



# Revision of the *Boophis majori* group (Amphibia: Mantellidae) from Madagascar, with descriptions of five new species

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A systematic revision of the Malagasy frogs hitherto attributed to the *Boophis difficilis* group is presented. The *difficilis* holotype is not conspecific with other specimens hitherto named *Boophis difficilis* but belongs to the *B. tephraeomystax* group based on lack of webbing between fingers and the presence of heterogeneously granular ventral skin. *Rhacophorus difficilis* Boettger, 1892 is considered as junior synonym of *Boophis tephraeomystax*. The *Boophis difficilis* group is dissolved and its species are transferred to a new species group named after *Boophis majori*, the oldest of the included taxa. All species of the *B. majori* group, their type specimens, and their geographical distributions are revised based on new morphological, bioacoustic and ecological data. Five new species of the group from the eastern rainforests of Madagascar are described. Morphological differentiation within the *B. majori* group is low, although some species can be distinguished by characters such as snout–vent length, relative tympanum size, or coloration. The most reliable character for species identification are advertisement calls which are strikingly different between most species of the group. Species diversity in *Boophis* is highest in central eastern Madagascar and gets lower at the northern and southern borders of the island. Available data do not allow a comprehensive phylogenetic analysis of the *B. majori* group, but a northern subgroup of small species without red coloration and a southern subgroup of larger species with distinct red pigments can be distinguished. Osteological data for *B. miniatus* are provided. Within *Boophis*, representatives of all species groups except the *B. tephraeomystax* group are characterized by a synapomorphic reduction of the anterolateral hyoidal process.

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## INTRODUCTION

The genus *Boophis* Tschudi, 1838 is endemic to Madagascar and adjacent islands. *Boophis* was considered a synonym of the Oriental genus *Rhacophorus* by Guibé (1978), but was re-established by Blommers-Schlösser (1979b) who distinguished eight phenetic species groups. Most *Boophis* are arboreal frogs with a typical treefrog habitus (enlarged finger discs, broad and anteriorly rounded head, large eyes, no dorsolateral ridge).

In the most recent classification Glaw & Vences

(1994) recognized seven *Boophis* species groups. According to these authors the *Boophis difficilis* group consists of five named species: *Boophis difficilis* (Boettger, 1892), *Boophis majori* (Boulenger, 1896), *Boophis miniatus* (Mocquard, 1902), *Boophis blommersae* Glaw & Vences, 1994 and *Boophis marojezensis* Glaw & Vences, 1994. These species are characterized by small size (snout–vent length of males 21–33 mm), a predominantly brownish (never green) back, often with hourglass shaped markings, a whitish (not transparent) venter, and the lack of a distinct canthus rostralis. Many species have reddish colour on the legs, feet, webbing or other skin areas of the body (sometimes only visible when preserved). As far as is known, these species live alongside brooks. The

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advertisement calls of the five hitherto known species have been described by Glaw & Vences (1992a,b, 1994).

Another species, *Boophis rhodoscelis*, shares many characters typical for the *difficilis* group (small size, brownish back, reddish webbing on the feet). However, this species has a distinct canthus rostralis, typical for the *B. goudoti* group. Blommers-Schlösser (1979b) considered this species a member of the *Boophis rhodoscelis* group which included *B. rhodoscelis*, *B. difficilis*, *B. miniatus* and *B. majori*. In a subsequent work, Blommers-Schlösser & Blanc (1991) assigned *B. rhodoscelis* to the *B. goudoti* group. This arrangement was followed by Glaw & Vences (1994) and is confirmed by new data on the call of *B. cf. rhodoscelis* (Glaw & Vences, 1997a), which is more similar to that of the *goudoti* group (low frequency). Furthermore the re-examination of the type material of *B. rhodoscelis* and that of *Rhacophorus andrangoloaka* and *R. brevirostris* confirmed the opinion of Guibé (1978) and Blommers-Schlösser & Blanc (1991) that the latter taxa are synonyms of *B. rhodoscelis* and not referable to any of the species of the *difficilis* group (Glaw & Vences, 1997a).

Re-examination of type specimens of *Boophis* species demonstrated important differences between the type of *Rhacophorus difficilis* Boettger, 1892 and other specimens so far attributed to *Boophis difficilis*. Furthermore, new field surveys in the rainforests of eastern Madagascar revealed several previously unrecognized *Boophis* species. Since no synonyms are available, new names have to be coined for all of them. In the present paper we revise the taxa which have been included in the *B. difficilis* group, provide clarifications on the status of the taxon *difficilis*, and describe five new *Boophis* species. Additionally, we give first osteological data for one representative of the group (*B. miniatus*) and brief considerations on the intrageneric relationships of *Boophis*, and discuss the importance of bioacoustic and morphological differentiation for the taxonomy of anurans.

We here follow Vences & Glaw (2001) and include the genus *Boophis* together with the genera *Mantidactylus*, *Mantella*, *Aglyptodactylus* and *Laliostoma* in the family Mantellidae (see also the molecular phylogram of Richards & Moore, 1998). Additionally, known differences between ranids and rhacophorine frogs are extremely low and mainly based on the existence of an intercalary element between the terminal and sub-terminal phalanges in rhacophorines. The limited value of this character has recently been demonstrated (Glaw *et al.*, 1998).

## MATERIAL AND METHODS

Specimens were generally collected at night with the aid of electric torches by trying to localize calling males.

At least one specimen of each species was only captured after its identification as calling male by observation of calling behaviour with vocal sac inflation. Field observations, unless otherwise stated, were made by F. G. Advertisement calls were recorded by different persons with different portable tape recorders and external microphones. Bioacoustic analyses were made by F. G. with the sound analysing system MEDAV Spekro 3.2. Temporal measurements are given as range followed by mean  $\pm$  standard deviation and number of analyzed units (*N*) in parentheses.

Most specimens were fixed in 96% ethanol and subsequently stored in 70% ethanol; only a few MRSN specimens were fixed in 10% formalin and subsequently stored in 70% ethanol. All examined ZMA specimens collected by R. Blommers-Schlösser had been fixed in formalin.

Morphometric measurements were done by M. V. with a precision calliper to the nearest tenth of a millimetre. Measurements taken were: snout-vent length (SVL), maximum head width (measured at a point immediately posterior to the eyes) (HW), head length (measured from posterior maxillary commissure to snout tip) (HL), horizontal eye diameter (Eye), horizontal tympanum diameter (Tym), eye-nostril distance (Eye-Ns), distance between nostril and snout tip (Ns-St), internarial distance (Ns-Ns), foot length (measured from foot-tarsus articulation to the tip of longest toe) (FoL), foot length including tarsus (measured from tibiotarsal articulation to the tip of longest toe) (FoTL), hindlimb length (measured from anus to the tip of longest toe) (HiL), forelimb length (measured from axil to the tip of longest finger) (ForL), hand length (measured from carpus-hand articulation to the tip of longest finger) (HaL).

Morphometric data were processed statistically with SPSS for Windows. The term shank is here used to refer to the part of the leg containing the tibia, and thigh is used for the part of the leg containing the femur. Webbing formula follows Savage & Heyer (1967) as modified by Myers & Duellman (1982) and Savage & Heyer (1997). To facilitate comparisons, in the holotype descriptions we also give the formula used by Blommers-Schlösser (1979a) and most subsequent authors who published accounts on Malagasy anurans. The Savage & Heyer (1967) system includes the toe disks in the determination of the webbing formula, whereas the Blommers-Schlösser (1979a) system does not (see drawings in Glaw & Vences, 1994). In the Blommers-Schlösser formula, the absence of webbing is here symbolized by a hyphen (-), whereas in the Savage & Heyer formula we only include those fingers and toes with recognizable webbing. To describe the amount of webbing relative to subarticular tubercles, we numbered these tubercles 1–3, beginning from the disks. In the text, the Blommers-Schlösser formula is

**Table 1.** Collecting localities which are mentioned in the text, their exact location, and recorded species. Localities are arranged alphabetically. Sources: [1] coordinates and altitudes according to Carleton & Schmidt (1990); [2] coordinates and altitudes according to Raxworthy & Nussbaum (1994; altitude according to their collecting localities of *B. miniatus*); own collecting localities within this range; [3] according to Andreone *et al.* (1995); [4] according to Brygoo (unpubl.); [5] Isaka 700 m alt. according to Brygoo (unpubl.). Mid-altitude refers to an altitude between c. 500 and 1100 m, low altitude to 0–500 m

Locality name	Altitude	Coordinates	Species recorded
near Ambalamarina (Andringitra)	>1000 m	22°07'S/46°56'E	<i>B. majori</i>
Ambanizana	10–20 m	15°35'S/49°56'E	<i>B. marojezensis</i>
Ambatolahy	800 m	21°15'S/47°24'E	<i>B. miniatus</i>
Ambohimitombo (= Ambohimitambo)	1200 m [1]	20°43'S/47°23'E [1]	<i>B. majori</i>
An'Ala	840 m	18°56'S/48°28'E	<i>B. pyrrhus</i> , <i>B. picturatus</i> , <i>B. marojezensis</i>
Andasibe (= Perinet)	915 m [1]	18°56'S/48°25'E [1]	<i>B. pyrrhus</i> , <i>B. miniatus</i> , <i>B. picturatus</i> , <i>B. feonnyala</i>
Andohahela	c. 400 m [3]	24°47'S/46°51'E	<i>B. haematopus</i>
Anjanaharibe	mid-altitude	13°37'S/49°36'E [4]	<i>B. marojezensis</i>
Ankeniheny	900 m	19°10'S/48°2'E	<i>B. pyrrhus</i>
Besariaka	850–940 m	14°50'S/49°36'E	<i>B. marojezensis</i>
Foizana (equals Fizoana?)	low altitude	15°20'S/49°57'E	<i>B. tephraeomystax</i> (holotype of <i>R. difficilis</i> )
Ifanadiana	450 m	21°18'S/47°38'E	<i>B. miniatus</i> , <i>B. pyrrhus</i>
Isaka-Ambobo	mid-altitude [5]	?	<i>B. miniatus</i>
Mandraka	1220 m [1]	18°55'S/47°56'E [1]	<i>B. marojezensis</i>
Mantady	900 m	18°53'S/48°25'E	<i>B. pyrrhus</i>
Marojezy Camp I	300 m	14°26'S/c. 49°46'E	<i>B. marojezensis</i>
Marojezy Camp III	700 m	14°26'S/c. 49°46'E	<i>B. vittatus</i>
Montagne d'Ambre (incl. Les Roussettes)	650–1150 m [2]	12°32'S/49°10'E [2]	<i>B. blommersae</i>
Nahampoana	c. 300 m	24°58'S/46°58'E	<i>B. miniatus</i> , <i>B. haematopus</i>
Base of Pic St. Louis (near Tolagnaro)	<300 m	25°00'S/46°59'E	<i>B. miniatus</i>
Ranomafana	600 m	21°15'S/47°27'E	<i>B. marojezensis</i>
Tsararano	700 m	14°55'S/49°41'E	<i>B. marojezensis</i>
Vohiparara	c. 1000 m	21°13'S/47°22'E [1]	<i>B. majori</i> , <i>B. picturatus</i> , <i>B. marojezensis</i>

preceded by 'BS', the Savage & Heyer formula by 'SH' in parentheses.

Osteological data were taken from alizarin/alcian blue stained specimens (method modified after Dingerkus & Uhler, 1977; see Plösch, 1991).

The following institutional abbreviations are used: BM (Natural History Museum, London), MNHN (Muséum National d'Histoire Naturelle, Paris), MRSN (Museo Regionale di Scienze Naturali, Torino), UMMZ (University of Michigan, Museum of Zoology), ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn), ZMA (Zoologisch Museum, Amsterdam), ZSM (Zoologische Staatssammlung, München).

Table 1 gives a summary of longitudes, latitudes, and altitudes of all localities referred to in the text.

## RESULTS

### IDENTITY OF *RHACOPHORUS DIFFICILIS* BOETTGER, 1892

In 1892, Oskar Boettger described a new anuran species as *Rhacophorus difficilis*, based on one male (?) specimen collected at Foizana in eastern Madagascar. In his monograph on Malagasy frogs, Guibé (1978) considered the species as synonym of *Rhacophorus tephraeomystax*, a species widely distributed at low-altitude localities along the coast of Madagascar.

During her fieldwork in Malagasy rainforests, Blommers-Schlösser (1979b) found three similar small *Boophis* species which were mainly distinguished by bioacoustic characters and slight morphological differences. She considered one of these species, collected

near the eastern mid-altitude locality Andasibe, as conspecific with the type of *Rhacophorus difficilis*, and redefined this taxon as *Boophis difficilis* mainly based on the following characters: (1) SVL of males 27–31 mm; (2) mean ratio Tym/Eye 0.36; (3) fringes along lower arm and tarsus well developed; (4) nostrils much nearer to tip of snout than to eye; (5) nostrils strongly protruding; (6) skin on the back smooth. Subsequent studies (Blommers-Schlösser & Blanc, 1991; Glaw & Vences, 1992a,b, 1994) followed this definition, and also assigned specimens from a population near Tolagnaro in south-eastern Madagascar to *B. difficilis* (Glaw & Vences, 1992b, 1994).

To clarify the identity of *Rhacophorus difficilis*, we undertook a detailed re-examination of the holotype which is given in the following.

*Redescription of the holotype.* SMF 6762, probably a male (weakly developed nuptial pads recognizable). (Figures 1, 2). Body slender; head slightly longer than wide, slightly wider than body; snout slightly pointed in dorsal and lateral view; nostrils directed laterally, protuberant; canthus rostralis moderately developed, concave; loreal region weakly concave; tympanum rather distinct, rounded, its diameter about 1/2 of eye diameter; distinct supratympanic fold; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct; choanae medium-sized, rounded. Arms slender; subarticular tubercles single; no distinct metacarpal tubercles recognizable; fingers without webbing; finger length  $1 < 2 < 4 < 3$ , when fingers 2 and 4 are adpressed to each other terminal finger disks do not get in contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches between eye and nostril; feet dessicated, due to their bad state of preservation, measuring of webbing formula is not possible; a small inner metatarsal tubercle is recognizable; toe disks shrunken, but probably originally well developed; toe length  $1 < 2 < 3 = 5 < 4$ . Skin on the upper surface smooth, throat and chest smooth, venter very granular, with larger granules posteriorly than anteriorly; ventral surface of thigh slightly granular, some distinct granules in the anal region. Coloration nearly completely faded. A brown band between the eyes is recognizable. Three light brown crossbands on the shank. For measurements see Table 2.

A photograph of the holotype of *difficilis* was given in Boettger (1913: pl. 29). A comparison of this picture with Figure 1 suggests that the specimen was already in a state of conservation not significantly better than today. No additional information which could be used for a diagnosis of *difficilis* from other *Boophis* is found in the original description (Boettger, 1892) nor in Boettger (1913).

There are obvious differences of the holotype to the

populations considered as *B. difficilis* by Blommers-Schlösser (1979b), Blommers-Schlösser & Blanc (1991), and Glaw & Vences (1992a,b, 1994). The distinctive states of the *difficilis* type are the following (states found in the populations previously attributed to *difficilis* given in parentheses): (1) lack of webbing between fingers (webbing between fingers present; Fig. 2); (2) first finger very short (Fig. 2); when fingers are adpressed, terminal disks of first and second fingers do not contact (first finger less short; when fingers are adpressed, terminal disks of first and second fingers do contact); (3) ventral skin heterogeneously granular, more coarse posteriorly than anteriorly (ventral skin homogeneously granular, posteriorly not coarse); (4) head slightly pointed in dorsal view (head rounded in dorsal view).

On the other hand, the *difficilis* type is similar by all characters mentioned above to *Boophis tephraeomystax*. Its size (28.7 mm SVL) comes very close to the smallest adult male of *B. tephraeomystax* measured by us (29.0 mm SVL). The type locality of *difficilis* is Foizana in eastern Madagascar. We did not find this locality on current maps. It seems to refer to Fizoana near Maroantsetra, near sea level (see also map in Blommers-Schlösser & Blanc, 1991). *Boophis tephraeomystax* is a common species in and near Maroantsetra (pers. obs.). As close direct comparison did not yield any distinctive features between the *difficilis* type and specimens of *B. tephraeomystax*, we hereby confirm Guibé's (1978) decision to include *difficilis* in the synonymy of *tephraeomystax*.

#### DEFINITION OF THE *BOOPHIS MAJORI* GROUP

Species groups in *Boophis* have always been named after the oldest included species (Blommers-Schlösser, 1979b; Blommers-Schlösser & Blanc, 1991; Glaw & Vences, 1994), as was done in species groups of other anuran genera (e.g. Duellman, 1970). *Rhacophorus difficilis* Boettger, 1892 is here considered as junior synonym of *Boophis tephraeomystax*. *Boophis difficilis* is therefore no longer available as a name for the phenetic species group that contains *Boophis majori*, *B. miniatus*, *B. blommersae* and *B. marojezensis*. The next oldest species is *B. majori* (Boulenger, 1896). We therefore dissolve the *B. difficilis* group and replace it by a newly created *B. majori* group in all following considerations.

