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Integrative taxonomy of Malagasy treefrogs: combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of *Boophis*

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Abstract

We describe ten new species of treefrogs assigned to the genus *Boophis* (Anura: Mantellidae) and resurrect two species from synonymy, based on materials collected during fieldwork in Madagascar, carried out mainly between 2000 and 2007. Our comparative database assembled over the past years comprises fresh material for molecular analysis from all 58 nominal *Boophis* species, and advertisement call recordings from all except three species. We follow an integrative approach and combine molecular, bioacoustic and morphological evidence to diagnose the new species. In most cases, the new species have uncorrected molecular divergences of over 4–5% in the mitochondrial 16S rRNA gene to their closest relatives. In some cases the divergences are lower (2–2.5%) but are then accompanied by distinct differences in advertisement calls or morphology. *Boophis piperatus* **sp. nov.** from Ranomafana National Park is a small brown species assigned to the *B. majori* group that is similar to *B. miniatus* but differs in morphology and advertisement calls. *Boophis arcanus* **sp. nov.** is assigned to the *B. majori* group as well and is known from only two female specimens from a site close to Ranomafana; it is described mainly based on its strong genetic differentiation (> 7.2% to all other species). *Boophis entingae* **sp. nov.** is a species of the *Boophis goudoti* group occurring in northern Madagascar, similar to and sympatric with *B. brachychir*, but with a strongly different advertisement call. *Boophis roseipalmatus* **sp. nov.** belongs to the *B. goudoti* group, is similar to *B. madagascariensis*, and appears to replace this species in most of northern Madagascar, with possible areas of sympatry in the north east. *Boophis spinophis* **sp. nov.** is an enigmatic, morphologically highly divergent species from Ranomafana National Park that belongs into the *B. goudoti* group but differs from all other spe-

cies in the group by having distinct dermal tubercles along the lateral parts of the shank and around the elbow. *Boophis praedictus* **sp. nov.** is a sibling species of *B. albilabris* in the *B. albilabris* group, diagnosable by its red iris periphery and distributed in rainforest along the east coast. *Boophis sandrae* **sp. nov.** belongs to the *B. luteus* group and is superficially similar to the sympatric *B. elenae*, but has a faster call and smaller body size. *Boophis miadana* **sp. nov.** and *B. haingana* **sp. nov.**, both in the *B. albipunctatus* group and syntopically occurring at Andohahela National Park, are related to *B. ankaratra* and *B. schuboeae* and differ mainly by their advertisement calls. *Boophis luciae* **sp. nov.**, also in the *B. albipunctatus* group, differs from the sympatric *B. albipunctatus* and *B. sibilans* by having slightly smaller body size and different advertisement calls. We furthermore resurrect *Rhacophorus obscurus* Boettger, 1913 (as *Boophis obscurus* in the *B. goudoti* group) from the synonymy of *Boophis goudoti* as well as *Rhacophorus andrangoloaka* Ahl, 1928 (as *Boophis andrangoloaka* in the *B. microtympanum* group) from the synonymy of *Boophis rhodoscelis*, and propose to consider *Rhacophorus brevirostris* Ahl, 1928 as junior synonym of *Boophis andrangoloaka*. We discuss our integrative methodological approach and the different lines of evidence used to delimitate the species described or resurrected herein. By applying IUCN Redlist criteria, we evaluate the threat status of the species considered: six species are classified Data Deficient (*B. arcanus, B. haingana, B. miadana, B. piperatus, B. praedictus, B. spinophis*), four Vulnerable (*B. andrangoloaka, B. entingae, B. roseipalmatus, B. sandrae*), and two Least Concern (*B. luciae, B. obscurus*).

Key words: Amphibia: Anura: Mantellidae; *Boophis*; cryptic species; DNA barcoding; integrative taxonomy; Madagascar

Introduction

The amphibian fauna of Madagascar is characterized by a high species diversity of currently 250 species of frogs and, especially, by a high degree of endemism which amounts to 100% in native species (Glaw & Vences 2007). Most species belong to the family Mantellidae, and one of the largest mantellid genera is *Boophis* Tschudi, with 58 currently recognized species (Cadle 2003; Glaw & Vences 2007; Vallan *et al.* 2010). *Boophis* are usually arboreal frogs, with the exception of a few montane species that can be more terrestrial in areas where no trees or bushes are found. *Boophis* can be divided in two major clades, one with stream-breeding specialists found mainly in rainforest or montane habitats, and a second with species breeding in ponds that occur in rainforests as well as in arid regions of western and southern Madagascar. Early results indicating that the pond-breeding *Boophis* may not be monophyletic (Vences *et al.* 2002) are contradicted by new analyses based on more extensive sampling of taxa and molecular characters (Glaw & Vences 2006; Glaw *et al.* 2006). Consequently, pond breeders are classified in a separate subgenus, *Sahona* Glaw & Vences, 2006, whereas all other (stream-breeding) species of *Boophis* are classified in the nominal subgenus *Boophis*. This latter subgenus is by far more diverse, and is divided in eight species groups (Glaw & Vences 2006; Wollenberg *et al.* 2008; Köhler *et al.* 2008): the *Boophis albilabris* group, *B. albipunctatus* group, *B. goudoti* group, *B. luteus* group, *B. majori* group, *B. mandraka* group, *B. microtympanum* group, and the *B. ulftunni* group. At least the *B. majori* group is known to be non-monophyletic (e.g., Glaw & Vences 2006; Raharivololoniaina *et al.* 2006; Randrianiaina *et al.* 2009); however, after a number of recent changes (e.g., Glaw & Vences 2006) most of these groups probably do represent clades. Independent from the phylogenetic status of these *Boophis* species groups, they are a very useful tool by subdividing this species-rich genus into manageable units that are then more accessible for taxonomic revision. Each of the groups consists of phenetically similar species assigned to the groups on the basis of combining several morphological characters (even if the defining character states of each group do not necessarily represent synapomorphies).

In general, *Boophis* are very vocal frogs that emit their loud advertisement calls almost exclusively at night. Because bioacoustic evidence has been extensively used in the taxonomy of Malagasy frogs (Köhler *et al.* 2005), and the calls of most *Boophis* are known (Vences *et al.* 2006), the taxonomic knowledge of this group can be considered comparatively well assessed. The available data sets also allow a relatively fast recognition of new, undescribed species, and the possibility of basing species records of many *Boophis* on solely their characteristic calls led to a relatively good knowledge of their distribution (Vences *et al.* 2008).

Although in some aspects *Boophis* are better known than other groups of Malagasy frogs, there is also a significant lack of knowledge. Because the search for these arboreal animals is successful mainly at night by locating calling males, the females are still unknown for a large number of species. In addition, the bioacoustic approach in taxonomy has revealed the existence of many cryptic species of *Boophis*, with very small or non-existing morphological differences but very distinct call differences to their often sympatric closest relatives (e.g., Andreone *et al.* 1995; Glaw & Vences 1997c; Glaw *et al.* 2001; Vences & Glaw 2002; Vences *et al.* 2005a). Subsequent molecular studies have revealed that these sibling species are also characterized by strong genetic divergences (e. g. Vences *et al.* 2002; Köhler *et al.* 2005), whereas chromosomal characters in the genus seem to show limited variation (Aprea *et al.* 2004).

A recent comprehensive survey combining molecular, bioacoustic and morphological evidence on materials collected during multiple field expeditions to Madagascar over the past 20 years has revealed the presence of a large number of divergent genealogical lineages, most of which correspond to taxa or populations characterized also by bioacoustic and/or morphological characters (Vieites *et al.* 2009). These "Confirmed Candidate Species" (CCS; Vieites *et al.* 2009) are, with high probability, new species that require taxonomic studies in order to receive a valid scientific name, by either new descriptions or resurrection of synonyms. Of altogether 126 CCS identified in the Malagasy anuran fauna, 21 corresponded to *Boophis*, indicating that taxonomic work on this genus is overdue.

Here we combine the available evidence on molecular, morphological and bioacoustic differentiation of various CCS in *Boophis*, based on our comparative database assembled over the past years comprising fresh material for molecular analysis from all 58 described *Boophis* species, and advertisement call recordings from all except three species. Based mainly on materials collected during field work in Madagascar between 2000 and 2007, we apply an integrative taxonomy approach to describe ten new species and resurrect two species from synonymy. In this, we largely follow an evolutionary or general lineage concept, defining species as evolutionary independent lineages (see de Queiroz 2007; Padial *et al.* 2009). Following the rationale of Vieites *et al.* (2009) for CCS recognition, we consider differences in sexual premating recognition systems (i.e., advertisement calls), and occurrence in syntopy without admixture, as particularly important arguments supporting species status.

Materials and methods

Frog specimens were collected at night by opportunistic searching, using torches and head lamps and by locating calling frogs. Specimens were euthanized in a chlorobutanol solution, fixed in 95% ethanol, and preserved in 70% ethanol. Localities were georeferenced with GPS receivers using the WGS84 datum system. Locality information was plotted on schematic maps (Appendix 10). Specimens studied in this paper are deposited in the collection of the California Academy of Sciences, San Francisco (CAS), Museo Regionale di Scienze Naturali, Torino (MRSN), Naturhistorisches Museum Bern (NMBE), Université d'Antananarivo, Département de Biologie Animale, Antananarivo (UADBA), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), Zoölogisch Museum Amsterdam (ZMA), Zoologisches Museum Berlin (ZMB), and the Zoologische Staatssammlung München (ZSM). FGMV, FGZC and ZCMV refer to F. Glaw and M. Vences field numbers; FAZC refers to F. Andreone field numbers; GA to Gennaro Aprea field numbers; RJS to Jasmin Randrianirina field numbers; LR to Liliane Raharivololoniaina field numbers. Terminology for biogeographic regions of Madagascar follow Boumans *et al.* (2007) (see also Glaw & Vences 2007).

Morphology. Specimens examined are listed in Appendices 1–8. Morphological measurements (in millimetres) were all done by M. Vences with digital calipers (precision 0.01 mm) 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), FORL (forelimb length), and RHL (relative hindlimb length). The definition of these measurements, terminology and description scheme follow Glaw *et al.* (2001), and Glaw & Vences (1997a) for eye colouration. Webbing formulae follow Blommers-Schlösser (1979).

We use the term "not recognizable" if a structure was not clearly discernable from the surrounding tissue.

Bioacoustics. Calls were recorded in the field using different types of tape recorders (Sony WM-D6C, Tensai RCR-3222) and external microphones (Sennheiser Me-80, Vivanco EM 238). Most recordings were sampled at 22.05 kHz and 16-bit resolution and computer-analysed using the software Adobe Audition version 1.5. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points). Spectrograms were obtained at Hanning window function with 256 or 512 bands resolution. Temporal measurements are given as range, with mean ± standard deviation in parentheses. We measured air temperature (to the nearest 0.1°C) with digital devices in close distance to calling frogs. The number of recordings did not allow for temperature corrections. Bioacoustic variables analysed are provided in Table 1. Definition of variables and terminology in call descriptions follow Köhler (2000). Classification of call types was done according to the social context observed during calling and the researchers' experience. Distress calls were emitted only when the frog individual was grabbed. Advertisement calls were those emitted regularly under usual mating conditions without extraordinary dense male aggregations. Calls emitted under latter conditions were usually interpreted as aggressive or territorial calls.

The amount of bioacoustic differences between species was evaluated following Vieites *et al.* (2009): we considered differences to be weak when the general call structure was similar and differences quantitative, i.e., referring to temporal or frequency variables that are known to be under influence of temperature and/or body size and/or motivation of calling specimen, and being detectable only or mainly by statistical analyses taking into account these covariables. Strong differences are those with differences in general call structure (e.g., pulsed versus melodious notes, different arrangement of note types) or in temporal variables that are largely independent from temperature, body size and motivation.

DNA extraction and sequencing. Total genomic DNA was extracted using proteinase K (final concentration 1 mg/mL), and isolated by a standard salt extraction protocol (Bruford *et al.* 1992). A fragment of the mitochondrial large ribosomal subunit (16S rRNA) was amplified via polymerase chain reaction (PCR) using the primers 16Sar-L and 16Sbr-H (Palumbi *et al.* 1991). PCRs were performed in 25 μL reactions using 50 ng genomic DNA, 10 pmol of each primer, 15 nmol of each dNTP, 50 nmol additional $MgCl_2$, 2.5 μL of PCR buffer (10 mm Tris-HCl, pH 8.3, 50 mm KCl, 1.1 mm $MgCl_2$ and 0.01% gelatine), and 1 U of Taq DNA polymerase. PCR conditions were as follows: an initial denaturation step at 94°C for 90 s; 35 cycles at 94°C for 30 s, annealing temperature of 53°C for 45 s, extension at 72°C for 60–120 s; final extension of 10 min at 72°C. PCR products were purified using QIAquick spin columns (QIAGEN) or ExoSAP-It (Amersham) prior to cycle sequencing. A 10 μL sequencing reaction included 1–2 μL of template, 2.5 μL of sequencing buffer, 1 μL of 2 pmolar primer, 0.4 μL of ABI sequence mix (BigDye Terminator version 3.1 sequencing standard, Applied Biosystems) and 3.2–4.2 μL of water. The sequence reaction was 39 cycles of 10 s at 94°C, 10 s at 49°C and 4 min at 60°C. Sequence data collection and visualization were performed on ABI 3730 and 3130 automated sequencers (Applied Biosystems). Sequences were deposited in GenBank; voucher specimens, localities and GenBank accession numbers of samples used are provided in Appendix 11. The 16S fragment length included about 500 base pairs.

Data analysis. 16S sequences were edited and aligned using SeqMan (DNASTAR inc.) and Bioedit (Hall 1999). Based on a full tree with one representative of all species and candidate species of Malagasy frogs (Vieites *et al.* 2009) we selected subsets of taxa, usually with representatives of all species in one species group, and constructed phylogenetic trees of those, adding all individual sequences available for these species. To each sequence set we added one outgroup sequence that according to previously published data (Glaw & Vences 2006; Vieites *et al.* 2009) is clearly phylogenetically more distant from all ingroup sequences than

these are to each other, but as close as possible to the ingroup clade to allow an unambiguous alignment of the variable (loop) portions of the DNA sequences. We used *Boophis jaegeri* (*B. luteus* group) as outgroup for the *B. albipunctatus* group; *Boophis ankaratra* (*B. albipunctatus* group) for the *B. luteus* group; and *Boophis tephraeomystax* (subgenus *Sahona*) as outgroup for the rest of analyses. The sequence set in each tree was selected so that it contains all those species that are morphologically similar to the newly described or resurrected species, and thus to provide evidence for the genetic distinctness of these from all those species that may be difficult to distinguish morphologically. We emphasize that the main purpose of these trees is to visualize that species as defined herein constitute monophyletic units regarding their mitochondrial genome (for which the 16S rRNA gene is representative), with conspecific sequences usually very similar or identical to each other and highly distinct from those assigned to other (morphologically similar) species (with exception of *B. obscurus* where we assume introgression; see below). It is not the goal of the trees to clarify the phylogenetic relationships among the species; for this purpose, the DNA fragment used is insufficient (Vieites *et al.* 2009) and more extensive multi-gene datasets are currently in preparation (manuscript by K. C. Wollenberg and collaborators).

The alignments of the separate sequence sets required inclusion of only few indels that were included in the analyses as missing data. Total length of separate alignments was different due to (1) a different number of indels in the diferent sequence sets and (2) missing data at the beginning or end of the sequences; we adjusted the alignments so that not more than 40% of the sequences had missing data at the beginning or end.

Phylogenetic analyses were performed using the programs PAUP 4b10* (Swofford 2002), and Mrbayes 3.1 (Ronquist & Huelsenbeck 2003). We performed both Bayesian and maximum-parsimony (MP) analyses in order to check for consistency in the results from different methods that are based on different assumptions of molecular evolution. MP analyses were performed in PAUP 4b10* using heuristic searches with tree-bisection–reconnection (TBR) branch swapping, step addition starting tree, and random addition sequence with 2000 replicates.

For the Bayesian analysis, we used MrModeltest version 2.2 (Nylander 2004) to choose the appropriate model of sequence evolution for each partition. We used a neighbour-joining (NJ) tree with Jukes–Cantor 69 substitution model of the whole data set as starting tree. The models selected were GTR+I+G for all data sets. Analyses consisted of four Markov chains that ran for 10×10^6 generations, sampled every 1000 generations, with a random starting tree and default priors. The burn-in was empirically estimated by plotting –ln L against the generation number, and the trees corresponding to the first 5 million generations discarded.

For interpreting the phylogenetic tree, we considered bootstrap values of 70% and higher, and Bayesian support values of 0.95 and higher, as relevant support; however, we emphasize again that the trees (Figs. 1, 7, 16, 18, 21) were not primarily calculated as a tool to infer intrageneric phylogenetic relationships in detail but to visualize genetic differences.

Uncorrected pairwise genetic distances were calculated using PAUP* and manually transformed into percentages. For interpretation of molecular divergences, largely on the basis of the results of Fouquet *et al.* (2007) and Vieites *et al.* (2009), we classify pairwise distances in the 16S rRNA gene as follows: low divergence, below threshold of 3%; moderate divergence, 3–5%; high divergence, above 5%; very high divergence, above 7%.

Taxonomy and description of new species

***Boophis piperatus* sp. nov.**
(Fig. 2, Appendix 9)

Remark. This species was referred to as *Boophis* sp. aff. *rhodoscelis* "Ranomafana" in Glaw & Vences (2007:152–153) and as *Boophis* sp. 30 by Vieites *et al.* (2009).

Holotype. ZSM 377/2004 (ZCMV 320), adult male (call voucher), from Ranomafana, Andranoroa river, near Ranomafanakely, 21°14.872' S, 47°22.580' E; 1138 m above sea level (a.s.l.), southeastern Madagascar, collected on 28 January 2004 by I. De la Riva and M. Vences.

Paratypes. ZSM 378/2004 (ZCMV 328), female, same data as holotype; ZSM 379/2004 (ZCMV 338), male, ZSM 380/2004 (ZCMV 339), female, ZSM 381/2004 (ZCMV 341), adult male (call voucher), UADBA 24317 (ZCMV 342), sex unknown, ZSM 382/2004 (ZCMV 345), male, ZFMK 90151 (formerly ZSM 383/2004 [ZCMV 346]), male, all with same data as holotype, but collected on 29 January 2004; ZSM 299/2006 (ZCMV 3363), adult male (seen calling), Andranoroa river, no further data, but probably collected February/March 2006.

Etymology. The specific name is a Latin adjective meaning "peppered", referring to the finely spotted dorsum, particularly evident in the holotype.

Diagnosis. 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 (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*). Assigned to the *Boophis majori* group based on the following combination of characters: small size (male SVL 28-30 mm); single subgular vocal sac; presence of vomerine teeth; smooth dorsal skin without folds, spines or tubercles; absence of distinct heel flaps or spines; presence of webbing between fingers; non-transparent ventral skin; brownish dorsal ground colour without green elements; occurrence of red colour on the hidden parts of the thighs and on the webbing of the feet. *Boophis piperatus* differs from all described species in the *B. majori* group by strong genetic differentiation (see below) and advertisement calls (see Glaw *et al.* 2001 and Vences *et al.* 2006, for comparative data on the calls of the other species). In brief, *B. piperatus, B. feonnyala, B. miniatus,* and *B. picturatus* differ from all other species in the group by having advertisement calls (call type 2 as described below) that are series of pulsed notes that directly follow each other, with a very short or almost missing inter-note interval. Among these species, the notes of *B. piperatus* are distinctly longer (135-283 ms) than those of *B. picturatus* (50-131 ms) and *B. miniatus* (35-85 ms), while no obvious difference exists between calls of *B. piperatus* and *B. feonnyala.* Morphologically, the new species differs from the three northern species of the *Boophis majori* group (*B. blommersae, B. marojezensis* and *B. vittatus*) by the presence of red colour on thighs and feet in preservative, and distinctly from *B. pyrrhus* and *B. haematopus* by the colouration in life and in preservative (see photographs in Glaw & Vences 2007). It differs from the syntopic *B. majori* by having larger size in males (SVL 27.9–29.6 mm vs. 21.5–24.5 mm) and females (SVL 36.2–36.9 mm vs. 29.0–29.2 mm, see Glaw *et al.* 2001 for comparative data) and different colour in preservative (e. g. ground colour of back brown vs. reddish). It differs from *B. miniatus* and *B. picturatus* by different iris colouration in life (see photographs in Glaw & Vences 2007) and from *B. feonnyala* by slightly different size in males (SVL 27.9–29.6 mm vs. 25.0–25.4 mm), a more strongly pointed snout, and lack of dark stripes or reticulations in the iris. It differs from the superficially similar species *B. rhodoscelis* and *B. andrangoloaka* by strong genetic differences and longer notes in advertisement calls (see call descriptions of those species below).

Description of the holotype. Adult male, SVL 28.7 mm. Body moderately slender; head slightly longer than wide, slightly wider than body; snout slightly subacuminate in dorsal view, moderately obtuse in lateral view; nostrils directed laterally, slightly nearer to tip of snout than to eye; canthus rostralis sharp in cross section, slightly concave in dorsal view, loreal region slightly concave; tympanum distinct, rounded, TD 56% of ED; supratympanic fold thin, distinct; vomerine odontophores distinct, well-separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, elongated. Tongue posteriorly bifid, free. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1), 2i(1.5), 2e(1), 3i(2), 3e(1.75), 4(1.25);

relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation reaching a little beyond tip of snout when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0.25), 2i(0.5), 2e(0), 3i(0.75), 3e(0.25), 4i(1.25), 4e(1.25), 5(0.25); relative length of toes 1<2<5=3<4; toe discs enlarged. Skin finely granular on dorsal surfaces, smooth on throat, chest, and ventral surface of thighs, coarsely granular on belly. A tissue sample was removed from the right thigh.

Measurements (in mm): SVL 28.7, HW 10.2, HL 10.8, ED 4.1, END 2.5, NSD 2.1, NND 2.9, TD 2.3, TL 16.4, HAL 9.1, FOL 13.1, FOTL 22.7.

After almost four years in preservative, ground colour of upper surface of head, dorsum and legs pale brown with tiny cream and dark brown flecks; upper lip cream with brown flecks; a canthal dark brown stripe from eye to tip of snout, outlined by a cream line above; a pale brown triangle from interorbital region to tip of snout. Tiny red flecks on tip of snout, supratympanic fold and dorsal surface of digits; posterior surface of thighs with irregular, diffuse red markings; lower flanks and ventral surfaces creamy yellow.

In life, dorsal surfaces pale brown with scattered small, darker flecks. Lower flanks cream with irregular greenish grey blotches. A paler triangle on head and a dark canthal stripe. Upper surfaces of thighs and shanks the same colour as dorsum, with darker diffuse bars. Iris golden with brown irregular markings around the pupil; iris periphery black, followed by green posteriorly (Fig. 2). Ventral life colouration of holotype unknown.

Variation. Morphometric variation is given in Appendix 1. Overall, paratypes are similar to the holotype. There can be large cream blotches on upper lip; females are larger and red colouration in preservative is more intense and extended than in males. At least one specimen was observed calling in the wild (emitting notes of type 1) and had a single subgular vocal sac that was moderately inflated during calls.

Natural history. As reported first by Vences *et al.* (2006) under the name "*Boophis* sp. aff. *rhodoscelis* (Ranomafana)", calling males of this species were found at night, 1–2 m high in the vegetation along Andranoroa river, in a rather disturbed area next to the edge of rainforest. Some single specimens were emitting call type 1 as described below while others were emitting call type 2 described below. Call type 2 was emitted in "waves" by a chorus of numerous specimens. Call type 3 that Vences *et al.* (2006) preliminarily assigned to this species in fact belongs to the syntopic *Boophis* sp. aff. *majori* "long calls" (Glaw & Vences 2007). Specimens were regularly encountered at the same site during visits in 2004 and 2006. They often were sitting on leaves on tree branches overhanging the water, sometimes also in bushes at some meters distance from the river edge.

Vocalization. Calls of *B. piperatus* may contain two different call types (Fig. 3). Type 1 consists of a series of pulsed notes emitted in fairly regular intervals. Each note contains 2–8 indistinct pulses. Within the call, notes show an increase in amplitude and duration, with the two terminal notes usually being the longest and loudest. Call type 2 is a vocalization with strongly pulsed notes, separated by only very short intervals. Compared to call type 1, it is significantly higher in frequency and several parallel narrow frequency bands are present in the spectrogram. Numerical parameters for the different call types of the Ranomafana population are as follows: Call type 1: call duration, 1100–2000 ms (1474 ± 336; n = 5); note duration, 18–50 ms (34 ± 10; n = 17); inter-note intervals, 121–310 ms (163 ± 47; n = 18); note repetition rate, 5.4–6.0 notes/second; dominant frequency range 2800–3500 Hz, maximum call energy at 2870–3180 Hz. Call type 2: call duration, 3260–3300 ms (n = 2); note duration, 135–283 ms (253 ± 38; n = 16); inter-note interval, 29–63 ms (43 ± 9; n = 15); note repetition rate, 3.1–3.4 notes/second; pulse rate approximately 300 pulses/second; dominant frequency range, 3600–5200 Hz, maximum call energy at 4170–4710 Hz (Vences *et al.* 2006, CD 1, track 57, call sections 1 & 2).

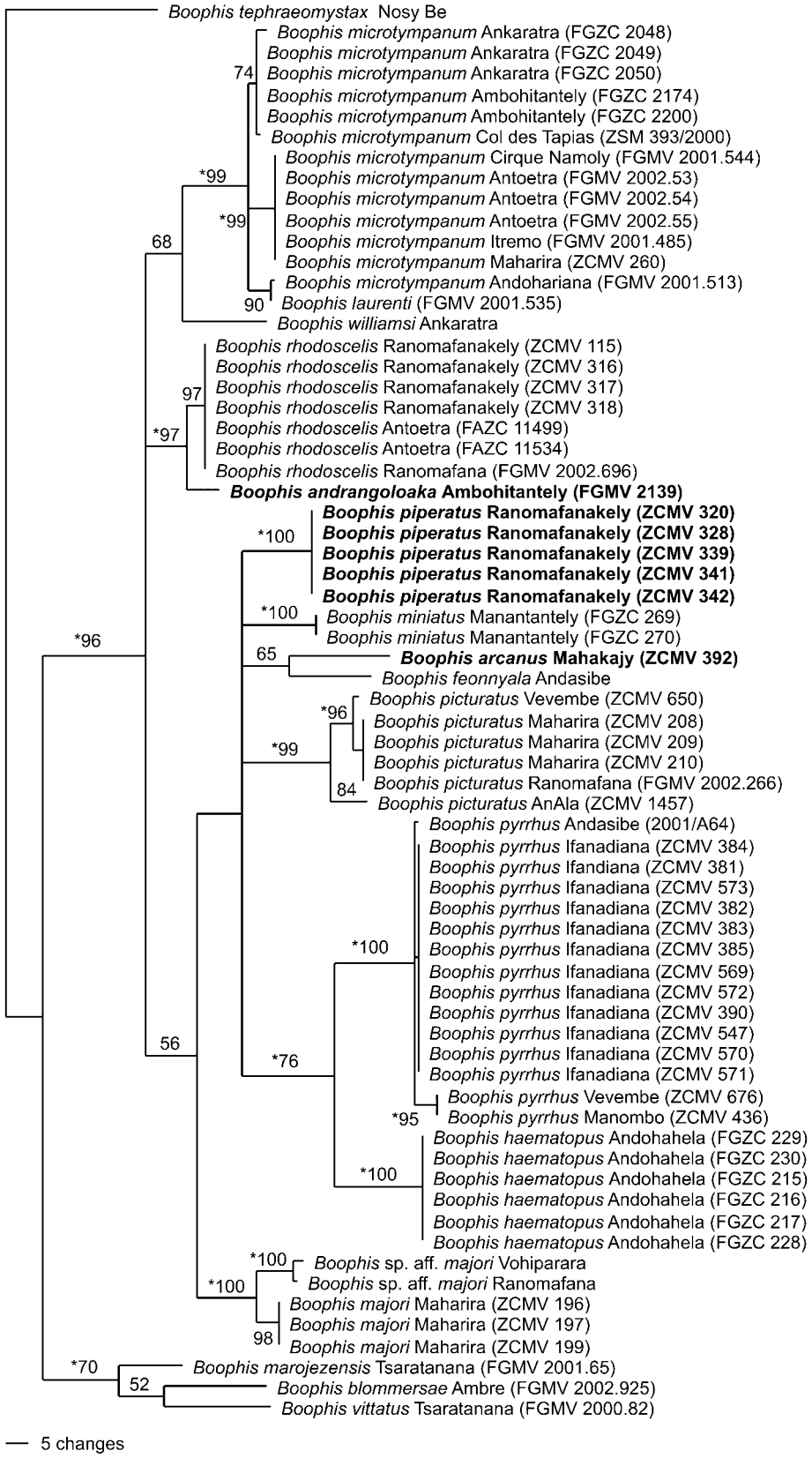


FIGURE 1. Maximum parsimony 16S rRNA phylogram for species in the *Boophis majori* and *B. microtympanum* groups. From 480 total characters, 336 were constant and 129 parsimony informative. MP searches retained 39 trees of which a strict consensus is shown. Consensus support values higher than 50, from 2000 bootstrap replicates, are shown; an asterisk indicates Bayesian posterior probabilities equal or higher than 95%. Species newly described or resurrected herein are in bold.



FIGURE 2. Male holotype of *Boophis piperatus* **sp. nov.** (ZSM 377/2004) from Ranomafana.

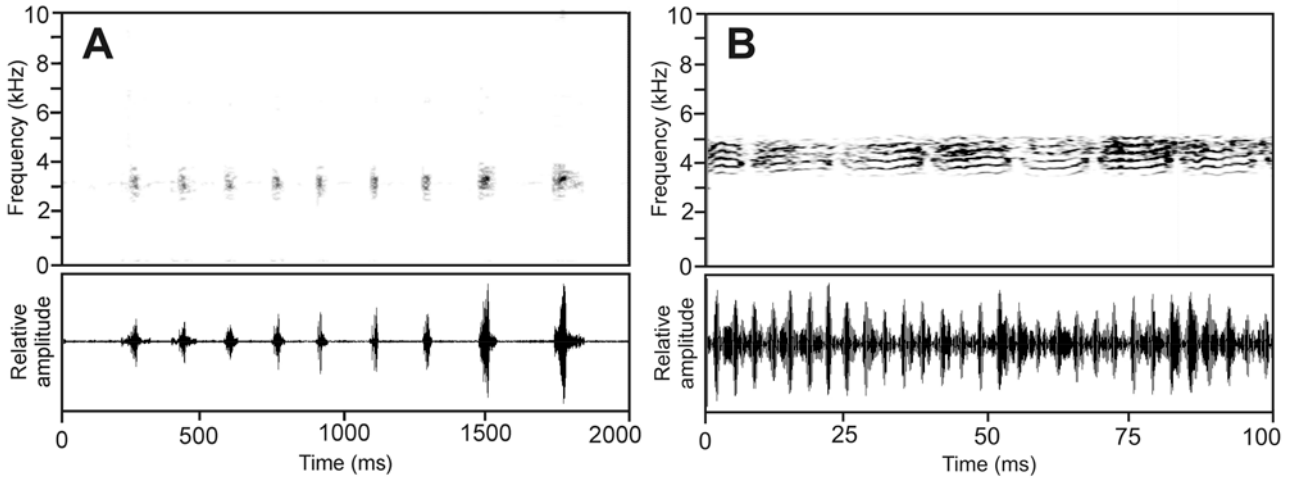


FIGURE 3. Spectrograms and waveforms of calls of *Boophis piperatus* **sp. nov.** from near Vohiparara, Ranomafana National Park (recorded on 28 January 2004, air temperature 20–21°C): (A) call type 1, (B) call type 2 (see text).

Molecular relationships. According to the phylogenetic tree (Fig. 1) this species belongs into a clade that also contains *B. arcanus* (described below), *B. feonnyala*, *B. haematopus*, *B. majori*, *B. miniatus*, *B. picturatus*, and *B. pyrrhus*. This clade receives only very low support [56% bootstrap support (BS); Bayesian posterior probability (BPP) not significant (< 0.95)], and relationships among the included species are largely unresolved. This clade largely corresponds to the *Boophis majori* group (see Glaw & Vences 2006), except for three species (*B. blommersae*, *B. marojezensis*, and *B. vittatus*) that are grouped with high support in a separately placed clade (BS 70%, BPP significant). Apparently, the *B. majori* group *sensu lato* consists of two lin-

eages, one (the *B. majori* group sensu stricto) that is here placed sister to the *B. microtympanum* group (with *B. andrangoloaka, B. laurenti, B. microtympanum, B. rhodoscelis, B. williamsi*; BS 96%, BPP significant), and a second clade with *B. blommersae, B. marojezensis,* and *B. vittatus* that may merit a status as separate species group. The molecular differentiation among all species in the *B. majori* group *sensu stricto* is high. *Boophis piperatus* is genetically highly divergent: pairwise distances are 5.3% to *B. miniatus*, 7.7% to *B. majori*, 8.5% to *B. feonnyala*, and >7% to all other species in the clade. All sequenced individuals of *B. piperatus* have identical sequences in the 16S rRNA fragment studied. The analysis also indicates divergences (2.8%) among sympatric specimens assigned to *B. majori* sensu lato, indicating that the specimens named *B.* sp. aff. *majori* "long calls" by Glaw & Vences (2007) (with strongly divergent call structure) may represent a further distinct, undescribed species (see also Vieites *et al.* 2009).

Distribution. At present *Boophis piperatus* is only reliably known from its type locality, Andranoroa river near Ranomafanakely, in the Southern Central East of Madagascar, along the road connecting Vohiparara with National Road RN7 Antananarivo-Fianarantsoa (Appendix 10).

***Boophis andrangoloaka* (Ahl, 1928) - bona species**
(Fig. 4, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *rhodoscelis* "Ambohitantely" in Glaw & Vences (2007:151–152) and as *Boophis* sp. 34 in Vieites *et al.* (2009).

Identity of the northern populations of *Boophis rhodoscelis* and resurrection of *Boophis andrangoloaka.* The identity of *B. rhodoscelis* has long remained uncertain because of the limited natural history data available on this species. Glaw & Vences (1997b) provided the first bioacoustic data based on one adult male specimen from Ambohitantely, at the western border of the Northern Central East region, which showed morphological similarities to the types of *B. rhodoscelis.* Since this time, evidence has accumulated in several respects indicating that more than one species may be included in *Boophis rhodoscelis* sensu lato. First, a second male specimen was collected at Ambohitantely which is similar morphologically and bioacoustically to the previously collected specimen. Second, several morphologically similar specimens were collected near Ranomafana in the southern central east (Andranoroa river near Ranomafanakely; 21° 14.872' S, 47° 22.580' E; 1138 m a.s.l., collected on 29 January 2004 by M. Vences and I. De la Riva). This locality is in the same general region as the type locality of *Rhacophorus rhodoscelis* Boulenger, 1882 ("East Betsileo"), and thus this population is best considered to represent typical *B. rhodoscelis.* These new specimens, however, differ by chromatic and morphological details, a moderate genetic differentiation, and differences in advertisement calls, from those collected at Ambohitantely (see Diagnosis, Vocalizations, and Comparative call data below). We conclude that these differences are best reflected by considering specimens from the two populations as distinct species, and as a classificatory consequence we propose to apply the name *Boophis rhodoscelis* to the animals from Ranomafana, and to revalidate the name *Boophis andrangoloaka* for the specimens from Ambohitantely.

Diagnosis. 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, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species, especially *B. rhodoscelis*. Species group assignment of *B. rhodoscelis* has long been controversial, and is therefore not straightforward for *B. andrangoloaka* based on morphology alone. Its morphological characters are congruent with species of the *B. majori* species group: small size (male SVL 28–30 mm); single subgular vocal sac; presence of vomerine teeth; smooth dorsal skin without

folds, spines or tubercles; absence of distinct heel flaps or spines; presence of webbing between fingers; non-transparent ventral skin; brownish dorsal ground colour without green elements; occurrence of red colour on the hidden parts of the thighs and on the webbing of the feet. Molecular data, however, clearly place *B. androngoloaka* as well as *B. rhodoscelis* in the *B. microtympanum* group (see Glaw & Vences 2006; Vieites *et al.* 2009), and in this group, *B. andrangoloaka* is distinguished from the other included species (except *B. rhodoscelis*) by its smaller size, brownish dorsal colour without distinct dorsal markings (vs. green or brown with distinct rounded markings or reticulations), and presence of red colour on hidden parts of thighs and webbing of the feet (vs. absence); furthermore, from *B. microtympanum* and *B. laurenti* it differs by having a brownish (vs. green) iris and strongly different advertisement calls; and from *B. williamsi*, by absence of orange markings on the dorsum, and tympanic region colour darker than flanks and dorsum. *Boophis andrangoloaka* also shows similarities to some species in the *B. goudoti* group (see Glaw & Vences 1997b) but can be distinguished from all species in the group by presence of red colour on the hidden parts of thighs and webbing. This latter chromatic character is shared with *B. rhodoscelis* and is also found in several species of the *B. majori* group; this probably led Blommers-Schlösser (1979) to group *B. rhodoscelis* with species today included in the *B. majori* group. However, all species in the *B. majori* group have advertisement calls that strongly differ from those of *B. andrangoloaka* (and of *B. rhodoscelis*), and they furthermore can be diagnosed by mostly lacking a tympanic region of distinctly darker colouration than the flanks and dorsum, and by lacking a distinct dark marbling on the throat. *Boophis andrangoloaka* is most similar to *B. rhodoscelis* but differs by (1) a moderate genetic divergence (see below), (2) a longer and slower call (note duration 178–198 vs. 56–100 ms; interval duration 208–265 ms vs. 93–152 ms; see below), (3) on average, a larger size (male SVL 28–30 mm vs. 25–28 mm), (4) a less contrasted ventral colour pattern with a more weakly defined light frenal stripe and a more weakly defined dark tympanic region, (5) a less contrasted ventral marbling, and (6) a slightly curved (vs. straight) supratympanic fold.

