

SALAMANDRA

German Journal of Herpetology



Published by
Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V.
Salzhemmendorf, Germany

VOLUME 62 · NUMBER 1

15 FEBRUARY 2026

Contents

Articles:

TIUTENKO, A. & M. F. BATES: Two centuries of confusion: the status of <i>Boaedon fuliginosus</i> and <i>Boaedon capensis</i> , and the resurrection of <i>Boaedon unicolor</i> (Serpentes: Lamprophiidae: Lamprophiinae: Boaedontini)	1
VAISSI, S., M. SHARIFI & V. AKMALI: Landscape features drive dispersal patterns in the vulnerable Yellow-spotted Mountain Newt, <i>Neurergus derjugini</i> (Caudata: Salamandridae)	27
QIAN, T. Y., S. MA, C. LI, L. LUAN, Y. X. WANG & J. P. JIANG: Vocalizations of four species of Asian treefrogs (Anura: Rhacophoridae) from Medog County, Xizang Autonomous Region, China	33
BASHAM, E. W., M. D. MASOTTI, B. O. JIMENEZ, D. RAZAFITSIMALONA, G. M. ANDRIANATENAINA, A. RAKOTOARISON, F. GLAW, P. C. WRIGHT & M. VENCES: New species of treefrog of the <i>Boophis goudotii</i> group from the isolated Ivohiboro Protected Area in south-eastern Madagascar	42

Correspondence:

CARMO, L. F., I. R. DIAS, G. TANAJURA, O. ROJAS-PADILLA, M. SOLÉ & C. V. MIRA-MENDES: Revisiting the bioacoustics of <i>Sphaenorhynchus prasinus</i> (Anura: Hylidae): new data on vocalization of a lime treefrog from northeastern Brazil, including topotypes	53
--	----

Titel page:

Paratype specimen of *Boophis samuelsabini* sp. n. from Ivohiboro Protected Area in south-eastern Madagascar. Photo: MIGUEL VENCES.

ISSN 0036-3375

© 2026 Deutsche Gesellschaft für Herpetologie und Terrarienkunde, Salzhemmendorf, Germany.
E-mail: salamandra@dght.de.

All rights at the Deutsche Gesellschaft für Herpetologie und Terrarienkunde. Reproduction in any form only with written permission of the society. Layout: BIRGIT RÖDDER, Am Wusthahn 7, 57537 Forst, Germany. Delivery to book dealers: DGHT-Geschäftsstelle, Vogelsang 27, 31020 Salzhemmendorf, Germany.





New species of treefrog of the *Boophis goudotii* group from the isolated Ivohiboro Protected Area in south-eastern Madagascar

EDMUND W. BASHAM¹, MATTEO D. MASOTTI², BEATRIZ OTERO JIMENEZ²,
DENIS RAZAFITSIMALONA³, GEORGES M. ANDRIANATENAINA³, ANDOLALAO RAKOTOARISON^{4,5},
FRANK GLAW⁶, PATRICIA C. WRIGHT^{2,3} & MIGUEL VENCES⁷

¹Department of Integrative Biology, University of Texas, Austin, Texas, 78712, USA

²Department of Anthropology, Stony Brook University, Stony Brook, New York 11794, USA

³Centre ValBio Research Station, Ranomafana, 101 Madagascar

⁴Mention Environnement, Université de l'Itasy, Faliarivo Ambohidanerana, 118 Soavinandriana Itasy, Madagascar

⁵School for International Training, VN 41A Bis Ambohitsoa, 101 Antananarivo, Madagascar

⁶Zoologische Staatssammlung München (ZSM-SNSB); Münchhausenstr. 21, 81247 München, Germany

⁷Zoologisches Institut, Technische Universität Braunschweig, Mendelssohnstr. 4, 38106 Braunschweig, Germany

Corresponding author: MIGUEL VENCES, ORCID 0000-0003-0747-0817,
e-mail: m.vences@tu-braunschweig.de

Manuscript received: 27 October 2025

Accepted: 26 January 2026 by JÖRN KÖHLER

Abstract. We describe a new species of treefrog of the *Boophis goudotii* group from Ivohiboro, a sacred forest in the South-east of Madagascar and recently established protected area. Based on a molecular phylogeny inferred from DNA sequences of the mitochondrial 16S rRNA gene, *Boophis samuelsabini* sp. n. is sister to the clade of *B. madagascariensis* and *B. roseipalmatus* but differs from these species by genetic distances of 4.8–6.3%. The new species has an advertisement call consisting of various note types similar to its closest relatives, *B. madagascariensis* and *B. roseipalmatus*, but is distinguished morphologically from them by smaller body size and presence of a pattern of reticulated dermal folds on the dorsum. This discovery highlights the poor state of exploration of remnant highland forests in the South East of Madagascar which can be expected to harbour additional microendemic species in need of conservation measures.

Key words. Amphibia, Anura, Mantellidae, *Boophis samuelsabini* sp. n., Ivohiboro, microendemism.

Introduction

Among the anuran family Mantellidae, endemic to Madagascar and the Comoran island of Mayotte, the genus *Boophis* includes 87 species of tree frogs (FROST 2025), separated in ten species groups (BLOMMERS-SCHLÖSSER 1979, BLOMMERS-SCHLÖSSER & BLANC 1991, GLAW & VENCES 2006, HUTTER et al. 2018, 2022). Despite their arboreal habits, *Boophis* are relatively conspicuous frogs and most species are regularly observed and collected (HUTTER et al. 2022). Male advertisement calls are powerful and a dominant component of the nocturnal soundscape in Madagascar's rainforests (VENCES et al. 2008, HUTTER et al. 2022). The *Boophis goudotii* group is a species-rich clade within the genus (HUTTER et al. 2018), which, taking into account the latest species descriptions (GLAW et al. 2010, VENCES et al. 2010, KÖHLER et al. 2011), currently contains 16 nominal species.

Although new species or deep genetic lineages of amphibians are regularly described from a variety of environ-

ments and geographical regions within Madagascar, an emerging trend is their discovery from small, previously neglected fragments of original habitat persisting in the largely degraded matrix, e.g., in miniaturized leaf chameleons (GLAW et al. 2012, 2022, RAKOTOARISON et al. 2024) or different groups of frogs (e.g., GEHRING et al. 2010). Even if very small and often degraded, these forest fragments allow for the persistence of microendemic species whose wider area of occupancy may already have been lost due to slash-and-burn agriculture and other anthropogenic influences. Because a substantial proportion of Madagascar's biota can survive in somewhat degraded forest or forest edges (e.g., VALLAN et al. 2004, NDRIANTSOA et al. 2017), the protection of these minute remnant habitats can be of high importance in conservation management.

The Ivohiboro Protected Area (IPA), located in the Ihorombe Region of south-eastern Madagascar and legally established in 2023, is one such forest managed by a consortium composed of the Madagascar Institut pour la Conser-

vation des Ecosystèmes Tropicaux (MICET), the biological station CentreValbio, the Rainforest Trust, and stakeholders from surrounding villages (OTERO JIMENEZ et al. 2023). Though it has been highly fragmented over years of anthropogenic disturbance, the ~ 850 ha of humid forest within the IPA retain high levels of biodiversity, with numerous species of amphibians, reptiles, birds, lemurs, invertebrates, and other taxa (BARTYLAK et al. 2022, FAHMY et al. 2023, OTERO JIMENEZ et al. 2023, GIERLASIŃSKI et al. 2024). In the same local region of Madagascar, several other isolated forest fragments have yielded remarkable herpetofaunal discoveries, including microendemic species such as *Boophis laurenti* and *Mantidactylus bourgati* (BELLUARDO et al. 2021).