The *B. majori* group is defined as follows within the genus *Boophis* (modified after Blommers-Schlösser & Blanc, 1991): (1) vomerine teeth present; (2) single subgular vocal sac in calling males; (3) webbing between external fingers more than 1/3 of their length; (4) shank longer than foot; (5) no dermal flaps or tubercles on heels; (6) legs with dark crossbands; (7) egg deposition and larval development mostly in running

**Table 2.** Morphometric measurements (all in mm) of the specimens considered in the present study. Status of specimens is given after the locality: HT – holotype, PT – paratype, LT – lectotype, PLT – paralectotype. TT – tibiotarsal articulation reaches (1) the eye, (2) between eye and nostril, (3) nostril, (4) between nostril and snout tip, (5) snout tip, (6) beyond snout tip, (7) well beyond snout tip

Locality	Collection number	SVL	HW	HL	Eye	Tym	Eye–Ns	Ns–St	Ns–Ns	ForL	HaL	HiL	FoTL	FoL	TT
<i>Rhacophorus difficilis</i> (male?)															
Foizana (HT)	SMF 6762	28.7	9.4	10.0	3.3	1.7	2.5	1.9	2.5	16.7	8.3	44.7	18.0	10.5	2
<i>B. tephraeomystax</i> (males)															
Nosy Be	MNHN 1994.1042	38.6	11.9	13.3	3.8	2.5	3.4	2.7	2.7	22.6	10.0	59.7	26.6	16.0	1
Madagascar (LT)	MNHN 1994.1040	38.2	11.6	12.3	4.3	2.6	3.3	2.2	2.7	22.7	10.3	57.2	24.1	14.0	2
Ankarana	ZFMK 62202	34.0	11.8	13.1	4.7	2.2	3.3	2.6	2.9	17.7	9.0	55.4	24.1	14.9	2
Ranohira	ZFMK 59863	35.9	12.3	13.1	4.4	2.6	3.2	2.9	3.2	21.4	10.2	57.0	24.9	15.5	3
Andasibe	ZFMK 60031	29.0	10.7	11.9	4.0	1.9	2.7	2.4	2.6	16.5	8.1	47.2	20.4	12.6	3
Tolagnaro	ZFMK 52650	40.2	14.2	14.8	4.6	2.9	3.7	2.8	3.4	24.0	11.4	65.4	28.8	18.5	3
Ambanja	ZFMK 52651	40.2	12.5	14.2	4.0	2.5	3.3	2.7	2.9	24.0	11.7	65.9	28.4	18.0	2
<i>B. majori</i> (males)															
Ambohitombo (LT)	BM 1947.2.7.67	23.7	8.5	8.8	3.3	1.6	2.0	1.6	2.1	15.1	7.4	39.0	17.0	10.0	2
Vohiparara	ZFMK 62672	21.6	7.5	7.5	2.7	1.3	1.7	1.7	1.7	14.0	6.9	37.6	16.2	9.5	6
Vohiparara	ZFMK 62673	21.5	8.1	7.8	3.0	1.4	1.5	1.6	2.2	15.4	7.1	38.6	16.6	9.6	6
Vohiparara	ZFMK 62674	21.5	8.1	8.2	2.8	1.8	1.8	1.8	2.0	14.5	6.8	39.1	16.9	10.1	6
Andringitra	ZFMK 57394	24.5	8.8	9.0	3.6	1.4	1.7	2.0	2.1	16.1	7.5	40.9	17.8	10.2	3
Andringitra	ZFMK 57395	23.8	8.4	9.0	3.4	1.5	1.8	1.7	2.2	15.3	7.2	41.4	17.0	10.3	5
Andringitra	ZFMK 57396	23.2	8.4	8.5	3.0	1.1	2.0	2.0	2.5	15.5	7.6	41.0	17.2	16.5	5
Andringitra	ZFMK 57397	24.0	8.3	8.5	3.2	1.3	1.8	1.8	2.4	14.6	7.6	41.0	17.3	10.3	2
<i>B. miniatatus</i> (males)															
Isaka-Ambobo (HT)	MNHN 1901.386	28.6	9.6	9.9	3.8	1.9	2.5	1.7	2.4	18.0	8.2	46.8	19.8	11.0	2
Pic St. Louis	ZFMK 52635	31.9	11.2	11.0	4.4	2.4	2.7	2.5	3.4	20.2	9.3	53.5	22.5	13.0	5
Pic St. Louis	ZFMK 53626	26.1	10.2	10.1	4.2	2.3	2.4	2.2	2.7	16.6	7.9	44.9	19.5	11.4	3
Pic St. Louis	ZFMK 53627	26.2	10.5	10.2	4.0	2.2	2.1	2.2	2.8	15.6	8.8	46.3	19.0	11.6	5
Nahampoana	ZFMK 53628	30.9	11.4	11.1	4.0	2.3	2.4	2.4	3.2	20.7	9.5	53.5	22.1	12.4	6
Nahampoana	ZFMK 53629	28.7	10.9	11.3	4.5	2.3	2.2	2.3	2.8	—	8.9	50.2	21.6	12.4	6
Nahampoana	ZFMK 53630	26.6	9.9	10.5	4.0	2.2	2.1	2.2	2.9	17.2	8.4	47.2	19.9	11.5	7
Nahampoana	ZFMK 53631	29.6	11.0	10.8	4.1	2.4	2.2	2.4	2.8	17.0	8.5	46.2	19.5	11.3	7
Ambatolahy	MRSN A323	23.8	8.6	8.8	3.6	1.5	2.1	1.6	2.2	15.5	7.3	41.1	18.0	11.0	3
Ifanadiana	MRSN A713	24.5	8.4	8.8	3.5	1.8	1.8	1.8	2.4	15.2	7.7	44.0	18.2	10.6	6
Ifanadiana	MRSN A1646.2	24.6	8.3	8.6	3.1	1.8	1.7	1.6	2.1	15.0	7.4	43.7	18.0	10.4	7
Ifanadiana	MRSN A1646.3	25.1	9.0	9.1	3.3	1.7	1.8	1.9	2.1	14.8	7.3	42.3	18.7	10.8	6
Ifanadiana	MRSN A1646.4	23.1	7.8	8.2	3.2	1.6	2.0	1.6	2.2	15.1	7.2	41.6	16.1	9.1	7
Ifanadiana	MRSN A1646.5	24.1	8.2	8.6	3.4	1.7	1.8	1.8	2.2	14.7	7.3	42.6	17.3	10.0	6
Ifanadiana	MRSN A1646.6	25.5	8.7	9.3	3.5	2.0	1.8	1.9	2.4	16.1	7.6	43.8	18.3	10.5	5

continued

Table 2 – continued.

Locality	Collection number	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	Ns-Ns	ForL	HaL	HiL	FoTL	FoL	TT
<i>B. blommersae</i> (males)															
M. d' Ambre (HT)	ZFMK 57398	24.3	8.6	8.7	3.3	1.4	1.7	1.7	1.9	14.7	7.3	39.5	17.9	10.3	3
M. d' Ambre (PT)	ZFMK 57399	24.8	9.2	9.2	3.3	1.5	2.0	1.7	2.5	15.2	7.6	40.6	17.5	10.7	3
M. d' Ambre (PT)	ZSM 562/1999	24.6	9.4	8.8	3.5	1.4	1.7	1.8	2.5	14.7	7.6	40.9	17.5	10.6	3
Les Roussettes	MNHN 1975.2469	26.5	9.8	8.9	3.5	1.7	2.2	2.2	2.7	16.3	7.9	43.8	17.6	10.9	3
Les Roussettes	MNHN 1975.2470	24.7	9.4	8.4	3.5	1.5	2.2	2.1	2.8	14.9	6.6	42.1	17.5	10.3	4
<i>B. marojezensis</i> (males)															
Marojezy (HT)	ZFMK 57401	25.7	9.7	9.8	3.4	1.3	2.0	2.2	2.7	15.0	7.6	43.2	17.9	10.3	3
Marojezy (PT)	ZSM 567/1999	24.9	9.5	9.2	3.8	1.4	2.0	2.0	3.0	14.4	7.4	43.8	18.1	10.4	5
Marojezy	ZFMK 59956	25.6	10.3	9.9	3.5	1.3	2.4	2.2	2.4	17.1	7.9	44.8	19.0	11.1	3
Marojezy	MNHN 1975.2471	22.9	8.9	8.8	3.9	1.6	2.1	1.8	2.5	15.9	7.1	39.3	16.9	9.6	3
Besariaka	MRSN A1841	27.0	9.6	9.5	3.6	1.4	2.0	2.0	2.5	16.3	8.5	45.7	19.2	11.6	3
Besariaka	MRSN A1842	26.9	9.8	9.8	3.5	1.6	2.2	2.0	2.4	17.6	8.7	45.4	20.3	11.6	3
Besariaka	MRSN A1840.1	22.6	8.1	8.2	2.7	1.2	1.7	1.7	2.1	14.5	6.6	36.8	16.6	9.8	3
Besariaka	MRSN A1840.2	22.8	8.1	8.2	3.2	1.2	1.7	1.6	2.2	14.7	7.4	38.9	16.4	9.9	5
Besariaka	MRSN A1839.2	21.7	8.1	7.8	3.1	1.2	1.7	1.7	2.0	14.9	7.5	38.5	16.2	9.6	5
Besariaka	MRSN A1839.3	22.7	8.2	8.1	3.2	1.1	1.8	1.8	2.3	15.6	7.4	39.6	17.3	9.1	6
Besariaka	MRSN A1839.4	22.8	7.9	8.1	3.0	1.3	1.6	1.7	2.3	14.7	7.3	38.4	16.5	9.4	6
Besariaka	MRSN A1839.5	22.2	7.7	7.9	3.0	1.1	1.7	1.8	2.1	15.4	7.2	40.3	16.4	9.8	7
Besariaka	MRSN A1839.6	23.6	8.7	8.6	2.9	1.2	1.7	1.8	2.5	15.6	7.5	42.7	17.7	10.3	7
Besariaka	MRSN A1839.7	21.8	7.8	8.3	3.1	1.4	1.8	1.7	2.2	14.9	6.8	37.3	16.2	9.9	6
Tsararano	MRSN A1838	20.7	7.6	7.8	3.2	1.2	1.8	1.8	2.1	14.2	6.8	38.8	16.4	9.4	7
Tsararano	MRSN A1837	23.9	8.1	8.3	3.0	1.2	1.9	1.7	2.0	13.2	7.8	37.3	15.6	9.3	1
Tsararano	MRSN A1835.2	23.4	7.9	8.1	3.1	1.1	1.6	1.9	2.2	14.4	7.1	40.4	17.2	10.2	3
Tsararano	MRSN A1835.1	23.6	8.0	8.3	3.0	1.2	1.7	1.9	2.2	15.0	7.5	40.5	16.1	9.2	3
Tsararano	MRSN A1834	21.8	7.5	7.9	3.0	1.4	1.6	1.6	2.2	14.7	6.7	38.1	15.4	8.6	6
Anjanaharibe	MRSN A1833.1	25.4	9.4	9.6	2.9	1.4	1.9	2.0	2.3	16.4	8.0	43.5	17.6	10.4	3
Anjanaharibe	MRSN A1833.2	25.8	9.1	9.5	3.0	1.5	2.0	1.8	2.2	15.7	7.9	41.9	17.5	10.3	3
Ambanizana	MRSN A1831.1	22.7	8.3	8.5	3.2	1.2	1.5	1.8	2.0	14.5	7.0	39.4	15.3	8.8	2
Ambanizana	MRSN A1831.2	22.7	8.1	8.5	3.4	.9	1.5	1.6	1.9	13.2	7.0	38.9	16.0	9.3	5
Ambanizana	MRSN A1831.3	23.0	8.2	8.5	3.2	1.1	1.8	1.8	2.3	15.0	6.9	40.2	17.0	9.0	5
Ambanizana	MRSN A1831.4	23.1	8.2	8.6	3.3	1.2	1.7	1.8	2.4	14.2	7.5	39.3	16.8	9.8	3
An'Ala	ZFMK 60085	21.3	7.9	7.9	2.7	1.2	1.6	1.6	2.2	15.2	7.2	39.6	16.2	9.3	7
An'Ala	ZFMK 60086	21.3	8.1	8.9	3.1	1.1	1.8	1.7	2.2	14.0	6.9	39.3	16.0	9.2	7
An'Ala	ZFMK 60087	21.9	8.0	8.0	3.1	1.2	1.8	1.9	2.1	14.7	6.8	39.7	16.0	8.8	6
An'Ala	ZFMK 60088	22.5	7.9	8.2	3.3	1.2	1.7	1.6	2.1	14.2	6.8	38.3	16.2	9.6	6
An'Ala	ZFMK 60089	21.5	7.6	7.6	3.0	.9	1.6	1.6	1.9	15.0	6.5	38.6	15.6	8.9	7

continued

Table 2 – continued.

Locality	Collection number	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	Ns-Ns	ForL	HaL	HiL	FoTL	FoL	TT
Mandraka?	MNHN 1984.11	22.3	9.0	8.7	3.4	1.6	1.9	2.0	2.3	15.2	7.1	41.2	18.7	11.9	7
Mandraka	ZMA 7104 (1136)	24.4	8.5	8.7	2.8	1.2	1.8	1.9	2.2	15.6	8.7	42.9	18.0	11.3	3
Mandraka	ZMA 7104 (1142)	23.8	8.6	8.5	2.8	1.2	1.8	1.8	2.1	15.6	8.0	41.1	17.6	10.2	6
Mandraka	ZMA 7104 (1134)	25.2	8.8	9.0	3.0	1.3	1.9	2.0	2.2	16.7	8.3	44.7	19.2	11.3	6
Mandraka	ZMA 7104 (1139)	24.0	9.0	9.1	3.0	1.1	1.8	2.1	2.3	16.4	8.0	40.3	18.2	10.6	5
Mandraka	ZMA 7103 (1042)	23.1	8.6	8.6	2.7	1.3	2.0	2.0	2.4	16.1	8.3	42.5	18.0	10.8	3
Mandraka	ZMA 7103 (1048)	23.9	9.0	8.8	3.1	1.2	1.7	1.8	2.3	15.2	8.1	43.1	18.0	11.3	5
Mandraka	ZMA 7103 (1045)	23.4	8.6	9.0	3.0	1.1	2.1	2.0	2.5	14.7	7.7	43.9	18.6	10.9	6
Ranomafana	ZFMK 62300	23.0	8.3	8.5	3.2	1.3	1.3	1.5	2.1	16.2	7.6	39.2	17.1	9.9	3
Vohiparara	MRSN A658	22.0	8.1	8.2	3.1	1.6	1.7	1.6	2.0	14.7	7.5	40.0	16.9	9.8	6
Vohiparara	MRSN A1650	20.0	7.3	7.6	3.1	1.6	1.7	1.5	2.2	13.4	6.6	37.1	15.5	9.0	5
<i>B. pyrrhus</i> (males)															
Andasibe (PT)	ZFMK 52633	26.9	10.3	10.5	3.2	1.4	2.4	2.0	2.7	16.4	8.2	47.5	20.1	11.7	6
Andasibe (HT)	ZSM 582/1999	28.2	9.9	10.6	3.7	1.4	2.6	2.1	2.4	17.5	8.8	49.2	20.3	11.9	6
Andasibe (PT)	ZFMK 59865	26.8	9.8	9.4	3.4	1.5	2.5	2.0	2.7	17.1	8.5	48.0	19.6	11.4	6
Andasibe (PT)	MRSN A278	27.8	10.3	10.8	3.7	1.6	2.5	2.1	2.6	16.8	8.6	47.5	20.4	11.8	5
Andasibe (PT)	ZMA 7099 (1029)	31.6	10.4	11.0	3.8	1.7	2.4	2.2	2.6	19.1	9.3	49.1	21.6	12.8	3
Andasibe (PT)	ZMA 7099 (1030)	27.6	9.4	10.0	3.6	1.3	2.4	2.0	2.4	17.8	9.0	49.5	22.2	12.9	6
Andasibe (PT)	ZMA 7099 (1028)	28.3	9.8	10.5	4.0	1.5	2.2	2.0	2.7	16.3	8.1	44.5	18.7	11.6	1
Andasibe (PT)	ZMA 7099 (1031)	28.2	10.0	10.4	3.6	1.3	2.4	2.2	2.2	17.4	8.6	48.6	21.1	12.5	6
Andasibe (PT)	ZMA 7099 (1032)	28.7	10.0	10.6	3.5	1.5	2.4	2.2	2.4	18.1	8.5	48.5	20.6	12.0	6
Andasibe (PT)	ZMA 7099 (1027)	28.4	9.8	10.5	3.8	1.4	2.2	2.0	2.8	20.2	8.9	48.0	20.6	12.0	3
Andasibe (PT)	ZMA 7098 (952)	26.1	9.0	9.8	3.6	1.5	2.5	2.1	2.3	17.0	8.8	46.3	19.5	10.8	6
Ifanadiana	MRSN A367	28.7	10.0	10.4	3.5	1.3	2.4	1.8	2.2	17.7	8.8	47.8	21.3	12.4	5
<i>B. haematopus</i> (males)															
Nahampoana (HT)	ZSM 583/1999	26.8	10.1	10.3	4.2	1.3	2.2	2.4	2.7	17.1	8.3	46.2	19.4	11.7	5
Nahampoana (PT)	ZFMK 53633	25.4	9.8	9.9	3.9	1.4	2.1	2.0	3.0	15.7	8.1	46.3	19.2	11.4	6
Nahampoana (PT)	ZFMK 52634	28.2	—	—	—	1.3	—	—	—	17.6	7.9	46.8	18.8	10.8	6
Andohahela (PT)	MRSN A725.1	28.3	10.3	10.9	3.7	1.7	2.1	2.1	2.7	18.3	9.0	48.5	20.8	12.6	4
Andohahela (PT)	MRSN A725.2	26.0	9.2	9.3	3.9	1.7	1.6	1.7	2.3	17.3	8.3	44.3	29.4	11.7	5
Andohahela (PT)	MRSN A1591.1	25.4	9.5	9.6	3.2	1.6	1.8	2.1	2.7	17.0	8.7	42.5	19.0	11.2	3
Andohahela (PT)	MRSN A1591.2	26.4	9.1	9.6	3.4	1.5	2.0	1.9	2.5	17.2	8.3	46.3	17.4	11.1	5
<i>B. picturatus</i> (males)															
An'Ala (HT)	ZSM 584/1999	27.7	10.1	10.3	4.0	2.0	2.2	2.1	2.8	18.4	9.2	51.2	22.0	12.8	6
Andasibe (PT)	ZFMK 52636	30.8	11.2	11.2	3.3	2.0	2.6	2.5	2.7	19.7	9.2	52.2	22.5	13.2	5
Andasibe (PT)	ZFMK 60021	30.0	10.7	11.2	3.7	1.8	2.4	2.4	3.0	18.7	9.5	51.8	21.7	13.0	4
Andasibe (PT)	ZFMK 60022	28.7	10.5	11.1	3.7	2.0	2.4	2.2	3.2	17.8	9.2	51.0	21.7	12.5	6