Redescription of the lectotype. ZMB 30510 (Appendix 9), adult female (designated by Glaw & Vences 1997b), SVL 37.4 mm. Body moderately slender; head slightly longer than wide, approximately as wide as body; snout rounded in dorsal and lateral view, nostrils directed laterally, slightly nearer to eye than to tip of snout; canthus rostralis rounded in cross section, straight in dorsal view; loreal region slightly concave; tympanum distinct, round; TD 54% of ED; supratympanic fold distinct; vomerine odontophores distinct, small, forming two elongated patches, positioned posteromedial to choanae; choanae medium-sized, rounded. Tongue bifid posteriorly, free behind. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers scarcely webbed, with lateral dermal fringes; webbing formula 1(1.5), 2i(1.), 2e(1), 3i(2), 3e(1.5), 4(1.25); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation reaching the eye when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes moderately webbed; webbing formula 1(0.25), 2i(1), 2e(0.5), 3i(1.25), 3e(1), 4i(1.5), 4e(1.5), 5(0.5); relative length of toes 1<2<5=3<4; toe discs enlarged. Skin smooth on dorsal surfaces, slightly granular on throat, coarsely granular on chest, belly and ventral surfaces of thighs.

Measurements (in mm): SVL 37.4, HW 12.5, HL 13.0, ED 4.6, END 2.5, NSD 2.7, NND 3.7, TD 2.5, TL 17.8, HAL 11.4, FOL 17.2, FOTL 28.0.

In preservative, ground colour of upper and lower surfaces of head, dorsum, and limbs beige, with small brown flecks and irregular markings on dorsum, flanks, lips, tympanic region, and limbs, which have a barred pattern; a cream labial stripe extending below tympanic region to the level of insertion of hind limb. Ventral parts greyish beige with brown markings on throat and chest. There are no data on colour in life of the lectotype.

New material. ZSM 5190/2005 (FGZC 2139), adult male (call voucher), from Ambohitantely Special Reserve, large swamp near administration buildings of the reserve, 18°11.967'S, 47.16.853'E, 1580 m a.s.l., central Madagascar, collected on 18 January 2005 by L. du Preez and M. Vences. ZFMK 60134, adult male

(call voucher), collected between the road RN4 and Ambohitantely Special Reserve, on 8 April 1995 by F. Glaw and D. Vallan.

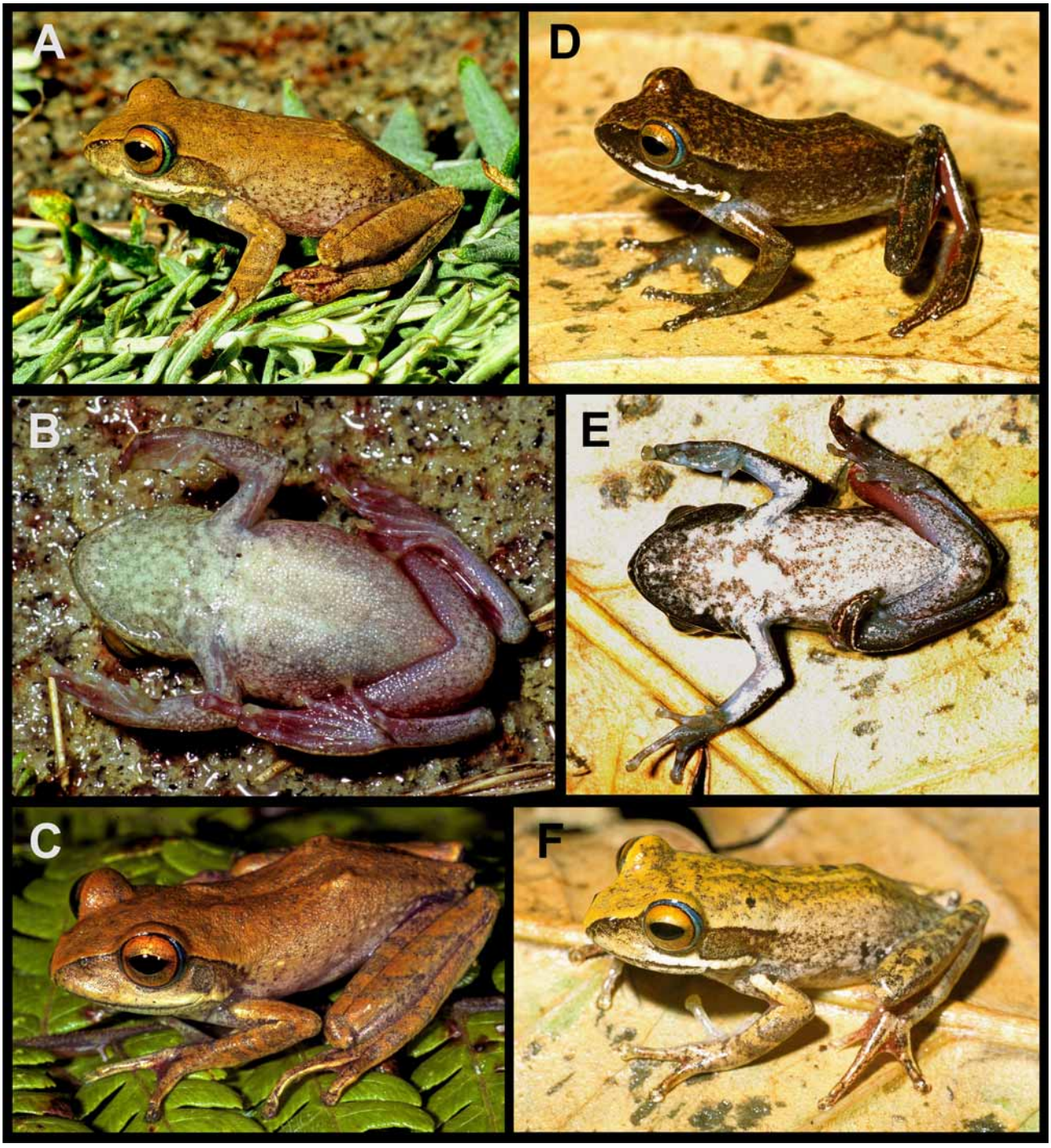


FIGURE 4. Dorsolateral view (A) and ventral view (B) of male of *Boophis andrangoloaka* (FGZC 2139) from Ambohitantely; (C) dorsolateral view of *Boophis andrangoloaka* (ZFMK 60134) from Ambohitantely; dorsolateral view (D) and ventral view (E) of a dark coloured specimen of *Boophis rhodoscelis* from Ranomafanakely; (F) dorsolateral view of a light coloured specimen of *Boophis rhodoscelis* from Ranomafanakely.

Variation. Morphometric variation is given in Appendix 1. The male specimen from Ambohitantely, ZSM 5190/2005 (Fig. 4), is overall quite similar to ZFMK 60134 and the lectotype, but in preservative it exhibits a marked dark stripe from temporal region to snout, outlined above with a cream stripe along the supratympanic fold, the upper eyelid, and the canthus rostralis, ending at the tip of the snout. The foot webbing, upper surfaces of toes, internal surfaces of tarsi, posterior surfaces of shank and anterior and posterior

surfaces of thighs are reddish purple. Calling specimens were not observed in detail during call emission but as far as recognizable upon capture had a single subgular vocal sac.

Natural history. In 2005, two to three males were heard calling late at night (no calls were heard before 22:00 h; see also Vences *et al.* 2006) when large and noisy choruses of *Heterixalus rutenbergi* and *H. betsileo* had largely fallen silent. The single collected specimen was sitting ca. 1 m high in the vegetation, next to some isolated trees, in a large exposed swampy area formed by a slow moving stream. Distance to the next patch of closed forest was 100–200 m. Calls were emitted after intervals of some minutes. A further specimen had been collected in 1995 in the same general area under similar conditions, calling at 1.5 m height in the vegetation (Glaw & Vences 1997b).

Vocalization. Calls of *Boophis andrangoloaka* are arranged in long series of notes emitted in regular intervals. A call series recorded on 18 January 2005 at Ambohitantely had a duration of 17.65 seconds and contained 43 notes. Notes are distinctly pulsed and show irregular amplitude modulation, with lowest energy in the middle of the note. Distinct frequency bands are recognisable in the spectrogram (Fig. 5A). Numerical call parameters are as follows: note duration, 178–198 ms (189 ± 7; n = 28); inter-note intervals, 208–265 ms (229 ± 18; n = 28); note repetition rate, 2.4 notes/second; 54–61 pulses/note; pulse repetition rate, 320 pulses/second; dominant frequency range 1600–3200 Hz, maximum call energy at 2470–2730 Hz (Vences *et al.* 2006, CD 1, track 56). These data largely coincide with those of another specimen recorded at Ambohitantely, as reported by Glaw & Vences (1997b), as *Boophis* cf. *rhodoscelis*).

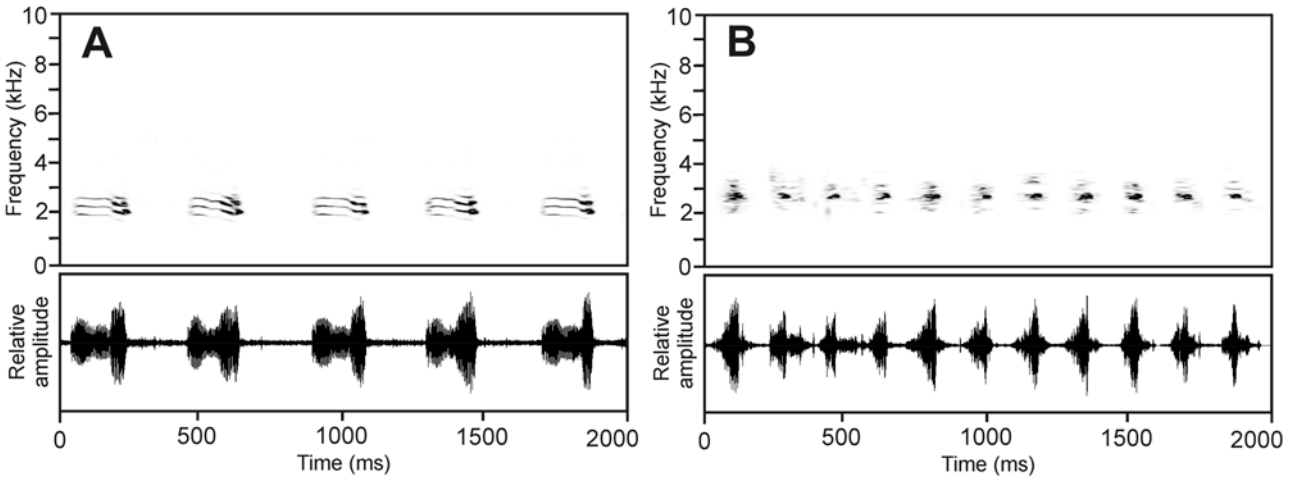


FIGURE 5. Spectrograms and waveforms of advertisement calls of: (A) *Boophis andrangoloaka* from Ambohitantely Special Reserve (recorded on 18 January 2005, air temperature app. 18°C); (B) *Boophis rhodoscelis* from Ranomafanakely, Ranomafana National Park (recorded on 28 January 2004, air temperature app. 21°C).

Comparative call data. As first reported by Vences *et al.* (2006), male specimens of *Boophis rhodoscelis* were observed in 2005 calling at night from low positions (perch heights below 1.0 m) within dense vegetation in a partly degraded forest bordering an exposed swampy area at the edge of Ranomafana National Park (locally known as Ranomafanakely), formed by a slow-moving stream. The call is of very low intensity which increases towards the end, and calling males are therefore difficult to find. The call of *B. rhodoscelis* consists of a long series of soft pulsatile notes repeated at regular intervals. Clearly separated pulses within notes are not recognizable. A note series recorded on 28 January 2004 at Ranomafanakely had a total length of 22.6 seconds (Fig. 5B). Numerical call parameters are as follows: note duration, 56–100 ms (80 ± 13; n = 24); inter-note intervals, 93–152 ms (119 ± 17; n = 25); note repetition rate, 4.6–5.0 notes/second; dominant frequency range 2000–3400 Hz, maximum call energy at 2490–3060 Hz (Vences *et al.* 2006, CD 1, track 55).

Additional synonyms. The type locality of *B. andrangoloaka* is Andrangoloaka in the Northern Central East of Madagascar. Although this site is not in the immediate vicinity of Ambohitantely, it is in an area that

has biogeographic links with Ambohitantely (e.g., haplotypes of the lizard *Phelsuma lineata* from Ambohitantely also occur in Antananarivo and in Fierenana, two localities not very far from Andrangoloaka, see Boumans *et al.* 2007). Biogeographically it would thus be possible that the same species occurs in Ambohitantely and Andrangoloaka, which further supports our decision to propose the resurrection of the name *Boophis andrangoloaka* and apply it to the Ambohitantely population.

One additional taxon is currently considered as junior synonym of *Boophis rhodoscelis* and needs to be discussed (see Glaw & Vences 1997b): *Rhacophorus brevirostris* Ahl, 1928 (type locality: northwestern Madagascar without further information). The two nomina, *andrangoloaka* and *brevirostris*, were described by E. Ahl in the same publication (Ahl 1928); the types of these two *nomina* were collected by J. M. Hildebrandt, and it is obvious that the locality data of parts of the Hildebrandt collection are dubious (see discussion in Vences & Glaw 2001, 2004). This is also true for the type locality of *Rhacophorus brevirostris* because no species similar to *Boophis rhodoscelis* is known from northwestern Madagascar. ZMB 30518, the holotype of *Rhacophorus brevirostris* Ahl, 1928 (Appendix 9), is quite similar to the *B. andrangoloaka* lectotype in general colouration; it has some brown, irregular, moderately large spots on flanks. In the absence of reliable locality data and considering this general similarity of the types, we propose to consider *Rhacophorus brevirostris* as a junior synonym of *Boophis andrangoloaka*.

Molecular relationships. According to Glaw & Vences (2006), *B. andrangoloaka* and *B. rhodoscelis* belong in the *B. microtympanum* group. This group is here not resolved as monophyletic lineage, probably due to insufficient informative sites in the short DNA fragment analysed. However, *B. andrangoloaka* is clearly placed sister to *B. rhodoscelis* with high support (97% BS, BPP significant; Fig. 1). The molecular differentiation among these two species is low (2.4%). *Boophis andrangoloaka* and *B. rhodoscelis* are both highly divergent from other species of the *B. microtympanum* group (6.2–7.5%) and the *B. majori* group (8.2–12.6%). The analysis further provides evidence for a significant and complex differentiation among mitochondrial lineages assigned to *B. laurenti* and *B. microtympanum* (up to 2.5% divergence), indicating that this complex of species is also in need of taxonomic revision (see also Glaw & Vences 2007).

Distribution. Under the current definition, two sites are reliably known for *Boophis andrangoloaka*, its type locality Andrangoloaka and Ambohitantely Special Reserve (Appendix 10).

***Boophis arcanus* sp. nov.**
(Fig. 6, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *miniatus* "Mahakajy" by Glaw & Vences (2007:154–155) and as *Boophis* sp. 29 by Vieites *et al.* (2009). First data on this species were possibly given by Andreone (1994), who recorded a small brown *Boophis* from the Ranomafana area as *B. miniatus*. Glaw *et al.* (2001) gave further information on the corresponding voucher specimens from Ifanadiana, a locality not far from Mahakajy. These specimens may belong to *B. arcanus*, but since no reliable male specimens of *B. arcanus* are known, and no genetic data are available for the Ifanadiana specimens, this hypothesis cannot be tested at present.

Holotype. ZSM 298/2006 (ZCMV 3370), adult female, from Mahakajy, 21° 16.753' S, 47°31.823' E, 577 m a.s.l., southeastern Madagascar, collected on 1 March 2006 by T. Rajaofiarison, E. Rajeriarison and M. Vences.

Paratype. UADBA 24299 (ZCMV 392), adult female, Mahakajy reserve, 21°16.753'S, 47°31.823'E, 577 m a.s.l., collected on 1 February 2004 by E. Edwards and M. Vences.

Etymology. The specific name is derived from the Latin adjective "arcanus", meaning "hidden" or "secret". It refers to the fact that this cryptic species is extremely difficult to identify based on morphological characters only, and that we were unable to collect more than two specimens despite intensive searches during three visits to the type locality.



FIGURE 6. Female paratype of *Boophis arcanus* **sp. nov.** (UADBA 24299) from Mahakajy.

Diagnosis. 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), enlarged terminal discs of fingers and toes, lateral metatarsalia separated by webbing, absence of outer metatarsal tubercle, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis majori* group based on the following combination of characters: small size (female SVL 34 mm); smooth dorsal skin without folds, spines or tubercles; presence of vomerine teeth; absence of distinct heel flaps or spines; presence of webbing between fingers; non-transparent ventral skin; brownish dorsal ground colour without green elements; occurrence of red colour on the hidden parts of the thighs and on the webbing of the feet; and molecular phylogenetic relationships (Vieites *et al.* 2009). *Boophis arcanus* differs from all described species in the *B. majori* group by strong genetic differentiation (> 7.2% to all other species, see below). It furthermore differs from the three northern species of the *Boophis majori* group (*B. blommersae, B. marojezensis* and *B. vittatus*) by the presence of red colour on thighs and feet in preservative and distinctly from *B. pyrrhus* and *B. haematopus* by colouration in life and in preservative (both species with a dorsal hourglass marking; *B. pyrrhus* with a reddish brown and *B. haematopus* with a light greenish brown dorsum with many small spots; see photographs in Glaw & Vences 2007; vs. almost uniformly brown in *B. arcanus*). It differs from *B. majori* by its larger female size (SVL 34.3 mm in *B. arcanus* vs. 29.0–29.2 mm in *B. majori*) and different colour in preservative (e. g. ground colour of back brown vs. reddish). It differs from *B. miniatus* and *B. picturatus* by having different iris colouration in life (*B. miniatus* with red colour and *B. picturatus* often with bluish colour in the outer iris area; both species without a pattern of dark vertical stripes; see photographs in Glaw & Vences 2007; vs. uniform with distinct dark vertical stripes in *B. arcanus*) and from *B. feonnyala* and *B. piperatus* by details of life colouration (a lighter ground colour and often with a pattern of fine dark spots especially in *B. piperatus*, vs. almost uniformly brown in *B. arcanus*) and strong genetic differentiation.

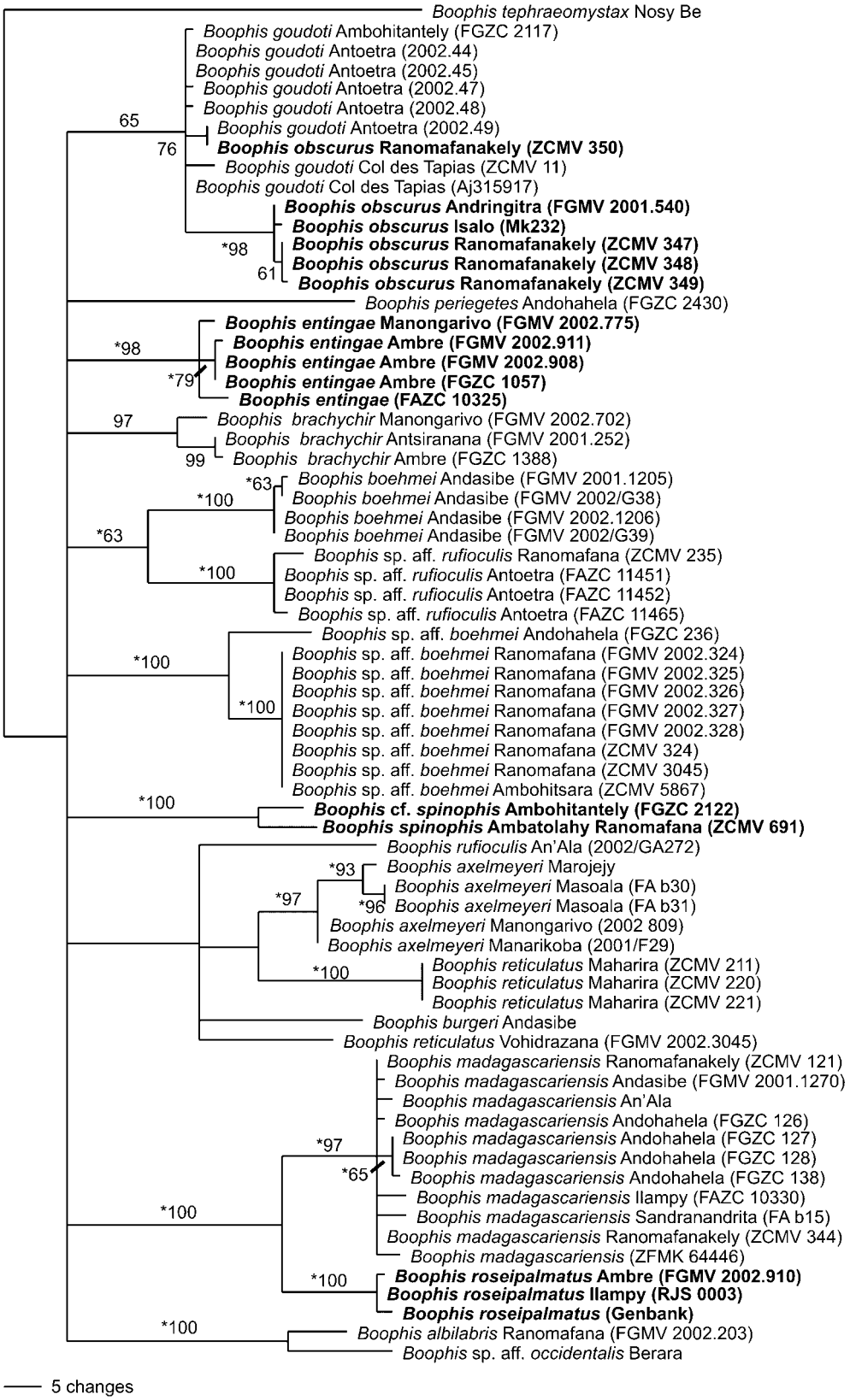


FIGURE 7. Maximum parsimony 16S rRNA phylogram of species of the *Boophis goudoti* group. From 510 total characters, 340 were constant and 130 parsimony informative. MP searches retained 3681 trees of which a strict consensus is shown. Consensus support values higher than 50, from 2000 bootstrap replicates, are shown; an asterisk indicates Bayesian posterior probabilities equal or higher than 95%. Species newly described or resurrected herein are in bold.

Description of the holotype. Female, in relatively good state of preservation (a large tissue sample was taken from the right thigh and a smaller sample from the left thigh), SVL 34.3 mm. Body slender; head slightly longer than wide, wider than body; snout rounded in dorsal view, obtuse in lateral view, nostrils directed laterally, slightly nearer to tip of snout than to eye; canthus rostralis sharp in cross section, slightly concave in dorsal view, loreal region slightly concave; tympanum distinct, rounded, TD 44% of ED; supratympanic fold distinct; vomerine odontophores distinct, well separated in two round patches, positioned posteromedial to choanae; choanae medium-sized, rounded. Tongue bifid, free posteriorly. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers moderately webbed; webbing formula 1(1.5), 2i(1.25), 2e(1.25), 3i(2), 3e(1.25), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs distinctly enlarged. Hindlimbs slender; tibiotarsal articulation reaching snout tip when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle very small and indistinct; no outer metatarsal tubercle; webbing between toes well-developed, webbing formula 1(0), 2i(0.25), 2e(0), 3i(1), 3e(0), 4i(1), 4e(1), 5(0.25); relative length of toes 1<2<5=3<4; toe discs enlarged. Skin on dorsal surfaces smooth, very finely granular on throat and chest, coarsely granular on belly; few slightly enlarged tubercles ventrally under the cloacal opening.

Measurements (in mm): SVL 34.3, HW 12.3, HL 12.8, ED 5.0, END 3.1, NSD 2.6, NND 3.5, TD 2.2, TL 19.2, HAL 10.6, FOL 15.5, FOTL 26.6.

After 1.5 years in preservative, dorsal surfaces brown with fine red and black dots. Back with a large, but poorly developed, hourglass-like pattern that is slightly darker than the surrounding skin. Three distinct dark crossbands on forelimbs, two on hindlimbs. Concealed parts of thighs reddish. Terminal tips of fingers and toes partly red, dorsally as well as ventrally. Webbing between toes pink. Throat dirty white with a brownish band along the jaw. Chest cream white, belly yellowish. Lateral parts of fifth toe and tarsus dark brown.

Variation. The paratype (deposited in UADBA) was superficially similar to the holotype but was not available for a detailed morphological examination. Its dorsal life colouration (see Glaw & Vences 2007: 155, photo 5) was largely uniformly brown with few scattered black spots and dots on back and extremities. The inguinal region had a bluish shade. The iris was silvery with vessel-like lines and the iris periphery was blue. Ventral life colouration unknown.

Natural history. Two females of this species have been found at Mahakajy in 2004 and 2006. Despite repeated visits to the site, no unknown calls were heard, indicating either that reproduction takes place elsewhere or is seasonal. Specimens were sitting, at night, on leaves 1–2 m high in bushes at the edge of disturbed rainforest.

Molecular relationships. *Boophis arcanus* is placed in the *B. majori* group sensu stricto according to the mitochondrial phylogenetic analysis (see account of *B. piperatus* above). Its position within this lineage is not resolved (Fig. 1), but its genetic divergences are remarkably high: 7.3% to *B. miniatus,* 8.2% to *B. piperatus*, 8.4% to *B. feonnyala*, and >9% to all other species.

Distribution. At present, *Boophis arcanus* is only reliably known from its type locality, Mahakajy Private Reserve in the southern-central east of Madagascar, along the road Ranomafana-Ifanadiana (Appendix 10).

***Boophis brachychir* (Boettger, 1882)**
(Fig. 8, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *brachychir* by Glaw & Vences (2007:162). The picture shown by these authors (Glaw & Vences 2007:163, photo 3) as *B. brachychir* does not show *B. brachychir* but *B. entingae,* described below, and the depicted specimen was collected at Andampy (Tsaratanana), not at Manongarivo.

Identity and redefinition. The original description of *Boophis brachychir* is based on a single specimen of 71 mm snout-vent length from Nosy Be island. The species was considered as a junior synonym of *Boophis*

madagascariensis since Guibé (1947), but was resurrected by Glaw & Vences (1992) after the discovery of a species similar but clearly different from *B. madagascariensis* at Benavony, on the mainland just opposite of Nosy Be. Nevertheless the identity of this species remained difficult to assess as the holotype was never traced after the species description and is considered lost (Blommers-Schlösser & Blanc 1991; G. Köhler, pers. comm.). Curiously, *B. brachychir* was not rediscovered on Nosy Be despite intensive recent surveys (see Andreone *et al.* 2003). However, a search in Herpnet (http://www.herpnet.org/) revealed that two *Boophis madagascariensis*-like specimens from Nosy Be are available in the collection of the California Academy of Sciences. We therefore redescribe and redefine *Boophis brachychir* based on these two specimens (CAS 156770, collected near Beomby in 1984 by L. G. Hoevers and CAS 156812 collected near Andranobe in 1983 by L. G. Hoevers) which are adult males with distinct nuptial pads.

Redescription. Based on specimen CAS 156812 (Appendix 9), adult male, SVL 41.5 mm. Body moderately slender; head longer than wide, slightly wider than body; snout long, rounded in dorsal and lateral view, nostrils directed laterally, nearer to eye than to tip of snout; canthus rostralis sharp in cross section, straight in dorsal view, reaching the tip of snout; loreal region slightly concave; eye large; tympanum distinct, rounded, TD 67% of ED; supratympanic fold thin, clearly distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, elongated. Tongue posteriorly bifid, free. Arms moderately slender; a pointed dermal appendage on elbow; subarticular tubercles single, round; inner palmar tubercle narrow, elongated, in close contact with nuptial pad; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1.5), 2i(1.5), 2e(0.75), 3i(2), 3e(1.5), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hind limbs slender; a pointed dermal appendage on heel; tibiotarsal articulation reaching tip of snout when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0), 2i(0.25), 2e(0), 3i(0.75), 3e(0), 4i(0.75), 4e(0.75), 5(0.25); relative length of toes 1<2<3<5<4; toe discs enlarged. Skin smooth on dorsal surfaces, finely granular on throat and chest, coarsely granular on belly, granular on ventral surface of thighs.

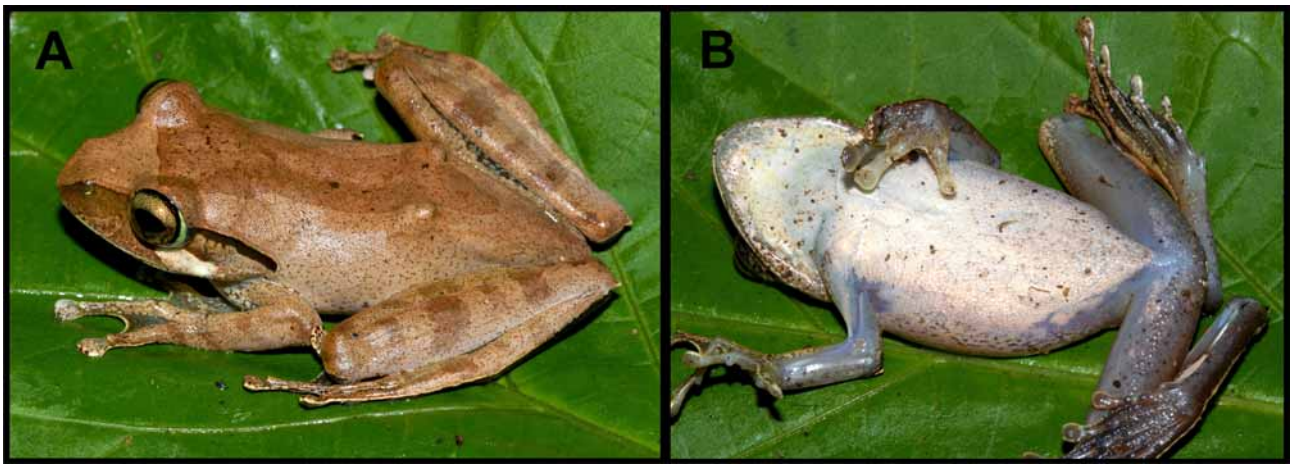


FIGURE 8. Male of *Boophis brachychir* (ZSM 2157/2007) from Forêt d'Ambre Special Reserve: (A) dorsolateral view; (B) ventral view.

Measurements (in mm): SVL 41.5, HW 14.3, HL 16.4, ED 5.8, END 3.4, NSD 3.3, NND 4.2, TD 3.9, TL 23.1, HAL 12.4, FOL 18.3, FOTL 30.5.

In preservative, ground colour of upper surface of head, dorsum and legs pale brown with darker, irregular, diffuse markings and some dark brown small blotches; legs barred; flanks pale beige; a fine cream stripe on upper lip. Almost no reticulated pattern on posterior surface of thighs and no whitish subocular bar recognizable. Ventral surfaces creamy beige. Colour in life unknown.

Variation. Morphological variation is given in Appendix 2. The background colouration of dorsal surfaces is always brown, but the pattern varies from mostly uniform to a pattern consisting of small, scattered grey (in preservative) lichenous blotches (ZSM 933/2003, male) or irregular blackish blotches (ZSM 586/2001). Specimens ZSM 897/2003, ZSM 2156/2007 (FGZC 1219), juveniles, and ZSM 2157/2007 (FGZC 1220), female, have a pinkish grey (in preservative) triangle between eyes and snout and two dorsolateral bands of the same colour connected on the sacral region; they also have an oblique, white subocular bar. The supratympanic fold is bordered inferiorly by a dark brown stripe in some specimens. No remarkable variation exists in ventral pattern. Calling specimens were not observed in detail during call emission but as far as recognizable upon capture had a single subgular vocal sac.

Referred specimens. ZSM 993/2003, Camp Norbert, Manongarivo, 5 February 2003, collected by F. Glaw, R. D. Randrianiaina and M. Vences; ZSM 2155/2007, 2156/2007, 2227/2007, 2228/2007 (males), ZSM 2157/2007, 2230/2007 (females), Forêt d'Ambre Special Reserve, 12°28'00" S, 49°13'37" E, 470 m a.s.l., collected on 12 March 2007 by P. Bora, F. Glaw and J. Köhler.

Natural history. At Manongarivo, calling specimens were observed at perch heights of about 2 m in bushes in a largely cleared and degraded area near rainforest, at a distance of at least 15 m from a larger fast-flowing stream with alternating rocky and sandy bottom. At Forêt d'Ambre, non-calling specimens were observed at night in the vegetation of a degraded forest, at perches 0.5–2 m above the ground.

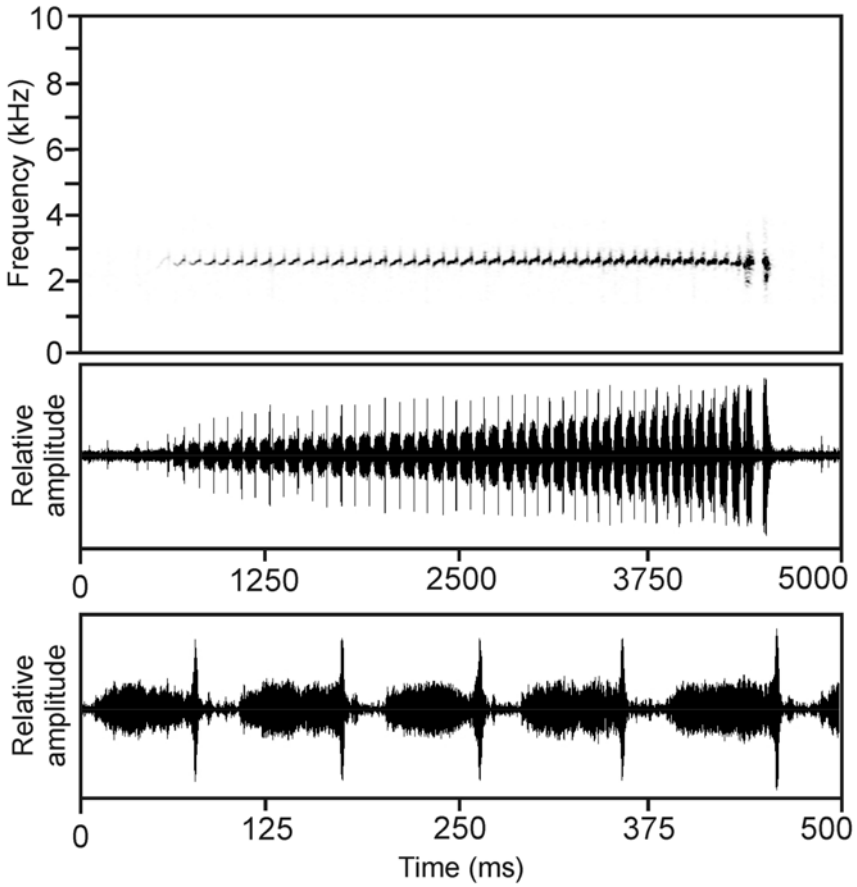


FIGURE 9. Spectrogram, corresponding waveform and expanded waveform of the advertisement call of *Boophis brachychir* from Manongarivo Special Reserve (recorded on 1 February 2003, air temperature 24.5°C).

Vocalization. The call of *B. brachychir* from Manongarivo Special Reserve is a long series of short whistles, repeated in very fast succession (Fig. 9). Notes are separated by very short intervals only. Overall amplitude as well as note repetition rate is increasing towards the end of the call. Each note shows some amplitude modulation, with a distinct energy peak at its end. The call ends with two "noisy" pulsatile notes which may

also be emitted separately. Numerical call parameters are as follows: call duration, 4015 ms (n = 1); 45 notes/call; note duration, 50–78 ms (62 ± 9; n = 26); inter-note interval, 20–30 ms (24 ± 2; n = 26); note repetition rate, 10.7–13.0 notes/second. Dominant frequency range 2400–3100 Hz, maximum call energy at 2610–2720 Hz. Pulsatile notes may be of slightly longer duration, 68–94 ms (n = 5), and their call energy is distributed in a slightly wider frequency band (1500–3400 Hz). These pulsatile notes are emitted at irregular intervals (Vences *et al.* 2006, CD 1, track 62, as *Boophis* sp. aff. *brachychir*).