Recent field surveys carried out in Ivohiboro (Fig. 1) revealed the presence of several amphibian species requiring taxonomic description (BASHAM et al. in review). These comprised a specimen of a *Guibemantis* that was recently described as new species, *G. sioka* (HUTTER et al. 2025), a probable new microhylid of the genus *Anodonthyla* which will be revised in subsequent studies, and a *Boophis* with morphological and genetic affinities to *B. madagascariensis* and *B. roseipalmatus* (BASHAM et al. in review). Here, we provide additional data on this *Boophis*, including evidence for its concordant genetic and morphological divergence, and formally name and describe it as new species.

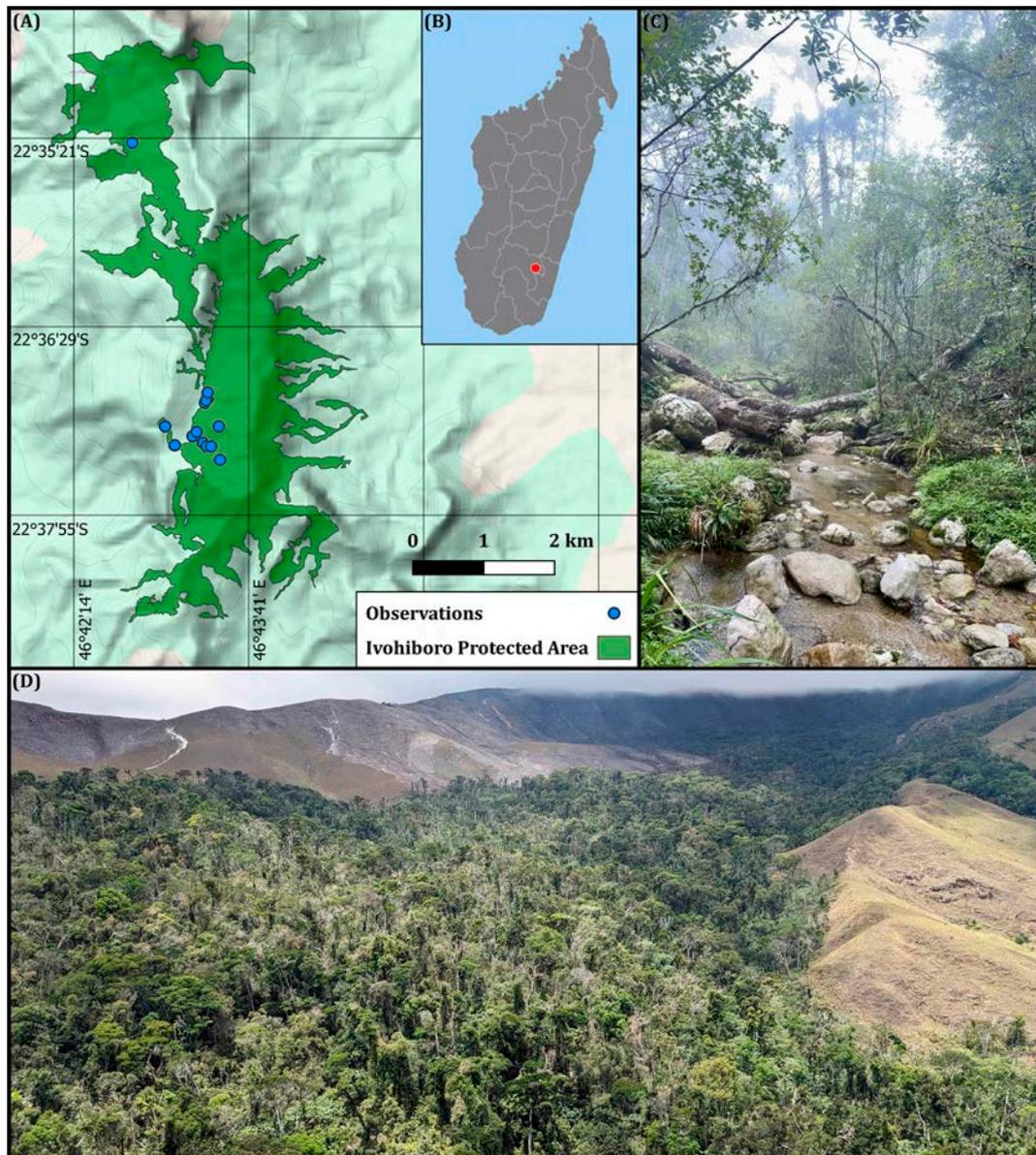


Figure 1. Map of Ivohiboro Protected Area with observation sites (A), with an inset of Madagascar showing the site location (B). (C–D) Photos of the habitat at Ivohiboro; C shows a representative view of the forest with a relatively large stream but note that the new species was found mostly in smaller, slow-moving streams (photograph by Mai Fahmy).

Materials and methods

Frogs of the target species were captured mostly at night and located by opportunistic searching, using torches and head lamps. Specimens were anesthetized with MS222 and subsequently euthanized with an overdose of the same substance. Tissue samples for genetic analyses were excised from the euthanized specimens and preserved in 96% ethanol. Specimens were then fixed in 96% ethanol, preserved in 70% ethanol, and deposited in the collections of the Université d'Antananarivo, Mention Zoologie et Biodiversité Animale, Madagascar (UADBA), and the Zoologische Staatssammlung München, Germany (ZSM). Collected voucher specimens were labelled with field numbers of F. GLAW (FGZC); several of these have not yet received final catalogue numbers in the respective collections and are therefore here referred to under the provisional acronyms UADBA-FGZC and ZSM-FGZC. Individuals observed by EB in 2023 could not be collected due to permitting issues, and were given field identifiers of MA (Analarny subsite) and MI (Ivohiboro subsite) (BASHAM et al. in review). During the 2023 fieldwork; 27 individuals were observed, 21 were photographed, 18 were swabbed, and 13 swabs yielded DNA of sufficient quality for sequencing. MA and MI identifiers were used for GenBank submission related to the 16S sequences derived from swabs. A table with all specimens (and their individual SVL measurements and recorded microhabitat) is available from Zenodo (<https://doi.org/10.5281/zenodo.18324260>). Other institutional codes and field numbers refer to sequences retrieved from GenBank and can be found in the respective publications referencing these sequences.

Morphological measurements (in millimetres) were taken by MV with a digital calliper to the nearest 0.1 mm. Abbreviations are: SVL (snout–vent length), HW (greatest head width), HL (head length), ED (horizontal eye diameter), END (eye–nostril distance), NSD (nostril–snout tip distance), NND (nostril–nostril distance), TD (horizontal tympanum diameter), TL (tibia length, actually referring not to the tibia bone but to the shank), HAL (hand length), HIL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus), and FORL (forelimb length). The definition of measurements, terminology and the description scheme follow GLAW et al. (2010) and VENCES et al. (2010), and GLAW & VENCES (1997) for eye colouration. Webbing formulae follow BLOMMERS-SCHLÖSSER (1979).

