

Two new treefrogs of the *Boophis rappiodes* group from eastern Madagascar (Amphibia Mantellidae)

M. VENCES¹ and F. GLAW²

¹ Institute for Biodiversity and Ecosystem Dynamics, Zoological Museum, University of Amsterdam, PO Box 94766, 1090GT Amsterdam, The Netherlands

(E-mail: m.vences@t-online.de)

² Zoologische Staatssammlung, Münchhausenstr. 21, D-81247 München, Germany (E-mail: Frank.Glaw@zsm.mwn.de)

Received 21 March 2002, accepted 22 May 2002

Two new sibling species of *Boophis* Tschudi 1838 are described from Andasibe in central-eastern Madagascar. Both are small greenish treefrogs with a translucent ventral skin and without lateral fringes along lower arm and tarsus, and are thereby assignable to the phenetic *B. rappiodes* group. *Boophis bottae* n. sp. is morphologically similar to *B. rappiodes* (Ahl 1928) and occurs syntopically with this species. It strongly differs from its sibling by advertisement calls (long trill notes instead of two-pulse notes), and by a reddish-brown dorsal pattern which does not fade soon in ethanol, often covering the entire back (vs a red pattern that largely fades in ethanol in *B. rappiodes*). *Boophis tasymena* n. sp. is similar to *B. erythrodactylus* (Guibé 1953) but differs in advertisement calls (notes composed of two instead of four-seven pulses) and lack of red colour on tips of fingers and toes. A lectotype is designated for *B. erythrodactylus*. The discovery of the two new species in addition to the revised distributional information for *B. rappiodes*, *B. erythrodactylus* and *B. viridis* Blommers-Schlösser 1979 confirms that mid-elevational central-eastern Madagascar is the centre of diversity for many Malagasy amphibian groups but has a relatively low degree of endemism. DNA sequence divergence was high within each pair of sibling species (6-7% in a fragment of the mitochondrial 16S rRNA gene), suggesting that their reproductive isolation was not a recent event and probably predates the Pleistocene.

KEY WORDS: Amphibia, Anura, Mantellidae, *Boophis viridis*, *Boophis rappiodes*, *Boophis erythrodactylus*, *Boophis bottae* n. sp., *Boophis tasymena* n. sp., Madagascar, advertisement calls, distribution.

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INTRODUCTION

With currently more than 45 species, the treefrog genus *Boophis* is one of the most speciose groups of Malagasy anurans. It is part of an endemic frog radiation (RICHARDS et al. 2000) which has recently been defined as the family Mantellidae (VENCES & GLAW 2001). *Boophis* was first recognized as a natural unit and divided into seven species groups by BLOMMERS-SCHLÖSSER (1979). Later, BLOMMERS-SCHLÖSSER & BLAKE (1991) assigned all known species in the genus to these groups, while GLAW & VENCES (1994) proposed some modifications to the grouping. According to the molecular data of RICHARDS et al. (2000), who studied representatives of five of the seven species groups (sensu GLAW & VENCES 1994), *Boophis* is a monophyletic assemblage.

One characteristic pattern in *Boophis* is the high proportion of sibling species which are well defined by advertisement calls and partly by colouration, but virtually indistinguishable by external morphology. This pattern has received particular attention by BLOMMERS-SCHLÖSSER (1979) in her treatment of the *Boophis rappiodes* group. She assigned two described species (*B. rappiodes* and *B. erythrodactylus*) to this group and described two new taxa (*B. mandraka* and *B. viridis*). She found all these species in central-eastern Madagascar, at her collecting localities Mandraka and Andasibe, and demonstrated close syntopy of two species (*B. erythrodactylus*, *B. mandraka* Blommers-Schlösser 1979) at one site (Mandraka). All species of the *B. rappiodes* group are small, basically greenish-coloured treefrogs with a translucent venter in life, reminiscent of the Neotropical Glass frogs of the family Centrolenidae. When preserved, the often diagnostic colour pattern is lost: the greenish colour changes first to pale yellow and then to whitish. If present, the red pattern often becomes brownish or fades to white. Although a few morphological characters are known to distinguish some of the species as defined by BLOMMERS-SCHLÖSSER (1979) (e.g., the position of the nostrils, which are closer to the eye in *B. mandraka* but closer to the snout tip in the other species), in general the *B. rappiodes* group exemplifies the difficulties in distinguishing sibling Malagasy frog species better than most other species assemblages (paralleled, however, by the *B. luteus* group; e.g., ANDREONE 1993, ANDREONE et al. 1995).

The recent intensive survey work carried out in several parts of eastern Madagascar revealed that the species inventory of Madagascar's herpetofauna is far from being complete (GLAW & VENCES 2000). Several of the newly discovered forms are assignable to the *B. rappiodes* group. In the present paper, we describe two of these as new species, partly revise the two species *B. rappiodes* and *B. erythrodactylus*, and provide new information about the distribution and advertisement calls of *B. viridis*. A revision of the remaining representative of the group, *B. mandraka*, and two new sibling species will be published elsewhere.

MATERIALS AND METHODS

Specimens were collected at night, mainly by locating calling males with the aid of electric torches. They were euthanised using chlorobutanol, fixed in 90% ethanol and preserved in 70% ethanol. Samples of femur muscle were preserved in pure 90% ethanol; DNA was extracted from these tissue samples, and a fragment of the mitochondrial 16S rRNA gene (560 nucleotides) was amplified and sequenced using protocols given in VENCES et al. (2000).

Morphological measurements of the preserved specimens were taken by the senior author with callipers to the nearest 0.1 mm: SVL (snout-vent length), HW (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), HAL (hand length), FORL (forelimb length), HIL (hindlimb length), FOI (foot length), FOIL (foot length including tarsus). The webbing formula is given according to BLOMMERS-SCHLÖSSER (1979).

Vocalizations were recorded using portable tape recorders with an external microphone (Vivanco EM 238) and were analyzed with the MEDAV sound analyzing system Spektro 3.2. Temporal measurements are given as range, with mean \pm standard deviation, and number of temporal units measured, in parentheses.

Institutional abbreviations used are as follows: MNHN (Muséum National d'Histoire Naturelle, Paris); UADBA (Université d'Antananarivo, Département de Biologie Animale) (numbers given refer to the fieldnumbers of different collectors; UADBA-MICE1, collection of the MICE1 team; UADBA-RD, collection of D. Rakotomalala; UADBA-MV, collection of M. Vences; UADBA-FG/MV, collection of F. Glaw and M. Vences); ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn); ZMA (Zoologisch Museum Amsterdam); ZMB (Zoologisches Museum der Universität, Berlin); ZSM (Zoologische Staatssammlung München). Coordinates and altitudes of localities are given according to GLAW et al. (2001) or given at first mention.

DNA sequences were submitted to public databases; EMBL/Genbank accession numbers are the following (voucher specimens in parentheses): *Boophis bottae* n. sp. (ZSM 344/2000, AJ314817); *Boophis erythrodactylus* (ZSM 324/2000, AJ314814); *Boophis rappiodes* (ZSM 347/2000 and UADBA-FG/MV 2000.59), AJ314815 and AJ314816; *Boophis tasymena* n. sp. (ZFMK 62888), AF215339; *Boophis viridis* (ZSM 338/2000, AJ314818).

SPECIES ACCOUNTS

Boophis viridis Blommers-Schlösser 1979

Boophis viridis BLOMMERS-SCHLÖSSER 1979. *Name-bearing type*: holotype ZMA 7100A, adult male, collected by R. Blommers-Schlösser on 14 November 1972. *Type locality*: "near Perinet (high-road R.N. 2 at km 142)" according to original description (Perinet being the old French name of Andasibe). *Other types*: paratypes ZMA 7100B, two adult males.

Identity and diagnosis. See Table 1 for morphometric measurements. A member of the *Boophis rappiodes* group as recognizable by relatively small size (SVL 29–31 mm in males, 32–35 mm in females; Table 1 and BLOMMERS-SCHLÖSSER 1979), greenish and slightly translucent dorsal colouration (during the day; at night more reddish), translucent venter (inner organs can be clearly seen through the skin in live specimens) and absence of lateral fringes along lower arm and tarsus (Fig. 1). Distinguishable from all other species of the group by the larger size of males (below 27 mm in all other species), characteristic iris colouration (inner iris area

Table 1.

Morphometric measurements (all in mm) of samples of species of the *Boophis raptoides* group. For abbreviations of variables, see Materials and methods. Other abbreviations: HT, holotype; PT, paratype; LT, lectotype; PLT, paralectotype; M, male; F, female; SA, subadult. Relative hindlimb length (RHL) is the position reached by the tibiotarsal articulation when the hindlimb is adpressed along the body.