continued

Table 2 – continued

Locality	Collection number	SVL	HW	HL	Eye	Tym	Eye-Ns	Ns-St	Ns-Ns	ForL	HaL	HiL	FoTL	FoL	TT
Andasibe (PT)	ZFMK 60023	27.4	10.0	10.5	3.6	1.9	2.5	2.2	2.9	16.7	8.4	48.0	20.5	12.0	5
An'Ala (PT)	ZFMK 62261	27.8	10.7	10.9	3.9	1.7	2.7	2.4	3.0	17.1	8.3	49.1	20.5	11.8	6
Andasibe	ZMA 7163 (953)	33.3	12.0	12.4	4.2	2.5	2.4	2.7	3.4	20.3	10.0	54.5	24.2	14.2	2
Andasibe	ZMA 7162 (657)	30.1	10.3	10.9	4.0	2.1	2.2	2.2	3.2	16.2	8.9	47.2	20.5	12.0	1
Andasibe	ZMA 7162 (714)	30.4	11.1	11.2	4.2	2.5	2.2	2.4	3.1	18.6	9.5	51.3	21.7	12.5	1
Vohiparara	ZFMK 62282	26.3	9.7	10.0	3.7	2.0	2.1	1.9	2.3	17.1	8.0	44.2	17.6	11.3	3
Vohiparara	ZFMK 62283	26.2	10.4	10.3	3.6	2.0	1.9	2.0	2.6	15.5	7.7	45.0	18.8	10.6	4
Vohiparara	ZFMK 62284	25.8	9.9	10.0	3.4	2.1	2.0	2.2	2.6	17.0	8.2	45.1	19.3	11.8	3
Vohiparara	ZFMK 62302	22.8	8.6	6.9	2.9	1.3	2.0	1.8	2.2	14.9	7.1	40.7	16.7	9.5	6
<i>B. feonyala</i> (males)															
Andasibe (HT)	ZSM 585/1999	25.1	9.2	9.0	3.8	1.7	2.1	2.1	2.7	15.1	7.0	42.6	17.6	10.3	4
Andasibe (PT)	ZFMK 60004	25.0	9.0	9.1	3.9	1.6	2.1	2.0	2.4	15.2	7.5	43.4	18.4	11.0	4
Andasibe (PT)	ZFMK 60005	25.4	8.9	9.3	3.7	1.6	2.3	2.2	2.4	17.1	7.9	46.3	19.9	11.4	6
Andasibe (PT)	ZFMK 60006	25.3	9.6	9.4	3.7	1.6	2.4	2.0	2.5	15.6	8.0	41.1	18.0	10.4	2
<i>B. vittatus</i> (males)															
Marojejy (HT)	ZSM 586/1999	24.1	9.1	8.9	3.6	1.6	2.0	2.0	2.2	15.4	7.2	41.5	17.5	9.9	7
Marojejy (PT)	ZFMK 59890	24.1	8.5	8.9	3.6	1.6	2.1	1.7	2.1	14.6	6.8	39.5	16.4	9.3	5
Marojejy (PT)	ZFMK 59891	23.1	8.0	8.1	3.1	1.4	2.1	1.8	2.2	12.8	6.7	37.8	16.0	9.4	2
Marojejy (PT)	ZFMK 59892	23.8	8.4	8.4	3.7	1.3	2.1	1.6	2.1	14.6	6.8	38.3	15.7	8.6	5
Marojejy (PT)	ZFMK 60121	25.4	8.6	8.8	3.6	1.3	2.0	1.7	2.3	14.8	7.1	40.9	16.4	9.2	3
Marojejy (PT)	ZFMK 60122	24.7	8.9	8.8	3.8	1.1	1.8	1.8	2.4	15.1	7.0	40.3	17.3	10.1	3
<i>B. tephraeomystax</i> (females)															
Madagascar (PLT)	MNHN 4584	49.1	15.7	16.8	5.2	2.6	4.5	3.6	3.8	28.6	13.6	77.8	35.5	20.9	1
Nosy Be	MNHN 1660	46.5	15.1	15.8	4.9	2.8	4.3	2.9	3.0	30.4	13.4	75.9	34.2	20.4	3
Nosy Be	MNHN 1994.1041	40.6	14.6	15.2	4.1	2.4	3.8	2.9	3.3	26.4	12.0	69.7	31.1	18.1	3
<i>B. majori</i> (females)															
Vohiparara	ZFMK 62675	29.0	10.3	9.7	3.3	1.9	2.3	2.1	2.2	19.5	9.8	—	—	—	—
Ambohitombo (PLT)	BM 1947.2.7.66	29.2	10.0	10.0	3.6	1.6	2.0	1.7	2.0	18.5	8.5	47.7	20.2	11.9	2
<i>B. miniatus</i> (females)															
Ifanadiana	MRSN A1646.1	35.3	12.1	12.5	3.8	2.0	2.9	2.4	3.3	21.0	10.2	60.0	25.2	15.0	3
unknown locality	ZFMK 48166	37.7	13.9	14.3	4.2	2.3	3.2	3.0	3.8	21.7	10.8	56.3	25.3	14.9	2
<i>B. marojezensis</i> (females)															
Mandraka	ZMA 7103 (1044)	31.8	11.8	11.7	3.8	1.6	2.5	2.6	3.0	21.3	10.5	55.8	24.9	14.9	2
Besariaka	MRSN A1839.1	33.0	11.6	11.7	3.9	1.9	2.6	2.6	3.2	19.3	10.2	53.7	23.3	13.4	3
<i>B. pyrrhus</i> (female)															
Andasibe (PT)	ZFMK 59866	37.0	13.2	14.0	4.3	1.7	3.3	3.5	3.9	23.4	11.2	60.9	26.7	15.4	3s





**Figure 1.** Ventral and dorsal views of (A,B) the holotype of *Boophis difficilis* (SMF 6762) and (C,D) a paratype of *Boophis pyrrhus* (ZFMK 59865) which was previously considered as *Boophis difficilis* according to Blommers-Schlösser (1979b). Note the differences in head shape, relative length of second and third finger, and ventral skin granules.

water; (8) dorsal integument of breeding males not more granular than of females; (9) SVL of adult males 21–33 mm; (10) dorsal ground coloration brownish

(without green); (11) weakly developed canthus rostralis; (12) venter whitish or reddish (not transparent). Some other characters are typical for several but not



**Figure 2.** Hand of (A) the holotype of *Rhacophorus difficilis* (SMF 6762) and (B) a paratype of *Boophis pyrrius* (ZFMK 59865) in ventral view. Note the absence of webbing in the *difficilis* type.

all species of the group: (13) tibiotarsal articulation often reaches beyond snout tip (at least in some specimens of all species treated here except *B. blommersae*); (14) webbing or other areas of the skin with distinct red pigments; (15) often a dark dorsal hourglass marking.

In the diagnoses of each of the following species accounts, we first give a general statement of the diagnostic features of the corresponding species. Then, we provide a comparison with all species which had already been treated in the previous accounts. In these pairwise comparisons, we do not emphasize all faint differences which may exist, but focus on up to three main characters (beside advertisement calls which alone would suffice to clearly characterize each of the species) which can be used for diagnosis. Original measurements of all specimens are given in Table 2, morphometric ratios of the different species in Table 3, and details of webbing formulae in Table 4.

## SPECIES ACCOUNTS

### *BOOPHIS MAJORI* (BOULENGER, 1896)

#### *Identity*

*Boophis majori* was described as *Rhacophorus majori* based on a syntype series from Ambohimombo in eastern Madagascar. Blommers-Schlösser (1979b)

designated a lectotype and assigned specimens collected at Mandraka to this species. There are no detailed call data from the Mandraka population, but available evidence indicates that it does not belong to *B. majori* but to *B. marojezensis*, as will be discussed below. Other species that have been confused with *B. majori* are *B. miniatus* and *B. blommersae* (see below). Glaw & Vences (1994) assigned specimens from a mid-altitude locality in the Andringitra mountains to *B. majori*, mainly relying on coloration and size. Recently F. G. found new specimens of the Andringitra form, including one female, at Vohiparara (near Ranomafana). In fact, the dorsal coloration and morphology of some specimens from these two populations are very similar to the *majori* types (especially to the female paralectotype BM 1947.2.7.66: rather uniformly beige back; reddish coloration above the eyes). Based on these similarities we consider the populations from Andringitra and Vohiparara (Fig. 3) as *Boophis majori*.

#### *Diagnosis*

Characterized by the structure (Fig. 4) and low frequency of its vocalizations (dominant frequency of 2950–3650 Hz, versus 3650–c. 7000 Hz in the other species) and by its golden-yellow iris coloration with a blue-green or green-grey iris periphery in life. At least

**Table 3.** Morphometric ratios of males in the species of the *B. majori* group and *B. tephraeomystax*. Calculated according to original data presented in Table 2

Species	N	SVL	Tym/Eye	Eye–Ns/Ns–St	HiL/SVL	FoL/SVL	HaL/SVL
<i>Rhacophorus difficilis</i> HT	1	28.7	0.52	1.32	1.56	0.37	0.29
<i>B. tephraeomystax</i>	7	36.6±4 29.0–40.2	0.58±0.08 0.47–0.66	1.26±0.13 1.1–1.5	1.59±0.05 1.5–1.64	0.43±0.03 0.37–0.46	0.28±0.01 0.26–0.29
<i>B. majori</i>	8	23.0±1.3 21.5–24.5	0.46±0.09 0.37–0.64	0.98±0.07 0.85–1.06	1.75±0.05 1.67–1.82	0.48±0.1 0.42–0.71	0.32±0.01 0.3–0.33
<i>B. miniatus</i>	15	26.6±2.7 23.1–26.6	0.53±0.04 0.42–0.59	1.06±0.16 0.92–1.47	1.73±0.07 1.56–1.8	0.42±0.02 0.38–0.46	0.30±0.01 0.29–0.34
<i>B. blommersae</i>	5	25.0±0.9 24.3–26.5	0.44±0.03 0.40–0.49	1.03±0.09 0.94–1.18	1.66±0.03 1.63–1.7	0.42±0.01 0.41–0.43	0.30±0.02 0.27–0.31
<i>B. marojezensis</i>	41	23.2±1.6 20.0–27.0	0.40±0.06 0.26–0.52	0.99±0.08 0.83–1.17	1.75±0.07 1.56–1.88	0.43±0.03 0.39–0.53	0.32±0.02 0.29–0.36
<i>B. pyrrhus</i>	12	28.1±1.4 26.1–31.6	0.40±0.03 0.36–0.45	1.17±0.08 1.09–1.33	1.71±0.08 1.55–1.79	0.43±0.02 0.41–0.47	0.31±0.01 0.29–0.34
<i>B. haematopus</i>	7	26.6±1.2 25.4–28.3	0.42±0.07 0.31–0.5	0.97±0.08 0.86–1.05	1.72±0.05 1.66–1.82	0.43±0.02 0.38–0.45	0.31±0.02 0.28–0.34
<i>B. picturatus</i>	13	26.3±2.7 22.8–33.3	0.54±0.06 0.44–0.62	1.03±0.09 0.89–1.14	1.72±0.07 1.57–1.85	0.43±0.02 0.4–0.46	0.31±0.01 0.29–0.33
<i>B. feonnyala</i>	4	25.2±0.2 25.0–25.4	0.43±0.02 0.41–0.45	1.07±0.09 1–1.2	1.72±0.08 1.62–1.82	0.43±0.02 0.41–0.45	0.30±0.02 0.28–0.32
<i>B. vittatus</i>	6	24.2±0.8 23.1–25.4	0.39±0.07 0.29–0.45	1.15±0.13 1–1.31	1.64±0.04 1.61–1.72	0.39±0.02 0.36–0.41	0.29±0.01 0.28–0.3

**Table 4.** Comparative amount of webbing on some fingers and toes on which interspecific differences were noted within the *B. majori* group. The webbing extension is given as number of phalanges free of webbing, not counting the terminal disks (as in the webbing formula notation of Blommers-Schlösser, 1979a)

Species	Hand 3e	Hand 4	Foot 1	Foot 3e	Foot 5
<i>B. majori</i>	1.5	1	0–0.5	0.5	0.500
<i>B. blommersae</i>	2	1.5	0.25	0.5	0.5
<i>B. marojezensis</i>	2	1–1.5	0.25–0.5	0.5	0.5
<i>B. miniatus</i>	1.5–2	1	0–0.5	0–0.5	0–0.25
<i>B. pyrrhus</i>	2	1	0–0.5	0–0.5	0.5
<i>B. haematopus</i>	1.5	1	0	0	0.5
<i>B. vittatus</i>	2	1	0–0.5	0	0.5
<i>B. feonnyala</i>	1.5	1	0.25	0–0.5	0
<i>B. picturatus</i>	1.5	1	0.5	0–1	0.5

some red colour on the ventral part of feet and legs is present. Distinguished from *Boophis rhodoscelis* by the lack of a distinct canthus rostralis and from *B. cf. rhodoscelis* by different calls (see Glaw & Vences, 1997a).

*Distribution*

The species is known from three localities in central eastern Madagascar (latitudinal range 20°43'–22°07'S, altitudinal range 1000–1200 m above sea level). Type locality: Ambohitombo forest (lectotype BM

1947.2.7.67; paralectotypes 1947.2.7.66 and two additional specimens according to Blommers-Schlösser, 1979b). Other localities: forest near Ambalamarina, Andringitra mountains (ZFMK 57394–57397); Vohi-parara (ZFMK 62672–62675).

Five localities included in Blommers-Schlösser & Blanc (1991) must be discussed here: Mandraka is based on specimens collected by Blommers-Schlösser (1979b) which are here referred to *B. marojezensis*. The locality Les Roussettes (Montagne d'Ambre) probably refers to two specimens (MNHN 1975.2469 and 1975.2470) which differ from *B. majori* by larger SVL

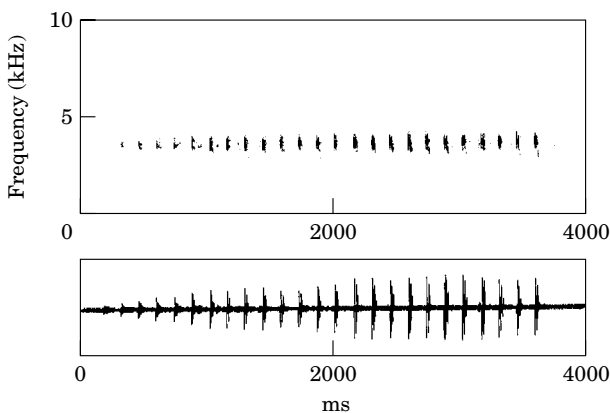


**Figure 3.** *Boophis majori*, specimen from Vohiparara (ZFMK 62675).

and dorsal coloration; they are here referred to *B. blommersae*. The locality Marojezy probably is based on one specimen (MNHN 1975.2471) which is here referred to *B. marojezensis*. The two localities Ankaratra and Chaines Anosyennes cannot be attributed at present to any species since we found no vouchers for these localities in the MNHN or ZMA, although most localities of Blommers-Schlösser & Blanc (1991) refer to these collections (Blommers-Schlösser, pers. comm.). We propose to delete these two localities as distribution records of *B. majori* until new data become available.

#### Morphology and coloration

Measurements and morphometric ratios of the lectotype, one paralectotype and eight specimens held in the ZFMK collection are given in Tables 2 and 3. Webbing formula between fingers is (SH) II 2–3<sup>+</sup> III



**Figure 4.** Sonagram and oscillogram of a call of *Boophis majori* from Andringitra. The call consists of a series of notes of type 1. Recorded on 15 January 1994 at c. 18°C.

2<sup>+</sup>–2 IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(1.5), 4(1); webbing formula between toes is (SH) I (1-1<sup>+</sup>)–(1<sup>+</sup>-2) II 1–(1-2<sup>+</sup>) III 1<sup>+</sup>–(2<sup>+</sup>-3) IV (2<sup>+</sup>-3)–(1-1<sup>+</sup>) V respectively (BS) 1(0-0.5), 2i(0.5-1), 2e(0), 3i(1-1.5), 3e(0.5), 4i(1.5-2), 4e(1.5-2), 5 (0-0.5).

Life coloration (after photographs of at least four males and one female) on head, dorsum and dorsal side of the legs beige to dark brown (with dispersed fine dark pigment). Sometimes dark spots and/or some small white spots on the dorsal surface. Grey crossbands on the hindlegs generally present, but sometimes indistinct. Chest and venter white, throat translucent grey-blue in males, white in one female (ZFMK 62675). Ventral surface of hands, feet, webbing, shank and thigh with different extension of red colour. In the female the red areas are especially extended, whereas in one male the red colour is less distinct and restricted to the ventral side of the thigh. Iris golden-yellow (sometimes with beige or brown colour around the pupil) and with a blue-green or green-grey iris periphery in life. A colour photograph of a male from Andringitra is published in Glaw & Vences (1994: plate 17).

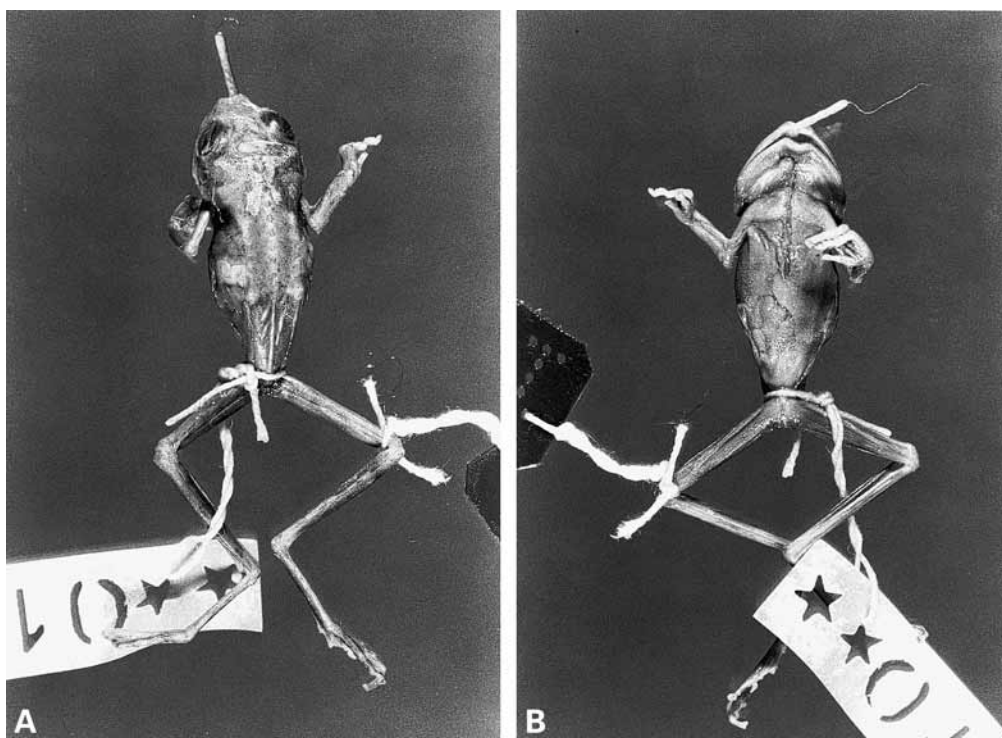
#### Habits

Calling activity was observed at night in January and March along brooks in primary forest from branches 2–4 m above the ground. One couple from Vohiparara laid a clutch of dark eggs the 5 March 1996. One day later embryonic development was already recognizable.

#### Call

A short description of calls from Andringitra (recorded 15 January 1994 at c. 18°C air temperature) was provided by Glaw & Vences (1994). New recordings are available from Vohiparara (recorded 3 March 1996 at c. 22°C). Three note types can be distinguished.

Type 1 is an unharmonious note with a duration of 19–33 ms (mean  $29 \pm 3$  ms,  $N=24$ ) in Andringitra and 23–53 ms (mean  $33 \pm 10$  ms,  $N=11$ ) in Vohiparara. Notes are arranged in series; duration of intervals between notes is 108–130 ms (mean  $115 \pm 6$  ms,  $N=23$ ) in Andringitra and 102–205 ms (mean  $133 \pm 31$  ms,  $N=10$ ) in Vohiparara. Note repetition rate is 6.3/s in Andringitra and 5.5/s in Vohiparara. There are 26–47 ( $N=2$ ) notes per call in Andringitra and 11–12 ( $N=2$ ) in Vohiparara, duration of a note series is 3800–7593 ms ( $N=2$ ) in Andringitra and 1675–2634 ms (mean  $2272 \pm 426$  ms,  $N=5$ ) in Vohiparara. Frequency is 2700–4050 Hz (dominant frequency 3300–3650 Hz) in Andringitra and 2350–3950 Hz (dominant frequency 3000–3250 Hz) in Vohiparara. Notes from Andringitra consist of three distinct pulses whereas pulses are only faintly distinguishable in notes from Vohiparara. Pulse



**Figure 5.** Holotype of *Boophis miniatus* (MNHN 1901.386); (A) dorsal, and (B) ventral view.

duration (Andringitra) is 3–8 ms ( $N=12$ ), duration of intervals between pulses is also 3–8 ms ( $N=8$ ).