For the genetic analysis, we used a fragment of the mitochondrial 16S rRNA gene often used for DNA barcoding of Malagasy frogs (VIEITES et al. 2009). We extracted DNA from tissue samples and sequenced the PCR-amplified fragment using standard protocols (GLAW et al. 2010, VENCES et al. 2010), and with primers 16Sar-L and 16Sbr-H of PALUMBI et al. (1991). Sequences were resolved on a capillary sequencer by LGC Genomics (Berlin, Germany), quality-checked in CodonCode Aligner (CodonCode Corporation), trimmed in MEGA7 (KUMAR et al. 2016), and aligned using the G-INS-I option of MAFFT (KATO & STANDLEY 2013) as implemented in Concatenator (VENCES et al. 2022).

A Maximum Likelihood tree under the GTR+G model, with node support assessed using 500 full (“thorough”) bootstrap replicates, was inferred in RAXML (STAMATAKIS 2014) as implemented in raxmlgui (EDLER et al. 2020). Uncorrected pairwise sequence distances (p-distances) were calculated in MEGA7 using default parameters. All new sequences were submitted to GenBank (accession numbers PV386819, PV386828–PV386840, PX900032–PX900033). The alignment and treefile are available from Zenodo (<https://doi.org/10.5281/zenodo.18324260>).

Vocalizations were extracted from videos recorded in the field using a Google Pixel 8a cell phone with built-in microphone. Recordings were re-sampled at 22.05 kHz and 32-bit resolution and analyzed using the software Cool Edit Pro 2.0. Temporal parameters were measured in the oscillograms. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points) at Hanning window function. Spectrograms were produced at Blackman window function with 256 bands resolution. Temporal measurements are summarized as range with mean \pm standard deviation in parentheses. Description, terminology, and methods follow those recommended by KÖHLER et al. (2017), using the call-centered terminological scheme. Representative cuts of the calls in WAV format have been uploaded to the Zenodo repository (<https://doi.org/10.5281/zenodo.18324260>).

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:7F38A5E2-D68C-49E5-8F31-CEBoCF092117. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: salamandra-journal.com, [Zenodo.org](http://zenodo.org).

Results

The ML tree inferred from 518 bp of 16S sequences (Fig. 2) supported placement of the new species from Ivohiboro within the *B. goudotii* group, in a maximally supported (Bootstrap support BS = 100%) clade consisting of *B. madagascariensis*, *B. roseipalmatus*, and the focal lineage from Ivohiboro. Within this clade, *B. madagascariensis* was sister to *B. roseipalmatus* (BS = 87%).

Uncorrected pairwise distances of the focal lineage from Ivohiboro in the 16S fragment studied amounted to 5.1–6.3% in comparison with *B. madagascariensis* and 4.8–5.1% in comparison with *B. roseipalmatus*. The uncorrected dis-

tances between *B. madagascariensis* and *B. roseipalmatus* were 5.2–6.1%. Within-lineage distances amounted up to 1.4% in *B. madagascariensis*, 0.2% in *B. roseipalmatus*, and 0.4% in the focal lineage from Ivohiboro.

Morphologically, specimens of the focal lineage from Ivohiboro were similar to *B. madagascariensis* in their rather uniform beige to light brown dorsum, lack of reddish color on feet and webbing, beige-yellowish, mostly uniform iris, gray-bluish iris periphery, and distinct spine on elbow and tibiotarsal articulation. However, they were characterized by comparatively smaller body size (up to 48 mm; vs. 52–81 mm in adult *B. madagascariensis* and 60–87 mm in adult *B. roseipalmatus*; GLAW et al. 2010), and distinct dermal reticulations on the dorsum in most specimens which are much more indistinct or entirely lacking in *B. madagascariensis* and *B. roseipalmatus*. This size range also includes the holotypes of *B. madagascariensis* (65 mm; PETERS 1874) and *B. roseipalmatus* (66.2 mm; GLAW et al. 2010). For more detailed comparisons, see Diagnosis below.

The combination of phylogenetic position, strong mitochondrial genetic divergence, and distinct morphological differences to its closest relatives support a status as distinct species for the focal lineage from Ivohiboro. We therefore proceed in formally naming and describing this lineage.

Taxonomy

Boophis samuelsabini sp. n.

Figs 3–5

ZooBank LSID: urn:lsid:zoobank.org:act:58A2498F-0041-4400-BEBF-660082A916F5

Holotype: ZSM 600/2025 (field number FGZC 12502) collected by B. OTERO JIMENEZ, D. RAZAFITSIMALONA and G. M. ANDRIANATENAINA at 6.45 pm, 7 October 2024 at Ivohiboro Protected Area (22°36'59.0" S 46°43'20.5" E; 1200 m a.s.l.), South East of Madagascar.