Catalogue number	Status	Sex	Locality	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOI	RHL
<i>Boophis viridis</i>																	
ZFMK 60012	—	M	Andasibe	29.5	11.5	10.9	1.7	4.0	2.6	1.9	2.7	18.8	8.7	50.0	20.6	12.0	beyond snout tip
ZFMK 60013	—	M	Andasibe	29.1	11.6	11.1	1.9	3.5	2.4	2.2	2.6	18.1	8.9	49.2	21.2	12.2	snout tip
ZFMK 53620	—	F	Andasibe	34.1	13.4	13.3	1.6	4.1	3.2	2.3	3.4	22.3	10.2	60.1	25.4	15.0	slightly beyond snout tip
ZFMK 60014	—	F	Andasibe	32.0	11.7	11.8	1.8	3.8	2.7	1.9	2.7	20.1	9.7	54.9	23.3	13.7	nostril
ZFMK 62211	—	F	Andasibe	35.1	12.9	12.7	2.1	5.6	2.9	2.2	3.1	22.1	10.7	62.0	25.8	15.1	beyond snout tip
<i>Boophis mandraka</i>																	
ZFMK 59815	—	M	Mandraka	22.1	8.8	8.0	1.3	3.1	1.8	1.9	2.8	12.7	7.7	39.9	17.0	10.3	snout tip
ZFMK 59816	—	M	Mandraka	23.2	9.3	8.3	1.4	3.3	1.5	2.1	2.9	13.8	7.7	40.0	17.4	10.7	snout tip
<i>Boophis raptoides</i>																	
ZMB 30540	HT	M	Ankoraka	25.1	9.0	9.0	1.6	3.2	2.2	1.7	2.8	14.9	7.3	43.6	17.8	10.5	beyond snout tip
ZFMK 53621	—	M	Nahampoana	24.0	9.6	8.8	1.4	3.3	2.0	1.7	3.0	13.9	6.6	41.9	17.7	10.3	beyond snout tip
ZFMK 53622	—	M	Nahampoana	25.1	10.0	9.5	1.7	3.6	2.3	2.0	3.0	16.5	7.7	43.8	18.3	11.1	beyond snout tip
ZFMK 53624	—	M	Andasibe	20.4	7.7	7.4	1.4	3.1	1.5	1.3	2.3	13.9	6.9	38.3	15.8	9.2	clearly beyond snout tip
ZFMK 53625	—	M	Andasibe	21.4	8.0	8.0	1.2	3.0	1.6	1.4	2.2	13.2	6.4	36.5	14.5	8.4	snout tip
ZSM 347/2000	—	M	Andasibe	24.2	9.0	8.8	1.3	3.1	2.1	1.4	2.7	15.0	7.0	42.7	17.8	10.0	beyond snout tip
ZSM 676/2001	—	M	Andasibe	22.7	8.8	8.0	1.1	3.2	2.0	1.5	2.0	13.5	6.7	40.2	16.5	9.3	beyond snout tip
ZFMK 53623	—	F	Andasibe	33.6	11.7	12.6	1.8	4.2	2.4	2.1	3.2	21.2	10.0	60.2	26.0	15.8	beyond snout tip
ZFMK 59869	—	F	Andasibe	32.7	11.2	10.9	1.6	3.6	2.2	2.3	3.4	19.0	9.1	53.7	22.4	14.8	anterior eye corner
ZFMK 62278	—	F	Vohiparara	30.0	10.8	10.6	1.7	3.0	2.4	2.1	3.2	18.6	8.6	50.2	21.4	13.0	snout tip
<i>Boophis borae</i> n. sp.																	
ZSM 678/2001	HT	M	Andasibe	24.2	9.0	8.7	1.4	3.4	2.0	1.5	2.2	15.5	6.9	43.0	17.3	10.4	beyond snout tip
ZSM 679/2001	PT	M	Andasibe	23.5	8.6	8.6	1.4	3.3	2.1	1.3	2.3	15.6	7.4	41.6	17.5	10.7	beyond snout tip
ZSM 344/2000	PT	M	Andasibe	21.9	8.1	8.2	1.4	3.3	1.6	1.4	2.4	15.0	6.9	37.7	16.3	9.6	beyond snout tip

(continued)

Table 1 (continued)

Catalogue number	Status	Sex	Locality	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOI	RHL
<i>Boophis erythrodactylus</i>																	
ZFMK 60015	PT	M	Andasibe	23.8	8.9	8.4	1.5	3.4	1.6	1.3	2.4	14.4	7.4	40.3	17.6	10.5	nostril
ZFMK 60016	PT	M	Andasibe	24.1	9.1	8.3	1.5	3.4	1.9	1.4	2.3	14.6	7.3	42.1	18.1	10.6	beyond snout tip
ZFMK 62220	PT	M	Andasibe	21.2	8.0	7.8	1.3	3.3	1.9	1.6	2.5	14.0	6.4	39.5	16.8	9.7	clearly beyond snout tip
ZFMK 62221	PT	F	Andasibe	35.1	12.7	12.5	1.8	4.0	2.4	2.2	3.4	20.7	9.8	56.7	24.2	15.0	nostril
<i>Boophis tasymena</i> n. sp.																	
MNHN 1994.1469	LT	M	Mahajebby	23.7	9.3	8.9	1.7	3.0	1.7	1.7	2.4	13.8	7.4	42.1	17.7	10.5	snout tip
MNHN 1953.171	PLT	M	Mahajebby	23.8	9.5	9.2	1.7	3.3	1.8	1.7	2.8	14.3	7.2	39.9	16.8	10.2	between eye and nostril
MNHN 1994.1470	PLT	SA	Mahajebby	21.3	7.8	7.6	1.2	2.8	1.6	1.6	2.5	12.4	6.3	37.7	15.4	9.3	snout tip
MNHN 1994.1471	PLT	SA	Mahajebby	21.2	8.2	7.6	1.4	2.8	1.7	1.2	2.2	14.8	6.1	36.9	15.6	9.4	snout tip
ZFMK 59813	—	M	Mandraka	24.6	9.6	9.1	1.7	2.7	2.0	1.5	2.6	16.4	8.0	44.0	18.8	11.4	beyond snout tip
ZSM 677/2001	—	M	Mandraka	24.2	9.2	8.5	1.7	3.3	2.0	2.0	2.8	15.9	7.4	43.2	18.0	10.5	snout tip
ZFMK 59814	—	F	Mandraka	33.0	11.9	11.1	2.2	3.1	2.5	1.7	2.9	20.4	10.0	53.7	23.8	14.2	nostril
<i>Boophis tasymena</i> n. sp.																	
ZSM 1085/2001	HT	M	Andasibe	22.7	8.7	8.0	1.7	3.0	1.9	1.6	2.4	13.8	7.0	39.6	17.2	10.2	snout tip
ZFMK 62225	PT	M	Andasibe	22.2	8.4	8.0	1.5	3.1	1.7	1.5	2.6	14.6	7.2	40.3	17.0	10.2	beyond snout tip
ZFMK 62243	PT	M	Mantady	21.0	8.2	7.5	1.4	2.7	1.6	1.4	2.0	13.6	6.4	38.7	16.1	9.6	clearly beyond snout tip
ZFMK 62244	PT	M	Mantady	21.9	8.3	7.5	1.5	3.0	2.0	1.5	2.3	15.2	7.0	38.9	16.3	9.8	snout tip
ZFMK 62262	PT	M	An'Ala	21.8	8.6	7.7	1.6	2.8	1.7	1.6	2.5	13.5	6.3	38.1	15.9	9.5	slightly beyond snout tip
ZFMK 62267	PT	M	An'Ala	21.8	8.5	7.8	1.5	3.0	1.7	1.2	2.3	14.9	6.6	38.0	16.2	9.6	beyond snout tip
ZFMK 62888	PT	F	Andasibe	32.3	11.1	11.0	2.2	3.0	2.4	1.7	3.1	19.0	8.7	53.3	23.1	13.5	nostril
Uncertain attribution																	
MNHN 1930.432	—	M	Vondrozo	24.5	9.3	8.7	1.5	3.1	2.3	1.8	2.6	15.6	7.7	40.8	17.5	10.3	nostril

brown, outer iris area blue), and by advertisement calls (unharmonious pulsed notes instead of pulsed click or trill notes of more harmonious structure).

Material examined. UADBA-MICET 331, 335, 344, 347 (Marotreh forest, 6 km S Ranomafana, 21°18.14'S, 47°27.4'E, 910 m elevation); UADBA-MICET 260-262, 304 (Ankopakopaka forest, 12 km NW Ikongo, 21°49.39'S, 47°20.20'E, 645 m elevation); UADBA-MV 2001.186, 2001.188-189 (Andasibe); ZFMK 53620, 60012-60014 and 62211 (Andasibe); ZSM 338/2000 and 675/2001 (Andasibe).

Natural history and advertisement calls. A few observations were reported by BLOMMERS-SCHLÖSSER (1979) and GLAW & VENCES (1994). According to published data and observations made in 1994-1996 and 2000-2001 at Andasibe, males generally call at night from leaves at 1-2 m above the ground, along (or up to 10 m away from) slow-moving brooks and streams, at forest edges. However, on 28 December 1994, during dry weather conditions, calling males were sitting on trees up to 5 m above the ground. Calling activity was recognized in the months October, November, December, and March. One pair in axillary amplexus (the female being ZFMK 62211) was observed on 31 January 1996 and laid 154 eggs in captivity. In contrast to the pale-yellowish eggs of *B. rappiodes*, *B. erythrodactylus*, and *B. bottae*, the eggs of *B. viridis* were dark brown. Another pair in amplexus was observed on 10 March 1996.

Advertisement calls were briefly described by GLAW & VENCES (1994); we here provide a more detailed description. Calls (recorded on 28 December 1994, in the evening around 19:00 hr) consisted of two note types. Notes of type 1 (Fig. 2) consisted of up to 40 pulses (pulse repetition rate about 135/sec) and had a duration of 131-295 msec (213 ± 41 msec, $n = 15$). They were sometimes arranged in series, with intervals of 347-755 msec (546 ± 129 msec, $n = 10$) between notes. The frequency ranged between 2150 and 3300 Hz. Each note was emitted as one expiration. Note type 2 generally consisted of three pulses (less frequently up to five pulses) and had a duration of 42-74 msec (53 ± 11 msec, $n = 9$). The intensity of the first pulse was usually lower than that of the following pulses. This note type was often emitted in short series of 2-3 notes; inter-note interval duration was 347-484 msec (420 ± 59 msec, $n = 6$). When both note types were combined (e.g., a note of type 1 followed by a series of notes of type 2), the note of type 1 was usually more intense.

Distribution. The species was originally known only from the type locality, Andasibe in central-eastern Madagascar, but was recorded from the Andringitra massif at 700-720 m altitude by RAXWORTHY & NUSSBAUM (1996). Recent collections by teams of the University of Antananarivo in the Ranomafana and Ikongo areas yielded one specimen (UADBA-MICET 331) which clearly can be assigned to *B. viridis* (as well as several additional specimens probably belonging to the species: UADBA-MICET 260-262, 304, 335, 344, 347).

Boophis rappiodes (Ahl 1928)

Rhacophorus rappiodes AHL 1928: Name-bearing type: holotype ZMB 30540, collected by BRAUN. Type locality: "Ankoraka, Sahambendrana (Zentral-Madagaskar)" according to the original description; corresponding to Akkoraka near Sahambendrana according to BLOMMERS-SCHLÖSSER & BLANC (1991). Other types: none.

