms) and higher in dominant frequency (785–828 Hz vs 526–534 Hz). For distinction from other newly described members of this species group, see their respective descriptions below.

Description of holotype. An adult male specimen in a moderately good state of preservation (Fig. 30). The abdomen is opened with the organs exposed. Tip of right third finger missing.

Body robust and rotund. Head broader than trunk, wider than long (HW/HL 1.59). Eyes quite small (ED/HL 0.28), pupils small, round. Snout rounded in dorsal and slightly truncate in lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril closer to tip of snout than to eye, slightly protuberant. Tympanum indistinct, round, TDH/ED 0.64. Supratympanic fold distinct, slightly raised, running straight from posterior corner of eye over tympanum, curving gently ventrally posterior to the tympanum. Slight colour border between lateral head and dorsal head, with the lateral head being lighter in colour. Superciliary spines absent, no white dots above the eyes. Dorsal skin smooth in preservative. Tongue broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth curved, with a dent each row marginally closer to midline than to lateral end, separated at the midline by a small gap. Choanae round and surrounded by pigment, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.386), strongly built. Fingers without webbing, moderately long, relative lengths $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth (Fig. 31). Finger tips not expanded, rounded. Finger subarticular tubercles distinct, whitish, flat; inner metacarpal tubercle broad and rounded, outer metacarpal/palmar tubercle indistinct, greyish. Hind limb strong, tibiotarsal articulation reaching between tympanum and eye when adpressed anteriorly along the body. TIBL/SVL 0.407. Inner metatarsal tubercle present, oblong, whitish, distinctly raised. Outer metatarsal tubercle absent. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third, third toe just exceeding the base of the second phalange of the fourth toe; subarticular tubercles indistinct; toe tips slightly enlarged, rounded (Fig. 31).

After 20 years in preservative, the base colour is a coffee brown across the dorsum, and a lighter brown on the limbs. The central dorsum is immaculate, bordered either side by greyish wavy patterns riddled with tiny white points, giving an overall ‘milky way’ impression. There is a slight colour border between the dorsal colour and the lateral head, with the lateral head lighter in colour than the dorsal surface. The inguinal region bears several large white spots which also extend onto the anterior thigh. There are also several white spots on the posterior thigh, ventral shank, and dorsal foot. The ventral thigh is light brown flecked with cream. The ventral feet are a light chocolate brown. A light annulus is present before the terminal phalange of each finger and toe. The legs lack crossbands dorsally. The arms have a single crossband on the lower arm. The palmar surface is

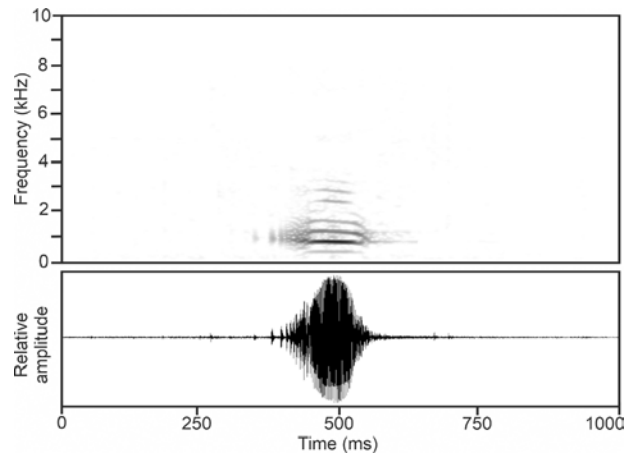


Figure 45. Advertisement call of *Rhombophryne sonaliae* sp. nov., recorded at Torotorofotsy in 2004. Audiospectrogram and corresponding oscillogram of one advertisement call at 1000 ms time scale. Recording band-pass filtered at 110–8000 Hz.

grey-brown. The chin is light brown, the ventral abdomen flecked with cream. The cloaca region is unmarked, and there is no blackish bar above it. The colouration in life was not recorded.

Variation. Type series SVL 33.0–44.7 mm ($n = 5$ adults). For variation in other measurements, see Table S6. Morphology is highly consistent. Third toe consistently reaching the second phalangeal articulation of the fourth toe or barely exceeding it. The most distinctive and constant feature is the diffuse light brown to grey stripe running from the eye toward the inguinal region flecked with tiny white specks, and distinct whitish or yellowish spots on the anterior and posterior thigh, inguinal region, and ventral shank. Only in MRSN A2620 are these spots not clearly defined and rather small. In all other specimens they are extremely strongly defined. Ventral colour likewise consistent, but varying over the posterior abdomen from covered in flecks (ZSM 467/2005) to almost immaculate (MRSN A5034). Chin dark in all available specimens. The referred specimen, BMNH 1986.28, is somewhat smaller than the rest of the type series, and its dorsal colouration is more mottled.

Call. The advertisement call recorded on 21 February 2004 (15:20 h) at Torotorofotsy (air temperature 19.1 °C) consists of a single pulsed note of moderate duration repeated at long irregular intervals (Fig. 45). Calls (= notes) exhibit distinct amplitude modulation, with call energy starting at low level, constantly increasing to about two thirds of the call’s duration where energy reaches its maximum, followed by a decrease towards the call’s end. Pulses are more narrowly spaced in the last two thirds of the call’s duration and very short in duration, with each pulse having around 1 ms duration, but impossible to measure exactly. In the first third of the call, pulses are longer in duration (5–7 ms) and repeated less rapidly. It is not possible to count the number of pulses per note (= call), but pulse repetition rate can roughly be calculated for each section of the note. Numerical parameters of 4 analysed calls

from 2 individuals are as follows: call duration (= note duration) 207–228 ms (219 ± 10 ms); inter-call intervals apparently long and irregular and not measured (probably poorly motivated calling; see Köhler et al. 2017); pulse repetition rate within first half of the call approximately 130–190 pulses/second, within second half of the call approximately 370–420 pulses/second; dominant frequency 785–828 Hz (805 ± 23 Hz); prevalent bandwidth 350–4000 Hz; numerous parallel frequency bands recognizable within the last two thirds of the call, representing a reflection of pulse rate (see Köhler et al. 2017). The call recording analysed herein has been published on the audio CD by Vences et al. (2006) as ‘*Plethodontohyla alluaudi*’ (CD 3, track 28). Assignment to this species is tentative, as the calling individual was not vouchered.

Etymology. We dedicate this species to Sonali Garg, in recognition of her substantial contributions to knowledge of taxonomy and biogeography of South and Southeast Asian frogs, especially microhylids (e.g., Garg et al. 2018, 2019, 2022; Garg and Biju 2019).

Distribution. Evidently widespread in eastern to north-eastern Madagascar, but seldom encountered. Definitive records come from (1) Andasibe (type locality), (2) Torotorofotsy, (3) Iampirano, (4) Tsararano, (5) Maromizaha (Ratsimbazafy et al. 2008), and (6) Mandraka (Blommers-Schlösser 1975). We have examined a referable specimen from (7) Zahamena (BMNH 1986.28). It has also been recorded in the (8) Ambatovy-Analamay region (Raselimanana 2010), and (9) An’Ala (Vallan et al. 2004). Elevation: ca 500–1200 m a.s.l.

Natural history. *Rhombophryne sonaliae* **sp. nov.** is a semi-fossorial or detriticolous species found in mid-elevation humid forest. Calling activity occurs mostly during or shortly after rain, often during the day but probably also at night. The captured calling male from Torotorofotsy was calling during the day from a burrow in the forest floor under the leaf litter. The gut contents of MRSN A2620 included four large termites (each ca 9 mm long), the remains of a katydid (shanks 10.8 mm), a whole spider, a staphylinid rove beetle (ca 9 mm), and three small ants, as well as two parasitic worms. There was only little detritus other than these arthropods in the gut. Those of MRSN A5034 contained a beetle tentatively assigned to Elateridae (click beetles), measuring 10.6 mm, a beetle elytrum, pieces of an ant, and a few large pieces of leaf, as well as two small parasitic worms. Field notes on ZFMK 52765 indicate that it had a caterpillar, among other things, in its stomach. Vallan et al. (2004) recorded a slight increase in detection of this species after logging of forest in An’Ala, but this may have been coincidental. Blommers-Schlösser (1975) found a female under a fallen tree trunk at 1200 m a.s.l. Referred specimen UADBA-A 62371 (MSZC 1480) was collected calling (including in response to playbacks) after rain at 10h13 in the morning on 13 March 2026. It was calling from under ca 10 cm of soil at the base of a tree; whilst excavating it, we encoun-

tered an adult *Plethodontohyla notosticta*, an adult *Paradoxophyla* cf. *palmata*, and a putative adult *Madascincus* cf. *nanus*.

Karyotype. The karyotype was originally described by Blommers-Schlösser (1976) based on a female from Mandraka (as ‘*Mantipus alluaudi*’). It consists of 10 large and 16 small pairs of chromosomes ($2n = 26$). Pair 4 subtelocentric, pairs 3, 7, 10, and 13 submetacentric. Aprea et al. (2007) provided a new description based on the holotype (ZSM 3/2002, as ‘*Plethodontohyla alluaudi*’). They reported both the fourth and the eleventh chromosome pairs to be subtelocentric. Nucleolar organiser regions were located in a peritelomeric position on the long arm of the second chromosome pair. Centromeric bands were DAPI positive.

Rhombophryne anatalia **sp. nov.**

<https://zoobank.org/445D5185-1A76-4AE2-8224-8E051D08CB82>

Figures 2, 4–7, 30, 31, 46, 47

Remark. MRSN A5477, a specimen housed in the same jar as MRSN A5524, the specimen of *R. maraorao* **sp. nov.** discussed above, likewise allegedly comes from Tsingy de Bemaraha in western Madagascar, but agrees morphologically with *R. anatalia*. We are confident that this specimen, too, was collected in northeastern Madagascar. However, as for *R. maraorao*, we do not include the mislocated specimen in the diagnosis of the species (also because we lack DNA sequence data on it), in order to avoid introducing errors, but recognise that it is probably referable to *R. anatalia* **sp. nov.** nonetheless.

Informal names. This species was listed as ‘*Rhombophryne* sp. 1’ by Vieites et al. (2009) and ‘*Rhombophryne* sp. Ca01’ by Scherz et al. (2016b) and Belluardo et al. (2022), and ‘*Rhombophryne* sp. 1’ and ‘UCS “Sp. 1”’ by Carné and Vieites (2024).

Justification of the new species. The new species was found to be the sister species of *R. sonaliae* **sp. nov.** (described above) with high support based on a multigene phylogeny (Belluardo et al. 2022). The genetic divergences between these two lineages is >3.8% uncorrected p distance in the 16S3’ fragment, and thus at a level typically indicative of species-level differentiation in Malagasy frogs (Vieites et al. 2009). We found absence of haplotype sharing between *R. anatalia* **sp. nov.** and *R. sonaliae* **sp. nov.** and between *R. anatalia* **sp. nov.** and any other *Rhombophryne* species in the analysed fragment of the nuclear gene RAG1 (Fig. 4). Morphologically, the two lineages differ in relative toe length (see Diagnosis below). Taken together, and based on other example of pairs of species of Malagasy frogs allopatrically distributed in the North East vs. Northern Central East of Madagascar, we consider the hypothesis of these two lineages

representing two distinct species as most likely, although we acknowledge the need for in-depth study of their contact zone. In the highly unlikely case future studies will find the two nomina to be subjective synonyms, we recommend as first reviser action to give priority to *sonaliae* over *anatalia*.

Holotype. MRSN A2696 (RJS 0597) an adult female, collected on 15 February 2002 at ‘Camp 7’ Antsiranana Faritany (15.4177°S, 49.9403°E, ca. 800 m a.s.l.), Amparihy, Masoala Peninsula, Analanjirofo Region, north-eastern Madagascar, by J.E. Randrianirina (Figs 30, 31, 47).

Paratypes. Two specimens: MRSN A4544 (FAZC 10314; Fig. 46), and MRSN A4600 (FAZC 10304), two ovigerous adult females, collected on 11 and 12 December 1999 (respectively) at ‘Camp 5’ Menamalona (15.3812°S, 49.9878°E, ca 800 m a.s.l.), Ilampy Corridor, Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by F. Andreone and J.E. Randrianirina.

Assignment of specimens. The paratype MRSN A4544 is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ FJ559295; Vieites et al. 2009). COI is so far not available for this species. The 16S3’ sequence of the holotype is identical to that of this specimen (OL780571) and has also been sequenced for 16S5’ (OL780600). Both paratypes conform well with the holotype in morphology (MRSN A4544 could only be examined from photographs; Fig. 46). The assignment of MRSN A4600 is further confirmed by molecular taxonomic identification (Fig. 2). MRSN A2696 and MRSN A4544 are present in the RAG1 haplotype network (Fig. 4).

A further specimen, MRSN A2584 (RJS 0348), is recovered by molecular taxonomic identification as conspecific, but could not be examined morphologically. Database records indicate that this should be a *Spinomantis* specimen, indicating some kind of specimen or metadata mix-up. To avoid confusion, we have not designated this specimen as a paratype.

Definition. Within the *R. laevipes* group, this species is sister to *R. sonaliae* **sp. nov.** (described above) based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) medium to large body size, adult SVL 34.3–37.9 mm; (2) head wider than long (HW/HL 1.56–1.76); (3) moderately small eyes (ED/HL 0.31–0.35); (4) relatively long hindlimbs (HIL/SVL 1.51–1.58); (5) small inner metatarsal tubercle (IMTL/FOL 0.11–0.13); (6) outer metatarsal tubercle absent; (7) second finger subequal to fourth; (8) third toe distinctly longer than fifth, reaching the second phalange of the fourth toe; (9) dorsal skin smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence of large white inguinal spots on a black background, and a light-brown dorsolateral stripe broadening from the eye towards the inguinal region; (13) presence of large white or yellowish spots on a black background on the posterior thigh and ventral surfaces of the shanks; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne anatalia **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘G’ at site 259, ‘C’ at site 654, and ‘G’ at site 739. No diagnostic sites were identified for 16S3’.

Diagnosis. Within the genus *Rhombophryne*, *R. anatalia* **sp. nov.** can usually be distinguished from all species except *R. sonaliae* **sp. nov.** described above by the presence of a light brown dorsolateral stripe expanding from the eyes towards the inguinal region. However, as this trait is not always present (Fig. 46A), additional traits are necessary for a reliable diagnosis.

Rhombophryne anatalia **sp. nov.** can easily be distinguished from *R. testudo*, *R. coudreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** by smooth skin (vs rough), absence of chin barbels (vs general presence), longer hindlimbs (HIL/SVL 1.51–1.58 vs 1.10–1.41); from *R. mangaben-*

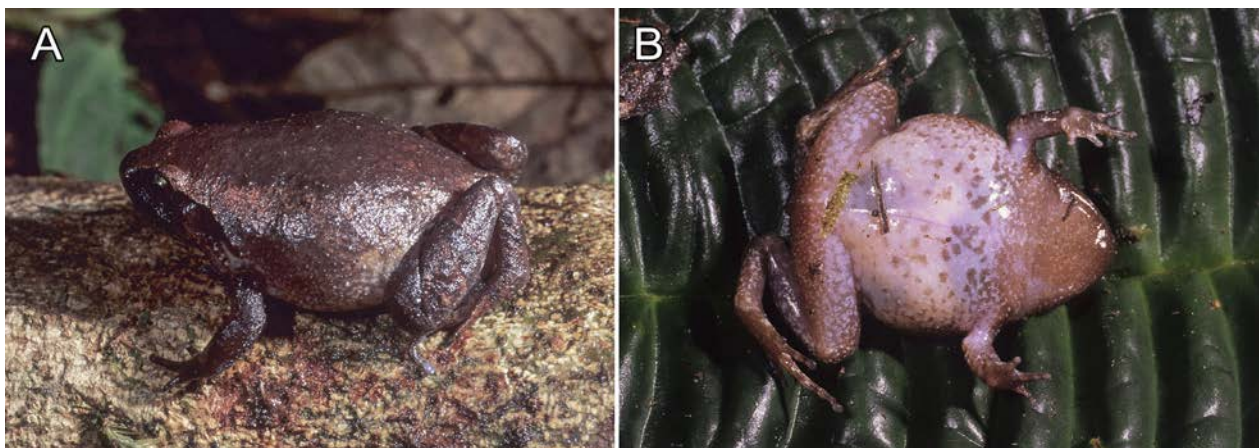


Figure 46. *Rhombophryne anatalia* **sp. nov.** adult female paratype MRSN A4544 (FAZC 10314) in life from Menamalona (Masoala Peninsula). Shown in **A** dorsolateral and **B** ventral view.

Description of holotype. Specimen in a moderately good state of preservation, though slightly soft (Fig. 30). An incision made along the left flank to assess the sex, and part of the tongue taken as a tissue sample. Small ova, ovaries, and fallopian tubes clearly visible.

Body robust and rotund. Head wider than long (HW/HL 1.76). Eyes quite small (ED/HL 0.31), slightly depressed, pupils small, oval. Snout rounded in dorsal and slightly truncate in lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril equidistant between tip of snout and eye, slightly protuberant. Tympanum indistinct, round, TDH/ED 0.59. Supratympanic fold distinct, slightly raised, dark brown, running straight from posterior corner of eye over tympanum, curving gently ventrally posterior to the tympanum to above the forearm's insertion. Lateral head similar in colour to dorsal head, except for the supratympanic fold. Superciliary spines absent, one subtle light dot above each eye. Dorsal skin smooth in preservative. Tongue partly taken as tissue sample, originally broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth curved, without pronounced height variation, separated at the midline by a small gap. Choanae round and surrounded by pigment, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.380), strongly built. Fingers without webbing, moderately long, relative lengths $1 < 2 < 4 < 3$ on left hand, $1 < 4 < 2 < 3$ on right, in both cases distinctly so (Fig. 31). Finger tips not expanded, rounded. Finger subarticular tubercles distinct, whitish, flat; inner metacarpal tubercle broad and rounded, outer metacarpal/palmar tubercle indistinct, greyish. Hind limb strong, tibiotarsal articulation reaching between tympanum and eye when addressed anteriorly along the body. TIBL/SVL 0.428. Inner metatarsal tubercle present, oblong, whitish, distinctly raised. Outer metatarsal tubercle absent. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third, third toe extending to the middle of the second phalange of the fourth toe; subarticular tubercles slightly distinct; toe tips slightly enlarged, rounded (Fig. 31).

After 19 years in preservative, the base colour is a coffee brown across the dorsum, and a darker brown on the limbs. The dorsum is mottled brown, with a clear V-shaped marking over the suprascapular region. Behind the eyes, running patterns towards the inguinal region, are lighter brown wavy patterns riddled with tiny white points, very similar to *R. sonaliae* **sp. nov.** No distinct colour difference between the lateral and dorsal head except on the supratympanic fold, which is dark brown. The inguinal region bears several large white spots which also extend onto the anterior thigh, on a dark brown background. There are also several white spots on the posterior thigh, ventral shank, and dorsal foot. The ventral thigh is mostly cream, mottled with light brown. The ventral feet are a light brown. A light annulus is present before the terminal phalange of each finger and toe. The legs have distinct crossbands on the thigh, shank, tarsus, and foot. The arms have a single crossband on the lower arm. The palmar

surface is grey-brown. The chin is light brown, the ventral abdomen mostly cream, with a few brown flecks. The cloaca region is unmarked, and there is no blackish bar above it.

Variation. SVL 34.3–37.9 mm ($n = 2$). For variation in other measurements see Table S6. MRSN A4600 has a distinctly different skin texture in preservative, and is also much less mottled than the holotype. It lacks the V-shaped marking of the dorsum and the crossbands on the legs of the holotype. MRNS A4544 likewise lacks the V-shaped marking on the dorsum, but does have the crossbands on its legs.

Call. The call of this species is unknown.

Etymology. The Malagasy adjective *anatala* meaning ‘in the forest’, in reference to the habitat of this species in the rainforests of Masoala. Used as an invariable noun in apposition.

Distribution. This species is only known from (1) Amparihy (type locality) and (2) Menamalona on the Masoala Peninsula. Elevation: 778–800 m a.s.l.

Natural history. Little is known of the ecology of this species, but we presume that it is similar to its sister species, *R. sonaliae* **sp. nov.**, in its ecology and behaviour; see the account of that species, above.

Rhombophryne kotrobaratra **sp. nov.**

<https://zoobank.org/058798DB-5703-447F-BBB9-5F912923531A>

Figures 2, 4–7, 30, 31, 48, 49

Informal names. This species was listed as ‘*Rhombophryne* sp. 10’ by Vieites et al. (2009) and ‘*Rhombophryne* sp. Ca10’ by Scherz et al. (2015b), Lambert et al. (2017), Scherz (2020), and Belluaro et al. (2022), and ‘*Rhombophryne* sp. 10’ and ‘UCS “Sp. 10”’ and ‘UCS “Sp. 20”’ by Carné and Vieites (2024). A specimen of this species (MRSN A2610) was mistakenly figured as the specimen MRSN A2620 of ‘*R. sp. Ca19*’ by Belluaro et al. (2022).

Justification of the new species. The new species was found to be the sister species of *R. sp. Ca15* from Betampona of which no further data are available (see account on this candidate species below). Together, the clade of these two lineages is sister to all other species of the *R. laevipes* group based on a multigene phylogeny (Belluaro et al. 2022) which by itself already excludes conspecificity with any of the other nominal species. Genetic divergence of *R. kotrobaratra* **sp. nov.** to all other nominal species of *Rhombophryne* is $>7.5\%$ uncorrected p distance in the 3'-terminal fragment of 16S and thus much higher than the 3% level typically indicative of species-level differentiation in Malagasy frogs (Vieites et al.

2009). There is no haplotype sharing in the analysed fragment of the nuclear gene RAG1 between *R. kotrobaratra* **sp. nov.** and any other species of the *Rhombophryne* genus in the analysed dataset (Fig. 4). Furthermore, it also differs from other nominal species in the *R. laevipes* group by morphological characters (see Diagnosis below), and its status as distinct species is therefore beyond doubt. More research is necessary to understand the status of *R. sp. Ca15* (see below).

Holotype. MRSN A2990 (RJS 0581), an adult female, collected on 17 February 2002 at ‘Camp 7’ Antsiranana Faritany (15.4177°S, 49.9403°E, ca. 778 m a.s.l.), Amparihy, Masoala Peninsula, Analanjirofo Region, north-eastern Madagascar, by J.E. Randrianirina (Figs 30, 31).

Paratypes. Nine specimens: MRSN A2610 (FAZC 10312; Fig. 48A–C), an adult male, and MRSN A2599 (FAZC 10307), an adult female, collected on 11 and 13 December 1999 (respectively) at ‘Camp 5’ Menamalona (15.3812°S, 49.9878°E, ca 800 m a.s.l.), Ilampy Corridor, Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by F. Andreone and J.E. Randrianirina; MRSN A1845 (FN 6310), an adult female, collected on 3 December 1996 in Antsarahany Tsararano (ca 14.9067°S, 49.6867°E, ca 700 m a.s.l.), Sava Region, northeastern Madagascar, by F. Andreone (Fig. 48E, F); MRSN A2609 (FN 7519; Fig. 49), an adult male, and MRSN A2601 (FN 7560), an adult female, collected on 23 and 24 November 1998 (respectively) at ‘Camp 2’ Beanjada (15.2638°S, 49.9583°E, ca 1000 m a.s.l.), Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by F. Andreone and J.E. Randrianirina; UADBA-A-APR 12594, UADBA-A-APR 12541, and UADBA-A-APR 12563, a putative male and two small juveniles (respectively), collected on 16–19 May 2016 at mid-elevation in Marojejy National Park (14.4559°S, 49.7749°E, 765–780 m a.s.l.), Sava Region, northeastern Madagascar, by A.P. Raselimanana; UADBA-A-APR 12765, an adult female, collected on 1 June 2016 at mid-elevation in southwestern Marojejy National Park (14.5074°S, 49.6153°E, 835 m a.s.l.), Sava Region, northeastern Madagascar, by A.P. Raselimanana.

Assignment of specimens. The paratype MRSN A2610 (FAZC 10312) is used as the reference specimen for this species in 16S rRNA barcoding (16S5’ AY594073; Andreone et al. 2005; 16S3’ AY594111; Vieites et al. 2009). The holotype is used as the reference specimen for COI barcoding (COI OL790134; Belluardo et al. 2022). The 16S sequence of the holotype differs from the 16S reference sequence by eight mutations and three gaps in the 16S3’ fragment (98% identical; OL780580). All paratypes and referred specimens conform well with the holotype in morphology; no further specimens are sequenced. MRSN A2990 and MRSN A2610 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. laevipes* group, this species along with *R. sp. Ca15* represents the sister clade of all

other group members based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) medium body size, adult SVL 24.1–33.0 mm; (2) head wider than long (HW/HL 1.46–1.64); (3) moderately small eyes (ED/HL 0.34–0.44); (4) long hindlimbs (HIL/SVL 1.81–1.92); (5) small inner metatarsal tubercle (IMTL/FOL 0.09–0.11); (6) outer metatarsal tubercle sometimes present; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin granular with scattered warts in life; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of distinct inguinal spots; (13) presence of bright orange colouration on the hidden surfaces of the legs in life; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne kotrobaratra **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany heleanae* MZ751042): in 16S5’, ‘C’ at site 288, ‘T’ at site 355, and ‘T’ at site 402. No diagnostic sites were identified for 16S3’.

Diagnosis. Within the genus *Rhombophryne*, *R. kotrobaratra* **sp. nov.** is highly distinctive, and can be distinguished from all other species by the combination of orange colouration on the hidden surfaces of the legs (otherwise present only in the *R. ellae* species group and *R. mavokely* **sp. nov.**), absence of inguinal ocelli (present in *R. ellae* and *R. quentini* **sp. nov.**), and long legs (HIL/SVL 1.81–1.92 vs 1.50–1.61 in *R. mavokely* **sp. nov.**, 1.40–1.80 in the *R. ellae* species group). It also typically has a distinctive dark chevron dorsally, which can be useful to distinguish it from most other species. These chevrons and in general the presence of a rather tubercular dorsal skin appear to distinguish the species from all other nominal species in the *R. laevipes* group.

Description of holotype. An ovigerous adult female in an excellent state of preservation (Fig. 30). Right arm removed as a tissue sample, and a slit made along the right flank to check the sex. The abdomen is full of highly developed ova.

Body robust. Head wider than long (HW/HL 1.55), distinctly narrower than abdomen. Eyes moderately small (ED/HL 0.41), slightly depressed, pupils lenticular. Snout rounded in dorsal and lateral view. Canthus rostralis indistinct, concave. Loreal region weakly concave, oblique. Nostril closer to tip of snout than to eye, very slightly protuberant. Tympanum indistinct, round, TDH/ED 0.55. Supratympanic fold indistinct, weakly raised, curving slightly from posterior corner of eye to above the forearm’s insertion. Lateral head similar in colour to dorsal head. Superciliary spines absent. Dorsal skin smooth in preservative. Tongue partly taken as tissue sample, originally broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth curved,

without height variation, separated at the midline by a small gap. Choanae oval, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.407) and narrow. Fingers without webbing, moderately long, relative lengths $1 < 4 < 2 < 3$, second finger distinctly longer than fourth (Fig. 31). Finger tips not expanded, rounded. Finger subarticular tubercles distinct, whitish, flat; inner

metacarpal tubercle distinct and rounded, outer metacarpal/palmar tubercle distinct and oblong, cream. Hind limb strong with particularly thick and robust thighs, tibiotarsal articulation reaching the snout when adpressed anteriorly along the body. TIBL/SVL 0.520. Inner metatarsal tubercle present, oblong, whitish, distinctly raised. Outer metatarsal tubercle present as a faint lightening of the general area. Toes not webbed; toes unreduced, toe

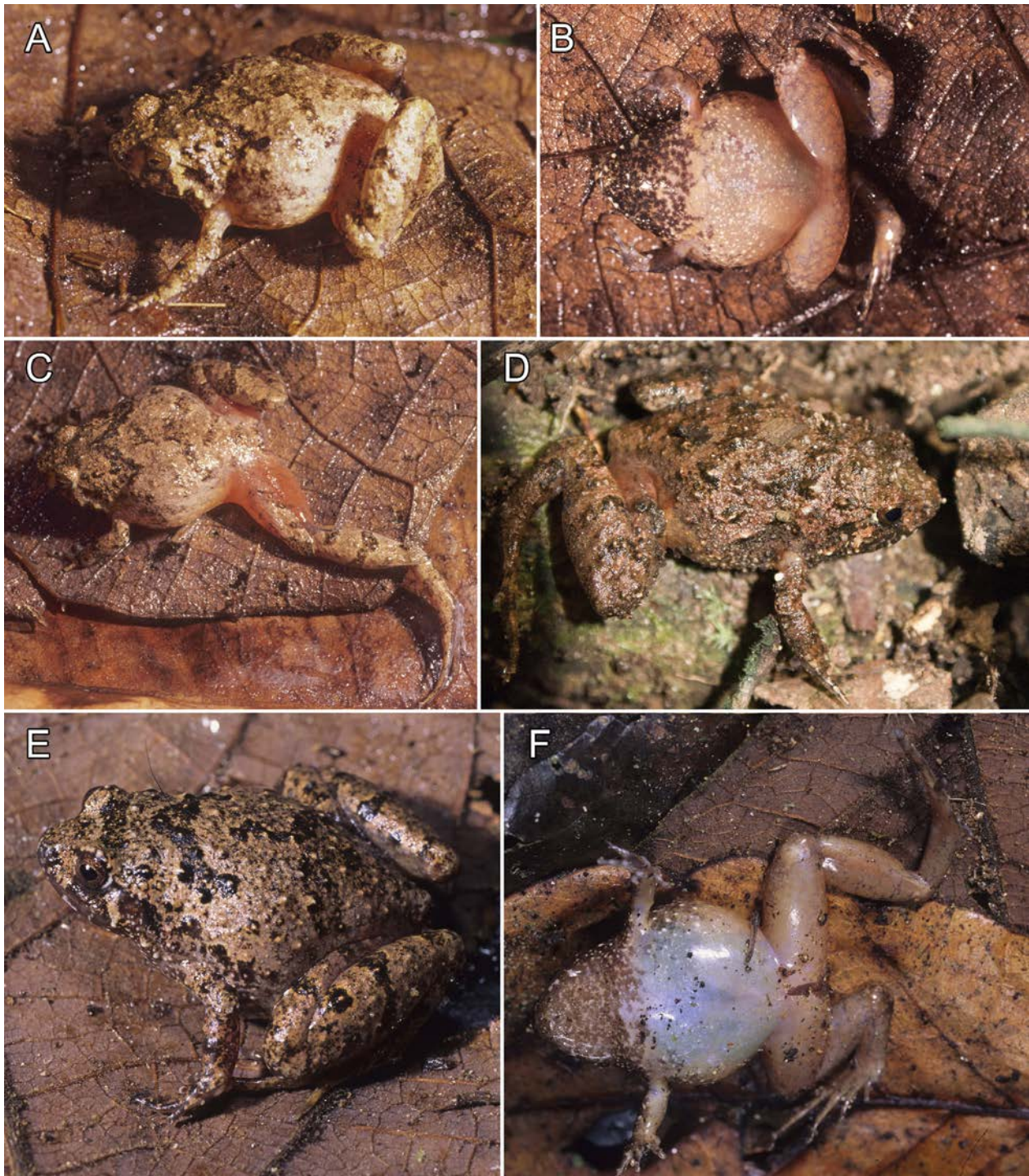


Figure 48. *Rhombophryne kotrobaratra* **sp. nov.** in life. **A–C** adult male paratype MRSN A2610 (FAZC 1031), from Menamalona, Masoala Peninsula, in **A** dorsolateral, **B** ventral, and **C** dorsal view with left leg stretched. **D** An uncollected individual referable to *R. kotrobaratra* **sp. nov.** in dorsolateral view, photographed by Éric Mathieu near ‘Camp 2’ in Marojejy National Park, ca 600–700 m a.s.l. **E, F** adult female paratype MRSN A1845 (FN 6310), from Antsarahany Tsararano, in **E** dorsolateral and **F** ventral view. Notice the reddish orange colouration on the legs in life in **C** and **D**.

consistently includes the dark chevron marking over the suprascapular region. The posterior chevron varies from highly distinct (MRSN A2609), to its least distinct in the holotype (Fig. 30). The legs of APR 12765 and APR 12594 are distinctly narrower than the rest of the type series. These specimens are also greyer in colour, possibly as a result of differences in preservation method. The ventral surface of APR 12765 is covered in tiny round dark markings that are clearly distinct from melanosomes. These structures are absent from all other specimens.

Call. The call of this species is not known.

Etymology. The Malagasy noun *kotrobaratra* meaning ‘thunder and lightning’, in reference to the typical conditions under which this frog emerges, during stormy weather with heavy rain. Used as an invariable noun in apposition.

Distribution. This species is known from (1) the western Masoala Peninsula: Amparihy (type locality), Menamalo-na, and Beanjada, and (2) Antsarahana’ny Tsararano, and (3) Marojejy (Fig. 48). It occurs at intermediate elevations (ca 600–1000 m a.s.l.).

Natural history. *Rhombophryne kotrobaratra* **sp. nov.** is a semi-fossorial or detriticolous species found in low- to mid-elevation humid forest. Specimens collected by APR were active at night on wet thick leaf litter covering the forest floor, after a heavy rain late in the afternoon. All observed individuals were found in almost-closed-canopy forest.

Rhombophryne sp. Ca15

Remark. This candidate species was identified by Bel-luardo et al. (2022) based on the specimen DLR 620 (extraction number ACP3194), which has been sequenced for the mitochondrial markers 16S3’ (OL780581), 16S5’ (OL780604), 12S (OL780590), COB (OL853700), and COI (OL790135), and the nuclear markers BDNF (OL853691), POMC (OL780557), RAG1 (PZ377035), RAG2 (OL780561), SACS-A (OL853704), and KIAA1239 (OL780539). It has also been referred to as ‘*R. sp. 15*’ and ‘*UCS “Sp. 15”*’ by Carné and Vieites (2024). Other than its collection locality (Betampona Strict Nature Reserve, central eastern Madagascar), we have no further data on this specimen. Based on its phylogenetic position, it appears to be the closest relative of *R. kotrobaratra*. No specimens were available to us at this time and it was not possible to assess this species taxonomically, but it is distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘T’ at site 288, ‘T’ at site 413, and ‘C’ at site 642; in 16S3’, ‘G’ at site 899, ‘A’ at site 1026, ‘G’ at site 1267, and ‘T’ at site 1276.

Osteology of the *Rhombophryne laevipes* species group

Material examined. This description is based on the following specimens: *R. laevipes* (MNHN 1893.285; Fig. 34), *R. botabota* (ZSM 358/2005; Fig. 37), *R. nilevina* (KU 340897; Fig. 40), *R. sonaliae* **sp. nov.** (ZSM 3/2002; Fig. 44), *R. anatala* **sp. nov.** (MRSN A2696; Fig. 47), and *R. kotrobaratra* **sp. nov.** (MRSN A2609; Fig. 49). The left arm of MRSN A2609 has been removed at the mid-humerus, its fourth toe on the right foot has been amputated near the middle of the first tarsal, and the right femur of KU 340897 is broken and healed near its distal end. V8 and the sacrum are fused in the vertebral column of ZSM 3/2002, presumably a developmental defect. Several of its finer bones are poorly ossified. This is true also of MNHN 1893.285, though to a lesser extent.

The *Rhombophryne laevipes* species group is osteologically rather homogeneous, showing mostly generalist, terrestrial features without obvious adaptations to digging. Here, we provide a description of the osteology of the group that highlights particularly diagnostic features of each species.

The skull is broader than long, and rather consistent in relative dimensions in all species. The braincase of *R. kotrobaratra* **sp. nov.** appears to extend further forward than all other members of the group (Fig. 49D).

Dorsal investing bones. Nasals closely abutting or contacting the frontoparietals in all species except *R. botabota*, in some cases in contact with calcified portions of the sphenethmoid. The maxillary process of the nasal is oriented posterolaterally and runs towards the neopalatine, but does not come close to contacting it or the maxilla in any species. The dorsal surface of the nasal and the maxillary process have an anterolateral concavity (similar to *R. maraorao* **sp. nov.** and *R. coudreaui* from the *R. testudo* species group), most pronounced in *R. nilevina* and *R. sonaliae* **sp. nov.** The maxillary process of most species tapers distally, but in *R. kotrobaratra* **sp. nov.** it is narrower and tapers only at the distal tip.

The frontoparietals are rather conserved in this group. All species have a distinct dorsal process. The lateral ventrally descending flange extends almost the full length of the frontoparietal, and encloses less than half of the lateral braincase.