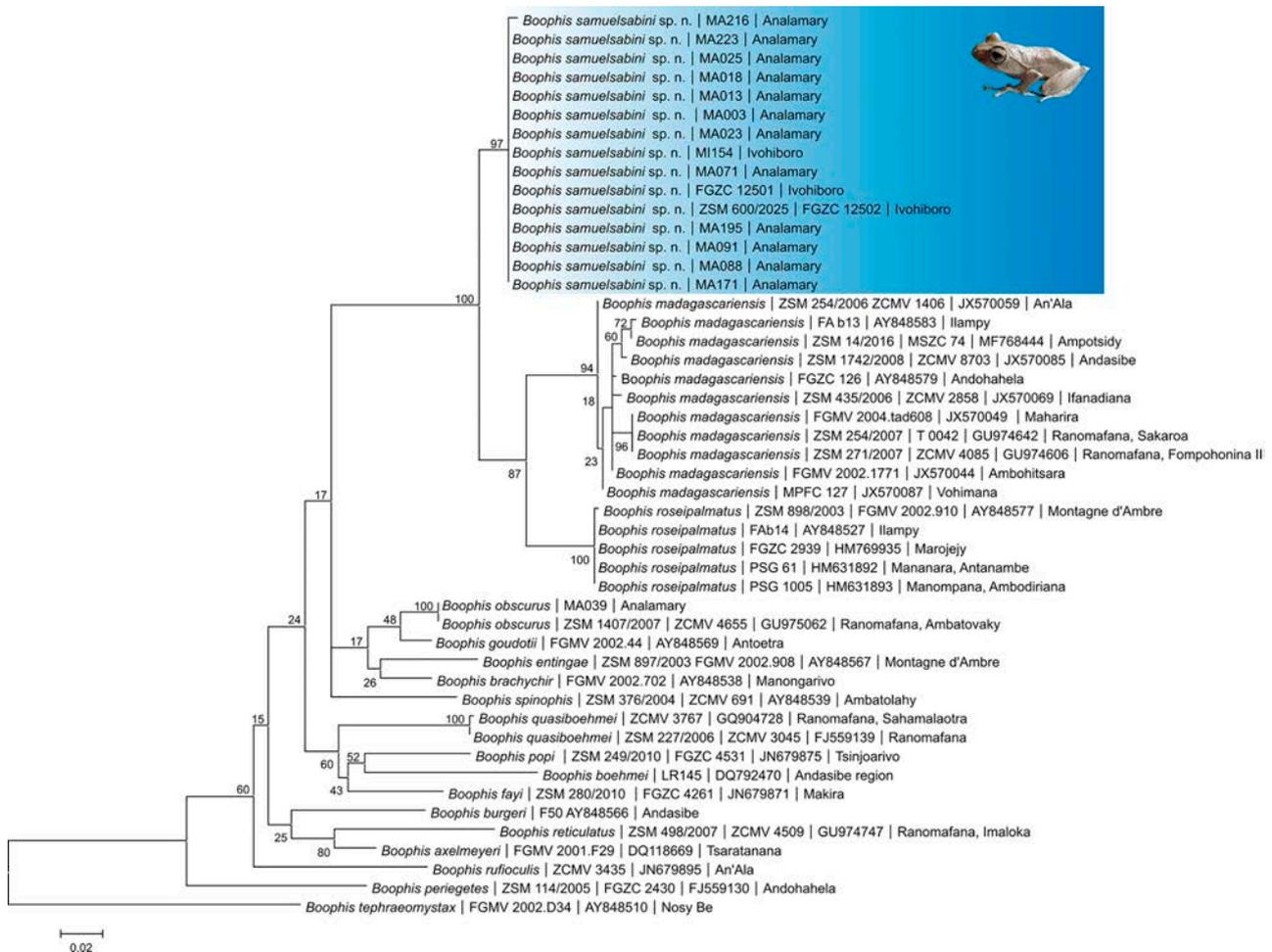


Figure 2. Maximum Likelihood phylogenetic tree inferred from a DNA alignment of 518 bp of the mitochondrial 16S rRNA gene. Numbers at nodes are bootstrap support values in percent (500 replicates). The sampling included all available sequences of *B. samuelsabini* sp. n., representative sequences of its closest relatives *B. madagascariensis* and *B. roseipalmatus* from across their range, and single sequences of all other species in the *B. goudotii* group. A sequence of *B. tephraeomystax* (subgenus *Sahona*) was used as outgroup.

Paratypes: Four specimens, all adult males. UADBA-FGZC 12501, with same collection data as holotype. ZSM-FGZC 12864, ZSM-FGZC 12866 and UADBA-FGZC 12867, collected by M. VENCES, S. RAKOTOMANGA, R. ANDRIAMIHANTASON, T. RAKOTOARIZAFY and A. RAZAFIMANANTSOA on 1 January 2026 at the type locality.

Available names: As discussed by GLAW et al. (2010), the nomen *Rhacophorus herthae* AHL, 1929 is currently considered as synonym of *B. madagascariensis* and needs to be taken into account as possible earlier name for the lineage described here. *Rhacophorus herthae* is based on a holotype in the Zoologisches Museum Berlin (ZMB 31577) of 25 mm SVL from Akkoraka, central Madagascar (see GLAW et al. 2010). This specimen shows a typical, contrasted color regularly observed in subadult *B. madagascariensis*, but not in any of the Ivohiboro specimens, including relatively small-sized specimens (e.g., MA88: 22 mm SVL; MA75: 27 mm SVL). Furthermore, the original description of *R. herthae*

does not make any reference to dermal ridges on the dorsum and describes the dorsal skin as smooth (AHL 1929). We therefore conclude that *R. herthae* is unlikely to be conspecific with the Ivohiboro specimens and continue considering the name as junior synonym of *B. madagascariensis*.

Definition: Assigned to the genus *Boophis* based on the presence of an intercalary element between ultimate and penultimate phalanges of fingers and toes (verified by external examination), presence of nuptial pads and absence of femoral glands in males, absence of gular glands in males, enlarged terminal discs of fingers and toes, lateral metatarsalia separated by webbing, absence of outer metatarsal tubercle, and molecular phylogenetic relationships (Fig. 2). Assigned to the *Boophis goudotii* group based on the following combination of characters: relatively large size (male SVL > 30 mm); beige to brown (not green) dorsal colour; non-transparent ventral skin, absence of red



Figure 3. Specimens of *Boophis samuelsabini* sp. n. in life: (A) paratype UADBA-FGZC 12501; (B) individual MA013 (not collected); (C) individual MA171 (not collected); (D) individual MA171 (not collected); (E) individual MA02 (not collected); (F) individual MA013 (not collected).

ventral colour; presence of dermal flaps or tubercles on heels and elbows; presence of webbing between fingers; presence of vomerine teeth; presence of white tubercles ventrally under the cloacal opening; presence of a well-defined canthus rostralis, and molecular phylogenetic relationships.

Diagnosis: The new species differs from all described species in the *B. goudotii* group by strong genetic differentiation, with pairwise 16S divergence of 5.1–6.3% to all the other species of the group. It further differs from *B. goudotii*, *B. obscurus* and *B. periegetes* by presence of distinct dermal flaps on heels (vs. absence) and from *B. goudotii*, *B. periegetes* and syntopic *B. obscurus* by smaller body size (male SVL as far as known < 40 mm vs. > 50 mm; *B. obscurus* from some other sites, e.g. Isalo, are smaller but still

> 42 mm); from *B. axelmeyeri*, *B. boehmei*, *B. quasiboehmei*, *B. popi*, and *B. rufiocularis* by absence of red pigment in the iris (vs. presence), and furthermore from *B. boehmei* and *B. quasiboehmei* by reticulated dorsum (vs. smooth) and larger body size (male SVL > 31 mm vs. < 31 mm); from *B. fayi* by absence of greenish color in the iris (vs. presence) and dorsal reticulations (vs. smooth dorsum); from *B. burgeri* by a whitish iris periphery (vs. blue); from *B. reticulatus* by comparatively weakly expressed dorsal reticulation (vs. strongly expressed) and uniformly colored head (vs. usually light patches laterally on head); from *B. brachychir* and *B. entingae* by reticulated dorsum (vs. smooth), uniform color on dorsum and head (vs. usually with black color lining the dorsolateral fold ventrally and often with large brown patch on dorsum), and smaller body size (male SVL as far as known < 40 mm vs. usually > 40 mm); from its