Type 2 is a longer unharmonious note which is also arranged in series. Recordings from Andringitra were too noisy to allow a detailed analysis. At Vohiparara note duration is 189–236 ms (mean  $214 \pm 12$  ms,  $N=25$ ), duration of intervals between notes is 196–280 ms (mean  $233 \pm 25$  ms,  $N=24$ ), duration of a note series is up to more than 8000 ms, notes per call are up to more than 17, note repetition rate is 2.1–2.3/s. Frequency is 2250–4150 Hz, dominant frequency is 2950–3250 Hz. Intensity of notes of type 2 is high at the beginning of the note and decreases towards the end of the note.

Type 3 is a short click which is given isolated or at the end of a series of note type 2. Duration of one such note is 21 ms, frequency is 2500–3950 Hz, dominant frequency is 3150–3350 Hz.

#### *BOOPHIS MINIATUS* (MOCQUARD, 1902)

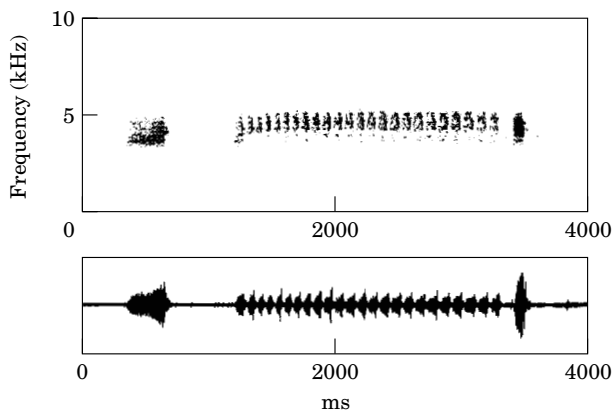
##### *Identity*

*Boophis miniatus* was described as *Rhacophorus miniatus* based on a single specimen (Fig. 5) collected in a forest between Isaka and the valley of Ambobo, near Tolagnaro in southeastern Madagascar. Glaw & Vences



**Figure 6.** *Boophis miniatus*; specimen from the base of Pic St. Louis near Tolagnaro (ZFMK 52635).

(1992a,b) considered specimens collected near Tolagnaro (Fig. 6) as belonging to this species. Morphometrically, all these specimens correspond well with the holotype of *B. miniatus* by having a relatively large SVL, and by a large relative tympanum size (Tables 2, 3). Also, the type locality is located close to Tolagnaro.



**Figure 7.** Sonagram and oscillogram of a call of *Boophis miniatus* from the base of Pic St. Louis (near Tolagnaro). The call consists of one note of type 3, followed by a series of notes of type 1 and one note of type 2. Recorded on 1 January 1992 at 23°C.

#### Diagnosis

Characterized by its vocalizations (series of 18–28 unharmonious notes with a note repetition rate of 11–12/s and a dominant frequency of 4400–4800 Hz, see Fig. 7). The relative tympanum size of *B. miniatus* has the largest mean value found in the *B. majori* group (Table 3). Most measured specimens have a tympanum/eye ratio larger than 0.5 (below 0.5 only in one out of 15 measured male specimens, Table 2), a value only occasionally found in other species of the *B. majori* group (see comparisons in the species accounts below). Distinct red colour on the webbing between toes is present in *B. miniatus*. The species is further distinguished from *B. majori* by tympanum size (only one out of eight measured males of *B. majori* had a tympanum/eye ratio above 0.5), and by its generally reddish outer iris coloration (vs. uniformly golden-yellow iris in *B. majori*).

#### Distribution

The species is known from four localities in central eastern and south-eastern Madagascar (latitudinal range 21°15'–25°00'S, altitudinal range <300–800 m above sea level). Type locality: forest between Isaka and Ambobo [Ambolo] according to Blommers-Schlösser & Blanc (1991), holotype MNHN 1901.386 (no paratypes). Specimens collected near the type locality are ZFMK 52635 and ZFMK 53626–53627 (from the base of Pic St. Louis near Tolagnaro) and ZFMK 53628–53631 (from Nahampoana).

The records from the Ranomafana area given by Andreone (1994) are corroborated by the voucher specimens MRSN A323 from Ambatolahy and A713 and A1646.1–6 from Ifanadiana. These specimens show a characteristic coloration (uniformly beige back with

small black spots) also seen in one specimen from Nahampoana (ZFMK 53626), and a large relative tympanum size. In some body proportions and SVL, however, they differ from the Tolagnaro series. We consider them tentatively as subadult specimens (males) and attribute them to *B. miniatus*, since the single female from Ifanadiana (MRSN A1646.1) is similar in body proportions to specimens from the Tolagnaro region.

Raxworthy & Nussbaum (1994) recorded *B. miniatus* at Montagne d'Ambre based on own voucher specimens and on MNHN 1975–2469 and 1975–2470. This record is clearly due to confusion with *Boophis blommersae* (see below). Raxworthy & Nussbaum (1996a) recorded *B. miniatus* for Andringitra, but did not record *B. majori* from this locality. Taking into account the difficult taxonomic situation in the *B. majori* group, and the fact that the same authors obviously confused also *B. blommersae* with *B. miniatus* (see below), we do not consider the record of *B. miniatus* from Andringitra until morphological and bioacoustic data of the corresponding vouchers (probably in UMMZ) are presented.

Two male specimens collected by R. Blommers-Schlösser near Andasibe (ZMA 7162) are here referred to *B. picturatus* based on their iris coloration (see below).

#### Morphology and coloration

Measurements and morphometric ratios of the holotype and 16 specimens held in the ZFMK, MRSN and ZMA collections are given in Tables 2 and 3. Webbing formula between fingers is (SH) II (2-2<sup>+</sup>)–3<sup>+</sup> III (2<sup>+</sup>–3)–2 IV respectively (BS) 1(-), 2i(-), 2e(1-1.5), 3i(2.5), 3e(1.5-2), 4(1); webbing formula between toes is (SH) I (1-1<sup>+</sup>)–(1<sup>+</sup>-2) II 1–(2-2<sup>+</sup>) III (1-1<sup>+</sup>)–2<sup>+</sup> IV (2<sup>+</sup>-3)–(1-1<sup>+</sup>) V respectively (BS) 1(0-0.5), 2i(0.5-1), 2e(0), 3i(1-1.5), 3e(0-0.5), 4i(1.5), 4e(1.25-2), 5(0-0.25).

Life coloration (after photographs of at least six males) on head, dorsum and dorsal side of the legs beige to reddish brown (sometimes with dispersed fine dark pigment). Yellowish dorsolateral bands from the snout tip to the vent can be present. Grey or brown crossbands on the hindlegs. Chest and venter white, throat translucent grey to blue in males. Red colour at least on the ventral surface of feet and webbing, sometimes also extending on to shank and thigh. Iris generally reddish externally and silvery around the pupil, but sometimes no distinct red colour is visible on the iris. Iris periphery blue-grey. Colour photographs are published in Glaw & Vences (1994: plate 21) and in Andreone & Randriamahazo (1997: fig. 21).

#### Osteology

After cleared and stained specimen ZFMK 53631. Frontoparietals divided along their whole length, the

division anteriorly and posteriorly becoming broader, notch-like; anteriorly neither reaching palatines nor anterior eye margin, largely separated from nasals, laterally slightly overlapping with sphenethmoid; more or less rectangular along their whole length except the anterior margin, reaching more to the front laterally than medially; thus anterior edge of the whole fronto-parietal complex appearing with a small central notch. Nasals very small, of elongated shape, obliquely directed backwards; medially largely separated from each other. Sphenethmoid well developed, dorsally undivided, ventrally divided at the centre of its anterior edge; reaching anteriorly less far than nasals, in contact but not overlapping with these.

Teeth present on maxilla and premaxilla. Vomer present, with a small, posteriorly directed comb-like dentigerous process and three spine-like, laterally and downwards directed processes. Vomerine teeth distinct on vomerine dentigerous process. Palatines present and distinct. Central processus of parasphenoid ends anteriorly as irregular, fibrous structure and does clearly not reach the palatines. Atlantal cotyles widely separated.

Omosternum largely ossified, short, unforked at its base. Sternum largely ossified, conical, anteriorly clearly broader than posteriorly, unforked at its base. Squamosal with distinct zygomatic and posterior process; zygomatic process shorter than posterior process. There are eight presacral vertebrae; sacral diapophyses only slightly enlarged. Calcified intercalary element between terminal and subterminal phalanges of fingers and toes present. Terminal phalanges of fingers and toes slightly, but distinctly Y-shaped. Two distinct free distal tarsal elements. Hyalia thin, with laterally curved anterior processes. No anterolateral processes of hyoidal plate present. Presence or absence of posterolateral processes can not be ascertained due to poor alcian blue staining.

One additional cleared and stained specimen (ZFMK 48166; female with uncertain locality) largely agrees with the described osteological characters. Fronto-parietals are posteriorly not completely divided and more distinctly notched at their anterior margin. Nasals are not in contact with sphenethmoid. Anterior process of parasphenoid ends straight, nearly at the height of the palatines. Omosternum very slightly forked. Posterolateral hyoidal processes recognizable; no anterolateral processes.

### Habits

Calling activity was observed at the base of Pic St. Louis near Tolagnaro on 1 January 1992 and at Nahampoana on March 1992. Calling males were sitting at about 1 m height on vegetation along slowly running parts of brooks, inside and outside of forest, at night.

One dissected female (MRSN A1646) contained 248 dark brown eggs with a diameter of 1.7 mm.

### Call

A short description of calls was provided by Glaw & Vences (1992b, 1994). Vocalizations (recorded on 1 January 1992 at the base of Pic St. Louis near Tolagnaro at 23°C) consist of at least three note types (Fig. 7).

Type 1 is unharmonious, indistinctly pulsed and is repeated in series of 18–28 notes (mean  $22.4 \pm 4.0$ ,  $N=8$ ). Note duration is 38–85 ms (mean  $59 \pm 13$  ms,  $N=48$ ), duration of intervals between notes is 14–39 ms (mean  $25 \pm 5$  ms,  $N=48$ ). There is a slight tendency for note duration to increase towards the end of the call. Duration of a series of note type 1 is 1516–2419 ms (mean  $1895 \pm 376$  ms,  $N=5$ ), note repetition rate is 11–12/s. Interval between two note series is often less than one second. Frequency is 3200–5350 Hz (dominant frequency 4400–4800 Hz).

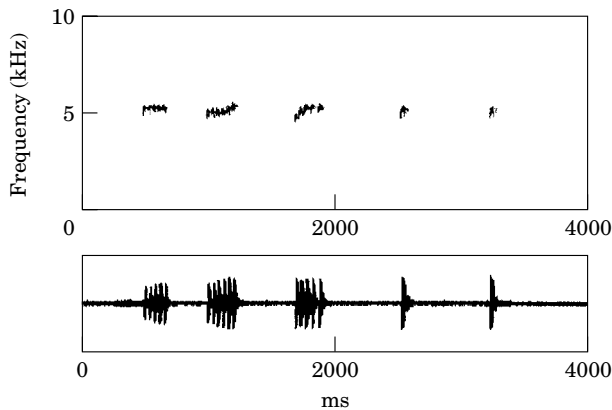
Type 2 is an unharmonious single note with a duration of 65–156 ms (mean  $98 \pm 25$  ms,  $N=14$ ). One analysed note (duration 111 ms) consists of about 20 pulses, resulting in a pulse repetition rate of 180/s. Notes of type 2 can either follow a series of type 1 notes after an interval of 27–161 ms (mean  $115 \pm 44$  ms,  $N=7$ ), or can be given as a single, isolated note or in a short series of up to four notes. In the latter case duration of intervals between notes is 1829–1945 ms (mean  $1893 \pm 59$  ms,  $N=3$ ). Frequency is slightly lower than in notes of type 1 (3000–5000 Hz, dominant frequency 3650–4800 Hz).

Only two notes of type 3 were recorded. They are unharmonious, and their duration is 261 and 315 ms. Interval between them is 665 ms. One of the notes (duration 315 ms) consists of about 57 pulses, resulting in a pulse repetition rate of 181/s. Frequency is 3250–4800 Hz, a distinct dominant frequency is not recognizable.

### *BOOPHIS BLOMMERSAE* GLAW & VENCES, 1994

#### Diagnosis

Characterized by its vocalizations (trills consisting of 4–7 pulses, pulse repetition rate 22–26/s, dominant frequency 4700–5100 Hz, see Fig. 8). Distinct red colour on the webbing between toes is absent. Further distinguished from (a) *B. majori* by less extensive hand webbing which reaches only second subarticular tubercle externally on third finger and not reaching first subarticular tubercle on fourth finger, and by lack of red coloration on webbing (present in *B. majori*); (b) from *B. miniatus* by a smaller tympanum size (none of the measured males of *B. blommersae* reaching a tympanum/eye ratio of 0.5 or larger as typical for



**Figure 8.** Sonagram and oscillogram of a call of *Boophis blommersae* from Montagne d'Ambre. The call consists of three notes of type 1, followed by two notes of type 2. Recorded on 14 March 1994 at 23°C.



**Figure 9.** Holotype of *Boophis blommersae* (ZFMK 57398) from Montagne d'Ambre.

*B. miniatus*) and by the lack of red coloration on webbing (present in *B. miniatus*).

#### Distribution

The species is only known from the type locality in northern Madagascar (latitude 12°32'S, altitudinal range probably 650–1150 m [as *B. miniatus*], compare Raxworthy & Nussbaum, 1994): Montagne d'Ambre (holotype ZFMK 57398 [Fig. 9] and paratypes ZFMK 57399 and ZSM 562/1999, all collected by F. Glaw, N. Rabibisoa and O. Ramilison 14.3–21.3.1994). Additional specimens (same locality and collectors) have been deposited at the herpetological collection of the University of Antananarivo.

The specimens MNHN 1975.2469 and 1975.2470 from Les Rousettes (Montagne d'Ambre) have been referred in the past either to *B. majori* or to *B. miniatus*

(Blommers-Schlösser & Blanc, 1991, 1993; Raxworthy & Nussbaum, 1994). The eye/tympanum ratio of these specimens (0.43–0.49, lower than in almost all *miniatus* specimens) and their lack of red colour ventrally on legs, or on the webbing, contradict their attribution to *B. miniatus*. The latter character also distinguishes them from *B. majori*. Despite intensive surveys, we did not find *B. majori* at Montagne d'Ambre; the two specimens are therefore here attributed to *B. blommersae*.

#### Morphology and coloration

Measurements and morphometric ratios of the types and two specimens held in the MNHN collection are given in Tables 2 and 3. Webbing formula between fingers is (SH) II 2–3<sup>+</sup> III 3–2<sup>+</sup> IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(2), 4(1.5); webbing formula between toes is (SH) I 1<sup>+</sup>–2 II 1–2 III 1<sup>+</sup>–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V respectively (BS) 1(0.25), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(1.25), 4e(1.25), 5(0.5).

#### Colour in life

After photographs of three males. Dorsal coloration very variable. One specimen is nearly uniformly light brown with finely dispersed dark brown pigment and indistinct crossbands on the legs. Another specimen is brown with a dark brown hour-glass marking on the dorsum and distinct crossbands on the legs. The third specimen is dark brown with yellow spots resembling lichens on head, dorsum, arms and legs. Chest and venter white, throat translucent greyish, ventral surface of arms and legs light brown without any red colour. Iris silvery, golden or brownish. Iris periphery grey-green. A colour photograph is published in Glaw & Vences (1994: pl. 19).

#### Habits

In primary rainforest of Montagne d'Ambre numerous males began calling at dusk alongside forest brooks, sitting at a height of 0.5–1.5 m in the vegetation.

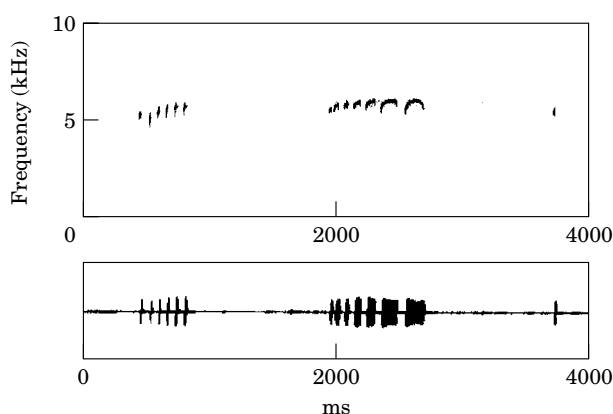
#### Call

Shortly described by Glaw & Vences (1994). Recorded on 14 March 1994, 1730 h, at Montagne d'Ambre (23°C). Two note types are distinguished.

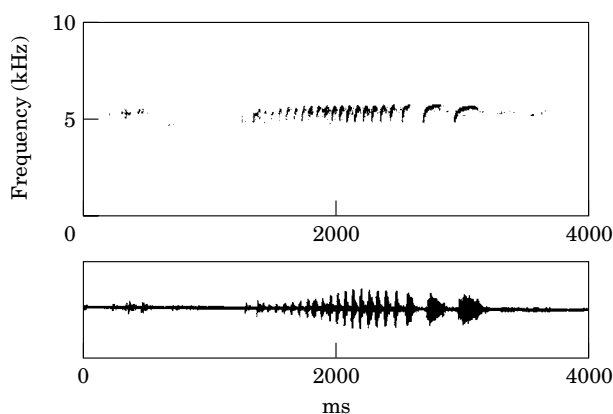
Type 1 is a pulsed trill with a duration of 156–284 ms (mean  $228 \pm 36$  ms,  $N=16$ ) consisting of 4–7 (mean  $5 \pm 1$ ,  $N=14$ ) pulses. Pulse duration is 15–43 ms (mean  $29 \pm 6$  ms,  $N=71$ ), duration of intervals between pulses is 4–32 ms (mean  $13 \pm 6$  ms,  $N=59$ ), pulse repetition rate is 22–26/s. Frequency is 4450–5200 Hz, dominant frequency is 4700–5100 Hz.

Type 2 is a short click with a duration of 31–65 ms (mean  $47 \pm 11$  ms,  $N=8$ ), reminding one of an isolated





**Figure 10.** Sonogram and oscillogram of two calls of *Boophis marojezensis* from Ambanizana. The first call is a series of notes of type 2, the second call is a series of notes of type 1. Recorded on 1 July 1995 at 20°C.



**Figure 11.** Sonogram and oscillogram of a call of *Boophis marojezensis* from An'Ala. The call is a series of notes of type 1. Recorded on 12 February 1995 at 21.5°C.

pulse of note type 1 but being distinctly longer. Frequency is 4550–5350 Hz, dominant frequency is 4750–5200 Hz.

A call generally begins with 2–5 notes of type 1 followed by 2–4 notes of type 2. Duration of intervals between notes of type 1 is 287–579 ms (mean  $436 \pm 111$  ms,  $N=11$ ), of intervals between one note of type 1 and one note of type 2 is 585–1002 ms (mean  $725 \pm 166$  ms,  $N=5$ ), of intervals between notes of type 2 is 597–714 ms (mean  $662 \pm 59$  ms,  $N=3$ ). Independently from note types, duration of intervals tends to be lower at the beginning of the call than at the end of the call.