Identity. During fieldwork in Andasibe, central-eastern Madagascar, we noted that *B. rappiodes* as defined by BLOMMERS-SCHLÖSSER (1979), BLOMMERS-SCHLÖSSER

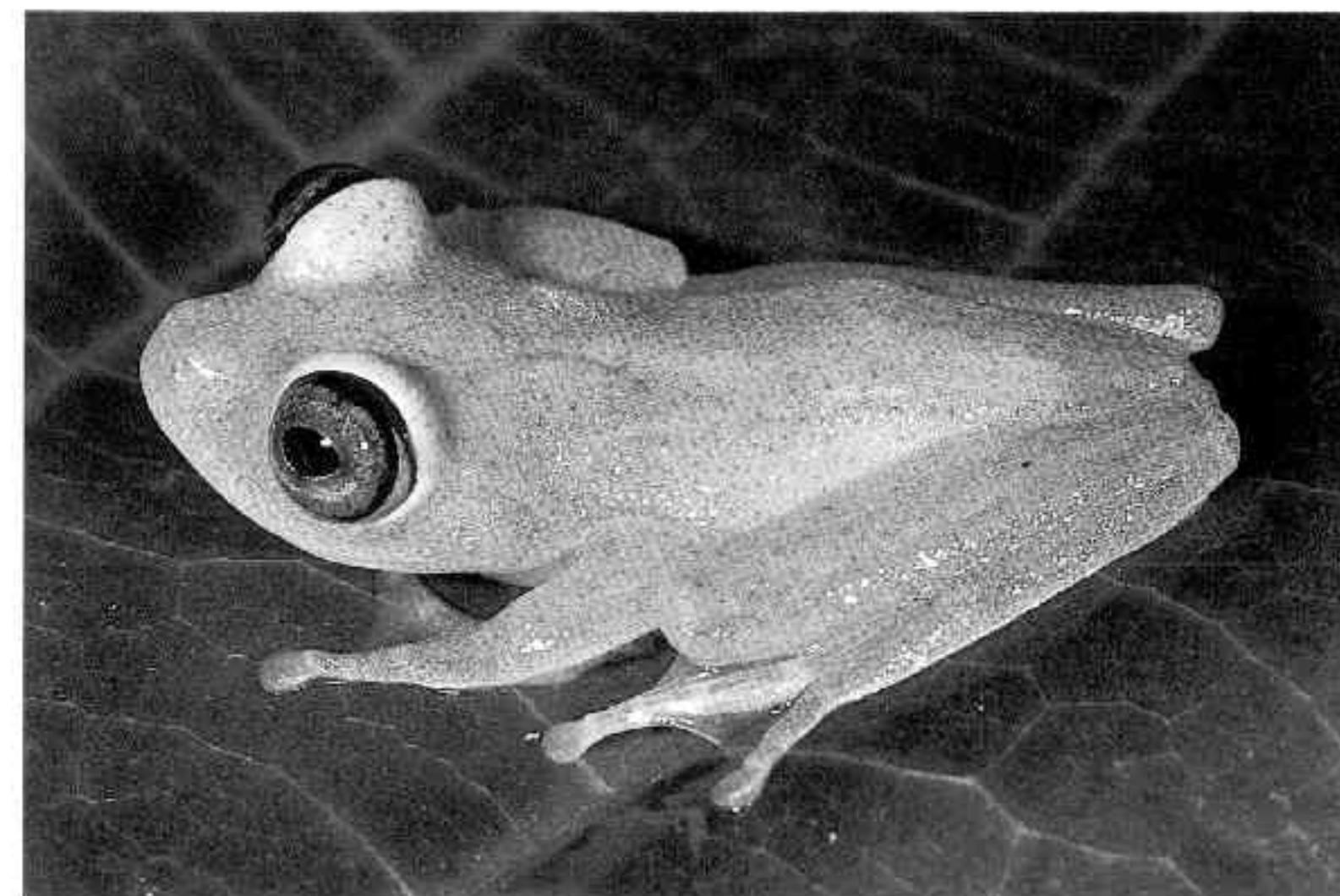


Fig. 1. — *Boophis viridis*, adult specimen from Andasibe.

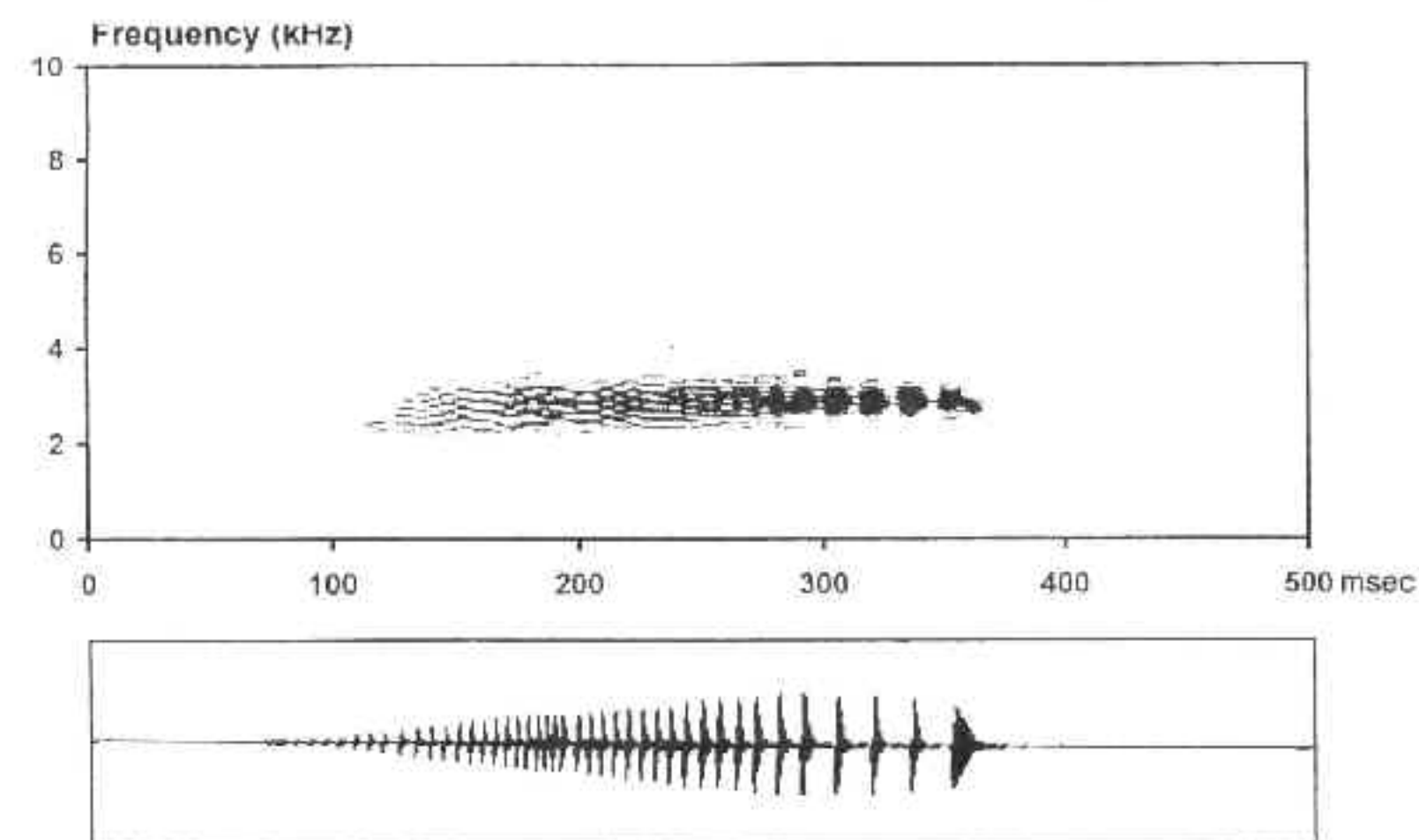


Fig. 2. — Sonagram and oscillogram of a note of type 1 of *Boophis viridis*, recorded at Andasibe.

& BLANC (1991) and GLAW & VENCES (1994) was actually a mix of two different forms. One form had extensive reddish-brown markings on its greenish back, which in preservative changed into a persistent brownish pattern, and a call that included long trills, sometimes preceded and followed by click notes. Specimens of the second form often had less extensive and usually bright red markings on the greenish back (Fig. 3), which in ethanol faded after a few days or weeks, and had calls consisting of short click series only. The two forms were observed syntopically at Andasibe, while at Nahampoana in south-eastern Madagascar only the second form was found and trill calls were not heard. DNA sequences (560 nucleotides of the 16S rRNA gene) differed in the two forms; 38 substitutions and 3 indels were found, corresponding to a total pairwise sequence divergence of 7.3%. Altogether, the evidence is overwhelming that the two forms are reproductively isolated and constitute two separate species. The holotype of *Boophis rappiodes* is in rather good state of preservation (despite the contrary statement of GUIBÉ 1978) and clearly shows remains of a light dorsolateral band on each side (presumably yellow in life) running from the nostril over the eye along the supratympanic fold, fading in the shoulder region. Except for a fine dark spotting all over the dorsum, no other pattern is recognizable. This agrees exactly with specimens from Nahampoana (ZFMK 53621-53622) which are clearly attributable to the form with little dark pigment on the back. We therefore conclude that this form must be considered as *Boophis rappiodes* (Ah! 1928), while the species with more dark pigment on the back will be described below.

Diagnosis. See Table 1 for morphometric measurements. A member of the *Boophis rappiodes* group as recognizable by small size (males 20-25 mm, females 30-34 mm), greenish and slightly translucent dorsal colouration, translucent venter (inner organs can be clearly seen through the skin in live specimens) and absence of lateral fringes along lower arm and tarsus (Fig. 3). Distinguished from *Boophis mandraka* by nostril position (closer to snout tip vs slightly closer to eye), iris colour (absence of distinct reticulations on a light beige iris), usual presence of red markings on the back (vs generally absent) and continuation of dorsolateral stripes from eye to supratympanic fold (vs restricted to snout tip-eye). Distinguished from *B. viridis* by smaller size and presence (vs absence) of yellowish dorsolateral stripes. For distinction from *B. erythrodictylus* and the two new species described herein, see below.

Material examined. UADBA-FC/MV 2000.59 (Andasibe); ZFMK 53621-53622 (Nahampoana); ZFMK 53623-53625 and 59869 (Andasibe); ZFMK 62278 (Vohiparara); ZMB 30450 (holotype; Ankarak); ZSM 347/2000 and 676/2001 (Andasibe).