Distribution. Under the definition proposed here, *Boophis brachychir* is known from (1) its type locality Nosy Be (with precise localities Andranobe and Beomby), (2) Manongarivo Special Reserve, (3) Forêt d'Ambre Special Reserve, and (4) near Antsiranana (Appendix 10).

***Boophis entingae* sp. nov.**
(Fig. 10, Appendix 9)

Remark. This species has been referred to as *Boophis brachychir* by Glaw & Vences (1992, 1994, 2007:162–163) and as *Boophis* sp. 11 by Vieites *et al.* (2009). The pictures 3, 4a and 4b in Glaw & Vences (2007:163) all show *B. entingae* (see account above for *B. brachychir*).

Holotype. ZSM 2083/2007 (FGZC 1057), adult male (call voucher), from Montagne d'Ambre National Park, northern Madagascar, ca. 12°29'38"S, 49°10'55" E, app. 750 m a.s.l., collected on 25 February 2007 by P. Bora, H. Enting, F. Glaw, A. Knoll and J. Köhler.

Paratypes. ZSM 897/2003 (FGMV 2002–908), juvenile, Montagne d'Ambre, collected on 18 February 2003 by F. Glaw, R. Randrianiaina and A. Razafimanantsoa; ZSM 624/2001 (FGMV 2001.158), adult male (call voucher), from Tsaratanana massif, Manarikoba forest, Andampy (Camp 0), 14°02'32"S 48°45'42"E, ca. 730 m a.s.l., collected on 10–11 February 2001 by F. Andreone, F. Mattioli, J. Randrianirina and M. Vences; ZSM 830/2003 (FG/MV 2002–0775) and ZSM 831/2003 (FGMV 2002–0776), two adult males from Manongarivo, Camp 0, collected on 1 February 2003, by F. Glaw, R. D. Randrianiaina and M. Vences; ZSM 852/2003 (FG/MV 2002–0822), adult male, and ZSM 858/2003 (FG/MV 2002–0829), juvenile, both from Manongarivo, Camp 1, collected on 3 February 2003 by F. Glaw, R. D. Randrianiaina and M. Vences; ZSM 899/2003 (FG/MV 2002–0911), female, Montagne d'Ambre, collected on 17–18 February 2003 by F. Glaw, R. Randrianiaina and A. Razafimanantsoa; ZSM 214/2004 (FGZC 418), Montagne d'Ambre, collected on 21 February 2004 by F. Glaw, M. Puente, R. Randrianiaina and A. Razafimanantsoa; ZSM 2081/2007 (FGZC 1055), from Montagne d'Ambre, 12°29'38"S, 49°10'55" E, ca. 750 m a.s.l., collected on 25 February 2007 by P. Bora, H. Enting, F. Glaw, A. Knoll and J. Köhler; ZFMK 53637–53639, three adult males from near Benavony, collected on 16 February 1992 by F. Glaw and J. Müller-Jung.

Etymology. We dedicate this species to Hildegard Enting (Frankfurt/Main). Her help with logistics, field work and preparation of specimens during two Madagascar expeditions contributed significantly to their success.

Diagnosis. 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, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis goudoti* group based on the following combination of characters: relatively large size (male SVL 47–58 mm); brownish dorsal ground colour; non-transparent ventral skin, absence of red ventral colour; presence of dermal flaps or tubercles on heels and elbows; presence of webbing between fingers; single subgular vocal sac; presence of vomerine teeth; presence of white tubercles ventrally under the cloacal opening; presence of a sharp canthus rostralis, and molecular phy-

logenetic relationships (see Vieites *et al.* 2009). *Boophis entingae* differs from all described species in the *B. goudoti* group by strong genetic differentiation (see below) and from *B. boehmei*, *B. rufioculis*, *B. axelmeyeri*, *B. reticulatus*, *B. madagascariensis*, *B. goudoti*, *B. obscurus*, and *B. periegetes* by advertisement calls: in brief, calls of *B. goudoti*, *B. madagascariensis* and *B. obscurus* are irregular croaks and moans rather than the regular series of 2–4 moans of *B. entingae;* the calls of *B. brachychir* and *B. periegetes* are melodious whistles rather than moans of noisy structure; calls of *B. boehmei* are series composed of two different note types; calls of *B. axelmeyeri* and *B. rufioculis* are composed of series of much shorter notes than those of *B. entingae.* The strongest similarities are with calls of *B. reticulatus* which however emits regularly a second call type (a rapid series of short notes) unknown from *B. entingae*. *Boophis entingae* furthermore differs from *B. boehmei*, *B. rufioculis*, *B. burgeri*, *B. reticulatus* and *B. axelmeyeri* by larger size (SVL of males 46.5–58.5 mm vs. 27–43 mm) and iris colouration. It differs from *B. goudoti* and *B. periegetes* by presence of distinct dermal flaps on heels (vs. absence). It differs from *B. madagascariensis* by presence of a usually distinct, sharply outlined brown marking that extends from upper eyelids and the interorbital region to the posterior dorsum (vs. absence). It differs from *B. brachychir* by its larger size (SVL of males 46.5–58.5 mm vs. 38.8–46.9 mm) and a reticulated pattern on posterior surfaces of thighs which is absent in *B. brachychir*. From *B. obscurus*, resurrected herein, *B. entingae* is distinguished by the absence of dorsal spicules in breeding males (vs. presence in *B. obscurus*), presence of a heel tubercle (vs. absence), and apparently smaller size of males (46.5–58.5 mm vs. 42–82 mm). From *B. roseipalmatus* it differs by the smaller size of males (46.5–58.5 mm vs. 59–68 mm, see Appendix 2) and absence of pinkish colour on webbing and iris periphery.

Description of holotype. Adult male, SVL 53.3 mm. Body moderately slender; head longer than wide, wider than body; snout long, sub-elliptical in dorsal view, obtuse to acuminate in lateral view; nostrils directed laterally, nearer to eye than to tip of snout; canthus rostralis sharp in cross section, straight in dorsal view, reaching the tip of snout; loreal region concave posteriorly, almost straight anteriorly; eye large; tympanum distinct, rounded, TD 61% of ED; supratympanic fold narrow, prominent; vomerine odontophores distinct, well separated in two elongated patches, positioned median between choanae; choanae medium-sized, rounded. Tongue removed for tissue sample. Arms moderately slender; a small pointed dermal appendage on elbow; thin dermal fold on outer edge of lower arm; subarticular tubercles single, round; inner palmar tubercle narrow, elongated, partly fused with nuptial pad; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1.5), 2i(1.5), 2e(1), 3i(2), 3e(1.25), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hind limbs slender; a pointed dermal appendage on heel; tibiotarsal articulation reaching between nostril and tip of snout when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle medium-sized, distinct, elongated; no outer metatarsal tubercle; toes moderately webbed; webbing formula 1(0), 2i(0.75), 2e(0), 3i(0.75), 3e(0), 4i(1), 4e(1), 5(0.25); relative length of toes 1<2<3=5<4; toe discs enlarged. Skin smooth on dorsal surfaces, smooth on throat and chest, coarsely granular on belly, granular on ventral surface of thighs, prominent scattered tubercles around cloaca.

Measurements (in mm): SVL 53.3, HW 18.2, HL 19.7, ED 7.0, END 3.9, NSD 4.6, NND 5.7, TD 4.3, TL 28.5, HAL 17.3, FOL 24.3, FOTL 39.4.

After six months in preservative, ground colour of upper surface of head, dorsum and limbs greyish brown, with few irregularly scattered black spots; irregular, indistinct dark blotch posterior to eyelids; supratympanic fold bordered with dark brown; upper lip creamy white; outer edges of lower arm with thin white line, bordered by thin brown line ventrally; dorsal surfaces of limbs indistinctly barred; flanks pale beige, with some brown spots in groin; two whitish dots of enlarged tubercles in cloacal region; indistinct beige supracloacal line; posterior surfaces of thighs greyish pale with dark brown reticulation; ventral surfaces creamy beige, with some pale greyish mottling on belly and ventral surfaces of thighs.

In life, ground colour of upper surface of head, dorsum and legs pale grey, with few irregularly scattered black spots; sharply outlined creamy pale brown blotch on middorsum, its corners extending to interorbital

region and upper eyelids anteriorly, posteriorly fading at level of urostyl; supratympanic fold bordered with black; loreal region with greyish brown shade; outer edges of lower arm and tarsus with thin white line, bordered by thin blackish line ventrally; dorsal surfaces of limbs with creamy pale brown transversal bars; flanks whitish, with some brown spots in groin; two white dots corresponding to enlarged tubercles in cloacal region; indistinct white supracloacal line; posterior surfaces of thighs light blue with blackish reticulation; throat, chest and venter creamy white, with some indistinct pale greyish mottling on belly; ventral surfaces of thighs, palmar and plantar surfaces with weak bluish to pinkish tint and indistinct pale grey mottling. Iris copper, with some fine black spotting, outer iris area black, iris periphery turquoise green.

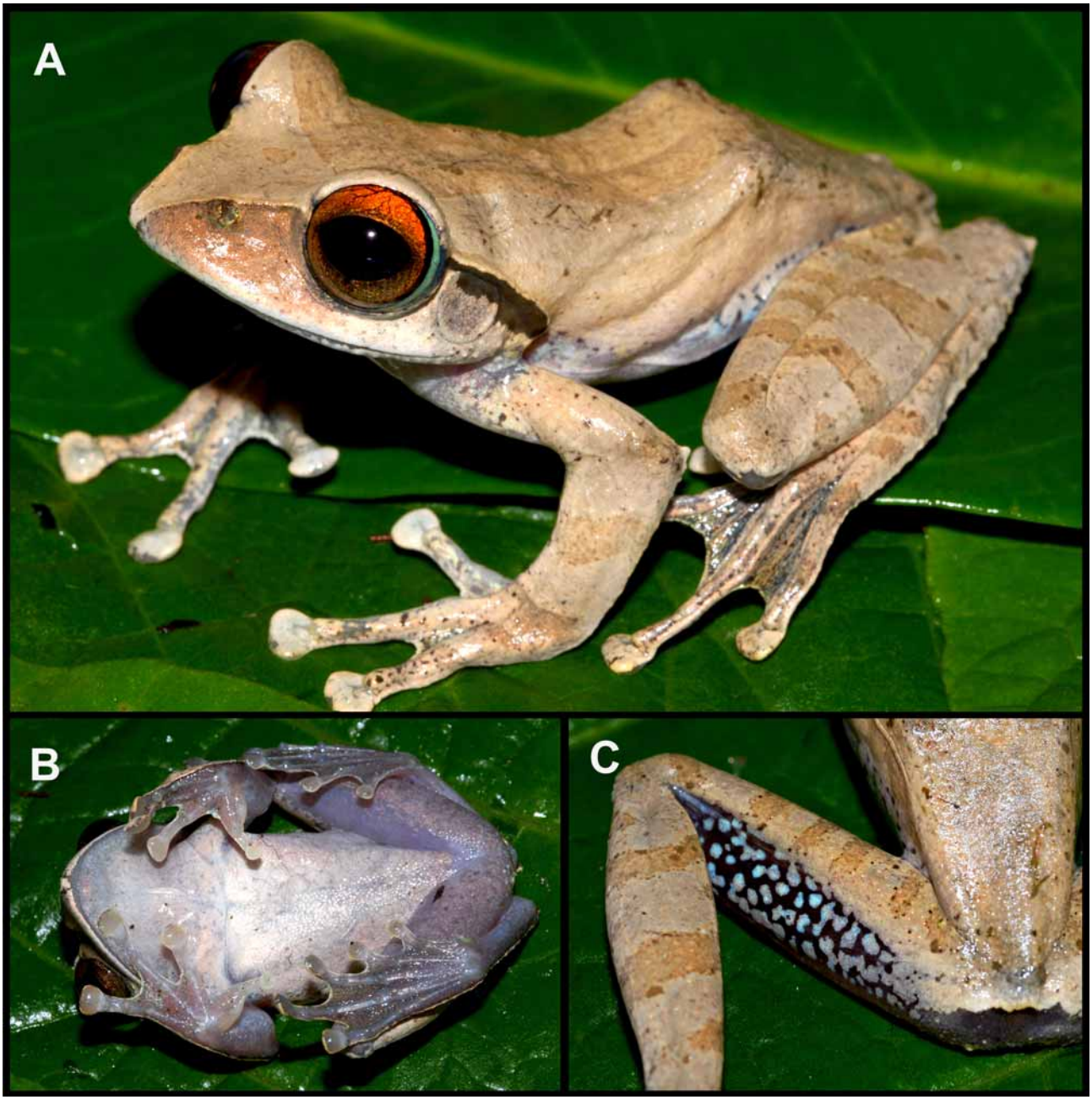


FIGURE 10. Male holotype of *Boophis entingae* **sp. nov.** (ZSM 2083/2007): (A) dorsolateral view; (B) ventral view; (C) detail showing colouration of posterior surfaces of thigh.

Variation. Morphological variation is given in Appendix 2. In preservative, the ground colouration of dorsal surfaces varies from grey to brown, with a variable pattern from mostly uniform to a pattern consisting of diffuse dark brown blotches and minute black flecks. Specimen ZFMK 53639 (male) lacks the dark stripe

under the supratympanic fold, and has well-marked minute spicules on dorsal surface. Some specimens (ZSM 624/2001, 830–831/2003, 852/2003, males) have a pale triangle between eyes and snout and two faint, broad dorsolateral bands of the same colour delimiting a darker inverted triangle on middorsum. There is no remarkable variation in ventral colouration. Likewise, there is no sexual dimorphism in colour pattern, but females are larger than males (maximum SVL in females 86.5 vs. 58.5 mm in males). Calling specimens during call emission had a single subgular vocal sac that was only weakly inflated.

Natural history. Males call at night along rainforest streams, from perch heights about 1–2 m. Streams where this species was found were often relatively slow-moving and with a sandy bottom.

Vocalization. The call of *B. entingae* from Benavony and Montagne d'Ambre was already briefly described by Glaw & Vences (1992, 1994) as that of *B. brachychir.* Call type 1 consists of pulsatile notes which might be arranged in series of 2–3. The general harmonic structure becomes unharmonious at the end of the note. Frequency is distributed in a relatively broad frequency bands. Sometimes a second call type is emitted, consisting of short click notes of about 60 ms duration (Glaw & Vences 1994). In addition to these already published data, we here describe call type 1 recorded at Manongarivo Special Reserve and Andampy (Tsaratanana), as well as the distress call recorded at Montagne d'Ambre National Park. Call type 1 from Manongarivo (Fig. 11A): note duration, 232–310 ms (280 ± 30; n = 6); inter-note interval, 226–245 ms (n = 3); note repetition rate (within series), approximately 2 notes/second; dominant frequency range 1700–3200 Hz, maximum call energy at 2200–2360 Hz (Vences *et al.* 2006, CD 1, track 61, as *B. brachychir*). Call type 1 from Andampy, Tsaratanana, recorded in 2001 at 25–26 °C air temperature is almost identical to call type 1 from Manongarivo in spectral and temporal characters: note duration, 227–331 ms (276 ± 39; n = 10); inter-note interval (within series), 168–214 ms (190 ± 20; n = 5); note repetition rate (within series), 2.0–2.3 notes/second; dominant frequency range 1900–3300 Hz, maximum call energy at 2530–2600 Hz. The distress call (Fig. 11B) consists of a long pulsed note. Note duration is 589–712 ms (641 ± 43; n = 8). Frequency is distributed in a very broad band of approximately 500–15000 Hz. Several distinct frequency bands are recognizable. Between 500–10000 Hz, 15 of such bands are present, separated from each other by a frequency gap of approximately 500–700 Hz; maximum call energy is at 4740–6790 Hz (Vences *et al.* 2006, CD 1, track 61, as *B. brachychir*).

Comparative call data. The call of *B. entingae* differs significantly from that of *B. brachychir* longer note duration, longer inter-note intervals and much slower note repetition rate. For a detailed comparison, see the numerical parameters of *B. brachychir* calls from Manongarivo Special Reserve provided above.

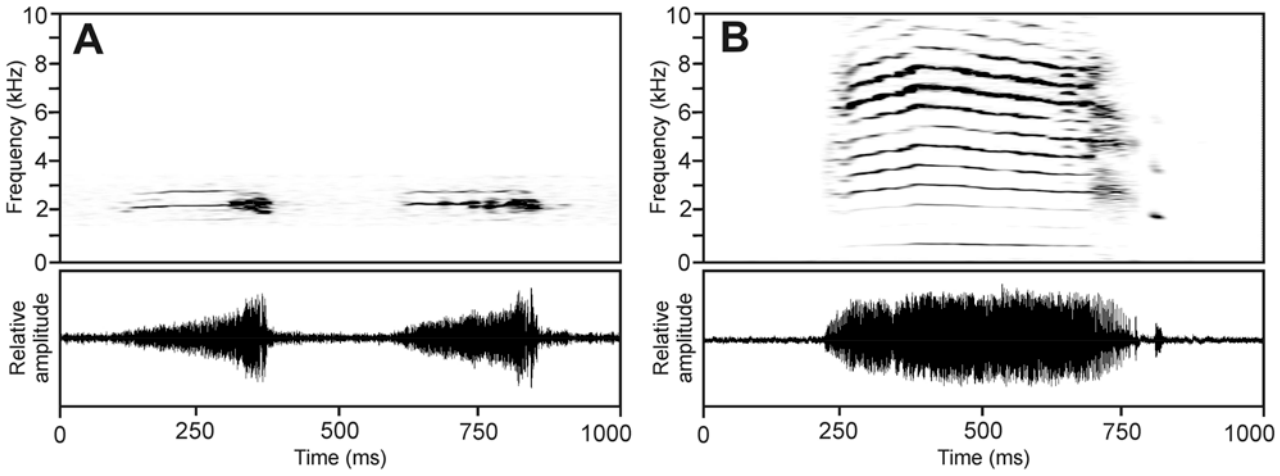


FIGURE 11. Spectrograms and waveforms of calls of *Boophis entingae* **sp. nov.**: (A) advertisement call from Manongarivo Special Reserve (recorded on 2 February 2003, air temperature 22°C); (B) distress call from Montagne d'Ambre National Park (recorded on 14 March 1994, air temperature 21.2°C).

Molecular relationships. The molecular phylogenetic analysis is unable to resolve relationships among species in the *B. goudoti* group (Fig. 7), probably due to a limited number of informative sites in the short 16S rRNA fragment studied. However, each species is resolved as a clearly and usually strongly supported monophyletic unit (except for *B. obscurus*, see below). The analysis also indicates that several species as currently understood comprise highly divergent mitochondrial lineages, such as *B. reticulatus, B. rufioculis,* and *B. boehmei* (each with differences between specimens from the Andasibe and Ranomafana regions). *Boophis brachychir* and *B. entingae* are each monophyletic clades and show high genetic divergences to each other (4.5–5.7%) and to other species in the *B. goudoti* group (4.5–11.5%), while within each of these species the divergences are low: 1.8% between *B. brachychir* from Montagne d'Ambre and Manongarivo, and 1.1% between *B. entingae* from Montagne d'Ambre and Manongarivo. Both species show comparatively low divergences of 4.5–5.3% to *B. goudoti* and *B. obscurus* (resurrected below), whereas the divergences to *B. madagascariensis* and *B. roseipalmatus* (described below) are higher (8.9–11.5%).

Distribution. *Boophis entingae* is known from its type locality, Montagne d'Ambre National Park, and from Manongarivo Special Reserve (campsites 0 and 1), Tsaratanana Strict Nature Reserve (Manarikoba forest, Andampy campsite), and Benavony (Appendix 10).

***Boophis roseipalmatus* sp. nov.**
(Fig. 12, Appendix 9)

Remark. Part of the population from Montagne d'Ambre referred to as *B. madagascariensis* by Glaw & Vences (1994) belongs to this species, as does *Boophis* sp. aff. *madagascariensis* "North" in Glaw & Vences (2007:164–165) and D'Cruze *et al.* (2008), and *Boophis* sp. 12 as used in Vieites *et al.* (2009).

Holotype. ZSM 211/2004 (FGZC 414), adult male, from Montagne d'Ambre National Park, app. 12°31' S, 49°10' E, 1000 m a.s.l., northern Madagascar, collected on 21 February 2004 by F. Glaw, M. Puente, R. Randrianiaina and A. Razafimanantsoa.

Paratypes. ZFMK 90152 (formerly ZSM 898/2003 [FG/MV 2002-910]), adult female, Montagne d'Ambre, collected on 17–18 February 2003 by F. Glaw, R. D. Randrianiaina and A. Razafimanantsoa ZSM 905/2003 (FG/MV 2002–0924), adult female, from Montagne d'Ambre, collected on 19 February 2003 by F. Glaw, R. D. Randrianiaina and A. Razafimanantsoa; ZSM 210/2004 (FGZC 412), ZSM 212/2004 (FGZC 415), ZSM 220/2004 (FGZC 429), three adult females, and ZSM 213/2004 (FGZC 417), one adult male, all from Montagne d'Ambre, collected on 21 February 2004 by F. Glaw, M. Puente, R. Randrianiaina and A. Razafimanantsoa; ZSM 2071/2007 (FGZC 1015), adult male from Montagne d'Ambre, Voie des milles arbres, 12°31'00" S, 49°10'36" E, 1050 m a.s.l., northern Madagascar, collected on 23 February 2007 by P. Bora, H. Enting, F. Glaw, A. Knoll and J. Köhler.

Etymology. The specific name is an adjective derived from the Latin "roseus", meaning pink, and "palma", meaning hand surface. It refers to the pink colour of webbing between fingers in life, diagnostic for the species.

Diagnosis. 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 (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis goudoti* group based on the following combination of characters: large size (male SVL 60–69 mm); brownish dorsal ground colour; non-transparent ventral skin; no distinct red (but pinkish) colour on ventral surface; presence of dermal flaps on heels and elbows; presence of webbing between fingers; single subgular vocal sac; presence of vomerine teeth; presence of

white tubercles ventrally under the cloacal opening, presence of a sharp canthus rostralis; and molecular phylogenetic relationships (see Vieites *et al.* 2009). *Boophis roseipalmatus* differs from all described species in the *B. goudoti* group by strong genetic differentiation (see below) and the usually distinct pink webbing between the fingers. It furthermore differs from *B. boehmei*, *B. rufioculis*, *B. burgeri*, *B. reticulatus*, and *B. axelmeyeri* by its larger size (SVL of males 60–69 mm in *roseipalmatus* vs. 27–43 mm in the other mentioned species) and different iris colouration (absence of red colour in the outer iris area as is typical for *B. axelmeyeri*, *B. boehmei*, and *B. rufioculis*; absence of a pattern of dark stripes typical for *B. reticulatus*; no distinct blue iris periphery as in *B. boehmei* and *B. burgeri*. It differs from *Boophis goudoti*, *B. obscurus*, and *B. periegetes* by the presence of distinct dermal flaps on heels. It differs from *B. brachychir* by its larger size (SVL of males 60–69 mm vs. 39–47 mm) and absence of the sharply outlined brown marking that extends from between the eyes to the posterior back present in *B. brachychir*. It differs from *B. entingae* by its larger size (male SVL 60–69 mm vs. 47–58 mm) and absence of a reticulated pattern on the concealed parts of the thighs. It differs from the most similar *B. madagascariensis* by the absence of a spotted pattern on the concealed parts of the thighs, and by the often pink colour of the webbing between fingers in life.

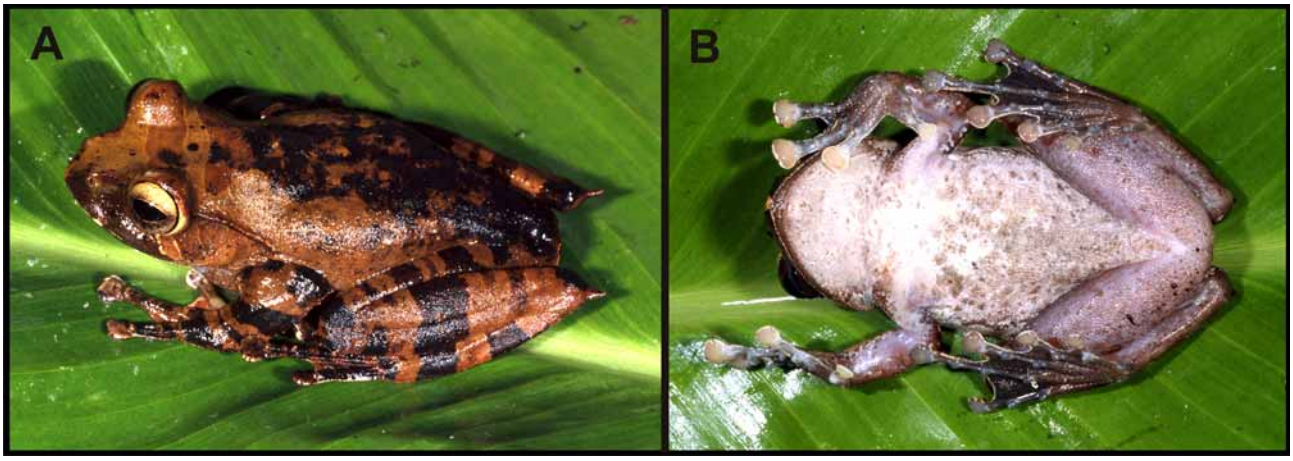


FIGURE 12. Male holotype of *Boophis roseipalmatus* **sp. nov.** (ZSM 211/2004) from Montagne d'Ambre National Park: (A) dorsolateral view; (B) ventral view.

Description of the holotype. Adult male, SVL 66.2 mm. Body moderately robust; head wider than long, slightly wider than body; snout subacuminate in dorsal view, obtuse in lateral view, nostrils directed laterally, nearer to tip of snout than to eye; canthus rostralis sharp in cross section, concave in dorsal view, reaching the tip of snout; loreal region concave; tympanum distinct, rounded, TD 55% of ED; supratympanic fold clearly distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae large, elongated. Tongue bifid posteriorly, free behind. Arms moderately robust; a short pointed dermal appendage on elbow; subarticular tubercles single, round; inner palmar tubercle elongated, in close contact with nuptial pad; nuptial pad creamy yellow, covering dorsal and posterior surfaces of first finger and dorsal surface of basis of second finger; outer palmar tubercle rounded, poorly distinct; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1.5), 2i(1.5), 2e(0.50), 3i(1.75), 3e(1), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hind limbs moderately slender; a pointed dermal appendage on heel; tibiotarsal articulation reaching tip of snout when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0), 2i(0.25), 2e(0), 3i(0.75), 3e(0), 4i(0.75), 4e(0.75), 5(0); relative length of toes 1<2<3=5<4; toe discs enlarged. Skin smooth on dorsal surfaces, finely granular on throat and chest, coarsely granular on belly and ventral surface of thighs, and with larger whitish tubercles ventrally under the cloacal opening.

Measurements (in mm): SVL 66.2, HW 24.3, HL 23.8, ED 7.6, END 5.5, NSD 4.7, NND 6.6, TD 4.2, TL 35.6, HAL 20.8, FOL 29.3, FOTL 47.4.

After almost four years in preservative, ground colour of upper surface of head, dorsum and legs brown with blackish brown, irregular connected blotches on dorsum; a pale brown oblique stripe going backwards from eye to lip, bordered by a thin cream line. Upper lip and loreal region brown, darker than top of head and dorsum. Dark brown bars on limbs, hands and feet. Toe webbing creamy brown. Ventral surfaces beige, creamy yellow on chest and ventral surfaces of fore limbs.

In life, ground colour of back brown with a distinct irregular blackish pattern that consists of few isolated black spots anteriorly and a connected blackish network of blotches posteriorly that covers most of the back. A slightly darker brown stripe is present between the eyes. A light brown spot bordered by a thin beige line is present between the posterior part of eye and upper jaw. Head sides anterior to this spot are darker brown than dorsally. Hindlimbs and forelimbs with very contrasting blackish bands, which are rather irregularly arranged. Dorsal surface of fingertips brown. Webbing between fingers pink, pinkish-brown between toes. Iris golden with brownish pigment around the pupil, posterior iris periphery beige. Ventral side dirty whitish on chest, light brownish on belly and darker brownish on hindlimbs.

Variation. The morphometric variation of *B. roseipalmatus* is given in Appendix 3. There is sexual dimorphism in size, females attaining a SVL of 86.6 mm while maximum SVL observed in males is 68.4 mm. The colouration is very variable. The number and extent of black spots and markings on the back can be much less than in the holotype (e.g. ZSM 211/2004, Fig. 12) or even reduced to an almost uniform reddish brown or blackish-brown back. Specimens strongly marbled with beige and dark brown also occur. All specimens have pink webbing, especially between fingers and (often less distinct) between toes. Fingertips are dorsally brown, grey, or whitish. The dark crossbands on the hindlimbs range from very distinct to poorly recognizable. The iris colour can be uniformly beige, but is mostly silvery or golden with brownish or even reddish pigment around the pupil. The posterior iris periphery of undisturbed specimens is mostly beige. In frogs displaying defense behaviour (inflation of the body), the skin of the iris periphery is slightly protruded and a pink stripe above the eye becomes visible. The ventral colouration ranges from whitish with grey mottling to largely brown with grey mottling, sometimes with a pink shade. The throat is mostly dirty whitish or greyish. A darker dorsal colouration seems to be correlated with a comparatively darker ventral colouration.

Natural history. Specimens were found at night in rainforest, on the vegetation, at perch heights of 0.5–2 m. Nothing else is known on the habits of this species.

Molecular relationships. Although relationships among most species of the *B. goudoti* group are not resolved (see molecular differentiation section of *B. brachychir* above), the molecular tree (Fig. 7) places *B. roseipalmatus* as sister species of *B. madagascariensis* with maximum support (BS 100%, BPP significant). Each of these species is a monophyletic lineage as well. The two species are highly divergent from each other (4.9–6.1%) whereas divergences within *B. roseipalmatus* (up to 0.6%) and *B. madagascariensis* (up to 1.7%, differentiating the sample from Ilampy from the other specimens) are lower. Two molecular samples provided by F. Andreone (see Fig. 7) also indicate sympatry of these two species in north-eastern Madagascar (Ilampy), but the corresponding specimens were not examined by us.

Distribution. At present *Boophis roseipalmatus* is known from its type locality, Montagne d'Ambre National Park, as well as lower elevations in the same area known as Fontenay Nature Park and Forêt d'Ambre Special Reserve (see D'Cruze *et al.* 2008; Appendix 10). Based on analyses of DNA barcoding data by F. Andreone (see Fig. 7) it also occurs at Masoala (Ilampy campsite), and own preliminary data (not included herein) indicate its possible occurrence at Marojejy (in sympatry with *B. madagascariensis*).

Available names. Due to the similarities of *Boophis madagascariensis* (Peters, 1874) and *Rhacophorus herthae* Ahl, 1929 with *B. entingae* and *B. roseipalmatus* a discussion about the identity of the former two taxa is provided here. *Boophis madagascariensis* was described as *Rhacophorus madagascariensis* Peters, 1874 from the imprecise type locality "Madagascar" based on a single holotype (ZMB 8217) from the collec-

tion of Crossley. Bauer *et al.* (1995) considered this specimen, together with ZMB 10473 from Betsileo, collected by Hildebrandt, as syntypes, but this interpretation is not justified from the original description. We therefore consider ZMB 10473 not as syntype of *B. madagascariensis* and recognize only a single holotype which is also in agreement with Guibé (1978) and with Blommers-Schlösser & Blanc (1991). According to the original description of Peters (1874) and the accompanying figure (Tafel 1) the holotype (ZMB 8217) has numerous scattered white spots on the inner parts of the thighs which are still well visible. This chromatic character is a distinct difference to all known specimens of *B. roseipalmatus* that have largely uniformely coloured thighs without light spots. The holotype of *B. madagascariensis* differs from *B. entingae* by the absence of a distinct, sharply outlined brown marking that extends from upper eyelids and the interorbital region to the posterior dorsum. Such a marking is not recognizable in the holotype and not visible on the figure in the original description. A further difference is the size of the dermal heel flap which is broad, large and triangular in the *B. madagascariensis* holotype and much narrower smaller and tubercle-shaped in *B. entingae*. Finally, the holotype has two distinct whitish dots ventrally under the cloaca on the proximal parts of the thighs which are absent or indistinct in most individuals of *B. entingae*.

Rhacophorus herthae Ahl, 1929 was described based on a single juvenile holotype (ZMB 31577) of 25 mm SVL from Akkoraka, central Madagascar. There are only poorly recognizable light spots on the inner parts of the thighs although this could be due to the poor state of the holotype. There are two distinct whitish dots ventrally under the cloaca on the thighs and a fine transversal brown line in the neck as typical in many specimens of *Boophis madagascariensis* from central eastern Madagascar, but no trace of a sharply outlined brown marking on the back that is typical for most *B. entingae*. We therefore confirm the synonymy of *Rhacophorus herthae* with *Boophis madagascariensis* which had been proposed already by Guibé (1978).

***Boophis spinophis* sp. nov.**
(Fig. 13, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. by Glaw & Vences (2007:164–165) and as *Boophis* sp. 15 in Vieites *et al.* (2009).

Holotype. ZSM 376/2004 (ZCMV 691), adult male, from Ambatolahy forest, 21°14.632' S, 47°25.573' E, 915 m a.s.l., southeastern Madagascar, collected on 10 February 2004 by D. R. Vieites and C. Woodhead.

Etymology. The specific name is used as a noun in apposition and makes reference to the unique morphology of this species. In fact, when first examining the single specimen, we were unable to decide whether it belonged to the genus *Boophis*, or to the genus *Spinomantis* in the subfamily Mantellinae. The specific name is therefore a composite of these two generic names, and also makes reference to the dermal flaps and tubercles and tubercles and spines characterizing the species.

Diagnosis. 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 the male, absence of gular glands in the male, enlarged terminal discs of fingers and toes, lateral metatarsalia separated by webbing, absence of outer metatarsal tubercle, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis goudoti* group based on the following combination of characters: relatively large size (male SVL 57 mm), brownish dorsal ground colour, non-transparent ventral skin, absence of red ventral colour; presence of webbing between fingers; apparently single subgular vocal sac; presence of vomerine teeth; and especially the molecular phylogenetic relationships of the species (see Vieites *et al.* 2009). *Boophis spinophis* differs distinctly from all described species in the *B. goudoti* group by strong genetic differentiation (see below), dorsal colouration and distinct dermal tubercles along the lateral parts of the tarsus and around the elbow (in life). It furthermore differs from *B. boehmei*, *B. rufioculis*,

B. burgeri, *B. reticulatus*, and *B. axelmeyeri* by its larger size (SVL of the single known male 56.5 vs. 27–43 mm in the other mentioned species, see Glaw & Vences 2007) and from most of these species by iris colouration (absence of red colour in the outer iris area as is typical for *B. axelmeyeri*, *B. boehmei*, and *B. rufioculis*; presence of a strong pattern of dark stripes in iris which are absent in *B. burgeri* and usually less expressed in *B. reticulatus*). It also differs from *B. goudoti* and *B. periegetes* by the presence of a distinct dark pattern in the iris.

Description of the holotype. Adult male, SVL 56.5 mm. Body moderately slender; head approximately as long as wide, slightly wider than body; snout rounded in dorsal and lateral view, nostrils directed laterally, slightly nearer to tip of snout than to eye; canthus rostralis moderately sharp in cross section, but comparatively indistinct, slightly concave in dorsal view, loreal region slightly concave; tympanum distinct, rounded, TD 41% of ED; supratympanic fold thin, distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, elongated. Tongue posteriorly bifid, free.

Arms slender; distal subarticular tubercles of fingers 1, 3 and 4 bifid, round; metacarpal tubercles not recognizable; fingers scarcely webbed, with lateral dermal fringes; webbing formula 1(1), 2i(2), 2e(1.25), 3i(2), 3e(1.5), 4(1.5); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation reaching nostril when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0), 2i(0.25), 2e(0), 3i(0.5), 3e(0), 4i(0.75), 4e(0.75), 5(0); relative length of toes 1<2<5=3<4; toe discs enlarged. Dorsal skin smooth with small warts, smooth on throat and chest, granular on belly and ventral surfaces of thighs. Heel, lateral parts of tarsus, external finger and elbow region were covered with distinct dermal tubercles in life, which however are poorly recognizable in preservative. A tissue sample was removed from the right thigh.



FIGURE 13. Male holotype of *Boophis spinophis* **sp. nov.** (ZSM 376/2004) from Ambatolahy.

Measurements (in mm): SVL 56.5, HW 20.0, HL 20.1, ED 6.8, END 4.4, NSD 4.7, NND 6.8, TD 6.8, TL 29.9, HAL 18.7, FOL 26.5, FOTL 42.9.