Neurocranium. The sphenethmoid varies from fully ossified and covering the anterolateral wall of the braincase (*R. anatala* **sp. nov.**, *R. kotrobaratra* **sp. nov.**), to weakly ossified but covering the anterolateral wall of the braincase (*R. nilevina*, *R. botabota*, *R. sonaliae* **sp. nov.**), to almost totally unossified (*R. laevipes*).

The exoccipital varies little in shape across this group. The posteromedial face of the dorsal extension is convex in *R. anatala* **sp. nov.** but flatter in most other species. The exoccipitals do not meet medially. The prootic is well ossified in all species, and varies little in shape among species.

The septomaxilla is rather consistent in shape across the group. The medial ramus is apparently present in all

species except *R. sonaliae* **sp. nov.** and *R. botabota*, but see our previous comments on the septomaxilla and its ossification, and why it should not be relied upon as a diagnostic feature in micro-CT scans (Scherz et al. 2017a).

The columella is rather similar in shape and structure among species.

Ventral investing and palatal bones. The cultriform process of the parasphenoid is broad in all species except *R. kotrobaratra* **sp. nov.**, where it is much narrower and longer. The alary processes of *R. sonaliae* **sp. nov.** are proportionally rather short, compared to the other species.

The anterior portion of the vomer is triradiate, nearly crescentic in some species. It is comparatively larger in *R. laevipes* and *R. sonaliae* **sp. nov.** than the other species, but this may be an artefact of its degree of ossification. The posterior portion of the vomer is curved (*R. kotrobaratra* **sp. nov.**, *R. laevipes*, *R. botabota*) or sigmoid (*R. anatalia* **sp. nov.**, *R. nilevina*, *R. sonaliae* **sp. nov.**). It bears distinct teeth in all species. There is a distinct diastema in the vomerine teeth of *R. kotrobaratra* **sp. nov.** The neopalatine, which lies dorsally on top of the vomer, is a curved flattened rod-like structure, but has a rounded to spatulate anterior projection near the midline in all species. The vomers and neopalatines are separated medially by a small gap.

Maxillary arcade. Maxillary teeth are present in all species, but are largest in *R. sonaliae* **sp. nov.** The premaxilla is fairly uniform across species. The maxilla is not especially deep in any species. Its lateral surface is concave in *R. sonaliae* **sp. nov.** and to some extent in *R. laevipes*. The facial process is bluntly raised in *R. botabota* and *R. kotrobaratra* **sp. nov.**, but more triangular in the other species. It is widely separated from the maxillary process of the nasal. The contact with the anterior ramus of the quadratojugal is extensive.

Suspensorium. The anterior ramus of the quadratojugal is curved in *R. kotrobaratra* **sp. nov.**, but straight in all other species. The contact with the squamosal is fairly brief.

The ventral ramus of the squamosal is rather straight, posteriorly flared. The otic and zygomatic rami are of similar length in all species, and form a gentle continuous curve in all species except *R. nilevina*, where they are rather angled relative to one another in dorsal view (Fig. 40D).

The pterygoid is quite consistent among species, varying predominantly in the position of the lateral groove.

Mandible. The mentomeckelians of all species are small and hourglass-shaped. The dentary is thin and laminar. The angulosplenial is robust. The coronoid process is low but distinct, largest in *R. laevipes*. The posterior process (articular facet) is weakly expanded.

Pectoral girdle. The coracoids are medially strongly flared, with a long medial contact facet. Clavicles present

and curved. The scapula and cleithra do not differ sufficiently for further comment.

The humeral crests are strongly developed in all species. The crista ventralis extends half the length of the humerus in all species except *R. kotrobaratra* **sp. nov.**, where it is ca one third of the humerus. The crista lateralis is present but weakly developed. The radioulna does not show remarkable variation.

Ossification of the hand bones is very low in *R. sonaliae* **sp. nov.**, and quite low in *R. laevipes*. Carpals 2, 3–5, element Y, radiale and ulnare present. The prepollex is absent or unossified in the specimens of *R. laevipes* and *R. sonaliae* **sp. nov.** examined. Among the other species, it is moderately large. The digital formula of all species is the same (2-2-3-3), and terminal phalanges consistently end with small knobs.

Vertebral column. Transverse processes of V2 perpendicular to body axis in all species except *R. botabota*, where they are angled posteriorly. Transverse processes of V2–4 distinctly broader than V5–8. Transverse processes of V5–8 broader than or roughly as broad as centrum is wide in *R. sonaliae* **sp. nov.**, *R. nilevina*, *R. laevipes*, and *R. anatalia* **sp. nov.**; substantially shorter than centrum is wide in *R. botabota* and *R. kotrobaratra* **sp. nov.** The sacrum is as wide as V4 in all species, its anterior edge quite straight, angled posteriorly. The diapophyses are very weakly flared in *R. botabota* and *R. kotrobaratra* **sp. nov.**, and more strongly flared in the other species (most strongly in *R. laevipes*). The urostyle has a dorsal ridge along 60–90% of its length, but the posterior tip is free in all species.

Pelvic girdle. Iliac shafts with strong dorsal crests in all species. The oblique groove and dorsal prominence are present in all species, most distinctly so in *R. nilevina* and *R. sonaliae* **sp. nov.**, and most weakly so in *R. kotrobaratra* **sp. nov.** The femur lacks a posterior ridge. The tibiofibula and tarsus do not bear further comment. The toe formula is standard (2-2-3-4-3). The prehallux is small, comprised of two elements. The state in *R. sonaliae* **sp. nov.** and *R. laevipes* cannot be commented upon because of the low ossification. Terminal phalanges of all toes short and knobbed.

Rhombophryne ellae species group

Rhombophryne ellae Scherz, 2020

Figures 2, 4–7, 50–53

Holotype. ZSM 76/2018 (MSZC 0534), an adult or subadult female, collected on 28 December 2017 in ‘Montagne d’Ambre National Park (12.5066°S, 49.1746°E, 892 m a.s.l.)’, Diana Region, northern Madagascar by M.D. Scherz, J.H. Razafindraibe, A. Razafimanantsoa, O. Randriamalala, S.M. Rasolonjavato, R. Tiavina, E.Z. Latenkamp, and A. Rakotoarison (Figs 50, 51, 52A–D, 53).

Paratypes. None.

Referred specimens. ZSM 903/2003 (FGMV 2002.0918), an unsexed adult, collected on 18 February 2003 in Montagne d'Ambre National Park (no precise coordinates available), Diana Region, northern Madagascar by F. Glaw, R.D. Randrianiaina, and A. Razafimanantsoa (Fig. 52E, F); ZSM 222/2004 (FGZC 432), a juvenile specimen, collected on 20 February 2004 in Montagne d'Am-

bre National Park (no precise coordinates available), Diana Region, northern Madagascar, by F. Glaw, M. Puente, R. Randrianiaina, and A. Razafimanantsoa.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S3' MT371794; Scherz 2020) and COI barcoding (COI MT372330; Scherz 2020), and is present in the RAG1 haplotype network (Fig. 4). No other specimens

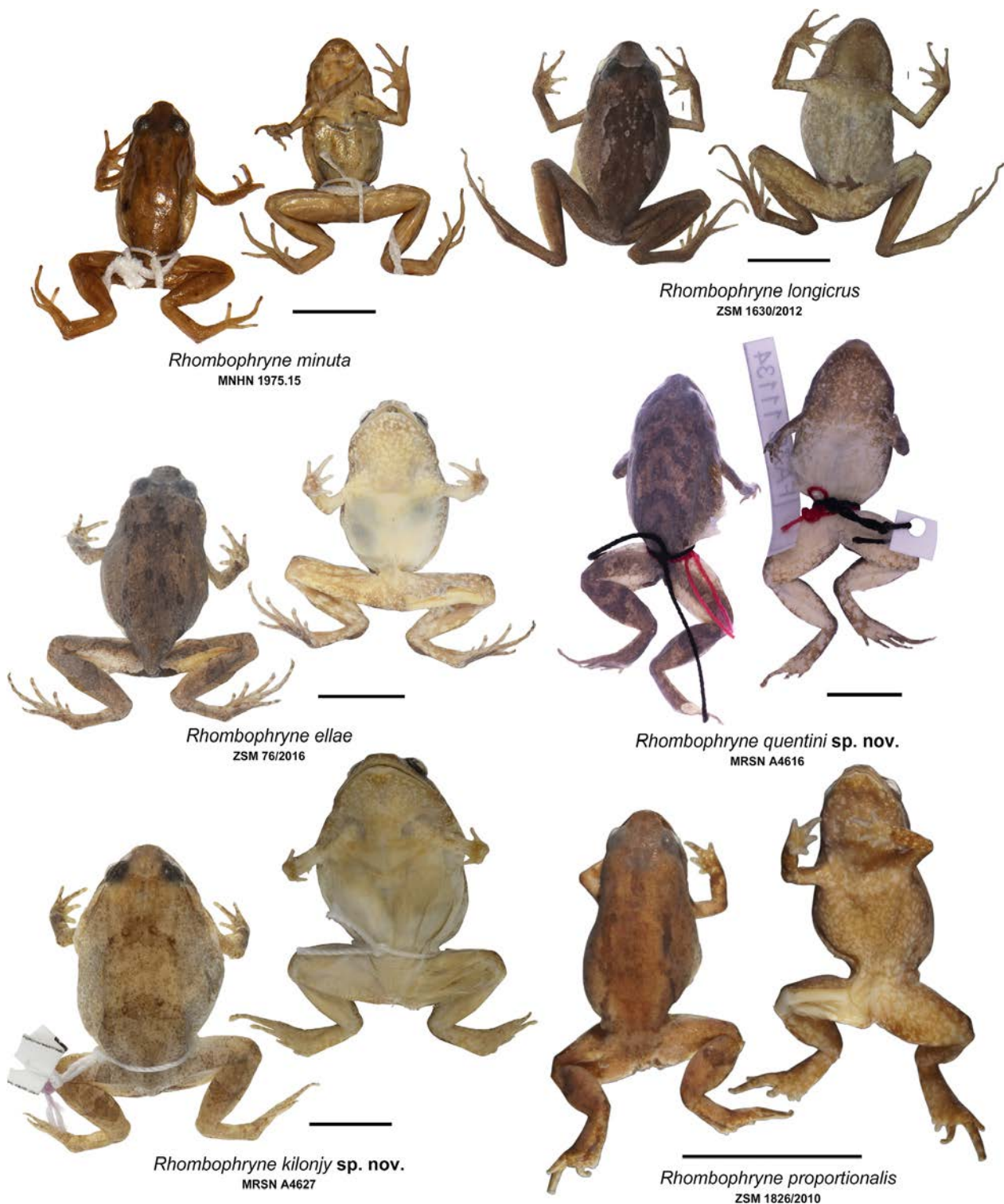


Figure 50. Name-bearing type specimens of species in the *Rhombophryne ellae*, *R. proportionalis*, and *R. minuta* species groups in dorsal (left) and ventral (right) views. Scale bars = 10 mm.

of the species have yet been sequenced. Both of the newly referred specimens conform well with the holotype in morphology.

Definition. Within the *R. ellae* group, this species is sister to a clade consisting of *R. quentini* **sp. nov.** and *R. kilonjy* **sp. nov.** (described below) based on molecular phylogenetic data. It is characterised by the possession of the following unique suite of characters: (1) medium body size, adult SVL 24.9 mm; (2) head wider than long (HW/HL 1.47); (3) moderately small eyes (ED/HL 0.38); (4) relatively long hindlimbs (HIL/SVL 1.71); (5) small inner metatarsal tubercle (IMTL/FOL 0.9); (6) outer metatarsal tubercle weakly pronounced; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence of large black inguinal ocelli bordered with white; (13) presence of bright orange colouration on the hidden surfaces of the legs in life; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne ellae is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S3', 'G' at site 1025, and 'A' at site 1074 (16S5' not available for this species).

Diagnosis. Within the genus *Rhombophryne*, *R. ellae* can be distinguished from all species except *R. quentini* **sp.**

nov. described below by the combination of distinctive white-outlined black inguinal ocelli with reddish orange colouration on the hidden surfaces of the legs. For distinction from *R. quentini* **sp. nov.** and *R. kilonjy* **sp. nov.**, see the description of those species, below.

Variation. In the original description, Scherz (2020) reported on the single specimen known to him at that time. ZSM 903/2003 (Fig. 52E, F) and ZSM 222/2004, agree very well with the original description both in morphology and in colouration. The dorsal skin of ZSM 903/2003 is slightly more granular than the type specimen, and the skin on the underside of the legs is darker grey. ZSM 222/2004 appears faded in colour. Morphometric measurements are provided in Table S7.

Call. The call of this species is unknown.

Etymology. Eponym for Ella Z. Lattenkamp, partner of MDS.

Distribution. This species is only known from (1) Montagne d'Ambre National Park (type locality).

Natural history. *Rhombophryne ellae* is a semi-fossorial or detriticolous species found in mid-elevation humid forest; its ecology is poorly known. Gut contents of the holotype included 'three whole ants and one ant head, seemingly belonging to two different species (one of the whole ants is diminutive), the head of a jumping spider (Salticidae), and the elytra and other body parts of a beetle.' (Scherz 2020: 319).



Figure 51. Ventral views of hands and feet, and lateral views of heads of name-bearing type specimens of members of the *Rhombophryne ellae*, *R. proportionalis*, and *R. minuta* species groups. Not to scale. * = mirrored for conformity.



Figure 52. *Rhombophryne ellae* in life. Photographed in rainforest in Montagne d'Ambre National Park. **A–D** adult female holotype ZSM 76/2018 (MSZC 0534) from Montagne d'Ambre in **A** posterior, **B** dorsal, **C** ventral, and **D** dorsolateral view; **E, F** unsexed adult ZSM 903/2003 (FGMV 2002.0918), a specimen referred to *R. ellae* based on morphology and colour, in **E** dorsolateral and **F** ventral view. Notice the inguinal spot with a thin white outline visible in **A** and **D** and the vibrant orange of the posterior thighs in **A** that is totally hidden when the legs are folded as in **B** and **D**.

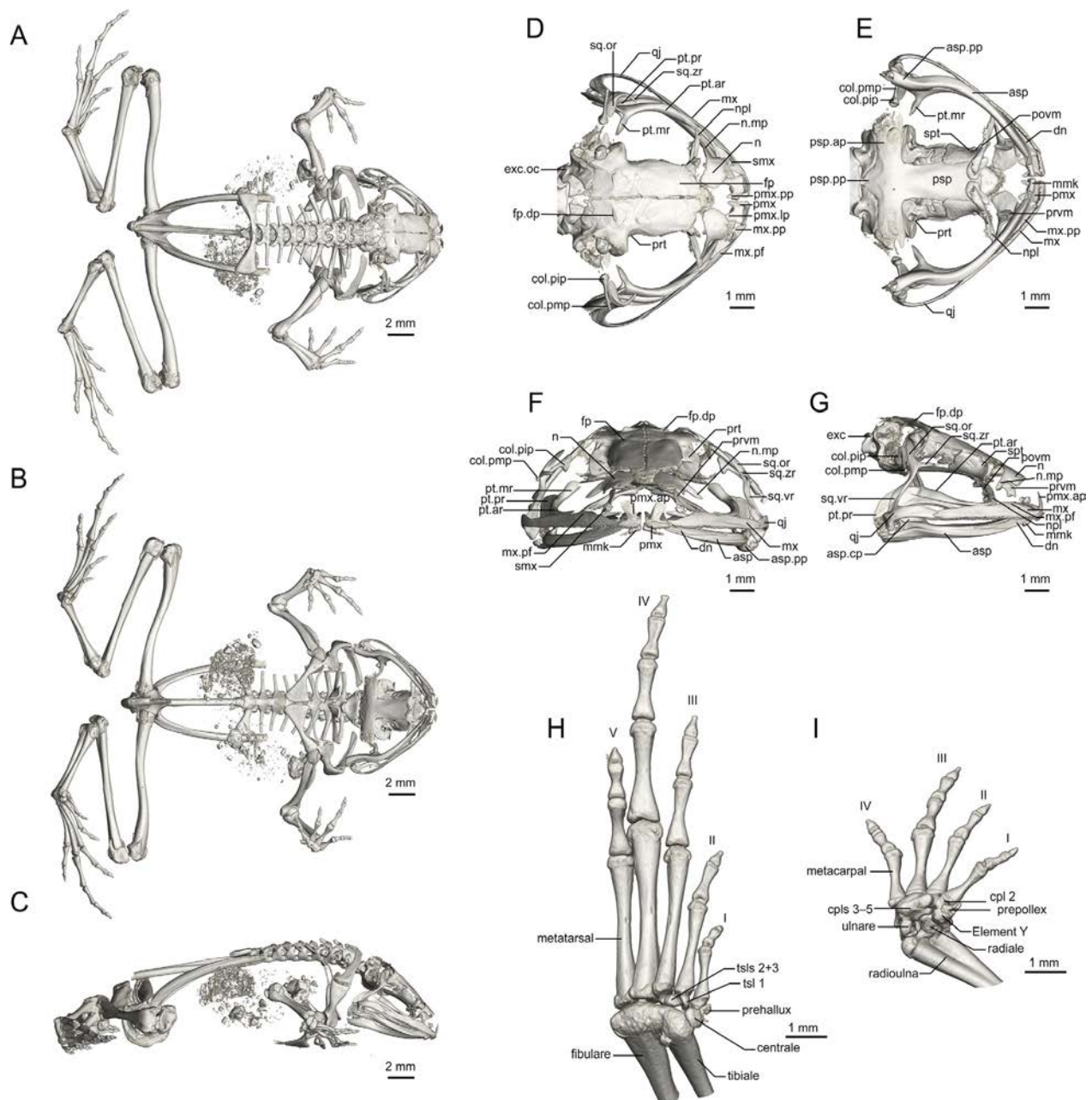


Figure 53. Skeleton of *Rhombophryne ellae* holotype ZSM 76/2018 (MSZC 0534). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** include small stones. Abbreviations are given under Materials and Methods.

Rhombophryne quentini sp. nov.

<https://zoobank.org/C8BE387D-E861-49B6-85B5-31805710E5DF>

Figures 2, 4–7, 50, 51, 54, 55

Remark. This species was figured as possibly representing *Rhombophryne guentherpetersi* by Glaw and Vences (2007).

Informal names. This species was listed as ‘*Rhombophryne* sp. 3 Tsaratanana’ by Wollenberg et al. (2008), ‘*Rhombophryne* sp. 7’ by Vieites et al. (2009), “‘*Rhombophryne*” sp. Ca07 Tsaratanana’ by Scherz et al. (2016b),

‘*Rhombophryne* sp. Ca07’ by Belluardo et al. (2022), ‘*Plethodontohyla* sp. 2’ by Andreone et al. (2009), and ‘*Rhombophryne* sp. 7’ and ‘UCS “Sp. 7”’ by Carné and Vieites (2024).

Justification of the new species. The new species is sister to *R. kilonjy* sp. nov., and these two species are together sister to *R. ellae*, as part of the *R. ellae* group that is phylogenetically distinct from other *Rhombophryne* (Belluardo et al. 2022). From *R. ellae*, the new species differs by a high genetic divergence of 6.3% uncorrected p distance in the 16S3’ fragment and thus distinctly higher than the 3% level typically indicative of species-level differentiation in Malagasy frogs (Vieites et al. 2009). There is no haplotype sharing between *R. quentini* sp. nov. and

R. ellae in the analysed fragment of the nuclear gene RAG1 (Fig. 4). Furthermore, it also consistently differs from *R. ellae* by various morphological and osteological characters, especially its pronounced metatarsal tubercle (see Diagnosis below), and its status as distinct species is therefore beyond doubt. See also the Justification section for *R. kilonjy* **sp. nov.** below.

Holotype. MRSN A4616 (FAZC 11134), an adult female, collected on 9 February 2001 at ‘Camp 1’ Antsahamanara (ca 14.045°S, 48.784°E, ca 1000 m a.s.l.), Manarikoba, Réserve Naturelle Intégrale de Tsaratànana, Diana Region, northern Madagascar, by F. Andreone, F. Mattioli, J.E. Randrianirina, and M. Vences (Figs 50, 51, 54A, B).

Paratypes. 12 specimens: MRSN A4615 (FAZC 11129; Fig. 55), MRSN A4617 (FAZC 11133), and MRSN A3248 (FAZC 11161 = FGMV 2001.G46 tissue sample), MRSN A4638 (FAZC 11169), four unsexed adults, MRSN A4628 (FAZC 11060), a juvenile, MRSN A4604 (FAZC 11048), an unsexed individual of uncertain maturity, MRSN A3656 (FAZC 11062; Fig. 54C, D), an adult female, MRSN A4629 (FAZC 11059; Fig. 54E, F), a subadult female, MRSN A4595 (FAZC 11151), an adult probable female (ambiguous genitalia), and MRSN A4630 (FAZC 11146) and MRSN A4631 (FAZC 11084), and UADBA-A 28193 (MV 2001.134), three adult males, all with same collection data as the holotype, but collected on 4–13 February 2001

Referred specimens. BMNH 1987.2297 (field number ‘9’), an unsexed adult, collected on 12 February 1988 at ‘Camp B’ in Manongarivo Special Reserve (14.067°S, 48.283°E, 350 m a.s.l.) by C.J. Raxworthy conforms morphologically with this species, but is not genetically verified. Due to its lower elevational distribution and geographical separation from other records, it is here tentatively included in the circumscription of *R. quentini* **sp. nov.**

Assignment of specimens. The paratype MRSN A3248 (FAZC 11161 = FGMV 2001.G46) is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ and 16S5’ EU341108; Vieites et al. 2009). The holotype is used as the reference specimen for this species in COI barcoding (COI OL790133; Belluardo et al. 2022). The sequence of the holotype is identical to the sequence of the reference specimen for 16S in 16S3’ (OL780577), and differs by one mutation in 16S5’ (99.8% identical; OL780602). All paratypes and referred specimens conform well with the holotype in morphology. Assignment of specimens MRSN A4615, MRSN A3248, MRSN A4604 and MRSN A4617 is further confirmed by molecular taxonomic identification (Fig. 2). Unsequenced, morphologically identified specimens MRSN A4638, MRSN A4628, MRSN A3656, MRSN A4629, MRSN A4595, MRSN A4630, MRSN A4631, UADBA-A 28193 were also collected at the type locality, and can be assigned to the species morphologically. MRSN A4604, MRSN A4615, and MRSN A3248 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. ellae* group, this species is sister to *R. kilonjy* **sp. nov.** (described below) based on molecular phylogenetic data (not shown). It is characterised by the possession of the following unique suite of characters: (1) small to medium body size, adult SVL 21.4–30.1 mm; (2) head wider than long (HW/HL 1.31–1.66); (3) moderately small eyes (ED/HL 0.32–0.43); (4) relatively long hindlimbs (HIL/SVL 1.44–1.80); (5) small inner metatarsal tubercle (IMTL/FOL 0.6–0.12); (6) outer metatarsal tubercle very distinct; (7) second finger subequal, shorter than, or seldom longer than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence of large black inguinal ocelli bordered with white; (13) presence of reddish orange colouration on the hidden surfaces of the legs in life; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne quentini **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘A’ at site 264, ‘C’ at site 301, and ‘T’ at site 369 (but note that its sister species, *R. ellae*, has not been analysed for this fragment); in 16S3’, ‘C’ at site 1138, ‘T’ at site 1139, and ‘T’ at site 1216.

Diagnosis. Within the genus *Rhombophryne*, *R. quentini* **sp. nov.** can be distinguished from all other *Rhombophryne* except *R. ellae* by the combination of distinctive white-outlined black inguinal ocelli with reddish orange colouration on the hidden surfaces of the legs. From *R. ellae* and almost all other *Rhombophryne* species, it can be distinguished by the very pronounced outer metatarsal tubercle in adults (vs weakly pronounced). It can further be distinguished from *R. ellae* by smaller relative tympanum size (TDH/ED 0.43–0.61 vs 0.62). The skeleton of *R. quentini* **sp. nov.** also seems to differ from that of *R. ellae* in the following traits: posterior edge of nasal with a bend in it (vs continuous in *R. ellae*), less acute angle between zygomatic and otic rami of squamosal as seen in dorsal view, anterior ramus of pterygoid lying abreast of the dorsal edge of the maxilla (vs running along the lingual edge), coracoids medially only weakly flared (vs strongly), shorter transverse processes on presacral vertebrae 5–8, and oblique groove and dorsal prominence weak (vs distinct). For osteological distinction from *R. kilonjy* **sp. nov.**, see the description of that species, below.

Description of holotype. Specimen in a moderately good state of preservation, though slightly soft (Figs 50). An incision made along the right flank to assess the sex, and part of the right foot taken as a tissue sample. Small ova, ovaries, and fallopian tubes clearly visible.

Body robust and rotund. Head wider than long (HW/HL 1.43). Eyes fairly small (ED/HL 0.33), pupils small, round. Snout slightly pointed in dorsal and slightly trun-

cate in lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril approximately equidistant between tip of snout and eye, slightly protuberant. Tympanum distinct, round, TDH/ED 0.52. Supratympanic fold indistinct, slightly raised, partly melanised, running straight from posterior corner of eye over tympanum, curving gently ventrally posterior to the tympanum to anterior to the forearm's insertion. Lateral head similar in colour to dorsal head. Superciliary spines absent. Dorsal skin smooth in preservative. Tongue broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth with a strong diastema, the medial elements distinct, separated from one another at the

midline by a small gap. Choanae round, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.382), moderately slender. Fingers without webbing, relative lengths $1 < 4 < 2 < 3$, second finger distinctly longer than fourth (Fig. 51). Finger tips not expanded, rounded. Finger subarticular tubercles distinct, greyish, flat; inner metacarpal tubercle slender and rounded, outer metacarpal/palmar tubercle distinct, greyish, paired. Hind limb strong, tibiotarsal articulation reaching eye when adpressed anteriorly along the body. TIBL/SVL 0.443. Inner metatarsal tubercle present, oblong, whitish, distinctly raised. Outer metatarsal tubercle highly distinct, rounded and raised.

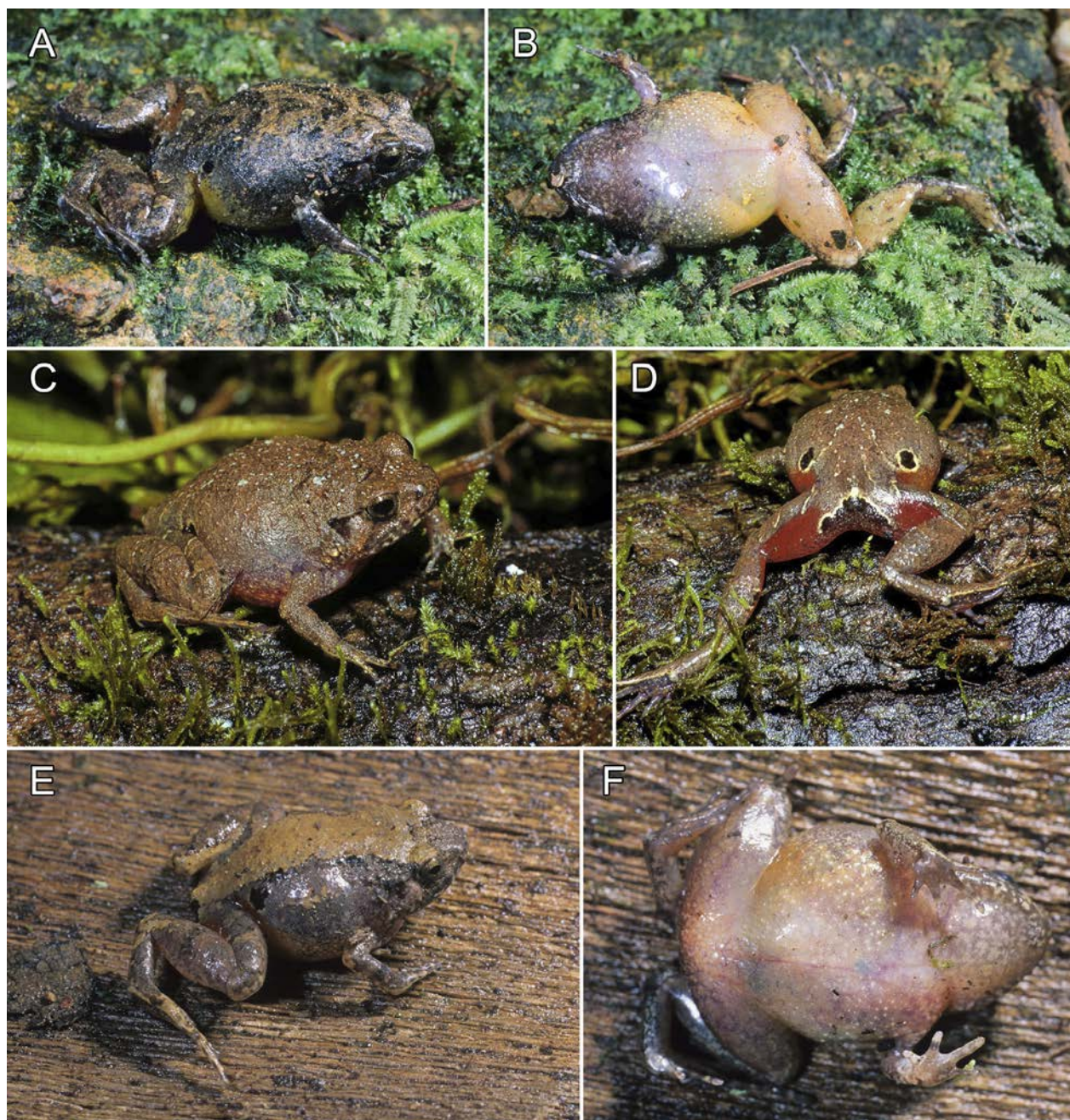


Figure 54. *Rhombophryne quentini* sp. nov. in life. Specimens photographed at Manarikoba, Tsaratàna Strict Nature Reserve in life. **A, B** adult female holotype MRSN A4616 (FAZC 11134) in **A** dorsolateral and **B** ventral view; **C–D** adult female paratype MRSN A3656 (FAZC 11062) in **C** dorsolateral and **D** posterior view; **E, F** subadult female paratype MRSN A4629 (FAZC 11059) in **E** dorsolateral and **F** ventral view.

Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles highly distinct, elongated, grey; toe tips distinctly enlarged, especially of fourth toe, rounded to subacuminate (Fig. 51).

After 22 years in preservative, the base colour is a dark greyed brown across the dorsum and flanks, including the dorsal limbs. The dorsum is marked with darker brown chevrons, specifically one over the suprascapular region and a second over the iliac region. Between the chevrons are additional patches of this darker brown. There are distinct, oblong inguinal ocelli that are a rich dark brown in colour with a very thin whitish edge. No distinct colour difference between the lateral and dorsal head. The supratympanic fold is dark brown from the eye to the tympanum, and then the colour stops. The dorsal hindlimbs bear indistinct crossbands that line up with the leg folded, in the same colours as the dorsum and chevrons. The ventral

foot surface is almost black but for the tubercles (metatarsal and subarticular), which are light grey. The anterior and posterior thigh is pale cream in preservative (this was bright orange in life; Fig. 54A, B), as is the ventral thigh and shank. A distinct, almost black trapezoid is present around the cloaca. The dorsal foot is mottled cream and coffee brown. A light annulus is present before the terminal phalange of each finger and toe. The arms have a single crossband on the antebrachium. The dorsal hand is lighter medially than laterally; the ventral hand is light brown. The chin is mottled light brown with cream flecks, fading to completely cream over the sternal region into the immaculate abdomen.

Variation. SVL of adults 22.1–30.1 mm (n = 10); among sexed adults, males 22.1–25.8 mm (n = 3), females 24.9–26.5 mm (n = 3); thus, very little sexual size dimorphism. For variation in other measurements, see Table S7. This

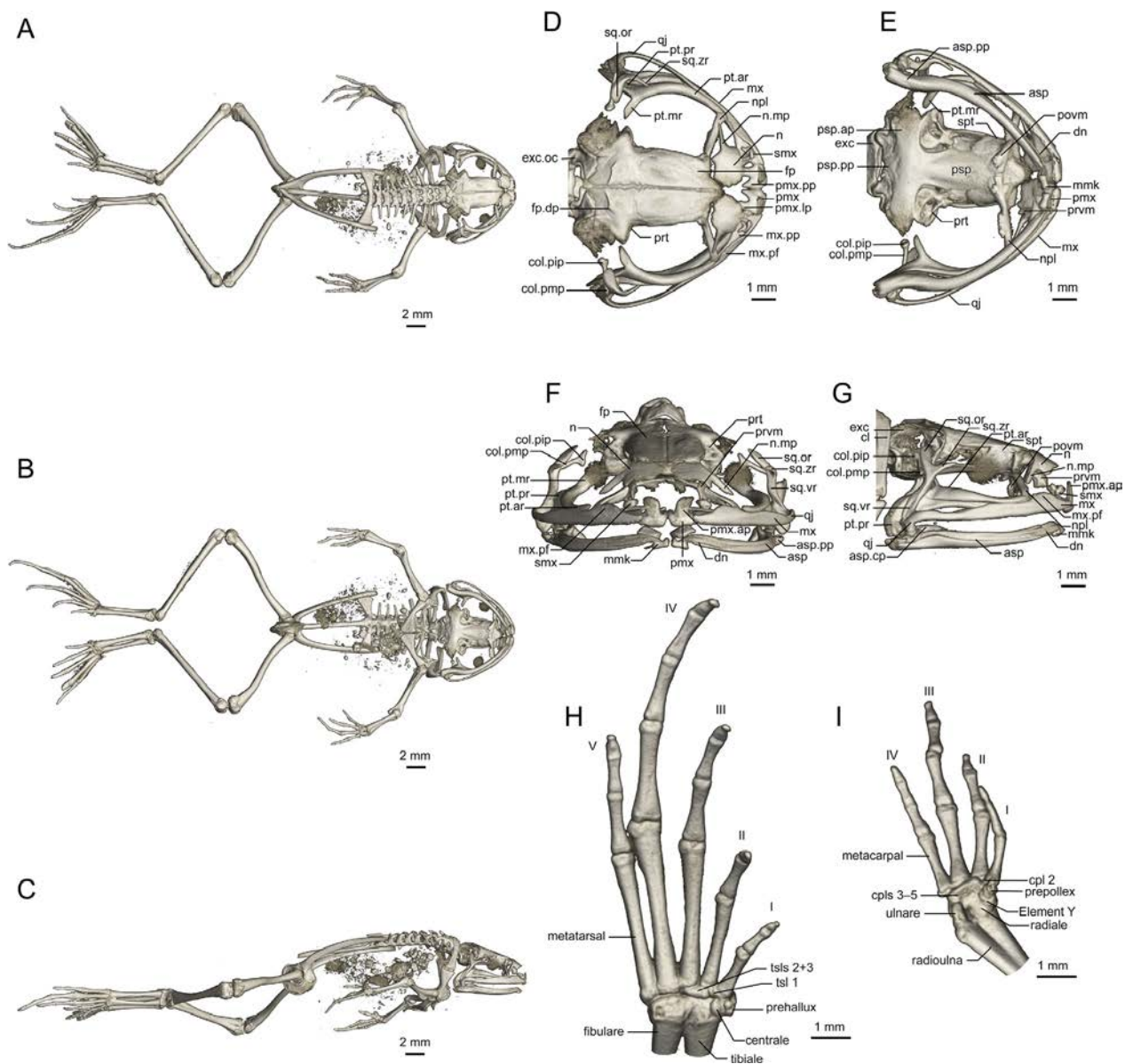


Figure 55. Skeleton of *Rhombophryne quentini* **sp. nov.** paratype MRSN A4615 (FAZC 11129). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Gut contents in **A–C** include small stones. Abbreviations are given under Materials and Methods.

species is based on an exceptionally large series of specimens, which are however mostly phenotypically homogeneous. The pronounced outer metatarsal tubercle is always present, though it is less obvious in the smallest specimens. All specimens have pale posterior and anterior thighs and ventral shanks in preservative, where they were orange in life; distinct blackish inguinal ocelli with narrow whitish outline in most individuals; and a dark brown trapezoid around the cloaca. Most specimens have a series of dark chevrons on the dorsum, especially one in the suprascapular region. Subadult female MRSN A4629 has a highly distinct colouration, with a broad vertebral stripe from the head to the cloaca (Fig. 54E, F) not seen in any other individuals, but otherwise matches the other specimens well. The chins of almost all specimens are lighter and more flecked with cream than the holotype. The adult male UADBA-A 28193 has a rich coffee brown chin. This specimen also has more patterning on its ventral shanks than most others. In most individuals, the second finger is shorter than the fourth, unlike the holotype; this is not a diagnostic character.