Natural history and advertisement call. Calling males were observed at night 2-3 m high in the vegetation along a large, slow-moving stream at Andasibe (sometimes more than 10 m from the water), and about 1 m high in the vegetation along a rather large and noisy brook at Nahampoana, at forest edges or outside primary forest. At Nahampoana, advertisement calls were recorded on 4 January 1992 at 18:30 hr (air temperature about 25 °C). Each note consisted of two pulses; duration of inter-note intervals was 2800-5400 msec. Duration of single pulses was 13-21 msec ($n = 6$), duration of inter-pulse intervals was 40-45 msec ($n = 3$). The frequency was between 2500 and 3500 Hz. Similar calls were recorded at Andasibe (from specimen ZSM 347/2000; Fig. 4). The second pulse had generally a higher intensity and longer duration than the first pulse. Duration of the first pulse of a note was



Fig. 3. — *Boophis rappiodes* (ZFMK 59869), adult female from Andasibe.

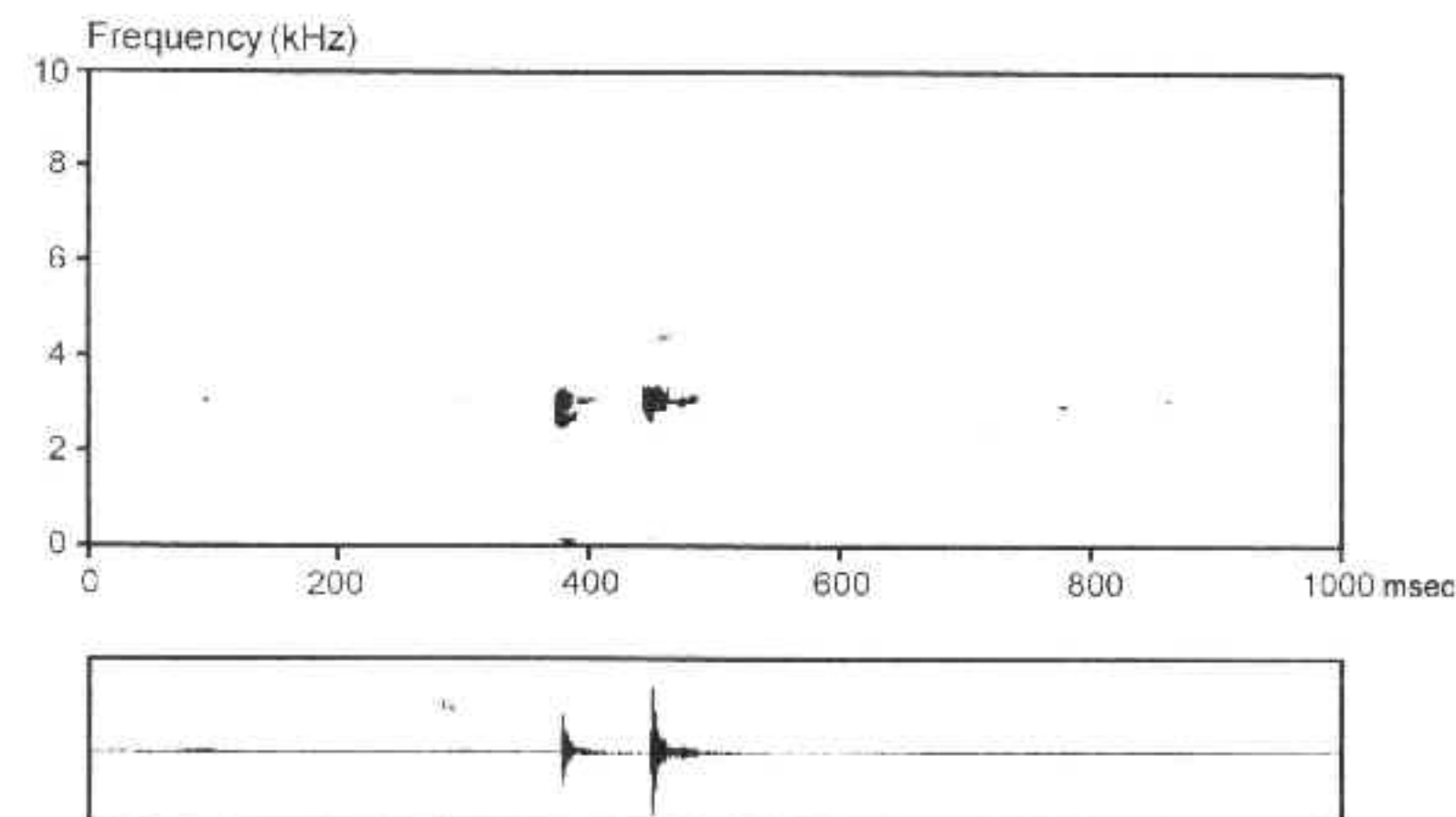


Fig. 4. — Sonogram and oscillogram of a call of *Boophis rappiodes*, recorded from specimen ZSM347/2000 at Andasibe.

9.29 msec (14 ± 7 msec, $n = 9$); duration of inter-pulse intervals was 42–62 msec (55 ± 6 msec, $n = 9$); duration of the second pulse was 11–27 msec (20 ± 7 msec, $n = 9$). The frequency ranged between 2500 and 3400 Hz.

Distribution. Besides the holotype from (1) Ankoraka and specimens collected by us at (2) Andasibe, (3) Nahampoana, and (4) Vohiparara, BLOMMERS-SCHLÖSSER & BLANC (1991) recorded *B. rappiodes* from three additional localities, Mandraka, Moramanga and Anosibe. These records are probably based on ZMA 7161 and 7168, tadpoles and young from Mandraka, and ZMA 7166, tadpoles "collected along the road from Moramanga to Anosibe at km 27" (BLOMMERS-SCHLÖSSER 1979). As it is not known at present how the tadpoles and young of *B. rappiodes* can be distinguished from those of *B. bottae* n. sp. (see below), we consider these sites as in need of confirmation. Also the identity of *B. rappiodes* records from Marojejy, Anjanaharibe-Sud and Tsararano in north-eastern Madagascar (RAXWORTHY et al. 1998, ANDREONE et al. 2000, RASOIMANANA et al. 2000) remains to be revised.

Boophis bottae n. sp.

Identity. This is the *B. rappiodes*-like species with distinct dark pigment on the back and trill calls (see above). Calls of this species were attributed to *B. rappiodes* by GLAW & VENCES (1994).

Diagnosis. A member of the *Boophis rappiodes* group as recognizable by small size (males 21–24 mm, one female 35 mm), greenish and slightly translucent dorsal colouration, translucent venter (inner organs can be clearly seen through the skin in live specimens) and absence of lateral fringes along lower arm and tarsus. Distinguished from *B. mandraka* by nostril position (closer to snout tip than to eye vs slightly closer to eye), and iris colour (absence of distinct reticulations on a light beige iris). Distinguished from *B. viridis* by smaller size, iris colouration, and presence (vs absence) of yellowish dorsolateral stripes. Distinguished from *B. erythrodactylus* by lack of reddish colour of fingertips, and from *B. erythrodactylus* and *B. tasymena* n. sp. (see below) by lack of regular pattern of red dorsal spots. By morphology and colouration, *B. bottae* n. sp. is most similar to *B. rappiodes*. It is distinguished, however, by a more extensive dark pattern on the dorsum. This difference is most distinct in living or freshly preserved specimens; while the dorsal pattern in *B. rappiodes* is intensely red, and remains red in preservative before it eventually fades, the pattern in *B. bottae* is reddish-brown in life and becomes persistently dark brown in preservative, often covering almost the entire dorsum (Fig. 5). Additionally, *B. bottae* is easily distinguished by its advertisement calls as no other species of the *B. rappiodes* group emits long trill calls composed of double click notes (Fig. 6).

Holotype. ZSM 678/2001, adult male, collected by M. Vences and D. Vieites on 16 February 2001 close to Andasibe (at a bridge on the road between the National Road 2 and the Andasibe village), central-eastern Madagascar $18^{\circ}56'S$, $48^{\circ}25'E$, ca 900 m elevation.

Paratypes. UADBA-MV 2000.194 and 2000.196, ZSM 679/2001, three adult males, same collection data as holotype; UADBA-FG/MV 2000.60 and ZSM 344/2000, two adult males, collected by F. Glaw and M. Vences on 9 February 2000 at the type locality; ZFMK 60015–60016, two adult males, collected by F. Glaw on 28 December 1994 at Andasibe; ZFMK 62220–62221, one adult male and one adult female, collected by F. Glaw on 9 February 1996 at Andasibe.