#### *BOOPHIS MAROJEZENSIS* GLAW & VENCES, 1994

##### Diagnosis

Characterized by its vocalizations (series of 3–21 notes, generally starting as short click notes while the last notes generally have a harmonic structure and a much



**Figure 12.** Paratype of *Boophis marojezensis* from Marojezy (ZSM 567/1999).

increased duration, see Figs 10, 11). Distinct red colour on the webbing between toes is absent. Further distinguished from (a) *B. majori* by less extensive hand webbing which reaches only second subarticular tubercle externally on third and not reaching first subarticular tubercle on fourth finger, and by lack of red coloration on webbing (present in *B. majori*); (b) from *B. miniatus* by a smaller tympanum size (only three out of 41 measured males of *B. marojezensis* reaching a tympanum/eye ratio of 0.5 or larger as typical for *B. miniatus*) and by the lack of red coloration on webbing (present in *B. miniatus*); (c) from *B. blommersae* by vocalizations (single click notes followed by longer harmonic notes in *B. marojezensis* vs. pulsed trills in *B. blommersae*).

##### Distribution

The species is known from eight localities in central eastern and north-eastern Madagascar (latitudinal range  $14^{\circ}26'–21^{\circ}15'S$ , altitudinal range 300–1220 m above sea level). Type locality: Marojezy (holotype ZFMK 57401 and paratype ZSM 567/1999 [Fig. 12] both collected by F. Glaw, N. Rabibisoa and O. Ramilison 27–31 March 1994 at Camp 1, about 300 m above sea level); ZFMK 59956, collected 3 March 1995 at the same locality as the type specimens. Tentatively, we also consider specimens from the following localities as *B. marojezensis*: Ambanizana (A1831.1–4); Besariaka (MRSN A1839.1–7, A1840.1–2, A1841, A1842); Tsararano (MRSN A1834, A1835, A1837, A1838), Anjanaharibe (MRSN A1833.1–2), An'Ala (ZFMK 60085–60089), Ranomafana National Park (ZFMK 62300; Fig. 13), Vohiparara (MRSN A658, A1650). We also attribute the specimen MNHN 1975.2471 from Marojezy to this species which was formerly identified as *B. majori* by Blommers-Schlösser & Blanc (1991).



**Figure 13.** *Boophis marojezensis*; specimen from Ranomafana (ZFMK 62300).

Blommers-Schlösser (1979b) collected a series of *Boophis* at Mandraka (ZMA 7095; 7102–7105; a total of 32 males and 1 female) which she assigned to *B. majori*. Their morphometric characters fit well with those of both *B. marojezensis* and *B. majori*, which are very similar morphometrically. Calls of this population were not analysed, but the general description “The mating call resembles high chirping of birds” (Blommers-Schlösser, 1979b: 280) fits much better with the call patterns of *B. marojezensis* than with those of *B. majori*. Additionally, the Mandraka specimens lack distinct reddish coloration on the legs and many of them have a light vertebral stripe which is common in *B. marojezensis* but not known in *B. majori*.

#### *Morphology and coloration*

Measurements and morphometric ratios of the types and 41 additional specimens are given in Tables 2 and 3. In the types, webbing formula is (SH) II 2–3<sup>+</sup> III 3–2 IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(2), 4(1) between fingers and (SH) I 1<sup>+</sup>–2 II 1–2 III 1<sup>+</sup>–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V respectively (BS) 1(0.25), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(1.25), 4e(1.25), 5 (0.5) between toes. In the populations from central eastern Madagascar, webbing is slightly more reduced: (SH) II 2–3<sup>+</sup> III 3–2<sup>+</sup> IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(2), 4(1.5) between fingers and (SH) I 1<sup>+</sup>–2 II (1–1<sup>+</sup>)–2 III 1<sup>+</sup>–3 IV 3–1<sup>+</sup> V respectively (BS) 1(0.5), 2i(1), 2e(0–0.5), 3i(1), 3e(0.5), 4i(2), 4e(2), 5(0.5) between toes.

#### *Colour in life*

After photographs of at least 11 males. Dorsal coloration very variable. Dorsal ground colour beige to brown. Some specimens from An’Ala and Ranomafana (Fig. 13) have irregular brownish, lichen-like spots (with whitish border) on head and dorsum which may

help to camouflage the frog in its resting place during the day (comparable spots were only found in *B. blommersae* in which the spots are uniformly yellowish on a dark ground colour). Some specimens have dark hour-glass markings on the dorsum or a light median line from snout tip to vent. *B. marojezensis* (from An’Ala and Mandraka) and *B. picturatus* (from Vohiparara, see below) are the only species of *Boophis* in which a light median stripe on the dorsum is known to occur. Chest and venter white, throat translucent greyish, ventral surface of arms and legs light brown without any red colour. Iris externally (or only above) orange-red or yellowish, silvery (in specimens from An’Ala and Ranomafana) or brown (in the specimen from Marojezy) around the pupil. Iris periphery blue (light green in the specimen from Marojezy). A colour photograph has been published in Glaw & Vences (1994: pl. 18).

#### *Habits*

Calling males in Marojezy were observed in March along a brook on vegetation 2–4 m above the ground. In populations from the localities Mandraka, An’Ala and Ranomafana calling activity was observed in all months between November and March (pers. obs.; Blommers-Schlösser, 1979b [as *B. majori*]). In Anjanaharibe calling activity was observed in January and February, in Tsararano in November and December, and in Besariaka in May and June (pers. obs.). One dissected female (MRSN A1839–1) contained 133 yellowish eggs with a diameter of 1.8 mm.

#### *Call*

Recordings from the type locality Marojezy were shortly described by Glaw & Vences (1994). Calls from that locality are very similar to those of the syntopic species *Boophis englaenderi*. Additionally, call recordings from Ambanizana (recorded on 1 July 1995 at 20°C), An’Ala (recorded on 12 February 1995 at 21.5°C) and Vohiparara (recorded on 4 March 1996 at c. 21°C) are available. Two note types can be distinguished.

Type 1 is a harmonious, frequency-modulated whistle; 3–21 notes are arranged in a series. Note duration often distinctly increases towards the end of the call. As examples for this increase we give duration of successive notes of one call from all four localities: Marojezy (140 ms–180 ms–230 ms); Ambanizana (69 ms–30 ms–33 ms–34 ms–40 ms–49 ms–90 ms–122 ms–152 ms); An’Ala (20 ms–31 ms–27 ms–27 ms–23 ms–23 ms–27 ms–27 ms–23 ms–31 ms–27 ms–31 ms–35 ms–55 ms–145 ms–172 ms); Vohiparara (60 ms–55 ms–59 ms–62 ms–76 ms–95 ms–100 ms–119 ms–111 ms–115 ms–119 ms–100 ms). Temporal and spectral parameters of note

**Table 5.** Temporal and spectral parameters of calls of *B. marojezensis* from different localities

	Marojezy	Ambanizana	An'Ala	Vohiparara
Note duration [ms]	140–230	22–152 (mean $66 \pm 35$ , $N=30$ )	10–189 (mean $38 \pm 40$ , $N=60$ )	33–155 (mean $92 \pm 32$ , $N=27$ )
Interval duration [ms]	90 ms	16–77 (mean $44 \pm 12$ , $N=26$ )	31–127 ms (mean $44 \pm 19$ , $N=57$ )	39–93 (mean $55 \pm 12$ , $N=24$ )
Notes/call	3–5	5–9 (mean $7.5 \pm 1.8$ , $N=8$ )	19–21 (mean $20.3$ , $N=3$ )	10–12 (mean $11$ , $N=2$ )
Note repetition rate [ $s^{-1}$ ]		9–10.8 (mean $9.6 \pm 0.8$ , $N=4$ )	12–12.9 (mean $12.5$ , $N=3$ )	7.1–7.6 (mean $7.4$ , $N=2$ )
Call duration [ms]		554–980 (mean $782 \pm 177$ , $N=4$ )	1546–1746 (mean $1640 \pm 101$ , $N=3$ )	1323–1692 (mean $1508$ , $N=2$ )
Frequency [Hz]	3500–4500	4700–6250	4900–5600	4900–6100
Dominant freq. [Hz]		5600–6200	5000–5500	5300–5900
Frequency modulation	present	present	present	present

type 1 series are summarized in Table 5 for each locality.

Type 2 is a short click note which is either given separately or arranged in short series. It was not observed in An'Ala. Note type 2 series consist of up to 6 notes (note duration 11–15 ms, interval duration 54–69 ms,  $N=5$ ; frequency 4700–5700 Hz) in calls from Ambanizana, or of up to 4 notes (note duration 11–27 ms,  $N=10$ ; interval duration 48–54 ms,  $N=5$ ; frequency 4700–5450 Hz, dominant frequency 4950–5350 Hz) in calls from Vohiparara.

There are relevant differences between the analysed calls. Mean duration of notes of type 1 shows important inter- and intrapopulational differences as indicated by high differences between means of populations and high standard deviations. The differences in note duration within a single call reflect this variability which may be largely caused by different motivation of the calling males. The differences in frequency between Marojezy and the remaining localities may be explained by the larger size of Marojezy males. However, we cannot exclude that the specimens here subsumed under the name *B. marojezensis* may in fact belong to two different species.

#### Tadpoles

A description of tadpoles from Mandraka (attributed to *B. majori*) was given by Blommers-Schlösser (1979b). Since the adults from this locality belong to *B. marojezensis*, it is probable that the description of tadpoles from this locality also refers to *B. marojezensis*.

### DESCRIPTIONS OF NEW SPECIES

#### *BOOPHIS PYRRHUS* SP. NOV.

(Figs 14, 15, 18)

*Remarks.* This species was considered as *Boophis difficilis* by Blommers-Schlösser (1979b) and Glaw & Vences (1992a,b, 1994).



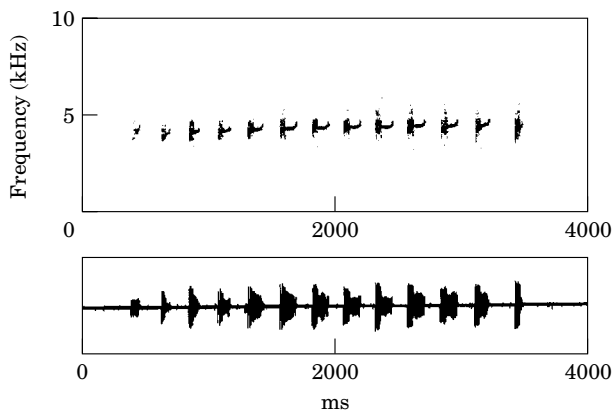
**Figure 14.** Male and female *Boophis pyrrhus* sp. nov. (Andasibe).

*Holotype.* ZSM 582/1999 (originally ZMFK 53634), adult male, collected on 9 January 1992 at Andasibe ( $18^{\circ}56'S$ ;  $48^{\circ}25'E$ , about 900 m above sea level), central eastern Madagascar by F. Glaw and J. Müller-Jung.

*Paratypes.* ZFMK 52633, adult male, collected on 15 February 1991 at Andasibe, by F. Glaw & M. Vences; ZFMK 59865, adult male and ZFMK 59866, adult female, collected on 24 February 1994 at Andasibe, by F. Glaw; MRSN A278, adult male, collected on 4 January 1992 at Andasibe by F. Andreone; ZMA 7098 (one adult male) and ZMA 7099 (six adult males) from Andasibe (collecting data see Blommers-Schlösser, 1979b).

#### Diagnosis

Characterized by its vocalizations (series of 12–17 notes, in which each note is unharmonious and pulsed at the beginning, becoming harmonious and unpulsed



**Figure 15.** Sonogram and oscillogram of a call of *Boophis pyrhus* sp. nov. from Andasibe. Recorded on 30 January 1992 at 22.8°C.

towards its end, see Fig. 15), and by its unique dorsal ground coloration (reddish brown with many small dark spots in life [see Fig. 14], pinkish with dark spots in alcohol) with a sandglass-shaped marking on the back. Distinct red colour on the webbing between toes is absent.

Further distinguished from (a) *B. majori* by absence of distinct red colour on webbing (present in *majori*), larger SVL (males 26.1–31.6 mm vs. 21.5–24.5 mm), and silvery-white iris (golden-yellow in *majori*); (b) *B. miniatus* by absence of distinct red colour on webbing and smaller tympanum (none of 12 measured male specimens reaching tympanum/eye ratio values of 0.5 or higher as typical in *miniatus*); (c) *B. blommersae* and *B. marojezensis* by a generally more extensive hand webbing which reaches first subarticular tubercle on fourth finger.

#### Description of holotype

Body slender; head as long as wide, broader than body; snout slightly pointed in dorsal view, angular in lateral view; nostrils directed laterally, protuberant; canthus rostralis slightly developed, concave; loreal region weakly concave; tympanum not very distinct, small sized, rounded, its diameter about 2/5 of eye diameter; moderately distinct supratympanic fold; single sub-gular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth distinct; choanae medium-sized, ovoid. Arms slender; subarticular tubercles single; outer and inner metacarpal tubercle not recognizable; fingers with webbing, formula (SH) II 2<sup>+</sup>–3<sup>+</sup> III 3–2 IV respectively (BS) 1(-), 2i(-), 2e(1.5), 3i(2.5), 3e(2), 4(1); comparative finger length 1<2<4<3, when fingers 2 and 4 are adpressed to each other terminal finger disks get in contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches beyond snout tip; feet with a small

elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well developed; webbing formula (SH) I 1–2 II 1–2 III 1–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V respectively (BS) 1(0), 2i(1), 2e(0), 3i(1), 3e(0), 4i(1.5), 4e(1.5), 5(0.5), lateral metatarsalia separated; comparative toe length 1 ≤ 2 ≤ 3 ≤ 5 ≤ 4. Skin on the upper surface smooth, throat and chest smooth, venter and ventral surface of thigh slightly granular, anal region strongly granular. For measurements of the holotype see Table 2.

#### Colour of holotype in preservative

Dorsum pinkish with a brown, roughly sandglass-shaped marking. A narrow dark line extends dorsally between the eyes. Upper surfaces of thigh, shank, foot except first, second and third toe, forearm and first finger pinkish, with rather distinct narrow dark crossbands on forearm, thigh, shank, and tarsus. Upper surface of fourth and fifth toe and first, second, and third finger yellowish white. Webbing between fingers and toes yellowish white. The ventral side is yellowish white except for the anterior half of the belly which is whitish. The ventral sides of the tarsus and of the outer metatarsalia are dark brown.

The pinkish dorsal coloration is made up of many very small indistinct reddish spots (agglomerations of red pigment cells); density of these pigment cells in each spot decreases towards the edge. The ground colour is beige and consists of whitish pigment cells. The dark dorsal markings consist of black pigment cells (melanophores) which are mixed with this ground coloration; small dark spots (dense agglomerations of melanophores) are scattered into the dark areas. These dark spots seem to correspond with skin glands since a distinct pore is recognizable in the centre of each spot.

#### Colour in life

Based on colour photographs of at least five males and one female. Head, dorsum, and upper surface of arms and legs are beige, orange or reddish-brown with numerous small reddish spots. A brownish-greyish sand-glass shaped marking on the back. This marking is composed of two triangles. The anterior triangle is formed by a brownish-greyish line between the eyes and two lines running from the eye to the centre of the back. The inner surface of this triangle is often of the same colour as the surrounding dorsum. The inner surface of the posterior triangle is brownish-grey. Yellowish spots are often present on the back, especially on the posterior part. The crossbands on the hindlegs are brown. Flanks whitish. Upper surface of fingers and toes often yellowish. Ventral side white in the centre, more transparent posteriorly and on the ventral side of legs; throat beige-grey. No red colour on legs,

feet or webbing. Some white granules in the anal region. Iris around the pupil silvery-white with a vertical dark line in the dorsal and ventral parts of the iris. Externally, there is a metallic blue ring in the males and a blackish ring in the female. Iris periphery metallic blue in males, grey in the female. Colour photographs are published in Glaw & Vences (1992b: pl. 29; 1994: pl. 20).

#### Variation

The finger and toe webbing of the paratypes agrees well with that of the holotype. ZFMK 59865 has (SH) II 2–3<sup>+</sup> III 3–2 IV between fingers, ZFMK 52633 has (SH) I 1<sup>+</sup>–2 II 1–2 III 1–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V between toes, and ZFMK 59866 has (SH) I 1–2 II 1–2 III 1<sup>+</sup>–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V between toes.

#### Etymology

Derived from Greek *pyrrhos* meaning fiery red, referring to the typical red colour of this species after preservation in alcohol.

#### Distribution

The species is known from five mid-altitude localities in central eastern Madagascar (latitudinal range 18°53'–21°18'S, altitudinal range 450–915 m above sea level). Andasibe (type specimens), An'Ala (sighting and call records by F. Glaw in 1995 and 1996), Mantady reserve (sighting and call records by F. Glaw 10.2.1996), Ankeniheny (sighting by F. Glaw in 1994), Ifanadiana (MRSN A367).

#### Habits

Calling activity was observed in all months between November and April (pers. obs; Blommers-Schlösser, 1979b). Calling males were sitting alongside slow or fast running brooks (sometimes 20–30 m away from water) in rainforest and secondary vegetation, on vegetation 1–2 m above the ground. A couple was observed on 24 February 1994. Another couple (female 35 mm, male 28 mm SVL) from Andasibe, found on 1 April 1995, laid a clutch consisting of dark fertilized eggs during the following night in captivity.

#### Call

Briefly described by Glaw & Vences (1992a,b, 1994). Recordings were made on 30 January 1992, 1930 h, at Andasibe (at 22.8°C). Two note types can be distinguished.

Type 1 is unharmonious and pulsed (4–6 pulses recognizable) at the beginning, becoming harmonious and unpulsed towards its end. Series consist of 12–17 notes (mean  $13.6 \pm 1.4$ ,  $N=9$ ). Note duration is

50–142 ms (mean  $109 \pm 29$  ms,  $N=105$ ), duration of intervals between notes is 114–212 ms (mean  $145 \pm 22$  ms,  $N=96$ ). The last note of a series often consists only of its unharmonious component and is distinctly shorter than the other notes. The interval between the first two notes of a series has the longest duration. Duration of a note type 1 series is 2928–3487 ms (mean  $3202 \pm 194$  ms,  $N=8$ ), note repetition rate is 4–4.2/s. Intensity of the first notes of a series is lower than of the following notes. Interval between two note series is 19 812–25 835 ms (mean  $23 439 \pm 2050$  ms,  $N=7$ ). Frequency is 4000–4200 Hz, 4250–4400 Hz in the melodious component. Type 2 is, as type 1, initially unharmonious, becoming harmonious at its end, but is not given as a distinct series. Relative duration of harmonious vs. unharmonious component is rather variable, resulting in notes with reduced harmonious respectively unharmonious component. Note duration is 81–109 ms (mean  $95 \pm 10$  ms,  $N=7$ ). Notes of type 2 either follow a note type 1 series after an interval (duration 2905 ms,  $N=1$ ), or are given as irregular series with variable intervals of 2897–18 025 ms (mean  $10 879 \pm 5031$  ms,  $N=7$ ) between notes. Frequency is 2800–5300 Hz, dominant frequency is 4100–4650 Hz.