Call. The call of this species is unknown.

Etymology. MDS wishes to dedicate this new frog species to his son, Quentin Artemis Lattenkamp, in the hope that it will continue to encourage his love for animals.

Distribution. This species is only known from (1) Manarikoba on the western side of the Tsaratànana Strict Nature Reserve (type locality). A putative record from the southern side of Manongarivo Special Reserve (BMNH 1987.2297) at 350 m a.s.l. should be validated with further material from this area. Elevation: ca 1000 m a.s.l.

Natural history. *Rhombophryne quentini* sp. nov. is a semi-fossorial or detriticolous species found in mid- and possibly also low-elevation humid forest. The gut of MRSN A3656 contained pieces of a blattodean that must have been relatively large in life, a diminutive ant, a flatbug (family Aradidae), and several unidentifiable arthropod pieces. According to Andreone et al. (2009),

Rhombophryne quentini sp. nov. was one of the most frequently encountered species in pitfall traps in Manarikoba; they captured 22 individuals in pitfall traps.

Karyotype. The karyotype of MRSN A3656 was described by Aprea et al. (2007) under the name '*Plethodontohyla* sp. aff. *minuta*', with the incorrect locality 'Masoala'. It was described to have $2n = 26$, with a telocentric eighth chromosome pair. Nucleolar organiser regions were located on the long arms of the sixth chromosome pair. Centromeric bands were CMA₃ and DAPI negative.

Rhombophryne kilonjy sp. nov.

<https://zoobank.org/2BAD5123-5309-46F7-8ECE-143AB8FDF4A>

Figures 2, 5–7, 50, 51, 56, 57

Informal names. This species was referred to as '*Plethodontohyla* sp.' by Andreone et al. (2001), '*Rhombophryne* sp. aff. *alluaudi*' by Penny et al. (2016), and '*Rhombophryne* sp. (UCS)' by Penny et al. (2017). It has not been sequenced previously.

Justification of the new species. The new species is sister to *R. quentini* sp. nov. (described above), and these two species are together sister to *R. ellae*, as part of the *R. ellae* group that is phylogenetically distinct from other *Rhombophryne* (Belluardo et al. 2022). Museum sequencing yielded 0.4× coverage for 117 bp of the 16S3' marker, and 0.9× coverage for 272 bp of the 16S5' marker, but even these fragmentary data are sufficient to assign this species to this group, and identify it as the sister of *R. quentini* sp. nov. The genetic distance towards other members of the species group ranges from 5.13 % in 16S3' to 12.4% in 16S5' (which might be exaggerated based on the fragmented state of the DNA; Table S3) and all members share a diagnostic 'G' at site 338 in the concatenated 16S alignment. It is morphologically distinct

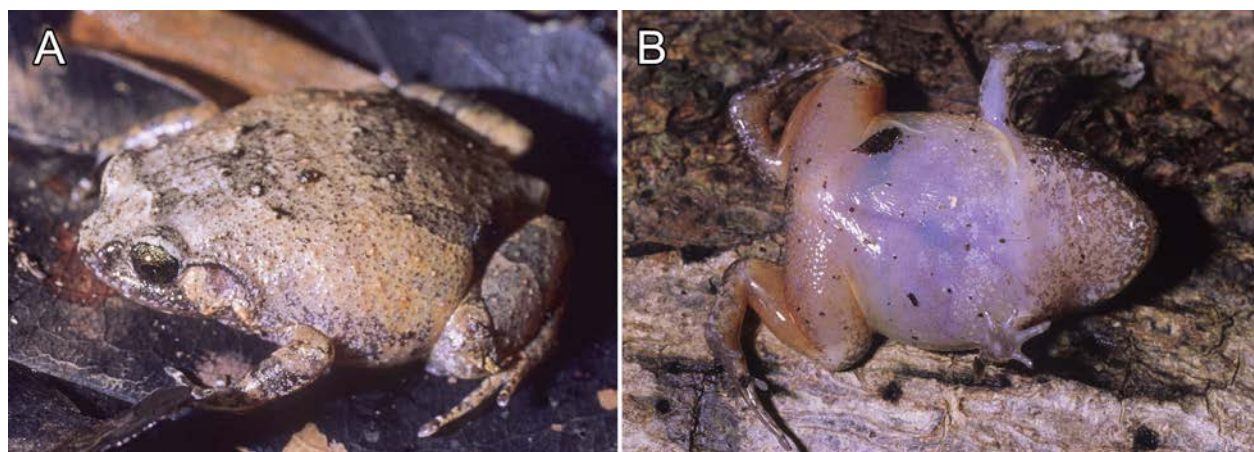


Figure 56. *Rhombophryne kilonjy* sp. nov. adult female holotype MRSN A4627 (FAZC 10505) from Berara, Sahamalaza Peninsula. Shown in **A** dorsolateral and **B** ventral view.

from both *R. ellae* and *R. quentini* **sp. nov.** by lacking inguinal ocelli (vs presence), and several osteological features relating to bones of the skull, and the humerus (see the diagnosis, below), and also from *R. ellae* by a distinct outer metatarsal tubercle (vs weakly pronounced).

Holotype. MRSN A4627 (FAZC 10505), an adult female, collected on 12 February 2000 in Berara (ca 14.3°S, 47.92°E, ca 170 m a.s.l.), Sahamalaza Peninsula, Sofia Region, northwestern Madagascar, by F. Andreone, J.E. Randrianirina, and M. Vences (Figs 51, 52, 57, 58).

Paratypes. Three specimens: MRSN A4601 (FAZC 10557), MRSN A4610, and MRSN A4611 (FAZC 10558), three juveniles, all with the same collection data as the holotype but collected on 14–16 February 2000.

Assignment of specimens. The three paratypes were collected at the type locality, and can be assigned to the species morphologically. There are no known *Rhombophryne* from the same locality with which these specimens could be confused, and they also could not be confused with any other cophyline microhylid species known from this area. The species does not currently have a reference specimen for DNA barcoding, and has not been sequenced for the RAG1 marker.

Definition. Within the *R. ellae* group, this species is sister to *R. quentini* **sp. nov.** based on molecular phylogenetic data. It is characterised by the possession of the following unique suite of characters: (1) medium body size, adult SVL 27.3 mm; (2) head wider than long (HW/HL 1.65); (3) moderately small eyes (ED/HL 0.42); (4) relatively long hindlimbs (HIL/SVL 1.40); (5) small inner metatarsal tubercle (IMTL/FOL 0.11); (6) outer metatarsal tubercle present but indistinct; (7) second finger shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli; (13) presence of reddish orange colouration on the hidden surfaces of the legs in life; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenic; and (15) clavicles present, thin, curving.

Rhombophryne kilonjy **sp. nov.** is furthermore distinguished from all other *Rhombophryne* species by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042), which were identified visually, as inclusion in the MoI analysis would have distorted the results due to insufficiently complete sequences: in 16S5' 'T' at site 446, 'C' at site 468, 'C' at site 580, 'G' at site 600, 'G' at site 601, and 'T' at site 670; in 16S3' 'T' at site 964, and 'T' at site 1004.

Diagnosis. Within the genus *Rhombophryne*, *R. kilonjy* **sp. nov.** can be distinguished from all other *Rhombophryne* except *R. ellae*, *R. quentini* **sp. nov.**, *R. kotrobaratra* **sp. nov.**, *R. mavokely* **sp. nov.**, and *R. ornata* by the presence of reddish orange colouration on the hidden surfaces of the legs. From *R. ellae* and almost all oth-

er *Rhombophryne* species, it can be distinguished by the pronounced outer metatarsal tubercle in adults (vs weakly pronounced), except *R. quentini* **sp. nov.** It can be distinguished from *R. quentini* **sp. nov.** and *R. ellae* by the absence of inguinal ocelli. Superficially it is rather similar to *R. mavokely* **sp. nov.**, but it differs from that species by absence of a black spot on the supratympanic fold (vs presence), larger body size (SVL 27.3 mm vs 21.2–21.3 mm), and presence of a distinct outer metatarsal tubercle (vs indistinct). Based on the specimens examined, the skeleton of *R. kilonjy* **sp. nov.** also differs from those of *R. ellae* and *R. quentini* **sp. nov.** in the following traits: broader prootic, columella with a dorsal extension to the pars interna plectri (vs without a dorsal extension), parasphenoid cultriform process narrowing anteriorly (vs not narrowing anteriorly), higher coronoid process of the angulosplenic (vs lower), humeral crista lateralis distinct (vs weakly developed).

Description of holotype. Specimen in an excellent state of preservation (Fig. 50). An incision made along the left flank to assess the sex, and part of the left thigh muscle taken as a tissue sample. Developing ova are clearly visible in the body cavity.

Body rotund. Head wider than long (HW/HL 1.65). Eyes moderately small (ED/HL 0.43), pupils small, oval. Snout somewhat boxy in dorsal and rounded in lateral view, with a small protrusion at the snout tip. Canthus rostralis indistinct, concave. Loreal region weakly concave, slightly oblique. Nostril closer to eye than to tip of snout, slightly protuberant. Tympanum indistinct, oval, TDH/ED 0.47. Supratympanic fold indistinct in preservative, visible only as melanised curve, but in life highly distinct, arcing strongly from posterior corner of eye over tympanum (Fig. 56). Lateral head similar in colour to dorsal head. Superciliary spines absent. Dorsal skin smooth in preservative, but finely granular in life (Fig. 56). Tongue broad, attached anteriorly, posteriorly free. Maxillary and vomerine teeth present, vomerine teeth with a lateral diastema, the medial elements distinct, separated from one another at the midline by a small gap. Choanae oblong, placed laterally in the roof of the mouth.

Forelimbs relatively short (FARL/SVL 0.366), moderately slender. Fingers without webbing, relative lengths $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth (Fig. 51). Finger tips not expanded, rounded. Finger subarticular tubercles distinct, cream, flat; inner metacarpal tubercle slender, outer metacarpal/palmar tubercle indistinct, cream, single. Hind limb strong, tibiotarsal articulation reaching approximately to the tympanum when adpressed anteriorly along the body. TIBL/SVL 0.367. Inner metatarsal tubercle present, oblong, whitish, distinctly raised. Outer metatarsal tubercle distinct, rounded and raised. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles weak, single; toe tips slightly enlarged, especially of fourth toe, rounded to subacuminate (Fig. 51).

After 24 years in preservative, the base colour was a grey-brown with darker brown speckles throughout, and

a darker brown area over the mid-dorsum in a broad strip. The dorsum is marked with two poorly defined darker brown chevrons, specifically one over the suprascapular region and a second over the iliac region. In each chevron are a small number of symmetrical white spots surrounded by dark brown. The inguinal region lacks any trace of ocelli. No distinct colour difference between the lateral and dorsal head. The supratympanic fold is dark brown from the eye to the tympanum, fading posteriorly. The dorsal hindlimbs bear indistinct crossbands that line up with the leg folded, in the same colours as the dorsum and chevrons. The ventral foot surface is dark brown. The anterior and posterior thigh is pale cream in preservative (this was reddish orange in life; Fig. 56), as is the ventral thigh and shank. A distinct, dark brown trapezoid is present around the cloaca. The dorsal foot is mottled cream

and light brown. A light annulus is present before the terminal phalange of each finger and toe. The arms have a single crossband on the antebrachium. The dorsal hand is lighter medially than laterally; the ventral hand is cream. The chin is mottled light brown with cream flecks, fading to completely cream over the sternal region into the immaculate abdomen.

Variation. The holotype is the only known adult, and measures 27.3 mm in SVL; measured juveniles ($n = 3$) ranged from 12.3–15.7 mm. For variation in other measurements, see Table S7. Juveniles are morphologically consistent with the holotype. The outer metatarsal tubercle is consistently distinct. The development of vomerine teeth is variable among the examined juveniles, with one specimen (MRSN A4611) lacking vomerine teeth (but the

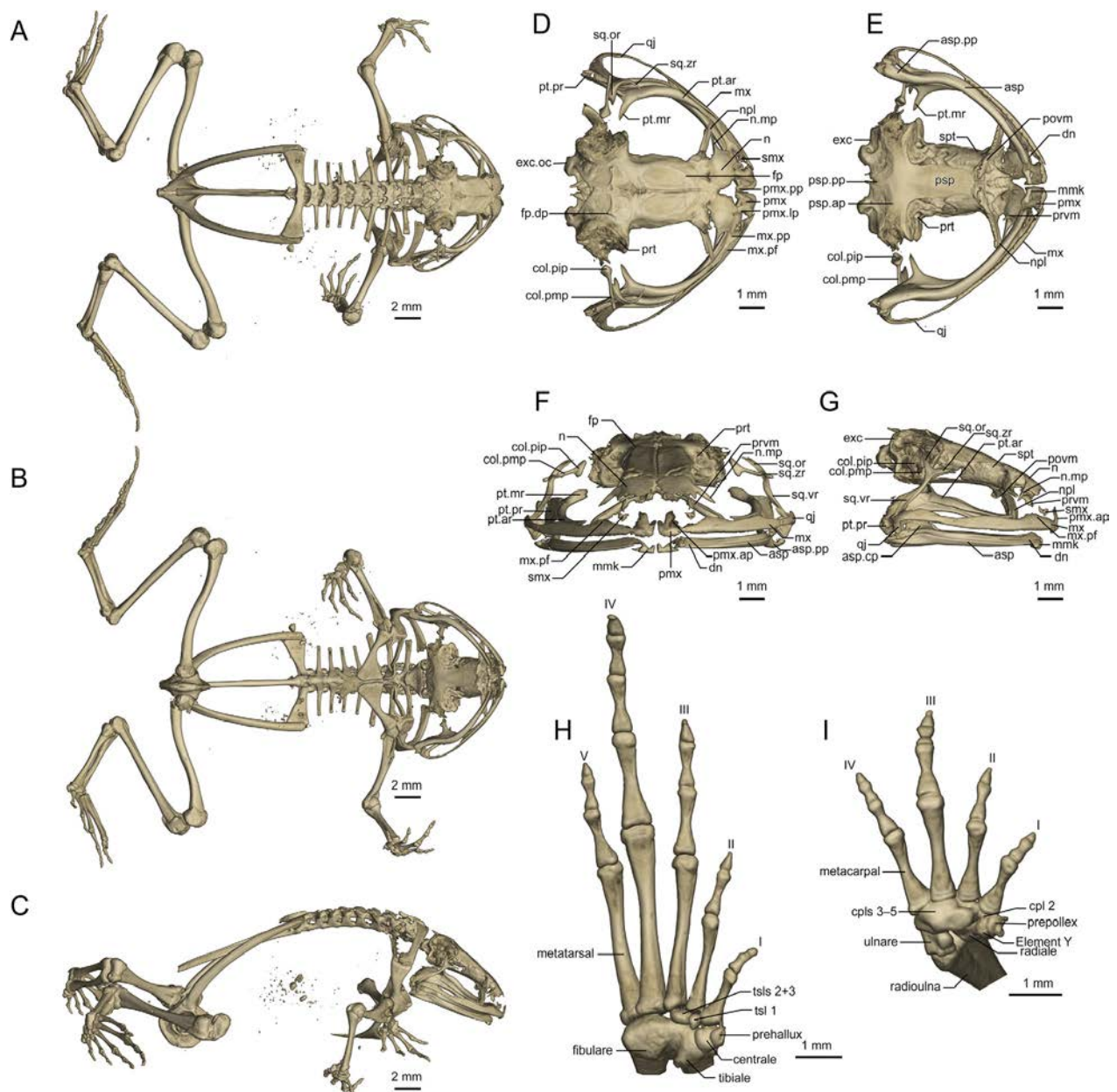


Figure 57. Skeleton of *Rhombophryne kilonjy* sp. nov. holotype MRSN A4627 (FAZC 10505). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

postchoanal portion of the vomer is clearly visible in the palate), whereas the other specimens have distinct and rather large vomerine teeth. All specimens lack inguinal spots. All specimens have at least a faint dark chevron on the dorsum.

Call. The call of this species is not known.

Etymology. The Malagasy noun *kilonjy* meaning ‘pebble’, in reference to the small, rotund shape of this species, reminiscent of a smooth pebble. Used as an invariable noun in apposition.

Distribution. This species is only known from (1) Berara on the Sahamalaza Peninsula (type locality). Elevation: 170–210 m a.s.l. (Andreone et al. 2001).

Natural history. *Rhombophryne kilonjy* **sp. nov.** is a semi-fossorial or detriticolous species known only from low-elevation western dry forest, drier than the localities of all other known *Rhombophryne*. One specimen was collected in a pitfall trap. No further specific details are known of its ecology.

Osteology of the *Rhombophryne ellae* species group

This description is based on the following specimens: *R. ellae* (ZSM 76/2018; Fig. 53), *R. quentini* **sp. nov.** (MRSN A4615; Fig. 55), *R. kilonjy* **sp. nov.** (MRSN A4627; Fig. 57). The fourth toe of the left foot of MRSN A4615 has been amputated in the middle of the first tarsal. The right humerus, crista ventralis of the left humerus, and the left ilium of MRSN A4627 are fractured. The specimens are well-ossified.

The *Rhombophryne ellae* species group is osteologically homogeneous, showing generalist, terrestrial features without obvious adaptations to digging. Here, we provide a description of the osteology of the group that highlights particularly diagnostic features of the three species. An osteological description of *R. ellae* was also given by Scherz (2020).

The skull is broader than long, slightly more rounded in *R. quentini* **sp. nov.** than *R. ellae*, and shorter and broader in *R. kilonjy* **sp. nov.**

Dorsal investing bones. Nasals closely abutting or contacting the frontoparietals. The maxillary process of the nasal is thin, oriented posterolaterally, and runs towards the neopalatine, but does not come close to contacting it or the maxilla. The posterior edge of the nasal plate is continuous with the posterior edge of the maxillary process in *R. ellae* and *R. kilonjy* **sp. nov.**, but not in *R. quentini* **sp. nov.**

The frontoparietals bear a transverse ridge with a raised dorsal process (different from the *R. laevipes* species group, where the dorsal process arises without a ridge). The lateral ventrally descending flange is shallow, enclosing only the upper-most edge of the braincase.

Neurocranium. The sphenethmoid is fully ossified, and covers around half of the anterolateral wall of the braincase. It does not differ appreciably among the three species. The exoccipital is likewise conserved, with only subtle differences in the surface of the posterior surface of the dorsal extension. The exoccipitals do not meet medially. The prootic is well-ossified, and is broader in *R. kilonjy* **sp. nov.** than the other species, but otherwise does not differ substantially in shape. The septomaxilla has a consistent shape, with a distinct medial ramus present. The columella in *R. kilonjy* **sp. nov.** has a dorsal extension to the pars interna plectri, giving it a somewhat tear-drop shape, compared to the lenticular shape of *R. ellae* and *R. quentini* **sp. nov.**

Ventral investing and palatal bones. The cultriform process of the parasphenoid is slightly broader in *R. quentini* **sp. nov.** than *R. ellae* and *R. kilonjy*; it narrows anteriorly in *R. kilonjy*. It has a distinct ‘waist’ in *R. ellae* and *R. quentini* **sp. nov.**, but not in *R. kilonjy* **sp. nov.** The alae are distally poorly ossified and only weakly pointed, compared to the *R. laevipes* species group.

The anterior portion of the vomer is triradiate. It is poorly defined in our scan of *R. quentini* **sp. nov.** The posterior portion of the vomer is curved and bears two distinct sets of teeth separated by a sizeable diastema. The neopalatine, which lies dorsally on top of the postchoanal vomer, is a curved flattened rod-like structure, but has a rounded to spatulate anterior projection near the midline in all three species. The vomers and neopalatines are separated medially by a small gap.

Maxillary arcade. Maxillary teeth are present in all three species. The premaxilla is uniform in the group, with a substantially longer lingual process than palatine process. The maxilla is not especially deep, with a blunt and broad facial process that is widely separated from the maxillary process of the nasal. The contact with the anterior ramus of the quadratojugal is comparatively brief.

Suspensorium. The anterior ramus of the quadratojugal is weakly curved, almost straight. The contact with the squamosal is fairly brief.

The ventral ramus of the squamosal is rather straight and narrow, with a fine posterior crest. The otic ramus is longer than the zygomatic ramus, and the two rami form an acute angle in dorsal view (narrower in *R. ellae* than *R. quentini* **sp. nov.** and *R. kilonjy* **sp. nov.**). The otic ramus is nearly perpendicular to the longitudinal axis of the skull.

The pterygoid is consistent in structure. The anterior ramus of the pterygoid runs along the lingual edge of the maxilla in *R. ellae* and *R. kilonjy* **sp. nov.**, but appears to lie abreast the dorsal edge of the maxilla in *R. quentini* **sp. nov.**

Mandible. The mentomeckelians are small and hour-glass-shaped. The dentary is thin and laminar. The angulosplenial is robust. The coronoid process is low but distinct, being lowest in *R. quentini* **sp. nov.** and highest in

R. kilonjy **sp. nov.** The posterior process (articular facet) is weakly expanded.

Pectoral girdle. The coracoids are medially more strongly flared in *R. kilonjy* **sp. nov.** than in *R. ellae*, which in turn is more strongly flared than in *R. quentini* **sp. nov.** Clavicles present and curved. The scapula and cleithra do not differ sufficiently for further comment.

The humeral crests are moderately developed. The crista ventralis extends half the length of the humerus. The crista lateralis is present but weakly developed in *R. ellae* and *R. quentini* **sp. nov.**, and distinct in *R. kilonjy* **sp. nov.** The radioulna does not show remarkable variation.

Carpals 2, 3–5, element Y, radiale and ulnare present. The prepollex is small, much shorter than the first metacarpal. The digital formula of both species is the same (2-2-3-3), and terminal phalanges consistently have small knobs.

Vertebral column. Transverse processes of V2 are perpendicular to body axis. Transverse processes of V2–4 are distinctly broader than V5–8. Transverse processes of V5–8 broader than or roughly as broad as centrum is wide; relatively longer in *R. ellae* and *R. kilonjy* **sp. nov.** than in *R. quentini* **sp. nov.** The sacrum is as wide as V4, its anterior edge slightly concave, oriented laterally. The diapophyses are flared. The urostyle has a dorsal ridge along ~70% of its length in *R. ellae* **sp. nov.** and *R. quentini* **sp. nov.**, nearly the full length in *R. kilonjy* **sp. nov.**

Pelvic girdle. Iliac shafts with weak dorsal crests. The oblique groove and dorsal prominence are weakly present in *R. quentini* **sp. nov.** and *R. kilonjy* **sp. nov.**, but distinct in *R. ellae*. The femur lacks a posterior ridge. The tibiofibula and tarsus do not bear further comment. The toe formula is standard (2-2-3-4-3). The prehallux is small, comprised of one or two elements (not clear from scans).



Figure 58. *Rhombophryne proportionalis* adult male holotype ZSM 1826/2010 (ZCMV 12404) from Bepia, Tsaratànana Massif, in life. Shown in **A** lateral, **B** dorsolateral, and **C** ventral view.

KU937808; Scherz et al. 2016b) and COI barcoding (COI KF611640; Perl et al. 2014). Both paratypes agree morphologically with the holotype and are topotypical. Assignment of specimen ZSM 1840/2010 is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 1826/2010 and ZSM 1840/2010 are present in the RAG1 haplotype network (Fig. 4).

Definition. This species is the sole member of the *R. proportionalis* group and phylogenetically distinct from all other *Rhombophryne* based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) diminutive body size, adult SVL 11.0–12.3 mm; (2) head wider than long (HW/HL 1.56–1.66); (3) comparatively large eyes (ED/HL 0.40–0.48); (4) relatively short hindlimbs (HIL/SVL 1.21–1.33); (5) small inner metatarsal tubercle (IMTL/FOL 0.07–0.14); (6) outer metatarsal tubercle variably present or absent; (7) second finger equal in length to fourth; (8) third toe distinctly longer than fifth, first toe highly reduced; (9) dorsal skin smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence of black inguinal spots or lines; (13) absence of distinctive markings along the posterior thigh; (14) pedomorphic skull without expansion of maxilla or posterior process of angulosplenial; (15) clavicles absent; and (16) advertisement call (based on 63 analysed calls by one individual) tonal, emitted in rapid, regular series, with (17) call duration 27–60 ms, (18) inter-call interval within series 45–88 ms (9–17 calls per series), and (19) dominant frequency 5162–5738 Hz.

Rhombophryne proportionalis is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'A' at site 496, 'C' at site 511, and 'G' at site 547; in 16S3', 'T' at site 966, 'C' at site 967, 'A' at site 1013 and 'T' at site 1165.

Diagnosis. Within the genus *Rhombophryne*, *R. proportionalis* can easily be distinguished from all other species by its much smaller body size (SVL 11.0–12.3 mm vs >16 mm). It also exhibits a host of miniaturised skeletal features, described in detail by Scherz et al. (2019b), that also set it apart from all congeners. Additionally, the advertisement call of *R. proportionalis* is unique for the genus in consisting of regular series of calls emitted in rapid succession (all other species with known calls emit single calls at much longer intervals).

Variation. As reported by Scherz et al. (2019b), adult SVL ranges from 11.0–12.3 mm; for other morphometric measurements, see Table S8. The type series is rather homogeneous, with a little variation in the shape of the head and supratympanic fold. Colouration is also rather consistent, though dorsolateral lines can be present or absent.

Call. The advertisement call recorded on 15 June 2010 (11:40 h) at Camp Bepia, Tsaratàna (air temperature

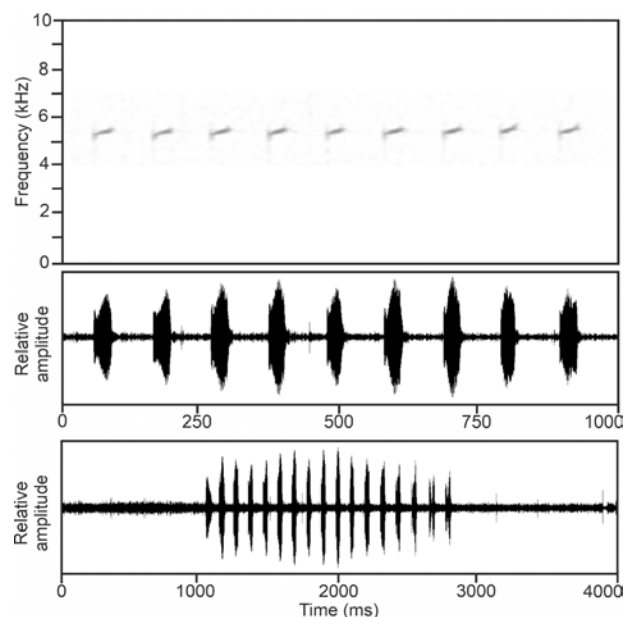


Figure 60. Advertisement calls of *Rhombophryne proportionalis*, recorded on the Tsaratàna Massif in 2010. Top: audiospectrogram and corresponding oscillogram of nine advertisement calls from a regular call series at 1000 ms time scale. Bottom: oscillogram at 4000 ms time scale depicting an entire call series containing seventeen calls. Recording band-pass filtered at 4000–7000 Hz.

unknown) from several individuals, consists of a high-pitched tonal note of short duration emitted in regular call series at regular and fast succession (Fig. 60). Each call exhibits slight amplitude modulation, with highest energy present at approximately the middle of the call's duration, with few calls at the end of call series exhibiting two separated energy peaks. Slight upward frequency modulation is evident in each call. Numerical parameters of 63 analysed calls are as follows: call duration (= note duration) 27–60 ms (45 ± 8 ms); inter-call intervals within regular call series 45–88 ms (63 ± 9 ms); number of calls per call series 9–17 (13 ± 3); duration of regular call series 893–1765 ms (1323 ± 291 ms); dominant frequency 5162–5738 Hz (5461 ± 123 Hz); prevalent bandwidth 5000–6300 Hz. Calls from the same recording have been described by Scherz et al. (2019b) using the note-centred terminological scheme.

Etymology. Latin feminine nominative singular adjective meaning 'proportional', in reference to the proportional dwarfism of the species.

Distribution. This species is only known from (1) Bepia on the Tsaratàna Massif (type locality), and (2) the nearby locality Andranomadio. Elevation: 2294–2503 m a.s.l. A record from Marojejy at 1300 m a.s.l. (Rakotoarimalala and Raselimanana 2023) requires verification.

Natural history. *Rhombophryne proportionalis* is a terrestrial or detriticolous species found in high-elevation humid forest. Males emit advertisement calls during the day. Nothing else is known of its natural history.

Osteology. The osteology of *Rhombophryne proportionalis* (Fig. 59) was described in detail by Scherz et al. (2019b). It is highly divergent from all other *Rhombophryne* species, as a result of its strongly miniaturised morphology.

Rhombophryne minuta species group

Rhombophryne minuta (Guibé, 1975)

Figures 2, 4–7, 50, 51, 61–64

Mantipus minutus Guibé, 1975

Plethodontohyla minuta — Blommers-Schlösser and Blanc (1991)

Rhombophryne minuta — Glaw and Vences (2007)

Remark. Several references to *R. minuta* actually refer to other species of *Rhombophryne*, including those from Manongarivo (Rakotomalala 2002) and Ambolokopatrika (Andreone et al. 2000).

The identity of this species was clarified by Glaw and Vences (2007) and Glaw et al. (2010b), and it was discussed further by Scherz et al. (2015a).

Holotype. MNHN 1975.15, an adult female, collected in November 1972 on the ‘Marojejy Massif, at altitude’, Sava Region, northeastern Madagascar, by C.P. Blanc (Figs 50, 51, 63).

Paratypes. Eight specimens: MNHN 1975.16–23, all with the same collection data as the holotype (Guibé 1975).

Referred specimens. ZSM 476/2005 (ZCMV 2003; Fig. 61A, B), ZSM 477/2005 (ZCMV 2004; Fig. 61C), two unsexed adults, and ZSM 359/2005 (FGZC 2897), ZSM 360/2005 (FGZC 2899), and UADBA-A-FGZC 2898, three unsexed presumed subadults, all collected on 17 February 2005 above ‘Camp Simpona’ (14.4408°S, 49.7399°E, ca 1700–1800 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by F. Glaw, M. Vences, and R.D. Randrianiaina.

Assignment of specimens. The specimen ZSM 360/2005 is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ and 16S5’ EU341106; Vieites et al. 2009) and COI barcoding (COI KF611591; Perl et al. 2014). Assignment of specimens ZSM 359/2005 and UADBA-A-FGZC 2898 is further confirmed by molecular taxonomic identification (Fig. 2), based on museum-

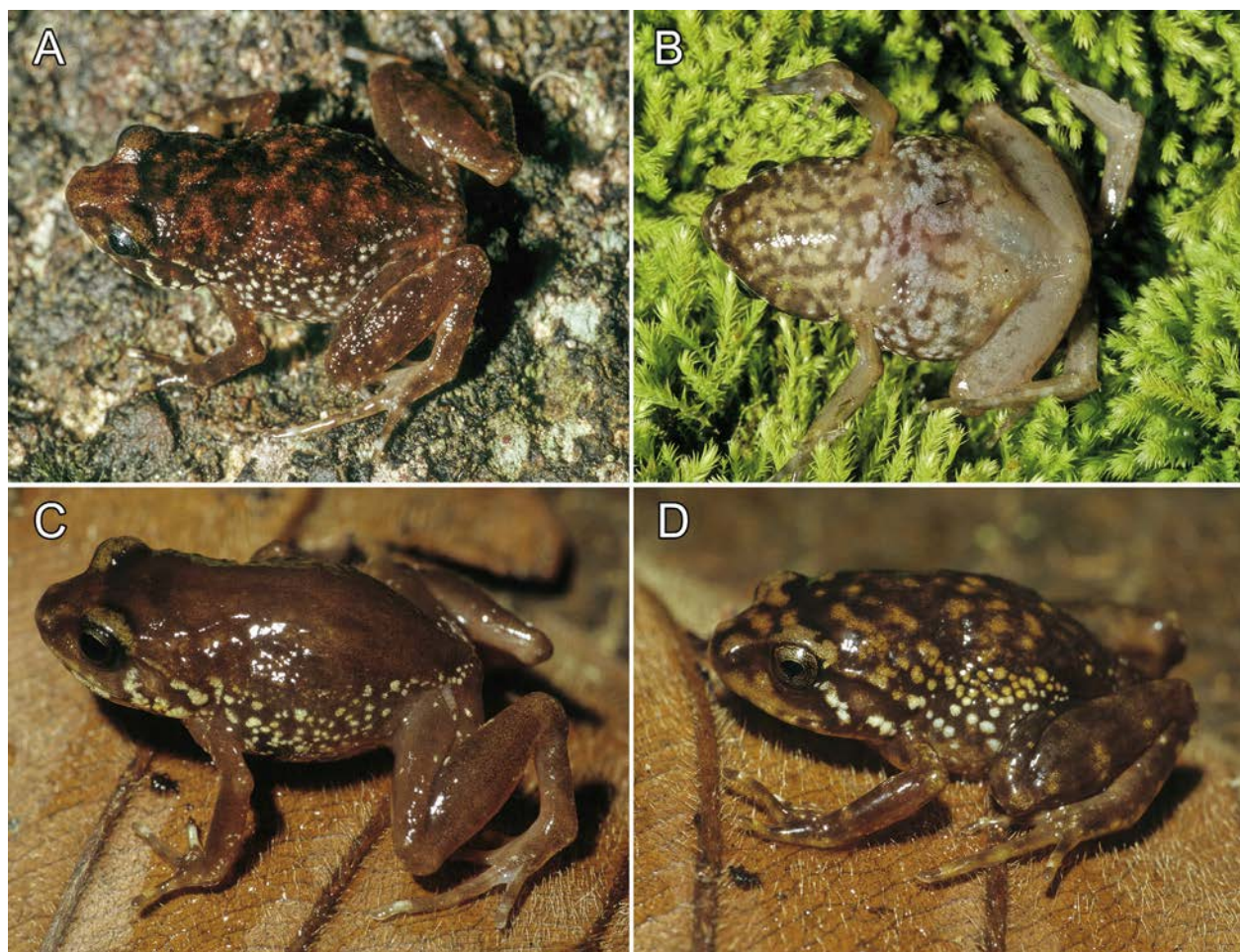


Figure 61. *Rhombophryne minuta* specimens in life. Photographed at ‘Camp Simpona’ in Marojejy National Park, in life. **A, B** unsexed adult ZSM 476/2005 (ZCMV 2003) in **A** dorsolateral and **B** ventral view; **C** unsexed adult ZSM 477/2005 (ZCMV 2004) in dorsolateral view; **D** an unidentified UADBA specimen in dorsolateral view. Not to scale.

ic sequences for 16S3' produced from the holotype (see Museomics section, above). The assignment of these specimens to this name, as well as ZSM 476/2005, ZSM 477/2005, is also supported by morphological comparison with the holotype. All of the referred specimens have been collected at the type locality. UADBA-A-FGZC 2898 is present in the RAG1 haplotype network (Fig. 4).

Definition. This species is sister to *R. longicrus*, the only other species of the *R. minuta* group, based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small body size, adult SVL 16.9–21.8 mm; (2) head wider than long (HW/HL 1.36–1.43); (3) moderately small eyes (ED/HL 0.42–0.45); (4) relatively long hindlimbs (HIL/SVL 1.73–1.82); (5) small

inner metatarsal tubercle (IMTL/FOL 0.08–0.09); (6) outer metatarsal tubercle absent or indistinct; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) presence or absence of faint dark oblong markings in the inguinal region; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosphenial; (15) clavicles present, thin, curving; and (16) advertisement call (based on 10 analysed calls by one individual) containing two pulses, with (17) call duration 114–162 ms, (18) inter-call interval 4660–8050 ms, and (19) dominant frequency 4030–4230 Hz.