After almost four years in preservative, ground colour of upper surface of head and dorsum brown with irregular darker blotches and small cream spots. Ground colour of ventral surfaces uniformly creamy yellow. In life, dorsal surfaces of head, body and limbs pale brown with pale green dots and larger, darker brown circular blotches with pale green inside. A whitish subocular bar between upper jaw, tympanum and eye. Iris golden with brown markings, more densely arranged at the edges of iris; upper eye periphery blue (Fig. 13).

Natural history. Largely unknown. The single known specimen was collected at night along a stream next to Ambatolahy, in disturbed rainforest, perched on the vegetation and not emitting any call.

Molecular relationships. This species turned out to be phylogenetically highly divergent from all other species in the *B. goudoti* group, with pairwise distances >9% to all species. Phylogenies based on additional mitochondrial genes (not shown here) confirm, however, that *B. spinophis* belongs indeed into this group. The sequence of the holotype and single specimen from Ambatolahy clusters with high support together with a sequence that refers to a juvenile specimen from Ambohitantely (ZSM 118/2005, not studied here). The divergence between these two sequences is quite high (3.5%), indicating that these two geographically distant populations are possibly not conspecific.

Distribution. At present *Boophis spinophis* is only reliably known from its type locality, a forest patch just outside Ranomafana National Park, near the village of Ambatolahy (Appendix 10). A second locality, Ambohitantely, is supported by DNA barcoding analysis (low pairwise sequence divergence) of a juvenile specimen from this site, but the corresponding sequence had a substantial differentiation and the identity of this population requires further study (see section on molecular relationships above).

***Boophis obscurus* (Boettger, 1913) - bona species**
(Fig. 14, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *goudoti* by Glaw & Vences (2007:164–165) and as *Boophis* sp. 13 in Vieites *et al.* (2009).

Resurrection of *Boophis obscurus*. *Boophis Goudotii* Tschudi, 1838 was the first frog species described from Madagascar. With just four lines, its original description written in Latin is very short and its type locality is only given imprecisely as "Madagascar" (Tschudi 1838). However, this description is in agreement with the widespread species from central Madagascar that is traditionally considered as *Boophis goudoti* and there is no character that would indicate its attribution to the form from the Ranomafana region. We therefore follow the definition of *B. goudoti* as used by Glaw & Vences (2007) whereas the morphologically similar species tentatively named *Boophis* sp. aff. *goudoti* (Glaw & Vences 2007) is in need of a scientific name. Numerous names are currently considered as synonyms of *Boophis goudoti*. The oldest available name is *Polypedates Goudotii* D. Bibr. var. *variolosa*, described by Steindachner (1864). The synonymy and Malagasy origin of this taxon is somewhat doubtful (see Guibé 1978: 72). According to the original description a row of skin tubercles is present on the integument located ventral sides of the metacarpal and metatarsal bones contradicting an attribution to the *B. goudoti* species group. The next oldest synonym, *Rhacophorus obscurus* Boettger, 1913, was described based on four specimens from Fianarantsoa. The male lectotype of this taxon (SMF 6763) shows distinct spines on the back and legs as is typical for *Boophis* sp. aff. *goudoti* and the description of Boettger (1913) agrees with this form as well. We therefore resurrect *Boophis obscurus* (Boettger, 1913) as valid species name for the form previously considered as candidate species *Boophis* sp. aff. *goudoti*.

Diagnosis. 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 fin-

gers and toes, lateral metatarsalia separated by webbing, absence of outer metatarsal tubercle, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis goudoti* group based on the following combination of characters: moderate to large size (male SVL 42–82 mm); brownish dorsal ground colour; non-transparent ventral skin; single subgular vocal sac; presence of vomerine teeth; presence of webbing between fingers; presence of a sharp canthus rostralis; and molecular phylogenetic relationships (see Vieites *et al.* 2009). *Boophis obscurus* differs distinctly from all described species in the *B. goudoti* group by its moderate to strong genetic differentiation (see below). It furthermore differs from *B. boehmei*, *B. rufioculis*, *B. burgeri*, *B. reticulatus*, and *B. axelmeyeri* by its larger size (SVL of males 42.4–81.9 mm vs. 27–43 mm) and iris colouration (absence of red colour in the outer iris area as is typical for *B. axelmeyeri, B. boehmei*, and *B. rufioculis*; absence of a pattern of dark stripes typical for *B. reticulatus*; no distinct blue iris periphery as in *B. boehmei*, *B. burgeri*, and *B. rufioculis*). It differs from *B. madagascariensis*, *B. roseipalmatus*, *B. entingae*, *B. brachychir*, *B. boehmei*, *B. rufioculis*, *B. burgeri*, *B. reticulatus*, and *B. axelmeyeri* by the absence of distinct dermal flaps or tubercles on heels. It differs from *B. spinophis* by the absence of distinct dermal tubercles along the lateral parts of the tarsus and around the elbow. It differs from *Boophis goudoti* by a dorsal colouration that usually includes orange-brown spots (hitherto not seen in *B. goudoti*) and a ventral colouration without yellow colour (yellow ventral colour being typical for *B. goudoti*). The new species is superficially also similar to *B. periegetes*, but breeding males can easily be distinguished from that species by the different types of skin rugosities (small keratinised spicules rather than larger warts), and by their advertisement calls (irregular pulsed croaking notes vs. whistling notes in *B. periegetes*; see below).



FIGURE 14. Male *Boophis obscurus* (UADBA uncatalogued) from Ranomafanakely.

Redescription (based on ZMA 20220). Adult male, SVL 63.2 mm. Body moderately robust; head longer than wide, slightly wider than body; snout long, rounded in dorsal view and lateral view, nostrils directed lat-

erally, nearer to eye than to tip of snout; canthus rostralis sharp in cross section, straight in dorsal view, almost reaching the tip of snout; loreal region concave; tympanum large, distinct, rounded, TD 83% of ED; supratympanic fold thick, clearly distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae large, elongated. Tongue posteriorly bifid, free. Arms moderately robust; subarticular tubercles single, round; inner palmar tubercle poorly distinct, elongated, in close contact with nuptial pad; nuptial pad creamy yellow, covering dorsal and posterior surfaces of first finger and dorsal surface of basis of second finger; outer palmar tubercle indistinct; fingers scarcely webbed and with lateral dermal fringes; webbing formula 1(1.5), 2i(1.5), 2e(1), 3i(2.25), 3e(1.75), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hind limbs moderately robust; tibiotarsal articulation barely reaching tip of snout when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle distinct, elongated; no outer metatarsal tubercle; toes moderately webbed; webbing formula 1(0), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(1.5), 4e(1.5), 5(0.25); relative length of toes 1<2<3=5<4; toe discs enlarged. Skin texture on dorsal surfaces smooth, but covered by small warts with keratinized black spicules, more abundant on the two posterior thirds of dorsum and upper surfaces of hind limbs. Ventral skin finely granular on throat and chest, coarsely granular on belly and ventral surface of thighs; keratinized spicules like those of dorsum (but not on the top of a wart) on venter and periphery of gular region, below the jaws.

Measurements (in mm): SVL 63.2, HW 21.3, HL 23.0, ED 6.8, END 4.6, NSD 5.4, NND 7.0, TD 5.7, TL 35.1, HAL 19.8, FOL 31.2, FOTL 49.5.

After almost four years in preservative, ground colour of upper surface of head, dorsum and legs brown with reddish brown, irregular blotches; warts grey with tiny black spicules; flanks brown with irregular cream blotches; an irregular, unconnected cream stripe along upper lip. Legs with dark brown bars. Ventral surfaces beige with irregular, diffuse brown blotches. Colouration of the holotype in life unknown.

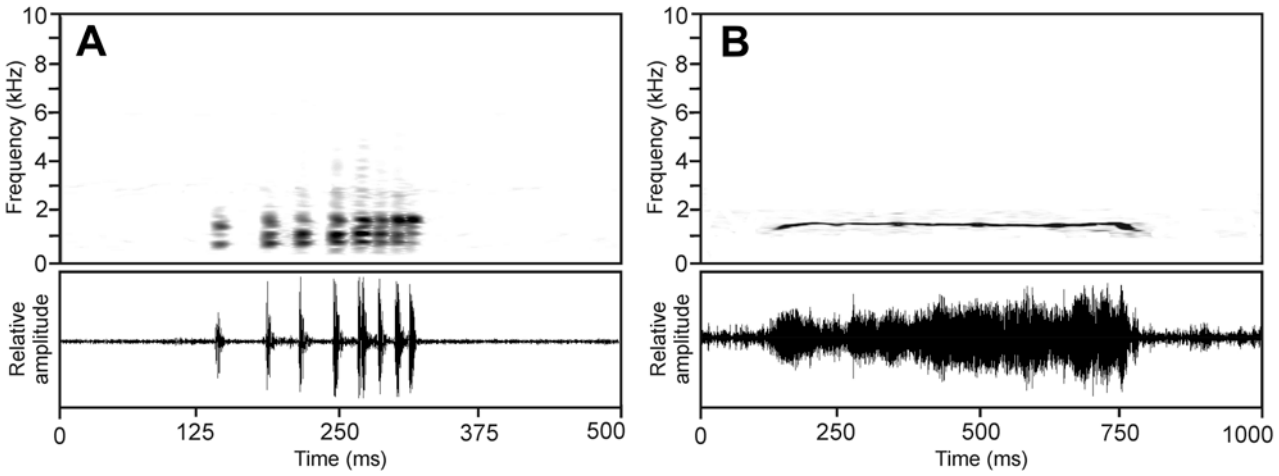


FIGURE 15. Spectrograms and waveforms of calls: (A) call type 1 of *Boophis obscurus* from near Vohiparara, Ranomafana National Park (recorded on 29 January 2004, air temperature app. 20.5°C); (B) advertisement call of *Boophis periegetes* from Andohahela National Park (recorded on 27 January 2005, air temperature app. 18°C)

New material. ZMA 20219 (ZCMV 347), ZMA 20220 (ZCMV 348), and UADBA 24309 (ZCMV 349), three adult males, from Ranomafana National Park, rice field close to Andranoroa river, near Ranomafanakely, 21°14.872' S, 47°22.580' E, 1138 m a.s.l., southeastern Madagascar, collected on 29 January 2004 by I. De la Riva and M. Vences; UADBA (ZCMV 5748, 5750, 5759), sex unknown, from Isalo National Park, collected on 15–16 February 2007 by M. Vences and J. Glos; ZMA 19452 (FG/MV 2002–1403), male, from the Maharira area, Ranomafana National Park, collected by E. Rajeriarison and T. Rajoafiarison in January 2003; ZSM 740/2001 (FGMV 2001.540), from Andohariana plateau (Andringitra), 22°10'49" S, 46°54'01" E, 2114 m, collected on 13–14 March 2001 by L. Raharivololoniaina, D. Rakotomalala, M. Vences and D. R.

Vieites; ZSM 2293/2007 (ZCMV 5774) and ZSM 2294/2007 (ZCMV 5781), two males, from Isalo, Cascade des Nymphes, collected on 16 February 2007 by M. Vences and J. Glos; ZSM 2292/2007 (ZCMV 5903), female, from Ambatovaky (road from Vohiparara to National Road RN7 Antananarivo-Fianarantsoa, at ca. 30 km direction from Vohiparara), collected on 1 March 2007 by M. Vences and P. Bora.

Variation. Morphometric variation is given in Appendix 4. No remarkable variation in colour pattern exists among the males from Ranomafana; two males from Isalo (ZSM 2293–2294/2007) also conform the general pattern of the holotype but are distinctly smaller. A male from Andringitra (ZSM 740/2001) is the largest specimen (81.9 mm SVL); it has poorly marked dorsal spicules, and marked brownish orange bars on limbs. The only female in our sample (ZSM 2292/2007) lacks spicules; it has a diffuse dorsal pattern of intermingled dark brown and brownish orange blotches, and limbs markedly barred. In life, paratypes had a dark reddish-brown dorsum, flanks yellowish, progressively becoming bluish downwards, with brown irregular blotches, and lower surfaces creamy white with brown markings. The iris was pale orange. In males, during call emission, a single subgular vocal sac was visible which however became only weakly extended.

Natural history. In the highlands of the Ranomafana area, specimens are regularly observed on the ground or on low perch heights along streams in more or less exposed areas next to rainforest. A chorus of calling specimens (reported as *Boophis* sp. aff. *periegetes* in Vences *et al.* 2006) was observed at night in slow-moving channels connecting rice fields close to rainforest. The specimens were sitting in close proximity of each other, at a rather exposed site at the borders of the canal or in the shallow water. At Andringitra, one large male was collected on the Andohariana plateau, above the tree line, next to a mountain stream during the day on the ground. At Isalo, males of the dwarf form here assigned to *B. obscurus* were observed at night calling from the ground or perched on branches and rocks in steep areas next to streams, and in areas were small amounts of water where constantly flowing and dripping and large boulders were creating small caves. Specimens were not in direct proximity but often at small distances of only a few meters from each other. Calls were also occasionally heard during the day.

Vocalization. Calls of *B. obscurus* are very variable and might be classified into several different call types like done for other species in the group, especially *B. madagascariensis* (Narins *et al.* 2000). However, our data do not allow for a proper classification, as calling motivation and the social context of our recordings remain largely unknown. We here describe some different types of vocalizations, being aware that several additional and/or intermediate call types may occur in this new species. What is here termed call type 1 might possibly represent some kind of advertisement call, as it is emitted with high energy and shows a relatively regular structure. It is a pulsed note with distinct temporal modulation of pulses. Type 2 is somehow similar, but is usually softer and shows more evenly distributed pulses within notes. Type 3 refers to various single clicks and shorter pulsed notes. Emission of these different note types does not seem to follow a particular pattern, as they rather appear randomly mixed and combined. Numerical call parameters for the different call types are as follows (Vences *et al.* 2006, CD 1, track 60): Call type 1 (Fig. 15A): note duration, 137–238 ms (187 ± 40; n = 5); notes repeated at irregular intervals; 8 pulses/note (n = 5), intervals between pulses, 4–41 ms (16 ± 11; n = 27); duration of inter-pulse intervals decreasing towards end of note; pulse repetition rate variable, approximately 20–70 pulses/second; dominant frequency range 400–3000 Hz, maximum call energy at 550–810 Hz. Call type 2: note duration, 206–360 ms (264 ± 33; n = 15), notes repeated at irregular intervals; pulses/note, 8–16 (11.6 ± 2.4; n = 12); intervals between pulses, 9–25 ms (16 ± 5; n = 25); pulse repetition rate approximately 32–36 pulses/second; dominant frequency range 400–1800 Hz, maximum call energy at 420–760 Hz. Call type 3 (no detailed analysis possible): various short notes, composed of 1–5 pulses, repeated at irregular intervals; note duration, 14–112 ms (n = 9); dominant frequency range similar to types 1 and 2.

Comparative call data. The call of *B. periegetes* consists of a long unpulsed whistle, usually emitted in groups of 3–4 notes (Fig. 15B). An increase in note duration is evident towards the end of such a series. Frequency is generally distributed in a very narrow band, but modulation is recognizable with a slight upward

sweep at the beginning and a distinct drop in frequency at the end of the note. Numerical call parameters are as follows: note duration, 225–637 ms (435 ± 147; n = 8); inter-note interval (within series), 320–967 ms (627 ± 243; n = 5); note repetition rate, approximately 0.6–1.8 notes/second; dominant frequency range 1100–1700 Hz, maximum call energy at 1320–1510 Hz (Vences *et al.* 2006, CD 1, track 59).

Molecular relationships. The molecular phylogeny places the sequences assigned to this species in a clade together with *B. goudoti.* Although this clade is only poorly supported (BS 65%, BPP not significant), the close relationships between these two species are beyond doubt based on analyses of further mitochondrial gene sequences (work in progress by K. C. Wollenberg). Also, it seems clear that the sequences assigned to each species (except one; see below) do each form a clade, despite the lack of such a topology in our tree (Fig. 7). Sequences assigned to *B. goudoti* and *B. obscurus* have divergences of 2.1–3.9%, depending on the length of the included fragment (in some specimens, fragments had many missing data in the generally quite conserved first section and sequence length for comparison was thus shorter and divergence values higher). One specimen morphologically clearly belonging to *B. obscurus* has a sequence identical to a specimen of *B. goudoti* from Antoetra, indicating either incomplete lineage sorting or, more probable, recent hybridization with mitochondrial introgression, as also known from other closely related mantellid species such as *Mantella aurantiaca* and *M. crocea,* and *Mantella baroni* and *M. cowani* (Chiari *et al.* 2004; Rabemananjara *et al.* 2007).

Distribution. At present, specimens assignable to *Boophis obscurus* are known from different sites in the Vohiparara region, in or near Ranomafana National Park: Andranoroa river, Ranomafanakely, and Ambatovaky (Appendix 10). Specimens that are substantially different in size are known from Andringitra National Park and Isalo National Park. An individual from Ambohimitombo (ZFMK 28862) shows the typical colour pattern of *B. obscurus* and may belong to this species as well, but this identification is in need of confirmation.

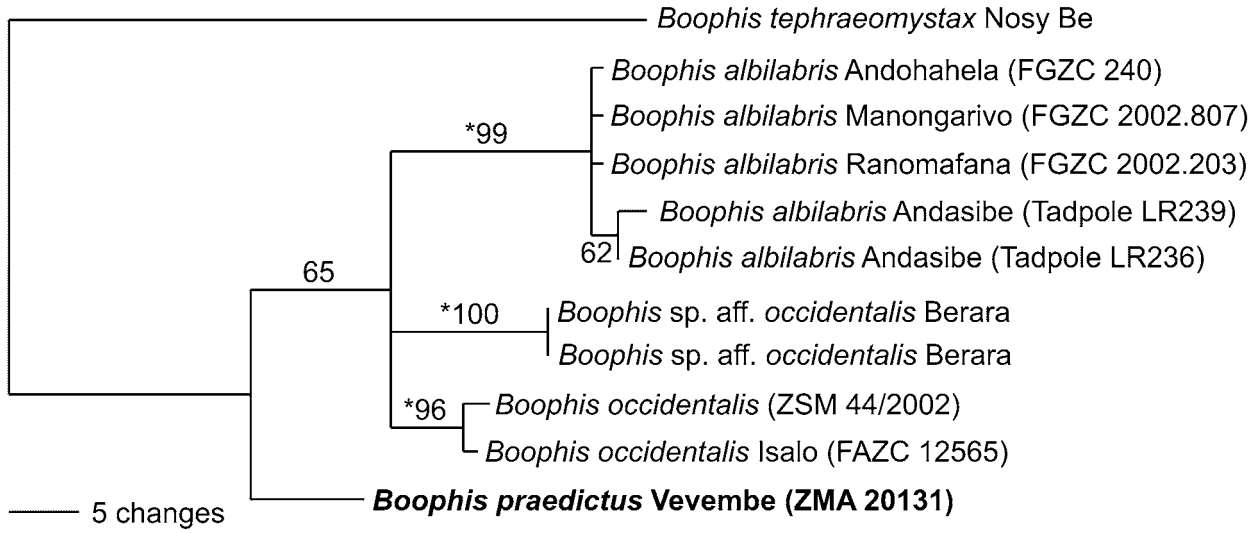


FIGURE 16. Maximum parsimony 16S rRNA phylogram for species in the *Boophis albilabris* group. From 535 total characters, 445 were constant and 35 parsimony informative. MP searches retained 6 trees of which a strict consensus is shown. Consensus support values higher than 50, from 2000 bootstrap replicates, are shown; an asterisk indicates Bayesian posterior probabilities equal or higher than 95%. The species newly described herein is in bold.

***Boophis praedictus* sp. nov.**
(Fig. 17, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *albilabris* "red eyes" by Glaw & Vences (2007:166–167) and as *Boophis* sp. 5 in Vieites *et al.* (2009).

Holotype. ZMA 20131 (ZCMV 678), adult female, from Vevembe, 22°47.686' S, 47°11.228' E, 581 m a.s.l., southeastern Madagascar, collected on 10 February 2004 by E. Rajeriarison and M. Vences.

Paratype. ZSM 478/2009 (ZCMV 11237), subadult female, from a campsite locally known as Ampofoko, Makira forest, 15°25'22.3" S, 49°07'15.1" E, 1034 m a.s.l.; collected on 22 June 2009 by M. Vences, D. R. Vieites, F. Ratsoavina, R.-D. Randrianiaina, E. Rajeriarison, T. Rajoafiarison and J. Patton.



FIGURE 17. Female holotype of *Boophis praedictus* **sp. nov.** (ZMA 20131) from Vevembe.

Etymology. The specific name is an adjective derived from the Latin "praedictus", meaning "previously mentioned", and refers to the fact that the existence of this species was known from a photograph published in 1993 in which its distinctive character, the red iris periphery, was clearly recognizable.

Diagnosis. 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), enlarged terminal discs of fingers and toes, lateral metatarsalia separated by webbing, absence of outer metatarsal tubercle, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis albilabris* group based on the following combination of characters: large size (female SVL 62–89 mm; Appendix 5); well developed webbing between fingers; presence of vomerine teeth; green colouration in life and colouration in preservative with a purple shade; presence of a white line along upper lip; molecular phylogenetic relationships (Vieites *et al.* 2009); and overall similarity to *B. albilabris*. *Boophis praedictus* differs from the other two described species in the *Boophis albilabris* group by strong genetic differentiation (see below). It further differs from *B. occidentalis* by its larger size and different body colouration (absence of yellow dorsolateral stripes) and iris colouration (yellowish iris and red iris periphery vs. turquoise iris and bluish posterior iris periphery), and from *B. albilabris* by a different colouration of the posterior iris periphery (red vs. whitish or greenish).

Description of the holotype. Adult female, SVL 89.3 mm. Body moderately slender; head slightly longer than wide, slightly wider than body; snout rounded in dorsal view, obtuse in lateral view, nostrils directed laterally, slightly nearer to tip of snout than to eye; canthus rostralis sharp in cross section, slightly concave in dorsal view, loreal region slightly concave; tympanum distinct, rounded, TD 60% of ED; supratympanic fold thin, distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, elongated. Tongue posteriorly bifid, free. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers broadly webbed and with lateral dermal fringes; webbing formula 1(1), 2i(1.5), 2e(0), 3i(1.25), 3e(0), 4(0); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation barely reaching nostril when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes almost fully webbed; webbing formula 1(0), 2i(0.25), 2e(0), 3i(0.25), 3e(0), 4i(0.25), 4e(0.25), 5(0); relative length of toes 1<2<5=3<4; toe discs enlarged. Skin finely granular on dorsal surfaces, smooth on throat and chest, coarsely granular on belly and ventral surfaces of thighs. A tissue sample was removed from the right thigh.

Measurements (in mm): SVL 89.3, HW 32.0, HL 33.3, ED 10.4, END 7.6, NSD 7.4, NND 9.5, TD 6.3, TL 45.8, HAL 27.9, FOL 40.8, FOTL 65.9.

After almost four years in preservative, ground colour of upper surface of head and dorsum dark greyish purple with scattered small, dark cream dots. A diffuse stripe at midflanks, paler than dorsum; lower flanks creamy yellow with irregular blotches of the same colour as dorsum. A creamy white, narrow stripe on upper lip, lateral edge of lower arm, tarsus, and heel. Ground colour of ventral surfaces uniformly creamy yellow; a dark greyish purple line along the lower jaw. Posterior surfaces of thighs cream with a purple reticulation. Posterior part of eye purplish.

In life, dorsal surfaces green with scattered small, cream dots. Lower flanks cream with irregular greenish grey blotches. A white, narrow stripe on upper lip, lateral edge of lower arm, tarsus, and heel. Upper surfaces of thighs and shanks the same colour as dorsum, with darker bars. Iris golden with brown reticulations, more densely arranged around the pupil; eye periphery red posteriorly (Fig. 17). Upper surface of fingers, toes and terminal discs reddish. Ventral life colouration of holotype unknown.

Natural history. A single female of this species was collected at night, sitting about 2 m high in the vegetation, along a stream in disturbed rainforest.

Molecular relationships. The phylogenetic tree of species assigned to the *Boophis albilabris* group (Fig. 16) provides evidence for a large molecular homogeneity of the species *B. albilabris* across its entire distribution range: sequences from Manongarivo in the Sambirano region in northern Madagascar showed almost no differences to sequences from Andasibe in the Northern Central East (0.6%), Ranomafana in the Southern Central East (0.4%), and Andohahela in the South East (0.2%). On the contrary, specimens from Berara forest (Sahamalaza Peninsula in the North West) previously assigned to *B. occidentalis* by Andreone *et al.* (2002) are divergent (3.1–3.3%) as compared to topotypical specimens from Isalo (see also Glaw & Vences 2007). The Berara population probably merits recognition as separate species and will be subject of a forthcoming study. The specimen of *B. praedictus* studied here is placed basally in the phylogeny and has a strong differentiation to all other species in the group (4.4–4.8% to *B. albilabris*; 4.4–4.6% to *B. occidentalis* and *B.* sp. aff. *occidentalis*).

Distribution. At present *Boophis praedictus* is known from (1) its type locality, Vevembe, and from three localities at the border between the Northern Central East and North East regions: from (2) Makira Reserve (paratype specimen), (3) Ambatovaky Special Reserve (Appendix 10), based on a photograph by C. J. Raxworthy reproduced in Blommers-Schlösser & Blanc (1993), and (4) Masoala based on a photograph by O. Jovanovic (not reproduced here) that shows a specimen probably belonging to this species as well, although the colour of the iris periphery is less distinctly visible. In both these photographs, the red iris periphery typical for *B. praedictus* is clearly recognizable.

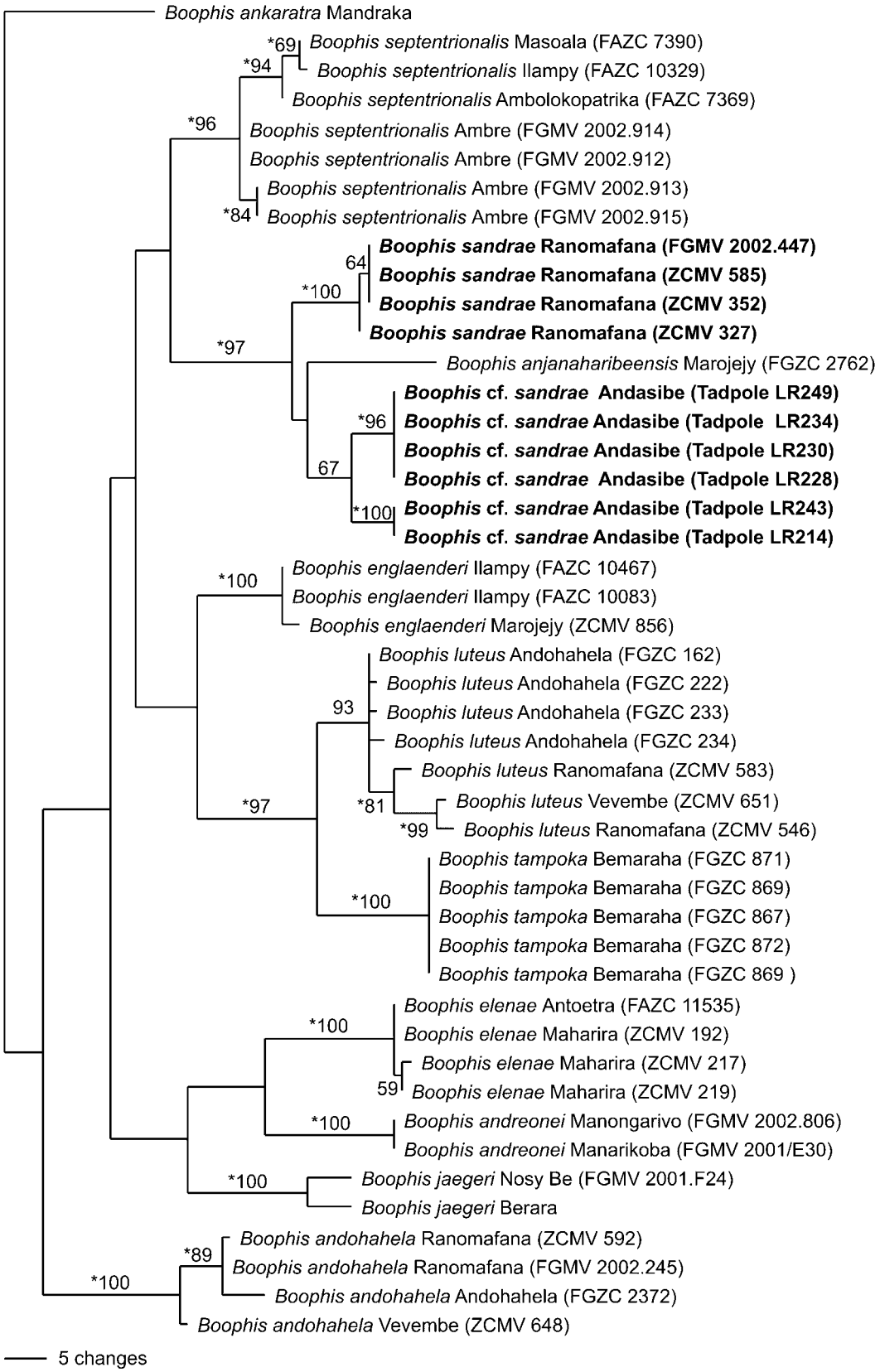


FIGURE 18. Maximum parsimony 16S rRNA phylogram for species in the *Boophis luteus* group. From 470 total characters, 347 were constant and 111 parsimony informative. MP searches retained 60 trees of which a strict consensus is shown. Consensus support values higher than 50, from 2000 bootstrap replicates, are shown; an asterisk indicates Bayesian posterior probabilities equal or higher than 95%. The species newly described herein is in bold.

Available names and justification. *Boophis albilabris* (Boulenger, 1888) was described based on a single adult holotype, reportedly a male specimen from "eastern Imerina". The Imerina, one of Madagascar's indigenous tribes, inhabit the central portion of the high plateau in the vicinity of Antananarivo, but *B. albilabris* is unlikely to have occurred in this now deforested area and the type most likely came from the rainforest escarpment to the east (Cadle 1995). The species so far usually considered to be *B. albilabris* (e.g., Cadle 1995; Andreone et al. 2002; Glaw & Vences 2007), and the species with red eye periphery here described as *B. praedictus,* both occur on the eastern escarpment. To assess the identity of the nomen *albilabris* we examined the holotype in the Natural History Museum, London (BMNH 1947.2.9.16) which is in moderately good state of preservation and we assume is probably a female, not a male specimen. The identity of this specimen is not unambiguous as it shares characters that seem to characterize either of the two species known, requiring a careful evaluation of its identity and the taxonomic consequences.

The two female type specimens of *B. praedictus* and photographs of additional females with reddish iris periphery assigned to that species seem to differ from most specimens assigned to *B. albilabris* by (1) the colouration of the flanks below the dorsolateral border which differs from the dorsal colouration, (2) more strongly developed white dermal ridge along the elbow and the lower arm, and (3) generally fewer, broader and less distinct crossbands on the hindlimbs. The holotype of *albilabris* is uniformly light purple, indicating that it probably was uniformly green in life, which agree with Boulenger's (1888) statement of a green colour in life in the original description. Crossbands on the hindlimbs are not recognizable, the skin on the flanks is shrinked and of greyish colour, and there is a prominent white ridge on heel and elbow. However, regarding the latter character, we have observed that this is a sexually dimorphic character in several species of the *B. albilabris* group (such as *B. occidentalis*), being in general more prominent in female specimens than in males, which have more muscular forelimbs (and most specimens assigned to *B. albilabris* known to us are males). The lack of crossbands on the limbs and the lack of purple (originally green) colour on the flanks can be due to fading of these pigments during the long period of preservation, and additionally weak expression of crossbands and dense marbling with colours other than green also occurs in some specimens of the species usually assigned to *B. albilabris.*

One additional piece of evidence to take in mind is the distribution of the two species. Although both occur in eastern rainforests, the species usually assigned to *B. albilabris* has been commonly encountered and photographed by multiple researchers and tourists in localities of mid-altitude (900–1100 m a.s.l.) of the eastern escarpment, some of which are close to the highland Imerina area (e.g. Andasibe). In contrast, the species described as *B. praedictus* has usually been found at lower elevations, and in particular in the north-east in Masoala. It is unlikely that any of these low-elevation localities would have been characterized as "eastern Imerina" by early collectors. However, the situation is complicated by the presence of *B. praedictus* at Makira at an elevation of above 1000 m a.s.l., and by its possible presence in An'Ala, a locality near Andasibe but at slightly lower elevation and known to contain faunal elements typical for low-elevation sites. This latter record is based on tadpoles only and became available after the present paper had been accepted for publication; it needs further study as it may indicate a contact zone between the two species between An'Ala and Andasibe. It also became recently clear that subadult specimens from Masoala and Mananara considered as separate candidate species *Boophis* sp. aff. *albilabris* "reticulated lips" (see Glaw & Vences 2007) probably correspond to subadults of *B. praedictus;* this provides another character (juvenile colour pattern) clearly distinguishing this form, and further confirms its presence at mainly east coast sites of low elevation. This evidence will be reported more in detail in forthcoming studies.

Eventually, the most important character distinguishing *B. praedictus* from the specimens usually assigned to *B. albilabris* is its red iris periphery. This is a conspicuous character that in our specimens, after several years in preservative, is still recognizable. Boulenger (1888) noted that the holotype of *albilabris* was green in life, suggesting that he had a fresh specimen or additional information available, but he did not mention any reddish iris periphery. Upon examination in 2009, the iris periphery of the *albilabris* holotype is uni-

formly light grey to silver without traces of red or orange colour, in full agreement with the species usually considered to be *B. albilabris.* There obviously remain doubts whether the colour of the iris periphery in the *albilabris* holotype may have faded over the past ca. 120 years, but there is no evidence that it was redddish in life shortly after preservation.

Summarizing, we conclude that there is no clear evidence supporting the *albilabris* holotype to be conspecific with the species here described as *B. praedictus*: similarities can either be explained by sexual dimorphism (heel and elbow ridges) or by partly faded colour pattern in the *albilabris* type (lack of limb crossbands and light flank colour) and furthermore fall into the variability of the species usually assigned to *B. albilabris.* In contrast, the lack of dark (red in life) pigment in the iris periphery and the type locality "Imerina" support that the species with light iris periphery common in the Andasibe and Ranomafana areas, and hence in at least some localities bordering the Imerina region, are to be considered as *B. albilabris.* Since this definition of *B. albilabris* is also in accordance with most accounts that provided data on the biology, morphology and colouration of this species (in particular Andreone 1993; Cadle 1995; Andreone *et al.* 2002), taxonomical stability is best served by accepting the evidence from biogeography and iris colour (although it is not unambiguous) and to continue the prevalent definition of *B. albilabris*, describing the mainly lowland species with red iris periphery as the new species *Boophis praedictus.*

***Boophis sandrae* sp. nov.**
(Fig. 19, Appendix 9)

Remark. Not surprisingly, due to their external similarity, largely similar call structure, and sympatric occurrence, *Boophis elenae* and *B. sandrae* have long been confused. In the original description of *B. elenae*, Andreone (1993) shows photographs of the holotype specimen (MRSN A69) in life, leaving no doubt about its identity due to the clearly visible reddish horizontal stripes in the iris which are absent in *B. sandrae*. Andreone (1993) mentions this iris character and attributes a further specimen (female paratype MRSN A71.2 from Ambatolahy) without iris stripes to *B. elenae* as well. Considering the new classification proposed herein, this specimen belongs instead to *B. sandrae*. Specimens of *B. sandrae* have been reported as "*B.* sp. aff. *elenae*" by Vences *et al.* (2006) and by Glaw & Vences (2007:168–169), and as *Boophis* sp. 22 in Vieites *et al.* (2009). See also section on Available names in the description of *Boophis luciae* below.

Holotype. ZMA 20133 (ZCMV 352), adult male, from Ranomafana, Andranoroa river, near Ranomafanakely, 21°14.872'S, 47°22.580'E, 1138 m a.s.l., southeastern Madagascar, collected on 29 January 2004 by I. De la Riva, D.R. Vieites and M. Vences.

Paratypes. ZFMK 62311–62312, male and female respectively, from Ranomafana village, 21°15.699'S, 47°27.571'E, 619 m a.s.l., collected on 5 March 1996 by F. Glaw, D. Rakotomalala and F. Ranaivojaona; ZMA 20132 (ZCMV 327), female, from Ranomafana, Andranoroa river near Ranomafanakely, 21° 14.872' S, 47° 22.580' E, 1138 m a.s.l., collected on 28 January 2004 by I. De la Riva and M. Vences; ZMA 19389 (FGMV 2002.447) from Ranomafana village (Hotel Manja), collected on 23 January 2003 by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas and D. R. Vieites; ZMA 20134–20135 (ZCMV 585–586), two males, from Ranomafana village, 21°15.699' S, 47°27.571' E, 619 m a.s.l., collected on 5 February 2004 by N. Fatroandrianjafinonjasolomiovazo; ZMA 20136 (ZCMV 631), male, from Ambatolahy forest, 21°14.632'S, 47°25.573'E, 915 m a.s.l., collected on 10 February 2004 by D. R. Vieites and C. Woodhead; ZMA 20137 (ZCMV 634), male, from the surroundings of Ranomafana National Park (probably from the village of Ranomafana; no further data available); ZSM 235/2006 (ZCMV 3003), male, from Ambatovory (upstream river Ambatolahy), 21°14.279' S, 47°25.487' E, 966 m a.s.l., collected on 26 February 2006 by P. Bora, Y. Chiari, T. Rajaofiarison, E. Rajeriarison, T. Razafindrabe and M. Vences; ZSM 236/2006 (ZCMV 3058), female, from Ambatolahy river, 21°14.632' S, 47°25.573' E, 915 m a.s.l., collected on 26 February 2006 by P. Bora, Y.