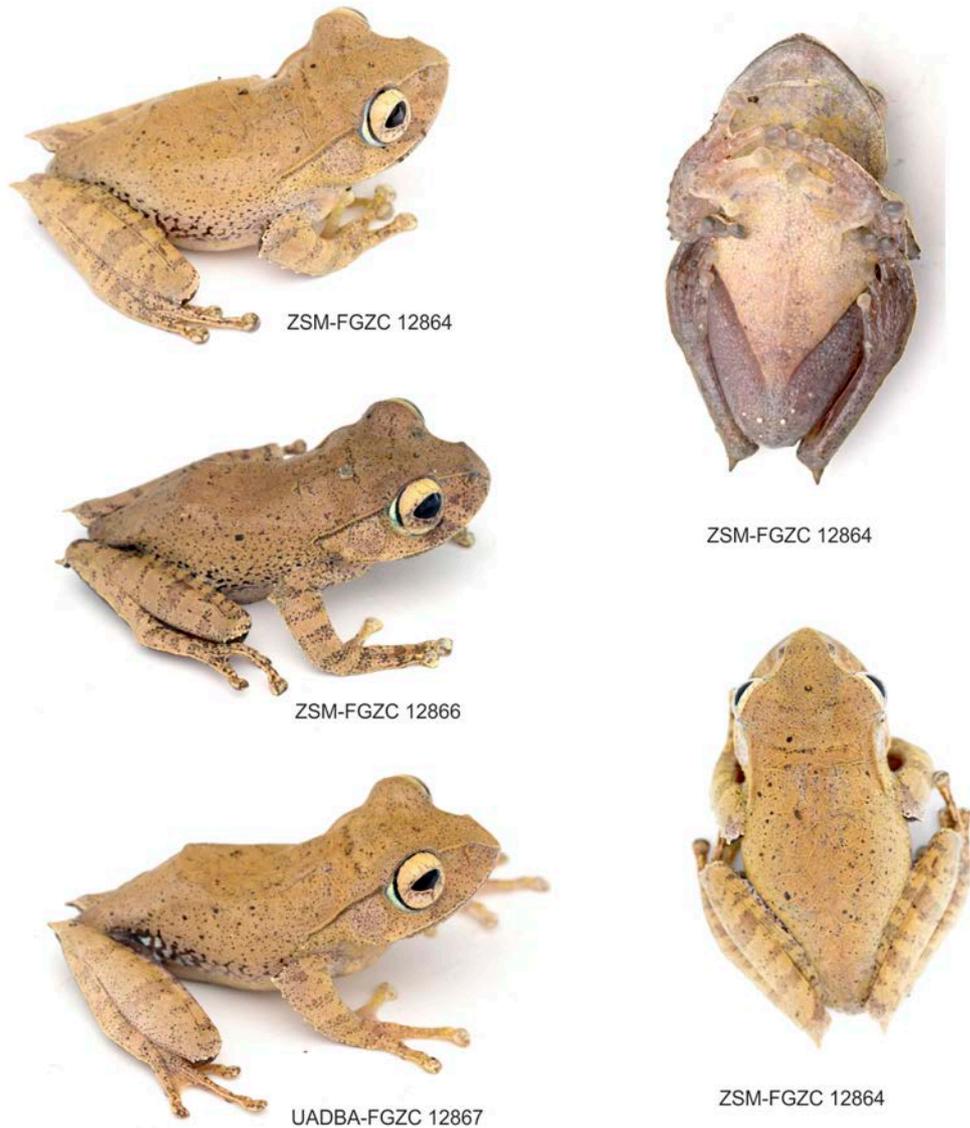


Figure 4. Dorsolateral views of three male paratypes, and dorsal and ventral views of one of these paratypes of *Boophis samuelsabini* sp. n. in life (specimens still uncatalogued and therefore here referenced with their field numbers; will be deposited in ZSM and UADBA).

closest relatives, *B. madagascariensis* and *B. roseipalmatus*, by reticulated dorsum (vs. usually smooth), distinctly smaller body size (male SVL as far as known < 40 mm vs. > 50 mm), and furthermore from *B. roseipalmatus* by absence of pinkish colour on webbing and iris periphery (vs. presence).

Description of the holotype: Adult male in a good state of preservation, tissue and skin removed ventrally from the thigh for DNA analysis (Fig. 5). Body moderately robust; head slightly wider than long, wider than body; snout slightly pointed in dorsal view, subacuminate in lateral view; nostrils directed laterally, slightly nearer to eye than tip of snout; canthus rostralis sharp, concave in dorsal view from eye to nostril; loreal region concave; eye large; tympanum distinct, rounded, TD 50% of ED; supratympanic fold prominent and straight; vomerine odontophores distinct, well separated in two rounded patches, positioned medially and posteriorly between choanae; choanae relatively small, rounded. Tongue wide, distinctly bifid and free posteriorly. Arms rather robust, lower arms with distinct lateral fringes which comprise about three smaller tubercles; a small but distinct pointed dermal appendage on elbow; subarticular tubercles single, round; inner palmar tubercle not unambiguously recognizable; fingers with traces of web between fingers 3 and 4, and without obvious lateral dermal fringes; relative length of fingers $1 < 2 < 4 < 3$ (finger 2 distinctly shorter than finger 4); finger discs enlarged; first finger with distinct, unkeratinized nuptial pad. Hind limbs slender; a distinct and prominent pointed dermal appendage on heel; tibiotarsal articulation reaches snout tip when hind limb is adpressed along body; lateral metatar-

sals largely separated by webbing; inner metatarsal tubercle small and distinct, elongated; no outer metatarsal tubercle; toes moderately webbed; webbing formula $1(0.75), 2i(1), 2e(0.5), 3i(1.5), 3e(0), 4i(2), 4e(2), 5(0.5)$; relative lengths of toes $1 < 2 < 3 < 5 < 4$; toe discs enlarged. Skin on dorsum largely smooth with fine reticulations in preservative; skin on dorsal faces of thigh, shank and tarsus smooth; skin smooth on throat and chest, slightly granular on belly with many granules dark pigmented; ventral faces of thighs and shanks finely granular, more coarsely granular with dark pigmented granules proximally on thighs, and with one prominent white tubercle on each side of the cloacal region. For measurements, see Table 1.

In preservative, after 3 months of preservation (Fig. 5), dorsally beige-cream with indistinct and poorly delimited large light brown patches on head and anterior dorsum and scattered small sharply delimited irregular black dots predominantly on posterior dorsum. Thighs, shanks, and feet with indistinct light brown crossbands. Ventrally cream, with a pattern of scattered dark brown spots on the belly which correspond to small and probably keratinized granules. Distinct brown pigment on tubercles on the ventral surface of hand and feet as well as most gland granules on the ventral side of thighs. Color in life of the holotype not documented.

Etymology: The species name is a patronym honoring SAMUEL SABIN, son of ANDREW SABIN, in recognition of the SABIN family's support for research and conservation of Madagascar's herpetofauna. Grammatically, the epithet is the genitive singular of a second-declension masculine noun.



Figure 5. Dorsal (left) and ventral (right) views of the preserved holotype ZSM 600/2025 (FGZC 12502) of *Boophis samuelsabini* sp. n.

Table 1. Morphometric measurements of holotype and paratypes of *Boophis samuelsabini* sp. n., all in mm. See Materials and methods for abbreviations.

Specimen voucher	ZSM 600/2025	UADBA-FGZC 12501	ZSM-FGZC 12864	ZSM-FGZC 12866	UADBA-FGZC 12867
Field number	FGZC 12502	FGZC 12501	FGZC 12864	FGZC 12866	FGZC 12867
Locality	Ivohiboro	Ivohiboro	Ivohiboro	Ivohiboro	Ivohiboro
Status	holotype	paratype	paratype	paratype	paratype
Sex	Male	Male	Male	Male	Male
SVL	36.2	35.6	37.0	36.5	36.8
HW	14.1	14.2	14.4	14.1	14.0
HL	13.8	14.0	15.0	14.9	14.6
TD	2.6	3.1	3.8	3.0	3.3
ED	5.2	4.6	5.6	5.1	5.5
END	3.0	3.0	3.3	3.3	2.9
NSD	3.2	3.4	3.4	3.2	3.5
NND	4.3	4.1	4.2	3.9	4.4
FORL	21.8	20.9	21.5	20.6	22.7
HAL	12.5	11.8	12.8	11.0	12.3
HIL	63.1	62.2	65.2	60.6	59.7
FOTL	27.0	26.6	28.4	26.5	26.1
FOL	16.5	16.0	16.9	15.7	15.4
TL	19.0	18.9	20.8	19.1	18.7

Variation: Based on available photos of several specimens, including the paratypes, in life (Figs 3–4), morphology is relatively uniform. Heel appendages and dorsal reticulation are visible in all specimens. Dorsal coloration in life ranges from cream to beige or light brown, but it is uncertain whether this in part reflects different white balance settings in the cameras used. Iris color is uniformly beige in most specimens, sometimes with some brown pattern (e.g., Fig. 3A); iris periphery is whitish or light bluish. BASHAM et al. (in review) recorded body sizes of 20 specimens of *B. samuelsabini* in their survey, but specimens were not reliably sexed and some of the values may refer to subadults. Adding the data of holotype and paratypes, the overall SVL range is 22.0–48.2 mm (mean 35.4; N = 25). Of these, 17 specimens measured between 32.0–38.2 mm, probably representing males given that the male holotype and paratypes fall within this range, and four specimens measured 45.4–48.2 mm which we hypothesize are females. A table with individual SVL measurements of all specimens is available from the Zenodo repository (<https://doi.org/10.5281/zenodo.18324260>).