Rhombophryne minuta is furthermore distinguished from all other *Rhombophryne* species analysed by the

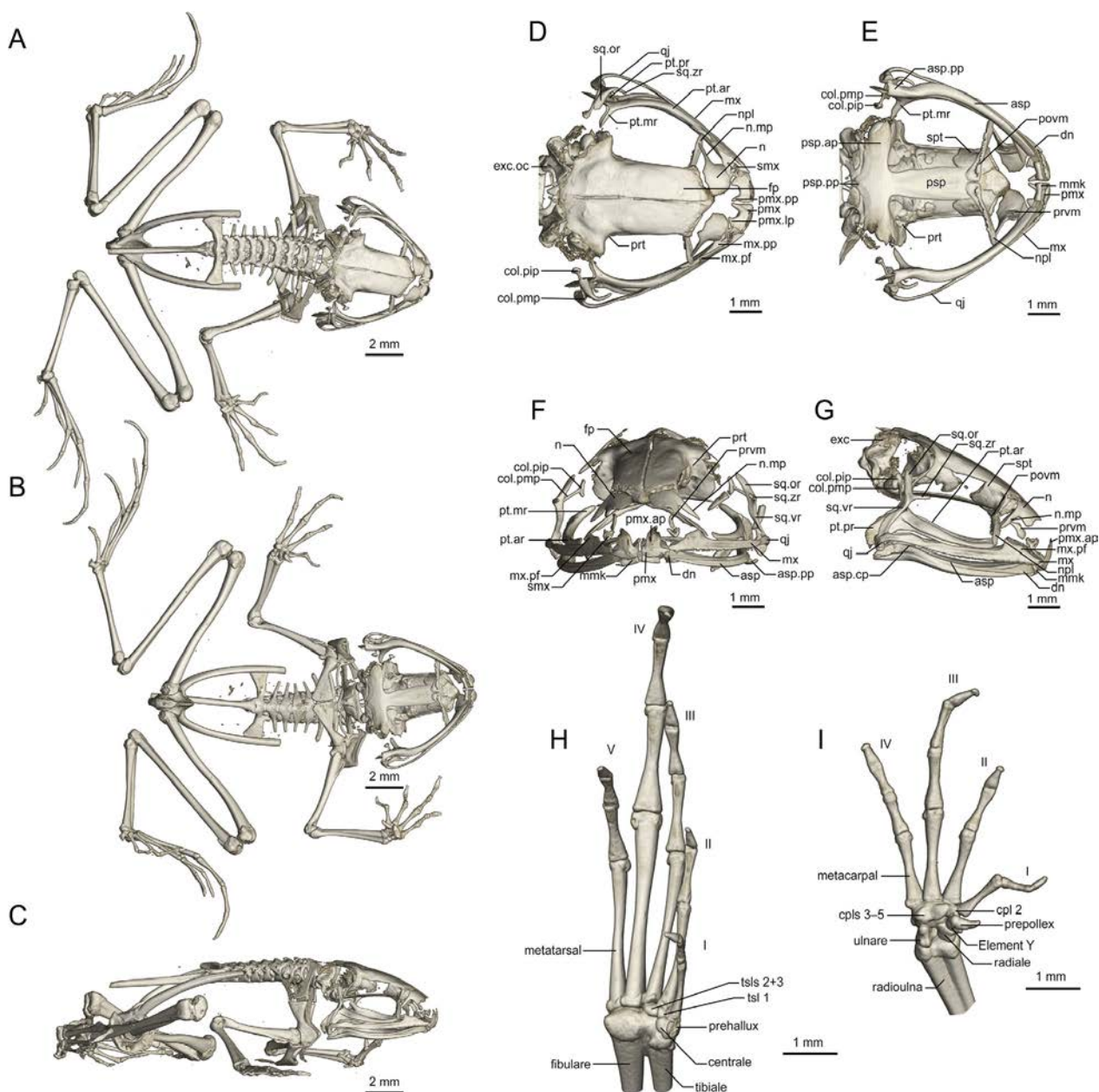


Figure 62. Skeleton of *Rhombophryne minuta* specimen ZSM 476/2005 (ZCMV 2003). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'G' at site 355, 'T' at site 566, and 'C' at site 592. No diagnostic sites were identified for 16S3'.

Diagnosis. Within the genus *Rhombophryne*, *R. minuta* can easily be distinguished from *R. testudo*, *R. cou-dreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** by its generally smaller size (SVL 16.9–21.8 mm vs 21.5–50), smooth skin (vs rough), absence of chin barbels (vs general presence), and much longer hindlimbs (HIL/SVL 1.73–1.82 vs 1.10–1.41); from *R. mangabensis* and *R. savaka* by its much longer hindlimbs (HIL/SVL 1.73–1.82 vs 1.37–1.60), and pulsed (vs tonal) advertisement call; from *R. mavokely* **sp. nov.** and members of the *R. ellae* species group by the absence of orange coloura-

tion on the posterior thigh and in the inguinal region (vs presence); from all members of the *R. laevipes* species group by smaller adult body size SVL 16.9–21.8 mm vs 24.1–57.2 mm), and absence of white spots in the inguinal region and on the posterior thigh (vs presence in most species); from *R. proportionalis* by larger adult body size (SVL 16.9–21.8 mm vs 11.0–12.3 mm); and from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence).

Rhombophryne minuta is most similar to its sister species, *R. longicrus*. It can be distinguished from that species by its smaller size (SVL 16.9–21.8 mm vs 23.8–28.0 mm), slightly smaller hand (HAL/SVL 0.28–0.28 vs 0.29–0.30), generally shorter tibia (TIBL/SVL 0.46–0.49 vs 0.49–0.52), and lack of dark colouration on the supratympanic region (vs presence).

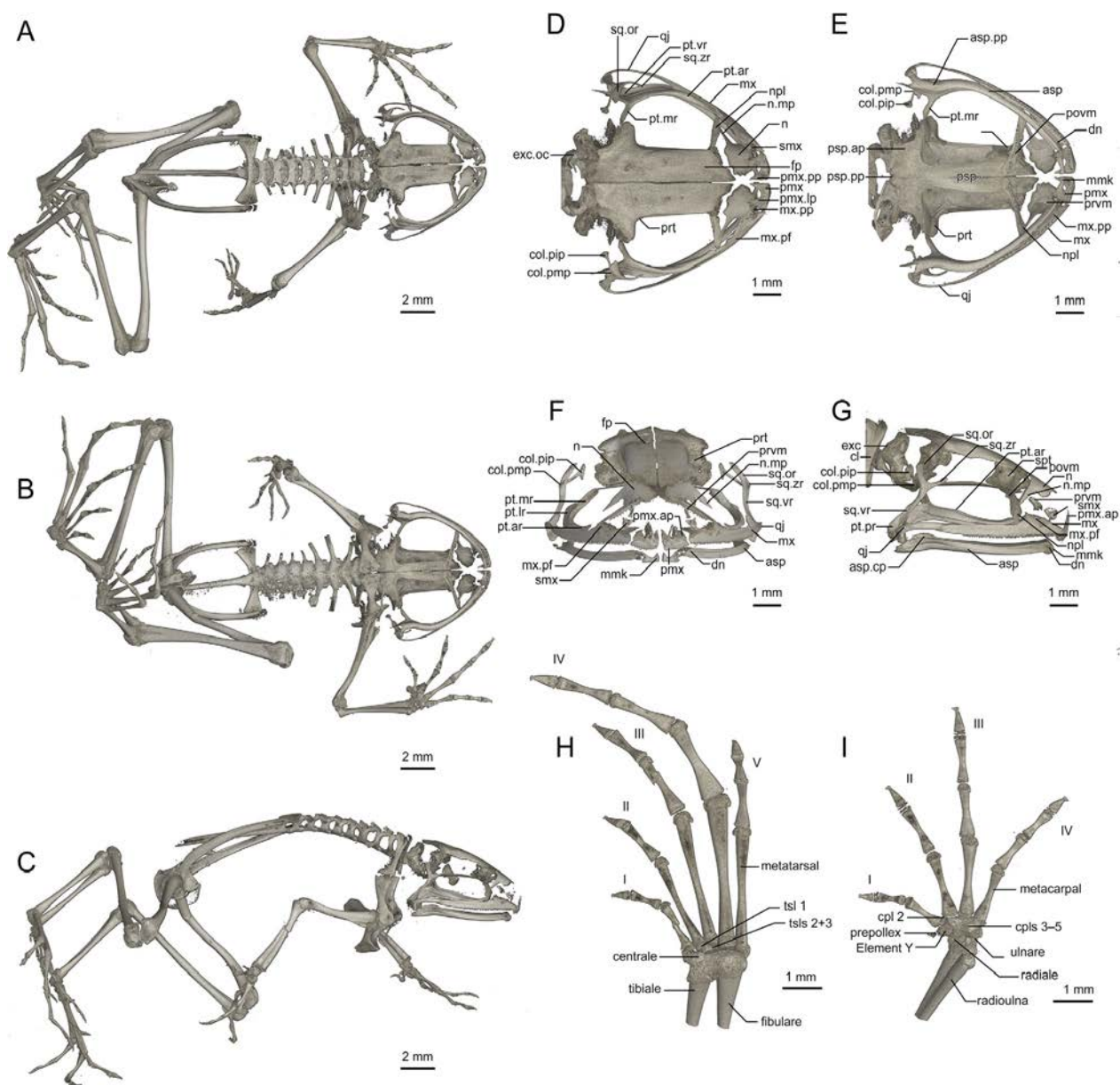


Figure 63. Skeleton of *Rhombophryne minuta* holotype MNHN 1975.15. **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** left foot in ventral view; **I** left hand in ventral view. Abbreviations are given under Materials and Methods.

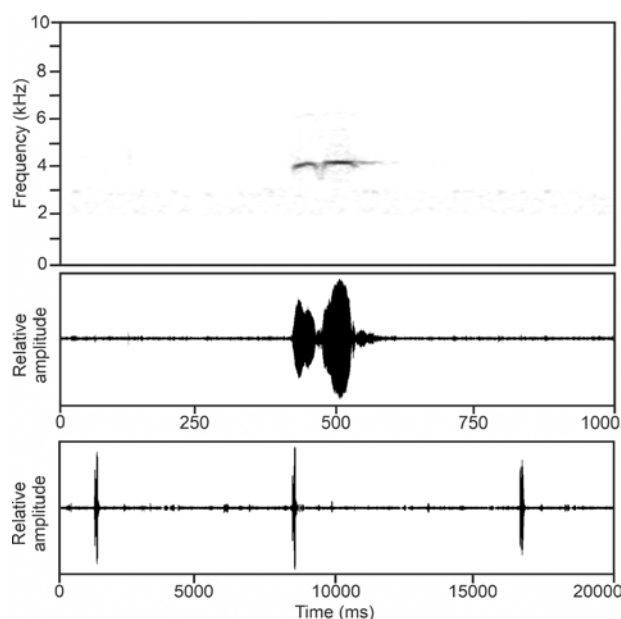


Figure 64. Advertisement calls of *Rhombophryne minuta*, recorded in Marojejy National Park in 2005. Top: audiospectrogram and corresponding oscillogram of one advertisement call at 1000 ms time scale. Bottom: oscillogram at 20,000 ms time scale showing pattern of call repetition (three calls). Recording high-pass filtered at 2000 Hz.

Redescription of holotype. A specimen in a good state of preservation (Fig. 50). Throat and pectoral girdle skin reflected to reveal pectoral girdle. A small incision along the right flank made to assess sex. Ovigerous female with ova at various stages of development. Part of the liver was taken through this incision for genetic analysis in 2021.

Body gracile. Head wider than long (HW/HL 1.36). Eyes fairly large (ED/HL 0.43), pupils small, round. Snout rounded in dorsal view, obtuse in lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique. Nostril closer to tip of snout than to eye, slightly protuberant. Tympanum indistinct, small, round, TDH/ED 0.36. Supratympanic fold distinct, raised, demarcated by a dark line, running from posterior corner of eye over tympanum and curving posteriorly to end above the insertion of the arm. Superciliary spines absent. A low sagittal fold runs from the tip of the snout to the middle of the body. Tongue relatively narrow, attached anteriorly, posteriorly free, rounded distally. Maxillary and vomerine teeth present, vomerine teeth forming two straight rows separated at the midline by a small gap. Choanae round, placed laterally in the roof of the mouth.

Forelimbs relatively long (FARL/SVL 0.50) and slender. Fingers without webbing, all long, relative lengths $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth (Fig. 51). Finger tips not expanded, rounded. Finger subarticular tubercles indistinct, whitish; inner metacarpal tubercle small, slightly rounded, outer metacarpal/palmar tubercle indistinct. Hind limb gracile, tibiotarsal articulation reaching the eye when adpressed anteriorly along the body. TIBL/SVL 0.46. Inner metatarsal tubercle present, distinctly raised, oblong, light brown. Outer

metatarsal tubercle absent. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles indistinct, greyish, flat, rather oblong; toe tips simple and round (Fig. 51).

After approximately 50 years in preservative, the colouration of the specimen is brown above and light tan below. Marbled brown and cream patterns of the venter that were illustrated by Guibé (1975) are still faintly visible. The dorsum does not have any distinctive patterning to it, but there are hints of dark patches in the inguinal region, and a dark spot on the left flank. One dark brown crossband is present on the lower arm. No crossbands on the hindlimbs.

Variation. SVL of adults 16.9–21.8 mm ($n = 3$), subadults 15.4–15.6 ($n = 2$). Insufficient sexed specimens exist to assess sexual size dimorphism. For variation in other measurements, see Table S9. Available specimens are largely phenotypically homogeneous. Colouration in life is somewhat variable (Fig. 61). Unlike the holotype, there are no inguinal markings in the other material we have examined.

Call. The advertisement call recorded on 17 February 2005 (21:00 h) near Camp Simpona, Marojejy National Park (air temperature $< 20^{\circ}\text{C}$), consists of a tonal note of moderate duration emitted at long and somewhat irregular intervals, not arranged in regular call series (Fig. 64). Each call (= note) exhibits distinct amplitude modulation, with two clearly separated pulses being evident, the second being slightly longer in duration and exhibiting higher call energy. Very slight overall upward frequency modulation is recognizable within each call, with a slight medium frequency drop between the two pulses. Numerical parameters of 10 analysed calls are as follows: call duration (= note duration) 114–162 ms (138 ± 17 ms); inter-call intervals 4660–8050 ms (6520 ± 1416 ms); dominant frequency 4030–4230 Hz (4143 ± 59 Hz); prevalent bandwidth 3500–6400 Hz; weak frequency band recognizable at approximately 6200 Hz. Calls from the same recording (Vences et al. 2006 CD 3, track 30) have been described by Glaw et al. (2010b) using a slightly different terminological scheme.

Etymology. Latin feminine nominative singular adjective meaning ‘very small’, presumably in reference to the comparatively small size of this species relative to other relatives.

Distribution. This species is only known from (1) high elevation on the Marojejy Massif (type locality). Elevation: 1700–1800 m a.s.l.

Natural history. *Rhombophryne minuta* is a scansorial species found in high-elevation humid forest. A scansorial species living in and on ericoid and lichenous vegetation near the tree line. Males call in the rainy season at night on low vegetation, up to 1 m above the ground (Glaw and Vences 2007).

***Rhombophryne longicrus* Scherz et al., 2015**

Figures 2, 4–7, 50, 51, 65, 66

Holotype. ZSM 1630/2012 (FGZC 3653), an adult female with immature oocytes, collected on 28 November 2012 in the montane forest of the Sorata Massif (ca 13.675°S, 49.439°E, ca 1580 m), Sava Region, northern Madagascar, by A. Rakotoarison, A. Razafimanantsoa, T. Rajoafiarison, F.M. Ratsavina, O. Hawlitschek, and F. Glaw (Figs 65A, B, 67).

Paratypes. One specimen: UADBA-A 60271 (FGZC 3651; Fig. 65C, D), an adult male, with the same collection data as the holotype.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S3' KR025898; Scherz et al. 2015a; 16S5' KY748101; Scherz et al. 2017a). Paratype UADBA-A 60271 is used as the reference specimen for this species in COI barcoding (COI OL790127; Belluardo et al. 2022). The paratype conforms well with the holotype in morphology, and is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 1630/2012 is present in the RAG1 haplotype network (Fig. 4).

Definition. This species is sister to *R. minuta*, the only other species of the *R. minuta* group, based on molecular phylogenetic data (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small to medium body size, adult SVL 23.8–28.0 mm; (2) head wider than long (HW/HL 1.22–1.39); (3) moderately small eyes (ED/HL 0.40–0.41); (4) relatively long hindlimbs (HIL/SVL 1.81–1.83); (5) small inner metatarsal tubercle (IMTL/FOL 0.08–0.09); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin smooth; (10) absence of chin barbels; (11) absence of pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne longicrus is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'T' at site 451, and 'T' at site 547; in 16S3', 'C' at site 1096, 'G' at site 1126, 'T' at site 1163 and 'A' at site 1315.

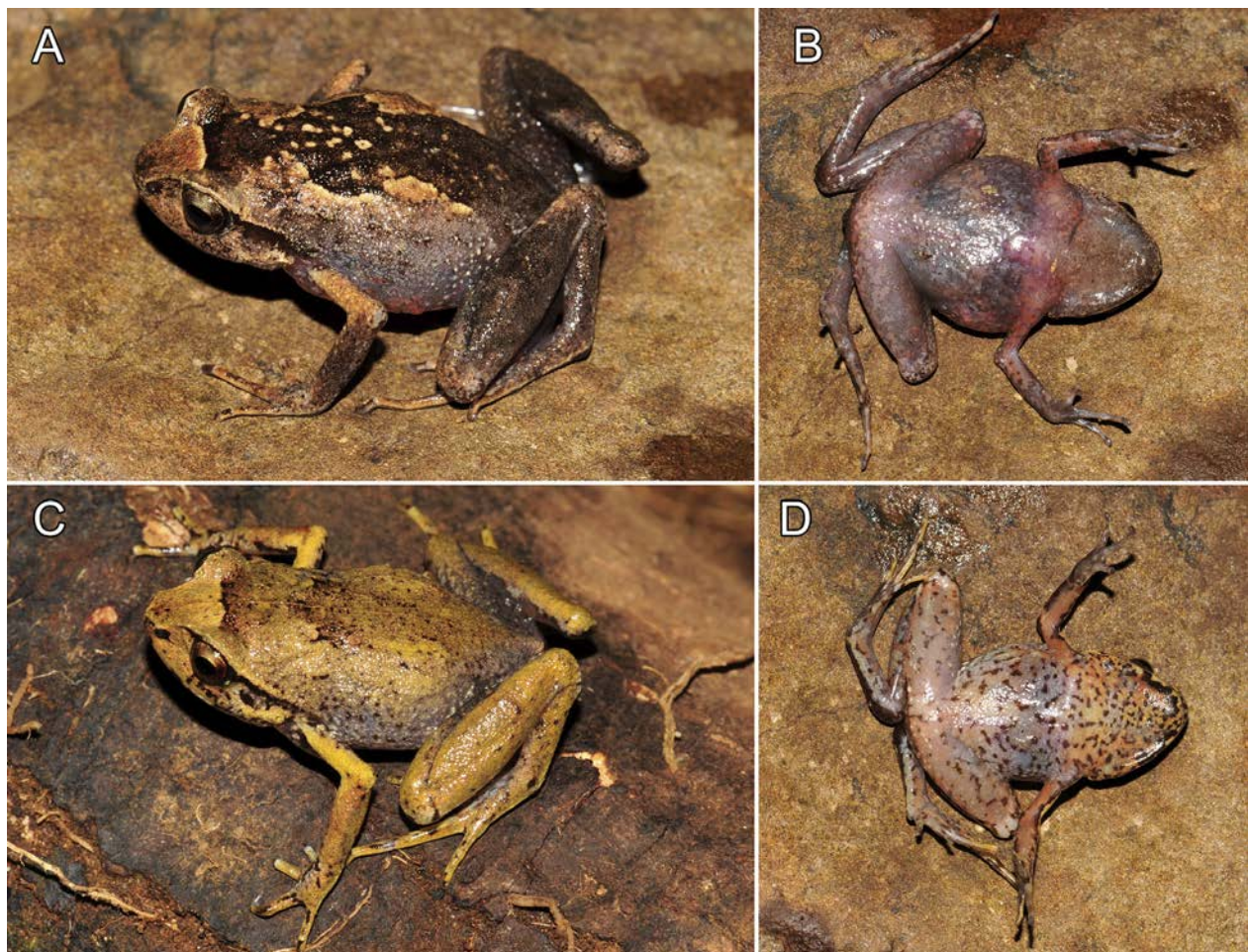


Figure 65. *Rhombophryne longicrus* specimens from Sorata, in life. **A, B** adult female holotype ZSM 1630/2012 (FGZC 3653) in **A** dorsolateral and **B** ventral view. **C, D** adult male paratype UADBA-A 60271 (FGZC 3651) in **C** dorsolateral and **D** ventral view.

Diagnosis. Within the genus *Rhombophryne*, *R. longicrus* can easily be distinguished from *R. testudo*, *R. coudreaui*, *R. matavy*, and *R. maraorao* **sp. nov.** by its smooth skin (vs rough), absence of chin barbels (vs general presence), and much longer hindlimbs (HIL/SVL 1.81–1.83 vs 1.10–1.41); from *R. mangabensis* and *R. savaka* by its much longer hindlimbs (HIL/SVL 1.81–1.83 vs 1.37–1.60); from *R. mavokely* **sp. nov.**, *R. kotrobaratra* **sp. nov.**, and members of the *R. ellae* species group by the absence of orange colouration on the posterior thigh and in the inguinal region (vs presence); from *R. kotrobaratra* **sp. nov.** further by absence of a dark chevron dorsally (vs presence); from *R. laevipes*, *R. nilevina*, *R. sonaliae* **sp. nov.**, and *R. anatalia* **sp. nov.** by smaller adult body size SVL 23.8–28.0 mm vs 33.0–57.2 mm), and absence of white spots in the inguinal region and on the posterior thigh (vs presence in most specimens); from *R. botabota* by more

gracile body (vs rotund) and longer hindlimbs (HIL/SVL 1.81–1.83 vs 1.41–1.75); from *R. proportionalis* by larger adult body size (SVL 23.8–28.0 mm vs 11.0–12.3 mm); and from all members of the *R. serratopalpebrosa* species group by the absence of superciliary spines (vs presence). For distinction from its sister species, *R. minuta*, see the account of that species, above. A detailed description of the species is given in Scherz et al. (2015a).

Variation. Both known specimens are highly similar to one another, but differ in size (SVL of male paratype 23.8 mm, female holotype 28.0 mm) and colouration, with the male being much yellower and having melanised flecks across its venter. For variation in morphometric measurements, see Table S9.

Call. The call of this species is not known.

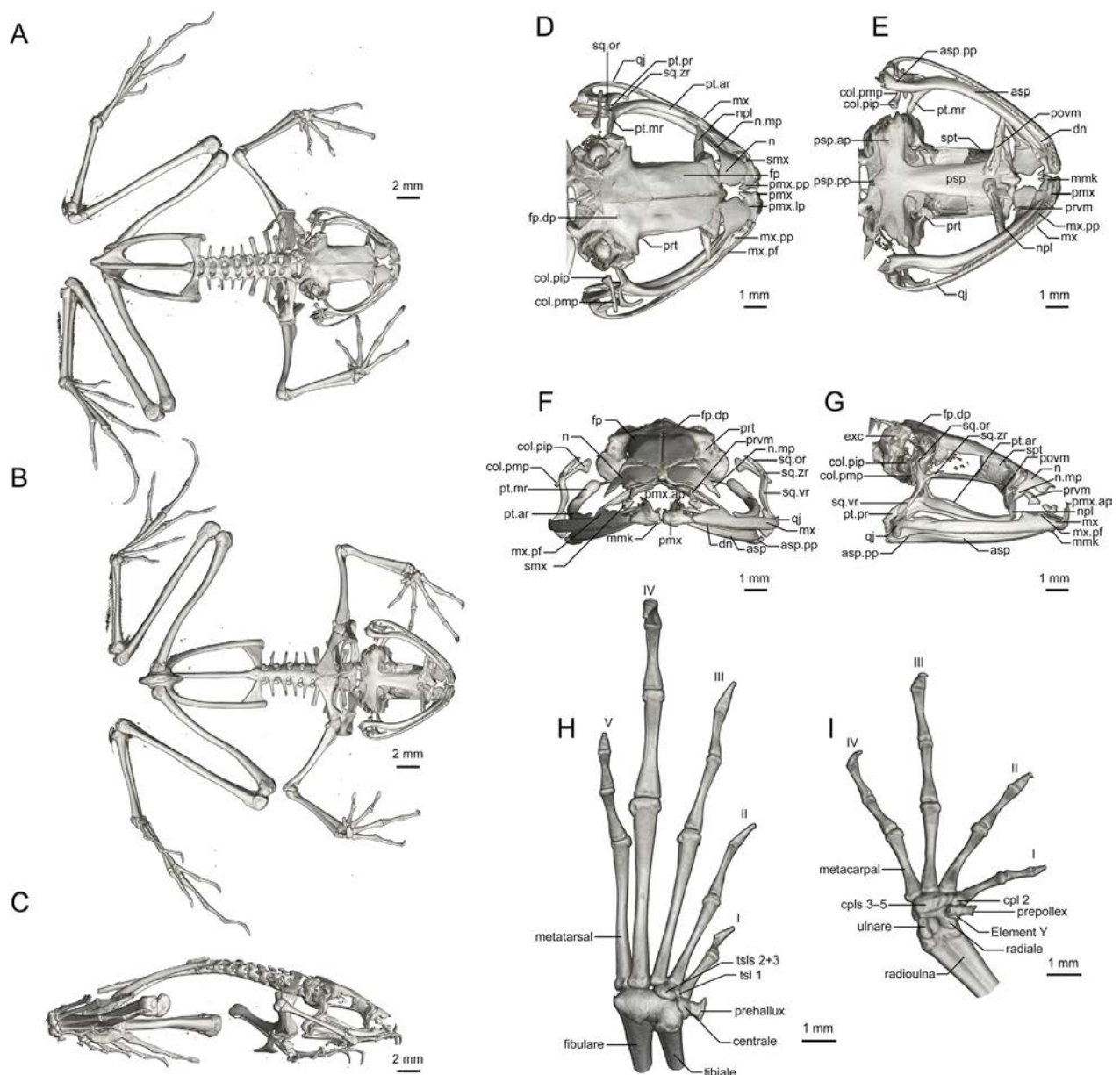


Figure 66. Skeleton of *Rhombophryne longicrus* holotype ZSM 1630/2012 (FGZC 3653). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

Etymology. Invariable Latin noun derived from the words *longus*, meaning ‘long’, and *crus* meaning ‘leg’, referring to the unusually long legs of this species.

Distribution. This species is only known from (1) high elevation on the Sorata Massif (type locality). Elevation: ca 1580 m a.s.l.

Natural history. *Rhombophryne longicrus* is a scansorial species found in high-elevation humid forest. Scherz et al. (2015a) documented the presence of small insects (mostly beetles) and a spider (probably Salticidae), along with moss, in the guts of the type specimens. The holotype contained >20 immature oocytes, the largest ranging from 1.3 to 1.6 mm in size. The authors speculated that this species may have a more saltatorial locomotion and lifestyle than its congeners. One of the type specimens was collected by A. Rakotoarison in a tree, sitting at the corner of a branch; this detail was forgotten from the original description, but could also suggest climbing behaviour, which has not previously been documented in this genus.

Osteology of the *Rhombophryne minuta* species group

Material examined. This description is based on the following specimens: *R. minuta* (ZSM 476/2005; Fig. 62; holotype MNHN 1975.15; Fig. 63), *R. longicrus* (ZSM 1630/2012; Fig. 66). All specimens are fully intact and well-ossified.

The *Rhombophryne minuta* species group is osteologically homogeneous, showing derived traits in the form of its elongated limbs and digits compared to other species groups. Here, we provide a description of the osteology of the group that highlights particularly diagnostic features of both species. An osteological description of *R. longicrus* was also given by Scherz et al. (2015a).

The skull is broader than long, but only marginally so in *R. minuta*.

Dorsal investing bones. Nasals closely approach but not contacting the frontoparietals. The maxillary process of the nasal is thin, oriented posterolaterally, and runs towards the neopalatine, but does not come close to contacting it or the maxilla. The posterior edge of the nasal plate is continuous with the posterior edge of the maxillary process in *R. longicrus*, but not in *R. minuta*.

The frontoparietals bear a low dorsal process, slightly more pronounced in *R. longicrus* than *R. minuta*, without a ridge. The lateral ventrally descending flange is moderately shallow, enclosing the upper edge of the braincase.

Neurocranium. The sphenethmoid is fully ossified, and covers just less than half of the anterolateral wall of the braincase. The exoccipital does not differ appreciably between the species. The exoccipitals do not meet medially. The prootic is well-ossified, but does not differ substantially in shape. The septomaxilla has a consistent shape, with a distinct medial ramus present. The pars interna

pectra of the columella is much more distinct from the pars media plectra in *R. minuta* than in *R. longicrus*.

Ventral investing and palatal bones. The parasphenoid is consistent among the species, having a very long cultriform process. The parasphenoid alae are slightly more anteriorly oriented in *R. minuta* than *R. longicrus*, and are only weakly pointed, compared to the *R. laevis* species group.

The anterior portion of the vomer is triradiate. In one specimen of *R. minuta* (ZSM 476/2005), it is asymmetrical, being almost crescentic on the right and subtriangular on the left; we therefore avoid further comment on it. The posterior portion of the vomer is straight or weakly curved and bears a continuous row of teeth without trace of a diastema. The neopalatine, which lies dorsally on top of the vomer, is a straight, flattened rod-like structure that expands medially, quite substantially in *R. minuta*. It lacks an anterior process near the midline in *R. minuta*, and has one on the left but not the right in *R. longicrus*. The vomers and neopalatines are separated medially by a small gap.

Maxillary arcade. Maxillary teeth are present in both species. The premaxilla is uniform in both species, with a much thinner lingual process than palatine process. The maxilla is not especially deep, with a very distinct and posteriorly pointed facial process that is widely separated from the maxillary process of the nasal. The contact with the anterior ramus of the quadratojugal is quite far posterior on the arcade, and is brief.

Suspensorium. The anterior ramus of the quadratojugal is weakly curved (*R. minuta*) or straight (*R. longicrus*). The contact with the squamosal is narrow.

The ventral ramus of the squamosal is rather straight and narrow, with a fine posterior crest. The otic ramus is longer than the zygomatic ramus, and the two rami are at a right-angle to one another in lateral view, as well as dorsal view. The otic ramus is nearly perpendicular to the longitudinal axis of the skull in *R. longicrus*, but angled somewhat posteriorly in *R. minuta*. The pterygoid is consistent in structure, with a comparatively narrow posterior ramus.

Mandible. The mentomeckelians are small and hourglass-shaped. The dentary is thin and laminar. The angulosplenial is shallow. The coronoid process is low but distinct. The posterior process (articular facet) is weakly expanded.

Pectoral girdle. The coracoids are slightly less robust in *R. minuta* than in *R. longicrus*. Clavicles present and curved. The scapula and cleithra do not differ sufficiently for further comment.

The humeral crests are weakly developed. The crista ventralis is exceptionally short, extending over less than a third of the length of the humerus—a state that is quite distinct from all other *Rhombophryne*. The crista lateralis is almost absent. The radioulna is comparatively long, but shows little variation between the species.

Carpals 2, 3–5, element Y, radiale and ulnare present. The prepollex is moderately small, about half the length of the first metacarpal. The digital formula of both species is the same (2-2-3-3). The terminal phalanges are long, ending in small knobs.

Vertebral column. The centra of *R. minuta* appear comparatively wider and shorter than in *R. longicrus*. Transverse processes of oriented anterolaterally. Transverse processes of V2–4 are distinctly broader than V5–8. Transverse processes of V5–8 much less narrow than centrum is wide. The sacrum is as wide as V4, its anterior edge practically straight, oriented laterally, the posterior edge sweeping back strongly. The diapophyses are flared. The urostyle has a dorsal ridge along ~50% of its length.

Pelvic girdle. Iliac shafts with weak dorsal crests. The oblique groove and dorsal prominence are distinct. The femur lacks a posterior ridge. The tibiofibula and tarsus are long, but do not bear further comment. The toe formula is standard (2-2-3-4-3). The prehallux is small, comprised of two elements.

Rhombophryne serratopalpebrosa species group

Note. The *Rhombophryne serratopalpebrosa* species group has received the greatest amount of attention of the genus in recent years (Scherz et al. 2014, 2015b, 2017a). To avoid unnecessary repetition, accounts of this species group are limited to type specimens, diagnoses, and any new data that have become available since 2017.

Rhombophryne serratopalpebrosa (Guibé, 1975)

Figures 2, 4–7, 67–70

Mantipus serratopalpebrosus Guibé, 1975

Plethodontohyla serratopalpebrosa — Blommers-Schlösser and Blanc (1991)

Rhombophryne serratopalpebrosa — Glaw and Vences (2007)

Remarks. All references to *Rhombophryne serratopalpebrosa* between 2005 and 2017 that did not refer specifically to the holotype of the species, were in fact referring to *R. regalis* (Scherz et al. 2017a). Previous references to *R. serratopalpebrosa* referred to any of a number of different members of the *R. serratopalpebrosa* species group; all of these references should therefore be carefully checked against the distribution and morphology of the other species mentioned here.

Until now, this species has only been known from the holotype, which is stained green and is in generally poor condition; it was redescribed by Scherz et al. (2014). A specimen collected by APR at high elevation on the Marojejy Massif is the first individual discovered that mor-

phologically matches the holotype. We obtained small fragments of the 5' fragment of 16S rRNA through museomics methods, which confirm identity with the holotype (Fig. 2). We therefore provide a detailed description of this specimen here.

Holotype. MNHN 1975.24, an adult female, collected on 29 November 1972 in the 'thickets at the summit of Marojejy', Sava Region, northeastern Madagascar, by C.P. Blanc (Guibé 1975: 1088).

Paratypes. None.

Referred specimen. UADBA 18258 (APR 04222), an adult female, collected at 11:00 am on 27 October 1996 at high elevation on the Marojejy Massif (14.4339°S, 49.7347°E, 1550 m a.s.l.), Sava Region, northeastern Madagascar, by A.P. Raselimanana. As stated above, the assignment of this specimen to this species is confirmed by molecular taxonomic identification (Fig. 2), in addition to be topotypical and conforming well morphologically with the holotype. RAG1 sequence of this species is so far not available.

Definition. The precise phylogenetic relationships of this species are poorly resolved, but it is possibly closely related to *R. regalis* and *R. vaventy* based on the existing but fragmentary DNA sequence data (Fig. 2). It is characterised by the possession of the following unique suite of characters: (1) medium body size, adult SVL 28.5–30.8 mm; (2) head wider than long (HW/HL 1.41–1.51); (3) moderately large eyes (ED/HL 0.38–0.38); (4) relatively long hindlimbs (HIL/SVL 1.87–1.88); (5) small inner metatarsal tubercle (IMTL/FOL 0.08–0.09); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin granular; (10) absence of chin barbels; (11) presence of four pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Diagnosis. Within the genus *Rhombophryne*, *R. serratopalpebrosa* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. Within the *R. serratopalpebrosa* species group, it can be distinguished from all species except *R. regalis* by the presence of an S-shaped dermal postnasal fold. It can be distinguished from *R. regalis* by its substantially larger size (SVL 28.5–30.8 mm vs 20.2–26.5 mm), strong supratympanic fold (vs weak), four superciliary spines (vs three), typically larger relative tympanum size (TDH/ED 0.72–0.75 vs 0.47–0.75), longer relative forearm length (FARL/SVL 0.55–0.60 vs 0.42–0.51), parasphenoid cultriform process not broadening anteriorly (vs broadening), absence of contact between exoccipitals ventromedially (vs presence), and narrow (vs broad) contact be-

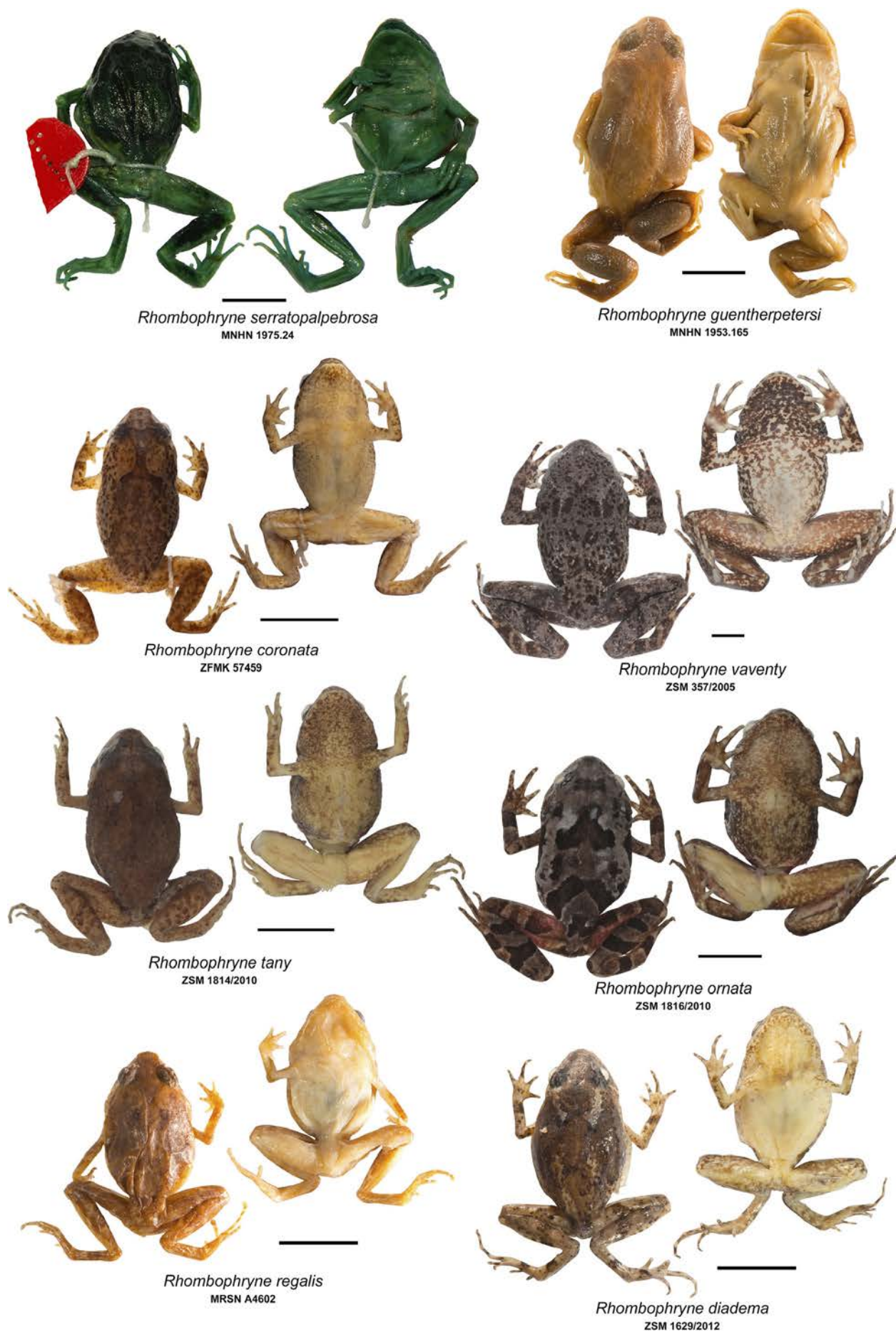


Figure 67. Name-bearing type specimens of species in the *Rhombophryne serratopalpebrosa* species group in dorsal (left) and ventral (right) views. Scale bars = 10 mm.

tween squamosal and quadratojugal. Based on the newly studied specimen, we can rule out the ossification of the pubis and stepping of the anterior edge of the ventral ramus of the squamosal as diagnostic traits to distinguish these two species, suggested by Scherz et al. (2017a). For distinction from new species described herein, see accounts below.