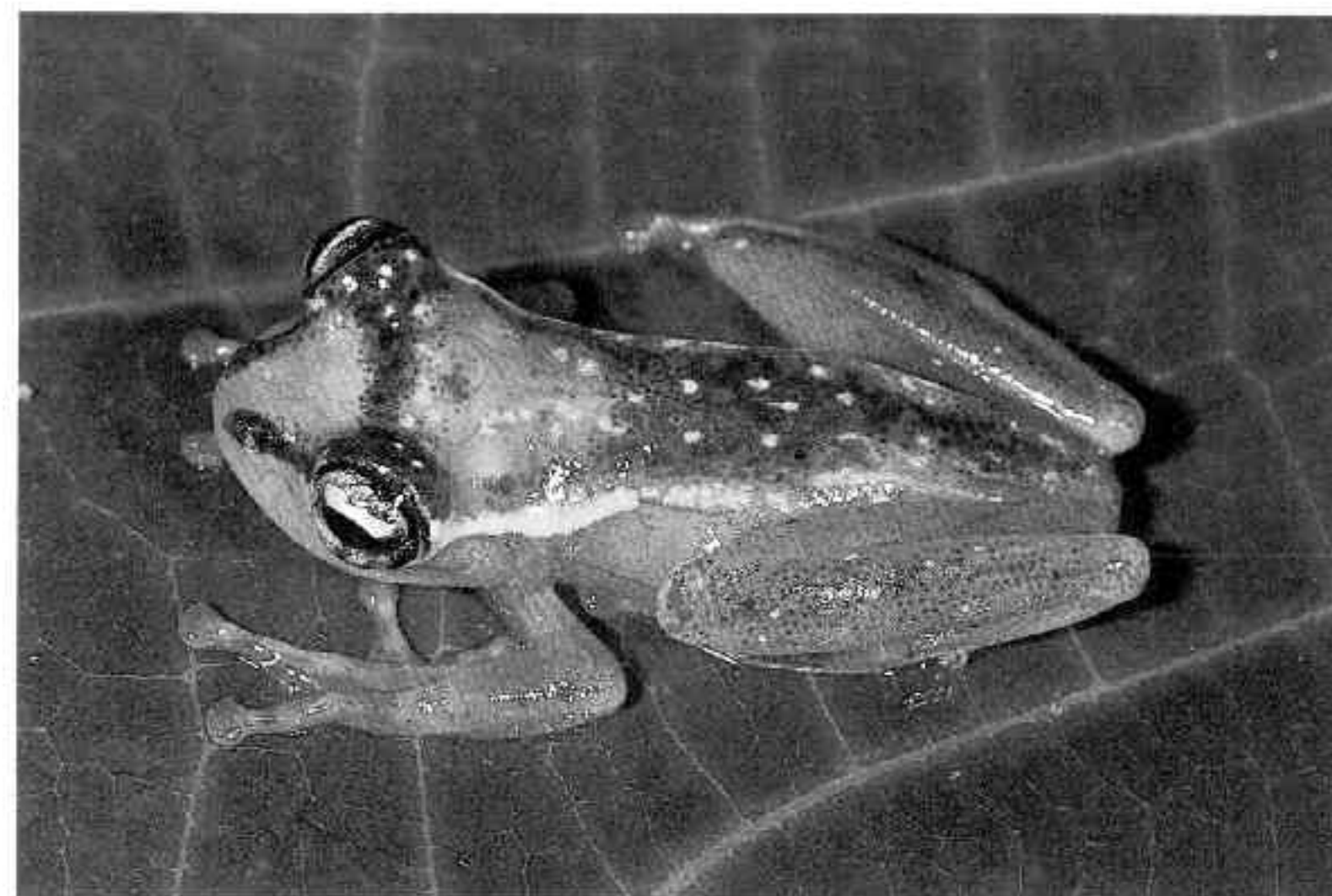


Fig. 5. — *Boophis bottae* n. sp. (paratype ZFMK 60016), adult male from Andasibe.

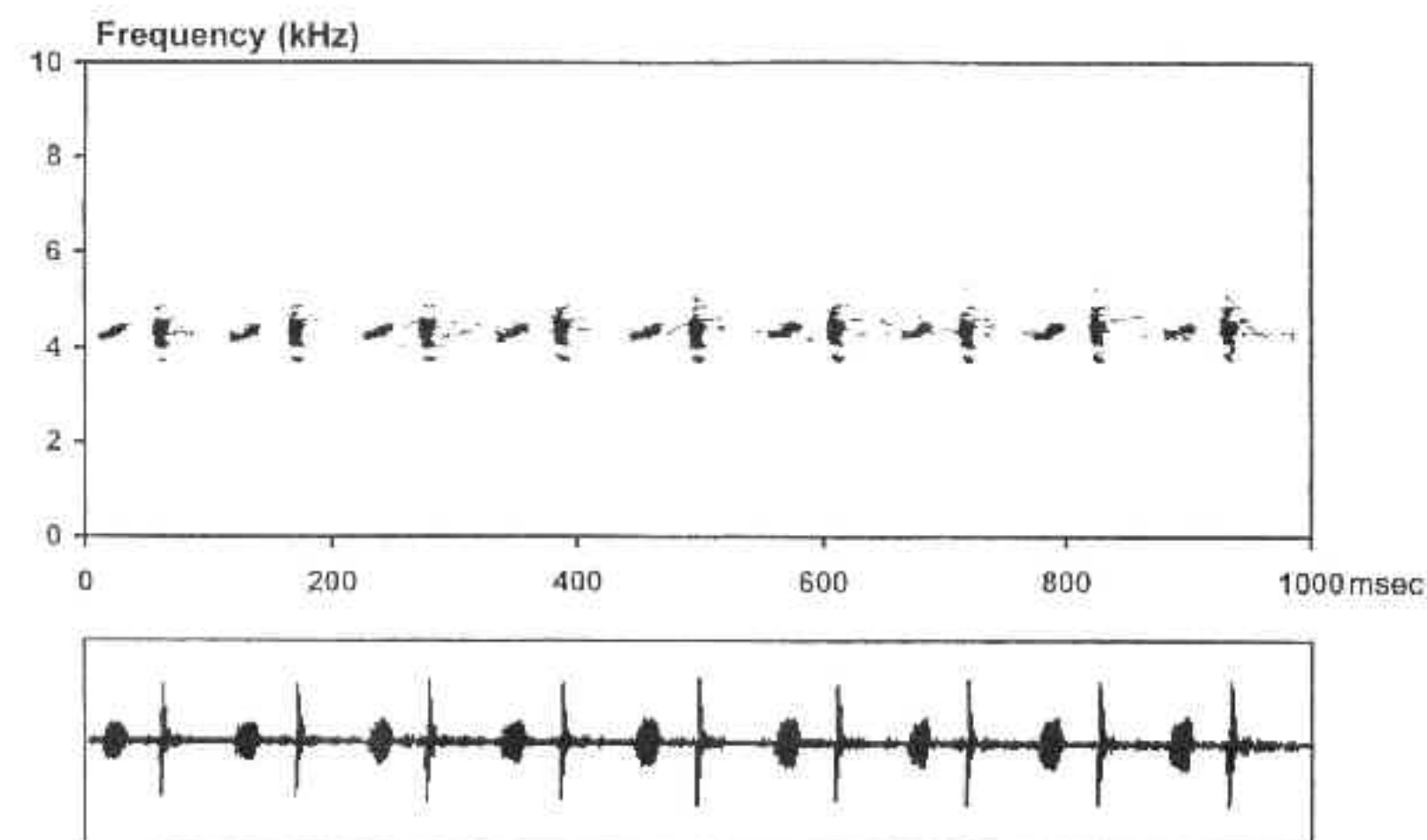


Fig. 6. — Sonagram and oscillogram of a section of a call of *Boophis bottae* n. sp. (series of notes of type 1), recorded at Andasibe.

Further material. UADBA-RD 1724 and 1732 (Vitanitelo, 15.5 km SE Vohitrafeno, 21°46.5'S, 47°20.8'E, 1100 m elevation); UADBA-MICET 19-21 (Mandriandry forest, 4.4 km SW Tolongoina, 21°35.3'S, 47°29.1'E, 750 m elevation); UADBA-MICET 144 and 147 (Ambahaka forest, 9 km NW Ambatofotsy, 21°44.2'S, 47°24.5'E, 750 m elevation). As no bioacoustic data of these specimens are known, we do not include them in the type series; they agree, however, with the type material in morphology and colouration.

Description of the holotype. SVL 24.2 mm. For measurements, see Table 1. Body slender; head wider than long, much wider than body; snout rounded in dorsal and lateral views, nostrils directed dorsolaterally, slightly protuberant, nearer to tip of snout than to eye; canthus rostralis moderately distinct, curved; loreal region concave; tympanum distinct, rounded, 41% of eye diameter; supratympanic fold rather indistinct and straight; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct, in two elongate aggregations, positioned posterolateral to choanae; choanae rounded. Arms slender, subarticular tubercles single; metacarpal tubercles not recognizable; fingers webbed; webbing formula 1 (1), 2i (1.5), 2e (1), 3i (2.25), 3e (1), 4 (1); relative length of fingers $1 < 2 < 4 < 3$, finger 2 distinctly shorter than finger 4; finger disks distinctly enlarged; unpigmented nuptial pads recognizable on the inner side of first finger. Hindlimbs slender; tibiotarsal articulation reaches beyond snout tip when hindlimb is adpressed along the body; lateral metatarsalia separated by the webbing; inner metatarsal tubercle recognizable, no outer metatarsal tubercle; webbing formula between toes 1 (0), 2i (0.5), 2e (0), 3i (0.5), 3e (0), 4i (1.5), 4e (1), 5 (0.25). Skin on the upper surface smooth; ventral skin smooth on throat where the presence of a vocal sac is clearly recognizable, slightly granular on belly; no distinct enlarged tubercles in the cloacal region.

After 5 months in preservative, the basic colour is beige-whitish. No further pigments are present on the flanks, while the whole dorsal side is irregularly covered with more or less intense dark pigment. This dark colour is interrupted by a pattern of small pigmentless spots. The area above the eyes is beige to reddish. The dorsal side of the legs is covered by few small dark pigment cells. The venter is unpigmented, the inner organs are visible through the translucent belly skin.

Variation. The paratypes agree largely in morphology and colouration with the holotype. The dark dorsal pattern is strongly expressed in the single female specimen (ZFMK 62221) and some males (ZFMK 62220), while in some other males (ZFMK 60016; Fig. 5) it is less distinct and sometimes relatively faint (ZFMK 60015). A dark inter-ocular stripe or band is always visible, and the dark pattern is always more intense on the posterior back. Two light dorsolateral bands are visible in most preserved specimens.

Colour in life. Based on colour slides of several paratype specimens (Fig. 5). The ground dorsal colour, including limbs, webbing and finger and toe disks is light greenish, more yellowish towards the flanks. Thin yellow dorsolateral stripes run from behind the eye to at least the forelimb insertion, sometimes along the whole body. Additionally, the dorsal surface has a pattern consisting of four general pigment types, but presence and extent of all of them is very variable. First, a red-brownish pattern is generally present above the eyes and as an inter-ocular band, and often as spots and larger markings on the posterior back. Second, a black pattern is often seen as very fine regular spotting on the back (probably consisting of single melanophores); often, the blackish pigment forms larger and more intense spots (probably dense layers of melanophores) at the center of the red-brownish

markings, i.e. above and between the eyes. Third, a pattern of bright red dorsal spots is often present; although sometimes intermediate states between these spots and the red-brown markings are observed, generally the red colour appears similar to that observed in *B. rappiodes*. Fourth, small dorsal yellow spots are often also observed. Few markings are present on fore- and hindlimbs. The venter is translucent. The iris is beige with a turquoise outer iris area and a brownish central marking in its lower part; the iris periphery is blue.

Etymology. Dedicated to Ursula Boti, ZFMK, in recognition of her invaluable help during the past 10 years.