Natural history: The species was locally abundant at the type locality. Males were observed calling at night from low vegetation directly overhanging small streams, typically perched on small branches, vines, palm fronds, or leaves. Calling activity commenced at dusk, and choruses often consisted of several males within close proximity; up to four males were recorded calling simultaneously from the same 2 × 2 m patch of understory shrubs beside a stream. Male choruses exhibited chain-like patterns of call initiation, with one male's call triggering responses from

nearby individuals. Vertical survey data using canopy access methods indicate that calling males primarily occupied perches within 0.5–2 m above ground, but one individual was captured at 7.2 m height, suggesting that outside of breeding activity the species may utilize higher strata of the understory and potentially canopy habitats.

Vocalizations: Advertisement calls recorded from an adult male in Ivohiboro on the 9th November 2024 at 21:25 (air temperature 19 °C, humidity 78%) consisted of pulsatile single-note calls (Fig. 6) which were repeated after irregular intervals (interval duration 9–10 seconds between three consecutively recorded calls). Call duration (= note duration) was 51–91 ms (mean 68 ms; N = 5). Calls contained 9–24 (mean 15.6; N = 5) pulses, with a pulse repetition rate of 147–264 pulses per second (mean 224/s; N = 5). There were no clearly recognizable silent intervals between pulses and in some cases pulses were not clearly distinguishable from each other. Pulses were most intense at the start of calls and intensity decreased gradually towards the end. Dominant frequency was 1291–1464 Hz (mean 1373 Hz; N = 5), and approximate prevalent bandwidth ranged between 900–2900 Hz. The recording also contains one short (ca. 25 ms) click note that likely was also emitted by this species, and in 2026 we heard also series of similar short notes probably emitted by this species (although the vocalizing specimen could not be observed in the moment emitting this kind of note). The large ranges of all temporal call variables, as well as the probable click note, indicate that advertisement calls of this species, as in the closely related *B. madagascariensis* (see NARINS et al. 2000) and probably in *B. roseipalma-*

tus (GLAW et al. 2010) are rather complex, and especially in highly motivated males may consist of various note types.

Distribution and conservation status: The species is so far only known from its type locality, Ivohiboro forest (750–1300 m a.s.l.; individuals were collected from 1000–1250 m a.s.l.) but may be present in other sites in the South East of Madagascar where remaining forests are under high anthropogenic pressure. Evaluating its conservation status is therefore not easy. Given the status of Ivohiboro as protected area, the species may be categorized as Least Concern based on IUCN criteria (IUCN Standards and Petitions Committee 2024), but could immediately shift to Critically Endangered if on-going decline in the extent and quality of its habitat in Ivohiboro would be noted, despite the site's protected area status. For a future IUCN Red List assessment of this species, the protection of Ivohiboro and the efficacy of the conservation measures in place for this protected area will therefore be crucial.

Discussion

The new species described herein, *Boophis samuelsabini*, has so far not been found at any other site in Madagascar except Ivohiboro Protected Area. Here, it is among the more common frog species, with 27 individuals recorded in the survey of BASHAM et al. (in review). Although the species can be distinguished from adults of its closest relatives, *B. madagascariensis* and *B. roseipalmatus*, readily by its smaller body size, it is possible that subadult *B. madagascariensis* from

other sites in the Southern Central East and South East of Madagascar may have been confused with *B. samuelsabini*. Confusion might also have happened with the similar-sized *B. reticulatus* which is relatively common in the area. However, molecular surveys, including numerous DNA sequences from tadpoles collected in Ranomafana National Park (e.g., STRAUSS et al. 2013, NDRIANTSOA et al. 2017), have not yielded any sequence of *B. samuelsabini*, suggesting that it may be absent or rare in Ranomafana. Recent research has revealed several frog species, such as *Guibemantis sioka* and *Gephyromantis cornucopia* (MIRALLES et al. 2023, HUTTER et al. 2025), which are probably restricted to forest areas at relatively high elevations (> 1000 m a.s.l.) in the South East of Madagascar, similar to the elevational range of *B. samuelsabini* (1000–1250 m a.s.l.). Future survey research is needed for this poorly prospected region, including forest remains > 1000 m in Ivohibe, Kalambatritra, and Chaines Anosyennes reserves.

The discovery of the new species also adds to recent findings of drastic differences in occurrence patterns and distribution ranges among closely related species of Malagasy anurans. While *B. samuelsabini* might be locally common, it seems to be geographically restricted while one of its closest relatives, *B. madagascariensis*, occupies a wide range spanning almost 1000 km along Madagascar's eastern rainforest band (GLAW & VENCES 2007). Similar examples of range-restricted vs. widespread species in the same region are *Guibemantis sioka* vs. *G. depressiceps* and *G. timidus* (HUTTER et al. 2025), or the range-restricted candidate species *Mantidactylus* sp. Ca55 and Ca56 vs. the widespread *M. guttulatus*, *M. lovei*, and *M. grandidieri*

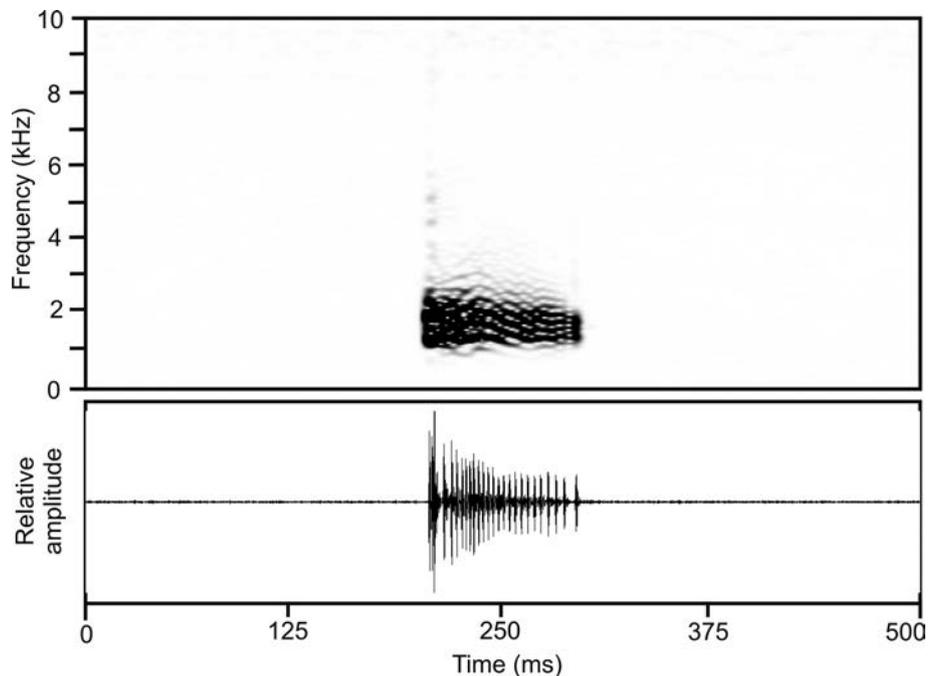


Figure 6. Audiospectrogram and corresponding oscillogram of a call emitted by a non-collected male of *Boophis samuelsabini* sp. n., recorded at the type locality on 9 November 2024 at 21:25 h.