#### *BOOPHIS HAEMATOPUS* SP. NOV.

(Figs 16–18)

#### Remarks

This species was considered as *Boophis difficilis* by Glaw & Vences (1992a,b, 1994) and Andreone & Rاندريامهازو (1997).

*Holotype*. ZSM 583/1999 (originally ZFMK 53632), adult male, collected on 4 January 1992, at Nahampoana (24°58'S/46°58'E), southeastern Madagascar, by F. Glaw and J. Müller-Jung.

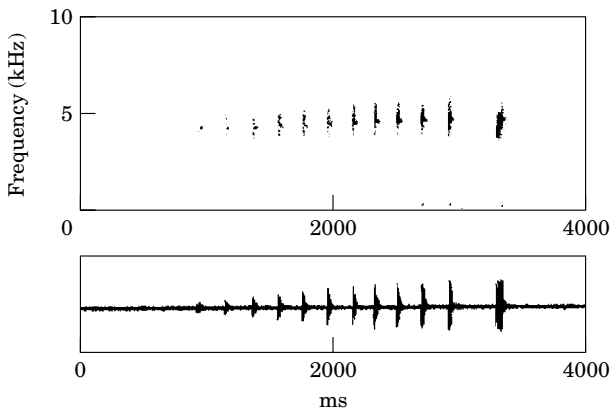
*Paratypes*. ZFMK 52634, adult male, collected on 1 March 1991, Nahampoana, by F. Glaw and M. Vences (Fig. 16); ZFMK 53633, adult male, same locality, date and collectors as holotype; MRSN A725-1, A725-2, adult males, collected on 11 November 1994, between Isaka-Ivondro and Eminiminy, Andohahela Strict Nature Reserve, by F. Andreone; MRSN A1591.1, A1591.2, adult males, collected on 29 April 1994, between Isaka-Ivondro and Eminiminy, by F. Andreone.

#### Diagnosis

Characterized by its vocalizations (series of 11–13 short notes with about 40 ms duration, a note repetition rate of 5/s and a dominant frequency of 4300–5000 Hz, see Fig. 17). Distinct red colour on the ventral side of legs, feet, hands and webbing is present.

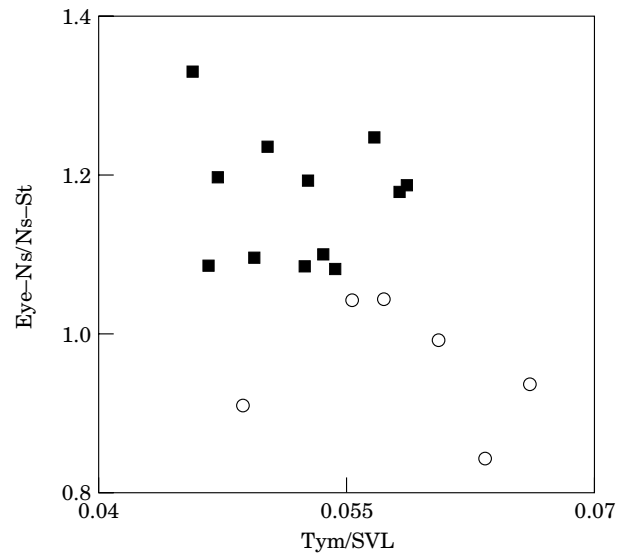


**Figure 16.** Paratype of *Boophis haematopus* sp. nov. (ZFMK 52634) from Nahampoana.



**Figure 17.** Sonagram and oscillogram of a call of *Boophis haematopus* sp. nov. from Pic St. Louis. Recorded on 30 December 1991 at c. 23°C.

Further distinguished from (a) *B. majori* by larger SVL (males 25.4–28.3 mm vs. 21.5–24.5 mm), and silver-beige iris (golden-yellow in *majori*); (b) *B. miniatus* by a smaller tympanum, only one out of seven measured specimens reaching a tympanum/eye ratio value of 0.5 (0.5 or higher being typical in *miniatus*); (c) *B. blommersae* and *B. marojezensis* by the presence of distinct red colour on the webbing and by a generally more extensive hand webbing which reaches first subarticular tubercle on fourth finger and further than second subarticular tubercle on the outer edge of third finger; (d) *B. pyrrhus* by lack of reddish dorsal ground coloration in life and preservative, presence of distinct red colour on the webbing (absent in *pyrrhus*), relative position of nostril (equidistant or nearer to eye than to snout tip in *haematopus*, nearer to snout tip in *pyrrhus*; ratio Eye–Ns/Ns–St 0.86–1.05 vs. 1.09–1.33;



**Figure 18.** Morphometric distinction between (■) *B. pyrrhus* and (○) *B. haematopus* by the ratios Tym/SVL and Eye–Ns/Ns–St. Calculated from original data in Table 2. Only males considered.

see also Fig. 18) and by call differences (although call structure and subjective sound to the human ear are similar in both species, the notes in a note series of *B. haematopus* are shorter and nearly have no harmonic component as compared to *B. pyrrhus*).

#### Description of holotype

Body slender; head as long as wide, distinctly broader than body; snout round shaped in dorsal and lateral view; nostrils directed laterally, protuberant; canthus rostralis moderately developed, slightly concave; loreal region weakly concave; tympanum not very distinct, small sized, rounded, its diameter about 1/3 of eye diameter; distinct supratympanic fold; single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct; choanae medium-sized, slightly ovoid. Arms slender; subarticular tubercles single; outer metacarpal tubercle not recognizable, inner metacarpal tubercle elliptical, weakly developed; fingers with webbing, formula (SH) II 2–3<sup>+</sup> III 2<sup>+</sup>–2 IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(1.5), 4(1); comparative finger length 1<2<4<3, when fingers 2 and 4 are addressed to each other terminal finger disks get in contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches tip of snout; feet with a small elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well developed; webbing formula (SH) I 1–2 II 1–2 III 1–2 IV 2<sup>+</sup>–1<sup>+</sup> V respectively (BS) 1(0), 2i(1), 2e(0), 3i(1), 3e(0), 4i(1), 4e(1.5), 5(0.5), lateral

metatarsalia separated; comparative toe length  $1 < 2 < 3 = 5 < 4$ . Skin on the upper surface smooth, throat and chest smooth, venter slightly granular, ventral surface of thigh granular, anal region strongly granular. For measurements of the holotype see Table 2.

#### *Colour of holotype in preservative*

Dorsum beige with a large symmetrical dark brown marking which extends from the eyes to the height of the inguinal region. The contrast between ground colour and dark marking is high, but the borders of the marking are poorly defined; on the posterior back both colours fade into each other. Dark colour is also present on the anterior of the head.

Upper surfaces of thigh, shank, foot except first, second and third toe, forearm and first finger beige with distinct dark brown crossbands. Upper surface of fourth and fifth toe and first, second, and third finger light beige. Postero-dorsal parts of thigh and webbing between toes and fingers deep red. The ventral side is yellowish white except for the belly which is whitish. Ventral sides of tarsus and, partly, of the lateral metatarsalia, as well as anal region, dark brown.

In the beige dorsal parts, many reflecting white pigment cells (iridophores) are recognizable. The dark dorsal markings are made up by numerous dark pigment cells which are not contracted, and extend star-like.

#### *Colour in life*

Based on photographs of four males. Dorsal coloration rather variable. Irregularly marmorated brownish or greyish with small reddish dots. Flanks light bluish. Tympanum not distinctly different from dorsal coloration. White spots along the upper lip can fuse to form a whitish band. Upper surfaces of arms and thighs similar to dorsal coloration. Three dorsal brownish crossbands on the thighs, sometimes rather indistinct. Chest and venter white; throat and posterior venter whitish to transparent bluish to grey; parts of ventral side of thigh, shank, tarsus, foot, hand and webbing deep red. Finger and toe disks ventrally yellow. White granules in the anal region. Iris silvery-beige with a vertical dark line in the dorsal and ventral parts. Iris periphery with a rather indistinct turquoise ring, especially in the posterior part. Additional dark lines can be present at the anterior and posterior corners of the iris. A colour photograph of ZFMK 52634 has been published in Glaw & Vences (1992b: pl. 30), whereas dorsal and ventral views have been figured in Andreone & Randriamahazo (1997: figs 13, 14).

#### *Variation*

The finger and toe webbing of the paratypes agrees well with that of the holotype. ZFMK 53633 has (SH) I 1–2 II 1–2 III 1–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V between toes.

#### *Etymology*

Derived from Greek *haima*, equals Latin *haema*-, meaning blood, and *pous*, equals Latin suffix *-pus* meaning foot. Referring to the deep red patterns at thighs and webbing of this species.

#### *Distribution*

Known from two localities in south-eastern Madagascar (latitudinal range 24°47'–25°00'S, altitudinal range 300–400 m above sea level): Nahampoana and Andohahela (see above).

#### *Habits*

Calling males were found at Nahampoana on vegetation alongside a brook in primary rainforest, sitting 1–2 m above the ground.

#### *Call*

A short description was given in Glaw & Vences (1992b: 77, 1994: 101), as *B. difficilis* from Tolagnaro. Recorded at Nahampoana on 30 December 1991 (at c. 23°C). Three different note types can be distinguished.

Type 1 is unharmonious, indistinctly pulsed and is arranged in series of 11–13 notes (mean  $11.6 \pm 0.9$ ,  $N = 5$ ). Note duration is 27–49 ms (mean  $40 \pm 4$  ms,  $N = 64$ ). Duration of intervals between notes is 138–332 ms (mean  $170 \pm 31$  ms,  $N = 57$ ). The interval between the last two notes of a series has the longest duration. Duration of note type 1 series is 2084–2514 ms (mean  $2248 \pm 167$  ms,  $N = 5$ ), note repetition rate is 5–5.3/s. Note intensity strongly increases from the first towards the last note of a series. Interval between two note series can last about 30 s. Frequency is 3600–5700 Hz, dominant frequency is 4300–5000 Hz.

Type 2 is a short, unharmonious and distinctly pulsed note. Note duration is 54–68 ms (mean  $61 \pm 4$  ms,  $N = 11$ ). A note consists of 8–12 pulses (mean  $10 \pm 1$ ,  $N = 11$ ). Pulse repetition rate is 140–179/s. Note type 1 series are followed by one note of type 2 after an interval of 345–4224 ms (mean  $2811 \pm 1364$  ms,  $N = 6$ ). Frequency is 3400–5500 Hz, dominant frequency is 3800–4800 Hz.

Type 3 is longer and more rapidly pulsed than type 2. Note duration is 83–88 ms (mean  $85 \pm 2$  ms,  $N = 6$ ). One note consists of about 25 pulses. Pulse repetition rate is about 300/s. Notes of type 3 follow notes of type 2 after an interval 9120–14 560 ms (mean  $11 041 \pm 1978$  ms,  $N = 6$ ).

One call series of a male showed the following arrangement of notes: 1232–1232–12232–1232–123–123. In this formula, 1 represents a series of type 1 notes, 2 and 3 represent single notes of type 2 and 3 respectively. Figure 17 shows a series of 10 notes of type 1 and one note of type 2.



**Figure 19.** Holotype of *Boophis picturatus* sp. nov. (ZSM 584/1999) from An'Ala.

**BOOPHIS PICTURATUS SP. NOV.**

(Figs 19–22)

*Remarks*

This species was considered as *B. miniatus* by Glaw & Vences (1992a). The same authors (1992b, 1994) characterized this species as *B. sp. c* (respectively *B. cf. miniatus*) and figured the paratype ZFMK 52636.

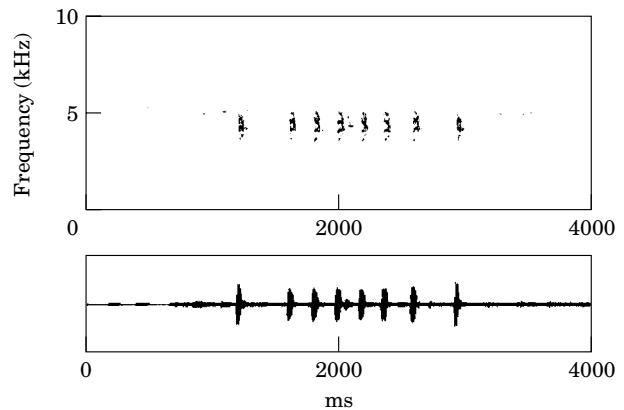
*Holotype.* ZSM 584/1999 (originally ZFMK 60078), adult male, collected on 11 February 1995 at An'Ala (18°56'S/48°28'E, about 840 m above sea level), central eastern Madagascar, by F. Glaw (Fig. 19).

*Paratypes.* ZFMK 52636, adult male, collected on 15 February 1991 at Andasibe, by F. Glaw and M. Vences; ZFMK 60021–60023, adult males, collected on 1 February 1995 at Andasibe, by F. Glaw; ZFMK 62261, adult male, collected on 3 February 1996 at An'Ala, by F. Glaw.

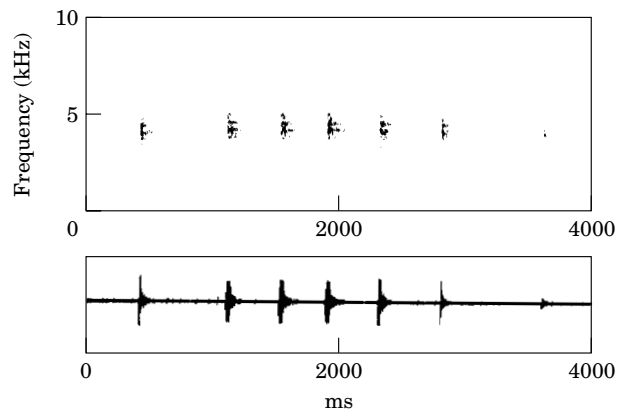
*Diagnosis*

Characterized by its vocalizations (single notes or short series of up to eight unharmonious notes, which are repeated rather irregularly, see Figs 20, 21), and by a large tympanum (mean tympanum/eye ratio is the second largest in the group after *B. miniatus*; only three out of 13 measured males had a tympanum/eye ratio below 0.5). Distinct red colour on the webbing between toes is present.

Further distinguished from (a) *B. majori* by blue iris periphery (blue-green or green-grey in *majori*) and larger tympanum size (only one out of eight measured *majori* males reached a tympanum/eye ratio above 0.5); (b) *B. miniatus* by lack of reddish colour on the outer iris area; (c) *B. blommersae* and *B. marojezensis* by the presence of distinct red colour on the webbing,



**Figure 20.** Sonagram and oscillogram of a call of *Boophis picturatus* sp. nov. from An'Ala. Recorded on 11 February 1995 at 21.5°C.



**Figure 21.** Sonagram and oscillogram of a call of *Boophis picturatus* sp. nov. from Vohiparara. Recorded on 28 February 1996 at c. 22°C.

by a generally more extensive hand webbing which reaches first subarticular tubercle on fourth finger and further than second subarticular tubercle on the outer edge of third finger, and by a larger tympanum (no *B. blommersae* and only three out of 41 *B. marojezensis* males reached a tympanum/eye ratio of 0.5 or higher); (d) *B. pyrrhus* by lack of reddish dorsal ground coloration in life and preservative, and presence of distinct red colour on the webbing (absent in *pyrrhus*), and a larger tympanum (no *B. pyrrhus* male reached a tympanum/eye ratio of 0.5 or higher); (e) *B. haematopus* by a larger tympanum (only one out of seven *B. haematopus* reached a tympanum/eye ratio of 0.5).

*Description of holotype*

Body slender; head as long as wide, distinctly broader than body; snout round shaped in dorsal view, angular in lateral view; nostrils directed laterally, protuberant;



canthus rostralis distinct, concave; loreal region weakly concave; tympanum distinct, medium sized, rounded, its diameter about 1/2 of eye diameter; moderately distinct supratympanic fold; single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth indistinct; choanae medium-sized, slightly ovoid. Arms slender; subarticular tubercles single; outer and inner metacarpal tubercle not recognizable; fingers with webbing, formula (SH) II 2–3<sup>+</sup> III 2<sup>+</sup>–2 IV respectively (BS) 1(-), 2i(-), 2e(1.5), 3i(3), 3e(1.5), 4(1); comparative finger length  $1 < 2 < 4 < 3$ , when fingers 2 and 4 are adpressed to each other terminal finger disks get in contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches beyond snout tip; feet with a small elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well developed; webbing formula (SH) I 1<sup>+</sup>–2 II 1–2 III 1<sup>+</sup>–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V respectively (BS) 1(0.5), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(1.5), 4e(1.5), 5(0.5), lateral metatarsalia largely separated; comparative toe length  $1 < 2 < 3 = 5 < 4$ . Skin on the upper surface smooth, throat and chest smooth, venter and ventral surface of thigh slightly granular, anal region with some tubercles. For measurements of the holotype see Table 2.

#### *Colour of holotype in preservative*

Dorsum pinkish beige with two symmetrical, sharply defined, contrasting dark brown markings; one large marking which is more or less triangular, extending from behind each eye to the middle of the back; the second, smaller marking forms a dorsal crossband at the height of the inguinal region. Anterior flank brownish; this brown coloration extends laterally along the head, sharply delimited by the canthus rostralis. Two distinct, rather large, pinkish beige roundish markings are present on the upper lip, one just posteriorly, the other just anteriorly to the eye.

Upper surfaces of thigh, shank, and forearm pinkish beige with dark crossbands. Upper surface of foot and hand, as well as webbing, posterior flank and ventral side red to bright red, except throat, chest, and ventral surface of forearm which are yellowish white. Ventral sides of tarsus and of lateral metatarsalia, as well as anal region, dark brown to blackish.

The beige dorsal coloration is made up by whitish pigment cells with reddish-brown intervals. The cellular composition of the dorsal dark brown markings is difficult to determine; only small black pigment cells (melanophores) are clearly recognizable. Distinct red, white, and black pigment cells are recognizable on the flanks; no single pigment cells are discernible in the red ventral coloration.

#### *Colour in life*

Based on photographs of eight males from Andasibe and An'Ala as well as four males from Vohiparara. The dorsal coloration of specimens from Andasibe and An'Ala is extremely variable, generally beige, brown or reddish. A distinct dark brown sand-glass shaped marking can be present on the back, but sometimes it is incomplete or indistinct. Often white spots along the upper lip, which can fuse to a more or less distinct white band. Indistinct grey crossbands are present or absent on the hindlegs. Fingers, toes and webbing at least partly red. The red areas appear especially extended in specimens with a highly contrasting dorsal colour pattern (beige with dark sand-glass shaped markings) in which the complete ventral surface of legs and parts of the venter are often red. Venter and anal region of the other specimens largely white, throat transparent light bluish-greenish, ventral parts of the legs transparent purple. Inner ring of iris brown. Sometimes a second whitish ring around the brown ring, which can fuse with the metallic turquoise outer ring. The outer ring is surrounded by a narrow black ring. Iris periphery blue, especially in the posterior part. Colour photographs of ZFMK 52636 are published in Glaw & Vences (1992b: pl. 32; 1994: pl. 22). Specimens from Vohiparara are different but less variable. The dorsum is beige with or without a dark hour-glass shaped marking. Three of four males are characterized by a yellow median line. The iris is golden yellow to light brown, the iris periphery is blue. The ventral surface has at most little and less distinct red colour on legs or webbing. Venter and anal region are white, the throat is transparent light bluish-greenish.