Natural history and advertisement calls. Calling males were regularly observed during the night at Andasibe, 1-3 m high in the vegetation along a slow-moving stream, in part syntopically with *B. rappiodes*. Advertisement calls recorded from ZFMK 62220 at Andasibe on 9 February 1996 (20:30 hr) at 23 °C air temperature had a complex structure. Note type 1 was a double click which corresponded to one expiration and was emitted in long trill series of up to 2800 msec (note repetition rate 8-9/sec). Each note consisted of one longer and one shorter click pulse (Fig. 6). Duration of the first, longer pulse was 21-27 msec (22 ± 2 msec, $n = 15$), duration of the second pulse was 7-11 msec (9 ± 1 msec, $n = 15$), inter-pulse interval duration was 26-29 msec (27 ± 1 msec, $n = 15$). Inter-note intervals in trill calls had a duration of 48-70 msec (54 ± 5 msec, $n = 13$). The frequency of the long pulses was 4050-4450 Hz with a dominant frequency of 4150-4350 Hz, the frequency of the short pulses was 3600-4900 Hz with a dominant frequency of 4200-4500 Hz. Notes of type 2 generally consisted of three pulses (the first pulse having a lower intensity) and were usually emitted at the end of one trill call with a note repetition rate of about 2/sec. Pulse duration was 7-28 msec (17 ± 9 msec, $n = 5$) for the first pulse, 21-26 msec (24 ± 2 msec, $n = 5$) for the second pulse, and 20-27 msec (24 ± 3 msec, $n = 5$) for the third pulse. Inter-pulse interval duration was 28-40 msec (33 ± 6 msec, $n = 5$) between first and second pulse and 14-25 msec (20 ± 4 msec, $n = 5$) between second and third pulse. Calls recorded on 27 February 1996 at Vohiparara had an almost identical structure; the duration differences between the two pulses of note type 1 were less distinct. The vocal sac was single subgular and remained partly inflated between calls.

Distribution. The species is known from (1) the type locality Andasibe, and from (2) the Ranomafana area. The latter locality is corroborated by our own call recordings and photographs from Vohiparara, and by UADBA specimens.

Boophis erythrodactylus (Guibé 1953)

Hyperolius erythrodactylus Guibé, 1953. *Name-bearing type:* lectotype by present designation, MNHN 1994.1469 (originally numbered 1953.171A), adult male, collected in September 1952 by R. Paulian. *Type locality:* "forêt de Mahajoby, près de Morafenobe, Ouest de Madagascar" according to the original description. *Other types:* paralectotypes, 1953.171, adult male, and 1994.1470-1471 (originally numbered 1953.171B-C), two subadult specimens, with same collecting data as lectotype.

Remarks. According to GUIBÉ (1953), the original syntype series of *Hyperolius erythrodactylus* consisted of three males and one female. We could determine the sex reliably in two (male) specimens only (MNHN 1953.171 and 1994.1469). These still show distinctly the many light (originally red; see GUIBÉ 1953) spots scattered on the dorsum, and a few very faint dark minute spots above the eyes. In contrast, in the subadults, the light spotted pattern is not recognizable, while the black pigment forms a faint interocular band on the dorsal head surface. Whether these two specimens are actually conspecific with the lectotype cannot be reliably assessed. Considering the identification of a sibling species described below as *B. tasymana* n. sp., it is important to stabilize the name *B. erythrodactylus* by designation of a lectotype. Of the two males, MNHN 1994.1469 was in a better state of preservation upon examination in May 2001, and we therefore choose it as lectotype.

Identity. *Boophis erythrodactylus* was defined by GUIBÉ (1953), BLOMMERS-SCHLÖSSER (1979) and BLOMMERS-SCHLÖSSER & BLANC (1991) largely by its characteristic colour pattern, with numerous red spots of similar size (whitish in ethanol) on a greenish back. During recent fieldwork, we observed that populations of frogs with this character differed in advertisement calls. While specimens from Mandraka, on which the observations of BLOMMERS-SCHLÖSSER (1979) were based, emitted notes composed of 4–7 pulses of rather low frequency (below 3500 Hz), those from other sites emitted notes composed of two or three click pulses of higher frequency (above 3500 Hz). DNA sequences (547 nucleotides of the 16S rRNA gene) of one specimen of each form (from Mandraka and Andasibe, respectively) differed from each other in 32 substitutions and 2 indels, corresponding to a total pairwise sequence divergence of 6.1%. The high genetic differentiation and consistent call differences indicate that the two forms correspond to distinct sibling species. Morphologically, we could not detect any significant difference between them, but the Mandraka specimens always had red tips of fingers and toes which were absent in the other individuals. According to GUIBÉ (1953), who examined the type specimens of *B. erythrodactylus* shortly after preservation, intense red colour was present on "Extrémité des trois doigts externes, ainsi que celle des trois orteils externes". The red colour on 2–3 external fingers and toes was also recognizable in May 2001 in the ZFMK and ZSM specimens from Mandraka examined (see below), 1–7 years after their fixation and preservation in ethanol. The presence of red colour on some external or all fingertips of specimens from Mandraka was also mentioned by BLOMMERS-SCHLÖSSER (1979). In contrast, specimens from Andasibe, Mantady and An'Ala (all with two-click calls) had no trace of red colour on any finger- or toe-tips. We therefore consider the species present at Mandraka (Fig. 7) as conspecific with the types of *B. erythrodactylus* from Mahajebby forest. Although the latter locality has been said to be in western Madagascar, it appears to be rather on the western slopes of the central plateau of Madagascar, and at least two species occurring at this site [*Mantidactylus opiparis* (Peracca 1893) and a new species of the *M. albofrenatus* group; VENCES & GLAW in press] are common in forests above 1000 m elevation such as the one at Mandraka (ca 1200 m).

Diagnosis. A member of the *Boophis rappiodes* group as recognizable by small size (males 20–25 mm, female 32–33 mm; Table 1 and BLOMMERS-SCHLÖSSER 1979), greenish and slightly translucent dorsal colouration, translucent venter (inner organs can be clearly seen through the skin in live specimens) and absence of lateral fringes along lower arm and tarsus. Distinguished from *Boophis mandraka* by

nostril position (closer to snout tip than to eye vs slightly closer to eye), and iris colour (absence of distinct reticulations on a light beige iris). Distinguished from *B. viridis* by smaller size. Distinguished from all species of the *B. rappiodes* group except for *B. tasymana* n. sp. (see below for a distinction from that species) by a regular dorsal pattern of similarly-sized red spots and red colour of (at least the external) tips of fingers and toes (Fig. 7).

Material examined. MNHN 1953.171 and 1994.1469–1471 (lectotype and three paralectotypes from Mahajebby forest); UADBA-MV 2001.206–207 (Mandraka); ZFMK 59813–59814 (Mandraka); ZSM 342/2000 and 677/2001 (Mandraka).

Distribution. The species is at present only known from (1) the type locality Mahajebby and (2) Mandraka. BLOMMERS-SCHLÖSSER & BLANC (1991) mentioned three other localities for the species, namely Andasibe (as Perinet), Manjakatempo and Vondrozo. The distributional information of these authors was almost exclusively based on the ZMA and MNHN holdings which were revised by us. The Manjakatempo locality was based on tadpoles (ZMA 7205–7206; BLOMMERS-SCHLÖSSER 1979) which most probably correspond to the species *Boophis ankaramitra* Andreone 1993 (GLAW & VENCES 1994 and unpublished data). The Andasibe locality was based on two males (ZMA 6929) collected along the "highroad R.N. 2 at km 142, alt 1100 m" (BLOMMERS-SCHLÖSSER 1979). Unfortunately, in the ZMA material, "the red colour has disappeared completely ..., probably because the collection was exposed to the light for some time" (BLOMMERS-SCHLÖSSER 1979). Therefore it is not possible, at present, to ascertain whether the specimens labeled ZMA 6929 are to be assigned to *B. erythrodactylus* or to *B. tasymana* n. sp. (see below). As the latter species is common in the Andasibe region, we consider the presence of *B. erythrodactylus* as in need of confirmation, although the syntopic occurrence of both taxa cannot be excluded. The locality Vondrozo is based on MNHN 1930.432. This specimen is in rather good state of preservation, but the colour pattern has faded completely. A reliable determination of this specimen (see Table 1 for measurements) is not possible, and we therefore propose to consider also the Vondrozo locality for *B. erythrodactylus* as in need of confirmation. As to the presence of *B. erythrodactylus* at Ranomafana (ANDREONE 1994), we suppose that this record was based on observations of the very similar *B. tasymana* n. sp. (see below) which is common in this area.

Natural history and advertisement calls. Calling males were observed about 2–3 m high in the vegetation along broad, fast-flowing streams, syntopically with *B. mandraka* (see also BLOMMERS-SCHLÖSSER 1979). Calls from Mandraka (recorded on 9 February 1994, 21:45 hr, at 23 °C air temperature) were series of usually 4–7 click pulses (sometimes up to 14 clicks) (Fig. 8). Duration of each pulse was 9–15 msec, pulse repetition rate was 9–10/sec. Inter-pulse interval duration was 99–109 msec. The frequency was between 1850 and 3500 msec, and often increased towards the last pulses of a call.

Boophis tasymana n. sp.

Identity. A *B. erythrodactylus*-like species with two- or three-pulse calls of high frequency, and without red tips on fingers and toes (see above).



Fig. 7. — *Boophis erythrodaetylus*, adult male from Mandraka (specimen preserved in UADBA collection).