(VENCES et al. 2025). At present, it is impossible to know whether the factors causing these differences are unique to each case, or indicate more general biogeographic or ecological patterns and processes; range-restricted species occur both in lowlands (*M. sp.* Ca55 and Ca56) and highlands (*G. sioka*, *B. samuelsabini*), and the differences are thus not obviously related to elevational segregation.

To better understand such macroecological patterns in Madagascar's amphibian fauna, it will first be necessary to assemble additional information on the natural history and life history of most species. Unfortunately, classical descriptive natural history work has fallen out of favor among researchers and funding agencies, and therefore, data on behavior, vocalization, microhabitat, tadpole morphology, or phenology are scarce or absent for most species in Madagascar's hyperdiverse amphibian assemblages, including *B. samuelsabini*. This species can be expected to have generalized exotrophic tadpoles living in streams, as known in the whole *B. goudotii* group (e.g., BLOMMERS-SCHLÖSSER 1979, BLOMMERS-SCHLÖSSER & BLANC 1991, RAHARIVOLONIAINA et al. 2006, RANDRIANIAINA et al. 2009, RASOLONJATOVO HIOMBIARILANTO et al. 2010). Future research in Ivohiboro should focus on obtaining such natural and life history data for its frog community, ideally in the rainy season, and coupled with additional collection of specimens to enable the taxonomic evaluation of additional candidate species that have already been identified from the site (BASHAM et al. in review). These efforts would benefit from parallel monitoring of forest condition and habitat quality, allowing changes in amphibian communities to be interpreted in the context of emerging threats, and providing a baseline to inform future conservation assessments.

Acknowledgments

We are grateful to the Malagasy authorities for approving research permit no. 354/24/MEDD/SG/DGGE/DAPRNE/SCB.Re from 17 September 2024 and export under permit 175N-EA07/MG25 from 22 July 2025. We are grateful to MICET, Centre Val-Bio Research Station, DINA ANDRIANOELY, and GEORGES RENE RAKONONIRINA for help with logistics. The work of the authors in the Ivohiboro Protected Area was supported by an anonymous donor to WISE Tropics Inc. Thanks to ANDY SABIN for his generous support. Additionally, we recognize BENJAMIN ANDRIAMIHAJA and DINA ANDRIANOELY with regards to planning and permitting of the initial survey work in Ivohiboro.

References

- AHL, E. (1929 "1928"): Neue Frösche der Gattung *Rhacophorus* aus Madagaskar. – *Zoologischer Anzeiger*, **75**: 311–318.
- BARTYLAK, T., P. KAYASTHA, M. ROSZKOWSKA, A. KEPÉL, M. KEPÉL & Ł. KACZMAREK (2022): Tardigrades of the Ivohibory forest (south-central Madagascar) with a description of a new *Bryodelphax* species. – *The European Zoological Journal*, **89**: 423–436.
- BASHAM, E. W., M. D. MASOTTI, I. E. SCHMEDER, M. VENCES, D. RAZAFITSIMALONA, G. M. ANDRIANATENAINA, D. ANDRIANOELY, C. M. ALLEN-LOVE, B. SCHEFFERS, K. R. ZAMUDIO & P. C. WRIGHT (in review): From ground to canopy: A molecularly verified herpetofaunal inventory of a Madagascar Protected Area. – *Journal of Herpetology*.
- BELLUARDO, F., D. D. QUIRÓS, J. LOBÓN-ROVIRA, G. M. ROSA, M. RASOAZANANY, F. ANDREONE & A. CROTTINI (2021): Uncovering the herpetological diversity of small forest fragments in south-eastern Madagascar (Haute Matsiatra). – *Zoosystematics and Evolution*, **97**: 315–343.
- BLOMMERS-SCHLÖSSER, R. M. A. (1979): Biosystematics of the Malagasy frogs. II. The genus *Boophis* (Rhacophoridae). – *Bijdragen tot de Dierkunde*, **49**: 261–312.
- BLOMMERS-SCHLÖSSER, R. M. A. & C. P. BLANC (1991): Amphibiens (première partie). – *Faune de Madagascar*, **75**: 1–379.
- EDLER, D., J. KLEIN, A. ANTONELLI & D. SILVESTRO (2020): raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAXML. – *Methods in Ecology and Evolution*, **12**: 373–377.
- FAHMY, M., D. ANDRIANOELY, P. C. WRIGHT & E. HEKKALA (2023): Leech-derived iDNA complements traditional surveying methods, enhancing species detections for rapid biodiversity sampling in the tropics. – *Environmental DNA*, **5**: 1557–1573.
- FROST, D. R. (2025): Amphibian Species of the World: an Online Reference. Version 6.1. – Electronic Database accessible at <https://amphibiansoftheworld.amnh.org/index.php>, accessed 3 March 2025. American Museum of Natural History, New York, USA.
- GEHRING, P. S., F. M. RATSOAVINA & M. VENCES (2010): Filling the gaps – amphibian and reptile records from lowland rainforests in eastern Madagascar. – *Salamandra*, **46**: 214–234.
- GIERLASIŃSKI, G., P. MAGNIEN, A. KEPÉL, K. WIŚNIEWSKI & A. LANGE (2024): *Kojderus maximus*, a new genus and species of Tessaratomidae (Hemiptera: Heteroptera), the first Natalicolinae from Madagascar. – *Acta Entomologica Musei Nationalis Pragae*, **64**: 327–335.
- GLAW, F., J. KÖHLER, I. DE LA RIVA, D. R. VIEITES & M. VENCES (2010): 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., J. KÖHLER, T. M. TOWNSEND & M. VENCES (2012): Rivaling the world's smallest reptiles: Discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar – *PLoS One*, **7**: e31314.
- GLAW, F., N. A. RAHARINORO, R. N. RAVELOJAONA, D. PRÖTZEL & M. VENCES (2022): New records of threatened leaf chameleons highlight unexpected genetic diversity of the *Brookesia decaryi*/*B. bonisi* species complex in western Madagascar. – *Der Zoologische Garten*, **90**: 71–80.
- GLAW, F. & M. VENCES (1997): Anuran eye colouration: definitions, variation, taxonomic implications and possible functions. – pp. 125–138 in: BÖHME, W., W. BISCHOFF & T. ZIEGLER (eds): *Herpetologia Bonnensis*. – Proceedings of the 8th Ordinary General Meeting of the Societas Europaea Herpetologica, Bonn.
- GLAW, F. & M. VENCES (2006): Phylogeny and genus-level classification of mantellid frogs (Amphibia, Anura). – *Organisms, Diversity & Evolution*, **6**: 236–253.