Chiari, T. Rajaofiarison, E. Rajeriarison, T. Razafindrabe and M. Vences; ZSM 237/2006 (ZCMV 3187), male, from Kidanavo bridge, 21°13.571' S, 47°22.176' E, 1152 m a.s.l., collected on 20 February 2006 by A. Meyer, L. du Preez, O. Verneau, D. R. Vieites and C. Weldon; ZSM 238/2006 (ZCMV 3371), female, from Mahakajy, collected on 1 March 2006 by T. Rajaofiarison, E. Rajeriarison and M. Vences; ZSM 665/2003 (FGMV 2002–0245), adult male, from point between Vohiparara and entrance to Ranomafana National Park, collected on 16 January 2003 by F. Glaw, M. Puente, L. Raharivololoniaina, M. Thomas and D. R. Vieites.

Etymology. This species is dedicated to Sandra Nieto Román, in recognition for her patience, interest and help during the field work and nights spent in the laboratory, by her husband, David R. Vieites.

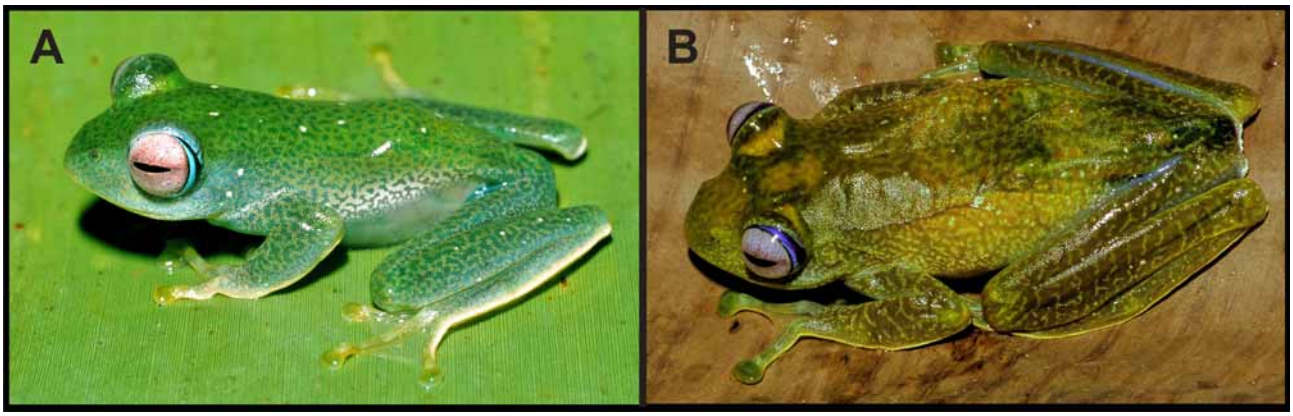


FIGURE 19. (A) Male holotype of *Boophis sandrae* **sp. nov.** (ZMA 20133) from Ranomafana; (B) female paratype of *Boophis sandrae* **sp. nov.** (ZSM 236/2006) from Ambatolahy.

Diagnosis. 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 axillary amplexus 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, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis luteus* group based on the following combination of characters: moderate size (male SVL 36–48 mm); absence of tubercles or flaps on heel and elbow; presence of webbing between fingers; indistinct canthus rostralis; presence of distinct white tarsal folds; dorsal colouration translucent green in life and yellow-whitish in preservative; absence of red ventral colour; ventral skin in life non-transparent; bilobed subgular vocal sac; presence of vomerine teeth; and molecular phylogenetic relationships. *Boophis sandrae* differs from all other species in the *Boophis luteus* group by strong genetic differentiation (see below) and by advertisement calls: in brief, the general call structure consisting of a long rapid series of short and unharmonious notes observed in *B. sandrae* is known from only in three other species in the group (*B. andreonei, B. anjanaharibeensis, B. elenae*), whereas other species have series of melodious whistling notes (*B. englaenderi, B. luteus, B. septentrionalis, B. tampoka*) or slow series of pulsed notes (*B. andohahela, B. jaegeri*); in calls of *B. elenae*, note repetition rate is lower and notes longer, and in *B. anjanaharibeensis*, call repetition rate is higher and notes shorter (see Comparative call data below); no obvious call differences exist to *B. andreonei* which however is a smaller species (SVL 31–33 mm vs. 36–48 mm in *B. sandrae*) without an obvious dorsal pattern of darker green spotting (vs. presence). *Boophis sandrae* differs from *B. luteus, B. anjanaharibeensis,* and the morphologically most similar species, *B. elenae,* by its iris colouration (without red vs. with thin red horizontal stripes or a broad ring of red colour). It further differs from *B. andohahela, B. septentrionalis* and *B. tampoka* by the absence of light yellowish dorsolateral lines (versus presence).

Description of the holotype. Adult male, SVL 35.8 mm. Body slender; head slightly longer than wide, wider than body; snout rounded in dorsal view, obtuse in lateral view, nostrils directed laterally, slightly nearer

to eye than to tip of snout; canthus rostralis sharp in cross section, straight in dorsal view, loreal region slightly concave; tympanum distinct, rounded, TD 36% of ED; supratympanic fold indistinct; vomerine odontophores distinct, well separated in two round patches, positioned posteromedial to choanae; choanae medium-sized, rounded. Tongue bifid, free posteriorly. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(-), 2i(1), 2e(1), 3i(2), 3e(1), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs moderately enlarged; distinct, well developed nuptial pad on inner side of first finger, unpigmented. Hindlimbs slender; tibiotarsal articulation reaching nostril when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; webbing between toes well-developed, lateral dermal fringes present; webbing formula 1(0), 2i(0.25), 2e(0), 3i(1), 3e(0), 4i(1), 4e(1), 5(0); relative length of toes 1<2<5=3<4; toe discs enlarged. Skin on dorsal surfaces smooth, very finely granular on throat, coarsely granular on chest and belly; a glandular area ventrally under the cloacal opening; no distinctly enlarged tubercles in the cloacal region. A tissue sample was removed from the right thigh.

Measurements (in mm): SVL 35.8, HW 12.1, HL 12.9, ED 5.5, END 2.4, NSD 3.3, NND 4.3, TD 2.0, TL 18.9, HAL 10.2, FOL 15.7, FOTL 25.7.

After almost four years in preservative, ground colour of flanks, dorsal and ventral surfaces uniformly creamy yellow. Skin above eye blackish. Nostril internally bordered with some dark pigment.

In life, ground colour of upper surface of head and dorsum light green with darker green spotting. A pale grey stripe at midflanks with dark green reticulations, below this stripe unpigmented. A bluish shade present on external edge of upper eyelid, loreal region, upper lip, tympanic region and borders of the concealed parts of the hindlimbs. Posterior iris periphery black, followed by light blue. Eye periphery black posteriorly (Fig. 19). White lateral fringes along lateral edge of lower arm, tarsus, and heel. Webbing yellowish green. Small, distinct white spots scattered on posterior part of head, back and hindlimbs. Dorsal surfaces of fingers and toes green, terminal discs green. Ventral life colouration of holotype unknown.

Variation. Morphological variation is given in Appendix 6. Females are larger, with an average of 144 % of male SVL. The paratypes are similar to the holotype. The dorsal colouration of the female paratype ZSM 236/2006 is more yellowish, especially on the flanks, and with three distinct yellow spots between the eyes. The forelimbs and hindlimbs are more brownish, with distinct light bands. The ventral surfaces of limbs are translucent bluish green, and the chest and belly translucent pinky white. Bones bluish green. Iris pale pink. In calling males we observed a bilobed subgular vocal sac.

Natural history. This species is common in the Ranomafana region. Its typical calls can be heard in dense rainforest but also very commonly in degraded or secondary forest and, in largely cleared areas, from large trees along streams and rivers. Calling specimens usually are perched quite high, often 2–4 m above the ground, and usually sit on thin branches rather than on leaves. In the later evening, pairs in axillary amplexus can be observed at lower heights in the vegetation along the streams. The species is often found in close syntopy with *B. luteus* but has not been recorded in the same stretch of stream with the externally similar *B. elenae*.

Vocalization. The call of *Boophis sandrae* consists of a very long series of short pulsed notes repeated in very fast succession. One such call (note series) recorded on 28 January 2004 near Vohiparara, Ranomafana National Park, had a duration of 33.6 seconds (Fig. 20A). Each note is distinctly pulsed and composed of 3–7 (4.7 ± 0.96; n = 30) pulses, which increase in amplitude towards the end of the note. Numerical call parameters are as follows: note duration, 13–23 ms (18.9 ± 2.4; n = 15); inter-note intervals, 35–43 ms (37.5 ± 2.6; n = 17); note repetition rate, 22 notes/second; dominant frequency range 2200–3500 Hz, maximum call energy at 2870–2970 Hz (Vences *et al.* 2006; CD 1, track 24). Another call series of 45 seconds duration recorded near Ranomafana on 1 March 1996 (at 22°C) exhibits the following parameters: note duration, 27–34 ms (30 ± 2; n = 11); inter-note intervals, 14–18 ms (16 ± 1; n = 10); note repetition rate, 22 notes/second; dominant

frequency range 2150–3600 Hz, maximum call energy at 3000–3200 Hz. Although there are slight differences in the measurements of note duration and inter-note intervals, the general character of both calls recorded is nearly identical and leaves no doubt that both belong to the same species. Differences are most probably due to different recording qualities (poor quality in the second mentioned recording).

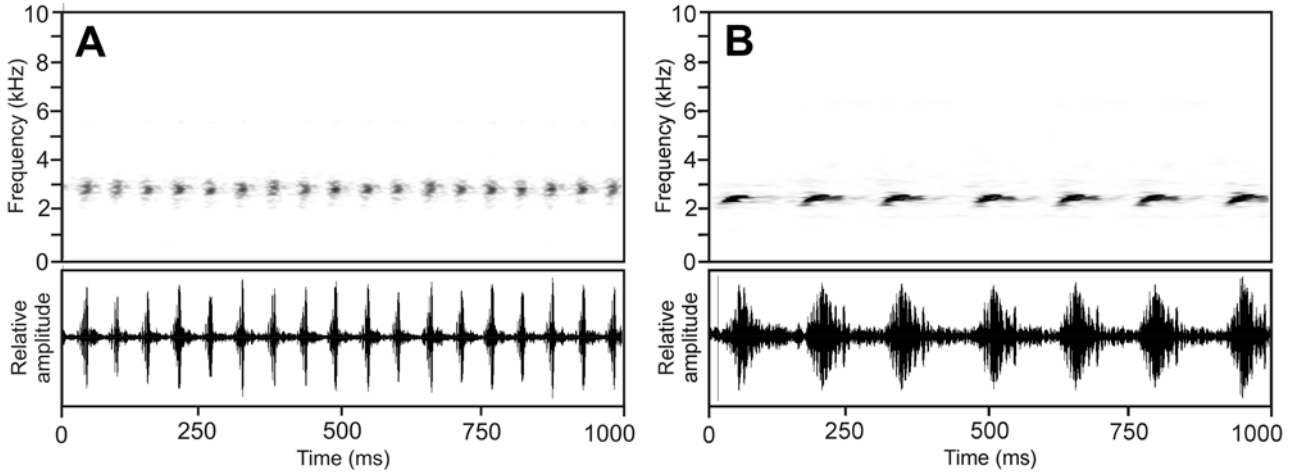


FIGURE 20. Spectrograms and waveforms of advertisement calls: (A) section of advertisement call of *Boophis sandrae* **sp. nov.** from near Vohiparara, Ranomafana National Park (recorded on 28 January 2004, air temperature 20–21°C); (B) advertisement call of *Boophis elenae* from Maharira Forest, Ranomafana National Park (recorded on 24 January 2004, air temperature app. 18.4°C).

Comparative call data. The sister species of *B. sandrae*, *B. anjanaharibeensis*, also emits long series of very short notes in rapid succession. In 2005, we were able to observe several specimens of this species emitting the call at Marojejy National Park, and our assignment of these call data to the species is thus reliable. In contrast, the calls tentatively assigned to the species by Andreone (1996) probably do not belong to this species (specimens were not observed calling by the author). These calls have a note repetition rate of 5.1 notes/second only, in contrast to approximately 40 notes/second observed by us in 2005. Compared to *B. sandrae*, note duration in *B. anjanaharibeensis* is much shorter (2–5 vs. 13–34 ms) and note repetition rate is much faster (40 vs. 22 notes/second), whereas maximum call energy is distributed roughly in the same frequency band (2950–3150 Hz) and inter-note intervals (18–27 ms) are also similar to *B. sandrae* (recording of *B. anjanaharibeensis* obtained at Marojejy National Park; Vences *et al.* 2006, CD 1, track 18). Also, calls of *B. elenae* consist of a long series of short pulsed notes, repeated in fast succession (Fig. 20B). However, note duration is longer and repetition rate significantly lower when compared to calls of *B. sandrae*. For detailed comparison, we here provide numerical parameters of the call of *B. elenae* recorded at Maharira forest (air temperature 18.4°C): duration of call series, 8877 ms; note duration, 78–110 ms (94 ± 9; n = 24); inter-note interval, 50–86 ms (66 ± 8; n = 24); note repetition rate, 6.1–6.4 notes/second; dominant frequency range 1900–2900 Hz, maximum call energy at 2510–2705 Hz (Vences *et al.* 2006, CD 1, track 19).

Molecular relationships. The phylogenetic tree of species in the *Boophis luteus* group (Fig. 18) shows a poor basal resolution, but some relationships among species are well resolved. As already indicated by a similar analysis (with fewer sequences of similar length; Köhler *et al.* 2007), *Boophis tampoka* is resolved sister to *B. luteus* (BS 97%, BPP significant), and *B. englaenderi* seems to be related to these (albeit without bootstrap or Bayesian support). *Boophis elenae* is grouped with *B. andreonei* and *B. jaegeri* (not supported by bootstrap or Bayesian support values), while the sympatric *B. sandrae* groups with *B. anjanaharibeensis* (BP 97%, BPP significant), and the *sandrae/anjanaharibeensis* lineage appears to be related to *B. septentrionalis* (no bootstrap or Bayesian support). *Boophis sandrae* (only topotypical specimens from the Ranomafana region considered) shows high genetic divergences to *B. anjanaharibeensis* (5.2–6.1%) and to all other representatives of the group (>7%). Interestingly, putative specimens of *B. sandrae* from Andasibe are genetically

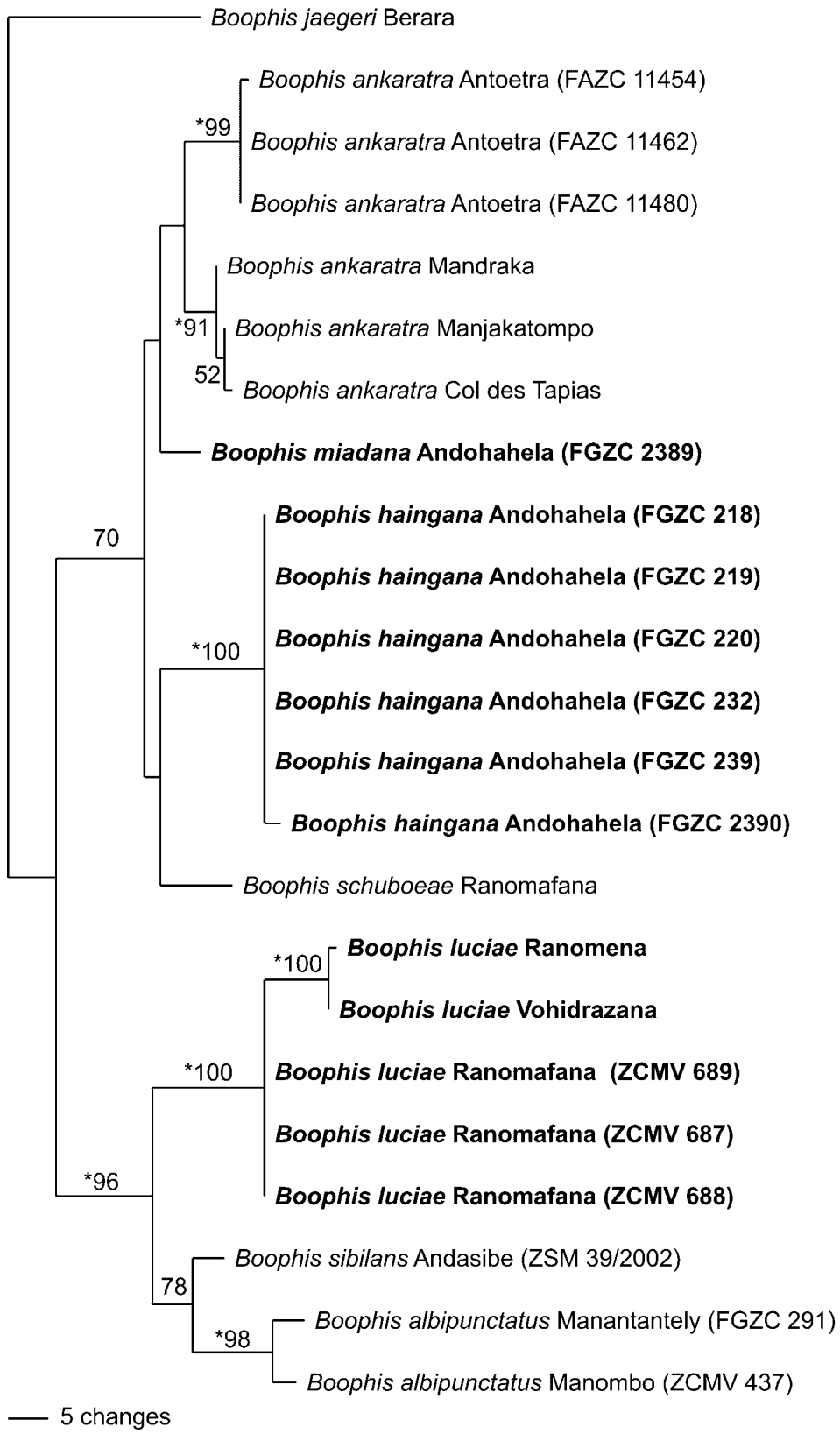


FIGURE 21. Maximum parsimony 16S rRNA phylogram for the *Boophis albipunctatus* group. From 485 total characters, 391 were constant and 72 parsimony informative. MP searches retained 26 trees of which a strict consensus is shown. Consensus support values higher than 50, from 2000 bootstrap replicates, are shown; an asterisk indicates Bayesian posterior probabilities equal or higher than 95%. Species newly described herein are in bold.

also quite divergent (2.8–5.0%) to topotypical specimens, and also comprise two sympatric lineages differentiated by 2.3% among each other. Because these sequences are based on tadpole specimens only (Rahariviloloniaina *et al.* 2006) the identity of this population cannot be further investigated here, but most probably they represent at least one further undescribed species.

Distribution. The distribution of *B. sandrae* encompasses various sites, all in the region around Ranomafana National Park, including Ambatolahy, Vohiparara, and Ranomafana village (Appendix 10). Similar specimens have been photographed and collected in the region around Andasibe, but based on tadpole sequences in Fig. 18 these specimens are strongly differentiated and may belong to another species.

***Boophis miadana* sp. nov.**
(Fig. 22, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *ankaratra* "Andohahela slow" by Glaw & Vences (2007:172–173) and as *Boophis* sp. 19 in Vieites *et al.* (2009).

Holotype. ZSM 5107/2005 (FGZC 2388), adult male, from Andohahela, near campsite of the 2005 expedition of P. Bora, F. Glaw and M. Vences, 24°32.642'S, 46°42.847'E, 1548 m a.s.l., collected on 26 January 2005 by P. Bora, F. Glaw & M. Vences.

Paratype. ZSM 5108/2005 (FGZC 2389), adult male, same collecting data as holotype.

Etymology. The specific name is used as a noun in apposition and is derived from the Malagasy word "miadana" meaning "slow", referring to the slow note repetition rate in advertisement calls of this species, especially in comparison to the syntopic *B. haingana.*

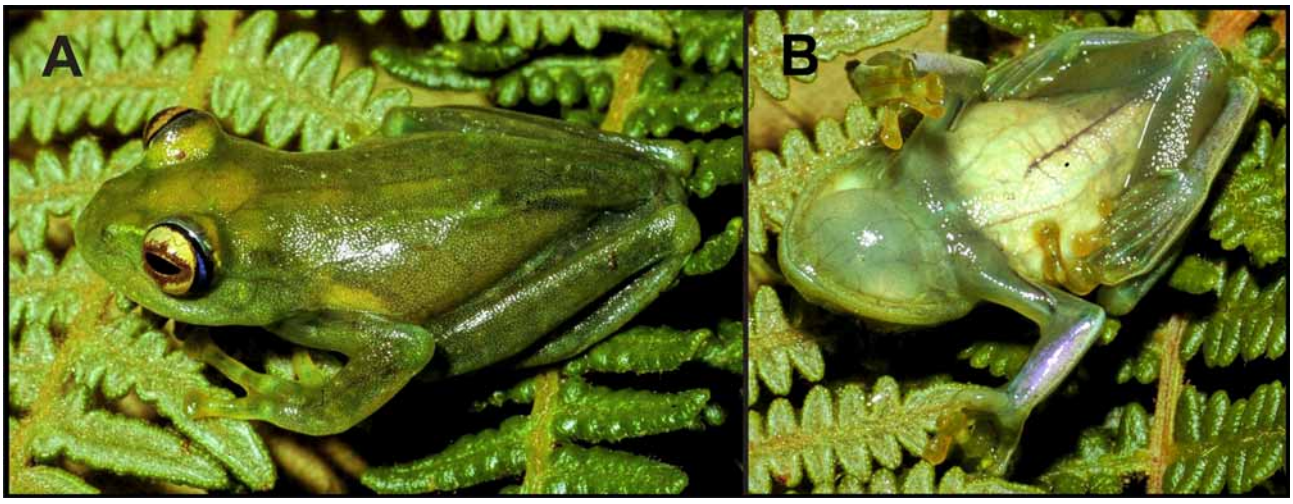


FIGURE 22. Male holotype of *Boophis miadana* **sp. nov.** (ZSM 5107/2005) from Andohahela, 1550 m a.s.l.: (A) dorsolateral view; (B) ventral view.

Diagnosis. 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), 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, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis albipunctatus* group based on the following combination of characters: small size (male SVL 26–27 mm); absence of tubercles or flaps on heel and elbow; presence of webbing between fingers; indistinct canthus rostralis; dorsal colouration translucent green in life and whitish-yellow in preservative; absence of red ventral colour; ventral skin in life non-transparent; single subgular vocal sac; presence

of vomerine teeth; molecular phylogenetic relationships; and high morphological similarity to *B. ankaratra* and *B. schuboeae.* The new species differs from all other species in the *Boophis albipunctatus* group by a moderate to strong genetic differentiation (see below) and by advertisement calls. Within the *B. albipunctatus* group, the new candidate species belongs to a clade of morphologically very similar species (*B. ankaratra, B. schuboeae, B. miadana,* and *B. haingana* as described below) characterized by (1) the lack of well-defined brown markings on the iris, and (2) lack of a dense dorsal spotting with small and sharply defined white spots. Within this complex, *B. miadana* is characterized by the longest duration of notes and of inter-note intervals (see Figs. 24–25 and Comparisons section below).

Description of the holotype. Adult male, SVL 25.5 mm. Body moderately slender; head slightly longer than wide, wider than body; snout rounded in dorsal and lateral view, nostrils directed laterally, nearer to eye than to tip of snout; canthus rostralis rounded in cross section, slightly concave in dorsal view, loreal region slightly concave; tympanum distinct, round, TD 44% of ED; supratympanic fold barely distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, rounded. Tongue posteriorly bifid, free. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1.5), 2i(1.5), 2e(1), 3i(2), 3e(1.5), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation reaching the tip of snout when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0.5), 2i(0.75), 2e(0.25), 3i(1), 3e(0.25), 4i(1.25), 4e(1.5), 5(0.5); relative length of toes 1<2<3<5<4; toe discs enlarged. Skin smooth on dorsal surfaces, finely granular on throat and chest, coarsely granular on belly and ventral surfaces of thighs. Muscle from right thigh was removed for tissue sample.

Measurements (in mm): SVL 25.5, HW 8.9, HL 9.1, ED 3.4, END 1.7, NSD 2.6, NND 2.8, TD 1.5, TL 14.1, HAL 8.6, FOL 11.5, FOTL 18.7.

After almost three years in preservative, ground colour of upper surfaces of head, dorsum, and limbs uniformly creamy yellow; dark pigmentations around nostrils. Ventral surfaces uniformly creamy yellow.
In life, the holotype was dorsally pale green, translucent, with few scattered, diffuse yellow flecks. Throat greenish blue, translucent; ventral skin transparent, visceral peritoneum white. Iris yellowish white, red around the pupil; a black ring surrounding the iris externally; from the pupil to the posterior part of eye, the colours are successively red, yellowish white, black, blue, and black again.

Variation. The topotypical specimen ZSM 5108/2005 is identical except for two small brown spots on dorsum. In calling males we observed a highly extensible single subgular vocal sac.

Natural history. Specimens were heard along a stream flowing through an exposed and largely unforested area at Andohahela. The stream was bordered by some trees and dense shrub vegetation at some sites, and distance to closed rainforest was 100–200 m. Along this stream, at night large mixed choruses of *Boophis andohahela* and *B. haingana* (see below) were heard. In between, a few specimens emitting a different call in very regular intervals could be detected, and two of these were eventually collected. They were sitting in dense shrub, on leaves at 1–2 m perch height.

Vocalization. The following description is based on recordings of the type specimens which were both identified as calling males. The call of *B. miadana* consists of a series of moderately long pulsed notes repeated in slow, but regular succession (Fig. 24A). Pulses within notes are clearly recognizable, but the slightly noisy recording prevents exact pulse counts. Numerous indistinct frequency bands are recognizable in spectrograms at high frequency resolution. Notes exhibit distinct amplitude modulation with energy constantly increasing towards the end of the note. Numerical parameters of calls from Andohahela National Park (1550 m a.s.l.) are as follows: duration of note series, 13.1 seconds; note duration, 239–309 ms (267 ± 24; n = 13); inter-note interval, 670–906 ms (746 ± 69; n = 11); note repetition rate, 1.0–1.2 notes/second; dominant frequency range 2100–3300 Hz, maximum call energy at 2720–2820 Hz (Vences *et al.* 2006, CD 1, track 30).

Comparative call data. Compared to calls of *B. ankaratra*, note duration in *B. miadana* is longer, as are intervals between notes (see Glaw & Vences 2002; Fig. 25). Moreover, pulses are clearly separated and the pulse rate within notes seems to be significantly higher in *B. ankaratra*. Calls of the sympatric *B. haingana* clearly differ by shorter note duration and significantly higher note repetition rate. Calls of *B. schuboeae* are more melodious, have shorter note duration and are repeated at a much higher rate (Fig. 25A).

Molecular relationships. The phylogenetic pattern observed in the subclade containing *Boophis miadana* (Fig. 21) is rather complex. This species is placed sister to *B. ankaratra*, but the bootstrap and Bayesian analyses provide no significant support for this placement; *B. haingana* (described below) and *B. schuboae* form a separate lineage. *Boophis ankaratra* itself is further divided into one lineage spanning much of its distribution area (here including specimens from Mandraka, Manjakatompo and Col des Tapias south of Antsirabe), and specimens from Antoetra. The latter individuals were collected by F. Andreone and showed rather slow calls (*Boophis* sp. aff. *ankaratra* "Antoetra slow" in Glaw & Vences 2007); their molecular differentiation from typical *B. ankaratra* (which seems to occur in the Antoetra region as well, but molecular data are not available) is 2.2–2.9% and their status requires a further in-depth study (see Comparisons below). The differentiation of *B. miadana* is 2.3–2.5% from typical *B. ankaratra* and 3.5% from *B. schuboeae*.

Taxonomic remarks. As discussed previously (Glaw & Vences 2002), a morphological differentiation of *B. ankaratra* and *B. schuboeae* is not possible, and this applies also to *B. miadana* (and *B. haingana*) as described herein, relative to *B. ankaratra* and *B. schuboeae* and to each other. All these species form a monophyletic group and are morphologically very similar, but can be distinguished by note duration and inter-note interval duration of their advertisement calls (Fig. 25).

The closest relationships of *B. miadana* are probably with *B. ankaratra*, although it is not grouped as its direct sister species in the molecular analysis. The two species are similar in having a relatively slow call, with long intervals and long notes (see comparative call data below). Such call parameters, in frogs, are known to differ with temperature and with state of sexual motivation, as also indicated by the calls of *B. haingana* from two sites of different elevation (and temperature) at Andohahela (Fig. 25). However, we are convinced that such temperature or motivational differences cannot explain the long note and interval durations of *B. miadana*. The calls of *B. ankaratra* are known to be rather similar across its range, from Ambohitantely to Andringitra, across a north-south transect of over 400 km in the central highlands of Madagascar (Glaw & Vences 2002). Even the slowest call recorded of *B. ankaratra* (from a male with very low motivation, calling only very sporadically in Itremo) still is characterized by, on average, a shorter inter-note interval (671 ms) than the calls of *B. miadana*, and note duration is consistently and distinctly shorter in this and all other available *B. ankaratra* recordings (range in six populations 94–204 ms; see data in Glaw & Vences 2002). Conversely, the calls of *B. miadana* were emitted by various highly motivated males that called very continuously at Andohahela.

A further candidate species of this complex exists, and was designated *Boophis* sp. aff. *ankaratra* "Antoetra slow" in Glaw & Vences (2007). This species was observed by F. Andreone in probable sympatry with *B. ankaratra* in the Antoetra region, which would strongly support its status as a separate, reproductively isolated species. A detailed revision of the respective material will be necessary, but it is probable that the specimens FAZC 11454, 11462 and 11480 belong to this new species. By molecular data, these species is grouped closer to *B. ankaratra* than to *B. miadana* (Fig. 21). If the identity of these specimens was verified, it would provide a further argument for the species status of *B. miadana* relative to *B. ankaratra*, although at present the underlying rationale is indirect and requires further study.

Distribution. At present, *Boophis miadana* is only reliably known from its type locality, Andohahela National Park, at elevations above 1500 m a.s.l. (Appendix 10).

***Boophis haingana* sp. nov.**
(Fig. 23, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *ankaratra* "Andohahela fast" by Glaw & Vences (2007:172–173) and as *Boophis* sp. 20 by Vieites *et al.* (2009).

Holotype. ZSM 5109/2005 (FGZC 2390), adult male, from Andohahela, near campsite of the 2005 expedition of P. Bora, F. Glaw and M. Vences, 24°32.642'S, 46°42.847'E, 1548 m a.s.l., southeastern Madagascar, collected on 26 January 2005 by P. Bora, F. Glaw and M. Vences.

Paratypes. UADBA 24749 and UADBA (FGZC 219, 220), three adult males, from Andohahela, between Isaka and Eminiminy, Camp 2, 24°44'18"S, 46°50'25"E, ca. 600 m a.s.l., collected on 1–4 February 2004 by F. Glaw, M. Puente, R. Randrianiaina and M. Thomas; UADBA (FGZC 2448, 2486, 2537), ZSM 5110/2005 (FGZC 2447), four males, and ZSM 5111/2005 (FGZC 2487), ZSM 5112/2005 (FGZC 2536), two females, all from Andohahela, stream at high altitude, ca. 45 minutes walking distance from holotype locality (no coordinates available), collected on 28–30 January 2005 by P. Bora, F. Glaw and M. Vences; ZFMK 90153 (formerly ZSM 122/2004 [FGZC 218]) and ZSM 129/2004 (FGZC 239), two adult males, from Andohahela, between Isaka and Eminiminy, Camp 2, 24°44'18"S, 46°50'25"E, ca. 600 m a.s.l., collected on 1–4 February 2004 by F. Glaw, M. Puente, R. Randrianiaina and M. Thomas.

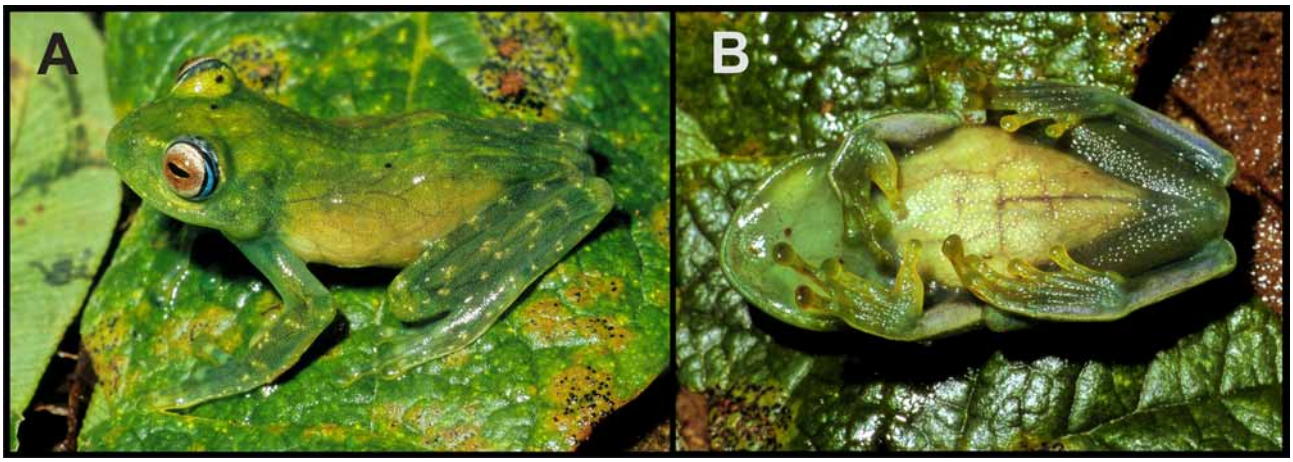


FIGURE 23. Male holotype of *Boophis haingana* **sp. nov.** (ZSM 5109/2005) from Andohahela: (A) dorsolateral view; (B) ventral view.

Etymology. The specific name is used as a noun in apposition and is derived from the Malagasy word "haingana" meaning "fast", referring to the fast note repetition rate in advertisement calls of this species, especially in comparison to the syntopic *B. miadana*.

Diagnosis. 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), 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, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis albipunctatus* group based on the following combination of characters: small size (male SVL 25–29 mm); absence of tubercles or flaps on heel and elbow; presence of webbing between fingers; indistinct canthus rostralis; dorsal colouration translucent green in life and yellow-whitish in preservative; absence of red ventral colour; ventral skin in life non-transparent; single subgular vocal sac; presence of vomerine teeth; molecular phylogenetic relationships; and its high morphological similarity to *B. ankaratra*. The new species differs from all other species in the *Boophis albipunctatus* group by a moderate to strong

genetic differentiation (see below). Within the *B. albipunctatus* group, the new species belongs to a clade of morphologically very similar species (*B. ankaratra, B. schuboeae, B. miadana,* and *B. haingana*) characterized by (1) the lack of well-defined brown markings on the iris, and (2) lack of a dense dorsal spotting with small and sharply defined white spots. Within this complex, *B. haingana* is characterized by the shortest duration of notes in advertisement calls (see Fig. 25 and Comparisons section below).

Description of the holotype. Adult male, SVL 25.7 mm. Body moderately slender; head as long as wide, wider than body; snout rounded in dorsal and lateral view, nostrils directed laterally, slightly nearer to eye than to tip of snout; canthus rostralis rounded in cross section, straight in dorsal view, loreal region slightly concave; tympanum distinct, round, TD 39% of ED; supratympanic fold barely distinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, rounded. Tongue posteriorly bifid, free. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1.5), 2i(1.5), 2e(1), 3i(2), 3e(1.5), 4(1); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation reaching the tip of snout when hind limb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0.5), 2i(0.75), 2e(0.25), 3i(1), 3e(0.25), 4i(1.25), 4e(1.25), 5(0.5); relative length of toes 1<2<3<5<4; toe discs enlarged. Skin smooth on dorsal surfaces, finely granular on throat and chest, coarsely granular on belly and ventral surfaces of thighs. Muscle from right thigh was removed for tissue sample.

Measurements (in mm): SVL 25.7, HW 9.3, HL 9.3, ED 3.3, END 2.1, NSD 2.4, NND 3.2, TD 1.3, TL 13.2, HAL 8.6, FOL 10.6, FOTL 18.1.