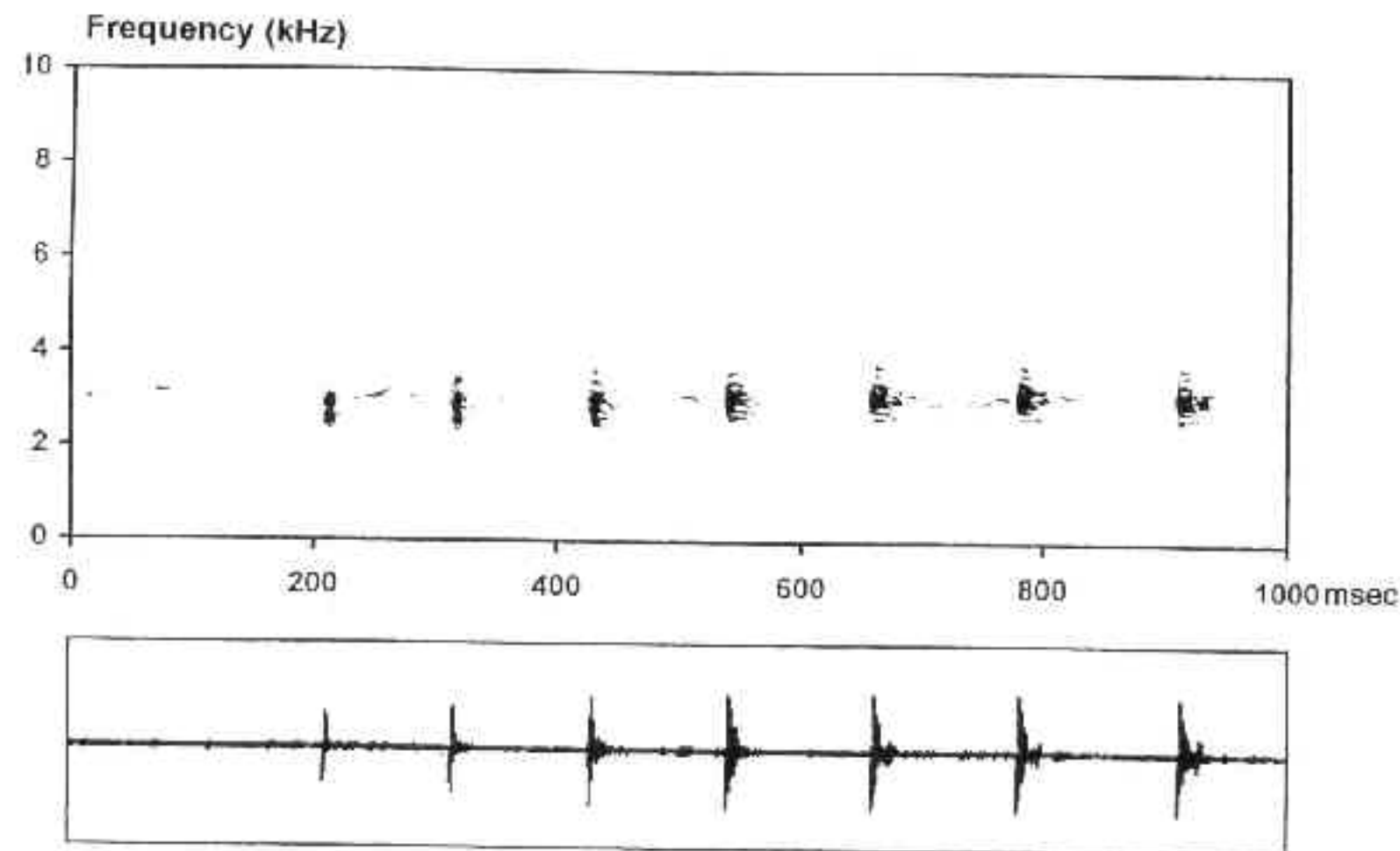


Fig. 8. — Sonogram and oscillogram of a call of *Boophis erythrodaetylus*, recorded at Mandraka.

Diagnosis. A member of the *Boophis rappiodes* group as recognizable by small size (males 21–23 mm, one female 32 mm; Table 1), greenish and slightly translucent dorsal colouration, translucent venter (inner organs can be clearly seen through the skin in live specimens) and absence of lateral fringes along lower arm and tarsus. Distinguished from *Boophis mandraka* by nostril position (closer to snout tip than to eye vs slightly closer to eye), and iris colour (absence of distinct reticulations on a light beige iris). Distinguished from *B. viridis* by smaller size. Distinguished from all species of the *B. rappiodes* group except for *B. erythrodaetylus* by a regular dorsal pattern of similarly-sized red spots. The species is most similar to *B. erythrodaetylus*, but differs in advertisement calls (2–3 click pulses vs 4–7 pulses), in the lack of red colour on the tips of fingers and toes (vs presence at least on the external fingers and toes; Fig. 9), and possibly in a smaller mean size of males (SVL 21–23 mm vs 24–25 mm in the samples analyzed by us; Table 1). It furthermore shows important genetic differences from *B. erythrodaetylus* (see Identity section of that species) which fully support its status as a distinct species.

Holotype. ZSM 1085/2001 (originally ZFMK 62224), adult male, collected by F. Glaw on 4 February 1996 at Andasibe, central-eastern Madagascar, 18°56'S, 48°25'E, ca 900 m elevation (Fig. 9).

Paratypes. ZFMK 62225, adult male, same collecting data as holotype; ZFMK 62243–62244, two adult males, collected by F. Glaw on 10 February 1996 at Mantady; ZFMK 62262 and 62267, two adult males, collected by F. Glaw on 3 February 1996 at An'Ala; ZFMK 62888, adult female, collected by F. Glaw, D. Rakotomalala and F. Ranaivojoana on 9–11 March 1996 at Andasibe.

Description of the holotype. SVL 22.7 mm. For measurements, see Table 1. Body slender; head wider than long, much wider than body; snout moderately truncated in dorsal and lateral views; nostrils directed laterally, slightly protuberant, nearer to tip of snout than to eye; canthus rostralis relatively indistinct, curved; loreal region slightly concave; tympanum distinct, rounded, 57% of eye diameter; supratympanic fold indistinct, relatively straight; tongue ovoid, distinctly bifid posteriorly; rudiments of vomerine teeth can be recognized posterolateral to choanae; choanae rounded. Arms slender, subarticular tubercles single; metacarpal tubercles not recognizable; fingers webbed; webbing formula 1 (1), 2i (1.25), 2e (1), 3i (2.25), 3e (2), 4 (1); relative length of fingers $1 < 2 < 4 < 3$, finger 2 distinctly shorter than finger 4; finger disks distinctly enlarged; unpigmented nuptial pads on inner side of first finger. Hindlimbs slender; tibiotarsal articulation reaches snout tip when hindlimb is adpressed along the body; lateral metatarsalia separated by the webbing; inner metatarsal tubercle present, outer metatarsal tubercle absent; webbing formula between toes 1 (0), 2i (0.5), 2e (0), 3i (1.25), 3e (0.5), 4i (2), 4e (2), 5 (0.5). Skin on the upper surface smooth; ventral skin smooth on throat, slightly granular on belly; no distinct enlarged tubercles in the cloacal region.

After more than 5 years in preservative, the main colouration is a dirty yellow-white. The whole dorsal area, including fore- and hindlimbs, is stippled with small, distinct red spots, all of more or less similar size. Large, intense red markings are present above the eyes, and are connected by a discontinuous red interocular stripe. The centre of these supraocular markings is covered by blackish pigment. No red colour is present on the tips of fingers and toes. The ventral side is completely unpigmented.



Fig. 9. — *Boophis tasymeria* n. sp. (holotype ZSM 1085/2001), adult male from Andasibe.

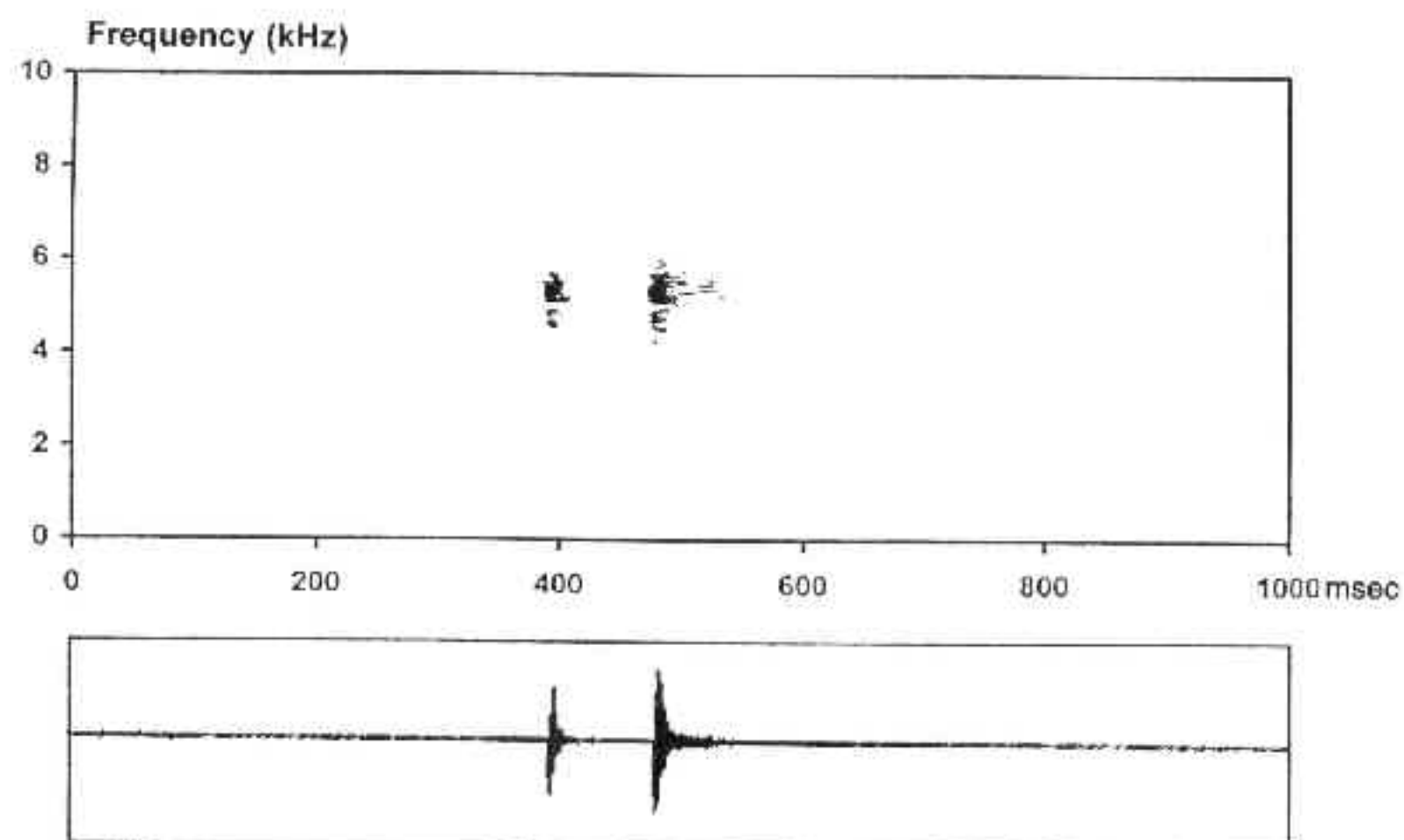


Fig. 10. — Sonogram and oscillogram of a call of *Boophis tasymeria* n. sp., recorded at Andasibe.

Variation. The paratypes agree well in morphology and colouration with the holotype. Most males (in preservative) have red patches above the eyes and a red inter-ocular line of different width and intensity. Generally, also some dark pigment is present at these places. In some specimens, three (ZFMK 62262) or four (ZFMK 62225) regularly spaced black spots are present on the tibia. Especially ZFMK 62225 is also characterized by two symmetric dark brown markings on the central back. The single female (ZFMK 62888) is characterized by the absence of any trace of supraocular or inter-ocular markings; the sole pattern in this specimen is the fine regular red spotting all over the dorsal surface. No trace of red colour on the tips of fingers or toes is visible in any specimen.