Description of UADBA 18258. An adult female in an excellent state of preservation (Fig. 69A). Slightly soft on the abdomen. Tissue sample taken from the right thigh, and a slit made in the right flank to assess the sex. Large yellowish ova present.

Overall extremely closely resembling MNHN 1975.24 as it looked before it was stained green. Body rhomboid. Head very wide, much wider than long (HW/HL 1.41). Eyes large and protuberant (ED/HL 0.37), pupils small, round. Snout rounded in dorsal and lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique, a distinct S-shaped postnasal fold. Nostril nearer to tip of snout than to eye, slightly protuberant. Tympanum distinct, large, oval, TDH/ED 0.75. Supratympanic

fold distinct, raised, not melanised, running in a slightly S-shaped curve, straight over the tympanum, curving ventrally behind it, and then posteriorly again toward the dorsal insertion of the forelimb. Lateral head similar in colour to dorsal head. Five superciliary spines of varying height and distinction present above each eye. Dorsal skin slightly shagreened, distinctly different in texture from flank and ventral skin. Ventral skin smooth. Tongue broad, attached anteriorly, posteriorly free, with a distinct raised, perpendicular ridge-like structure on its antero-dorsal surface. Maxillary and vomerine teeth present, vomerine teeth straight, not varying in height, separated from one another at the midline by a small gap. Choanae round, placed laterally in the roof of the mouth.

Forelimbs long (FARL/SVL 0.552), slender. Fingers without webbing, long, relative lengths $1 < 2 < 4 < 3$, second finger much shorter than fourth. Finger tips not expanded, elongated. Finger subarticular tubercles indistinct, cream, flat; inner metacarpal tubercle small and rounded, outer metacarpal/palmar tubercle indistinct, cream, single. Hind limb slender and long, tibiotarsal articulation reaching snout when adpressed anteriorly along



Figure 68. Ventral views of hands and feet, and lateral views of heads of name-bearing type specimens of members of the *Rhombophryne serratopalpebrosa* species group, plus the head, hand, and foot of a specimen of *R. sp. 'Ivohibe'*, UADBA 17420. Not to scale. * = mirrored for conformity.

the body. TIBL/SVL 0.493. Inner metatarsal tubercle present, oblong, cream, weakly raised. Outer metatarsal tubercle absent. Toes not webbed; toes unreduced, long, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles indistinct; toe tips elongated, not expanded.

After 29 years in preservative, the base colour is coffee brown, mottled across the whole body with a mixture of lighter and darker brown. The limbs are slightly lighter than the trunk in dorsal colouration. Flanks with small cream spots, but otherwise largely lacking noteworthy patterning: there are no inguinal spots or other markings; the hindlimbs are largely homogeneous, being more pigmented above than below, and forelimbs the same. No distinct

colour difference between the lateral and dorsal head. The upper lip has a thin white line running from below the eye to the nostril, and an oblique light marking from the posterior corner of the eye to the rictus anterior to the tympanum. There is a light patch lacking pigment on the left inguinal area, but this may be due to how tags were tied before they were attached at the right knee. Ventrally, the chin is light brown, and this colour fades gently to grey-brown over the abdomen. The ventral legs have a few small cream spots. The ventral hands and feet are cream-brown. There is no distinctive colouration around the cloaca.

Variation. SVL 28.5–30.8 mm ($n = 2$). For variation in other measurements, see Table S10. The newly examined



Figure 69. Currently described species in the *Rhombophryne serratopalpebrosa* species group. **A** *R. serratopalpebrosa* from high elevation in Marojejy National Park (UADBA 18258, adult female; no photos in life available; **B** *R. guentherpetersi* from Andranomadio (camp 4) on Tsaratànana Massif (ZSM 607/2014, adult male); **C** *R. coronata* from Ankeniheny (holotype ZFMK 57459, adult male); **D** *R. vaventy* from Camp Simpona in Marojejy National Park (holotype ZSM 357/2005, adult male); **E** *R. ornata* from Matsabory Maiky (Camp 2), on Tsaratànana Massif (holotype ZSM 1816/2010, adult male); **F** *R. tany* from Matsabory Maiky (Camp 2), on Tsaratànana Massif (holotype ZSM 1814/2010, presumed male); **G** *R. diadema* from Sorata (paratype ZSM 1628/2012, presumed male); **H** *R. regalis* from Antsinjorano in the Ambolokopatrika-Betaolana Forest (voucher number and sex unknown). Not to scale.

Holotype. MNHN 1953.165, an adult female, collected on an unknown date on the ‘Tsaratànana Massif’ (no precise coordinates, at ‘2600 m’ a.s.l.), northern Madagascar (Guibé 1973: 1181). Scherz et al. (2017a) stated that the collectors of this specimen were unknown, but the MNHN catalogue records J. Millot and J. Guibé as the collectors.

Paratypes. Four specimens: MNHN 1953.165A, a subadult female, MNHN 1953.165B, an adult female, with the same collection data as the holotype. MNHN 1973.592, a subadult female, and MNHN 1973.593, a juvenile, collected on 1 November 1966 on Mission ORSTOM by C.P. Blanc from the same locality as the holotype (Guibé 1973: 1181). Note: the MNHN catalogue records R. Paulian as the collector.

Referred specimens. ZSM 606/2014 (DRV 6220), an adult female, ZSM 607/2014 (DRV 6223; Fig. 69B), an adult male, UADBA-A 60775 (DRV 6210) and UADBA-A 60776 (ZCMV 12401), two unsexed adults, and UADBA-A 60782 (ZCMV 12435), a subadult, all collected on 16 June 2010 at ‘Camp 4’ Andranomadio (14.0801°S, 48.9854°E, 2503 m a.s.l.), Tsaratànana Massif, Diana Region, northern Madagascar by D. Vieites, M. Vences, R.D. Randrianiaina, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, F. Randrianasolo, F. Randrianasolo, and T. Rajoafiarison; ZSM 608/2014 (DRV 6231), an adult female, collected on 18 June 2010 at 14.0665°S, 48.9832°E, 2732 m a.s.l., Tsaratànana Massif, Diana Region, northern Madagascar, by D. Vieites, M. Vences, R.D. Randrianiaina, F.M. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, F. Randrianasolo, F. Randrianasolo, and T. Rajoafiarison.

Assignment of specimens. The specimen ZSM 606/2014 is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ KU724178; Scherz et al. 2016b; 16S5’ KY748098; Scherz et al. 2017a) and COI barcoding (COI OL790126; Belluardo et al. 2022). All paratypes and referred specimens conform well with the holotype in morphology. Assignment of specimen UADBA-A 60776 is further confirmed by molecular taxonomic identification (Fig. 2). UADBA-A 60776 is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. serratopalpebrosa* group, this species is placed in a clade containing *R. diadema*, *R. ornata*, and *R. tany* based on molecular phylogenetic data, but the exact relationships within that clade are poorly resolved (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) medium to large body size, adult SVL 27.3–35.7 mm; (2) head wider than long (HW/HL 1.35–1.42); (3) moderately large eyes (ED/HL 0.35–0.41); (4) relatively short hindlimbs (HIL/SVL 1.33–1.45); (5) small inner metatarsal tubercle (IMTL/FOL 0.10–0.13); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin slightly granular, with pronounced glandular swellings in the dorsolateral area of the trunk and on the tibia;

(10) absence of chin barbels; (11) presence of two small superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne guentherpetersi is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘C’ at site 369, ‘G’ at site 714, and ‘C’ at site 735; in 16S3’. No diagnostic sites were identified for 16S3’.

Diagnosis. Within the genus *Rhombophryne*, *R. guentherpetersi* can easily be distinguished from all other species (including all species newly described herein) by the presence of large, swollen tibial glands.

Call. The call of this species is unknown.

Etymology. Eponym for Günther Peters, German herpetologist.

Distribution. This species is only known from (1) high elevation on the Tsaratànana Massif (type locality). Elevation: 2503–2732 m a.s.l. Raxworthy et al. (2008) reported the species from 1450–2700 m a.s.l., but their identifications have not been verified by us, and the lower elevation records may refer to other species.

Natural history. *Rhombophryne guentherpetersi* is a semi-fossorial or detriticolous species found in montane forest and ericoid thicket. No further information on its natural history is available.

Rhombophryne coronata (Vences & Glaw, 2003)

Figures 2, 4–7, 67–69, 71, 72, 74

Plethodontohyla coronata Vences & Glaw, 2003

Rhombophryne coronata — Glaw and Vences (2007)

Remark. Belluardo et al. (2022) reported the candidate species *Rhombophryne* sp. Ca13, based on specimen KU 340732 (CRH 457; Fig. 71A), an adult female (containing 12 eggs), collected on 5 January in 2015 in Vohidrazana Private Reserve (18.9761°S, 48.4993°E, ca. 1150 m a.s.l.), Alaotra-Mangoro Region, central eastern Madagascar, by C.R. Hutter and S. Lambert. We here refrain from treating the taxonomy of that candidate species, because (1) it is very closely related to *R. coronata*, (2) we have not been able to identify any morphological features that distinguish these lineages (they are extremely similar both externally and osteologically; compare Figs 72 and 73), and (3) we lack bioacoustic data from *R. sp.* Ca13. Based on molecular phylogenetic data *Rhombophryne*

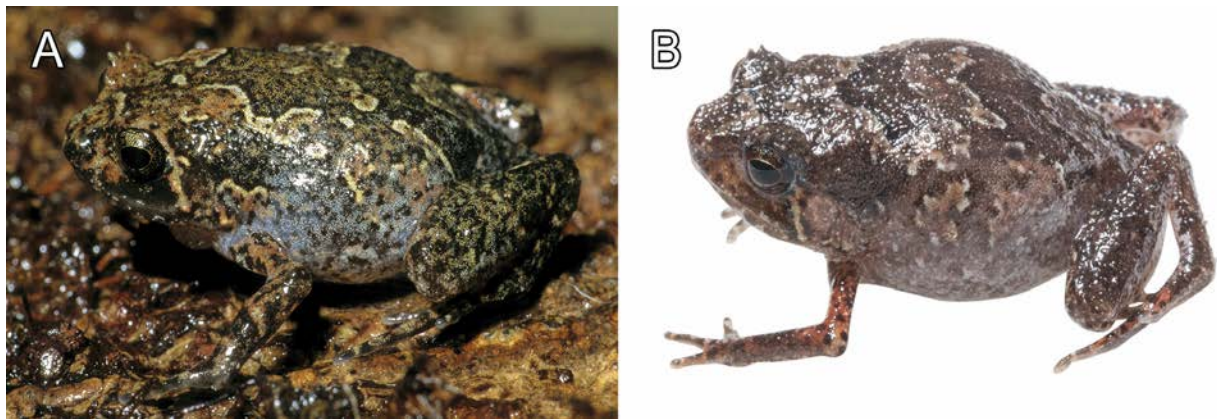


Figure 71. Comparison of *Rhombophryne coronata* and *R. sp. Ca13*. **A** *R. coronata* paratype ZSM 694/2001 (FGMV 2001.199) from Mandraka; **B** *R. sp. Ca13* specimen KU 340732 (CRH 457) from Vohidrazana Private Reserve. Not to scale.

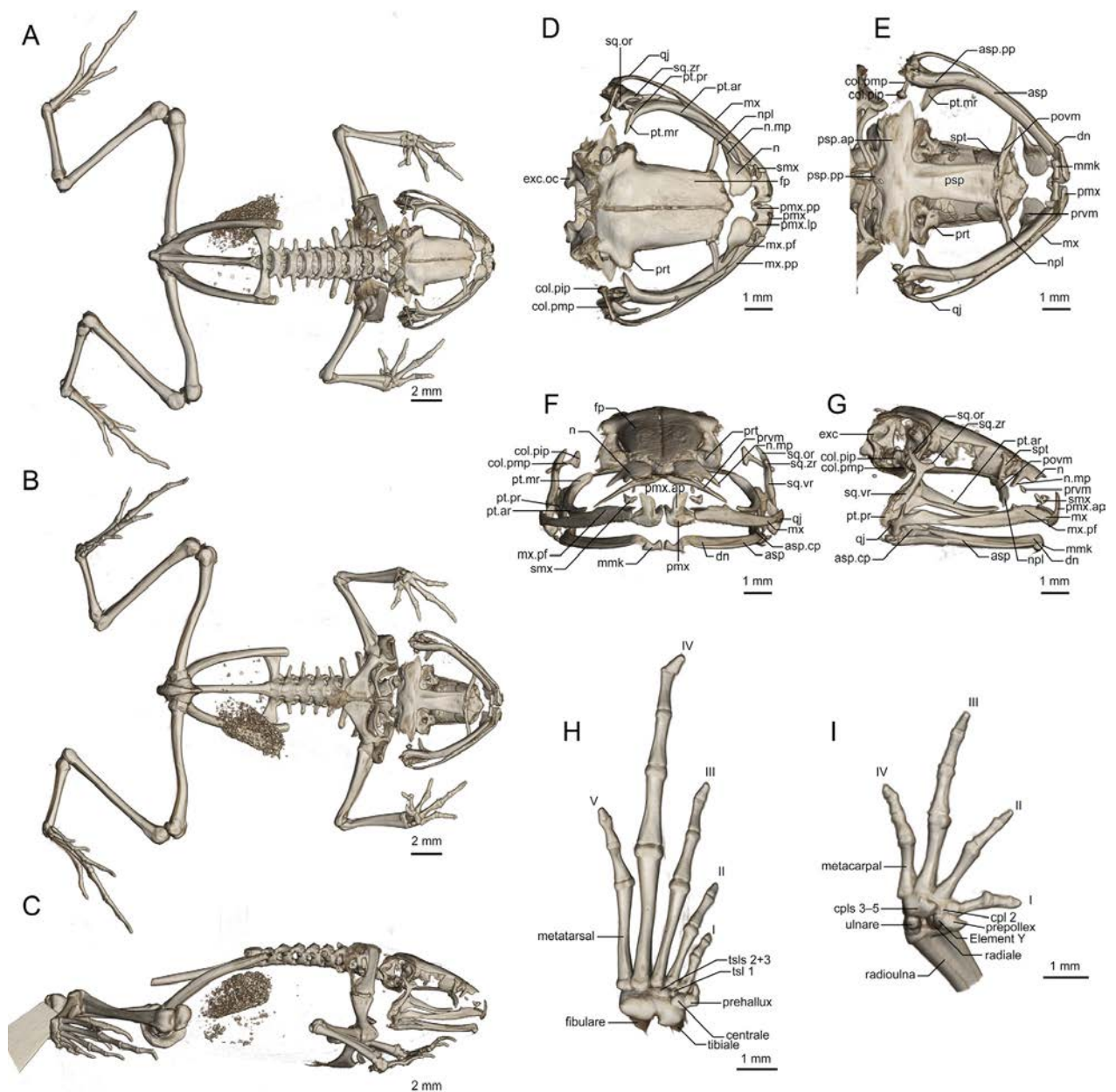


Figure 72. Skeleton of *Rhombophryne coronata* holotype ZFMK 57459. **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

coronata and *R. sp. Ca13* form a highly supported clade (Fig. 2). Our ASAP species delimitation retained *R. sp. Ca13* as a distinct species. However, data from the nuclear gene RAG1 reveal haplotype sharing between *Rhombophryne coronata* and *R. sp. Ca13* (Fig. 4). Altogether, this is weak evidence for species-level distinction, and we need additional material from more sites in this area in order to clarify the taxonomy of these frogs.

Holotype. ZFMK 57459, an adult male, collected on 19 February 1994 at Ankeniheny (19.167°S, 48.033°E, 900 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar, by F. Glaw, N. Rabibisoa, and O. Ramilison.

Paratypes. Two specimens: ZSM 694/2001 (FGMV 2001.199), and UADBA-A-FGMV 2001.200, two adult

males, collected on 16 February 2001 at Mandraka (18.917°S, 47.933°E, 1220 m a.s.l.), Analamanga Region, North Central East Madagascar, by M. Vences and D.R. Vieites.

Referred specimens. ZSM 473/2005 (ZCMV 2222) and ZSM 474/2005 (ZCMV 2223), two unsexed adults, collected in February 2005 in a pitfall trap in Andasibe (18.9362°S, 48.4122°E, 939 m a.s.l.), Alaotra-Mangoro Region, North Central East Madagascar, by R. Dolch and collaborators.

Assignment of specimens. The paratype ZSM 694/2001 (FGMV 2001.199) is used as the reference specimen for this species in 16S rRNA barcoding (16S3' and 16S5' EU341103; Vieites et al. 2009). A tissue sample with

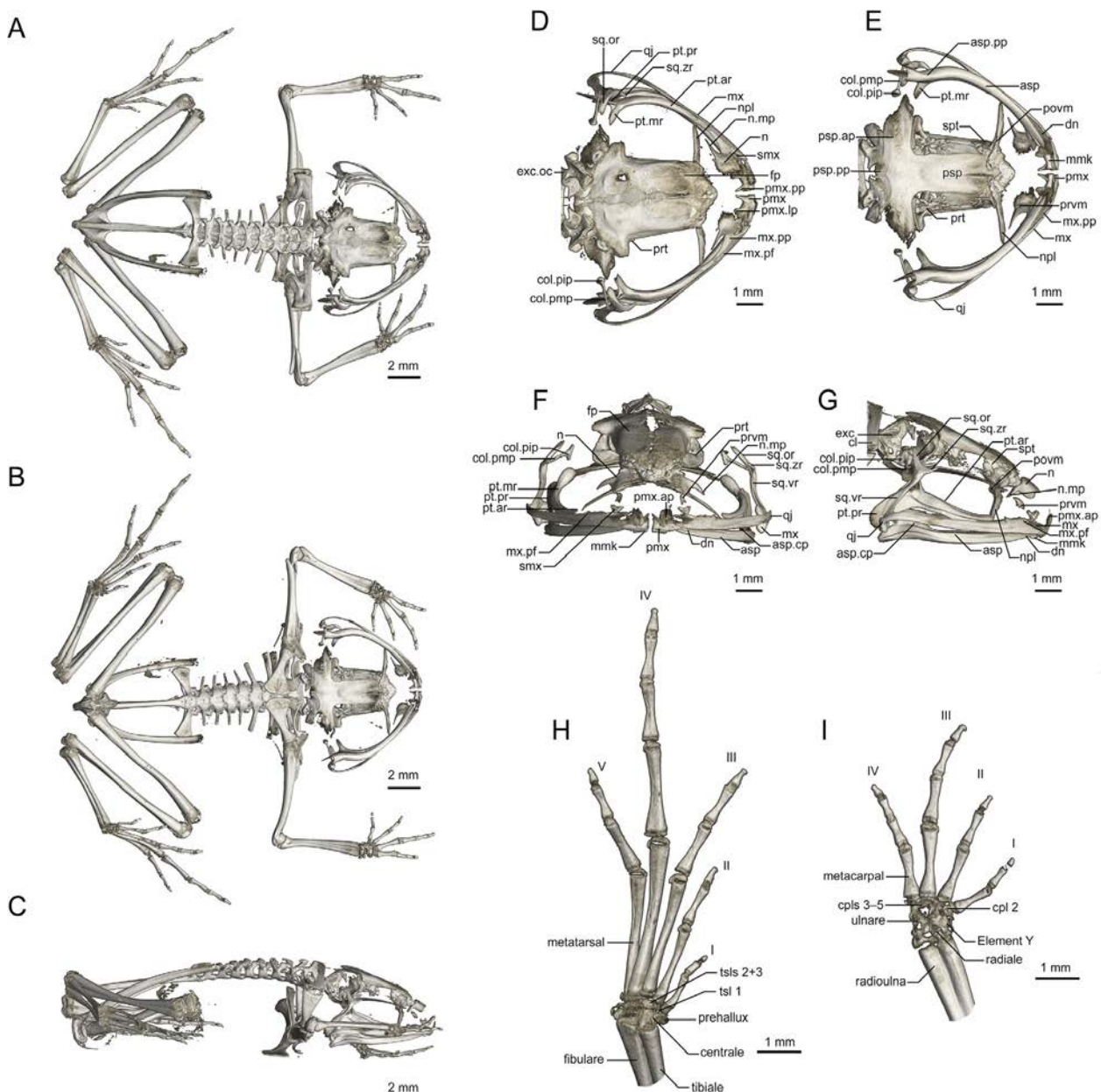


Figure 73. Skeleton of *Rhombophryne sp. Ca13* specimen KU 340732 (CRH 457). **A–C** Whole skeleton in **A** dorsal, **B** ventral, and **C** lateral view; **D–G** skull in **D** dorsal, **E** ventral, **F** anterior, and **G** lateral view; **H** right foot in ventral view; **I** right hand in ventral view. Abbreviations are given under Materials and Methods.

specimen number MV2001.A1 (corresponding to either ZSM 694/2001 or UADBA-A-FGMV 2001.200) is used as the reference for this species in COI barcoding (COI KF611586; Perl et al. 2014). All paratypes and referred specimens conform well with the holotype in morphology. Assignment of specimens ZSM 473/2005, and ZSM 474/2005 is further confirmed by molecular taxonomic identification (Fig. 2). MV2001.A1, ZSM 473/2005, and ZSM 474/2005 are present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. serratopalpebrosa* group, this species is sister to the unconfirmed candidate species *R. sp. Ca13* in a clade sister to all other nominal species based on molecular phylogenetic data (Fig. 2; Belluaro et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small body size, adult SVL 19.4–23.2 mm; (2) head wider than long (HW/HL 1.51–1.55); (3) moderately large eyes (ED/HL 0.41–0.46); (4) relatively short hindlimbs (HIL/SVL 1.28–1.47); (5) small inner metatarsal tubercle (IMTL/FOL 0.08–0.13); (6) outer metatarsal tubercle absent; (7) second finger subequal to fourth; (8) third toe distinctly longer than fifth, first toe reduced to a nub in some specimens; (9) dorsal skin finely granular; (10) absence of chin barbels; (11) presence of three small, equal-sized superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne coronata is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'T' at site 275, 'A' at site 288, and 'A' at site 381; in 16S3', 'A' at site 967, 'T' at site 1182, and 'A' at site 1322.

Diagnosis. Within the genus *Rhombophryne*, *R. coronata* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. Within the *R. serratopalpebrosa* species group, it is unique in possession of a reduced first toe. For further distinction from *R. serratopalpebrosa* and *R. guentherpetersi*, see the diagnosis of those species, above. It can further be distinguished from *R. vaventy* by much smaller adult body size (SVL 19.4–23.2 mm vs > 50 mm), and finely granular dorsal skin (vs rugose); from *R. ornata* by much smaller adult body size (SVL 19.4–23.2 mm vs up to 33.0 mm), three superciliary spines (vs two), and absence of reddish colouration on the thighs and inguinal region; from *R. tany* by slightly smaller adult body size (SVL 19.4–23.2 mm vs 24.6 mm), indistinct supratympanic fold (vs distinct), and shorter hindlimb (HIL/SVL 1.28–1.43 vs 1.56); from *R. regalis* by absence of S-shaped dermal postnasal fold, superciliary spines being of roughly equal size (vs three spines differing in size: 1st large, 2nd medium, 3rd diminutive), and shorter relative tibia length (TIBL/SVL

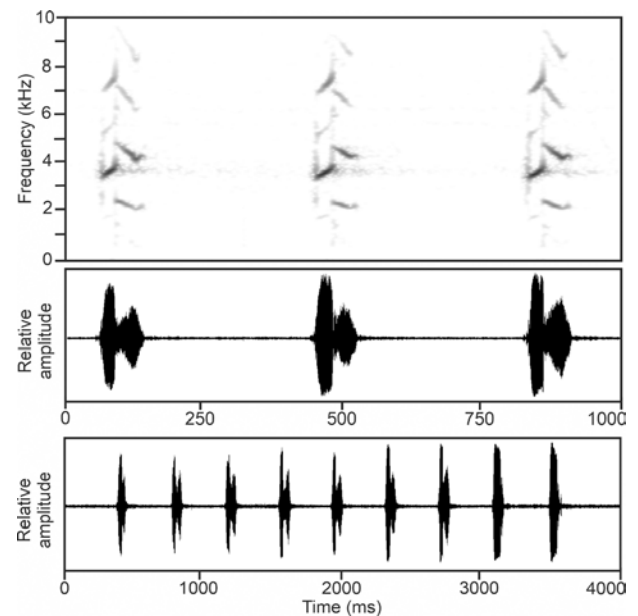


Figure 74. Advertisement calls of *Rhombophryne coronata* (presumably holotype ZFMK 57459), recorded at Ankeniheny in 1994. Top: audiospectrogram and corresponding oscillogram of three advertisement calls from a regular call series at 1000 ms time scale. Bottom: oscillogram at 4000 ms time scale depicting a regular call series containing nine calls. Recording high-pass filtered at 500 Hz.

0.35–0.39 vs 0.47–0.56); from *R. diadema* by superciliary spines being of roughly equal size (vs posterior-most spine being diminutive compared to the other two), smaller relative tympanum size (TDH/ED 0.37–0.59 vs 0.59–0.64), and shorter relative tibia length (TIBL/SVL 0.35–0.39 vs 0.44–0.46). For distinction from new species described herein, see accounts below.

A detailed description of the species is given in Vences and Glaw (2003) but we here add more data on the variation and distribution of the species, as well as a redescription of the call.

Variation. SVL 19.4–23.2 mm ($n = 4$). For variation in other measurements, see Table S10. Specimens are very consistent in anatomy, except one specimen (ZSM 474/2005, ZCMV 2223), which differs as follows: the fourth finger is longer than the second, but only slightly; in this specimen, the first finger is also visibly reduced, to a greater extent than in other specimens examined, whereas the first toe is not reduced, unlike other specimens examined.

Our measurements of the holotype of *R. coronata* differ in some points quite substantially from the original measurements of Vences and Glaw (2003), especially HL (5.7 mm vs 7.3 mm), NSD (1.3 vs 1.6 mm), TDH (1.4 vs 1.7 mm), HAL (4.7 vs 5.0 mm), FORL (13.2 vs 12.6 mm), FOTL (14.7 vs 14.4 mm), HIL (33.0 vs 30.6 mm), and IMCL (0.9 vs 1.1 mm). These differences are undoubtedly due to differences in measurement style; hence, we emphasise that all measurements reported in this paper were taken by the same measurer (MDS) based on the measurement scheme shown in Fig. 1.

Rhombophryne sp. Ca13 is extremely similar to *R. coronata* morphologically (Fig. 71). The one ovigerous adult female specimen we examined (KU 340732, CRH 457) differed from specimens of *R. coronata* by a longer forelimb (FORL/SVL 0.71 vs 0.32–0.59; FARL/SVL 0.48 vs 0.37–0.43), and hindlimb (TIBL/SVL 0.45 vs 0.35–0.39; HIL/SVL 1.63 vs 1.28–1.47); tibiotarsal articulation reaching the eye (vs the tympanum) when adpressed forward along the body. The skin texture and colour pattern, as well as the size distribution of superciliary spines, is, however, practically identical.

Call. The advertisement call recorded on 19 February 1994 (18:30–19:00 h) at Ankeniheny (air temperature 23.5 °C) consists of a short tonal note emitted in regular call series of variable duration (Fig. 74). Most calls (= notes) are composed of two recognizable pulses. These two-pulse calls exhibit a remarkable and complex pattern of frequency modulation, with a distinct upward sweep corresponding to the initial pulse, followed by a downward sweep corresponding to the second pulse. In addition, an upward shift in dominant frequency is recognizable in the second pulse (Fig. 74). Numerical parameters of 15 analysed calls are as follows: call duration (= note duration) 68–95 ms (83 ± 7 ms); inter-call intervals within regular call series 284–331 ms (308 ± 13 ms); number of calls per call series 5–12 (9 ± 3); duration of regular call series 1641–4468 ms (3162 ± 1119 ms); dominant frequency 3488–3660 Hz (3588 ± 81 Hz), with a second prominent peak present at 7200–7400 Hz; prevalent bandwidth 1800–9500 Hz; harmonic frequency bands recognizable with approximately 3500 Hz spacing up to 19,000 Hz. Calls from the same recording (Vences et al. 2006 CD 3, track 29) have been described by Vences and Glaw (2003) using a slightly different terminological scheme.

Etymology. Latin feminine nominative singular adjective meaning ‘crowned’, referring to the superciliary spines.

Distribution. This species is known from (1) Ankeniheny (type locality), (2) Mandraka, (3) Andasibe, (4) Berano (18.8371°S, 48.3185°E, 1126 m a.s.l.) (Rako-

toarisoa 2012) and (5) various sites locations in the Ambatovy-Analamay area (Raselimanana 2010). Records of the species from Zahamena (IUCN SSC Amphibian Specialist Group 2016c; Goodman et al. 2018) and other locality records given in Goodman et al. (2018) are in need of confirmation, since we have not seen any voucher specimens and there are no DNA sequences available. If *R. sp. Ca13* is considered conspecific, Vohidrazana will be added to the localities known for this species. Elevation: 900–1220 m a.s.l.

Natural history. *Rhombophryne coronata* is a semi-fossorial or detriticolous species found in mid-elevation humid forest. Adult males were found calling from the leaf litter (not inside burrows) at night in rainforest.

Rhombophryne vaventy Scherz, Ruthensteiner, Vences & Glaw, 2014

Figures 2, 4–7, 67–69, 75

Remark. The 3' fragment of the 16S gene sequences of specimen AMNH A167315 (referred to as ‘*R. cf. vaventy*’ in Belluardo et al. 2022 and ‘*R. sp. cf. vaventy*’ and ‘DCL “Sorata”’ by Carné and Vieites 2024) from Sorata is poorly differentiated from the homologous sequence of paratype UADBA-A-FGZC 2842, and our species delimitation results confirm that these are conspecific.

Holotype. ZSM 357/2005 (FGZC 2876), an adult male, collected on 17 February 2005 at ‘Camp Simpona’ (14.4367°S, 49.7434°E, 1326 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by F. Glaw, M. Vences, R.D. Randrianiaina.

Paratypes. One specimen: UADBA-A-FGZC 2842, an unsexed probable adult, with same collection data as the holotype but collected on 16 February 2005.

Referred specimens. ZSM 522/2016 (ZCMV 15278), an adult female, collected on 20 November 2016 near

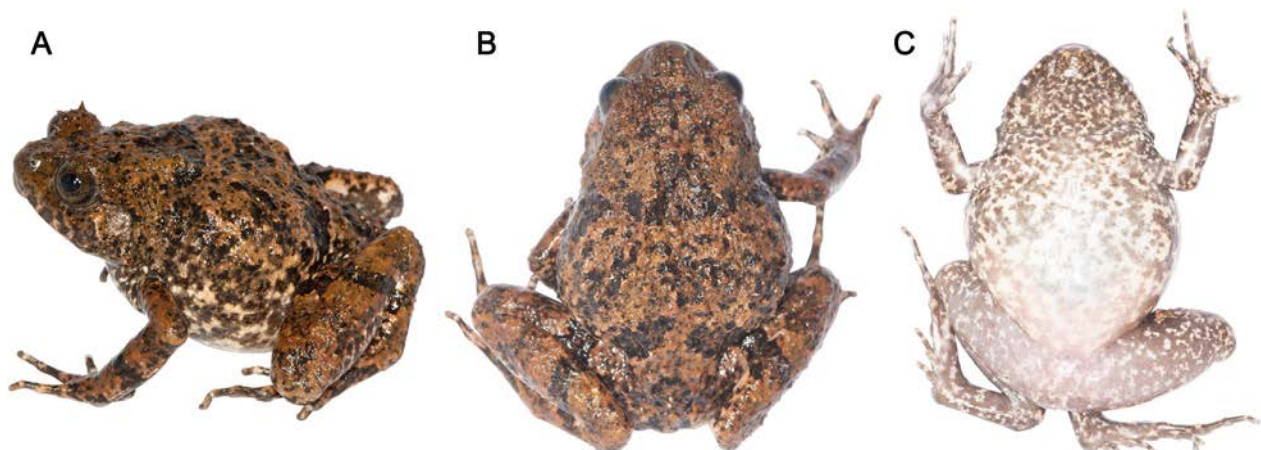


Figure 75. *Rhombophryne vaventy* in life. Photographed at ‘Camp Simpona’ in Marojejy National Park. **A–C** adult female: ZSM 522/2016 (ZCMV 15278) in **A** lateral, **B** dorsal and **C** ventral view.

‘Camp Simpona’ (14.4366°S, 49.7434°E, 1325 m a.s.l.), Marojejy National Park, Sava Region, northeastern Madagascar, by M.D. Scherz, A. Rakotoarison, M. Bletz, M. Vences, and J. Razafindralaibe (Fig. 75).

Based on our species delimitation analysis, AMNH A167315, a specimen of unknown sex and age, collected at Camp 1, Vohemar, Sorata Mountain (13.6858°S, 49.4419°E, ca 1300 m a.s.l.), Sava Region, northeastern Madagascar, is also attributable to this species. However, that specimen has not been examined, and this assignment remains tentative at present.

Assignment of specimens. The paratype UADBA-A-FGZC 2842 is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ and 16S5’ EU341107; Vieites et al. 2009) and COI barcoding (COI KF611595; Perl et al. 2014). The holotype is identical to this specimen in 16S3’ (GenBank: PZ418427) and differs by three gaps in a repetitive string of cytosines in 16S5’ (GenBank: PZ405243; Fig. 2). The paratype and ZSM 522/2016 conform well with the holotype in morphology, and are topotypical. ZSM 357/2005 and UABA-A-FGZC 2842 are present in the RAG1 haplotype network (Fig. 1).

Definition. Within the *R. serratopalpebrosa* group, this species is possibly closest related to *R. regalis* and *R. serratopalpebrosa* based on molecular phylogenetic data (Fig. 2). It is characterised by the possession of the following unique suite of characters: (1) large body size, adult SVL 51.9–58.6 mm; (2) head wider than long (HW/HL 1.56–1.70); (3) moderately large eyes (ED/HL 0.43–0.45); (4) relatively long hindlimbs (HIL/SVL 1.88–1.95); (5) small inner metatarsal tubercle (IMTL/FOL 0.11–0.14); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin rugose; (10) absence of chin barbels; (11) presence of four pronounced superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne vaventy is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘C’ at site 309, ‘C’ at site 385, ‘G’ at site 642; in 16S3’, ‘C’ at site 920, ‘A’ at site 1177, and ‘A’ at site 1217.