After almost three years in preservative, ground colour of upper surfaces of head, dorsum, and limbs creamy yellow; there is a brown small spot on dorsum and two more on head, one in the interorbital region and another on the right upper eyelid; dark pigmentation around nostrils. Ventral surfaces uniformly creamy yellow.

In life, the holotype was dorsally pale green, translucent, with scattered, diffuse yellow flecks, and three brown spots, one on dorsum and two on head. The throat was greenish blue, translucent; the ventral skin was transparent, and the visceral peritoneum white. Iris was white, red around the pupil, with a black ring surrounding the iris externally; from the pupil to the posterior part of eye, the colours are successively red, white, black, blue, and black again.

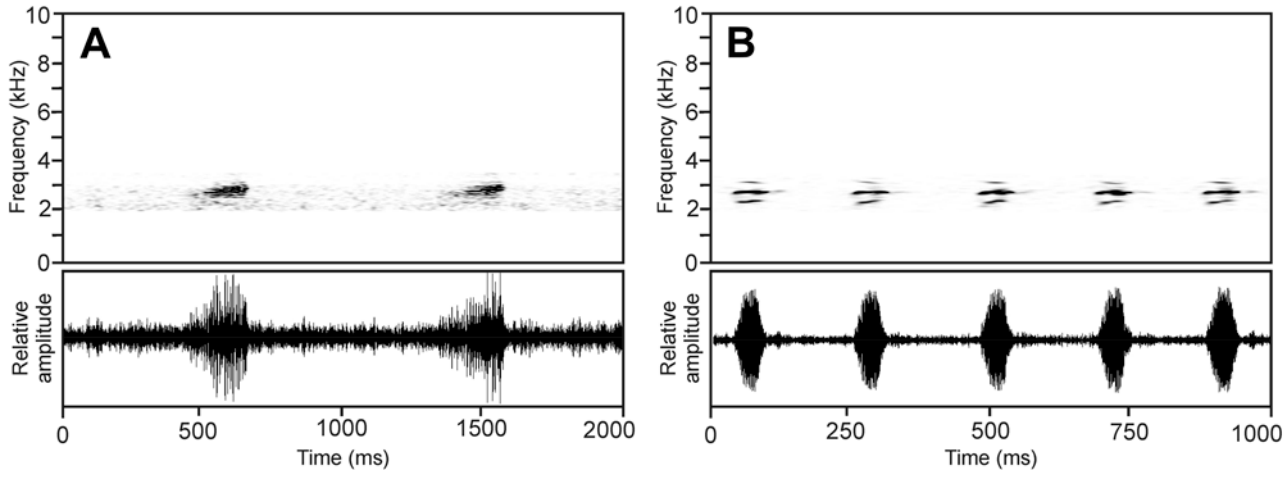


FIGURE 24. Spectrogram and waveform of advertisement calls of: (A) *Boophis miadana* **sp. nov.** from Andohahela National Park, 1550 m a.s.l. (recorded on 26 January 2005, air temperature app. 17.6°C); (B) *Boophis haingana* **sp. nov.** from Andohahela National Park, low altitude (recorded on 3 February 2004, air temperature app. 23.2°C).

Variation. Morphometric variation is given in Appendix 8. Females are larger, at average having approximately 136 % of male SVL. All collected specimens are very similar in colouration and external morphology. In calling males we observed a highly extensible single subgular vocal sac.

Natural history. At higher elevation of Andohahela National Park, specimens were collected in syntopy with *Boophis andohahela* and *B. miadana* (see above), along a stream flowing through an exposed and largely unforested area, at about 100–200 m from closed forest. Specimens were calling at night from perch heights of 1–2 m in the shrubby vegetation along the stream. At low elevations of Andohahela National Park, specimens were collected from perch heights of at least 2 m, in vegetation in closed rainforest at some distance from a stream.

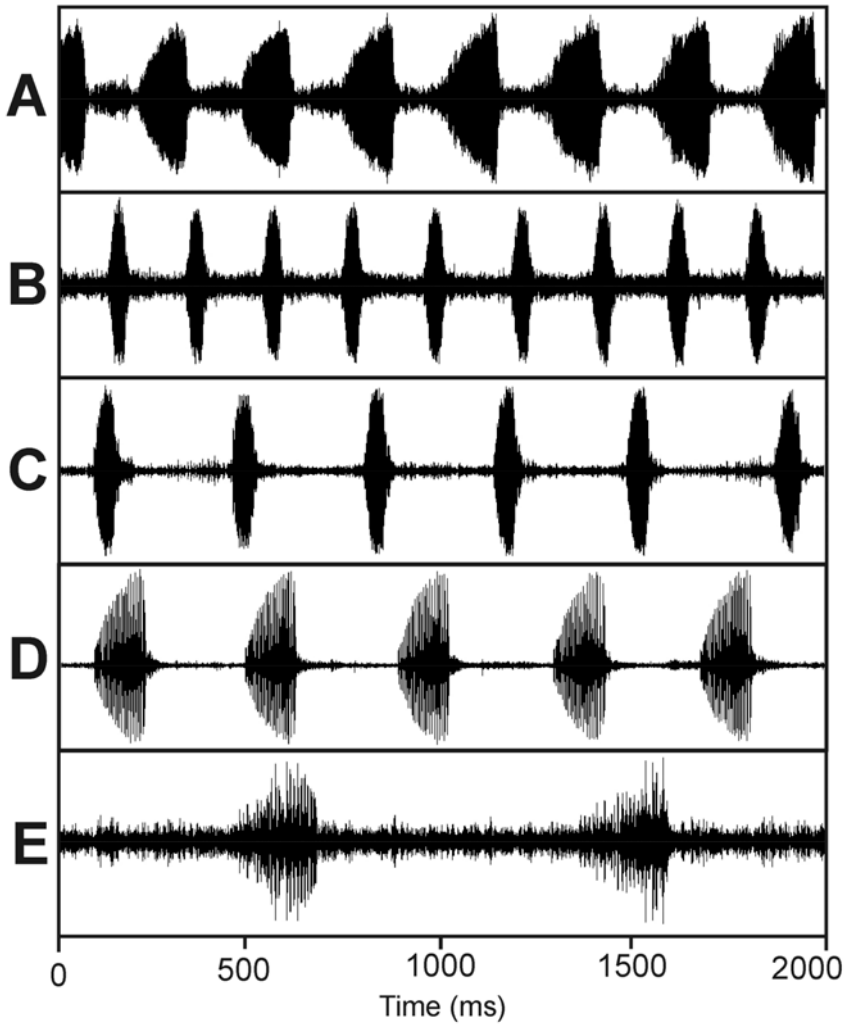


FIGURE 25. Comparative waveform sections (each 2000 ms duration) of advertisement calls of species in the *Boophis albipunctatus* group: (A) *Boophis schuboeae* (Ranomafana National Park, 23°C); (B) *Boophis haingana* **sp. nov.** (Andohahela National Park, low altitude, 23.2°C); (C) *Boophis haingana* **sp. nov.** (Andohahela National Park, 1600 m a.s.l., 17.6°C); (D) *Boophis ankaratra* (Manjakatompo, 18°C); (E) *Boophis miadana* **sp. nov**. (Andohahela National Park, 1550 m a.s.l., 17.6°C).

Vocalization. The call of *B. haingana* consists of a long series of short pulsatile notes repeated in fast and regular succession (Fig. 24B). Pulses within notes are clearly recognizable but not distinctly separated from each other, preventing exact counts. Three distinct frequency bands are evident in the spectrogram. With higher temperature, note repetition rate increases, but note duration roughly remains the same. Notes exhibit clear amplitude modulation, with maximum energy at the middle of the note. Here we present data for two

populations of the new species from Andohahela National Park, one from low altitude (600 m a.s.l., air temperature 23.2°C, recorded specimen ZSM 129/2004), and the other from 1550 m a.s.l. (air temperature 17.6°C). Low altitude population (Fig. 24B): duration of note series, 16.2 seconds; note duration, 36–60 ms (49 ± 7; n = 25); inter-note interval, 142–232 ms (184 ± 24; n = 25); note repetition rate, 4.2–4.5 notes/second; dominant frequency range 2200–3200 Hz, maximum call energy at 2770–2810 Hz. High altitude population: duration of note series, 28 seconds; note duration, 55–90 ms (72 ± 9; n = 29); inter-note interval, 245–365 ms (306 ± 32; n = 29); note repetition rate, 2.6–3.0 notes/second; dominant frequency range 2300–3200 Hz, maximum call energy at 2680–2880 Hz (Vences *et al*. 2006, CD 1, track 29).

Comparative call data. In comparison to calls of *B. ankaratra* and *B. schuboeae*, note duration in *B. haingana* is significantly shorter (see Glaw & Vences 2002; Fig. 25). Moreover, amplitude modulation of notes differs by the highest energy present in the middle of notes in *B. haingana* vs. at the end of the notes in *B. ankaratra* and *B. schuboeae*. Notes of *B. schuboeae* are generally of slightly pulsatile nature, but have a melodious character compared to *B. haingana*. Notes of *B. ankaratra* have distinctly separated pulses, whereas the pulses in notes of *B. haingana* are partly fused. Compared to calls of the syntopical *B. miadana*, note duration in *B. haingana* is much shorter and note repetition much faster (see above; Fig. 25).

Molecular relationships. The molecular phylogenetic analysis places *Boophis haingana* sister to *B. schuboeae* (Fig. 21) but this relationship receives no bootstrap or Bayesian support. Molecular divergence of *B. haingana* is 4.1–4.6% from *B. ankaratra*, 4.4–4.6% from *B. miadana*, and 4.6–4.8% from *B. schuboeae*. The single specimen of *B. haingana* studied from high elevations of Andohahela National Park differs by 0.4% from the low-altitude specimens which all have identical sequences.

Comparisons. See Comparisons section of *B. miadana* above for a general discussion of the morphological and bioacoustic differentiation in the clade of species formed by *B. ankaratra, B. haingana, B. miadana*, and *B. schuboeae.* The closest relationships of *B. haingana* are with *B. schuboeae.* The two species cluster in the molecular analysis (Fig. 21) albeit without significant support, and they are similar in their relative fast calls with short inter-note intervals. Recordings from low and high elevations at Andohahela demonstrate that the inter-note intervals in *B. haingana* strongly depend on the temperature and become distinctly larger at low temperatures. However, similar to what has been reported in *B. ankaratra* (see Glaw & Vences 2002), note duration of *B. haingana* appears to be unaffected by temperature, and the differences to *B. schuboeae* remain stable (Fig. 25), supporting their status as two different species differing by a distinct call.

Distribution. At present *Boophis haingana* is only reliably known from its type locality, Andohahela National Park (Appendix 10), where it occurs at both low and high elevations (600-1550 m a.s.l.).

***Boophis luciae* sp. nov.**
(Fig. 26, Appendix 9)

Remark. This species has been referred to as *Boophis* sp. aff. *sibilans* by Glaw & Vences (2007:172–173) and as *Boophis* sp. 17 in Vieites *et al.* (2009).

Holotype. ZSM 327/2000, adult male, from Vohidrazana, 18°57'57" S, 48°30'37" E, 731 m a.s.l., eastern Madagascar, collected on 10 April 2000 by F. Glaw.

Paratypes. UADBA (ZCMV 688), sex unknown, from near Ambatolahy, 21°14.632' S, 47°25.573' E, 915 m a.s.l., collected on 10 February 2004 by D. R. Vieites and C. Woodhead; ZFMK 60126–60129 and 60834, adult males, from Ranomena near Andasibe, collected on 2 April 1995 by F. Glaw and D. Vallan; ZFMK 64141, male, from the Ranomafana region, collected on 3–4 March 1996 by F. Glaw, D. Rakotomalala and F. Ranaivojaona; ZFMK 60041, adult male, from Andasibe, collected on 1 February 1995 by F. Glaw; ZFMK 62307, 62908, adult males, from Ranomafana, collected on 2 March 1996 by F. Glaw, D. Rakotomalala and F. Ranaivojaona; ZMA 20305 (ZCMV 595), adult female, ZMA 20306–20307 (ZCMV 687, 689), adult males,

from near Ambatolahy, 21°14.632' S, 47°25.573' E, 915 m a.s.l., collected on 9 February 2004 by D. R. Vieites and C. Woodhead; ZSM 63/2004, adult male, from Andohahela, between Isaka and Eminiminy, Camp 1, 24°45'31" S, 46°51'15" E, 247 m a.s.l., collected on 29–31 January 2004 by F. Glaw, M. Puente, R. Randrianiaina and M. Thomas; ZSM 328–329/2000, adult males, same data as holotype; ZSM 243/2006 (ZCMV 3033), adult male, ZSM 244/2006 (ZCMV 3057), adult female, from near Ambatolahy, 21°14.632' S, 47°25.573' E, 915 m a.s.l., collected on 26 February 2006 by P. Bora, Y. Chiari, E. Rajeriarison, T. Razafindrabe and M. Vences.

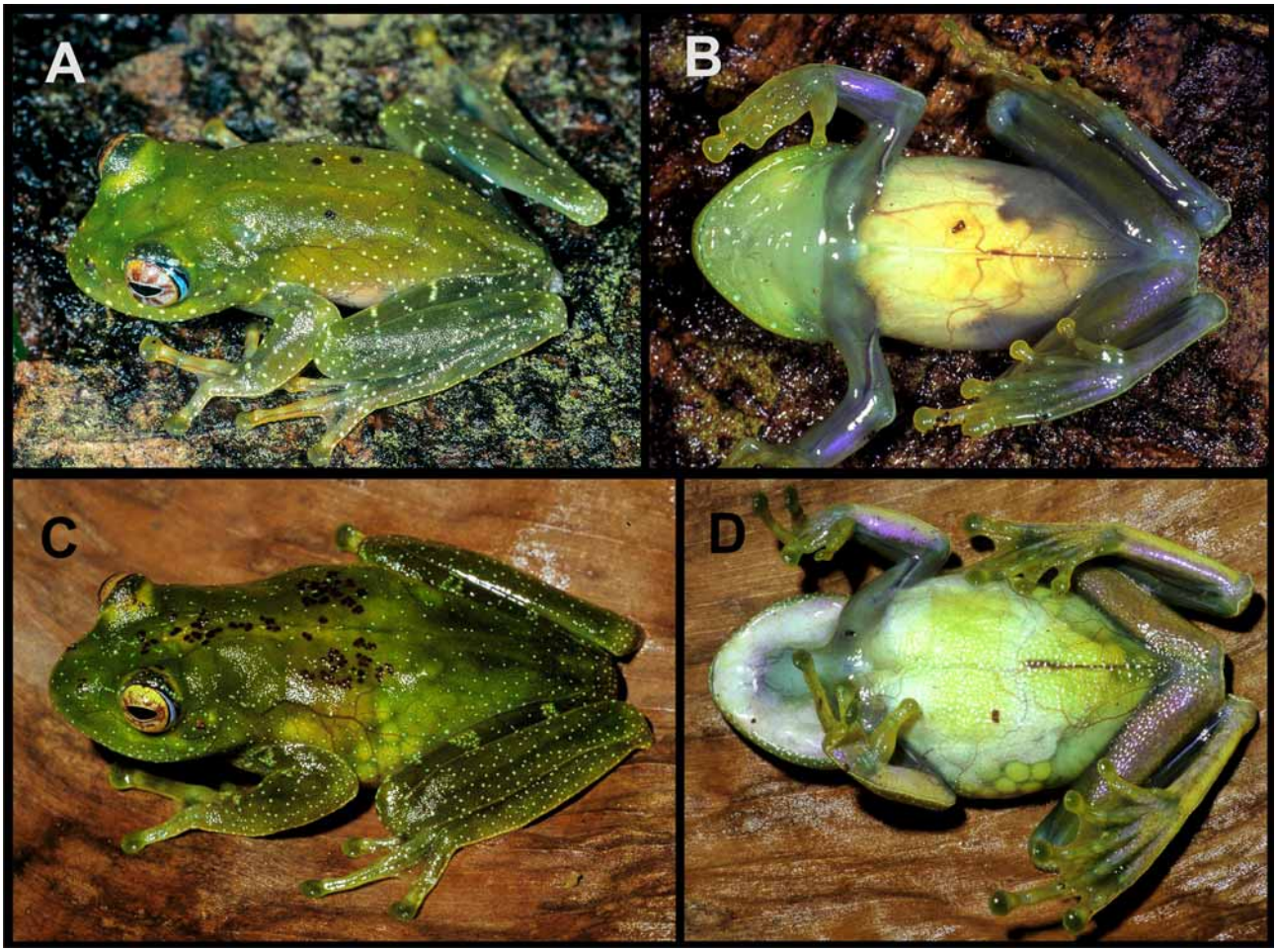


FIGURE 26. *Boophis luciae* **sp. nov.** in life: (A) dorsolateral view and (B) ventral view of male from Ranomena; (C) dorsolateral view and (B) ventral view of female from Ranomafana region showing mature eggs through transparent skin.

Etymology. Ignacio De la Riva dedicates this species to his daughter Lucia, as compensation for the time he spends doing field work abroad, something she rather dislikes.

Diagnosis. 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), absence of femoral glands in males, absence of gular glands in males, presence of axillary amplexus, enlarged terminal discs of fingers and toes, lateral metatarsalia separated by webbing, absence of outer metatarsal tubercle, molecular phylogenetic relationships (see Vieites *et al.* 2009 for a complete molecular analysis of *Boophis*), and overall similarity to other *Boophis* species. Assigned to the *Boophis albipunctatus* group based on the following combination of characters: small size (male SVL 24–31 mm); absence of tubercles or flaps on heel and elbow; presence of webbing between fingers; indistinct canthus rostralis; dorsal colouration translucent green with

many small white dots in life and yellow-whitish in preservative; absence of red ventral colour; ventral skin in life non-transparent; single subgular vocal sac; presence of vomerine teeth; molecular phylogenetic relationships; and its high morphological similarity to *B. albipunctatus* and *B. sibilans.* The new species differs from all other species in the *Boophis albipunctatus* group by its strong genetic differentiation (see below). Along a stream near Andasibe, *B. luciae* occurs in syntopy with *B. albipunctatus* and *B. sibilans*. Within the *B. albipunctatus* group, the new species belongs to a clade of morphologically very similar species (*B. albipunctatus, B. luciae, B. sibilans*) characterized by (1) presence of well-defined brown markings on the iris, and (2) presence of a dense dorsal spotting with small and sharply defined white spots. Within this complex of species, *B. luciae* is characterized by its usually smaller body size (male SVL of *B. luciae* 24–31 mm, mostly below 30 mm, vs. 28–34 mm in the other two species). It is further distinguished by its advertisement call: from *B. albipunctatus*, by a longer duration and different structure of notes (trill notes vs. short clicks; note duration 18–101, average 61 ms, vs. 19–43 ms), and from *B. sibilans* by the pulsed structure of its trill notes (vs. tonal unpulsed whistles; see Comparative call data below).

Description of the holotype. Adult male, SVL 28.5 mm. Body moderately slender; head as longer as wide, slightly wider than body; snout rounded in dorsal and lateral view, nostrils directed laterally, slightly nearer to tip of snout than to eye; canthus rostralis rounded in cross section, straight in dorsal view, loreal region slightly concave; tympanum distinct, round, TD 45% of ED; supratympanic fold indistinct; vomerine odontophores distinct, well separated in two elongated patches, positioned posteromedial to choanae; choanae medium-sized, rounded. Tongue posteriorly bifid, free behind. Arms slender, subarticular tubercles single, round; metacarpal tubercles not recognizable; fingers moderately webbed and with lateral dermal fringes; webbing formula 1(1), 2i(1.25), 2e(0.75), 3i(1.25), 3e(1.5), 4(1.25); relative length of fingers 1<2<4<3 (finger 2 distinctly shorter than finger 4); finger discs enlarged. Hindlimbs slender; tibiotarsal articulation reaching beyond the tip of snout when hindlimb is adpressed along body; lateral metatarsalia separated by webbing; inner metatarsal tubercle small, distinct, elongated; no outer metatarsal tubercle; toes broadly webbed; webbing formula 1(0), 2i(0.5), 2e(0.25), 3i(0.25), 3e(0), 4i(1), 4e(1), 5(0.25); relative length of toes 1<2<5=3<4; toe discs enlarged. Skin smooth on dorsal surfaces, granular on throat, chest, belly and ventral surfaces of thighs. The entire left forelimb was removed for tissue sample.

Measurements (in mm): SVL 28.5, HW 10.6, HL 10.6, ED 3.3, END 2.3, NSD 2.2, NND 3.0, TD 1.5, TL 45.8, HAL 9.8, FOL 12.6, FOTL 20.8.

After seven years in preservative, ground colour of upper and lower surfaces of head, dorsum, and limbs creamy yellow, with small dark spots or flecks on flanks, lips, tympanic region, and limbs; small brown flecks on central dorsum and around nostrils. Posterior part of eye purplish. There are no data on colour in life of the holotype.

Variation. Morphometric variation is given in Appendix 7. Females are larger, at average having approximately 154 % of male SVL. Overall, the paratypes are similar to the holotype. In life, dorsal surfaces of head, body and limbs translucent green with scattered small, cream dots; there are few scattered brown dots on head and dorsum, often especially concentrated in a group at each side of mid-dorsum. Upper surface of fingers, toes and terminal discs the same colour as dorsum. Lower flanks transparent. Ventral skin transparent, ventral peritoneum white. Ventral skin of limbs translucent with a bluish tone. Iris golden (orange near the border), with purple markings, more densely arranged around the pupil; eye periphery black posteriorly, then blue, and again black (Fig. 26). In calling males we observed a highly extensible single subgular vocal sac.

Natural history. Similar to *Boophis albipunctatus* and *B. sibilans*, calling males of *B. luciae* are often heard at night from high perches up to 4 m in the vegetation along streams in primary and degraded rainforest. In most cases, it is very difficult to observe the calling males, although along some streams this species occurs in rather high densities and non-calling specimens and pairs in axillary amplexus can be observed later at night on lower perches. Especially in the early evening, single individuals may emit only one of the two possible call types (see below).

Vocalization. Generally, calls of *Boophis luciae* (Fig. 27) may contain three different call types. Type 1 consists of a long series of trill notes (reminding whistles if heard in the field from a distance), emitted in regular intervals. Each trill note contains 5–10 distinctly separated pulses, whereby calls from the Ranomena population contain 5 pulses only. Call type 2 is a short series (maximum 1710 ms duration) of 9–13 whistles, with an increase in note duration towards the end of the series. Call type 3 consists of a short series of 3–6 click notes separated by long intervals, mostly followed by 1–2 whistles, or sometimes followed even by a long series of whistling notes as described for call type 2. Trills and whistles in calls of *B. luciae* show distinct frequency modulation, with frequency constantly increasing towards the end of the note. Numerical parameters for the different call types of the Ranomena (near Andasibe) population are as follows: Call type 1: note duration, 146–201 ms (176 ± 13; n = 58); inter-note intervals, 288–497 ms (376 ± 41; n = 55); note repetition rate, 1.7–2.0 notes/second. Call type 2: note duration, 18–101 ms (61 ± 18; n = 76); inter-note intervals, 39–106 ms (73 ± 16; n = 68); note repetition rate, 7.5–9.8 notes/second. Call type 3: note duration, 15–39 ms (27 ± 7; n = 18); inter-note intervals, 395–527 ms (459 ± 36; n = 13). Dominant frequency range 3000–4500 Hz, maximum call energy at 3600–4300 Hz. Numerical parameters for the different call types of the Vohiparara (Ranomafana) population are as follows: Call type 1: note duration, 152–213 ms (179 ± 12; n = 55); inter-note intervals, 250–529 ms (398 ± 43; n = 48); note repetition rate, 1.6–2.0 notes/second. Call type 2: note duration, 23–81 ms (61 ± 10; n = 48); inter-note intervals, 62–103 ms (84 ± 11; n = 43); note repetition rate, 6.6–7.6 notes/second. Call type 3: note duration, 26–41 ms (31 ± 7; n = 4); inter-note intervals, 467–599 ms (546 ± 70; n = 3). Dominant frequency range 2950–3900 Hz, maximum call energy at 3150–3800 Hz (see Vences *et al.* 2006, CD 1, track 27).

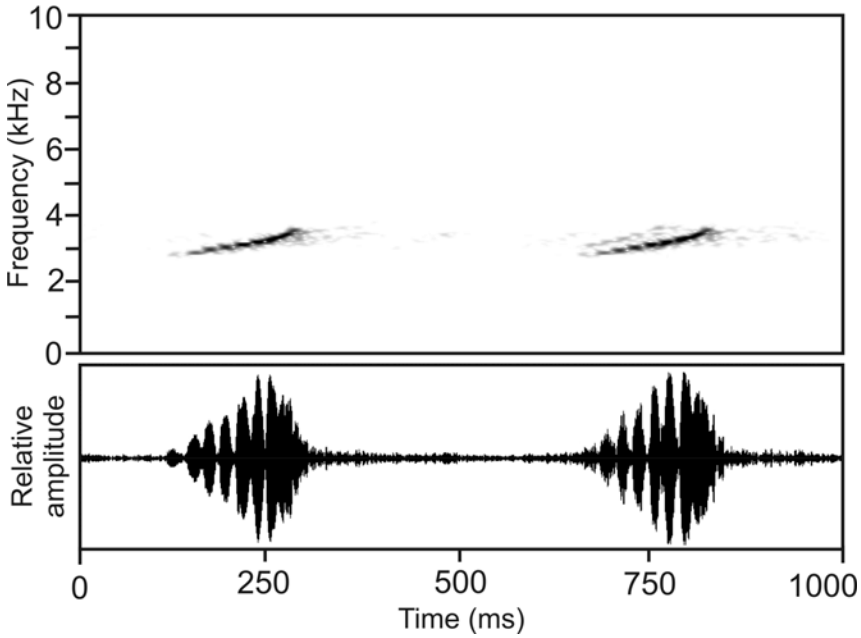


FIGURE 27. Spectrogram and waveform of call type 1 of *Boophis luciae* **sp. nov.** from Andasibe (recorded on 1 February 1995, air temperature 22°C).

Comparative call data. In comparison to sympatric *Boophis sibilans* from Andasibe, the call type 1 of *B. luciae* contains distinctly pulsed trill notes (vs. unpulsed whistles) which are usually emitted in much faster succession (mean inter-note interval 656 vs. 375 ms). Moreover, frequency modulation within whistles is far less pronounced in *B. sibilans*. Click notes are so far unknown in the latter species. For better comparison and in addition to the data provided by Glaw & Thiesmeier (1993), we here provide a more detailed analysis of call type 1 and 2 of *B. sibilans* from Andasibe (type locality): Call type 1: note duration, 151–186 ms (164 ± 9;

n = 34); inter-note intervals, 502–931 ms (656 ± 132; n = 33); note repetition rate, 0.9–1.6 notes/second. Call type 2: note duration, 32–150 ms (117 ± 30; n = 14); inter-note intervals, 113–239 ms (137 ± 37; n = 13); note repetition rate, 3.8–5.0 notes/second; maximum duration of call series, 3436 ms (14 notes, 4.1 notes/second). Dominant frequency range 2600–3450 Hz, maximum call energy at 2700–3300 Hz. Harmonic frequency bands are present at 5600–6100 Hz and 8450–9150 Hz (Vences *et al.* 2006, CD 1, track 26).

Molecular relationships. The phylogenetic tree of species assigned to the *Boophis albipunctatus* group (Fig. 21) provides evidence for two subclades that correspond well with morphological characters. The first subclade (supported by a bootstrap value of 70% but not by the Bayesian analysis) comprises *B. ankaratra, B. schuboeae*, and allied species (two of which are described as new herein, *B. miadana* and *B. haingana*); all these species are green with an irregular pattern of light mottling or with few to many (usually) ill-defined light dots on a green ground colour. The second subclade (BS 96%, BPP significant) contains three species characterized by a pattern of many very small but well-defined white dots on a green ground colour. Of these three species, *B. sibilans* and *B. albipunctatus* are grouped together (BP 78%, BPP not significant), whereas *B. luciae* is most basal. Genetic divergences of *B. luciae* are 4.8–6.2 to *B. sibilans* and 6.4–7.6% to *B. albipunctatus. Boophis sibilans* and *B. albipunctatus* differ by 3.5–3.8%. The two specimens of *B. albipunctatus* differ by 1.4% whereas the specimens of *B. luciae* from the Andasibe region (Ranomena and Vohidrazana) differ by 1.9–2.4% from those of the Ranomafana region.

Comparative material. So far, *B. albipunctatus* is known from few localities only (Andohahela, Manantantely, and Nahampoana in the South East; and Andasibe in the Northern Central East, where it occurs sympatrically with *B. sibilans* and *B. luciae*). We here provide measurements of one further specimen from Ambohitsara (ZSM 2290/2007) in the Southern Central East which is the first record of the species from this region. It was collected from a chorus of various individuals emitting the typical calls as described by Glaw & Thiesmeier (1993). Furthermore, one DNA sequence (see Fig. 21) of a specimen collected in Manombo Special Reserve, a coastal locality in South Eastern Madagascar, provides evidence for the occurrence of the species at this locality.

Distribution. *Boophis luciae* is known from Ambatolahy and other sites in and near Ranomafana National Park, from Andohahela National Park at lower elevations based on call recordings, and from An'Ala, Andasibe, Vohidrazana and Ranomena (near Andasibe) (Appendix 10).

Available names. Several names in the *Boophis luteus* group are potentially available as earlier names for the following four new species described in this paper: *Boophis sandrae, B. miadana, B. haingana*, and *B. luciae*. All species of the *Boophis luteus* group quickly loose the greenish colouration after preservation and fade to yellowish-white. For this reason and due to their morphological similarities it is notoriously difficult to identify preserved voucher specimens for which additional data are unknown. A lectotype (BMNH 1947.2.9.7) of *Rhacophorus luteus* var. *longicrus* Parker, 1925 was designated by Glaw & Vences (1992): Adult male (with nuptial pads recognizable on the first finger), SVL 33.2 mm, eye diameter 4.4 mm, eye-nostril distance 2.4 mm, nostril-snout tip distance 3.1 mm, tympanum diameter 1.6 mm, flanks with remains of white marbling, iris periphery with remains of blue colour. This taxon is considered as a junior synonym of *Boophis luteus* since long. Its small SVL (adult male 33.2 mm vs. 31.9–37.0 mm in *B. luteus*) and relatively small eyes (eye-diameter / SVL = 0.13 vs. 0.11–0.12 in *B. luteus*) argue for this synonymy and against an attribution to *Boophis sandrae* (male SVL 35.5–48.2 mm, eye-diameter / SVL = 0.11–0.15) or *B. elenae* (SVL 40.4–46.0 mm, eye-diameter / SVL = 0.11–0.12). *Rhacophorus anceps* Mocquard, 1902 (type locality Fort Dauphin) and *Rhacophorus isabellinus* Boettger, 1913 (type locality Moramanga) are based on single, poorly preserved and probably juvenile specimens. The former taxon was repeatedly considered as a dubious name (Guibé 1978, Blommers-Schlösser & Blanc 1991, Andreone 1993). An unambiguous attribution of both these taxa to any species of the *B. luteus* group appears impossible. We continue considering them as junior synonyms of *Boophis luteus*.

TABLE 1. Comparative numerical parameters among calls of *Boophis* species considered to have advertisement function. Temporal measurements are given in milliseconds (ms) as range, with mean ± standard deviation in parentheses. See text for more detailed descriptions of calls.

Species	Locality	Temp. [°C]	Note duration	Inter–note interval duration	Note repetition rate [notes/s]	Maximum call energy at [Hz]
B. piperatus (call type 1)	Vohiparara, Ranomafana	20–21	18–50 (34 ± 10)	121–310 (163 ± 47)	5.4–6.0	2870–3180
B. andrangoloaka	Ambohitantely	18.0	178–198 (189 ± 7)	208–265 (229 ± 18)	2.4	2470–2730
B. rhodoscelis	Ranomafanakely	21.0	56–100 (80 ± 13)	93–152 (119 ± 17)	4.6–5.0	2490–3060
B. brachychir	Manongarivo	24.5	50–78 (62 ± 9)	20–30 (24 ± 2)	10.7–13.0	2610–2720
B. entingae (call type 1)	Manongarivo	24.5	232–310 (280 ± 30)	226–245 (–)	2.0	2200–2360
B. obscurus (call type 1)	Vohiparara, Ranomafana	20.5	137–238 (187 ± 40)	extremely irregular	extremely irregular	550–810
B. periegetes	Andohahela	18.0	225–637 (435 ± 147)	320–967 (627 ± 243)	0.6–1.8	1320–1510
B. sandrae	Vohiparara, Ranomafana	20–21	13–23 (18.9 ± 2.4)	35–43 (37.5 ± 2.6)	22.0	2870–2970
B. elenae	Maharira Forest	18.4	78–110 (94 ± 9)	50–86 (66 ± 8)	6.1–6.4	2510–2705
B. miadana	Andohahela, 1600 m a.s.l.	17.6	239–309 (267 ± 24)	670–906 (746 ± 69)	1.0–1.2	2720–2820
B. haingana	Andohahela, 1600 m a.s.l.	17.6	55–90 (72 ± 9)	245–365 (306 ± 32)	2.6–3.0	2680–2880
B. ankaratra	Manjakatompo	18.0	116–129 (125 ± 4)	251–263 (257 ± 4)	2.5	2750–3000
B. schuboeae	Vohiparara, Ranomafana	23.0	96–182 (146 ± 21)	111-221 (140 ± 21)	3.4	3350–3500
B. luciae (call type 1)	Andasibe	22.0	146–201 (176 ± 13)	288–497 (376 ± 41)	1.7–2.0	3600–4300
B. sibilans (call type 1)	Andasibe	23.0	151–186 (164 ± 9)	502–931 (656 ± 132)	0.9–1.6	2700–3300

Discussion

Practical application of integrative taxonomy in Malagasy frogs

Historically, Malagasy amphibians were described solely on the basis of morphological characters of preserved specimens which in many cases led to biologically mistaken interpretations of variation. As discussed by Glaw & Vences (1994), especially many new species described by Ernst Ahl from Madagascar turned out to be synonyms and created taxonomic confusion. Blommers-Schlösser (1979) pioneered an approach that combines various sets of data to delimit species and decipher the true biological relationships among them. Besides morphology of adults, she studied their colouration in life, ecology, bioacoustics, tadpoles, chromosomes, and DNA content, which led to an enormous progress in the understanding of the systematics of Malagasy frogs. Three factors subsequently led to a veritable boom in the discovery of new species from

Madagascar from the beginning of the 1990s on (Köhler *et al.* 2005; Vieites *et al.* 2009). First, a strongly increased intensity of field work and collection activity that also included remote parts of Madagascar from where field data had been very scarce previously. Second, the understanding that advertisement calls in frogs are a highly stable character mediating sexual species recognition, and that differences in these calls consequently are a highly relevant character to distinguish species. And third, the development of economically convenient high-throughput methods to sequence standard DNA fragments and thus to develop DNA barcoding research programs.

Despite the implicit use of combined sets of characters in delimiting Malagasy amphibians since the works of Blommers-Schlösser (1979), it is only recently that species delimitation is seen as a Renaissance issue in systematics (Sites & Marshall 2004) and that advances have been made to provide an explicit theoretical backbone for the use of combined evidence in this process. On one hand, through the general lineage species concept (De Queiroz 1998; 2007) it is now widely understood among evolutionary biologists that almost all species concepts agree in defining species as population-level evolutionary lineages, and that the various species concepts refer to diagnostic characters of these lineages that become recognizable in a variable order and after different intervals of time. Secondly, there is a vivid and fruitful discussion about the novel concept of integrative taxonomy as introduced by Dayrat (2005). This concept rejects the superiority of any particular set of characters (morphological, behavioural, molecular) over others during the process of recognizing and diagnosing species, and advocates the combined and integrated use of various methodological approaches to study the variation in different suites of characters. However, the development of the integrative taxonomy concept is ongoing, and among the various proposed work protocols there are those that seek for congruence among data sets as a main criterion to delimit species boundaries (Cardoso *et al.* 2009) and those that argue that under certain circumstances differences in a single marker are sufficient to delimit a species, but that several lines of evidence indicate higher future stability of a species name (Padial *et al.* 2009).

Whereas the framework provided by the lineage species concept has been rapidly embraced by many systematists to delineate species boundaries (e.g. Wiens & Penkrot 2002; Sites & Marshall 2004; Wiens 2007), both the lineage species concept and need for an integrative taxonomy have been controversially debated and are only being gradually accepted by taxonomists (see reviews by Dayrat 2005; Padial & De la Riva 2006). The use of molecular data as major tool in species discovery has been criticised by both applied biologists and some taxonomists who argue for taxonomic conservatism grounded either in the requirement of providing evidences of morphological distinctiveness or of reproductive barriers to erect new species names (see Isaac *et al.* 2004). Padial & De la Riva (2006; 2007) argued against these views and claimed for the extensive use of molecular tools by taxonomists. However, if we consider species descriptions of amphibians published during the past two years in Zootaxa as representative, the majority of them does not include molecular evidence, and many others do not even use bioacoustic data along with the classical morphological diagnosis and description.