#### *Variation*

In all paratypes distinct vomerine teeth are recognizable. The finger and toe webbing of the paratypes agrees well with that of the holotype. Webbing between toes is (SH) I 2–2 II 1–2 III 1<sup>+</sup>–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V in ZFMK 62282, (SH) I 1<sup>+</sup>–2 II 1–2 III 2–2<sup>+</sup> IV 2<sup>+</sup>–1<sup>+</sup> V in ZFMK 52636.

#### *Etymology*

Derived from Latin *picturatus* meaning decorated with colour. Referring to the variable and beautiful dorsal colour patterns of this species.

#### *Distribution*

Known from three mid-altitude localities in central eastern Madagascar (latitudinal range 18°56'–21°13'S, altitudinal range 840–1000 m above sea level). Type material from Andasibe and An'Ala (see above). We also attribute specimens from Vohiparara (ZFMK



**Figure 22.** *Boophis picturatus* sp. nov. Specimen from Vohiparara (ZFMK 62284).

62282–62284, ZFMK 62302; Fig. 22), as well as three specimens from Andasibe collected by Blommers-Schlösser (1979b) to this taxon (ZMA 7162 and 7163). The iris coloration of the ZMA specimens (as visible in ZMA 7162 as figured by Blommers-Schlösser & Blanc, 1993: pl. 114) with a greenish-beige outer iris area and a dark brownish inner iris area agrees rather well with other *B. picturatus* specimens from Andasibe, but differs from *B. miniatus* in which the (beige) inner iris area is lighter than the (reddish) outer iris area.

#### Habits

Calling males were found in February and March along brooks in primary forest, sitting on vegetation between 1.5 and more than 3 m above the ground.

#### Call

Some data are given by Glaw & Vences (1992a: 51, as *B. cf. miniatus*; 1992b: 78, as *B. sp. c*; 1994: 102, as *B. sp. a*) but were based on recordings under artificial, captive conditions. Nevertheless, published data are in accordance regarding general call structure with new recordings from An'Ala (recorded on 11 February 1995 at 21.5°C) and Vohiparara (recorded on 28 February 1996 at c. 22°C). Generally, only one note type can be distinguished. Notes are unharmonious and are given separately or arranged in short series of up to 8 notes (Figs 20, 21). Note duration is 49–131 ms (mean  $75 \pm 21$  ms,  $N=24$ ) in An'Ala and 47–100 ms (mean  $75 \pm 19$  ms,  $N=6$ ) in Vohiparara. Duration of intervals between notes is very variable, 125–2197 ms (mean  $725 \pm 583$  ms,  $N=18$ ) in An'Ala and 284–625 (mean  $398 \pm 137$ ,  $N=5$ ) in Vohiparara. Frequency 3600–5500 Hz (dominant frequency 4100–4700 Hz) in An'Ala, 3000–5350 Hz (dominant frequencies 4000–4250 Hz and 4400–4600 Hz) in Vohiparara.



**Figure 23.** Paratype of *Boophis feonnyala* sp. nov. (ZFMK 60004) from Andasibe.

Recordings from Vohiparara also include a second, longer note type which was seldom heard. Duration of one such note is 222 ms (consisting of 14 pulses). Frequency is 3150–5200 Hz (dominant frequency 3900–4500 Hz).

#### *BOOPHIS FEONNYALA* SP. NOV.

(Figs 23, 24)

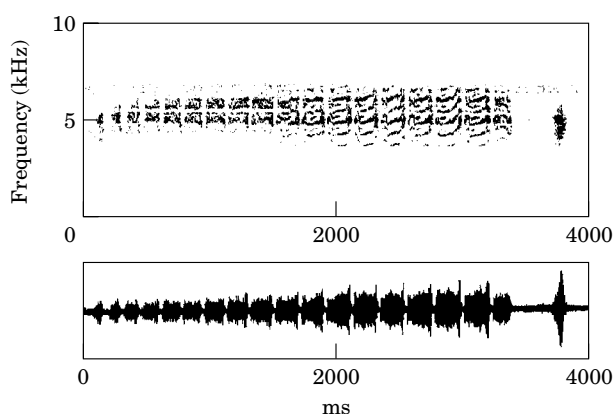
*Holotype.* ZSM 585/1999 (originally ZFMK 60003), adult male, collected on 1 April 1995 at Andasibe (18°56'S/48°25'E, about 900 m above sea level), central eastern Madagascar, by F. Glaw and D. Vallan.

*Paratypes.* ZFMK 60004–60006, adult males, same locality, date and collectors as holotype (Fig. 23).

#### Diagnosis

Characterized by its vocalizations (series of 18–20 long notes of about 160 ms duration and an interval duration between notes which is much shorter than the note duration [about 30 ms]; note repetition rate of about 5/s and dominant frequency of 4700–6000 Hz, see Fig. 24). Additionally characterized by the extensive webbing; beside *B. feonnyala*, only in some *B. miniatus* the webbing reaches the disk of the fifth toe (see Table 4). Distinct red colour on the webbing between toes is absent.

Further distinguished from (a) *B. majori* by larger SVL (males 25.0–25.4 mm vs. 21.5–24.5 mm) and absence of distinct red coloration on webbing (present in *B. majori*); (b) *B. miniatus* by a smaller tympanum (none of the measured *B. feonnyala* males reached a tympanum/eye ratio of 0.5 or higher as typical in *B. miniatus*), and absence of distinct red coloration on webbing (present in *B. miniatus*); (c) *B. blommersae* and *B. marojezensis* by a clearly larger extension of



**Figure 24.** Sonagram and oscillogram of a call of *Boophis feonnyala* sp. nov. from Andasibe. The call is a series of notes of type 1, followed by one note of type 2. Recorded on 1 April 1995 at c. 20°C.

hand and foot webbing which reaches the terminal disk on fifth toe, first subarticular tubercle on fourth finger and further than second subarticular tubercle on the outer edge of third finger; (d) *B. pyrrhus* by lack of reddish dorsal ground coloration in life and preservative; (e) *B. haematopus* by lack of distinct red coloration on webbing (present in *haematopus*); (f) *B. picturatus* by lack of distinct red coloration on webbing (present in *picturatus*), and by a smaller tympanum (none of the measured *B. feonnyala* males reached a tympanum/eye ratio of 0.5 or higher as typical in *B. picturatus*).

#### *Description of holotype*

Body slender; head as long as wide, broader than body; snout round shaped in dorsal and lateral view; nostrils directed laterally, protuberant; canthus rostralis distinct, concave; loreal region weakly concave; tympanum not very distinct, small sized, rounded, its diameter about  $\frac{2}{5}$  of eye diameter; distinct supratympanic fold; single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct; choanae medium-sized, ovoid. Arms slender; subarticular tubercles single; outer and inner metacarpal tubercle not recognizable; fingers with webbing, formula (SH) II 2–3<sup>+</sup> III 2<sup>+</sup>–2 IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(1.5), 4(1); comparative finger length  $1 < 2 < 4 < 3$ , when fingers 2 and 4 are adressed to each other terminal finger disks get nearly in contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches between nostril and snout tip; feet with a small elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well developed; webbing formula (SH) I 1<sup>+</sup>–2 II 1–2 III 1<sup>+</sup>–2<sup>+</sup> IV 2<sup>+</sup>–1 V respectively (BS) 1(0.25), 2i(1), 2e(0), 3i(1), 3e(0.5),

4i(1.5), 4e(1.5), 5(0), lateral metatarsalia separated; comparative toe length  $1 \leq 2 \leq 3 \leq 5 \leq 4$ . Skin on the upper surface smooth, throat and chest smooth, venter and ventral surface of thigh slightly granular, anal region granular. For measurements of the holotype see Table 2.

#### *Colour of holotype in preservative*

Dorsum beige with brown, both colours indistinctly fading into each other. Upper surfaces of thigh, shank, foot except first, second and third toe, forearm and first finger beige; indistinct dark brown crossbands on thigh and shank. Upper surface of fourth and fifth toe and first, second, and third finger light beige. Small red spots on postero-dorsal parts of thigh and on toes. Webbing between fingers and toes yellowish white. The ventral side is yellowish white except for the belly which is whitish. Ventral sides of tarsus and, partly, of the lateral metatarsalia, as well as anal region, dark brown.

The dorsal coloration is made up by irregularly scattered melanophores and white pigment cells. The red spots on thigh and toes are agglomerations of distinct red pigment cells.

#### *Colour in life*

Based on photographs of several specimens. Head, dorsum, upper surface of arms and legs beige. In some specimens very small dark and reddish spots are scattered on the whole dorsal surface, other specimens are nearly uniformly beige; 2–3 greyish crossbands on hindlegs. Tympanum not distinctly different from dorsal coloration. Belly white in the center, transparent greyish-beige posteriorly and towards the flanks. Throat rather transparent (light bluish), ventral surface of arms and legs beige, ventral sides of fingers and toes partly yellowish, anal region with white granules. No recognizable reddish coloration. Iris golden, often with a dark vertical line in the dorsal and ventral parts of the iris, sometimes additional dark lines in the iris. Iris periphery with a metallic turquoise ring, sometimes only visible in the posterior part or even not visible.

#### *Variation*

The finger and toe webbing of the paratypes agrees well with that of the holotype. Webbing between toes is (SH) I 1<sup>+</sup>–2 II 1–2 III 1–2<sup>+</sup> IV 2<sup>+</sup>–1 V in ZFMK 60004 and 60006.

#### *Etymology*

Derived from Malagasy *feon'ny ala* meaning voice of the forest. The species was discovered by its call while

the collectors were on the way to have dinner beside the artificial lake in front of the hotel Feon'ny ala.

#### Distribution

Known only from the type locality Andasibe (latitude 18°56'S, altitude 915 m above sea level).

#### Habits

Calling males were heard around an artificial lake in March and April, whereas calling males of the other species of the *majori* group were mainly found along running water. Calling activity started at dusk from vegetation 1–2 m above the ground.

#### Call

Recorded on 1 April 1995 at Andasibe (at c. 20°C). Two note types can be distinguished.

Type 1 is given in series of 18–20 notes ( $N=2$ ). Note duration is 64–205 ms (mean  $160 \pm 40$  ms,  $N=18$ ). Note intensity and note duration increase towards the end of a note series, but the last note of a series is shorter than the preceding note. Duration of intervals between notes is 21–61 ms (mean  $28 \pm 10$  ms,  $N=17$ ). Duration of one series of 18 notes is 3382 ms, resulting in a note repetition rate of 5.3/s. Frequency is 3450–6650 Hz, dominant frequencies are 4700–4900 Hz and 5800–6000 Hz.

Type 2 is a single unharmonious click note with a duration of 43–105 ms (mean  $81 \pm 19$  ms,  $N=7$ ). One note with a duration of 90 ms consists of about 17 pulses. Notes of type 2 are either given after a series of type 1 notes after an interval of 230–322 ms ( $N=2$ ), or separately before a note type 1 series, or as short series of up to 5 notes. In the latter case duration of intervals between type 2 notes is 1451–2304 ms (mean  $1717 \pm 349$  ms,  $N=5$ ). Frequency is 3500–5600 Hz, dominant frequency is indistinct. Figure 24 shows a series of 18 notes of type 1 followed by one note of type 2.

#### **BOOPHIS VITTATUS SP. NOV.**

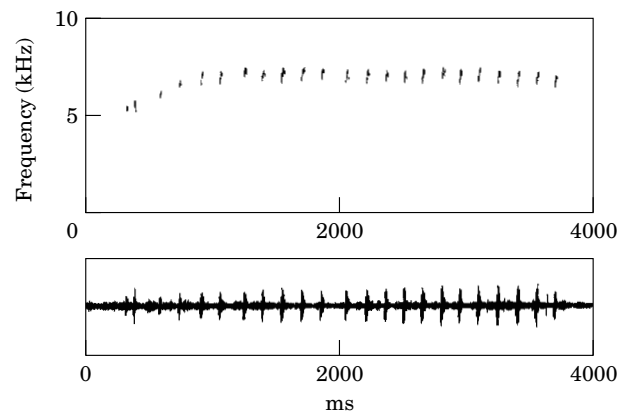
(Figs 25, 26)

*Holotype*. ZSM 586/1999 (originally ZFMK 59889), adult male, collected on 1 March 1995, Reserve Naturelle Integrale Marojezy, Camp 3 (14°26'S/c. 49°46'E, about 700 m above sea level), northeastern Madagascar, by F. Glaw & O. Ramilison.

*Paratypes*. ZFMK 59890–59892, 60121, 60122, adult males, same locality, date and collectors as holotype.

#### Diagnosis

Characterized by its vocalizations (series of 18–28 short 'click' notes of about 22 ms duration, a note



**Figure 25.** Sonagram and oscillogram of a call of *Boophis vittatus* sp. nov. from Marojezy. Recorded on 1 March 1995 at 22°C.

repetition rate of 6–7/s and a very high frequency of 6250–8250 Hz, see Fig. 25).

Further distinguished from (a) *B. majori* by its silvery beige iris with orange (golden-yellow in *majori*), and absence of distinct red colour on the webbing (present in *majori*); (b) *B. miniatus* by a smaller tympanum (none of the measured *B. vittatus* males reached a tympanum/eye ratio of 0.5 or higher as typical in *B. miniatus*), and absence of distinct red coloration on webbing (present in *B. miniatus*); (c) *B. pyrrius* by lack of reddish dorsal ground coloration in life and preservative, and by smaller SVL (males 23.1–25.4 mm vs. 26.1–31.6 mm); (d) *B. haematopus* by lack of distinct red coloration on webbing (present in *haematopus*), and by smaller SVL (males 23.1–25.4 mm vs. 25.4–28.3 mm); (e) *B. picturatus* by lack of distinct red coloration on webbing (present in *picturatus*), and by a smaller tympanum (none of the measured *B. vittatus* males reached a tympanum/eye ratio of 0.5 or higher as typical in *B. picturatus*); (f) *B. blommersae*, *B. marojezensis*, and *B. feonnyala*, as well as all other species of the *B. majori* group, by presence of dark dorsolateral bands (Fig. 26).

#### Description of holotype

Body slender; head as long as wide, broader than body; snout slightly pointed in dorsal view, rounded in lateral view; nostrils directed laterally, slightly protuberant; canthus rostralis distinct, concave; loreal region weakly concave; tympanum not very distinct, small sized, rounded, its diameter more than 2/5 of eye diameter; moderately distinct supratympanic fold; single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth present but indistinct, choanae medium-sized, ovoid. Arms slender; sub-articular tubercles single; outer and inner metacarpal



**Figure 26.** Specimen of *Boophis vittatus* sp. nov. from Marojezy, preserved in the collection of the University of Antananarivo.

tubercle not recognizable; fingers with webbing, formula (SH) II 2–3<sup>+</sup> III 3–2 IV respectively (BS) 1(-), 2i(-), 2e(1), 3i(2.5), 3e(2), 4(1); comparative finger length  $1 < 2 < 4 < 3$ , when fingers 2 and 4 are adpressed to each other terminal finger disks get in contact; well developed terminal finger disks. Legs slender; tibiotarsal articulation reaches clearly beyond snout tip; feet with a small elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well developed; webbing formula (SH) I 1<sup>+</sup>–2 II 1–2 III 1–3 IV 2<sup>+</sup>–1<sup>+</sup> V respectively (BS) 1(0.5), 2i(1), 2e(0), 3i(1), 3e(0), 4i(2), 4e(1.5), 5(0.5), lateral metatarsalia largely separated; comparative toe length  $1 < 2 < 3 = 5 < 4$ . Skin on the upper surface smooth, throat and chest smooth, venter and ventral surface of thigh slightly granular, anal region granular. For measurements of the holotype see Table 2.

#### *Colour of holotype in preservative*

Dorsum uniformly cream beige with distinct brown dorsolateral bands. Upper surfaces of thigh, shank, foot (except first, second and third toe), forearm and first finger beige; brown crossbands on thigh, shank and foot. Upper surface of fourth and fifth toe and first, second, and third finger yellowish white. Webbing between fingers and toes yellowish white. The ventral side is yellowish white except for the anterior belly which is whitish. Ventral sides of tarsus and of the lateral metatarsalia dark brown. The dorsal coloration consists of numerous white pigment cells with few scattered melanophores; the brown markings are made up by a higher melanophore density.

#### *Colour in life*

Based on photographs of a single specimen. Head, dorsum, upper surface of arms and legs beige. A brown band runs from the nostril above the eye to the middle of the back. Several small brown spots and a few larger spots are scattered on the dorsal surface. No distinct dark crossbands on hindlegs. Tympanum not distinctly different from dorsal coloration. Belly white and granular in the center, more smooth and transparent towards the flanks. Throat rather transparent (light bluish), ventral surface of arms and legs beige, ventral sides of finger and toe yellowish, anal region with white granules. No recognizable reddish coloration. Iris silvery-beige, dorsal part orange. Posterior iris periphery turquoise.

#### *Morphological variation*

In ZFMK 60121 and 59892 toe 5 is clearly longer than toe 3, whereas in ZFMK 60122, 59890, and 59891 toe 5 slightly longer than toe 3. ZFMK 59892 has only four toes on the left foot due to a malformation. Webbing of fingers and toes of the paratypes agrees well with that of the holotype.

#### *Etymology*

Derived from Latin *vittatus* meaning wearing a (ritual) band. Referring to the dark dorsolateral stripes typical for this species.

#### *Distribution*

Only known from the type locality Marojezy (latitude 14°26', altitude 700 m above sea level).

#### *Habits*

Calling males were sitting in the vegetation 0.5–2 m above the ground alongside a tiny brook in primary forest, at night.

#### *Call*

Recorded on 1 March 1995, 2130 h, at 22°C at the type locality. Two note types can be distinguished.

Type 1 is high-pitched, short, and arranged in series of 18–28 notes (mean  $21.8 \pm 3$ ,  $N = 10$ ). Note duration is 16–65 ms (mean  $33 \pm 10$  ms,  $N = 72$ ). Duration of intervals between notes is 58–305 ms (mean  $124 \pm 35$  ms,  $N = 68$ ). The interval between the last two notes of a series has mostly the longest duration. A note type 1 series generally lasts between 3000 and 4000 ms, with a note repetition rate of 6–7/s. Intensity is lower in the first notes of a series than in the last notes. Frequency is 6250–8250 Hz, no distinct

dominant frequency is recognizable. Frequency increases in the first half of a note, and decreases in its second half.

Type 2 is a very short, high pitched click-note and can be arranged in series of up to 6. Duration is 8–17 ms (mean  $13 \pm 3$  ms,  $N=13$ ). Duration of intervals between notes is 50–91 ms (mean  $61 \pm 12$  ms,  $N=11$ ). Frequency is 4700–6200 Hz.