Diagnosis. Within the genus *Rhombophryne*, *R. vaventy* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. Within the *R. serratopalpebrosa* species group, it can be distinguished from all species by its much larger body size (SVL 51.9–58.6 mm vs < 36 mm), and its rugose dorsal skin texture (vs smooth to granular).

A detailed description of the species is given in Scherz et al. (2014), but see also notes in Scherz et al. (2017a).

Variation. Adult SVL 51.9–58.6 mm; for variation in other measurements see Table S10. The newly collected female specimen is 6.7 mm larger than the male holotype; there may be some degree of sexual size dimorphism. In all other respects, it agrees closely with the types.

Call. The call of this species is unknown.

Etymology. The Malagasy adjective *vaventy* meaning ‘large’, in reference to the exceptionally large size of this species. Used as an invariable noun in apposition.

Distribution. Originally known only from (1) the Marojejy Massif (Rakotoarimalala and Raselimanana 2023 reported it from 1300±200 m a.s.l. and 1875±200 m a.s.l.), but here expanded to encompass (2) Sorata as well by the assignment of AMNH A167315. Elevation: ca 1300–1875 m a.s.l. (the upper elevation being rather uncertain).

Natural history. *Rhombophryne vaventy* is a semi-fossorial or detriticolous species found in mid- to high-elevation humid forest. The newly collected adult female specimen ZSM 522/2016 was found active on the ground during the day by local guides.

Rhombophryne ornata Scherz et al., 2015

Figures 2, 4–7, 67–69

Holotype. ZSM 1816/2010 (ZCMV 12384), an adult male, collected on 13 June 2010 at ‘Camp 2’ Matsabory Maiky (14.1526°S, 48.9573°E, 2021 m a.s.l.), Tsaratànana Massif, Diana Regions, northern Madagascar, by M. Vences, D.R. Vieites, R.D. Randrianiana, F. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison.

Paratypes. Five specimens: ZSM 1815/2010 (ZCMV 12382), UADBA-A 60834 (ZCMV 12381), UADBA-A 60835 (ZCMV 12383), UADBA-A 60734 (ZCMV 12455), and ZSM 2859/2010 (DRV 06156), five juvenile or subadult specimens, with same collecting data as the holotype except UADBA-A 60734, which was collected 15–20 June 2010.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ KP895584; Scherz et al. 2015b; 16S5’ KY748102; Scherz et al. 2017a) and COI barcoding (COI KF611583; Perl et al. 2014). All paratypes are topotypical and conform well with the holotype in morphology. Assignment of ZSM 1815/2010 and ZSM 2859/2010 is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 1816/2010 is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. serratopalpebrosa* group, this species is placed in a clade containing *R. diadema*, *R. guentherpetersi*, and *R. tany* based on molecular phylo-

genetic data, but the exact relationships within that clade are poorly resolved (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters (based on a set of four subadults and one adult): (1) medium body size, adult SVL up to 33 mm; (2) head wider than long (HW/HL 1.39–1.51); (3) moderately large eyes (ED/HL 0.40–0.45); (4) moderately long hindlimbs (HIL/SVL 1.46–1.64); (5) small inner metatarsal tubercle (IMTL/FOL 0.09–0.10); (6) outer metatarsal tubercle absent; (7) second finger subequal to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin somewhat rugose; (10) absence of chin barbels; (11) presence of two distinct superciliary spines; (12) presence of reddish colouration in inguinal region; (13) presence of reddish colouration on anterior and posterior surface of thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne ornata is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'T' at site 315, 'G' at site 345, 'T' at site 682, and 'C' at site 721. No diagnostic sites were identified for 16S3'.

Diagnosis. Within the genus *Rhombophryne*, *R. ornata* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. Within the *R. serratopalpebrosa* species group, it can be distinguished from all species by the presence of reddish orange colouration in the inguinal region and on the thigh (vs absent).

A detailed description of the species is given in Scherz et al. (2015b).

Call. The call of this species is not known.

Etymology. Latin feminine nominative singular adjective meaning 'ornate', in reference to the colourful appearance of this species, especially in contrast to other *Rhombophryne*.

Distribution. This species is only known from (1) Matsabory Maiky on the Tsaratànana Massif (type locality). Elevation: 2021 m a.s.l.

Natural history. *Rhombophryne ornata* is a semi-fossorial or detriticolous species found in high-elevation humid forest. Specimens were collected hiding under logs and stones in forest; one specimen contained a frog in its stomach, as well as insect and plant remains (Scherz et al. 2015b).

Rhombophryne tany Scherz et al., 2015

Figures 2, 4–7, 67–69

Remark. This species is only known from the holotype.

Holotype. ZSM 1814/2010 (ZCMV 12359), an adult male, collected on 13 June 2010 at 'Camp 2' Matsabory Maiky (14.15256°S, 48.95728°E, 2021 m a.s.l.), Tsaratànana Massif, Diana Region, northern Madagascar, by M. Vences, D. Vieites, R.D. Randrianaiaina, F. Ratsoavina, S. Rasamison, A. Rakotoarison, E. Rajeriarison, and T. Rajoafiarison.

Paratypes. None.

Assignment of specimens. The holotype and sole known specimen of the species is used as the reference specimen for this species in 16S rRNA barcoding (16S3' KP895585; Scherz et al. 2015b; 16S5' KY748104; Scherz et al. 2017a) and COI barcoding (COI KF611582; Perl et al. 2014). It is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. serratopalpebrosa* group, this species is placed in a clade containing *R. diadema*, *R. ornata*, and *R. guentherpetersi* based on molecular phylogenetic data, but the exact relationships within that clade are poorly resolved (Fig. 2; Belluardo et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) medium body size, adult SVL 24.6 mm; (2) head wider than long (HW/HL 1.53); (3) moderately large eyes (ED/HL 0.36); (4) relatively short hindlimbs (HIL/SVL 1.56); (5) small inner metatarsal tubercle (IMTL/FOL 0.07); (6) outer metatarsal tubercle absent; (7) second finger equal to fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin finely granular; (10) absence of chin barbels; (11) presence of two distinct superciliary spines; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne tany is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'A' at site 504, 'T' at site 557, 'T' at site 578, and 'G' at site 721. No diagnostic sites were identified for 16S3'.

Diagnosis. Within the genus *Rhombophryne*, *R. tany* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. For distinction from *R. serratopalpebrosa*, *R. guentherpetersi*, *R. coronata*, *R. vaventy*, and *R. ornata*, see the diagnosis of those species, above. It can be distinguished from *R. regalis* by the absence of an S-shaped dermal postnasal fold, two (vs three) superciliary spines, and stronger supratympanic fold; and from *R. diadema* by two (vs three) superciliary spines, stronger supratympanic fold, slightly shorter relative tibia length (TIBL/SVL 0.43 vs 0.44–0.46), prootics not in contact with parasphenoid alae (vs

in contact), parasphenoid cultriform process with parallel edges (vs broadening anteriorly), nasals anterolaterally displaced (vs not displaced), quadratojugal-squamosal contact narrow (vs broad), anterior edge of ventral ramus of squamosal weakly (vs distinctly) stepped, dorsal prominence of iliac shafts strong (vs weak), and possibly unossified pubis (vs partially ossified). For distinction from new species described herein, see accounts below.

A detailed description of the species is given in (Scherz et al. 2015b).

Call. The call of this species is unknown.

Etymology. The Malagasy adjective *tany* meaning 'brown', in reference to the overall brown colour of this species. Used as an invariable noun in apposition.

Distribution. This species is only known from (1) Matsabory Maiky on the Tsaratànana Massif (type locality). Elevation: 2021 m a.s.l.

Natural history. *Rhombophryne tany* is a semi-fossorial or detriticolous species so far known only from high-elevation bamboo forest (Scherz et al. 2015b).

Rhombophryne regalis Scherz et al., 2017

Figures 2, 5–7, 67–69

Holotype. MRSN A4602 (FN 7292), an adult male, collected on 13 December 1997 at 'Camp 3' Antsinjorano (14.5433°S, 49.4300°E, ca 980 m a.s.l.), Ambolokopatrika-Betaolana Forest, Sava Region, northeastern Madagascar, by F. Andreone, J.E. Randrianirina, and G. Aprea.

Paratypes. Five specimens: MRSN A4603 (FN 7146), an adult female, same collection data as the holotype; MRSN A4619, a subadult, and MRSN A4620, an adult female, collected on 6 December 1997 at 'Camp 2' Andranomadio (14.5400°S, 49.4383°E, ca 860 m a.s.l.), Ambolokopatrika-Betaolana Forest, Sava Region, northeastern Madagascar, by F. Andreone, J.E. Randrianirina, and G. Aprea; MRSN A4618, an adult female, collected on 26 June 1996 at Ambinanin'antsahamaloto (14.8283°S, 49.5958°E, ca 800 m a.s.l.), Besaria-ka Forest, Sava Region, northeastern Madagascar, by F. Andreone and J.E. Randrianirina; MRSN A6058, an adult female, collected in January 1996 at 'Camp W1' west slope of Anjanaharibe-Sud (Analabe; 14.7783°S, 49.4634°E, ca 1050 m a.s.l.), Sava Region, northeastern Madagascar, by F. Andreone, J.E. Randrianirina, and H. Randriamahazo.

Referred specimens. UADBA-A 14174 (APR 00650), UADBA-A 14205 (APR 00477), UADBA-A 14172 (APR 00476), an adult female, an unsexed adult, and a juvenile, respectively, collected between 23 and 29 October 2001 in Marojejy National Park (14.4183°S, 49.6014°E,

810 m a.s.l.), Sava Region, northeastern Madagascar, by A.P. Raselimanana.

Assignment of specimens. The holotype is used as the reference specimen for this species in 16S rRNA barcoding (under the incorrect name *R. serratopalpebrosa*) (16S3' EU341111; Vieites et al. 2009). It has not been sequenced for COI. All paratypes conform well with the holotype in morphology. RAG1 sequence of this species is so far not available.

Definition. Within the *R. serratopalpebrosa* group, the precise phylogenetic relationships of this species are poorly resolved, but it is possibly closely related to *R. serratopalpebrosa* and *R. vaventy* based on the existing but fragmentary DNA sequence data (Fig. 2). It is characterised by the possession of the following unique suite of characters: (1) small to medium body size, adult SVL 20.2–26.5 mm; (2) head wider than long (HW/HL 1.21–1.46); (3) moderately large eyes (ED/HL 0.35–0.40); (4) moderately long hindlimbs (HIL/SVL 1.64–1.84); (5) small inner metatarsal tubercle (IMTL/FOL 0.06–0.12); (6) outer metatarsal tubercle absent; (7) second finger slightly to distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin shagreened; (10) absence of chin barbels; (11) presence of three or four pronounced superciliary spines, the longest being anterior to the eye; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne regalis is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5', 'G' at site 302, 'A' at site 334, 'G' at site 598, 'T' at site 601, 'C' at site 603, 'A' at site 607, and 'C' at site 615 (noteworthy that the sequence was retrieved from museomics and some sites may result from low quality sequence data); in 16S3', 'A' at site 964, 'T' at site 982, 'G' at site 1199.

Diagnosis. Within the genus *Rhombophryne*, *R. regalis* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. Within the *R. serratopalpebrosa* species group, it can be distinguished from all species except *R. serratopalpebrosa* by the presence of an S-shaped dermal postnasal fold. For distinction from *R. serratopalpebrosa*, see the diagnosis of that species, above. For distinction from new species described herein, see accounts below.

Variation. The newly examined material from Marojejy (referred specimens, above) are clearly assignable to this species based on the presence of S-shaped postnasal fold, most enlarged first superciliary spine, dorsal skin texture. Measurements are given in Table S10.

Call. The call of this species is unknown.

Etymology. Latin feminine nominative singular adjective meaning ‘regal’, in reference to the superciliary spines.

Distribution. *Rhombophryne regalis* was originally described from (1) Anjanaharibe-Sud, (2) Ambolokopatrika-Betaolana forest (type locality), and (3) Besariaka (Scherz et al. 2017a). The newly referred material expands the range of the species to (4) Marojejy, supporting the findings of Rakotoarimalala and Raselimanana (2023), who reported it from ca 1300 m a.s.l. Elevation: ca 800–1300 m a.s.l. (the upper elevation being rather uncertain).

Natural history. *Rhombophryne regalis* is a semi-fossorial or detriticolous species found in mid-elevation humid forest. Specimens were found active on the ground during rainy weather at night (Scherz et al. 2017a).

Rhombophryne diadema Scherz et al., 2017

Figures 2, 4–7, 67–69

Remark. This species is only known from the type series.

Holotype. ZSM 1629/2012 (FGZC 3604), an adult female, collected between 26 and 30 November 2012 on the Sorata Massif (13.6817°S, 49.4411°E, 1339 m a.s.l.), Sava Region, northern Madagascar, by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F.M. Ratsoavina, and A. Razafimanantsoa.

Paratypes. Two specimens: ZSM 1628/2012 (FGZC 3731), an adult male, and UADBA-A 60289 (FGZC 3611), an ovigerous adult female, collected between 26 and 30 November 2012 at a creek above the campsite on the Sorata Massif (13.6780°S, 49.4404°E), Sava Region, northern Madagascar, by F. Glaw, O. Hawlitschek, T. Rajoafiarison, A. Rakotoarison, F.M. Ratsoavina, and A. Razafimanantsoa.

Referred specimens. ZSM 341/2016 (AEA 041), an unsexed adult, collected on 25 May 2016 in Andravory (13.7483°S, 49.5307°E, 1168 m a.s.l.), Sava Region, northeastern Madagascar, by S. Megson and co-workers. This specimen is referred on morphological grounds and has not been genetically verified.

Assignment of specimens. The paratype ZSM 1628/2012 (FGZC 3731) is used as the reference specimen for this species in 16S rRNA barcoding (16S3’ KU724171; Scherz et al. 2016a; 16S5’ KY748097; Scherz et al. 2017a). Paratype UADBA-A 60289 (FGZC 3611) is used as the reference specimen for this species in COI barcoding (COI OL790125; Belluaro et al. 2022). The holotype is identical to the 16S3’ reference sequence, except one insertion and an undetermined stretch (16S3’ PZ418419)

and differs by one mutation in the 16S5’ fragment (16S5’ PZ405231). All paratypes and referred specimens conform well with the holotype in morphology. Assignment of the paratypes is further confirmed by molecular taxonomic identification (Fig. 2). ZSM 1629/2012 is present in the RAG1 haplotype network (Fig. 4).

Definition. Within the *R. serratopalpebrosa* group, this species is placed in a clade containing *R. guentherpetersi*, *R. ornata*, and *R. tany* based on molecular phylogenetic data, but the exact relationships within that clade are poorly resolved (Fig. 2; Belluaro et al. 2022). It is characterised by the possession of the following unique suite of characters: (1) small body size, adult SVL 21.5–23.4 mm; (2) head wider than long (HW/HL 1.40–1.59); (3) moderately large eyes (ED/HL 0.38–0.44); (4) relatively long hindlimbs (HIL/SVL 1.66–1.89); (5) small inner metatarsal tubercle (IMTL/FOL 0.07–0.11); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin granular to rugose; (10) absence of chin barbels; (11) presence of three superciliary spines, the posterior-most being diminutive; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Rhombophryne diadema is furthermore distinguished from all other *Rhombophryne* species analysed by the following robust diagnostic nucleotide combination in the mitochondrial 16S rRNA gene (positions relative to the full 16S sequence of *Anilany helenae* MZ751042): in 16S5’, ‘T’ at site 266, ‘A’ at site 640, and ‘T’ at site 740; in 16S3’ ‘A’ at site 965, ‘T’ at site 1083, ‘T’ at site 1086, and ‘T’ at site 1329. No diagnostic sites were identified for 16S3’.

Diagnosis. Within the genus *Rhombophryne*, *R. diadema* can easily be distinguished from all species except other members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. For distinction from *R. serratopalpebrosa*, *R. guentherpetersi*, *R. coronata*, *R. vaventy*, *R. ornata*, *R. tany*, and *R. regalis*, see diagnoses of those species above. For distinction from the new species described herein, see accounts below.

Call. The call of this species is unknown.

Etymology. Latin feminine noun in apposition meaning ‘diadem’, in reference to the superciliary spines.

Distribution. This species is only known from (1) Sorata Massif (type locality). Elevation: 1339–1407 m a.s.l.

Natural history. *Rhombophryne diadema* is a semi-fossorial or detriticolous species found in mid-elevation humid forest. Individuals were found during the day in the leaf litter. The holotype contained at least 13 well-developed, yellow eggs (diameter 2.45 ± 0.25 mm) (Scherz et al. 2017a).

HL 0.33–0.43); (4) relatively long hindlimbs (HIL/SVL 1.66–1.89); (5) small inner metatarsal tubercle (IMTL/FOL 0.08–0.10); (6) outer metatarsal tubercle absent; (7) second finger distinctly shorter than fourth; (8) third toe distinctly longer than fifth; (9) dorsal skin shagreened; (10) absence of chin barbels; (11) presence of three to four pronounced superciliary spines, the longest being centrally over the eye; (12) absence of inguinal ocelli or spots; (13) absence of distinctive markings along the posterior thigh; (14) unfortified skull without expansion of maxilla or posterior process of angulosplenial; and (15) clavicles present, thin, curving.

Thus, this species can easily be distinguished from all species except other *Rhombophryne* except members of the *R. serratopalpebrosa* species group by the presence of distinct superciliary spines. It differs from *R. serratopalpebrosa* and *R. regalis* by the absence of an S-shaped dermal postnasal fold; from *R. regalis* by the longest superciliary spine being over the centre of the eye (vs the anterior-most spine in *R. regalis*); from *R. guentherpetersi* by the absence of large, swollen tibial glands (vs presence); from *R. coronata* by longer hindlimb (HIL/SVL 1.66–1.89 vs 1.28–1.43), first toe unreduced (vs usually reduced), superciliary spines varying in length (vs small and equally sized), and shagreened dorsal skin (vs finely granular), and sphenethmoid not appreciably extending anterior to the postchoanal vomer (vs extending anteriorly); from *R. vaventy* by much smaller adult body size (SVL 21.6–25.8 mm vs > 50 mm); from *R. ornata* by smaller adult body size (SVL 21.6–25.8 mm vs up to 33 mm), three to four superciliary spines (vs two), and probable absence of reddish orange colouration in the inguinal region and on the thigh (vs presence); from *R. tany* by longer hindlimb (HIL/SVL 1.66–1.89 vs 1.56), and three to four superciliary spines (vs two); and from *R. diadema* possibly by more shagreened dorsal skin and more distinct supratympanic fold, by the longest superciliary spine being over the centre of the eye (vs anterior two spines equal in length and posterior-most diminutive).

Generalised morphological description. SVL 21.6–25.8 mm (n = 8); for variation in other measurements, see Table S10. Body rhomboid, head rather triangular. Head wider than long, eyes fairly large, pupils small, round. Snout slightly pointed in dorsal and truncate in lateral view. Canthus rostralis distinct, concave. Loreal region concave, oblique, with no trace of an S-shaped curve posterior to the nostril. Nostril nearer to tip of snout than to eye, slightly protuberant. Tympanum indistinct, round. Supratympanic fold distinct, strongly raised, partly melanised, curving gently from posterior corner of eye over tympanum toward anterior insertion of the forearm. Lateral head similar in colour to dorsal head. Three to four distinct superciliary spines above each eye, the longest over the centre of the eye. Dorsal skin shagreened in most specimens. Ventral skin smooth. Tongue quite narrow, broadening posteriorly, attached anteriorly, posteriorly free, not lobed. Maxillary and vomerine teeth present, vomerine teeth rather straight, without any variation in

height, separated from one another at the midline by a small gap. Choanae oval, placed laterally in the roof of the mouth, slightly melanised.

Forelimbs rather long, slender. Fingers without webbing, relative lengths $1 < 2 < 4 < 3$, second finger distinctly shorter than fourth. Finger tips not expanded, rounded. Finger subarticular tubercles indistinct; inner metacarpal tubercle small, weakly developed, greyish, outer metacarpal/palmar tubercle indistinct, greyish, single. Hind limb slender. Inner metatarsal tubercle present, oblong, greyish, weakly raised. Outer metatarsal tubercle absent. Toes not webbed; toes unreduced, toe lengths $1 < 2 < 5 < 3 < 4$, fifth toe distinctly shorter than third; subarticular tubercles indistinct, grey; toe tips not enlarged, slightly pointed, especially fourth toe.

The base colour is a dark brown across the dorsum and flanks, including the dorsal limbs. The dorsum has several nearly black markings on it in all individuals, but vary in intensity; some individuals have lines that run slightly discontinuously from the suprascapular region toward the inguinal region roughly parallel to one another. No distinct inguinal spots present, no traces of cream-bordered markings present. No distinct colour difference between the lateral and dorsal head. The supratympanic fold is blackish above the tympanum, but otherwise dark brown. The hindlimbs lack distinct crossbands, but a concentration of these blackish markings on the mid-shank gives the impression of a crossband. The posterior thigh is not distinctly coloured. The foot is laterally dark brown, but medially creamy brown. A cream annulus is present before the terminal phalange of each finger and toe. The ventral foot is dark brown, fading to grey along the toes. No distinct colouration around the cloaca. The arms have several blacking markings, including a moderately large marking in the middle of the antebrachium. The dorsal hand is lighter medially than laterally; the ventral hand is light brown. The chin is mottled light brown with tan flecks, fading to completely tan over the sternal region into the immaculate abdomen.

Distribution. Specimens referred to this putative candidate species are from (1) the Pic d'Ivohibe Special Reserve (type locality), and (2) the corridor between Ivohibe and Andringitra. Raxworthy and Nussbaum (1996) recorded specimens probably referable to this species at 1625 m a.s.l. in Andringitra National Park, but also gave it a range from 1240 to 1300 m a.s.l. in the same table; it is not clear which range is correct, but the latter better matches the specimens discussed here. Elevation: ca 1200–1275 m a.s.l.

Natural history. This is a semi-fossorial or detriticolous species found in mid-elevation humid forest. Specimens of this species were caught in pitfall traps and on surveys by Raselimanana (1999). During the day they hide under thick leaf litter or under rotten logs. An individual (UADBA 17422, APR 01677) was found under a rotten log with tadpoles at 16:00 h in primary rain forest on a ridge. Regrettably, both the tadpoles and data pertaining to them have been lost.

Osteology of the *Rhombophryne serratopalpebrosa* species group

Note. The osteology of the *Rhombophryne serratopalpebrosa* species group was treated in detail by Scherz et al. (2017a). Here, we relate only the osteology of *R. sp. 'Ivohibe'* (based on specimen UADBA 17419; Fig. 76) to that description, rather than recounting the full osteology of the species group. The skeleton of UADBA 17419 has small defects in the frontoparietals and the right postchoanal vomer, which may be either fractures or developmental anomalies. The left maxilla is fractured at its anterior end, and the right quadratojugal close to its posterior end.

As noted by Scherz et al. (2017a), the degree of ossification in this species group is substantial. *Rhombophryne sp. 'Ivohibe'* is comparatively well ossified, with the extremities of all of its long limb bones, as well as its carpals and tarsals, ossified.

Dorsal investing bones. The nasals of *R. sp. 'Ivohibe'* are broadly separated from one another, and from the frontoparietals, as is typical for the group (except possibly *R. coronata*). Its frontoparietal does not contact the sphenethmoids anteriorly, and is distinctly separated from the prootics. It lacks a dorsal process, like most species in this group.

Neurocranium. A mineral deposit is present between the sphenethmoids of *R. sp. 'Ivohibe'*, as in several other species in this group. Its sphenethmoid has only a short anterior extension, typical for this group (unlike *R. coronata*). Its exoccipitals are well separated above and below.

Ventral investing and palatal bones. The cultriform process of the parasphenoid of *R. sp. 'Ivohibe'* broadens anteriorly, like in *R. coronata*, *R. guentherpetersi*, *R. regalis*, and *R. diadema*. The prechoanal portion of the vomer lacks rami (i.e., as the state in *R. guentherpetersi*, *R. diadema*, *R. regalis*, and *R. tany*). Vomerine teeth in *R. sp. 'Ivohibe'* are confined to a narrow patch either side of the midline, giving it perhaps the smallest set of vomerine teeth in the group. Its postchoanal vomer lacks obvious anterior projections, similar to *R. diadema*, *R. coronata*, *R. guentherpetersi*, *R. regalis*, and *R. tany*.

Maxillary arcade. The maxillary arcade of *R. sp. 'Ivohibe'* conforms perfectly with other members of the group.

Suspensorium. The articulation between the quadratojugal and the squamosal is narrow in *R. sp. 'Ivohibe'*, like *R. ornata*, *R. serratopalpebrosa*, *R. tany*, and *R. vaventy*. The anterior edge of the squamosal is smoothly, but weakly, sigmoidal, as in *R. vaventy*, *R. tany*, and *R. regalis*.

Mandible. The dentary of *R. sp. 'Ivohibe'* is poorly ossified. The coronoid process of its angulosplenial is strongly raised, as is typical for the group.

Pectoral girdle. The pectoral girdle of *R. sp. 'Ivohibe'* conforms with the rest of the group except for *R. guentherpetersi*. The crista ventralis of the humerus is rather short in *R. sp. 'Ivohibe'*, like in *R. diadema*, *R. coronata*, and *R. regalis*. The manus of *R. sp. 'Ivohibe'* appears to lack an ossified prepollex.

Vertebral column. The vertebrae of *R. sp. 'Ivohibe'* conform with the typical pattern for this species group except for *R. guentherpetersi*. The sacral diapophyses have straight edges perpendicular to the longitudinal axis of the body, as in most species in this group. The dorsal ridge of the urostyle in *R. sp. 'Ivohibe'* extends over half its length, i.e., like *R. diadema*, *R. ornata*, *R. coronata*, *R. tany*, and *R. vaventy*.

Pelvic girdle. The dorsal prominence of *R. sp. 'Ivohibe'* is pronounced, i.e., like *R. guentherpetersi*, *R. regalis*, *R. serratopalpebrosa*, and *R. tany*. The pubis of *R. sp. 'Ivohibe'* is unossified. It seems to lack a prehallux.

Specimens of uncertain affinity

MRSN A2600 (FN 7559). An adult male, collected on 24 November 1998 at Beanjada 'Camp 2' (15.267°S, 49.983°E, ca 1000 m a.s.l.), Masoala Peninsula, Analanjirofo Region, northeastern Madagascar, by F. Andreone and J.E. Randrianirina. For morphometric measurements, see Table S11. This specimen was originally identified as a member of *R. kotrobaratra*, but it does not conform morphologically with that species, being stockier, having a burnt-umber chin, very dark dorsal colouration without dorsal chevrons, reticulation on the posterior thigh, and a faint outer metatarsal tubercle. Morphologically it seems to resemble *R. quentini sp. nov.* most closely, but its outer metatarsal tubercle is less distinct, and it lacks inguinal spots. Its identity will require clarification with more specimens from the area and genetic data.

UADBA-A 61731 (ZCMV 11320). An unsexed specimen without collection data. For morphometric measurements, see Table S11. This specimen is assignable to the *R. mangabensis* species complex (*R. testudo* species group) based on its small size, colouration, and morphology. The lack of collection locality means that it cannot be further assessed at present.

UADBA 18260 (APR 04377), and UADBA 18261 (APR 04417). Specimens collected at high elevation in Marojejy National Park (14.4344°S, 49.7347°E, 1550 m a.s.l.) by A.P. Raselimanana; and also UADBA 08186 (NR 383) with unclear precise locality. For morphometric measurements, see Table S11. These specimens are possibly referable to *Rhombophryne vaventy*, but we here refrain from formally doing so because they have fewer superciliary spines and smoother dorsal skin. Genetic data are needed from these specimens to confirm their identity.

UADBA 14173 (APR 00599). A small specimen (17.4 mm) collected at intermediate elevation in Marojejy National Park (14.4183°S, 49.6014°E, 810 m a.s.l.), by A.P. Raselimanana, may be a juvenile of *R. vaventy* based on its numerous superciliary spines, absence of S-shaped postnasal fold, rugose dorsum, and hand and foot morphology. For morphometric measurements, see Table S11.

THC 305. An unsexed specimen, collected near Marojejy by T.R. Fulgence. This specimen has been sequenced for 16S3' (GenBank: MZ019244), but could not be included in our molecular phylogenetic analyses and species delimitation. It was identified as an unconfirmed candidate species by Carné and Vieites (2024), '*R. sp. alluaudi*' and 'UCS "Marojejy"'). It differs from the closely related *R. sonaliae* **sp. nov.** and other members of the *R. laevipes* group by a deletion of nine bases, AAGCGAGGA, as well as several single nucleotide mutations, and thus may well constitute a distinct species. We have not been

able to examine the specimen morphologically to assess its distinctness.

***Rhombophryne* sp. 'Ambohitantely'.** An uncollected individual observed in February 2023 by L. de Beer in Ambohitantely National Park (ca 18.173°S, 47.278°E), Analamanga Region, central Madagascar (Fig. 77). Morphologically, this specimen conforms well with the *R. laevipes* species group, but its assignment to a species is not clear: it lacks the dorsolateral stripes of *R. anatalia* **sp. nov.** and *R. sonaliae* **sp. nov.**; the chevrons and rough skin of *R. kotrobaratra*; and has white spots on the hidden portions of the hindlimb (Fig. 77C) unlike *R. botabota*. It is thus most similar to *R. laevipes* and *R. nilevina*. Of these, it is biogeographically closest to the range of *R. nilevina*, but it also appears to differ from that species in lacking a dark colour border between the eyes and the light area anterior to this (compare Fig. 39), and the venter is much lighter. Voucher specimens from this population are needed to verify its taxonomic status.

Key to the genus *Rhombophryne*

Here we present a key to adult individuals of the genus *Rhombophryne* that should be useable under field conditions. It focuses on morphological and colour-pattern features, proportions, and, in a few instances, advertisement-call features. It will not be possible in all cases to identify species of *Rhombophryne* based on in-situ photos alone. Notably, important diagnostic features on the thighs and inguinal region are often hidden in frogs that are sitting normally. For proper identification, photos would be needed that show the inguinal region and posterior thigh clearly.

1a	Adult SVL > 13 mm	2
1b	Adult SVL < 13 mm	<i>R. proportionalis</i>
2a	Superciliary spines absent.....	3
2b	Superciliary spines present	20
3a	Orange or yellow colouration on ventral, anterior, and/or posterior thighs present	4
3b	Orange or yellow colouration on ventral, anterior, and/or posterior thighs absent	8
4a	Blackish inguinal eye-spots often bordered with white present	5
4b	Blackish inguinal eye-spots absent	6
5a	Outer metatarsal tubercle distinct	<i>R. quentini</i> sp. nov.
5b	Outer metatarsal tubercle absent or indistinct.....	<i>R. ellae</i>
6a	Long hindlimbs (HIL/SVL > 1.70).....	<i>R. kotrobaratra</i> sp. nov.
6b	Short hindlimbs (HIL/SVL < 1.70).....	7
7a	Black spot present on supratympanic fold, SVL < 25 mm, outer metatarsal tubercle indistinct.....	<i>R. mavokely</i> sp. nov.
7b	Black spot absent on supratympanic fold, SVL > 25 mm, outer metatarsal tubercle distinct	<i>R. kilonjy</i> sp. nov.
8a	Light-brown dorsolateral bands from eyes towards inguinal region present.....	9
8b	Light-brown dorsolateral bands from eyes towards inguinal region absent	10
9a	Third toe much longer than joint between first and second metatarsal of fourth toe.....	<i>R. anatalia</i> sp. nov.
9b	Third toe hardly exceeds joint between first and second metatarsal of fourth toe.....	<i>R. sonaliae</i> sp. nov.
10a	Skin rough, head extremely broad, body round and robust	11
10b	Skin smooth or granular.....	14
11a	SVL > 30 mm.....	12
11b	SVL < 30 mm.....	13
12a	Chin barbels present.....	<i>R. testudo</i>
12b	Chin barbels absent.....	<i>R. matavy</i>
13a	Several chin barbels present, ED/HL 0.25–0.27, second finger at least slightly longer than the fourth	<i>R. maraorao</i> sp. nov.
13b	Few chin barbels present, ED/HL 0.29–0.31, second finger equal to fourth	<i>R. coudreaui</i>
14a	Habitus gracile, FARL/SVL ≥ 0.50.....	15
14b	Habitus plump, FARL/SVL < 0.50	16

15a	SVL < 22 mm, TIBL/SVL $\leq$ 0.49, dark colouration in supratympanic region absent.....	<i>R. minuta</i>
15b	SVL > 23 mm, TIBL/SVL $\geq$ 0.49, dark colouration in supratympanic region present	<i>R. longicrus</i>
16a	SVL < 24 mm.....	17
16b	SVL > 24 mm.....	18
17a	Weak diastema in vomerine teeth, TIBL/SVL > 0.43, inguinal spots absent, advertisement call duration 180–237 ms, dominant frequency 3300–3550 Hz	<i>R. mangabensis</i>
17b	Strong diastema in vomerine teeth, TIBL/SVL < 0.43, inguinal spots occasionally present, advertisement call duration 121–142 ms, dominant frequency 4144–4210 Hz.....	<i>R. savaka</i>
18a	SVL > 40 mm, white spots in inguinal region present or absent. Advertisement call pulsed, duration >208 ms, dominant frequency <700 Hz	19
18b	SVL < 35 mm, white spots in inguinal region absent. Advertisement call tonal, duration 161–201 ms, inter-call interval 2.5–2.7 s, dominant frequency 1256–1291 Hz.....	<i>R. botabota</i>
19a	Always with white or yellow spots in inguinal region and/or on the anterior, ventral, posterior thigh, and ventral shank. Advertisement call duration 208–254 ms, inter-call interval 1.5–2.2 s, dominant frequency 612–631 Hz. .	<i>R. laevipes</i>
19b	Often without white spots in inguinal region and/or on the anterior, ventral, posterior thigh, and ventral shank. Advertisement call duration 526–534 ms, inter-call interval 42–126 s, dominant frequency 526–534 Hz	<i>R. nilevina</i>
20a	S-curved skin fold posterior to nostril present.....	21
20b	S-curved skin fold posterior to nostril absent	22
21a	SVL > 28 mm, FARL/SVL > 0.52, four superciliary spines	<i>R. serratopalpebrosa</i>
21b	SVL < 28 mm, FARL/SVL < 0.52, three superciliary spines	<i>R. regalis</i>
22a	Tibial gland absent	23
22b	Tibial gland present.....	<i>R. guentherpetersi</i>
23a	Reddish colour absent on hindlimbs	24
23b	Reddish colour present on hindlimbs	<i>R. ornata</i>
24a	SVL < 45 mm.....	25
24b	SVL > 45 mm.....	<i>R. vaventy</i>
25a	2 superciliary spines.....	<i>R. tany</i>
25b	3 superciliary spines.....	26
26a	Anterior two superciliary spines much larger than third, TDH/ED $\geq$ 0.59, TIBL/SVL > 0.4	<i>R. diadema</i>
26b	All three superciliary spines equal in size, TDH/ED $\leq$ 0.59, TIBL/SVL < 0.4	<i>R. coronata</i>

Proposed revised conservation assessment of *Rhombophryne*

Based on the extensive revision of the taxonomy, natural history, and distribution knowledge of the specimens discussed herein, a comprehensive re-assessment of their conservation status is warranted and presented in Appendix 2. At present, 15 of the now 27 species of *Rhombophryne* have been assessed (<https://www.iucnredlist.org>), with 80% being Threatened (12 threatened: 1 CR, 10 EN,

1 VU; three non-threatened: 1 NT, 2 LC). Our proposed reassessment of all 27 species would bring this to 88.9% (24 threatened: 2 CR, 16 EN, 6 VU; 2 non-threatened: 0 NT, 2 LC; 1 DD). No change in status assessment is due to a genuine decline or improvement; all are based on new data. It is worth stressing, however, that in most cases we have erred towards conservative assessment proposals; strict interpretation of Criterion B of the IUCN Guidelines (IUCN 2012) would leave all of the species that we propose as VU, as EN instead, because they have

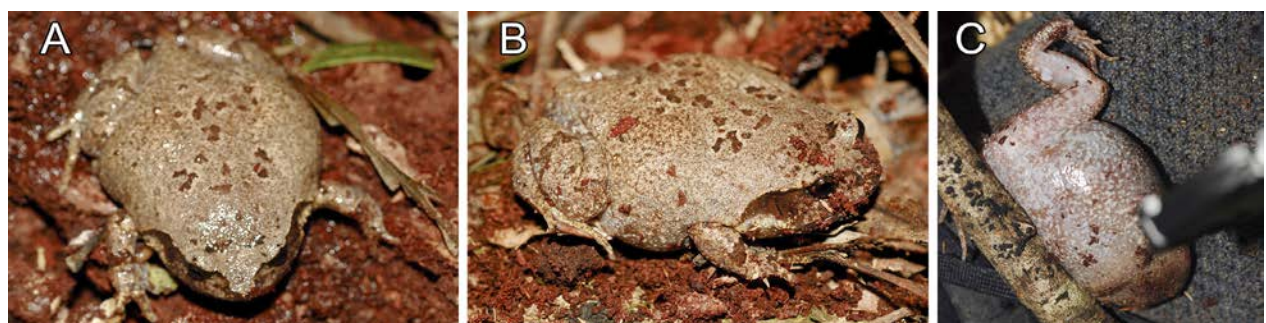


Figure 77. *Rhombophryne* sp. from Ambohitantely Special Reserve in **A** anterodorsal, **B** dorsolateral, and **C** ventral view. This is the only known record of a *Rhombophryne* from this forest. This individual was not collected or sampled, and no specimens exist in collections, to our knowledge. Photographs by Len de Beer. Used with permission.

extent of occurrence estimates <5000 km² and are found at five or fewer threat-defined locations.