Based on our experience, we are convinced that the potential of molecular data for initial diversity screening and identification of candidate species is unmatched by any other method (Vieites *et al.* 2009), although it is obvious that DNA barcoding alone is an insufficient basis for taxonomic species description, and molecular data are not automatically superior taxonomic characters. Nevertheless, analysis of DNA sequences can accelerate the taxonomic process by pointing more efficiently to those populations and individuals that merit further taxonomic study, and it is important that in times of a biodiversity crisis taxonomists make use of this extremely useful tool, whether they refer to it under the controversial term DNA barcoding or not (Vences *et al.* 2005b). In fact, in Madagascar, a massive DNA barcoding screening of adult frogs and tadpoles boosted the discovery of new amphibian species diversity to unprecedented levels (Köhler *et al.* 2005; Vieites *et al.* 2009), but only the combination with morphological and bioacoustic data will allow to understand which of the newly discovered genealogical lineages are best addressed as deep conspecific lineages and which merit description as new species.

In the present paper we followed this integrative taxonomy approach by reviewing and combining three major lines of evidence, molecular, bioacoustic and morphological. Two further lines of evidence for species delimitation can be relevant for amphibians but are so far underexplored, especially in Malagasy frogs. First, larval morphology is often rather uniform among sister species, but sometimes tadpoles of even closely related species can be strikingly different, e.g., between *Boophis majori* and an undescribed species named *B.* sp. aff *majori* "long calls" (Glaw & Vences 2007; Vieites *et al.* 2009). Second, ecological differences may be important criteria, assessable through field observations but also through ecological niche modeling based on remote sensing data (Raxworthy *et al.* 2007). The potential of these two sets of data in amphibian species delimitation requires further study.

Although strict concordance among all data sets is doubtless the most convincing rationale to delimit and describe a new species, in practice this is often hampered by the absence of clear differences in one or more data sets (Padial *et al.* 2009; Cardoso *et al.* 2009). An additional point that probably is even more relevant in practical applications is missing data. Molecular and bioacoustic information is usually absent from type specimens of related species and their junior synonyms, and often sample size of some deviant populations is quite small, or restricted to one sex only, which even impedes a full assessment of morphological variability. Because newly discovered species diversity usually is included in conservation priority assessments only after the new species have been named (see below), we argue that compromises are necessary between the urgent need to complete the taxonomic inventory of amphibians and other organisms in biodiversity hotspots such as Madagascar, and the requirement for ideal and complete integrative data sets for delimiting these new species.

Of the 12 species described or resurrected in this paper, there is only one (*B. spinophis*) that is immediately recognizable from all other Malagasy frogs by morphological characters. This species is also most strongly divergent in the molecular data set, while its advertisement call is unknown. Through detailed comparisons of morphology and life colouration, six additional species can be diagnosed: *B. andrangoloaka, B. entingae, B. praedictus, B. roseipalmatus, B. obscurus,* and *B. sandrae.* Four species are morphologically so similar to their closest relatives that a reliable morphological identification is not possible: *B. haingana, B. luciae, B. miadana,* and *B. piperatus.* For *B. arcanus,* only females are known and a reliable statement on possible morphological differences to other species such as *B. miniatus* is not possible at present. Thus, with the present state of knowledge, morphological data allow diagnosing seven out of the 12 species (58%) treated herein. Bioacoustic data are not available for *B. arcanus, B. roseipalmatus,* and *B. spinophis*. Of the remaining nine species, eight can be diagnosed by their calls (all except *B. obscurus*).

Fouquet *et al.* (2007), for Neotropical amphibians, provided evidence that an uncorrected threshold divergence of 3% in the 16S rRNA is a good compromise to be able to recognize, on one hand, most candidate species, and on the other hand, avoiding to flag too many intraspecific lineages for future taxonomic study. Most of the new species described herein are genetically strongly divergent to all other *Boophis* species, including their closest relatives, with uncorrected pairwise divergences often above 4–5% and amounting up to 7.3% in the comparison of *B. arcanus* with *B. miniatus*, and to >9% in the comparison of *B. spinophis* to other species in the *B. goudoti* group. However, in other cases, the newly recognized species are less divergent, such as *B. miadana* from *B. ankaratra* (2.2–2.9%), the resurrected *B. obscurus* from *B. goudoti* (2.1–3.9%), and the resurrected *B. andrangoloaka* from *B. rhodoscelis* (2.4%).

Table 2 summarizes the evidence available for species delimitation in the new species described and resurrected herein. The differences in part reflect biological reality; for instance, species of "green" *Boophis* in the *B. albipunctatus* group and *B. luteus* group simply are indistinguishable from their nearest relatives by morphology and colouration alone. However, there certainly are also differences in the quality of the evidence. Sympatric occurrence of a candidate species with its closest relative, without genetic admixture, and strictly correlated at least with a weak bioacoustic or morphological difference is decisive to consider them as full species, even if the genetic difference is low. This highly reliable evidence is available for *B. luciae* and *B. entingae,* probably for *B. roseipalmatus,* and partly for *B. sandrae* (which is sympatric with the morphologically closest species *B. elenae,* but allopatric with its sister species *B. anjanaharibeensis*).

TABLE 2. Evidence available for delimitation of the *Boophis* species newly described or resurrected from synonymy herein. Data refer to comparisons with the most similar close relative(s). Geography indicates whether the new species is known to occur sympatrically with its closest relative(s); morphology indicates non-existence or existence of strong or weak morphological differences; bioacoustics indicates existence of strong or weak differences in advertisement calls, DNA indicates classes of pairwise divergence in the 16S rRNA gene; haplotype sharing (hs) with related species is indicated as well; n. a., not available or applicable. For definitions of strength of bioacoustic and molecular differences, see Materials and Methods. *) strong differences to sympatric *B. elenae*, but moderate only to the allopatric sister species *B. anjanaharibeensis*.

Species	Geography	Morphology	Bioacoustics	DNA
B. piperatus	allopatric	no	weak	high
B. andrangoloaka	allopatric	weak	weak	low
B. roseipalmatus	probably sympatric	weak	n.a.	high
B. entingae	sympatric	weak	strong	high
B. spinophis	n.a.	strong	n.a.	very high
B. obscurus	allopatric	weak	no	low (hs)
B. praedictus	allopatric	weak	n.a.	high
B. arcanus	allopatric	n.a.	n.a.	very high
B. sandrae	(sympatric)	weak	(strong)*	high
B. miadana	allopatric	no	strong	low
B. haingana	allopatric	no	strong	moderate
B. luciae	sympatric	no	weak	high

Similarly, strong morphological differences like those of the unique *B. spinophis* are very reliable as long as it can be excluded that the differences are due to phenotypic plasticity, ontogenetic change or sexual dimorphism. Species here classified as having weak differences in advertisement calls such as in *B. entingae, B. miadana*, and *B. haingana* do not present completely different call structures as in many other sibling species of Malagasy frogs (e.g., Vences *et al.* 2006), but nevertheless the call differences detected do refer to parameters that are unlikely to be under strong influence of temperature or sexual motivation, and thus indicate a clear differentiation of these species in a signal that mediates prezygotic isolation.

In a few other species, the amount of evidence for their species status is clearly lower. This applies for instance to *B. obscurus* which is classified (Table 2) as having weak morphological differences from closely related species, because a clear diagnosis of non-breeding males and females is difficult. However, in this case we feel that the strong differences in male secondary sexual characters, correlated with constant colour differences and (albeit low) molecular differentiation do warrant a species status of *B. obscurus*, although we are aware that the complex of this species and *B. goudoti* clearly needs more work to understand the factors influencing their morphological variation. Ironically, the application of integrative taxonomy in the present study even led to the resurrection of *B. andrangoloaka*, one of the species described by Ahl (1928) although in the same publication, this author had described a second species (*Rhacophorus brevirostris*) that in fact is to be considered a synonym of *B. andrangoloaka*.

Conservation status of the new species

Assessments of conservation priorities are still mostly based on the category of species, for example to assess regional priorities in reserve planning. Kremen *et al.* (2008) based their proposal for areas to be included in Madagascar's reserve network on distribution modeling for a large number of taxa, and some of them were undescribed candidate species of frogs, but such approaches are still exceptions. Although Vieites *et al.* (2009) proposed a terminology to deal with undescribed species diversity, classifying newly identified

genealogical lineages as confirmed candidate species, unconfirmed candidate species, and deep conspecific lineages, the taxonomic description of newly identified species remains the central prerequisite to make them accessible for conservation and for further research. Efforts to complete the taxonomic inventory of Madagascar are therefore crucial for realistic conservation planning for the remarkable amphibian fauna of the island (Andreone *et al.* 2008a).

The recently updated Global Amphibian Assessment for Madagascar (Andreone *et al.* 2005; Andreone *et al.* 2008b), among described species, lists 66 threatened species of Malagasy frogs, of which 6 are considered to be Critically Endangered, 31 Endangered, and 29 Vulnerable. Only few *Boophis* are included among the threatened species: *B. williamsi* is Critically Endangered, *B. baetkei* and *B. tampoka* are Endangered and five species are Vulnerable: *B. andreonei, B. blommersae, B. haematopus, B. jaegeri*, and *B. sambirano* (Andreone *et al.* 2008b; Köhler *et al.* 2008).

All but one of the new species described here occur in at least one officially protected area (national park, strict nature reserve or special reserve), and most occur in more than one. The only exception is *B. arcanus* which is known from Mahakajy, a site receiving some protection as private reserve. We assume that this species may also be present at lowland sites within Ranomafana National Park.

Several of the species described herein are very incompletely known, especially with respect to their distribution. *Boophis spinophis* seems to be a very secretive species known only from one adult specimen and possibly from a juvenile from a second locality. *Boophis haingana* and *B. miadana*, as well as *B. arcanus* and *B. piperatus*, are known from single localities. *Boophis praedictus* is known from two female specimens as well, plus some unverified photographic records from a few more localities. For these six species, we propose the status of Data Deficient, and more field work is needed to obtain reliable information on their extent of occurrence and area of occupancy, as well as on their natural history and habitat requirements. We assume that *B. haingana, B. miadana, B. arcanus* and *B. piperatus* could possibly turn out to be true local endemics, and thus in the future may be included in a threatened category, possibly Vulnerable.

Two species occur in a relatively restricted range in northern Madagascar, and here their area of occupancy is rather limited to the remaining rainforest patches. Because of the continuing decline of extent and quality of habitat in this area, we thus consider *B. roseipalmatus* and *B. entingae* as Vulnerable based on IUCN criteria B1ab(iii). We also propose the Vulnerable category for two further species, *Boophis sandrae* and *B. andrangoloaka*. Of these, *B. sandrae* sensu stricto (i.e., excluding the genetically divergent *B.* cf. *sandrae* from the Andasibe region) according to current knowledge is restricted to the Ranomafana region, and interestingly here does not seem to commonly occur within the dense rainforests of Ranomafana National Park. On the contrary, this species is very common in forest edge situations and even in secondary habitat near rainforest, such as Ranomafana village. The call of this species is easy to recognize, but we have not heard it from other areas in the southern central east of Madagascar, or elsewhere. Although we assume that the extent of occurrence of this species is larger, its area of occupancy is certainly small and fragmented. On the other hand, because of its tolerance of moderate degrees of habitat destruction, currently we do not consider this factor as particularly severe for the species. We therefore propose the Vulnerable category based on criterion B1a. Recent records of *B. andrangoloaka* exist only for Ambohitantely Special Reserve. This is a small and fragmented protected area where continuous forest destruction takes place through fires (e.g., Vallan 2000). In general, very little forest habitat remains in the highlands of Madagascar, and although *B. andrangoloaka* seems to be rather a forest edge species, it very probably requires nearby forested habitat for its long-term survival. We therefore suggest to consider *B. andrangoloaka* as Vulnerable based on criterion B1ab(iii). Two further species are relatively widespread and appear to be common within their ranges: *B. luciae,* and *B. obscurus,* for which we propose the category of Least Concern.

Altogether, of the 12 new species described or resurrected herein, we propose to classify six as DD (of which possibly four could result to be threatened), four as VU, and two as LC. Compared to data from previously described species, this is a distinctly higher percentage of threatened species: 6 out of 57 described spe-

cies (11%), and 4 out of 13 new species (31%). This provides further evidence for the impact of undescribed diversity on conservation assessments (Vieites *et al.* 2009). In fact, the proportion of geographically localized and thereby potentially threatened species may be larger in yet undescribed species, and their neglection thus constitutes an important bias. We therefore urge taxonomists to combine different lines of evidence, including molecular data, in order to speed up the description of species diversity from biodiversity hotspots.

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APPENDIX 1. Morphometric measurements (all in mm) of type specimens of various *Boophis* species, and of comparative material. For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype (lectotype in case of *B. andrangoloaka*); *paratype.

Locality	Collection number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis piperatus **sp. nov.**																		
Ranomafana (Andranoroa river)	ZSM 378/2004*	ZCMV 328	F	36.2	12.8	13.4	2.5	4.7	3.1	3.0	3.2	10.8	22.0	63.3	27.4	16.4	20.3	9
Ranomafana (Andranoroa river)	ZSM 381/2004*	ZCMV 341	M	28.3	10.4	10.6	2.2	4.0	2.4	2.4	3.3	9.8	19.0	50.5	22.4	13.8	16.1	9
Ranomafana (Andranoroa river)	ZSM 380/2004*	ZCMV 339	F	36.9	13.0	13.3	2.4	4.7	3.1	2.7	3.6	11.9	23.4	63.6	28.7	18.0	20.2	9
Ranomafana (Andranoroa river)	ZSM 377/2004**	ZCMV 320	M	28.7	10.2	10.8	2.3	4.1	2.5	2.1	2.9	9.1	19.2	51.2	22.7	13.1	16.4	10
Ranomafana (Andranoroa river)	ZSM 379/2004*	ZCMV 338	M	28.2	10.0	10.8	2.1	4.2	2.4	2.1	2.7	9.0	17.4	51.1	21.5	12.8	15.9	10
Ranomafana (Andranoroa river)	ZSM 382/2004*	ZCMV 345	M	27.9	10.3	10.4	2.4	3.9	2.5	2.3	2.9	9.6	18.9	50.3	22.6	13.5	16.5	10
Ranomafana (Andranoroa river)	ZFMK 90151*	ZCMV 346	M	28.0	10.1	10.9	2.4	4.1	2.4	2.4	2.5	9.3	17.9	48.3	21.1	12.4	15.2	9
Ranomafana (Andranoroa river)	ZSM 299/2006*	ZCMV 3363	M	29.6	10.5	10.9	2.4	4.3	2.5	2.2	2.9	9.5	18.3	49.2	21.4	12.6	15.7	9
Boophis rhodoscelis																		
Ranomafanakely	ZSM 371/2004	ZCMV 115	M	25.4	9.2	9.3	2.0	3.5	1.9	2.2	2.6	7.3	15.9	40.9	18.6	10.9	12.6	6
Ranomafanakely	ZSM 372/2004	ZCMV 316	M	28.1	10.5	10.5	2.1	3.8	2.0	2.4	3.5	8.8	17.4	46.1	20.8	12.7	14.1	6
Ranomafanakely	ZSM 373/2004	ZCMV 318	M	25.5	8.7	9.5	2.0	3.8	1.7	2.5	2.9	7.9	16.0	41.5	18.6	11.6	12.9	4
Ranomafanakely	ZSM 374/2004	ZCMV 340	M	26.3	9.5	9.8	2.0	3.5	1.9	2.0	3.0	8.2	17.4	43.7	19.4	11.4	13.1	5
Ambohimitombo	ZFMK 28864	no	F	35.3	10.9	11.6	2.5	4.1	2.6	3.2	3.5	10.8	21.2	61.4	28.2	17.0	18.5	6
Ambohimitombo	ZFMK 28865	no	F	36.8	11.6	12.2	2.2	4.2	2.4	2.8	3.7	11.1	24.0	60.1	27.9	17.0	18.5	5
Boophis andrangoloaka																		
Ambohitantely	ZSM 5190/2005	FGZC 2139	M	30.2	10.8	10.7	1.9	4.4	1.8	2.1	3.2	9.3	19.6	50.1	22.4	13.5	14.5	5
Ambohitantely	ZFMK 60134	no	M	28.0	11.2	10.8	2.1	4.2	2.2	2.4	3.4	9.5	18.5	48.5	23.1	13.9	15.4	7
Andrangoloaka	ZMB 30510**	no	F	37.4	12.5	13.0	2.5	4.6	2.5	2.7	3.7	11.4	24.7	59.3	28.0	17.2	17.8	4
Dubious ("NW-Madagascar")	ZMB 30518	no	M	28.1	9.3	10.6	2.0	4.1	2.1	2.1	3.1	8.1	17.1	43.6	20.3	12.3	13.1	4
Boophis arcanus **sp. nov.**																		
Mahakajy	ZSM 298/2006**	ZCMV 3370	F	34.3	12.3	12.8	2.2	5.0	3.1	2.6	3.5	10.6	22.4	60.8	26.6	15.5	19.2	9

APPENDIX 2. Morphometric measurements (all in mm) of type specimens of *Boophis entingae,* and of comparative material of *B. brachychir.* For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Collection number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis brachychir																		
Nosy Be	CAS 156812	H1632	M	41.5	14.3	16.4	3.9	5.8	3.4	3.3	4.2	12.4	23.2	71.0	30.5	18.3	23.1	9
Nosy Be	CAS 156770	H1427	M	46.9	16.3	18.1	4.0	6.4	3.9	4.1	5.1	14.1	26.4	82.8	35.7	21.5	27.1	7
Manongarivo (Camp Norbert)	ZSM 993/2003	FGMV 2002.2331	M	46.6	17.0	17.9	3.9	7.2	3.8	4.0	5.0	15.0	29.5	78.1	33.4	20.6	24.7	7
Foret d'Ambre	ZSM 2157/2007	FGZC 1220	F	48.2	17.4	19.0	3.3	6.1	4.2	4.2	5.8	14.2	29.5	85.3	36.2	21.7	27.3	9
Foret d'Ambre	ZSM 2230/2007	FGZC 1389	F	62.2	22.3	23.4	3.9	6.5	5.1	5.2	7.4	19.0	37.0	107.3	46.6	26.7	34.8	9
Foret d'Ambre	ZSM 2227/2007	FGZC 1385	M	41.8	14.7	15.8	3.1	5.0	3.4	3.5	4.4	12.4	24.5	71.2	31.5	18.5	23.2	7
Foret d'Ambre	ZSM 2155/2007	FGZC 1218	M	43.6	14.8	16.6	3.2	5.3	3.2	3.9	5.1	12.9	26.0	76.9	33.0	19.7	25.0	10
Foret d'Ambre	ZSM 2228/2007	FGZC 1386	M	44.3	15.0	16.1	3.6	5.0	3.2	3.8	5.1	13.8	24.6	74.7	32.4	19.4	23.6	7
Foret d'Ambre	ZSM 2156/2007	FGZC 1219	M	38.8	14.2	15.1	3.1	5.6	3.3	3.4	4.3	12.5	24.6	68.2	28.9	17.1	22.5	10
Boophis entingae **sp. nov.**																		
Andampy (Tsaratanana)	ZSM 624/2001*	FGMV 2001.158	M	50.7	18.5	18.6	4.1	6.7	3.6	4.7	6.1	16.2	32.3	90.3	38.7	23.2	28.8	9
Manongarivo (Camp 1)	ZSM 852/2003*	FGMV 2002.822	M	57.2	20.1	21.3	4.2	6.8	4.2	4.8	6.4	17.9	33.8	97.3	44.1	26.8	33.4	8
Manongarivo (Camp 0)	ZSM 831/2003*	FGMV 2002.776	M	54.5	19.4	21.2	4.3	6.8	3.9	5.5	6.0	17.8	34.7	97.9	43.5	26.1	32.1	10
Manongarivo (Camp 0)	ZSM 830/2003*	FGMV 2002.775	M	54.2	18.0	20.7	3.9	6.9	4.0	4.7	5.4	16.9	33.1	94.4	41.9	24.9	30.9	9
Benavony	ZFMK 53639*	no	M	50.3	16.5	20.3	4.0	7.5	3.8	5.1	5.6	14.1	30.0	83.5	34.9	20.7	26.7	8
Benavony	ZFMK 53637*	no	M	46.5	16.7	18.1	3.9	7.0	3.6	4.5	5.4	14.0	27.0	79.5	33.9	20.2	25.8	7
Benavony	ZFMK 53638*	no	M	48.2	16.8	18.2	3.9	7.1	3.4	4.1	4.9	13.7	24.9	78.5	32.8	20.2	24.8	6
Manongarivo (Camp 1)	ZSM 858/2003*	FGMV 2002.829	F	86.5	30.0	31.3	6.1	10.3	5.9	6.7	8.7	26.1	53.0	147.4	64.5	40.2	47.9	7
Montagne d'Ambre	ZSM 2081/2007*	FGZC 1055	M	58.5	20.9	21.4	4.7	7.9	4.0	4.8	6.4	18.1	33.9	100.0	44.3	27.5	33.0	10
Montagne d'Ambre	ZSM 2083/2007**	FGZC 1057	M	53.3	18.2	19.7	4.3	7.0	3.9	4.6	5.7	17.3	33.8	88.7	39.4	24.3	28.5	8
Montagne d'Ambre	ZSM 899/2003*	FGMV 2002.911	F	71.4	24.6	23.8	4.4	8.8	4.7	5.0	7.4	19.9	40.8	116.2	50.1	30.5	38.1	6
Montagne d'Ambre	ZSM 214/2004*	FGZC 418	F	68.3	24.0	22.9	4.6	8.4	4.0	5.3	7.2	21.3	42.0	115.0	48.7	30.2	37.0	7

APPENDIX 3. Morphometric measurements (all in mm) of type specimens of *Boophis roseipalmatus* and of comparative material of *B. madagascariensis*. For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Collection number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis madagascariensis																		
Ambatolahy (Ranomafana)	ZSM 2312/2007	ZCMV 5827	M	54.5	19.8	19.7	4.2	6.6	3.7	4.5	6.0	16.9	32.7	89.0	38.8	23.4	28.5	6
Ambohitantely	ZSM 2310/2007	ZCMV 5667	M	53.1	19.0	19.0	4.4	7.0	3.8	4.3	5.5	16.9	32.5	89.4	38.9	23.0	27.8	7
Ambohitantely	ZSM 2311/2007	ZCMV 5671	M	57.0	22.1	21.5	5.0	7.7	4.1	4.7	6.0	17.5	34.0	95.2	40.7	24.3	30.9	9
Andasibe	ZSM 21/2002	FGMV 2001.1293	M	54.3	20.9	21.2	4.7	6.8	4.4	5.0	6.0	18.3	33.2	92.5	41.0	24.9	28.7	9
An'Ala	ZSM 255/2006	ZCMV 1440	M	56.5	21.7	22.5	4.6	7.7	4.3	5.1	6.6	17.9	34.9	91.8	40.0	24.5	29.0	7
An'Ala	ZSM 256/2006	ZCMV 1443	M	52.0	20.7	20.8	4.4	7.3	4.4	4.3	6.2	16.7	34.4	90.8	39.6	23.1	19.6	9
An'Ala	ZSM 254/2006	ZCMV 1406	M	56.4	20.7	21.3	4.5	6.8	4.5	5.3	6.6	17.0	31.2	92.9	40.5	23.2	29.9	7
Samalaotra (Ranomafana)	ZSM 258/2006	ZCMV 2998	F	72.1	27.6	25.9	5.1	7.9	5.1	6.0	7.4	23.5	46.1	123.5	51.3	32.1	38.2	7
Talatakely (Ranomafana)	ZSM 259/2006	ZCMV 3331	F	78.9	31.1	28.1	5.2	7.8	5.8	6.5	9.3	26.7	51.3	133.1	60.2	38.0	42.7	7
An'Ala	ZSM 257/2006	ZCMV 2454	F	81.3	30.3	29.3	5.2	8.3	6.2	6.2	8.1	25.8	47.5	134.9	62.2	37.9	43.7	7
Boophis roseipalmatus **sp. nov.**																		
Montagne d'Ambre	ZSM 220/2004*	FGZC 429	F	78.1	29.4	29.2	4.4	7.6	6.4	6.3	8.9	25.4	45.4	124.2	58.1	35.2	42.0	5
Montagne d'Ambre	ZSM 213/2004*	FGZC 417	M	68.4	24.9	24.2	3.5	7.8	5.0	5.0	7.3	20.2	41.0	111.0	49.2	29.5	35.5	6
Montagne d'Ambre	ZSM 905/2003*	FGMV 2002.924	F	86.6	33.9	31.2	5.2	9.1	6.7	6.5	9.5	29.5	52.4	138.1	60.9	39.7	46.6	6
Montagne d'Ambre	ZSM 210/2004*	FGZC 412	F	76.7	29.9	27.5	4.8	8.3	6.2	4.8	7.8	23.5	47.3	119.8	54.9	33.3	40.2	6
Montagne d'Ambre	ZFMK 90152*	FGMV 2002.910	F	68.7	27.5	26.4	4.4	6.9	6.0	5.2	6.8	21.8	44.4	120.0	51.5	31.3	39.0	10
Montagne d'Ambre	ZSM 212/2004*	FGZC 415	F	76.7	28.9	27.4	4.3	7.3	5.4	6.0	7.6	24.8	47.2	126.7	52.4	30.4	42.1	7
Montagne d'Ambre	ZSM 211/2004**	FGZC 414	M	66.2	24.3	23.8	4.2	7.6	5.5	4.7	6.6	20.8	40.9	109.7	47.4	29.3	35.6	7
Montagne d'Ambre	ZSM 2071/2007*	FGZC 1015	M	59.7	22.8	22.4	4.0	6.8	4.3	4.6	6.0	20.0	36.0	104.1	43.4	25.9	32.9	9

APPENDIX 4. Morphometric measurements (all in mm) of type specimens of *Boophis spinophis,* and of comparative material of *B. obscurus, B. goudoti* and *B. periegetes.* For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Collection number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis obscurus																		
Ambatovaky (Ranomafana)	ZSM 2292/2007	ZCMV 5903	F	74.9	28.3	26.1	5.8	9.0	5.2	6.7	8.3	24.4	47.1	127.2	59.0	36.8	40.8	9
Andranoroa river (Ranomafana)	ZMA 19452	FG/MV 2002.1403	M	67.5	22.2	22.1	5.0	6.8	4.4	6.4	6.4	19.0	(34.1)	no	50.3	31.6	35.5	no
Andranoroa river (Ranomafana)	ZMA 20220	ZCMV 348	M	63.2	21.3	23.0	5.7	6.8	4.6	5.4	7.0	19.8	40.4	105.9	49.5	31.2	35.1	7
Andranoroa river (Ranomafana)	ZMA 20219	ZCMV 347	M	64.4	20.6	22.1	4.1	6.2	3.9	6.2	6.6	19.1	35.6	103.7	47.1	30.4	31.9	6
Andohariana plateau (Andringitra)	ZSM 740/2001	FGMV 2001.540	M	81.9	27.7	26.8	5.6	9.1	4.6	7.4	9.6	25.2	46.1	132.6	59.3	39.4	40.1	7
Isalo	ZSM 2294/2007	ZCMV 5781	M	48.9	16.4	18.5	3.5	6.7	2.6	4.7	5.3	14.5	27.8	74.8	32.6	19.6	23.6	5
Isalo	ZSM 2293/2007	ZCMV 5774	M	42.4	14.4	15.8	3.1	5.8	3.0	4.1	4.8	13.0	69.0	30.4	22.3	18.8	21.9	7
Boophis goudoti																		
near Moramanga	ZSM 250/2006	ZCMV 3254	F	42.8	27.1	26.0	6.0	8.6	4.9	5.9	7.8	24.4	46.5	131.6	61.8	39.5	43.1	9
near Moramanga	ZSM 251/2006	ZCMV 3255	M	55.3	20.5	21.5	4.7	7.2	4.1	5.1	6.5	18.4	34.6	91.8	43.6	27.4	31.2	7
Tsiafajavona plateau (Ankaratra)	ZSM 741/2001	FGMV 2001.426	F	80.9	32.8	31.2	5.2	8.5	6.6	7.8	8.6	27.6	52.8	159.7	72.6	45.3	49.3	10
Tsiafajavona plateau (Ankaratra)	ZSM 742/2001	FGMV 2001.427	F	100.5	40.0	36.9	7.5	10.4	6.6	10.6	12.4	31.9	62.7	174.6	83.6	52.5	55.8	no
Manjakatompo	ZSM 391/2000	FGMV 2000.418	F	83.5	30.5	30.1	5.5	9.0	5.3	8.2	8.7	26.1	51.7	157.8	68.4	43.0	48.2	10
Ambohimirandrana (Ankaratra)	ZSM 248/2006	ZCMV 2527	M	70.7	26.8	26.5	5.1	7.6	4.6	6.4	7.5	23.1	43.6	129.2	57.4	36.8	40.2	10
Andasibe	ZSM 247/2006	ZCMV 2334	F	93.5	33.4	31.9	6.5	9.6	6.5	7.8	7.9	28.0	57.3	155.0	70.0	43.7	48.0	6
Antoetra	ZMA 19544	FGMV 2002.45	M	61.6	21.7	22.6	5.0	7.0	4.1	6.1	6.9	19.9	40.7	108.0	49.2	30.5	33.6	9
Antoetra	ZMA 19545	FGMV 2002.47	M	70.4	25.3	25.8	4.4	8.8	4.8	6.2	8.1	21.6	no	120.9	55.2	34.5	37.7	7
Boophis periegetes																		
Andohahela, 1500 m. alt.	ZSM 426/2005	FGZC 2441	M	59.7	20.7	20.8	3.5	7.7	3.8	5.3	7.1	20.4	37.8	103.4	45.1	28.2	33.5	7
Andohahela, 1500 m. alt.	ZSM 427/2005	FGZC 2500	F	80.0	31.8	29.8	5.1	9.4	5.9	7.4	9.3	27.9	49.8	143.1	62.5	41.0	44.2	9
Boophis spinophis **sp. nov.**																		
Ambatolahy	ZSM 376/2004**	ZCMV 691	M	56.5	20.0	20.1	2.8	6.8	4.4	4.7	6.8	18.7	33.4	90.3	42.9	26.5	29.9	7

APPENDIX 5. Morphometric measurements (all in mm) of type specimens of *Boophis praedictus,* and of comparative material of *B. albilabris.* For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Collection number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis praedictus **sp. nov.**																		
Vevembe	ZMA 20131**	ZCMV 678	F	89.3	32.0	33.2	6.3	10.4	7.6	7.4	9.5	27.9	49.0	146.3	65.9	40.8	45.8	6
Makira	ZSM 478/2009*	ZCMV 11237	F	62.3	25.3	24.0	3.4	6.9	5.1	5.4	6.2	20.2	38.5	110.9	49.2	28.1	35.4	10
Boophis albilabris																		
Andasibe	ZSM 220/2006	ZCMV 2331	M	93.1	32.8	30.3	(4.7)	9.8	7.4	6.8	9.4	27.4	53.2	145.0	67.5	43.7	44.8	5
Ambatolahy	ZSM 221/2006	ZCMV 2808	M	90.7	30.8	29.5	no	8.9	6.5	6.5	9.2	27.2	53.5	147.8	63.6	37.8	46.8	6
Ranomafana	ZSM 222/2006	ZCMV 2999	F	89.5	31.4	31.3	4.4	9.9	7.2	6.9	9.2	28.0	52.1	149.0	67.3	42.3	44.7	5
Ranomafana	ZSM 2288/2007	ZCMV 5889	F	76.1	29.1	29.0	(3.9)	9.2	6.2	6.5	8.5	24.2	44.8	136.5	62.8	39.2	43.5	10
Manongarivo	ZMA 19557	no	M	79.0	29.3	27.2	(4.0)	7.7	6.2	5.9	8.3	25.0	43.6	118.3	56.9	36.0	37.7	1
Andohahela	ZSM 130/2004	FGZC 240	M	97.1	33.8	31.8	(4.7)	9.0	6.8	7.2	9.6	28.0	54.1	160.4	69.7	45.0	47.8	6
Ranomafana	ZSM 654/2003	FGMV 2002–205	M	79.2	27.8	25.8	no	8.1	6.0	5.7	9.0	26.0	44.8	137.5	62.4	39.6	38.1	6

APPENDIX 6. Morphometric measurements (all in mm) of type specimens of *Boophis sandrae*, and of comparative material of other species of the *Boophis luteus* group. For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Catalogue number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis sandrae **sp. nov.**																		
Ranomafana, Andranoroa river	ZMA 20132*	ZCMV 327	F	52.7	17.5	17.9	3.0	6.3	3.5	4.8	6.1	15.4	32.1	87.3	38.5	24.0	27.0	7
Ranomafana, Andranoroa river	ZMA 20133**	ZCMV 352	M	35.8	12.1	12.9	2.0	5.5	2.4	3.3	4.3	10.2	20.8	58.2	25.7	15.7	18.9	6
Ranomafana village	ZMA 20134*	ZCMV 585	M	37.3	13.6	13.9	2.2	5.5	2.7	3.6	4.5	11.8	23.4	65.0	29.2	17.4	21.0	10
Ranomafana village	ZMA 20135*	ZCMV 586	M	48.2	16.4	17.3	2.5	6.5	3.1	4.6	5.9	15.4	29.2	88.8	39.1	23.8	28.0	10
Ambatolahy forest	ZMA 20136*	ZCMV 631	M	36.7	13.0	13.7	2.0	5.2	2.7	3.1	4.7	11.2	22.1	65.2	29.5	17.7	19.9	9
probably Ranomafana	ZMA 20137*	ZCMV 634	M	38.4	14.2	14.1	2.1	5.6	3.0	3.2	4.6	11.3	23.2	65.5	28.7	17.0	20.6	9
Ranomafana, near Vohiparara	ZSM 665/2003*	FGMV 2002.0245	M	37.2	12.5	12.7	2.4	4.2	2.7	3.0	4.3	12.0	23.7	62.1	27.6	16.4	20.4	6
Ranomafana, Ambatovory	ZSM 235/2006*	ZCMV 3003	M	43.6	14.8	15.8	2.3	5.9	3.0	3.9	4.9	13.7	26.1	81.1	36.4	22.0	26.0	10
Ambatolahy river	ZSM 236/2006*	ZCMV 3058	F	63.0	20.8	21.5	3.4	7.2	4.4	5.6	7.0	19.2	39.2	108.4	49.5	30.7	33.7	7
Ranomafana, Kidonavo bridge	ZSM 237/2006*	ZCMV 3187	M	35.5	11.7	12.7	2.0	5.1	2.4	3.4	4.2	10.4	21.8	58.2	26.4	16.2	18.5	7
Mahakajy	ZSM 238/2006*	ZCMV 3371	F	50.3	17.2	18.2	2.6	6.0	3.7	4.1	5.3	14.6	31.0	85.0	37.0	22.3	27.2	6
Ranomafana	ZFMK 62311*	no	M	38.8	14.0	13.9	2.2	5.3	2.5	3.7	4.6	11.6	23.0	70.2	30.4	18.4	22.2	7
Ranomafana	ZFMK 62312*	no	F	58.2	20.0	19.6	2.8	6.8	3.8	5.1	6.4	17.0	34.5	97.2	43.3	26.2	30.1	7
Boophis cf. *sandrae*																		
Nosy Boraha (wrong locality)	ZFMK 46022	no	F	55.5	18.8	18.9	2.9	6.6	3.4	5.2	6.9	15.7	32.3	94.4	42.3	25.7	29.7	9
Andasibe	ZFMK 50646	no	F	52.6	18.2	17.8	3.0	6.1	4.1	no	5.9	16.5	35.3	92.7	41.8	25.1	29.3	7
Andasibe	ZFMK 60027	no	M	42.6	15.4	16.1	2.3	6.1	3.0	3.8	5.0	13.9	26.2	76.1	33.4	20.5	24.0	10

APPENDIX 6. (continued)