Colour in life. Based on colour slides of the holotype and of several paratype specimens. The ground colour is greenish, including the limbs, webbing and finger and toe disks. Sometimes, the latter are of a more intense green than the limbs, but never show any red colour. The ventral side is translucent. Yellow dorsolateral lines run from the eye to the forelimb insertion. Dorsally two further pigment types are present to a variable extent: the bright red spotting; reddish-brown markings above the eyes and as an inter-ocular transversal band, but seldom as symmetric markings on the back. The iris is beige with a bright light blue outer area and a brownish central marking in its lower part; the iris periphery is blue.

Etymology. Derived from the Malagasy words tasy (pattern, spot) and mena (red) and referring to the characteristic red spotted pattern. The name is used as an invariable noun standing in apposition to the generic name.

Natural history and advertisement calls. Calling males were found at night sitting 1-3 m high in trees and shrubs along broad brooks, sometimes at distances of up to 20 m from the water. Calls recorded at Andasibe on 4 February 1996 at 19:30 hr (24 °C air temperature) and An'Ala on 3 February 1996 at 18:30 hr (23 °C air temperature) were very similar. They usually consisted of two pulses (Fig. 10). Pulse duration was 10-24 msec (17 ± 3 msec, $n = 46$), duration of inter-pulse intervals was 71-97 msec (81 ± 8 msec, $n = 23$). The frequency ranged between 3850 and 6100 Hz, the dominant frequency was 5000-5500 Hz. Calls recorded at Vohiparara on 3 March 1996 regularly contained also three-pulse notes. Pulse duration was 5-17 msec (7 ± 3 msec, $n = 17$), duration of inter-pulse intervals was 63-90 msec (77 ± 9 msec, $n = 11$). The frequency was 3700-5400 Hz, the dominant frequency 4250-4900 Hz. The vocal sac was single subgular, and each two- or three-pulse note was emitted as one expiration. The vocal sac did not remain inflated between calls, but was slightly inflated before the start of each call.

Distribution. Besides (1) the type locality Andasibe and the localities of paratypes, (2) Mantady and (3) An'Ala, the species is also known from (4) Vohiparara. The latter locality is corroborated by field observations and call recordings by F. Glaw (see call descriptions above).

DISCUSSION

In addition to the characters used here for distinguishing among the species of the *B. rappiodes* group, several others have been used in the literature and will

therefore be discussed in the following. BLOMMERS-SCHLÖSSER (1979) distinguished *B. viridis* by a strongly protruding nostril (vs slightly protruding in the other species). We do not consider this character to be very useful, especially as *B. viridis* is easily diagnosed by its size and general appearance. The more strongly protruding nostrils of *B. viridis* are recognizable in most individuals, but at least in one of our specimens, ZFMK 60013, the nostril state did not differ from other species of the group.

BLOMMERS-SCHLÖSSER (1979) also distinguished *B. rappiodes* by its shorter hand length (ratio HAL/SVL 0.26 vs 0.33 in the other species). In our sample (Table 1), mean relative hand length of *B. rappiodes* males was actually the lowest (0.299), but also the values of *B. viridis* (0.300), *B. bottae* (0.305) and *B. tasymena* males (0.308) were low, with largely overlapping ranges. Although relative hand length may be of some use to distinguish particular species (e.g., in our sample, *B. mandraka* males had a high mean value of 0.340), it is not a very useful diagnostic character according to our data.

In contrast, relative tympanum diameter, as used by BLOMMERS-SCHLÖSSER (1979) to characterize *B. erythrodactylus*, appears useful also according to our data set. Instead of the ratio TD/ED as used by BLOMMERS-SCHLÖSSER (1979), we preferred the ratio TD/SVL, as eye diameter can strongly depend on the state of fixation and preservation of the specimens. Considering males only, the highest mean values, 0.071 and 0.070, corresponded to *B. erythrodactylus* and its sibling *B. tasymena*, while the other species of the group ranged between 0.060 and 0.062. Even the minimum values of *B. erythrodactylus* (0.069) and *B. tasymena* (0.067) were higher than those of any other species except for *B. rappiodes* in which two individuals attained 0.068–0.069. We therefore confirm that relative tympanum diameter in *B. erythrodactylus* and *B. tasymena* is larger than in the other species of the group.

A further difference within the *B. rappiodes* group is relative female size. All species agree with the general trend that *Boophis* females are distinctly larger than males (in contrast to many species of the mantelline genus *Mantidactylus*). However, the relative mean male/female size ratio of *B. viridis* (87%) is distinctly higher than in the other species of the group (66–73% in *B. rappiodes*, *B. bottae*, *B. erythrodactylus* and *B. tasymena*). As female size is similar in *B. viridis* and the other species (Table 1), this indicates an evolutionary trend of male size differentiation independently of female size. It may be hypothesized that the derived state is the large male size with low sexual dimorphism in *B. viridis*. This species occurs syntopically with three other species of the *B. rappiodes* group at Andasibe (*B. rappiodes*, *B. bottae* and *B. tasymena*) and is bioacoustically the most divergent species of the group. It is well known that the frequency of vocalizations is inversely correlated with individual size (DUELLMAN & TRUEB 1986). It is therefore possible that the size diversification of this species has been influenced by factors of bioacoustic competition with other syntopic species of the *B. rappiodes* group. An alternative explanation for the relatively enlarged size of *B. viridis* males may be intraspecific male combats (SHINE 1979) which, however, have not been observed in this species.

The discovery and description of two additional species of the *B. rappiodes* group indicates that the centre of endemism of the group is in central-eastern Madagascar. Two further new species of the group, siblings to *B. mandraka*, were also discovered in this region (this complex of species will be revised elsewhere). According to the distribution maps of BLOMMERS-SCHLÖSSER & BLANC (1991), only

one dubious record of *B. mandraka* was then known from the Chaînes Anosyennes in the extreme south-east. The corresponding vouchers, MNHN 1973.1100–1101 and 1973.1103–1105, have distinct fringes along the lateral edge of the lower arm and tarsus, which are absent in the *B. rappiodes* group but typical of the *B. luteus* group (BLOMMERS-SCHLÖSSER & BLANC 1991); these specimens may actually belong to *Boophis andohahela* Andreone et al. 1995, *B. albipunctatus* Glaw & Thiesmeier 1993, or *B. sibilans* Glaw & Thiesmeier 1993. Thus, the record of *B. rappiodes* in Nahampoana (GLAW & VENCES 1994) was the first of a species of this group in far south-eastern Madagascar. Recent surveys recorded species of the group from the north-east: *B. mandraka* and *B. rappiodes* from Marojejy, Anjanaharibe-Sud, Tsararano, and *B. mandraka* from Ambolokopatrika (RAXWORTHY et al. 1998, ANDREONE et al. 2000, RASELIMANANA et al. 2000). However, at these northern and southern sites, only one or two species were found, while the Andasibe-Mandraka area in central-eastern Madagascar harbours at least eight species.

The elevational distribution of the group is largely confined to mid-elevations (700–1200 m). At north-eastern sites, *B. rappiodes* and *B. mandraka* were found between 500 and 1560 m (RAXWORTHY et al. 1998, ANDREONE et al. 2000, RASELIMANANA et al. 2000), while the south-eastern Nahampoana site, located at ca 300 m above sea level, is an exception. However, other typical mid-elevation species, such as *Boophis luteus* (Boulenger 1882), also reach lower elevations at Nahampoana.

Altogether, the new distributional and taxonomic information confirms that the high faunal diversity in mid-elevational central-eastern Madagascar (LEES 1996) is not a sampling artefact. On the other hand, the degree of endemism in this region may be lower than previously thought, and species thought to be exclusive to the environments of Andasibe are increasingly recorded also from other sites. According to our data, all species revised herein are known from at least one additional site, mostly in south-eastern Madagascar (Ranomafana area). The genetic differentiation (in the 16S rRNA gene; Table 2) of *Boophis tasymena* to *B. erythrodactylus* and *B. bottae* to *B. rappiodes* (6–7%) is of a similar order of magnitude as, for instance, that of *B. erythrodactylus* and *B. tasymena* to *B. rappiodes* (8%); it is lower than between *B. viridis* and the other species (9–10%), but still much higher than would be expected from the similar morphology of these sibling species. In a molecular phylogenetic analysis (VENCES et al. 2002), *B. bottae* was the sister species of *B. rappiodes*, and *B. tasymena* the sister species of *B. erythrodactylus*, as would be expected from the similarities in colouration and morphology. When the

Table 2.

Genetic differences between species of the *B. rappiodes* group. The values are total pairwise divergences in per cent (above diagonal) and total number of substitutions including indels (below diagonal) in the analyzed 16S rRNA gene fragment (560 nucleotides).

	<i>B. viridis</i>	<i>B. rappiodes</i>	<i>B. bottae</i>	<i>B. erythrodactylus</i>	<i>B. tasymena</i>
<i>B. viridis</i>	—	10.4%	9.8%	9.3%	9.8%
<i>B. rappiodes</i>	58	—	7.3%	8.0%	8.0%
<i>B. bottae</i>	55	41	—	8.5%	9.1%
<i>B. erythrodactylus</i>	52	45	45	—	6.1%
<i>B. tasymena</i>	55	45	51	34	—

usual rate estimate of 0.6% pairwise sequence divergence per million years is applied, the origin of these sibling species clearly predates the Pleistocene, as is common in rainforest species (MORITZ et al. 2000).

ACKNOWLEDGEMENTS

We are grateful to Dorothea Rakotomalala who assisted in the field and during examination of LADBA specimens; to Para Ranaivojaona and David Vieites for their help in the field. Wolfgang Böhme (Bonn), Rainer Günther (Berlin), Berthuis van Tuijl (Amsterdam), Alain Dubois and Annemarie Ohler (Paris) allowed examination of specimens held in their care. We are indebted to the Malagasy authorities for research and export permits. The work of both authors was made possible by a cooperation accord between the Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn and the Zoologische Staatssammlung München, with the Département de Biologie Animale, Université d'Antananarivo, and was financially supported by the Deutscher Akademischer Austauschdienst (DAAD).

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