Discussion

Tallying up the taxonomy of *Rhombophryne*

This revision has resulted in recognition of seven new *Rhombophryne* species, bringing the current tally to 27. It is clear from the several candidate species that we have not described in this work—either because of the ambiguity of their species status (*R. sp.* Ca13) or because insufficient numbers of specimens are available (*R. sp.* Ca15, *R. sp.* Ca16)—that the taxonomy of the genus is not yet fully resolved. Moreover, some unsequenced specimens are known to us that are not unambiguously assignable morphologically to any known species, and these, too, signify that there is still more diversity remaining to be described, if only enough material can be assembled. Further fieldwork, especially in key unstudied or understudied areas of the North Central East (e.g., Zahamena, Makira) and North East (e.g., the mountains between Tsaratànana and Anjanaharibe-Sud), will likely yield additional new species.

In the period between 1880 and 2007, new *Rhombophryne* species were described at a rate of roughly one species every 18 years to reach a total of seven species. Since 2007, 20 species have been described, including those named herein; a rate of roughly one every ten months (Fig. 3). Several of the most recently described species are amongst the most distinctive *Rhombophryne* species ever found. We can see three major drivers of the dramatic change in taxonomic progress on the species in this genus. Firstly, fieldwork has intensified in Madagascar since the 1990s, providing access to new material from areas that had previously been unexplored herpetologically. Secondly, genetic data, and especially comprehensive DNA barcoding (Vieites et al. 2009) and, more recently, the application of museomics approaches to older voucher specimens, has resulted in an enormous increase in the rate of description among all frogs in Madagascar, not just diamond frogs (Glaw et al. 2022). Thirdly, two additional sets of data have frequently been included in recent *Rhombophryne* publications that were seldom included before 2003: bioacoustic and osteological data. Both of these data types have strong diagnostic potential. Bioacoustic data have been rare but are highly diagnostic among *Rhombophryne* species, as is typical in frogs (Köhler et al. 2017). In this study, we have been able to add call data for several species; call data are now available from 12 of the 27 species. Access to osteological data thanks to affordable micro-CT scanning (Scherz et al. 2014, 2017a) has provided a large suite of morphological data that was not previously accessible without destroying the precious few specimens that are available. The integration of these data with DNA bar-

coding on freshly collected specimens from new areas has been key for identification and description of new species.

Diamond frogs of many shapes, colours, and sizes

With the revelations from genetic data (Andreone et al. 2005; Wollenberg et al. 2008), our understanding of the relationships of *Rhombophryne testudo* were completely transformed—no longer was it a monotypic genus, but it was revealed to have close affinities to a host of other terrestrial frogs, previously variously placed in *Mantipus*, *Mantiphrys*, and *Plethodontohyla*. The division of *Rhombophryne* into species groups (Belluardo et al. 2022) highlights this morphological diversity; contrast the stocky *R. ellae* species group with the long-legged terrestrial species of the *R. laevipes* species groups, the gracile *R. minuta* species group, the miniaturised *R. proportionalis* species group, the gracile to robust *R. serratopalpebrosa* species group, and the rotund *R. testudo* species group. In body length, diamond frogs range by a factor of more than 5, from the smallest adult (*R. proportionalis*) at 11.0, to the largest (*R. vaventy*) at 58.6 mm. The new picture that has emerged reveals a remarkable morphological diversity within the genus that will be interesting to explore with ancestral-state analyses once a more robust phylogenetic or phylogenomic tree becomes available—current instability regarding the deep nodes of the tree makes key relationships, such as those of *R. proportionalis* to the rest of the genus, unclear.

These morphological differences are likely also tied to ecological differences. However, data on *Rhombophryne* ecology are scarce, so we cannot yet infer what the differences in their morphology signify in terms of how they live, with the exception of the specialised burrowers. Although we have previously speculated that long limbs in the *R. minuta* species group may be an adaptation for long-distance leaping or scansorial habits (Scherz et al. 2015a), we currently lack the data to test such hypotheses. This remains a promising avenue for future research, indeed also at the level of the Cophylinae as a whole.

Another noteworthy feature of *Rhombophryne* is that, although they are generally brown frogs, they exhibit a subtle but substantial diversity in colour. Reddish ‘flash markings’ occur quite frequently on the hindlimbs of Malagasy frogs (Glaw et al. 2020). Reddish-orange colouration on the limbs occurs in members of four species groups of *Rhombophryne*: *R. ellae* species group (*R. ellae*, *R. quentini* **sp. nov.**, and *R. kilonjy* **sp. nov.**), *R. laevipes* species group (*R. kotrobaratra*), *R. testudo* species group (*R. mavokely* **sp. nov.**), and *R. serratopalpebrosa* species group (*R. ornata*). Based on their position in the phylogeny, the presence of this colouration in each species group likely represents an independent origin of the trait. Studies on its histological/chemical/genomic basis should be carried out to understand if this is achieved via a shared evolutionary pathway or differently each time.

Limb and inguinal spots also show up on *Rhombophryne* in several different ways: in the *R. laevipes* species group, as large white spots on the inguinal region, thigh, and ventral shank; in the *R. ellae* group as inguinal eye-spots (ocelli), with a black centre surrounded by a white or cream border; in various other species as simple brown or black oblongs in the inguinal region. Such spots are common occurrences in frogs and have a presumed anti-predatory function as false eyes (Hernández-Palma et al. 2023). However, it seems that, in diamond frogs—and in cophylines as a whole—there is no ‘one-size-fits-all’ solution, but rather, like for the other traits already discussed, a diversity of solutions that have been found to produce these kinds of markings. This is fortunate for the taxonomist and the field observer, as these have proved to be important diagnostic features, at least at the species-group level.

Future evolutionary work, based on a dated and better-resolved phylogeny than any currently available, will shed more light on these and other interesting facets of diamond frog evolution.

Biogeography of *Rhombophryne* — more like lace than tapestry

The distribution of *Rhombophryne* species across Madagascar is reminiscent of some other frog genera, such as *Gephyromantis*, with a concentration of diversity in northern and northeastern Madagascar, and representatives spread along the island’s eastern rainforest belt. A particular hotspot of diversity is Marojejy National Park. This 558.85 km² protected area has 11 of the 27 *Rhombophryne* species. Although a few of these species appear to be micro-endemic to the Marojejy Massif (*R. minuta*, *R. serratopalpebrosa*, and possibly *R. savaka*), several are also found in Sorata, Ambolokopatrika-Betaolana, Anjanaharibe-Sud, and other geographically connected, rainforest-clad massifs. In contrast, the Tsaratànana Massif has fewer species, but most are so far only known from this location. We hypothesise that this apparent pattern is rather due to poor exploration of the surrounding massifs, than any kind of topographical or biogeographic isolation, however.

Rhombophryne sp. ‘Ivohibe’ defines the southernmost extent of the genus, over 100 km farther south than the next-most-southern species, *R. nilevina* in Ranomafana National Park. We consider it possible that further fieldwork in poorly sampled areas like Midongy du Sud could yield further new species or range extensions. But overall, the genus is mostly restricted to the east, northeast, and north of the island, in contrast to, e.g., *Stumpffia* and *Plethodontohyla*, both of which range to the far southeast of Madagascar.

One surprising result emerging from the improved taxonomic coverage of this genus is the appearance of several truly widespread species. *Rhombophryne sonaliae* sp. nov. and *R. nilevina* cover enormous distributions; the former stretches from Andasibe in the North Central East to Tsararano in the northeast, and the lat-

ter stretches from Ranomafana in the South Central East to Tsaratànana in the north. The discovery of disparate specimens of such species highlights how incomplete our understanding of the distribution of the herpetofauna of Madagascar remains; similar revelations have recently emerged from *Anilany* (Petzold et al. 2025), *Boophis* (Vences et al. 2011), and *Wakea* (Carné et al. 2025). Previous conclusions that microendemism is widespread in Malagasy amphibians (Wollenberg et al. 2011; Brown et al. 2016)—especially cophyline microhylids (Wollenberg et al. 2008)—may be due to incompleteness of sampling. Only further fieldwork, especially in poorly sampled areas, will bring further clarity to this picture.

Collecting diamond frogs and natural history data about them

Given that *Rhombophryne* are not easy to find, it is remarkable that only two of the 27 species so far described are singleton specimens (*R. tany* and *R. kilonjy*). All other species have had at least one further specimen collected, either as part of their type series, or subsequently—here we have documented the second known specimens for *R. ellae* and *R. serratopalpebrosa*. Given that the number of available specimens of all species, is, on the whole, very small, additional material would be highly valuable.

Targeting fieldwork to collect *Rhombophryne* specimens requires specific attention to these rather secretive frogs. Particular attention must be paid to the season, as most species are most active and calling in the rainy season. The calls, especially of the larger species, carry over substantial distances, and in order to find the calling individual (key for a match of the call recording to the specimen), a substantial investment of time must be made. It can frequently be necessary to cross several hundred metres of dense forest. Most species call from concealed positions within the leaf litter, and some even in burrows (Lambert et al. 2017). This means that even once a calling individual has been narrowed down to within an area of ca 1 m², it can still take considerable time to find and catch it. However, in our experience, this is well-invested time and has yielded very valuable data on several species in the present work.

Three further methods have been successfully applied by us for the collection of *Rhombophryne* specimens. Firstly, active searching. Covering ground on foot, especially during or after rain, increases the chance of finding and catching *Rhombophryne* active on the forest floor. We have observed several species active this way, both at night and by day. Secondly, leaf-litter quadrats. Specifically, we have had good success finding *R. botabota* on the Marojejy Massif along natural rises where leaf-litter is dense, by simply scooping leaf litter into rice bags, and sorting it by hand. Often the act of scooping the leaf litter has already cause the frogs to leap away, at which point they can be captured. Finally, and perhaps most importantly, pitfall traps are an effective, if effort-intensive, method of collecting *Rhombophryne*. Notably, *R. quentini* sp. nov. was one of the most commonly collected

specimens in pitfall traps in Tsaratànana (Andreone et al. 2009). Unfortunately, this is not always successful, however; pitfall traps we set in Montagne d'Ambre in 2017 and 2018, as well as in Torotorofotsy in 2026, failed to capture any *Rhombophryne*. Nevertheless, this method is worthwhile for the other taxa that fall into the traps and should be included in all surveys.

Specimens alone are not the only thing that is needed for *Rhombophryne*. There are still major gaps in our knowledge of their ecology. No *Rhombophryne* egg or tadpole has ever been described, except a burrow full of *R. testudo* froglets (Köhler et al. 1997); the clutch of tadpoles found in association with a specimen of *R. sp.* 'Ivohibe' has not been located for study and may not have been collected. It is thus unclear if these are species that lay eggs in a jelly or foam nest that develop into nidicolous, endotrophic tadpoles, like in the rest of Cophylinae (Scherz et al. 2022b), or have some other reproductive mode, such as direct development. Courtship other than advertisement calls is totally unknown, as is whether or not the species are territorial. In terms of diet, only minimal data are available from a handful of specimens that we have dissected or micro-CT scanned.

Some of these gaps in our knowledge of diamond frog natural history could be addressed comparatively easily, for instance by more thorough investigation of existing museum specimens (dietary data), if permission can be obtained from museum curators to perform the necessary dissections; although we have recorded hard-bodied prey from micro-CT scans, dissections are still necessary to obtain insights into gut contents. The behavioural data, however—especially pertaining to reproductive mode—would best be fulfilled by captive-breeding projects, like those in place by Association Mitsinjo in eastern Madagascar (Edmonds et al. 2012; Rakotoarisoa et al. 2025). These have already had success with other Cophylinae, and we encourage future endeavours to keep and breed *Rhombophryne* species in captivity as well. In-situ observations of any such behaviours would be highly desirable, but such observations cannot easily be planned.

Are diamonds forever? Conservation outlook for *Rhombophryne*

Based on our summary of the conservation status of *Rhombophryne* species given above, it is evident that the overall conservation outlook for the genus is poor. 24 out of 27 species are listed or are proposed to be assessed as threatened, and one that is not remains Data Deficient, so may in truth be threatened as well. Only two species, *R. nilevina* and *R. sonaliae*, are suggested to be Least Concern due to their large distributions. However, as we have highlighted above, our knowledge of these frogs is still highly fragmentary. The past decade of work has yielded numerous range extensions, and consequently it is likely that ranges will continue to be expanded in the years to come. This may bring some currently Endangered species into the Vulnerable category, but it is not likely to bring many out of the threatened categories.

The greatest threat posed to these largely terrestrial frogs that are restricted to tropical or montane forests is loss of habitat. Species at low elevation are at the greatest risk, because they are closest to anthropogenic influence; *R. mavokely* **sp. nov.**, at the base of the Marojejy Massif, is at far greater risk due to logging and fire at the forest edge than is *R. minuta* sitting over 1500 m a.s.l. on the same massif. Fire is of significant concern, especially where people live near protected-area boundaries, because 'fires in Madagascar are overwhelmingly started by humans' (Frappier-Brinton and Lehman 2022), especially for slash-and-burn agriculture (tavy in Malagasy). Increasing drought in Madagascar (Gouveia et al. 2024) may favour fires. Rainforests in Madagascar burn exceptionally extensively (Joseph et al. 2024) and fire contributes to forest degradation and is becoming more frequent (Frappier-Brinton and Lehman 2022; Joseph et al. 2024; Ralimanana et al. 2022). Although landscape-scale fires (i.e., fires ≥ 21 ha in scale) in Madagascar are not thought to be a driver of forest loss (Phelps et al. 2022), small-scale fires, especially those made for tavy, are (Ralimanana et al. 2022).

Two species of *Rhombophryne* are proposed to be Critically Endangered: *R. kilonjy* **sp. nov.** and *R. matavy*. *Rhombophryne kilonjy* **sp. nov.** is known from a handful of specimens collected on the Sahamalaza Peninsula, which has highly fragmented forest and hosts a rather high level of micro-endemism (Andreone et al. 2001; Penny et al. 2014, 2016, 2017). *Rhombophryne matavy* is known only from low-elevation forest in Montagne d'Ambre National Park. In both cases, elevation is a significant factor in increasing their risk. On Montagne d'Ambre, there is ongoing illegal logging in the lower regions of the park (D'Cruze et al. 2008, 2010; our own pers. obs.). The resilience of these frogs to such habitat disturbance is unknown. The ability to manage them more actively, however, is limited by the total lack of knowledge on their ecology. Understanding their reproductive reproduction and natural history would be greatly beneficial for possible conservation efforts targeting these and other taxa.

Acknowledgements

This project is the cumulation of at least two dozen field campaigns carried out between 1991 and 2019. These campaigns were supported by dozens of grants by different funding bodies, too numerous to list. We are immensely grateful to all of the individuals who have provided us assistance in the field over the last 30 years, who are likewise too numerous to list here. Fieldwork was made possible by research and collection permissions issued by the Direction Générale des Forêts of Madagascar, to whom we are greatly indebted. All fieldwork was carried out in the framework of collaborations with the Department of Zoology and Animal Biology of the University of Antananarivo and with Parc Botanique et Zoologique de Tsimbazaza. The work of MDS and AP was supported by Deutsche Forschungsgemeinschaft grant SCHE 2181/1-1 of the SPP 1991 TaxonOMICS priority programme, and ERC Starting Grant 101162288 to MDS. The work of AC and FB was supported by Portuguese National Funds from FCT (Fundação para a Ciência e a Tecnologia) through the contract to AC [2020.00823.CEECIND/CP1601/

CT0003] and the doctoral fellowship to FB [PD/BD/128493/2017]. We thank the following individuals for providing photos: É. Matthieu, S. Zozaya, L. de Beer. F. Tillack and M.-O. Rödel provided access to specimens at the Museum für Naturkunde, Berlin. A. Ohler provided access to specimens from the Muséum National d'Histoire Naturelle, Paris.

References

- Andreone F (2003) Distribution record. *Plethodontohyla coudreaui*. Herpetological Review 34: 259.
- Andreone F, Glaw F, Mattioli F, Jesu R, Schimmenti G, Randrianirina JE, Vences M (2009) The peculiar herpetofauna of some Tsaratanana rainforests and its affinities with Manongarivo and other massifs and forests of northern Madagascar. Italian Journal of Zoology 76: 92–110. <https://doi.org/10.1080/11250000802088603>
- Andreone F, Glaw F, Nussbaum RA, Raxworthy CJ, Vences M, Randrianirina JE (2003) The amphibians and reptiles of Nosy Be (NW Madagascar) and nearby islands: A case study of diversity and conservation of an insular fauna. Journal of Natural History 37: 2119–2149. <https://doi.org/10.1080/00222930210130357>
- Andreone F, Randrianirina JE (2008) An unexpected *Rhombophryne* record at Tsingy de Bemaraha confirms the presence of cophyline frogs in western Madagascar. Zootaxa 1812: 46–48.
- Andreone F, Randrianirina JE, Jenkins PD, Aprea G (2000) Species diversity of Amphibia, Reptilia and Lipotyphla (Mammalia) at Ambolokopatrika, a rainforest between the Anjanaharibe-Sud and Marojeje massifs, NE Madagascar. Biodiversity and Conservation 9: 1587–1622.
- Andreone F, Vences M, Randrianirina JE (2001) Patterns of amphibian and reptile diversity at Berara Forest (Sahamalaza Peninsula), NW Madagascar. Italian Journal of Zoology 68: 235–241. <https://doi.org/10.1080/11250000109356414>
- Andreone F, Vences M, Vieites DR, Glaw F, Meyer A (2005) Recurrent ecological adaptations revealed through a molecular analysis of the secretive cophyline frogs of Madagascar. Molecular Phylogenetics and Evolution 34: 315–322. <https://doi.org/10.1016/j.ympev.2004.10.013>
- Andrianarimisa A, Andrianjakarivelo V, Rakotomalala Z, Anjerinaina M (2009) Vertébrés terrestres des fragments forestiers de la Montagne d'Ambatotsirongorongo, site dans le Système des Aires Protégées de Madagascar de la Région Anosy, Tolagnaro. Malagasy Nature 2: 30–51.
- Angel F (1938) Description d'un Amphibien nouveau, de Madagascar, appartenant au genre *Plethodontohyla*. Bulletin du Muséum National d'Histoire Naturelle (2e Série) 10: 260–261.
- Antonelli A, Smith RJ, Perrigo AL, Crottini A, Hackel J, Testo W, Farooq H, Torres Jiménez MF, Andela N, Andermann T, Andriamanohera AM, Andriambololonera S, Bachman SP, Bacon CD, Baker WJ, Belluardo F, Birkinshaw C, Borrell JS, Cable S, Canales NA, Carrillo JD, Clegg R, Clubbe C, Cooke RSC, Damasco G, Dhand S, Edler D, Faurby S, de Lima Ferreira P, Fisher BL, Forest F, Gardiner LM, Goodman SM, Grace OM, Guedes TB, Henniges MC, Hill R, Lehmann CER, Lowry PP, Marline L, Matos-Maraví P, Moat J, Neves B, Nogueira MGC, Onstein RE, Papadopoulos AST, Perez-Escobar OA, Phelps LN, Phillipson PB, Pironon S, Przelomska NAS, Rabarimanarivo M, Rabehevitra D, Raharimampionona J, Rajaonah MT, Rajaonary F, Rajaovelona LR, Rakotoarivino M, Rakotoarisoa AA, Rakotoarisoa SE, Rakotomalala HN, Rakotonasolo F, Ralaivelarisoa BA, Ramirez-Herranz M, Randriamamonjy JEN, Randriamboavonjy T, Randrianasolo V, Rasolohery A, Ratsifandrihamanana AN, Ravololomanana N, Razafiniary V, Razanajato H, Razanatoa E, Rivers M, Sayol F, Silvestro D, Vorontsova MS, Walker K, Walker BE, Wilkin P, Williams J, Ziegler T, Zizka A, Ralimanana H (2022) Madagascar's extraordinary biodiversity: Evolution, distribution, and use. Science 378: eabf0869. <https://doi.org/10.1126/science.abf0869>
- Aprea G, Odierna G, Andreone F, Glaw F, Vences M (2007) Karyological evolution and systematics of Malagasy microhylid frogs. Zoologischer Anzeiger 246: 23–41. <https://doi.org/10.1016/j.jcz.2006.10.001>
- Barbour T, Loveridge A (1929) Typical reptiles and amphibians in the Museum of Comparative Zoölogy. Bulletin of the Museum of Comparative Zoology 69: 205–360.
- Bauer AM, Günther R, Robeck HE (1996) An annotated type catalogue of the hemisotid, microhylid, myobatrachid, pelobatid and pipid frogs in the Zoological Museum, Berlin. Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe 72: 259–275. <https://doi.org/10.1002/mmnz.19960720205>
- Bellati A, Scherz MD, Megson S, Hyde Roberts S, Andreone F, Rosa GM, Noël J, Randrianirina JE, Fasola M, Glaw F, Crottini A (2018) Resurrection and re-description of *Plethodontohyla laevis* (Boettger, 1913) and transfer of *Rhombophryne alluaudi* (Mocquard, 1901) to the genus *Plethodontohyla* (Microhylidae: Cophylinae). Zoosystematics and Evolution 94: 109–135. <https://doi.org/10.3897/zse.94.14698>
- Belluardo F, Scherz MD, Santos B, Andreone F, Antonelli A, Glaw F, Muñoz-Pajares J, Randrianirina JE, Raselimanana AP, Vences M, Crottini A (2022) Molecular taxonomic identification and species-level phylogeny of the narrow-mouthed frogs of the genus *Rhombophryne* (Anura: Microhylidae: Cophylinae) from Madagascar. Systematics and Biodiversity 20: 1–13. <https://doi.org/10.1080/14772000.2022.2039320>
- Blommers-Schlösser RMA (1975) Observations on the larval development of some Malagasy frogs, with notes on their ecology and biology (Anura: Dyscophinae, Scaphiophryninae, and Cophylinae). Beaufortia 24: 7–26.
- Blommers-Schlösser RMA (1976) Chromosomal analysis of twelve species of Microhylidae (Anura) from Madagascar. Genetica 46: 199–210.
- Blommers-Schlösser RMA, Blanc CP (1991) Amphibiens (première partie). Faune de Madagascar 75: 1–397.
- Boettger O (1880a) Diagnoses Batrachiorum novorum insulae Madagascar. Zoologischer Anzeiger 3: 567–568.
- Boettger O (1880b) Diagnoses reptilium et batrachiorum novorum a Carolo Ebenau in insula Nossi-Bé madagascariensi lectorum. Zoologischer Anzeiger 3: 279–283.
- Boettger O (1881) Diagnoses reptilium et batrachiorum novorum ab ill. Antonio Stumpff in insula Nossi-Bé Madagascariensi lectorum. Zoologischer Anzeiger 4: 358–362.
- Boulenger GA (1882) Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. Second Edition. Taylor and Francis, London, 503 pp. <https://doi.org/10.5962/bhl.title.20903>
- Brown JL, Sillero N, Glaw F, Bora P, Vieites DR, Vences M (2016) Spatial biodiversity patterns of Madagascar's amphibians and reptiles. PLoS One 11: e0144076. <https://doi.org/10.1371/journal.pone.0144076>
- Bruford MW, Hanotte O, Brookefield JFY, Burke T (1992) Single-locus and multilocus DNA fingerprint. In: Hoelzel AR (Ed.) Molecular Genetic Analysis of Populations: A Practical Approach. IRL Press, Oxford, 225–270.

- Carné A, Vieites DR (2024) A race against extinction: The challenge to overcome the Linnean amphibian shortfall in tropical biodiversity hotspots. *Diversity and Distributions* 30: e13912. <https://doi.org/10.1111/ddi.13912>
- Carné A, Vieites DR, Ferrer X, Moreno M, ponz-Segrelles G, Rahagalala TNAA, Rakotomanga SE, Laca AR, Ratsoavina FM, van den Burg MP (2025) Microendemism in Madagascar: Small ranges or sampling gaps? The case of the frog *Wakea madinika*. *Salamandra* 61: 160–170.
- Clement M, Posada DC, Crandall KA (2000) TCS: A computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659.
- D'Cruze N, Köhler J, Franzen M, Glaw F (2008) A conservation assessment of the amphibians and reptiles of the Forêt d'Ambre Special Reserve, north Madagascar. *Madagascar Conservation & Development* 3: 44–54.
- D'Cruze N, Köhler J, Vences M, Glaw F (2010) A new fat fossorial frog (Microhylidae: Cophylinae: *Rhombophryne*) from the rainforest of the Forêt d'Ambre Special Reserve, northern Madagascar. *Herpetologica* 66: 182–191. <https://doi.org/10.1655/09-008r1.1>
- Dabney J, Knapp M, Glock I, Gansauge M, Weihmann A, Nickel B, Valdiosera C, García N, Pääbo S, Arsuag J, Meyer M (2013) Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proceedings of the National Academy of Sciences of the USA* 110: 15758–15763.
- de Queiroz K (1998) The General Lineage Concept of species, species criteria, and the process of speciation. In: Howard DJ, Berlocher SH (Eds) *Endless Forms: Species and Speciation*. Oxford University Press, Oxford, 57–75.
- deQueirozK (2007) Species concepts and species delimitation. *Systematic Biology* 56: 879–886. <https://doi.org/10.1080/10635150701701083>
- Edmonds D, Rakotoarisoa JC, Dolch R, Pramuk J, Gagliardo R, Andreone F, Rabibisoa N, Rabemananjara F, Rabesihanaka S, Robsomani-trandrasana E (2012) Building capacity to implement conservation breeding programs for frogs in Madagascar: Results from year one of Mitsinjo's amphibian husbandry research and captive breeding facility. *Amphibian & Reptile Conservation* 5: 57–69
- Eudeline R, Wang C, Scherz MD (2015) Predation attempt of *Rhombophryne laevipes* by *Compsophis albiventris*. *Herpetology Notes* 8: 393–394.
- Fedosov A, Achaz G, Gontchar A, Puillandre N (2022) mold, a novel software to compile accurate and reliable DNA diagnoses for taxonomic descriptions. *Molecular Ecology Resources* 22: 2038–2053. <https://doi.org/10.1111/1755-0998.13590>
- Fouquet A, Gilles A, Vences M, Marty C, Blanc M, Gemmell NJ (2007) Underestimation of species richness in neotropical frogs revealed by mtDNA analyses. *PLoS One* 2: e1109. <https://doi.org/10.1371/journal.pone.0001109>
- Frappier-Brinton T, Lehman SM (2022) The burning island: Spatiotemporal patterns of fire occurrence in Madagascar. *PLoS One* 17: e0263313. <https://doi.org/10.1371/journal.pone.0263313>
- Frost DR (2026) Amphibian Species of the World: An Online Reference. Version 6.2 Electronic Database accessible at <https://amphibiansoftheworld.amnh.org/>. American Museum of Natural History, New York, NY [accessed 26 June 2026].
- Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1–370. [https://doi.org/10.1206/0003-0090\(2006\)297\[0001:TA-TOL\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2006)297[0001:TA-TOL]2.0.CO;2)
- Fulton TL, Shapiro B (2019) Setting up an ancient DNA laboratory. In: Shapiro B, Barlow A, Heintzman PD, Hofreiter M, Pajmians JLA, Soares AER (Eds) *Ancient DNA: Methods and Protocols*. Springer New York, New York, NY, 1–13. https://doi.org/10.1007/978-1-4939-9176-1_1
- Gansauge M-T, Gerber T, Glocke I, Korlević P, Lippik L, Nagel S, Riehl LM, Schmidt A, Meyer M (2017) Single-stranded DNA library preparation from highly degraded DNA using T4 DNA ligase. *Nucleic Acids Research* 45: e79. <https://doi.org/10.1093/nar/gkx033>
- Garg S, Biju SD (2019) New microhylid frog genus from Peninsular India with Southeast Asian affinity suggests multiple Cenozoic biotic exchanges between India and Eurasia. *Scientific Reports* 9: 1906. <https://doi.org/10.1038/s41598-018-38133-x>
- Garg S, Senevirathne G, Wijayathilaka N, Phuge S, Deuti K, Manamendra-Arachchi K, Meegaskumbura M, Biju SD (2018) An integrative taxonomic review of the South Asian microhylid genus *Uperodon*. *Zootaxa* 4384: 1–88. <https://doi.org/10.11646/zootaxa.4384.1.1>
- Garg S, Sivaperuman C, Gogulakrishnan G, Chandramouli SR, Biju SD (2022) Hiding in plain sight: Rain water puddles in Nicobar Islands of India reveal abundance of a new frog species of the genus *Microhyla* Tschudi, 1838 (Anura: Microhylidae). *Zoological Studies* 61: 1–23. <https://doi.org/10.6620/ZS.2022.61-02>
- Garg S, Suyesh R, Das A, Jiang J, Wijayathilaka N, Amarasinghe AAT, Alhadi F, Vineeth KK, Aravind NA, Senevirathne G, Meegaskumbura M, Biju SD (2019) Systematic revision of *Microhyla* (Microhylidae) frogs of South Asia: A molecular, morphological, and acoustic assessment. *Vertebrate Zoology* 69: 1–71. <https://doi.org/10.26049/VZ69-1-2019-01>
- Glaw F, Crottini A, Rakotoarison A, Scherz MD, Vences M (2022) Diversity and exploration of the Malagasy amphibian fauna. In: Goodman SM (Ed.) *The New Natural History of Madagascar*. Princeton University Press, Princeton, NJ, 1305–1322.
- Glaw F, Köhler J, de la Riva I, Vieites DR, Vences M (2010a) Integrative taxonomy of Malagasy treefrogs: Combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of *Boophis*. *Zootaxa* 2383: 1–82.
- Glaw F, Köhler J, Vences M (2010b) A new fossorial frog, genus *Rhombophryne*, from Nosy Mangabe Special Reserve, Madagascar. *Zoosystematics and Evolution* 86: 235–243. <https://doi.org/10.1002/zoos.201000006>
- Glaw F, Scherz MD, Rakotoarison A, Crottini A, Raselimanana AP, Andreone F, Köhler J, Vences M (2020) Genetic variability and partial integrative revision of *Platypelis* frogs (Microhylidae) with red flash marks from eastern Madagascar. *Vertebrate Zoology* 70: 141–156. <https://doi.org/10.26049/VZ70-2-2020-04>
- Glaw F, Vences M (1992) A Fieldguide to the Amphibians and Reptiles of Madagascar. Vences & Glaw Verlags GbR, Cologne, 335 pp.
- Glaw F, Vences M (1994) A Fieldguide to the Amphibians and Reptiles of Madagascar. Vences & Glaw Verlags GbR, Cologne, 478 pp.
- Glaw F, Vences M (2002) *Rhombophryne testudo*. Correction of locality record. *Madagascar: Réunion. Herpetological Review* 33: 64.
- Glaw F, Vences M (2007) A Field Guide to the Amphibians and Reptiles of Madagascar. Third Edition. Vences & Glaw Verlags GbR, Cologne, 496 pp.
- Goodman SM, Raherilalao MJ, Wohlhauser S (Eds) (2018) *Les Aires Protégées Terrestres de Madagascar: Leur Histoire, Description et Biote/The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota*. Vol. II: Northern and Eastern Madagascar. Association Vahatra, Antananarivo, 806 pp.

- Gouveia CM, Silva M, Russo A (2024) The severity of dry and hot climate extremes and their related impacts on vegetation in Madagascar. *iScience* 27. <https://doi.org/10.1016/j.isci.2023.108658>
- Guibé J (1946) Sur la validité de *Mantipus laevipes* (Mocq.) (Batraciens-Microhylidae). *Bulletin du Muséum National d'Histoire Naturelle* (2e Série) 18: 50–51.
- Guibé J (1973) Batraciens nouveaux de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle* (3e Série) 171: 1169–1192.
- Guibé J (1975) Batraciens nouveaux de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle* (3e Série) 323: 1081–1089.
- Guibé J (1978) Les batraciens de Madagascar. *Bonner zoologische Monographien* 11: 1–140.
- Günther ACLG (1858) On the systematic arrangement of the tailless batrachians and the structure of *Rhinophrynus dorsalis*. *Proceedings of the Zoological Society of London* 1858: 339–352.
- Hahn EE, Alexander M, Stiller J, Grewe PM, Holleley CE (2024) Hot alkaline lysis gDNA extraction from formalin-fixed archival tissues. *PLoS One* 19: e0296491. <https://doi.org/10.1371/journal.pone.0296491>
- Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hernández-Palma TL, Rueda-Solano LA, Valkonen JK, Rojas B (2023) Predator response to the coloured eyespots and defensive posture of Colombian four-eyed frogs. *Journal of Evolutionary Biology* 36: 1040–1049. <https://doi.org/10.1111/jeb.14193>
- Howes GB, Ridewood W (1888) On the carpus and tarsus of the Anura. *Proceedings of the Zoological Society of London* 1888: 141–182. <https://doi.org/10.1111/j.1469-7998.1888.tb06691.x>
- Hutter CR, Andriampenanana ZF, Razafindraibe J, Rakotoarison A, Scherz MD (2018) New dietary data from *Compsophis* and *Alluaudina* species (Squamata: Lamprophiidae: Pseudoxyrhophiinae), and implications for their dietary complexity and evolution. *Journal of Natural History* 52: 2497–2510. <https://doi.org/10.1080/00222933.2018.1543732>
- Hutter CR, Cobb KA, Portik DM, Travers SL, Wood Jr PL, Brown RM (2021) FrogCap: A modular sequence capture probe-set for phylogenomics and population genetics for all frogs, assessed across multiple phylogenetic scales. *Molecular Ecology Resources* 22: 1100–1119. <https://doi.org/10.1111/1755-0998.13517>
- Hyde Roberts S, Daly C (2014) A rapid herpetofaunal assessment of Nosy Komba Island, northwestern Madagascar, with new locality records for seventeen species. *Salamandra* 50: 18–26.
- IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland and Cambridge, 38 pp.
- IUCN SSC Amphibian Specialist Group (2016a) *Boophis ankarakensis*. IUCN Red List of Threatened Species 2016: e.T68568328A68568331. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T68568328A68568331.en>
- IUCN SSC Amphibian Specialist Group (2016b) *Gephyromantis ambohitra*. IUCN Red List of Threatened Species 2016: e.T57458A84168942. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T57458A84168942.en>
- IUCN SSC Amphibian Specialist Group (2016c) *Rhombophryne coronata*. IUCN Red List of Threatened Species 2016: e.T57969A84180747. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T57969A84180747.en>
- IUCN SSC Amphibian Specialist Group (2016d) *Rhombophryne coudreaui*. IUCN Red List of Threatened Species 2016: e.T57970A84180885. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T57970A84180885.en>
- Joseph GS, Seymour CL, Rakotoarivelo AR (2024) Fire incongruities can explain widespread landscape degradation in Madagascar's forests and grasslands. *Plants, People, Planet* 6: 656–669. <https://doi.org/10.1002/ppp3.10471>
- Kalyaanamoorthy S, Minh BQ, Wong TK, von Haeseler A, Jermini LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587. <https://doi.org/10.1038/nmeth.4285>
- Keefe R, Blackburn DC (2020) Comparative morphology of the humerus in forward-burrowing frogs. *Biological Journal of the Linnean Society* 20: 1–13. <https://doi.org/10.1093/biolinnean/blaa092>
- Klages J, Glaw F, Köhler J, Müller J, Hipsley CA, Vences M (2013) Molecular, morphological and osteological differentiation of a new species of microhylid frog of the genus *Stumpffia* from northwestern Madagascar. *Zootaxa* 3717: 280–300. <https://doi.org/10.11646/zootaxa.3717.2.8>
- Köhler J, Glaw F, Vences M (1997) Notes on the reproduction of *Rhombophryne* (Anura: Microhylidae) at Nosy Be, northern Madagascar. *Revue française d'Aquariologie-Herpetologie* 24: 53–54.
- Köhler J, Jansen M, Rodríguez A, Kok PJR, Toledo LF, Emmrich M, Glaw F, Haddad CFB, Rödel M-O, Vences M (2017) The use of bioacoustics in anuran taxonomy: Theory, terminology, methods and recommendations for best practice. *Zootaxa* 4251: 1–124. <https://doi.org/10.11646/zootaxa.4251.1.1>
- Lambert SM, Hutter CR, Scherz MD (2017) Diamond in the rough: A new species of fossorial diamond frog (*Rhombophryne*) from Ranomafana National Park, southeastern Madagascar. *Zoosystematics and Evolution* 93: 143–155. <https://doi.org/10.3897/zse.93.10188>
- Laurence JD (1987) Rev. Richard Baron's "Compendium des Plantes Malgaches". *Taxon* 36: 39–46. <https://doi.org/10.2307/1221349>
- Laurent RF (1946) Mises au point dans la taxonomie des ranides. *Revue de Zoologie et de Botanique Africaines* 39: 336–338.
- Lê S, Josse J, Husson F (2008) FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software* 25: 1–18. <https://doi.org/10.18637/jss.v025.i01>
- Mertens R (1967) Die herpetologische Sektion des Natur-Museums und Forschungs-Institutes Senckenberg in Frankfurt a. M. nebst einem Verzeichnis ihrer Typen. *Senckenbergiana Biologica* 48: 1–106.
- Mocquard MF (1895) Sur une collection de reptiles recueillis à Madagascar par MM. Alluaud et Belly. *Bulletin de la Société Philomathique de Paris* (Huitième Série) 7: 112–136.
- Mocquard MF (1901) Note préliminaire sur une collection de Reptiles et de Batraciens recueillis par M. Alluaud dans le sud de Madagascar. *Bulletin du Muséum National d'Histoire naturelle* 7: 251–256.
- Mocquard MF (1909) Synopsis des familles, genres et espèces des reptiles écailleux et des batraciens de Madagascar. *Nouvelles Archives du Muséum* (5e Série) 1: 1–110.
- Müller F (1892) Siebenter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 10: 195–215.
- Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Noble GK (1931) *The Biology of the Amphibia*. McGraw-Hill, New York, NY & London, 577 pp.