## DISCUSSION

### MORPHOLOGICAL AND BIOACOUSTIC DIFFERENTIATION

All known species of the *Boophis majori* group are quite similar morphologically. Some species, e.g. *B. miniatus* and *B. pyrrhus*, differ in easily recognizable variables, such as relative nostril position and tympanum size, and thus can rather reliably be differentiated. The existence of species with intermediate characters, however, makes such an identification more difficult. The dilemma has been expressed by Duellman (1970) in his monograph on Central American hylid frogs: "Among the herpetological forms of life, frogs are notorious for their lack of definitive external characters." Due to the general soft configuration of amphibian bodies there is no such thing as an exact measure of any of the morphological variables. To reliably compare values, they must be measured by the same person, and without long interval between measurements. In fact, our absolute values of Tym/Eye ratios largely differ from those found by Blommers-Schlösser (1979b), although the respective intraspecific differences which she noted are in agreement with our findings. Even values for specimens measured by the same person at the same time can differ substantially depending on the state of preservation and of fixation of the specimens (Myers & Böhme, 1996).

Generally, morphological differences tend to be very low between closely related anuran species from Madagascar. Thus the resolution power of purely morphological analyses for the taxonomy and identification of sibling species is rather limited. Our data show that morphological differentiation in the *B. majori* group is not distinct enough to allow a completely reliable discrimination of all species based solely on morphological characters. A detailed univariate statistical analysis demonstrated significant differences in at least one variable between nearly all studied *Boophis* species, but in some cases similar differences also exist between populations of the same species (data not shown). On the other hand, the species can be easily identified by their advertisement calls, and species definitions in the *Boophis majori* group therefore are at present mainly based on bioacoustic data, as it also is the case in the *B. luteus* group (e.g. Andreone, 1996;

Andreone, Nincheri & Piazza, 1995), and partly in the *B. goudoti* group (Glaw & Vences, 1997a).

### SPECIES DIVERSITY

There is a remarkable increase of species recognition in the *B. majori* group. While Guibé (1978) recognized only a single species (*B. majori*), Blommers-Schlösser & Blanc (1991) recognized three, Glaw & Vences (1994) five. The current recognition of five additional new species brings up the total number from one to nine species within 20 years. Little doubt remains that the final total number of species in this group is even higher. A similar situation is found in the *B. luteus*-group: Guibé (1978) and Blommers-Schlösser & Blanc (1991) recognized only *B. luteus*, whereas 11 named species are distinguished at present and at least further four species are still undescribed (pers. obs.).

The rapid increase of species recognition is mainly due to the application of bioacoustic methods in the field. This remarkable example emphasizes that quick and economic methods are crucial to screen amphibian species diversity, to identify centres of endemism and to establish the conservational status of species, since otherwise many species will have disappeared before they are recognized as such.

### SAMPLE HETEROGENEITY

Specimens of the *B. majori* group collected by us were assigned to species based on bioacoustic and morphological characters including coloration. In most cases the different data sets revealed congruent results. However, there are three important exceptions in which the homogeneity of the species as defined by us is not clear. Using a conservative approach we considered only clearly different forms as separate taxa. Further studies are necessary to clarify the taxonomy of the following populations:

- (1) *Boophis picturatus* specimens from Vohiparara are smaller and differ distinctly by coloration of body and eye from specimens of the Andasibe area. Their call repertoire includes a second note type not heard in Andasibe. More data, especially from geographically intermediate populations are necessary to assess the relevance of the observed differences.
- (2) *Boophis miniatus* males from the Ranomafana region are smaller and have different body proportions than specimens from the Tolagnaro region. Their spotted colour pattern is only found in one out of seven Tolagnaro specimens. No call data are available for these Ranomafana populations. The morphological differences may be explained by the sampling dates: Most Ranomafana specimens were collected outside of the rainy season; they may be

subadults, showing juvenile morphometric patterns.

- (3) Most male *Boophis marojezensis* from the type locality Marojezy are relatively large (SVL 25–26 mm). In other populations (Mandraka, An'Ala, Ranomafana region), males generally do not reach 25 mm SVL. Only calls consisting of few (3–5 notes) are known from Marojezy, whereas other populations have up to 21 notes per call. However, only few calls were recorded at Marojezy, and number of notes per call may be a variable parameter, depending on the motivational state of the calling specimen.

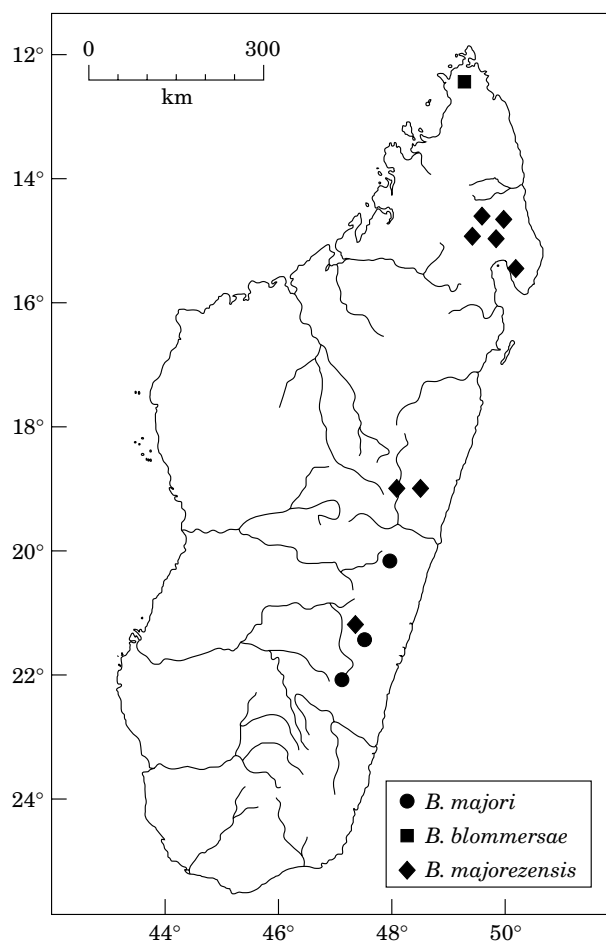
#### BIOGEOGRAPHY

Biogeographical regions within Madagascar based on distribution patterns of amphibians and reptiles were first sketched by Angel (1942) who only considered the reptiles, and slightly modified by Glaw & Vences (1994). According to these authors, Madagascar is divided into the Western and Eastern Domains which are further subdivided. The Western Domain consists of the Western, South-Western, and Southern regions, whereas the Eastern Domain contains the Sambirano (North-Western), Northern, Northern-Central, North-Eastern, Eastern, Central, Southern Central, and South-Eastern Regions. All rainforests are within the Eastern Domain.

Raxworthy & Nussbaum (1995) largely corroborated these divisions within northern Madagascar by an analysis of patterns of endemism and distribution of dwarf chameleons (genus *Brookesia*). They gave more exact definitions of the regions identified in northern Madagascar which they called Northwest (=Sambirano), Montagne d'Ambre (=North), Tsaratanana (=Northern-Central), Northeast, and East.

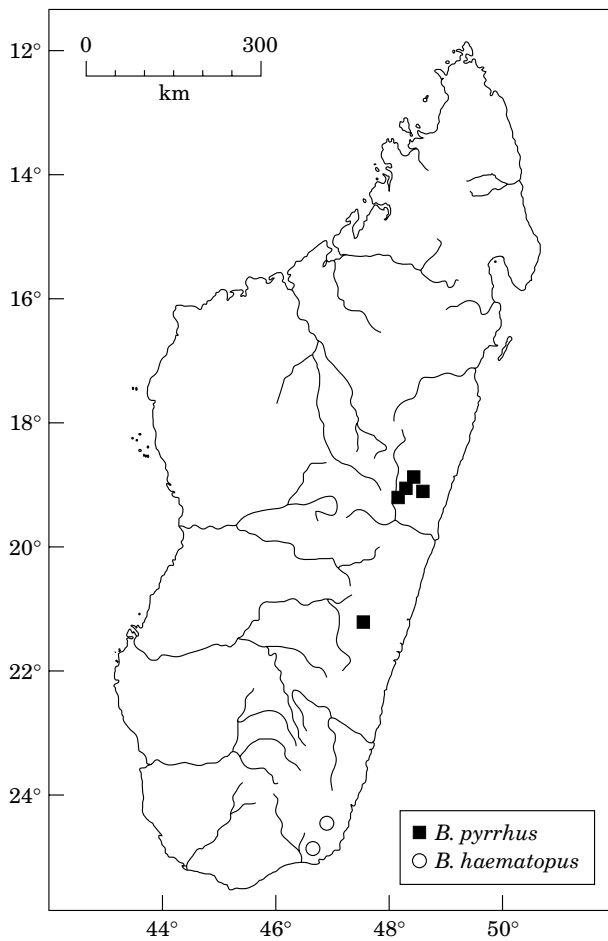
Biogeographical patterns of amphibians in Madagascar are still poorly understood although a detailed analysis was recently provided by Blommers-Schlösser & Blanc (1993). Many results of this study must already be considered as outdated, mainly due to two reasons: (a) recent field surveys revealed new locality records for many species and (b) species identification was mainly based on preserved material and therefore could not distinguish between morphologically similar sibling species. Although distributional data of *Boophis* are still very incomplete, two patterns observed in the *B. majori* group (Figs 27–29; Tables 6, 7) are worthy of mention.

- (1) There is a distinct increase in species diversity from north and from south towards the centre, with the highest diversity in the area around Andasibe (=Perinet). A similar situation can be observed in most other *Boophis* species groups (Table

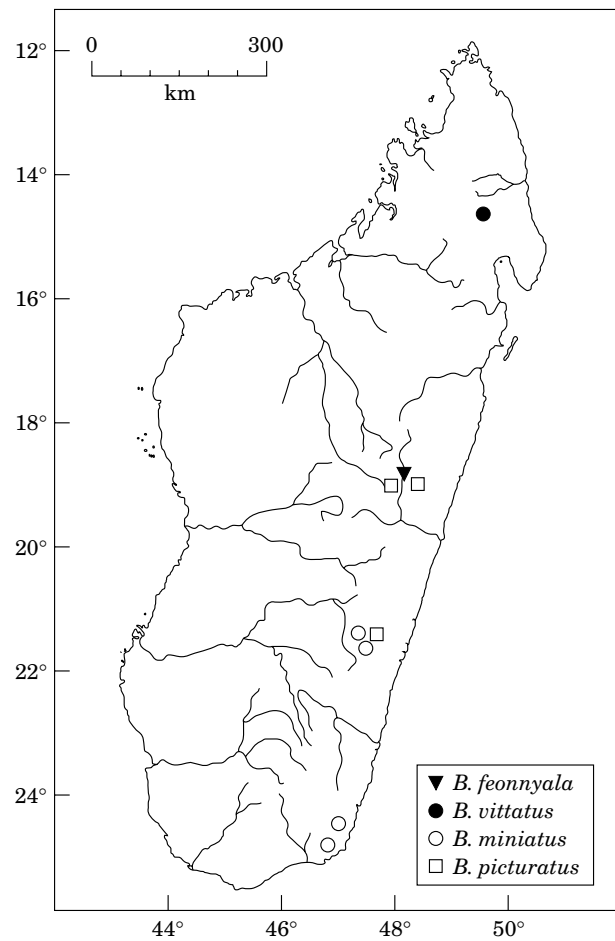


**Figure 27.** Distribution map of *Boophis blommersae*, *B. marojezensis* and *B. majori*. Positioning of symbols is only approximate; for exact coordinates, see Table 1.

7; the *B. albilabris* group and the *B. microtympaanum* group have a low species diversity and are not considered here). It corresponds well with the diversity gradients observed by Lees (1996) in satyrine butterflies. In several animal groups the highest diversity is found in central eastern Madagascar ("Perinet-effect"; Lees, 1996). The extraordinary anuran species diversity around Andasibe may have possible causes: (i) The complex mosaic of different humid primary and secondary habitat types within a small area is certainly a major pre-condition for high species diversity. (ii) The mid-latitude position of the Andasibe region encourages species which are mainly distributed in northern or southern Madagascar to extend into the Andasibe area. (iii) The mid-altitudinal position at about 900 m seems close to the maximum elevational limit for several coastal species (e.g. *Heterixalus madagascariensis*) and to the minimum elevational limit for highland species (e.g. *Boophis*



**Figure 28.** Distribution map of *Boophis pyrrhus* and *B. haematopus*. Positioning of symbols is only approximate; for exact coordinates, see Table 1.



**Figure 29.** Distribution map of *Boophis picturatus*, *B. miniatus*, *B. vittatus* and *B. feonnyala*. Positioning of symbols is only approximate; for exact coordinates, see Table 1.

*goudoti*) on the other hand. (iv) Andasibe is on the main route between the capital Antananarivo and the important harbour city Toamasina (Tamatave) and is therefore much more accessible than most other rainforests in Madagascar. This has led to an enormous bias of scientific studies in this region. (v) At least some species appear to be real endemics in the Andasibe area (e.g. *Mantella aurantiaca*). However, distribution patterns in the *B. majori* group do not indicate a high level of endemism. All species known from the Andasibe area except *B. feonnyala* have also been found in at least one other area as defined in Table 7.

- (2) Currently no members of the *B. majori* group are known from the Western Domain and the Sambirano region, and only one species (*B. blommersae*) is known from Montagne d'Ambre. Western Madagascar is rather dry, with only isolated patches of wetter forest, and the apparent lack of representatives of the *B. majori* group in this region

can be explained by the rareness of humid forest and brooks. In contrast, the Sambirano Region contains rainforest areas, and species of the *B. majori* group could well be expected to occur there. Also the *B. rappiodes* group has currently no known member in the Sambirano Region and Montagne d'Ambre, and the *B. tephraeomystax* group is only represented in both regions by the ubiquitous species *B. tephraeomystax* which does generally not occur in rainforests. A comparable situation is found in the Malagasy poison frogs (genus *Mantella*): only representatives of the *M. betsileo* group occur in the West, North, and North-West, whereas the other species groups are restricted to eastern and north-eastern Madagascar (pers. obs.). Rainforests of Sambirano and Montagne d'Ambre apparently have a relatively high endemicity at the species level in some groups such as dwarf chameleons (genus *Brookesia*; Raxworthy & Nuss-



**Table 6.** Locality records of species of the *B. majori* group and of *B. difficilis*, and their specific appurtenance according to the present revision. References are coded as follows: (1) Blommers-Schlösser (1979b); (2) Blommers-Schlösser & Blanc (1991); (3) Glaw & Vences (1992a); (4) Glaw & Vences (1992b); (5) Glaw & Vences (1994); (6) Raxworthy & Nussbaum (1994)

Record by	Locality	Record as	Correctly refers to
1,2,3,4,5	Andasibe	<i>B. difficilis</i>	<i>B. pyrrhus</i>
3,4,5	Nahampoana	<i>B. difficilis</i>	<i>B. haematopus</i>
3,4,5	Andasibe	<i>B. cf. miniatus</i>	<i>B. picturatus</i>
1,2	Andasibe	<i>B. miniatus</i>	<i>B. picturatus</i>
2,4	Marojezy	<i>B. majori</i>	<i>B. marojezensis</i>
1,2,4,5	Mandraka	<i>B. majori</i>	<i>B. marojezensis</i>
2,4	Montagne d'Ambre	<i>B. majori</i>	<i>B. blommersae</i>
6	Montagne d'Ambre	<i>B. miniatus</i>	<i>B. blommersae</i>

**Table 7.** Species diversity of *Boophis* species groups at different collecting areas, arranged from north to south. Data of the *B. majori* group from the present study, of the remaining groups from Glaw & Vences (1994, 1997a,b and pers. obs.). Localities of species of the *B. majori* group were grouped as follows: Montagne d'Ambre area (M. d'Ambre); Marojezy area (Marojezy; Tsararano); Andasibe area (Andasibe; Mantady; An'Ala; Ankeniheny); Ranomafana area (Ranomafana; Ifanadiana; Vohiparara; Ambatolahy); Andohahela area (Isaka-Ambobo; Andohahela; Nahampoana; Pic St. Louis)

Region	<i>B. majori</i> group	<i>B. luteus</i> group	<i>B. rappiodes</i> group	<i>B. goudoti</i> group	<i>B. tephraeomystax</i> group	Total
Sambirano	0	2	0	1	1	4
Montagne d'Ambre	1	1	0	2	0	4
Marojezy	2	4	1	3	2	12
Andasibe	5	4	5	6	6	26
Ranomafana	5	5	2	5	3	20
Andohahela	2	3	1	3	2	11

baum, 1995, 1996b) and cophyline frogs (Microhylidae) except *Anodonthyla* (pers. obs.), indicating that these regions were generally important for speciation events. However, the rather low species diversity of *Boophis* in the Sambirano and Montagne d'Ambre regions may indicate that these areas were less important for speciation of *Boophis*.

#### PHYLOGENY

No hypothesis of the intrageneric phylogeny of *Boophis* has yet been published (see Cadle, 1995). Blommers-Schlösser & Blanc (1991) characterized *Boophis* species groups by external characters and ecology, but did not polarize these rather variable characters phylogenetically. More relevant characters may be found in a comparative osteological study. One characteristic common to many *Boophis* is the lack of the anterolateral process of the hyoid plate, which is known from *B. goudoti* (Trewavas, 1933; Guibé, 1978), *B. rhodoscelis* (Trewavas, 1933) and *B. albilabris* (Cadle, 1995). Our osteological descriptions of two *B. miniatus*

specimens, representing the first published data of a species of the *B. majori* group, corroborate that the anterolateral process is also absent in this species. The process is also absent in *B. cf. sibilans*, *B. cf. erythroductylus* and *B. microtypanum* (pers. obs.), but is present in *B. tephraeomystax* (Liem, 1970; pers. obs.). Within the rhacophorines, only four species of the oriental genus *Chirixalus* and one species of *Polypedates* are known to share the absence of the anterolateral process (Liem, 1970; as alary process). The process is generally present in ranids (Liem, 1970; pers. obs.) and universally present in the Mantellinae (pers. obs.). Although an unequivocal outgroup comparison is not possible at present due to the chaotic systematics of ranoid frogs (Duellman & Trueb, 1986), it currently is most plausible to consider the absence of the anterolateral process in *Boophis* as derived. Since representatives of all *Boophis* species groups except the *B. tephraeomystax* group lack the process, the latter may represent an assemblage of basal *Boophis* taxa. Species of the *B. tephraeomystax* group breed in stagnant, shallow water bodies (Blommers-

Schlösser, 1979b; Glaw & Vences, 1994, 1997b), whereas nearly all other *Boophis* are brook breeders. Breeding in stagnant water may therefore be the pleiomorphic condition in *Boophis*.

The phylogenetic relationships within the *B. majori* group are still more difficult to assess. The monophyly of the group is not clear; all species are very similar morphologically, but no clearly defined synapomorphies of all species are known. However, it is possible to classify most species into two subgroups: (a) small species without red coloration (*B. blommersae*, *B. vittatus*, *B. marojezensis*), which mainly occur in northern Madagascar; (b) larger species with distinct red colour on body and/or web (*B. miniatus*, *B. picturatus*, *B. pyrrius*, *B. haematopus*). Only *B. feonyala* (relatively large, without distinct red) and *B. majori* (small, red webbing) do not clearly fit into this partition. Based on the structural similarities of the calls, *B. pyrrius* and *B. haematopus* are sister species.

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