- GLAW, F. & M. VENCES (2007): A field guide to the amphibians and reptiles of Madagascar, third edition. – Vences & Glaw Verlag.
- HUTTER, C. R., Z. F. ANDRIAMPENOMANANA, E. W. BASHAM, F. GLAW, M. D. MASOTTI, S. M. LAMBERT & M. VENCES (2025): A new species of mantellid frog of the genus *Guibemantis* from south-eastern Madagascar. – *Zootaxa*, **5647**: 260–274.
- HUTTER, C. R., S. M. LAMBERT, Z. F. ANDRIAMPENOMANANA, F. GLAW & M. VENCES (2018): Molecular phylogeny and diversification of Malagasy bright-eyed tree frogs (Mantellidae: *Boophis*). – *Molecular Phylogenetics and Evolution*, **127**: 568–578.
- HUTTER, C. R., M. VENCES & J. E. CADLE (2022): Mantellidae, Boophinae: *Boophis*. – pp. 1357–1360 in: GOODMAN, S. M. (ed.): *The New Natural History of Madagascar*. – Princeton University Press.
- IUCN Standards and Petitions Committee (2024): Guidelines for using the IUCN Red List categories and criteria, version 16. – IUCN, Gland, Switzerland.
- KATO K. & D. M. STANDLEY (2013): MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. – *Molecular Biology and Evolution*, **30**: 772–780.
- KÖHLER, J., F. GLAW, G. M. ROSA, P.-S. GEHRING, M. PABIJAN, F. ANDREONE & M. VENCES (2011): Two new bright-eyed treefrogs of the genus *Boophis* from Madagascar. – *Salamandra*, **47**: 207–221.
- KÖHLER, J., M. JANSEN, A. RODRÍGUEZ, P. J. R. KOK, L. F. TOLEDO, M. EMMRICH, F. GLAW, C. F. B. HADDAD, M.-O. RÖDEL & M. VENCES (2017): The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. – *Zootaxa*, **4251**: 1–124.
- KUMAR, S., G. STECHER & K. TAMURA (2016): MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. – *Molecular Biology and Evolution*, **33**: 1870–1874.
- MIRALLES, A., J. KÖHLER, F. GLAW, K. C. WOLLENBERG VALERO, A. CROTTINI, A. M. ROSA, L. DU PREEZ, P.-S. GEHRING, D. R. VIEITES, F. M. RATSOAVINA & M. VENCES (2023): An endless harvest: integrative revision of the *Gephyromantis boulengeri* and *G. blanci* complexes reveals six new species of mantellid frogs from Madagascar. – *Salamandra*, **59**: 1–41.
- NARINS, P. M., E. R. LEWIS & B. E. MCCLELLAND (2000): Hyperextended call note repertoire of the endemic Madagascar treefrog *Boophis madagascariensis* (Rhacophoridae). – *Journal of Zoology*, **250**: 283–298.
- NDRIANTSOA, S. H., J. C. RIEMANN, N. RAMINOSOA, M.-O. RÖDEL & J. GLOS (2017): Amphibian diversity in the matrix of a fragmented landscape around Ranomafana in Madagascar depends on matrix quality. – *Tropical Conservation Science*, **10**: 1–16.
- OTERO JIMENEZ, B., R. MONTAÑO, R. S. ROTHMAN, R. C. WILLIAMS & P. C. WRIGHT (2023): A surprising haven: The biodiversity of an old-growth forest amidst a scorched landscape in Madagascar. – *Conservation Science and Practice*, **5**: e12993.
- PALUMBI, S. R., A. MARTIN, S. ROMANO, W. O. McMILLAN, L. STICE & G. GRABOWSKI (1991): *The Simple Fool's Guide to PCR*, Version 2.0. – University of Hawaii Zoology Department, Honolulu, Hawaii.
- PETERS, W. C. H. (1874): Ueber neue Amphibien. – *Gesamtsitzung, Monatsberichte der Königlichen Preussischen Akademie des Wissenschaften zu Berlin*: 616–624.
- RAHARIVOLONIAINA, L., S. GROSJEAN, N. RASOAMAMPIONONA RAMINOSOA, F. GLAW & M. VENCES (2006): Molecular identification, description and phylogenetic implications of the tadpoles of 11 species of Malagasy treefrogs, genus *Boophis*. – *Journal of Natural History*, **40**: 1449–1480.
- RAKOTOARISON, A., A. F. HASINIAINA, F. GLAW & M. VENCES (2024): A new miniaturized species of leaf chameleon, genus *Brookesia*, from a littoral forest fragment in eastern Madagascar. – *Zootaxa*, **5506**: 533–547.
- RANDRIANIAINA, R.-D., L. RAHARIVOLONIAINA, C. PREUSS, A. STRAUSS, F. GLAW, M. TESCHKE, J. GLOS, N. RAMINOSOA & M. VENCES (2009): Descriptions of the tadpoles of seven species of Malagasy treefrogs, genus *Boophis*. – *Zootaxa*, **2021**: 23–41.
- RASOLONJATOVO HIOBIARILANTO, T., R.-D. RANDRIANIAINA, J. GLOS, A. STRAUSS & M. VENCES (2010): Description of ten tadpoles in the genus *Boophis* from Madagascar. – *Zootaxa*, **2694**: 1–25.
- STAMATAKIS, A. (2014): RAXML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. – *Bioinformatics*, **30**: 1312–1313.
- STRAUSS, A., R. D. RANDRIANIAINA, M. VENCES & J. GLOS (2013): Species distribution and assembly patterns of frog larvae in rainforest streams of Madagascar. – *Hydrobiologia*, **702**: 27–43.
- VALLAN, D., F. ANDREONE, V. H. RAHERISOA & R. DOLCH (2004): Does selective wood exploitation affect amphibian diversity? The case of An'Ala, a tropical rainforest in eastern Madagascar. *Oryx*, **38**: 410–417.
- VENCES, M., Y. CHIARI, M. TESCHKE, R.-D. RANDRIANIAINA, L. RAHARIVOLONIAINA, P. BORA, D. R. VIEITES & F. GLAW (2008): Which frogs are out there? A preliminary evaluation of survey techniques and identification reliability of Malagasy amphibians. – *Monografie del Museo Regionale di Scienze Naturali di Torino*, **45**: 233–253.
- VENCES, M., J. KÖHLER, A. CROTTINI & F. GLAW (2010): High mitochondrial sequence divergence meets morphological and bioacoustic conservatism: *Boophis quasiboehmei* sp. n., a new cryptic treefrog species from south-eastern Madagascar. – *Bonn zoological Bulletin*, **57**: 241–255.
- VENCES, M., S. PATMANIDIS, V. KHARCHEV & S. S. RENNER (2022): Concatenator, a user-friendly program to concatenate DNA sequences, implementing graphical user interfaces for MAFFT and FastTree. – *Bioinformatics Advances*, **2**: vbac050.
- VENCES, M., J.-B. RAMANAMANJATO, A. MIRALLES & F. GLAW (2025): A new giant stream frog (genus *Mantidactylus*) from south-eastern Madagascar (Amphibia, Mantellidae). – *Spixiana*, **47**: 297–300.
- VIEITES, D. R., K. C. WOLLENBERG, F. ANDREONE, J. KÖHLER, F. GLAW & M. VENCES (2009): Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. – *Proceedings of the National Academy of Sciences of the United States of America*, **106**: 8267–8272.