Locality	Catalogue number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis elenae																		
Maharira	ZMA 20300	ZCMV 217	M	44.3	15.5	15.4	2.6	5.2	3.1	4.2	5.5	13.0	27.0	73.2	32.9	20.0	23.0	7
Maharira	ZMA 20301	ZCMV 218	M	40.4	14.8	15.3	2.7	5.0	2.6	3.9	5.0	12.4	23.8	68.5	30.4	18.6	21.5	9
Maharira	ZMA 20302	ZCMV 219	M	43.7	15.7	16.6	2.7	5.4	3.0	4.6	6.1	13.5	27.0	74.0	33.0	19.6	23.1	7
Samalaotra (Ranomafana)	ZSM 245/2006	ZCMV 2984	F	52.2	19.0	19.4	3.0	6.2	3.5	5.1	6.7	16.5	33.3	91.0	40.3	24.7	28.3	9
Ranomena (Ranomafana)	ZSM 246/2006	ZCMV 3083	M	43.1	14.8	15.6	2.5	5.4	2.7	3.7	5.6	13.3	26.2	72.5	32.2	19.9	22.8	7
Boophis luteus																		
Andasibe	ZSM 343/2000	2000–64	F	55.8	18.7	18.1	3.1	6.2	3.7	4.5	6.1	16.5	36.9	99.5	44.3	27.2	30.7	10
Ranomafana village	ZMA 20260	ZCMV 584	F	49.5	17.7	18.1	2.8	6.0	3.7	4.1	5.3	15.8	32.4	88.9	36.9	22.4	27.8	10
Ranomafana, Andranoroa river	ZMA 20291	ZCMV 546	M	37.0	11.8	12.6	2.2	4.6	2.6	2.8	3.6	10.6	21.6	62.2	25.7	15.7	19.3	8
Isalo	ZSM 2308/2007	ZCMV 5764	M	33.6	11.6	11.0	1.9	3.9	2.5	3.2	3.5	9.0	20.2	54.1	24.0	14.7	17.1	7
Isalo	ZSM 2309/2007	ZCMV 5767	M	31.9	11.3	11.1	1.8	3.9	2.3	2.8	3.7	8.4	18.7	50.9	21.6	13.2	15.8	6
Boophis anjanaharibeensis																		
Marojejy	ZSM 413/2005	ZCMV 854	M	36.9	12.6	14.4	(1.9)	4.7	2.8	3.2	4.2	10.5	21.9	61.6	27.0	16.2	20.2	7
Marojejy	ZSM 414/2005	ZCMV 855	F	53.4	19.1	19.9	(2.5)	6.5	3.9	5.2	6.2	15.6	32.4	91.0	40.5	23.7	29.7	10
Boophis englaenderi																		
Marojejy	ZSM 418/2005	ZCMV 856	M	31.8	11.1	11.4	1.8	4.7	2.5	2.8	3.3	9.2	20.2	51.6	22.7	13.9	17.3	7
Marojejy	ZSM 419/2005	ZCMV 857	M	31.8	11.0	11.2	1.8	4.4	2.2	2.5	3.0	9.1	18.7	54.3	23.1	13.3	17.6	9
Marojejy	ZSM 420/2005	ZCMV 858	F	46.5	15.1	15.9	2.3	5.5	3.4	3.9	4.8	13.4	28.5	78.6	32.1	17.6	24.9	8

APPENDIX 7. Morphometric measurements (all in mm) of type specimens of *Boophis luciae*, and of comparative material of other species of the *Boophis albipunctatus* group. For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Catalogue number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis luciae **sp. nov.**																		
Ranomena (near Andasibe)	ZFMK 60129*	no	M	25.3	10.1	10.0	1.6	3.1	2.1	2.6	3.4	8.4	15.3	43.3	18.8	11.3	13.7	7
Ranomena (near Andasibe)	ZFMK 60127*	no	M	27.8	10.8	10.4	(1.5)	3.6	2.1	2.3	3.3	8.3	15.9	45.2	19.5	11.5	14.3	7
Ranomafana	ZFMK 64141*	no	M	25.2	9.5	9.4	no	2.7	2.5	2.5	2.8	no	no	40.6	18.1	10.6	12.8	5
Ranomena (near Andasibe)	ZFMK 60834*	no	M	25.8	10.4	10.1	no	3.6	2.2	2.7	3.1	8.3	15.8	41.8	17.9	11.0	12.9	5
Ranomena (near Andasibe)	ZFMK 60128*	no	M	24.4	9.5	9.5	1.7	3.3	2.1	2.4	2.9	7.1	13.9	39.3	16.5	9.6	12.4	7
Andasibe	ZFMK 60041*	no	M	28.4	11.1	10.3	no	3.5	2.2	2.4	3.3	8.8	17.4	46.5	19.8	12.0	14.8	7
Ranomafana	ZFMK 62307*	no	M	27.9	10.3	10.4	1.6	3.2	2.3	2.5	3.2	8.3	15.8	44.0	19.9	12.1	14.4	6
Ranomafana	ZFMK 62908*	no	M	30.1	10.8	10.6	1.6	3.5	2.5	2.3	3.4	9.5	20.0	50.3	21.0	12.5	15.7	7
Ranomena (near Andasibe)	ZFMK 60126*	no	M	23.9	9.7	9.5	1.4	3.0	2.0	2.5	3.0	7.6	15.2	41.3	17.6	10.3	12.5	6
Ambatolahy	ZMA 20305*	ZCMV 595	F	42.7	14.6	15.4	2.0	4.3	3.7	3.3	4.3	12.3	24.5	70.7	31.7	19.5	21.8	7
Ambatolahy	ZMA 20307*	ZCMV 689	M	30.8	11.3	10.9	1.6	3.8	2.7	3.0	3.1	10.1	18.8	51.5	13.3	12.7	16.8	7
Ambatolahy	ZMA 20306*	ZCMV 687	M	28.8	11.2	11.1	1.3	3.8	2.3	2.6	3.0	9.0	17.2	44.9	19.4	12.1	14.8	5
Andohahela	ZSM 63/2004*	FGZC 105	M	31.3	11.9	11.8	1.6	4.0	2.4	2.8	3.3	9.7	20.5	55.0	24.1	14.4	17.6	10
Vohidrazana	ZSM 327/2000**		M	28.5	10.6	10.6	1.5	3.3	2.3	2.2	3.0	no	17.3	47.7	20.8	12.6	14.9	7
Vohidrazana	ZSM 328/2000*		M	27.9	10.8	10.9	1.5	3.5	2.3	2.8	2.9	8.9	17.4	47.6	20.6	12.4	15.2	7
Vohidrazana	ZSM 329/2000*		M	26.9	10.0	10.4	1.3	3.4	2.1	2.3	2.9	8.6	17.1	46.3	20.3	12.1	14.3	7
Ambatolahy	ZSM 243/2006*	ZCMV 3033	M	28.7	11.0	11.3	1.5	3.7	2.3	2.5	3.2	9.8	18.0	48.2	21.0	12.1	15.5	7
Ambatolahy	ZSM 244/2006*	ZCMV 3057	F	42.1	14.6	14.6	2.0	4.1	3.2	3.7	3.9	12.9	26.7	69.9	30.7	18.3	21.9	9

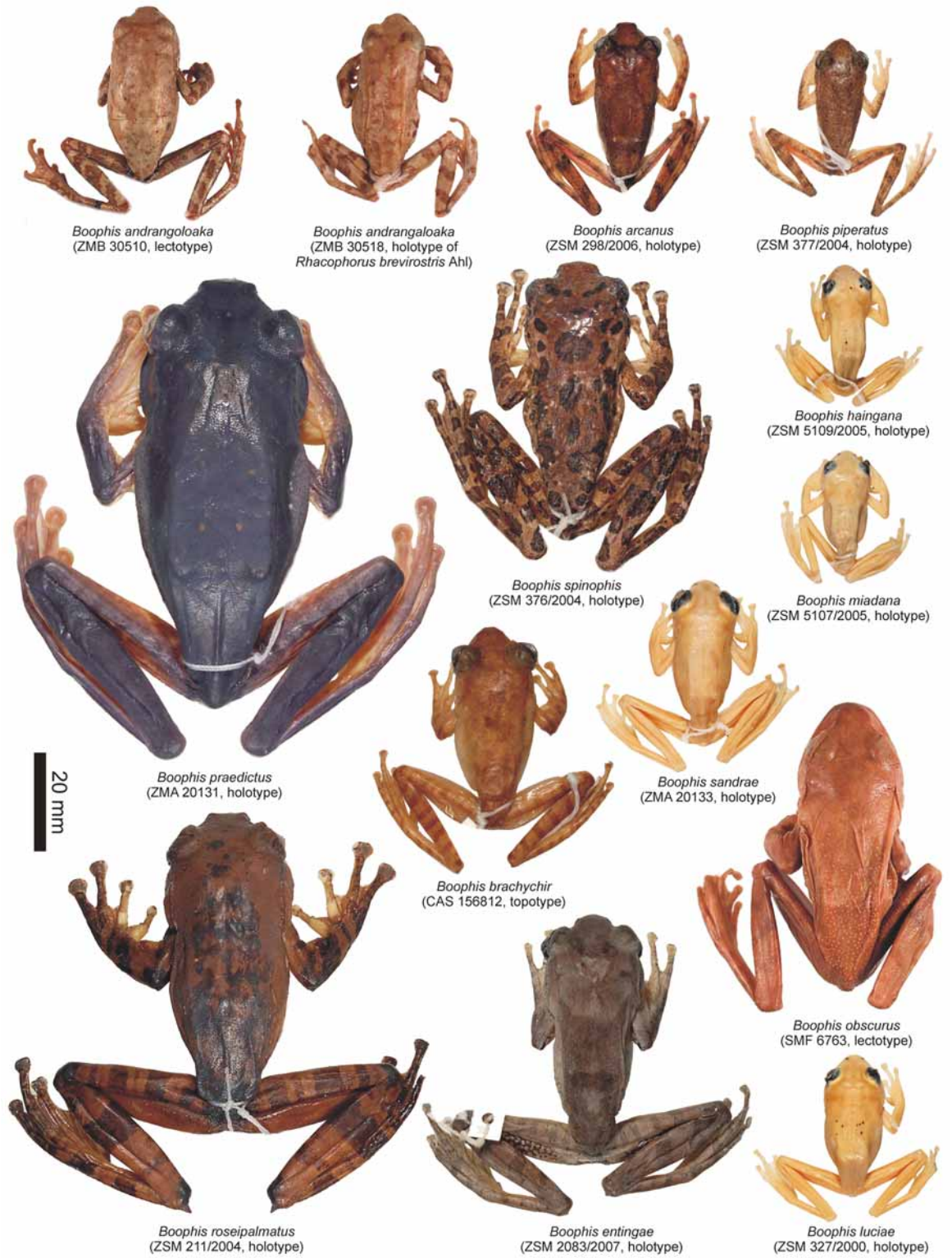
APPENDIX 7. (continued)

Locality	Catalogue number	Field number	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis sibilans																		
Andasibe	ZFMK 60035	no	M	28.4	10.2	10.4	1.8	3.3	2.1	2.6	3.6	8.4	17.4	47.1	20.1	12.2	14.9	7
Andasibe	ZFMK 62223	no	M	32.6	11.9	11.6	1.8	3.8	2.5	2.9	3.3	10.0	20.1	54.4	23.6	14.2	17.2	7
Andasibe	ZFMK 62219	no	M	27.6	10.4	10.6	no	3.3	2.3	2.5	3.4	8.3	16.8	46.8	20.1	11.5	15.2	5
Andasibe	ZFMK 60036	no	M	31.5	11.5	10.8	no	4.2	2.6	2.8	3.4	8.6	17.8	53.8	22.6	13.6	17.3	8
Andasibe	ZFMK 59873	no	M	34.2	13.2	12.8	no	3.8	2.8	3.0	3.7	9.3	19.5	53.5	23.3	13.7	16.2	5
Andasibe	ZFMK 60034	no	M	31.4	12.5	11.9	no	3.9	2.7	3.0	3.4	9.7	19.7	53.4	23.7	13.9	17.7	6
Andasibe	ZSM 39/2002	2001–1273	M	28.7	11.1	10.4	(1.5)	3.3	2.2	2.5	3.3	9.8	18.0	51.1	21.8	12.4	15.7	9
Boophis albipunctatus																		
Ambohitsara	ZSM 2290/2007	ZCMV 5934	M	34.3	12.8	13.7	1.7	4.1	3.0	2.6	3.7	9.7	21.4	57.0	23.9	13.7	18.6	7

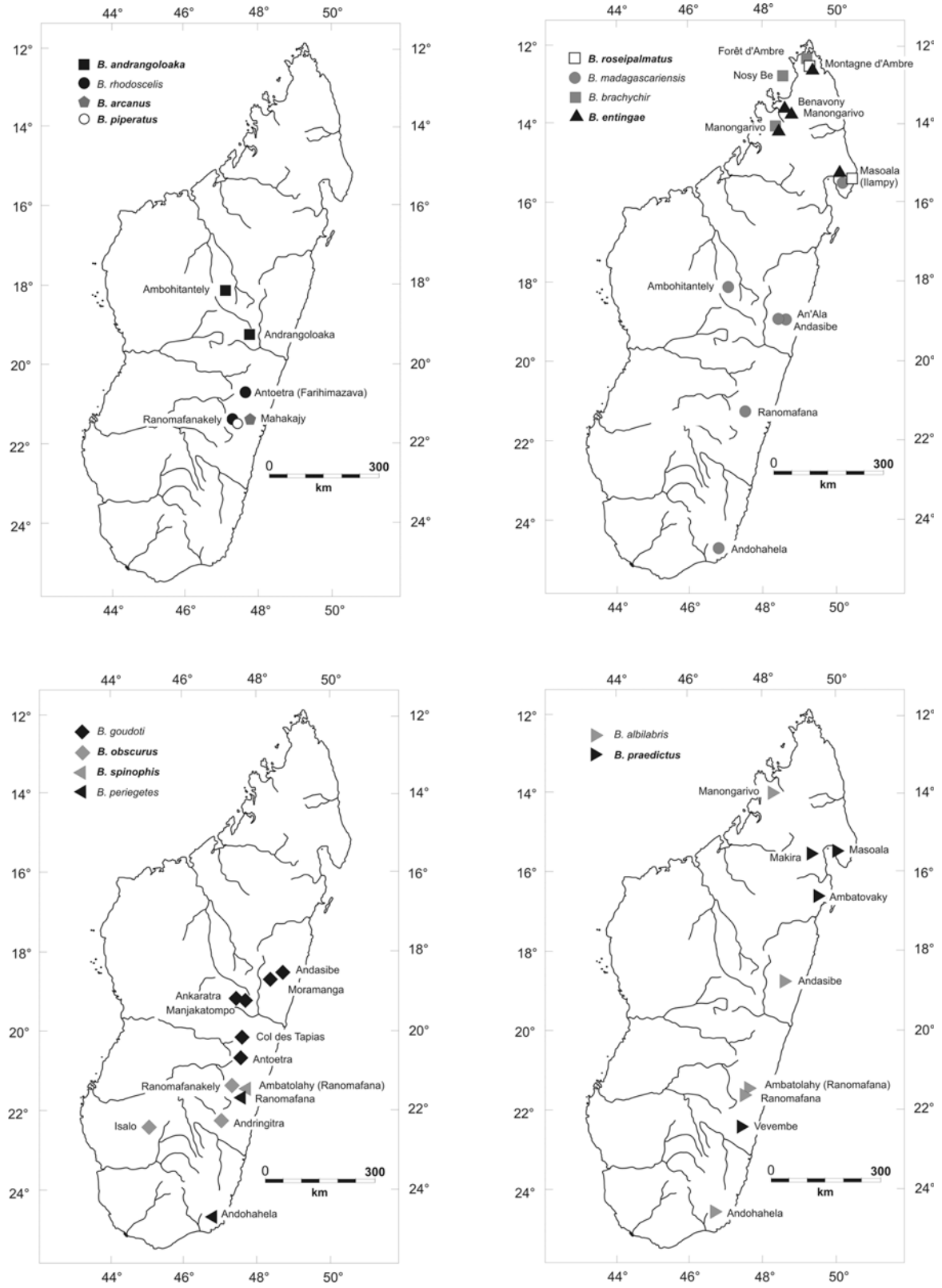
APPENDIX 8. Morphometric measurements (all in mm) of type specimens of *Boophis miadana* and *B. haingana.* For abbreviations of measurements, see Materials and methods. Relative hindlimb length (RHL) is given as the point reached by the tibiotarsal articulation when the hindlimb is adpressed along the body: (1) tympanum, (2) between tympanum and eye, (3) posterior edge of eye, (4) eye center, (5) anterior edge of eye, (6) between eye and nostril, (7) nostril, (8) between nostril and snout tip, (9) snout tip, and (10) beyond snout tip. **Holotype; *paratype.

Locality	Collection number	Field number	Sex	SVL	HW	HL	TD	ED	ENS	NSD	NND	HAL	FORL	HIL	FOTL	FOL	TL	RHL
Boophis miadana **sp. nov.**																		
Andohahela, 1550 m	ZSM 5107/2005**	FGZC 2388	M	25.5	8.9	9.1	1.5	3.4	1.7	2.6	2.8	8.6	16.8	42.5	18.7	11.5	14.1	9
Andohahela, 1550 m	ZSM 5108/2005*	FGZC 2389	M	26.8	9.7	9.1	1.5	3.4	2.1	3.0	2.9	8.3	17.2	43.2	19.2	11.9	13.3	5
Boophis haingana **sp. nov.**																		
Andohahela, 1550 m	ZSM 5112/2005*	FGZC 2536	F	36.3	13.1	13.1	1.9	4.5	2.7	3.5	4.7	11.2	23.9	59.4	26.9	16.4	18.1	5
Andohahela, 1550 m	ZSM 5109/2005**	FGZC 2390	M	25.7	9.3	9.3	1.3	3.3	2.1	2.4	3.2	8.6	17.1	42.5	18.1	10.6	13.2	6
Andohahela, 1550 m	ZSM 5110/2005*	FGZC 2447	M	24.8	9.3	9.3	1.5	3.5	1.9	2.4	3.2	8.0	17.0	43.0	18.4	11.7	13.4	9
Andohahela, 1550 m	ZSM 5111/2005*	FGZC 2487	F	37.0	12.9	12.6	1.8	3.7	2.7	3.0	3.7	11.4	23.7	61.4	27.4	16.5	19.1	7
Andohahela, 600 m	ZSM 129/2004*	FGZC 239	M	28.2	9.9	9.9	1.6	3.2	2.2	2.3	3.1	8.4	17.3	46.3	20.7	12.4	14.5	8
Andohahela, 600 m	ZFMK 90153*	FGZC 218	M	29.0	10.3	10.1	1.4	3.5	2.5	2.7	3.6	8.7	17.4	47.1	21.4	12.4	15.0	7

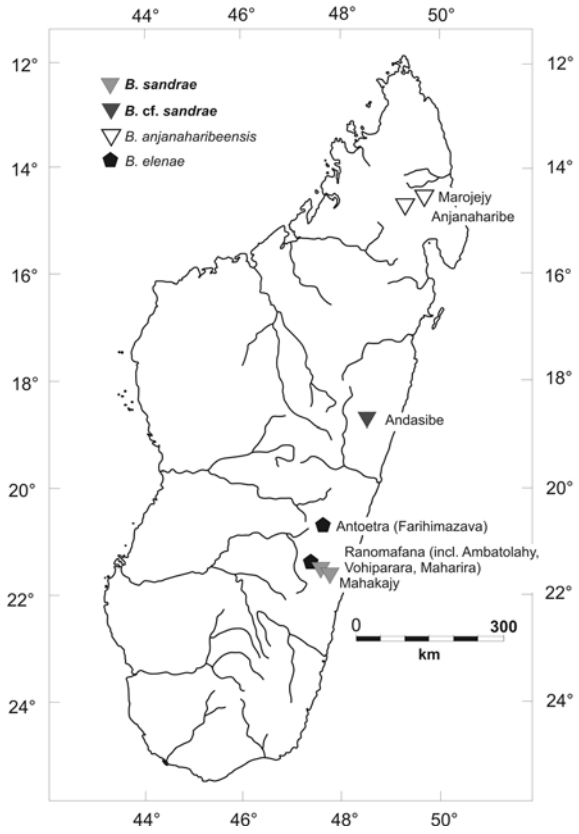
APPENDIX 9. Preserved name-bearing type specimens and topotypical reference specimens of *Boophis* species described, revalidated or discussed herein.

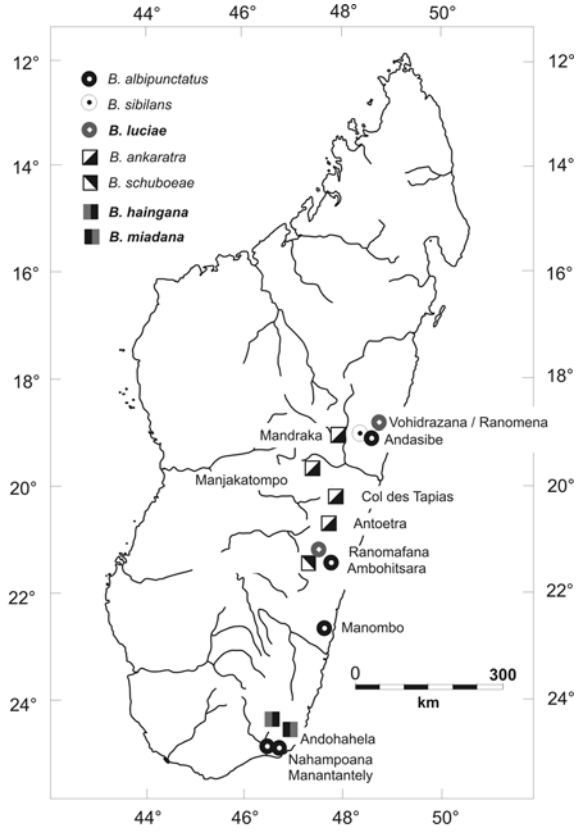


APPENDIX 10. Maps showing the distribution of the species newly described or resurrected herein, as well as of selected closely related species. In some cases, the symbols of nearby localities are placed next to each other for better visibility although strictly the symbols should be almost fully overlapping. Note that the maps are restricted to show reliable records, mainly based on materials studied herein, not necessarily all localities of material or observations assigned to the species. For more comprehensive distributional information, see species accounts and maps in Glaw & Vences (2007).



APPENDIX 10. Continued.





APPENDIX 11. List of voucher specimens and GenBank accession numbers for the 16S gene fragment used in the present study. Taxon names refer to those used in the present study. For abbreviations used in collection numbers see Material and Methods.

Taxon name	Locality	Voucher number	GenBank accession
Boophis albilabris	Andohahela	FGZC 240	AY848555
Boophis albilabris	Manongarivo	FGMV 2002.807	AY848556
Boophis albilabris	Ranomafana	FGMV 2002.203	AY848557
Boophis albilabris	Andasibe	LR 239	DQ792469
Boophis albilabris	Andasibe	LR 236	DQ792468
Boophis albilabris	Ranomafana	FGMV 2002.203	AY848557
Boophis albipunctatus	Manantantely	FGZC 291	AY848446
Boophis albipunctatus	Manombo	ZCMV 437	AY848455
Boophis andohahela	Ranomafana	ZCMV 592	AY848447
Boophis andohahela	Vevembe	ZCMV 648	AY848448
Boophis andohahela	Ranomafana	FGMV 2002.245	AY848456
Boophis andohahela	Andohahela	FGZC 2372	FJ559121
Boophis andrangoloaka	Ambohitantely	FGZC 2139	GU205779
Boophis andreonei	Manongarivo	FGMV 2002.806	AY848449
Boophis andreonei	Tsaratanana	FAZC	AY848450
Boophis anjanaharibeensis	Marojejy	FGZC 2762	FJ559122
Boophis ankaratra	Antoetra	FAZC 11454	AY848436
Boophis ankaratra	Antoetra	FAZC 11462	AY848437
Boophis ankaratra	Antoetra	FAZC 11480	AY848438
Boophis ankaratra	Mandraka	ZSM 400/2000	AJ315909
Boophis ankaratra	Manjakatompo	ZSM 367/2000	AJ315911
Boophis ankaratra	Col des Tapias	ZSM 399/2000	AJ315910
Boophis arcanus	Mahakajy	ZCMV 392	AY848632
Boophis axelmeyeri	Manongarivo	FGMV 2002.909	DQ118668
Boophis axelmeyeri	Manarikoba	FGMV 2001/F29	DQ118669
Boophis boehmei	Andasibe	FGMV 2001.1205	AY848559
Boophis boehmei	Andasibe	FGMV 2001.1206	AY848560
Boophis boehmei	Andasibe	FGMV 2002/G38	AY848561
Boophis boehmei	Andasibe	FGMV 2002/G39	AY848562
Boophis boehmei	Ambohitsara	ZCMV 5867	GU205773
Boophis brachychir	Manongarivo	FGMV 2002.702	AY848538
Boophis brachychir	Tsaratanana	FGMV 2001.252	AY848564
Boophis brachychir	Montagne d'Ambre	FGZC 1388	GU205772
Boophis burgeri	Andasibe	---	AY848566
Boophis burgeri	Marojejy	---	AF215336
Boophis cf. *sandrae*	Andasibe	LR 249	DQ792467
Boophis cf. *sandrae*	Andasibe	LR 243	DQ792466
Boophis cf. *sandrae*	Andasibe	LR 234	DQ792465
Boophis cf. *sandrae*	Andasibe	LR 230	DQ792464
Boophis cf. *sandrae*	Andasibe	LR 228	DQ792463

Boophis cf. *sandrae*	Andasibe	LR 214	DQ792462
Boophis cf. *spinophis*	Ambohitantely	FGZC 2122	GU205769
Boophis elenae	Antoetra	FAZC 11535	AY848469
Boophis elenae	Maharira	ZCMV 192	AY848470
Boophis elenae	Maharira	ZCMV 217	AY848471
Boophis elenae	Maharira	ZCMV 219	AY848472
Boophis englaenderi	Ilampy	FAZC 10467	AY848473
Boophis englaenderi	Ilampy	FAZC 10083	AY848474
Boophis englaenderi	Marojejy	ZCMV 856	FJ559124
Boophis entingae	Manongarivo	FGMV 2002.775	AY848537
Boophis entingae	Montagne d'Ambre	FGMV 2002.911	AY848563
Boophis entingae	Ilampy	FAZC 10329	AY848565
Boophis entingae	Montagne d'Ambre	FGMV 2002.908	AY848567
Boophis entingae	Montagne d'Ambre	FGZC 1057	GU205771
Boophis feonnyala	Andasibe	ZSM 313/2000	AJ315922
Boophis goudoti	Ambohitantely	FGZC 2117	GU205768
Boophis goudoti	Antoetra	FGMV 2002.44	AY848569
Boophis goudoti	Antoetra	FGMV 2002.45	AY848570
Boophis goudoti	Antoetra	FGMV 2002.47	AY848571
Boophis goudoti	Antoetra	FGMV 2002.48	AY848572
Boophis goudoti	Antoetra	FGMV 2002.49	AY848573
Boophis goudoti	Col des Tapias	ZCMV 11	AY848574
Boophis goudoti	Col des Tapias	---	AJ315917
Boophis haematopus	Andohahela	FGZC 229	AY848637
Boophis haematopus	Andohahela	FGZC 230	AY848638
Boophis haematopus	Andohahela	FGZC 215	AY848633
Boophis haematopus	Andohahela	FGZC 216	AY848634
Boophis haematopus	Andohahela	FGZC 2174	AY848635
Boophis haematopus	Andohahela	FGZC 228	AY848636
Boophis haingana	Andohahela	FGZC 218	AY848459
Boophis haingana	Andohahela	FGZC 219	AY848460
Boophis haingana	Andohahela	FGZC 220	AY848461
Boophis haingana	Andohahela	FGZC 232	AY848462
Boophis haingana	Andohahela	FGZC 239	AY848463
Boophis haingana	Andohahela	FGZC 2390	FJ559142
Boophis jaegeri	Berara	ZSM 413/2000	AJ315914
Boophis jaegeri	Nosy Be	ZSM 587/2001	FJ559125
Boophis laurenti	Andringitra	FGMV 2001.535	AY848575
Boophis luciae	Ranomena	ZFMK 62797	AF215338
Boophis luciae	Vohidrazana	ZSM 327/2000	AJ315913
Boophis luciae	Ranomafana	ZCMV 689	AY848445
Boophis luciae	Ranomafana	ZCMV 687	AY848443
Boophis luciae	Ranomafana	ZCMV 688	AY848444
Boophis luteus	Andohahela	FGZC 162	AY848482

Boophis luteus	Andohahela	FGZC 222	AY848483
Boophis luteus	Andohahela	FGZC 233	AY848484
Boophis luteus	Andohahela	FGZC 234	AY848485
Boophis luteus	Ranomafana	ZCMV 583	AY848486
Boophis luteus	Vevembe	ZCMV 651	AY848487
Boophis luteus	Ranomafana	ZCMV 546	AY848488
Boophis madagascariensis	Ranomafanakely	ZCMV 121	AY848576
Boophis madagascariensis	Andasibe	FGMV 2001.1270	AY848578
Boophis madagascariensis	An'Ala	ZFMK 62265	AF215337
Boophis madagascariensis	Andohahela	FGZC 126	AY848579
Boophis madagascariensis	Andohahela	FGZC 127	AY848580
Boophis madagascariensis	Andohahela	FGZC 128	AY848581
Boophis madagascariensis	Andohahela	FGZC 138	AY848582
Boophis madagascariensis	Ilampy	FAZC 10330	AY848583
Boophis madagascariensis	Sandrangato	---	AY848584
Boophis madagascariensis	Ranomafanakely	ZCMV 344	AY848585
Boophis madagascariensis	---	ZFMK 64446	GU205770
Boophis majori	Maharira	ZCMV 196	AY848586
Boophis majori	Maharira	ZCMV 197	AY848587
Boophis majori	Maharira	ZCMV 199	AY848588
Boophis marojezensis	Ambre	FGMV 2001.65	AY848595
Boophis miadana	Andohahela	FGZC 2389	FJ559141
Boophis microtympanum	Ankaratra	FGZC 2048	GU205775
Boophis microtympanum	Ankaratra	FGZC 2049	GU205776
Boophis microtympanum	Ankaratra	FGZC 2050	GU205777
Boophis microtympanum	Ambohitantely	FGZC 2174	GU205778
Boophis microtympanum	Ambohitantely	FGZC 2200	FJ559129
Boophis microtympanum	Col des Tapias	ZSM 393/2000	AJ315918
Boophis microtympanum	Cirque Namoly	FGMV 2001.544	AY848597
Boophis microtympanum	Andohariana	FGMV 2001.513	AY848599
Boophis microtympanum	Antoetra	FGMV 2002.53	AY848600
Boophis microtympanum	Antoetra	FGMV 2002.54	AY848601
Boophis microtympanum	Antoetra	FGMV 2002.55	AY848602
Boophis microtympanum	Itremo	FGMV 2001.485	AY848603
Boophis microtympanum	Maharira	ZCMV 260	AY848604
Boophis miniatus	Manantantely	FGZC 269	AY848639
Boophis miniatus	Manantantely	FGZC 270	AY848640
Boophis obscurus	Ranomafana	ZCMV 350	AY848609
Boophis obscurus	Andringitra	FGMV 2001.540	AY848568
Boophis obscurus	Isalo	ZCMV 5552	GU205774
Boophis obscurus	Ranomafana	ZCMV 347	AY848606
Boophis obscurus	Ranomafana	ZCMV 348	AY848607
Boophis obscurus	Ranomafana	ZCMV 349	AY848608
Boophis occidentalis	probably near Antoetra	ZSM 44/2002	AY341720

Boophis periegetes	Andohahela	FGZC 2430	FJ559130
Boophis picturatus	Vevembe	ZCMV 650	AY848641
Boophis picturatus	Maharira	ZCMV 208	AY848642
Boophis picturatus	Maharira	ZCMV 209	AY848643
Boophis picturatus	Maharira	ZCMV 210	AY848644
Boophis picturatus	Ranomafana	FGMV 2002.266	AY848610
Boophis picturatus	An'Ala	ZCMV 1457	EU252140
Boophis piperatus	Ranomafana	ZCMV 320	AY848627
Boophis piperatus	Ranomafana	ZCMV 328	AY848628
Boophis piperatus	Ranomafana	ZCMV 339	AY848629
Boophis piperatus	Ranomafana	ZCMV 341	AY848630
Boophis piperatus	Ranomafana	ZCMV 342	AY848631
Boophis praedictus	Vevembe	ZMA 20131	AY848528
Boophis pyrrhus	Andasibe	---	AY848646
Boophis pyrrhus	Ifanadiana	ZCMV 384	AY848651
Boophis pyrrhus	Ifanadiana	ZCMV 381	AY848645
Boophis pyrrhus	Ifanadiana	ZCMV 573	AY848647
Boophis pyrrhus	Ifanadiana	ZCMV 382	AY848649
Boophis pyrrhus	Vevembe	ZCMV 676	AY848648
Boophis pyrrhus	Ifanadiana	ZCMV 383	AY848650
Boophis pyrrhus	Ifanadiana	ZCMV 385	AY848652
Boophis pyrrhus	Ifanadiana	ZCMV 569	AY848655
Boophis pyrrhus	Ifanadiana	ZCMV 572	AY848658
Boophis pyrrhus	Ifanadiana	ZCMV 390	AY848653
Boophis pyrrhus	Manombo	ZCMV 436	AY848611
Boophis pyrrhus	Ifanadiana	ZCMV 547	AY848654
Boophis pyrrhus	Ifanadiana	ZCMV 570	AY848656
Boophis pyrrhus	Ifanadiana	ZCMV 571	AY848657
Boophis reticulatus	Vohidrazana	FGMV 2002.3045	AY848612
Boophis reticulatus	Maharira	ZCMV 211	AY848613
Boophis reticulatus	Maharira	ZCMV 220	AY848614
Boophis reticulatus	Maharira	ZCMV 221	AY848615
Boophis rhodoscelis	Ranomafanakely	ZCMV 115	AY848619
Boophis rhodoscelis	Ranomafanakely	ZCMV 316	AY848620
Boophis rhodoscelis	Ranomafanakely	ZCMV 317	AY848621
Boophis rhodoscelis	Ranomafanakely	ZCMV 318	AY848622
Boophis rhodoscelis	Antoetra	FAZC 11499	AY848616
Boophis rhodoscelis	Antoetra	FAZC 11534	AY848617
Boophis rhodoscelis	Ranomafana	FGMV 2002.696	AY848618
Boophis roseipalmatus	Ambre	FGMV 2002.910	AY848577
Boophis roseipalmatus	Ilampy	RJS 03	AY848527
Boophis roseipalmatus	---	---	AF261266
Boophis rufioculis	An'Ala	2002/GA272	AY848623
Boophis sandrae	Ranomafana	FGMV 2002.447	AY848439

Boophis sandrae	Ranomafana	ZCMV 585	AY848440
Boophis sandrae	Ranomafana	ZCMV 327	AY848441
Boophis sandrae	Ranomafana	ZCMV 352	AY848442
Boophis schuboeae	Ranomafana	FGMV 2002.1804	DQ068395
Boophis septentrionalis	Masoala	FAZC 7390	GU205765
Boophis septentrionalis	Ilampy	FAZC 10329	GU205766
Boophis septentrionalis	Montagne d'Ambre	FGMV 2002.914	GU205767
Boophis septentrionalis	Ambolokopatrika	FAZC 7369	AY848504
Boophis septentrionalis	Montagne d'Ambre	FGMV 2002.912	AY848505
Boophis septentrionalis	Montagne d'Ambre	FGMV 2002.913	AY848506
Boophis septentrionalis	Montagne d'Ambre	FGMV 2002.915	AY848507
Boophis sibilans	Andasibe	ZSM 39/2002	AY341718
Boophis sp. aff. *boehmei*	Ranomafana	FGZC 236	AY848529
Boophis sp. aff. *boehmei*	Ranomafana	FGMV 2002.324	AY848530
Boophis sp. aff. *boehmei*	Ranomafana	FGMV 2002.325	AY848531
Boophis sp. aff. *boehmei*	Ranomafana	FGMV 2002.326	AY848532
Boophis sp. aff. *boehmei*	Ranomafana	FGMV 2002.327	AY848534
Boophis sp. aff. *boehmei*	Ranomafana	FGMV 2002.328	AY848533
Boophis sp. aff. *boehmei*	Ranomafana	ZCMV 324	AY848536
Boophis sp. aff. *boehmei*	Ranomafana	ZCMV 3045	FJ559139
Boophis sp. aff. *majori*	Ranomafana	ZCMV 2976	FJ559151
Boophis sp. aff. *majori*	Vohiparara	---	AF215340
Boophis sp. aff. *occidentalis*	Berara	MRSN A2000	AJ314820
Boophis sp. aff. *occidentalis*	Berara	---	AJ314819
Boophis sp. aff. *rufioculis*	Ranomafana	ZCMV 235	AY848535
Boophis sp. aff. *rufioculis*	Antoetra	FAZC 11451	AY848551
Boophis sp. aff. *rufioculis*	Antoetra	FAZC 11452	AY848552
Boophis sp. aff. *rufioculis*	Antoetra	FAZC 11465	AY848553
Boophis sp. aff. *rufioculis*	Masoala	FAZC 7261	AY848548
Boophis sp. aff. *rufioculis*	Masoala	FAZC 7656	AY848549
Boophis spinophis	Ranomafana	ZCMV 691	AY848539
Boophis tampoka	Tsingy de Bemaraha	FGZC 871	EF682215
Boophis tampoka	Tsingy de Bemaraha	FGZC 869	EF682216
Boophis tampoka	Tsingy de Bemaraha	FGZC 867	EF682213
Boophis tampoka	Tsingy de Bemaraha	FGZC 872	EF682214
Boophis tampoka	Tsingy de Bemaraha	FGZC 869	EF682216
Boophis tephraeomystax	Nosy Be	ZSM 458/2000	AJ312114
Boophis vittatus	Montagne d'Ambre	FGMV 2002.925	AY848451
Boophis vittatus	Tsaratanana	FGMV 2000.82	GU205780
Boophis williamsi	Ankaratra	ZSM 734/2001	AY848624