- Padial JM, Miralles A, De La Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7: 16. <https://doi.org/10.1186/1742-9994-7-16>
- Paijmans JLA, Baleka S, Henneberger K, Taron UH, Trinks A, Westbury MV, Barlow A (2017) Sequencing single-stranded libraries on the Illumina NextSeq 500 platform. *arXiv*. <https://doi.org/10.48550/arXiv.1711.11004>
- Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The Simple Fool's Guide to PCR, Version 2.0. Privately published, University of Hawaii, Honolulu, HI, 45 pp.
- Parker HW (1934) Monograph of the Frogs of the Family Microhylidae. British Museum, London, 208 pp.
- Peloso PLV, Frost DR, Richards SJ, Rodrigues MT, Donnellan S, Matsui M, Raxworthy CJ, Biju SD, Lemmon EM, Lemmon AR, Wheeler WC (2016) The impact of anchored phylogenomics and taxon sampling on phylogenetic inference in narrow-mouthed frogs (Anura, Microhylidae). *Cladistics* 32: 113–140. <https://doi.org/10.1111/cla.12118>
- Peloso PLV, Raxworthy CJ, Wheeler WC, Frost DR (2017) Nomenclatural stability does not justify recognition of paraphyletic taxa: A response to Scherz et al. (2016). *Molecular Phylogenetics and Evolution* 111: 56–64. <https://doi.org/10.1016/j.ympev.2017.03.016>
- Penny SG, Andreone F, Crottini A, Holderied MW, Rakotozafy LS, Schwitzer C, Rosa GM (2014) A new species of the Boophis rapipoides group (Anura, Mantellidae) from the Sahamalaza Peninsula, northwest Madagascar, with acoustic monitoring of its nocturnal calling activity. *Zookeys*: 111–132. <https://doi.org/10.3897/zookeys.435.7383>
- Penny SG, Andreone F, Crottini A, Holderied MW, Rosa GM, Schwitzer C (2016) The Amphibians of the Sahamalaza Peninsula, Northwest Madagascar — Actions for their Conservation. Bristol Zoological Society, Bristol, 34 pp.
- Penny SG, Crottini A, Andreone F, Bellati A, Rakotozafy LMS, Holderied MW, Schwitzer C, Rosa GM (2017) Combining old and new evidence to increase the known biodiversity value of the Sahamalaza Peninsula, Northwest Madagascar. *Contributions to Zoology* 86: 273–296.
- Perl RGB, Nagy ZT, Sonet G, Glaw F, Wollenberg KC, Vences M (2014) DNA barcoding Madagascar's amphibian fauna. *Amphibia-Reptilia* 35: 197–206. <https://doi.org/10.1163/15685381-00002942>
- Peters WCH (1883) Über *Mantipus* und *Phrynocara*, zwei neue Batrachiergattungen aus dem Hinterlasse des Reisenden J. M. Hildebrandt von Madagascar. *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1883: 165–168.
- Petzold A, Glaw F, Mullin KE, Rakotoarison A, Raselimanana AP, Crottini A, Orozco-terWengel P, Köhler J, Prötzel D, Vences M, Hofreiter M, Scherz MD (2025) A preliminary assessment of the diversity of the frog genus *Anilany* from Madagascar (Microhylidae, Cophylinae) with description of a new species from western Madagascar. *Salamandra* 61: 70–94.
- Phelps LN, Andela N, Gravey M, Davis DS, Kull CA, Douglass K, Lehmann CER (2022) Madagascar's fire regimes challenge global assumptions about landscape degradation. *Global Change Biology* 28: 6944–6960. <https://doi.org/10.1111/gcb.16206>
- Phillips CA (2015) Herpetological type specimens in the University of Illinois Museum of Natural History: An update to the primary types. https://www.inhs.illinois.edu/files/8914/3110/1369/Prim_Types2015.pdf
- Posit team (2024) RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA.
- Puillandre N, Brouillet S, Achaz G (2021) ASAP: Assemble species by automatic partitioning. *Molecular Ecology Resources* 21: 609–620. <https://doi.org/10.1111/1755-0998.13281>
- R Core Team (2024) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rabearivony J, Raselimanana AP, Andriamazava MA, Thorstrom R, de Roland L-AR (2010) A new locality for the endangered microhylid frog *Scaphiophryne boribory* from northern Madagascar and a rapid survey of other amphibians of the Bemanevika region. *Herpetology Notes* 3: 105–109.
- Raherilalao MJ, Raselimanana AP, Soarimalala V, Goodman S (2016) Evaluation biologique de la flore et de la faune du Parc National de Masoala, Madagascar. Association Vahatra, Antananarivo, 116 pp.
- Rakotoarimalala F, Raselimanana AP (2023) Aperçu global de la tendance de la structure de la communauté herpétofaunique le long du gradient altitudinal du versant Est du Parc National de Marojejy au cours de ces 25 dernières années. *Malagasy Nature* 17: 165–186.
- Rakotoarisoa AJ (2012) Analyse comparative des communautés herpétofauniques de la forêt d'Ambatovy-Analamay, en vue de concevoir une approche de conservation convenable. Université d'Antananarivo, Antananarivo, 50 pp.
- Rakotoarisoa JC, Rakotoarison A, Rasoaantenaina S, Robsomanitrana E, Edmonds SSS, Soamiamampionona J, Tsimialomanana E, Wolf S, Edmonds D (2025) Captive breeding reveals insights into the ecology and reproductive biology of 11 little-known Malagasy frog species. *Zoo Biology* 44: 24–35. <https://doi.org/10.1002/zoo.21876>
- Rakotoarison A, Crottini A, Müller J, Rödel M-O, Glaw F, Vences M (2015) Revision and phylogeny of narrow-mouthed treefrogs (*Cophyla*) from northern Madagascar: Integration of molecular, osteological, and bioacoustic data reveals three new species. *Zootaxa* 3937: 61–89. <https://doi.org/10.11646/zootaxa.3937.1.3>
- Rakotoarison A, Glaw F, Vieites DR, Raminosoa NR, Vences M (2012) Taxonomy and natural history of arboreal microhylid frogs (*Platypelis*) from the Tsaratanana Massif in northern Madagascar, with description of a new species. *Zootaxa* 3563: 1–25.
- Rakotoarison A, Scherz MD, Bletz MC, Razafindrala JH, Glaw F, Vences M (2019) Diversity, elevational variation, and phylogenetic origin of stump-toed frogs (Microhylidae: Cophylinae: *Stumpffia*) on the Marojejy massif, northern Madagascar. *Salamandra* 55: 115–123.
- Rakotoarison A, Scherz MD, Glaw F, Köhler J, Andreone F, Franzen M, Glos J, Hawlitschek O, Jono T, Mori A, Ndriantsoa SH, Raminosoa Rasoamampionona N, Riemann JC, Rödel M-O, Rosa GM, Vieites DR, Crottini A, Vences M (2017) Describing the smaller majority: Integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. *Vertebrate Zoology* 67: 271–398. <https://doi.org/10.3897/vz.67.e31595>
- Rakotomalala D (2002) Diversité des reptiles et amphibiens de la Réserve Spéciale de Manongarivo, Madagascar. In: Gautier L, Goodman SM (Eds) Inventaire Floristique et Faunistique de la Réserve Spéciale de Manongarivo (NW Madagascar). Conservatoire et Jardin Botaniques de Genève, Geneva, 340–358.
- Ralimanana H, Perrigo AL, Smith RJ, Borrell JS, Faurby S, Rajaonah MT, Randriamboavonjy T, Vorontsova MS, Cooke RSC, Phelps LN, Sayol F, Andela N, Andermann T, Andriamanohera AM, Andriambololonera S, Bachman SP, Bacon CD, Baker WJ, Belluaro F, Birkinshaw C, Cable S, Canales NA, Carrillo JD, Clegg R, Clubbe C, Crottini A, Damasco G, Dhanda S, Edler D, Farooq H, de Lima Ferreira P, Fisher BL, Forest F, Gardiner LM, Goodman SM, Grace OM,

- Guedes TB, Hackel J, Henniges MC, Hill R, Lehmann CER, Lowry PP, Marline L, Matos-Maraví P, Moat J, Neves B, Nogueira MGC, Onstein RE, Papadopoulos AST, Perez-Escobar OA, Phillipson PB, Pironon S, Przelomska NAS, Rabarimanarivo M, Rabehevitra D, Raharimampionona J, Rajaonary F, Rajaovelona LR, Rakotoarivino M, Rakotoarisoa AA, Rakotoarisoa SE, Rakotomalala HN, Rakotonasolo F, Ralaiveloarisoa BA, Ramirez-Herranz M, Randriamamonjy JEN, Randrianasolo V, Rasolohery A, Ratsifandrihamanana AN, Ravololomanana N, Razafiniary V, Razanajatovo H, Razanatsoa E, Rivers M, Silvestro D, Testo W, Torres Jiménez MF, Walker K, Walker BE, Wilkin P, Williams J, Ziegler T, Zizka A, Antonelli A Madagascar's extraordinary biodiversity: Threats and opportunities. *Science* 378: eadf1466. <https://doi.org/10.1126/science.adf1466>
- Ramanamanjato J-B, McIntyre PB, Nussbaum RA (2002) Reptile, amphibian, and lemur diversity of the Malahelo Forest, a biogeographical transition zone in southeastern Madagascar. *Biodiversity and Conservation* 11: 1791–1807.
- Ramanamanjato J-B, Soanary CH (2011) The herpetofauna of Tsitongambarika Forest. In: BirdLife International (Ed.) Tsitongambarika Forest, Madagascar—Biological and socio-economic surveys, with conservation recommendations. BirdLife International, Cambridge, 34–41.
- Raselimanana AP (1999) L'herpétofaune. In: Goodman SM, Rasolonandrasana BPN (Eds) Inventaire Biologique de la Réserve Spéciale du Pic d'Ivohibe et du Couloir Forestier qui la Relie au Parc National d'Andringitra. Centre d'Information et de Documentation scientifique et technique, Antananarivo, 81–97.
- Raselimanana AP (2010) The amphibians and reptiles of the Ambatovy-Analamay region. *Malagasy Nature* 3: 99–123.
- Raselimanana AP, Raxworthy CJ, Nussbaum RA (2000) Herpetofaunal species diversity and elevational distribution within the Parc National de Marojejy, Mad[a]gascar. *Fieldiana Zoology (New Series)* 97: 157–174.
- Ratsimbazafy J, Ralison JM, Rabarison H, Randrianarison RM, Mensimana RM, Rasolondraibe LT, Rasoarivelo DS, Randrianasolo RM, Rakotosamimanana TH, Andrianandrasanana H (2008) Préservation de la biodiversité de Maromizaha. Antananarivo, 109 pp.
- Raxworthy CJ, Nussbaum RA (1994) A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation* 69: 65–73.
- Raxworthy CJ, Nussbaum RA (1996) Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: A study of elevational distribution and local endemism. *Fieldiana Zoology* 85: 158–170.
- Raxworthy CJ, Pearson RG, Rabibisoa N, Rakotondrazafy AM, Ramanamanjato J-B, Raselimanana AP, Wu S, Nussbaum RA, Stone DA (2008) Extinction vulnerability of tropical montane endemism from warming and upslope displacement: A preliminary appraisal for the highest massif in Madagascar. *Global Change Biology* 14: 1703–1720. <https://doi.org/10.1111/j.1365-2486.2008.01596.x>
- Rohland N, Siedel H, Hofreiter M (2004) Nondestructive DNA extraction method for mitochondrial DNA analyses of museum specimens. *BioTechniques* 36: 814–821.
- Rosa GM, Andreone F, Crottini A, Hauswaldt JS, Noël J, Rabibisoa NH, Randriambahiniarime MO, Rebelo R, Raxworthy CJ (2012) The amphibians of the relict Betampona low-elevation rainforest, eastern Madagascar: An application of the integrative taxonomy approach to biodiversity assessments. *Biodiversity and Conservation* 21: 1531–1559. <https://doi.org/10.1007/s10531-012-0262-x>
- Scherz MD (2020) Diamond frogs forever: A new species of *Rhombophryne* Boettger, 1880 (Microhylidae, Cophylinae) from Montagne d'Ambre National Park, northern Madagascar. *Zoosystematics and Evolution* 96: 313–323. <https://doi.org/10.3897/zse.96.51372>
- Scherz MD, Crottini A, Hutter CR, Hildenbrand A, Andreone F, Fulgence TR, Köhler G, Ndrantsoa SH, Ohler A, Preick M, Rakotoarison A, Rancilhac L, Raselimanana AP, Riemann JC, Rödel M-O, Rosa GM, Streicher JW, Vieites DR, Köhler J, Hofreiter M, Glaw F, Vences M (2022a) An inordinate fondness for inconspicuous brown frogs: integration of phylogenomics, archival DNA analysis, morphology, and bioacoustics yields 24 new taxa in the subgenus *Brygoomantis* (genus *Mantidactylus*) from Madagascar. *Megataxa* 7: 113–311. <https://doi.org/10.11646/megataxa.7.2.1>
- Scherz MD, Crottini A, Rakotoarison A (2022b) Microhylidae: Cophylinae, Microhylid frogs. In: Goodman SM (Ed.) The New Natural History of Madagascar. Princeton University Press, Princeton, NJ, 1382–1390.
- Scherz MD, Glaw F, Hutter CR, Bletz MC, Rakotoarison A, Köhler J, Vences M (2019a) Species complexes and the importance of Data Deficient classification in Red List assessments: The case of *Hylobatrachus* frogs. *PLoS One* 14: e0219437. <https://doi.org/10.1371/journal.pone.0219437>
- Scherz MD, Glaw F, Vences M, Andreone F, Crottini A (2016a) Two new species of terrestrial microhylid frogs (Microhylidae: Cophylinae: *Rhombophryne*) from northeastern Madagascar. *Salamandra* 52: 91–106.
- Scherz MD, Hawlitschek O, Andreone F, Rakotoarison A, Vences M, Glaw F (2017a) A review of the taxonomy and osteology of the *Rhombophryne serratopalpebrosa* species group (Anura: Microhylidae) from Madagascar, with comments on the value of volume rendering of micro-CT data to taxonomists. *Zootaxa* 4273: 301–340. <https://doi.org/10.11646/zootaxa.4273.3.1>
- Scherz MD, Hutter CR, Rakotoarison A, Riemann JC, Rödel M-O, Ndrantsoa SH, Glos J, Hyde Roberts S, Crottini A, Vences M, Glaw F (2019b) Morphological and ecological convergence at the lower size limit for vertebrates highlighted by five new miniaturised microhylid frog species from three different Madagascan genera. *PLoS One* 14: e0213314. <https://doi.org/10.1371/journal.pone.0213314>
- Scherz MD, Rakotoarison A, Hawlitschek O, Vences M, Glaw F (2015a) Leaping towards a saltatorial lifestyle? An unusually long-legged new species of *Rhombophryne* (Anura, Microhylidae) from the Sorata massif in northern Madagascar. *Zoosystematics and Evolution* 91: 105–114. <https://doi.org/10.3897/zse.91.4979>
- Scherz MD, Ruthensteiner B, Vences M, Glaw F (2014) A new microhylid frog, genus *Rhombophryne*, from northeastern Madagascar, and a re-description of *R. serratopalpebrosa* using micro-computed tomography. *Zootaxa* 3860: 547–560. <https://doi.org/10.11646/zootaxa.3860.6.3>
- Scherz MD, Ruthensteiner B, Vieites DR, Vences M, Glaw F (2015b) Two new microhylid frogs of the genus *Rhombophryne* with superciliary spines from the Tsaratanana Massif in northern Madagascar. *Herpetologica* 71: 310–321. <https://doi.org/10.1655/HERPETOLOGICA-D-14-00048>
- Scherz MD, Vences M, Rakotoarison A, Andreone F, Köhler J, Glaw F, Crottini A (2016b) Reconciling molecular phylogeny, morphological divergence and classification of Madagascan narrow-mouthed frogs (Amphibia: Microhylidae). *Molecular Phylogenetics and Evolution* 100: 372–381. <https://doi.org/10.1016/j.ympev.2016.04.019>
- Scherz MD, Vences M, Rakotoarison A, Andreone F, Köhler J, Glaw F, Crottini A (2017b) Lumping or splitting in the Cophylinae (Anura: Microhylidae) and the need for a parsimony of taxonomic changes: A response to Peloso et al. (2017). *Salamandra* 53: 479–483.

- Stephens M, Smith NJ, Donnelly P (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics* 68: 978–989.
- Straube N, Lyra ML, Paijmans JLA, Preick M, Basler N, Penner J, Rödel M-O, Westbury MV, Haddad CF, Barlow A, Hofreiter M (2021) Successful application of ancient DNA extraction and library construction protocols to museum wet collection specimens. *Molecular Ecology Resources* 21: 2299–2315. <https://doi.org/10.1111/1755-0998.13433>
- Trueb L (1968) Cranial osteology of the hylid frog, *Smilisca baudini*. *University of Kansas Publications, Museum of Natural History* 18: 11–35.
- Trueb L (1973) Bones, frogs, and evolution. In: Vial JL (Ed.) *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems*. University of Missouri Press, Columbia, MO, 65–132.
- Trueb L (1993) Patterns of diversity in the lissamphibian skull. In: Hanken J, Hall BK (Eds) *The Skull, Volume 2: Patterns of Structural and Systematic Diversity*. University of Chicago Press, Chicago, IL, 255–343.
- Tu N, Yang M, Liang D, Zhang P (2018) A large-scale phylogeny of Microhylidae inferred from a combined dataset of 121 genes and 427 taxa. *Molecular Phylogenetics and Evolution* 126: 85–91.
- Vallan D, Andreone F, Raherisoa VH, Dolch R (2004) Does selective wood exploitation affect amphibian diversity? The case of An'Ala, a tropical rainforest in eastern Madagascar. *Oryx* 38: 410–417. <https://doi.org/10.1017/S003060530400078X>
- van der Meijden A, Vences M, Hoegg S, Boistel R, Channing A, Meyer A (2007) Nuclear gene phylogeny of narrow-mouthed toads (Family: Microhylidae) and a discussion of competing hypotheses concerning their biogeographical origins. *Molecular Phylogenetics and Evolution* 44: 1017–1030. <https://doi.org/10.1016/j.ympev.2007.02.008>
- van der Meijden A, Vences M, Hoegg S, Meyer A (2005) A previously unrecognized radiation of ranid frogs in southern Africa revealed by nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 37: 674–685.
- Veith M, Lötters S, Andreone F, Rödel M-O (2004) Measuring and monitoring amphibian diversity in tropical forests. II. Estimating species richness from standardized transect censusing. *Ecotropica* 10: 85–99.
- Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*. Springer, New York, NY, 498 pp.
- Vences M, Glaw F (2003) New microhylid frog (*Plethodontohyla*) with a supraocular crest from Madagascar. *Copeia* 2003: 789–793. <https://doi.org/10.1643/ha02-285.1>
- Vences M, Glaw F, Marquez R (Eds) (2006) *The Calls of the Frogs of Madagascar*. 3 Audio CDs and booklet. Vol. Fonoteca Zoológica, Madrid, 44 pp.
- Vences M, Köhler J, Vieites DR, Glaw F (2011) Molecular and bio-acoustic differentiation of deep conspecific lineages of the Malagasy treefrogs *Boophis tampoka* and *B. luteus*. *Herpetology Notes* 4: 239–246.
- Vences M, Kosuch J, Glaw F, Böhme W, Veith M (2003a) Molecular phylogeny of hyperoliid treefrogs: Biogeographic origin of Malagasy and Seychellean taxa and re-analysis of familial paraphyly. *Journal of Zoological Systematics and Evolutionary Research* 41: 205–215. <https://doi.org/10.1046/j.1439-0469.2003.00205.x>
- Vences M, Miralles A, Brouillet S, Ducasse J, Fedosov A, Kharchev V, Kostadinov I, Kumari S, Patmanidis S, Scherz MD, Puillandre N, Renner SS (2021) iTaxoTools 0.1: Kickstarting a specimen-based software toolkit for taxonomists. *Megataxa* 6: 77–92. <https://doi.org/10.11646/megataxa.6.2.1>
- Vences M, Multzsch M, Gippner S, Miralles A, Crottini A, Gehring P-S, Rakotoarison A, Ratsoavina FM, Glaw F, Scherz MD (2022) Integrative revision of the *Lygodactylus madagascariensis* group reveals an unexpected diversity of little brown geckos in Madagascar's rainforest. *Zootaxa* 5179: 1–61. <https://doi.org/10.11646/zootaxa.5179.1.1>
- Vences M, Patmanidis S, Fodosov A, Miralles A, Puillandre N (2024a) iTaxoTools 1.0: Improved DNA Barcode Exploration with TaxID. In: DeSalle R (Ed.) *DNA Barcoding Methods in Molecular Biology*, vol 2744. Humana, New York, NY, https://doi.org/10.1007/978-1-0716-3581-0_18
- Vences M, Patmanidis S, Schmidt J-C, Matschiner M, Miralles A, Renner SS (2024b) Hapsolutely: A user-friendly tool integrating haplotype phasing, network construction, and haploweb calculation. *Bioinformatics Advances* 4: vbae083. <https://doi.org/10.1093/bioadv/vbae083>
- Vences M, Raxworthy CJ, Nussbaum RA, Glaw F (2003b) New microhylid frog (*Plethodontohyla*) from Madagascar, with semiarboreal habits and possible parental care. *Journal of Herpetology* 37: 629–636. <https://doi.org/10.1670/258-01A>
- Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences of the USA* 106: 8267–8272. <https://doi.org/10.1073/pnas.0810821106>
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York, NY, 260 pp.
- Wickham H, Averick M, Bryan J, Chang W, D'Agostino McGowan L, François R, Golemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Milton Bache S, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the Tidyverse. *The Journal of Open Source Software* 4: 1686. <https://doi.org/10.21105/joss.01686>
- Wollenberg KC, Vieites DR, Glaw F, Vences M (2011) Speciation in little: The role of range and body size in the diversification of Malagasy mantellid frogs. *BMC Evolutionary Biology* 11: 217. <https://doi.org/10.1186/1471-2148-11-217>
- Wollenberg KC, Vieites DR, van der Meijden A, Glaw F, Cannatella DC, Vences M (2008) Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. *Evolution* 62: 1890–1907. <https://doi.org/10.1111/j.1558-5646.2008.00420.x>

Appendix 1

Comparative morphological features of the species groups within *Rhombophryne*. + = presence, - = absence, ± = some species.

	<i>testudo</i> group	<i>laevipes</i> group	<i>ellae</i> group	<i>proportionalis</i> group	<i>minuta</i> group	<i>serratopalpebrosa</i> group
SVL (mm)	18.7–45.1	24.1–57.2	22.1–30.1	11.0–12.3	16.9–28.0	19.4–58.6
HIL/SVL	1.10–1.61	1.41–1.92	1.39–1.80	1.21–1.33	1.73–1.84	1.28–1.95
FARL/SVL	0.30–0.43	0.34–0.45	0.32–0.43	0.33–0.35	0.50–0.54	0.37–0.60
Clavicles	±	+	+	—	+	+
Premaxillary teeth	±	+	+	+	+	+
Maxillary teeth	±	+	+	+	+	+
Vomerine teeth	±	+	+	+	+	+
Superciliary spines	±	—	—	—	—	+
Black inguinal spots, sometimes with white outline	±	±	+	—	—	—
White inguinal spots	—	±	—	—	—	—
Red on legs	±	—	+	—	—	±
Dorsal skin	Smooth to rugose	Smooth to granular	Granular	Smooth	Smooth	Smooth to rugose

Appendix 2

Current and proposed IUCN Red List assessment of *Rhombophryne* species, following IUCN Guidelines (IUCN 2012). LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, EOO = Extent of Occurrence, TDL = Threat-defined location.

Species	Current Assessment	Proposed Assessment	Approx. EOO (km ²)	TDLs	Note
<i>R. testudo</i>	EN B1ab(iii)	EN B1ab(iii)	457	2	No significant changes from current assessment.
<i>R. coudreaui</i>	NT	EN B1ab(iii)	22	2	Taxonomic refinement reduces to just two TDLs. Ongoing decline in extent and quality of habitat.
<i>R. matavy</i>	CR B1ab(iii)	CR B1ab(iii)	48	1	No significant changes from current assessment.
<i>R. mangabensis</i>	VU D2	EN B1ab(iii)	300	4	Range extension to several localities on the Masoala Peninsula; no longer qualifies under criterion D2. Use of criterion B paradoxically increases perceived risk (VU→EN), but reflects threatened mainland populations, and is more consistent with other <i>Rhombophryne</i> species. EOO mostly water. Ongoing decline in extent and quality of habitat on Masoala Peninsula.
<i>R. savaka</i>	EN B1ab(iii)	EN B1ab(iii)	780	1	Refined elevational distribution suggests that it may not occur as far down as the park border, so its habitat within the protected areas of northern Madagascar is less threatened than previously thought. However, its potential distribution area is limited to a narrower elevational strip, reducing its potential distribution substantially. Retention of current assessment is recommended. EOO estimate is based on park boundaries and is probably wildly inaccurate due to narrow elevational distribution of the species.
<i>R. maraorao</i> sp. nov.	N/A	VU B1ab(iii)	3600	4	Ongoing decline in extent and quality of habitat.
<i>R. mavokely</i> sp. nov.	N/A	VU B1ab(iii)	1500	3	Ongoing decline in extent and quality of habitat.
<i>R. laevipes</i>	LC	VU B1ab(iii)	1000	2	IUCN record from Bemaraha is erroneous; populations in northern and eastern Madagascar mostly belong to <i>R. nilevina</i> . Two TDLs. Ongoing decline in extent and quality of habitat. Assessment in alignment with <i>Gephyromantis</i> (<i>Asperomantis</i>) <i>ambohitra</i> , which has a similar distribution (IUCN SSC Amphibian Specialist Group 2016b).
<i>R. botabota</i>	EN B1ab(iii)	VU B1ab(iii)	4190	2	No significant changes from current assessment, but status of EN with such a large EOO and two TDLs is inconsistent with other assessments.
<i>R. nilevina</i>	ND	LC	>20,000	4	Taxonomic reassessment (incorporation of specimens formerly assigned to <i>R. sp. Ca03</i>) renders this the most widespread <i>Rhombophryne</i> . Ongoing decline in extent and quality of habitat, but sufficiently widespread to not be at great risk.

Species	Current Assessment	Proposed Assessment	Approx. EOO (km ²)	TDLs	Note
<i>R. sonaliae</i> sp. nov.	N/A	LC	6200	~9	Ongoing decline in extent and quality of habitat, but no immediate threats to this species.
<i>R. anatala</i> sp. nov.	N/A	EN B1ab(iii)	380	1	Known from three specimens from two locations on the same mountain chain of the Masoala Peninsula, but likely to occur more widely. EOO based on continuous forest. Ongoing decline in extent and quality of habitat. EN status suggested to remain conservative.
<i>R. kotrobaratra</i> sp. nov.	N/A	VU B1ab(iii)	1600	3	Ongoing decline in extent and quality of habitat.
<i>R. ellae</i>	ND	EN B1ab(iii)	<400	1	Ongoing decline in extent and quality of habitat.
<i>R. quentini</i> sp. nov.	N/A	EN B1ab(iii)	1236	1	EOO estimated to conform with <i>R. ornata</i> , <i>R. tany</i> , and <i>R. guentherpetersi</i> , which occur under similar circumstances.
<i>R. kilonjy</i> sp. nov.	N/A	CR B1ab(iii)	<100	1	Ongoing decline in extent and quality of habitat. Assessment in line with <i>Boophis ankafensis</i> from the same locality (IUCN SSC Amphibian Specialist Group 2016a).
<i>R. proportionalis</i>	ND	EN B1ab(iii)	1236	1	EOO estimated to conform with <i>R. ornata</i> , <i>R. tany</i> , and <i>R. guentherpetersi</i> , which occur under similar circumstances.
<i>R. minuta</i>	EN B1ab(iii)	EN B1ab(iii)	780	1	No significant changes from current assessment. EOO estimate is based on park boundaries and probably wildly inaccurate due to narrow elevational distribution of the species.
<i>R. longicrus</i>	EN B1ab(iii)	EN B1ab(iii)	672	1	No significant changes from current assessment.
<i>R. serratopalpebrosa</i>	EN B1ab(iii)	EN B1ab(iii)	780	1	No significant changes from current assessment, except that a second, more recent specimen is now known. EOO estimate is based on park boundaries and probably wildly inaccurate due to narrow elevational distribution of the species.
<i>R. guentherpetersi</i>	EN B1ab(iii)	EN B1ab(iii)	1236	1	No significant changes from current assessment.
<i>R. coronata</i>	LC	DD	Unknown	5?	Taxonomic reassessment (ascribing specimens from Andringitra area as <i>R. sp.</i> ‘Ivohibe’) substantially reduces distribution. Taxonomic status of <i>Rhombophryne</i> sp. Ca13 also has significant implications for distribution, if distinct. Proposed to be Data Deficient until Zahamena and other northern locations are verified and the status of Ca13 is assessed; see Scherz et al. (2019a).
<i>R. vaventy</i>	EN B1ab(iii)	EN B1ab(iii)	2000	2	Addition of specimen from Sorata adds a second TDL, and expands EOO, but does not change overall assessment (as already discussed by Scherz et al. 2017a).
<i>R. ornata</i>	EN B1ab(iii)	EN B1ab(iii)	1236	1	No significant changes from current assessment.
<i>R. tany</i>	EN B1ab(iii)	EN B1ab(iii)	1236	1	No significant changes from current assessment.
<i>R. regalis</i>	ND	VU B1ab(iii)	600	4	Ongoing decline in extent and quality of habitat.
<i>R. diadema</i>	ND	EN B1ab(iii)	<50	2	Ongoing decline in extent and quality of habitat.

Supplementary Material 1

Figure S1

Authors: Scherz MD, Glaw F, Petzold A, Andreone F, Köhler J, Raselimanana AP, Hutter C, Belluardo F, Rakotoariason A, Hofreiter M, Vences M, Crottini A (2026)

Data type: .png

Explanation notes: Excerpt from the 3' end of the *Rhombophryne* 16S5' alignment, showing the position of sites in SMF 4241 relative to other *Rhombophryne* species that is identical to other specimens of *R. testudo*, and a unique combination within the genus, although no one site is diagnostic.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/vz.76.e172567.suppl1>

Supplementary Material 2

Tables S1–S17

Authors: Scherz MD, Glaw F, Petzold A, Andreone F, Köhler J, Raselimanana AP, Hutter C, Belluaro F, Rakotoari-son A, Hofreiter M, Vences M, Crottini A (2026)

Data type: .zip

Explanation notes: After extracting the “Tables S1–S17” archive, all tables are available in .xlsx format. **Table S1.** Micro-CT scans of *Rhombophryne* specimens included in this study with information on their Media IDs. Species names anticipate the taxonomic decisions proposed in this study. — **Table S2.** — Uncorrected pairwise distances within *Rhombophryne* in the 3’ fragment of the 16S rRNA mitochondrial barcode region. — **Table S3.** — Uncorrected pairwise distances within *Rhombophryne* in the 5’ fragment of the 16S rRNA mitochondrial barcode region. — **Table S4.** — List of localities mentioned in the text, geographical coordinates, elevation, and species of *Rhombophryne* occurring at the respective sites. Elevation is given as NA for general sites without specific information. — **Table S5.** — Morphometric measurements (all in mm) of voucher specimens of the *Rhombophryne testudo* species group. — **Table S6.** — Morphometric measurements (all in mm) of voucher specimens of the *Rhombophryne laevipes* species group. — **Table S7.** — Morphometric measurements (all in mm) of voucher specimens of the *Rhombophryne ellae* species group. — **Table S8.** — Morphometric measurements (all in mm) of voucher specimens of the *Rhombophryne proportionalis* species group. — **Table S9.** — Morphometric measurements (all in mm) of voucher specimens of the *Rhombophryne minuta* species group. — **Table S10.** — Morphometric measurements (all in mm) of voucher specimens of the *Rhombophryne serratopalpebrosa* species group. — **Table S11.** Morphometric measurements (all in mm) of voucher specimens of uncertain taxonomic affinity. — **Table S12.** Micro-CT scanning parameters used to produce scans used in this manuscript. — **Table S13.** Available molecular dataset for barcoded *Rhombophryne* specimens. Samples ID numbers are coded as follows: Angelica Crottini’s extraction codes (ACP; MR). Field collection numbers are coded as follows: Dina Ramamonjisoa’s field series (DLR), David Vieites’ field series (DRV), Franco Andreone’s field series (FAZC; FN), Frank Glaw’s field series (FGMV; FGZC), Miguel Vences’ field series (FGMV; MV; MVTIS; ZCMV), Mark Scherz’s field series (MSZC), Christopher Raxworthy’s field series (RAX), and Jasmin Randrianirina’s field series (RJS). Museum collection numbers are coded as follows: American Museum of Natural History, New York City, USA (AMNH), Biodiversity Institute of the University of Kansas, Lawrence, USA (KU), Museo Nacional Ciencias Naturales, Madrid, Spain (MNCN), Muséum National d’Histoire Naturelle, Paris, France (MNHN), Museo Regionale di Scienze Naturali, Torino, Italy (MRSN), Domaine des Sciences et Technologies, Université d’Antananarivo, Antananarivo, Madagascar (UADBA), and Zoologische Staatssammlung, Munich, Germany (ZSM). Species newly described in this study are highlighted in bold. Accession numbers in blue are newly published sequences from next-generation sequencing methods (from either hybrid enrichment or museomics), while those in red are from Sanger sequencing. Certain sequences were too incomplete or short to be accepted by NCBI; for these ‘see Zenodo’ is written; the full, aligned sequence is provided in the Zenodo archive at <https://doi.org/10.5281/zenodo.17247222>. — **Table S14.** Uncorrected pairwise distances in the mitochondrial rRNA 16S3’ marker, including specimens sequenced via museomics (note that these sequences are usually shorter, and their pairwise distances are therefore to be interpreted with caution). — **Table S15.** Uncorrected pairwise distances in the mitochondrial rRNA 16S5’ marker, including specimens sequenced via museomics (note that these sequences are usually shorter, and their pairwise distances are therefore to be interpreted with caution). — **Table S16.** Uncorrected pairwise distances in the mitochondrial rRNA 16S3’ marker, based only on modern specimens. — **Table S17.** Uncorrected pairwise distances in the mitochondrial rRNA 16S5’ marker, based only on modern specimens.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/vz.76.e172567.suppl2>