

A REVISION OF THE *SCAPHIOPHRYNE MARMORATA* COMPLEX OF MARBLED TOADS FROM MADAGASCAR, INCLUDING THE DESCRIPTION OF A NEW SPECIES

MIGUEL VENCES¹, CHRISTOPHER J. RAXWORTHY², RONALD A. NUSSBAUM³ AND FRANK GLAW⁴

¹*Institute for Biodiversity and Ecosystem Dynamics, Zoological Museum, Universiteit van Amsterdam, PO Box 94766, 1090 GT Amsterdam, The Netherlands*

²*American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA*

³*Division of Reptiles and Amphibians, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, USA*

⁴*Zoologische Staatssammlung München, Münchhausenstrasse 21, 81247 München, Germany*

A revision of the available material hitherto assigned to the endemic Malagasy microhylid toad *Scaphiophryne marmorata* finds this taxon to be a complex of three species. In this study we resurrect *Scaphiophryne spinosa* Steindachner, 1882 from the synonymy of *S. marmorata* and describe a new species from central eastern Madagascar. These three *Scaphiophryne* species are characterized by their distinctly expanded terminal finger discs, a character only shared with *S. gottlebei*. *S. spinosa* is characterized by a highly granular back, with large spiny tubercles above the forelimb insertion and in the tympanic region, while *S. marmorata* is dorsally covered by less prominent and more regular tubercles. The new species is distinguished from both *S. marmorata* and *S. spinosa* by its large body size (SVL 47-60 mm), a smoother dorsal skin, and reddish terminal finger discs in life. *S. spinosa* is distributed in low- and mid-altitude rainforests along the east coast, whereas the new species is only known from mid-altitude rainforest in the Fierenana region. In contrast, records of *S. marmorata* include eastern mid-altitude rainforests and several more arid western sites.

Key words: Amphibia, Anura, Madagascar, Microhylidae, frog taxonomy.

INTRODUCTION

Several of the anuran genera of Madagascar belong to diverse endemic radiations such as the Mantellidae or the microhylid subfamily Cophylinae (Vences & Glaw, 2001). Other genera, in contrast, are less speciose and have uncertain affinities within their respective higher taxa. Such genera are often distributed in the xeric regions of western Madagascar and show reproductive modes typical for arid environments (Vences *et al.*, 2000a).

One of these groups is the genus *Scaphiophryne*, which – together with the monotypic *Paradoxophyla* – is classified in the endemic subfamily Scaphiophryninae (Blommers-Schlösser & Blanc, 1991), or even in the separate family Scaphiophrynidae (Dubois, 1992). *Scaphiophryne* are unique in the morphology of their tadpoles, which are intermediate between the ranoid and the microhylid type (Wassersug 1984). They reproduce in lentic, often temporary waters, and lay a large number of small eggs (Blommers-Schlösser, 1975; Vences *et al.*, 2002a). This reproductive mode is typical for seasonal areas such as savannas (e.g. Rödel, 2000), but

several species of *Scaphiophryne* are also known from the mountains and rainforest areas of central and eastern Madagascar. According to Blommers-Schlösser & Blanc (1991) these comprise *Scaphiophryne madagascariensis*, *S. marmorata* and *S. pustulosa*. Three further species – *S. brevis*, *S. calcarata* and *S. gottlebei* – are known from western and southern Madagascar.

Vences *et al.* (2002b) provided evidence that the name *Pseudohemisus pustulosus* Angel & Guibé, 1945 is a junior synonym of *Calophrynus madagascariensis* Boulenger, 1882. Consequently, they applied the name *Scaphiophryne madagascariensis* to populations previously assigned to *S. pustulosa*, and verified that no available name exists for specimens from the Andringitra Massif in south-eastern Madagascar which has thus far been referred to as *S. madagascariensis*.

Scaphiophryne madagascariensis and the new form from Andringitra are known from high altitudes along the central mountain chain of Madagascar, and are characterized by lacking greatly expanded terminal discs on fingers and toes. In contrast, *S. marmorata* is known from forests in eastern Madagascar, and from relict forests in the arid west (Glaw & Vences, 1994). It is characterized by its expanded terminal finger discs (and slightly expanded toe discs), a state that so far was thought to be shared by only one further species, *S.*

Correspondence: M. Vences, Institute for Biodiversity and Ecosystem Dynamics, Zoological Museum, Universiteit van Amsterdam, PO Box 94766, 1090 GT Amsterdam, The Netherlands; *E-mail:* vences@science.uva.nl

gottlebei from Isalo in south-western Madagascar (Busse & Böhme, 1992). Recent fieldwork revealed the presence of additional species with this character in eastern Madagascar. We herein revise the material of green-coloured *Scaphiophryne* with expanded finger discs available to us, resurrect the name *Scaphiophryne spinosa* Steindachner, 1882 and describe one highly differentiated new species.

MATERIALS AND METHODS

The present revision is based on material in the following collections: The Natural History Museum, London (formerly British Museum of Natural History) (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Museo Regionale di Scienze Naturali, Torino (MRSN); Naturhistorisches Museum Wien (NMW); University of Michigan, Museum of Zoology (UMMZ); Zoölogisch Museum Amsterdam (ZMA); Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK); Zoologische Staatssammlung München (ZSM).

Specimens were measured with calipers to the nearest 0.1 mm. Measurements taken were SVL (snout-vent length), HW (head width at the maxillary rictus), HL (head length, from the maxillary commissure to the snout tip), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (horizontal tympanum diameter), HAL (hand length, from the carpal-metacarpal articulations to the tip of the longest finger), FORL (forelimb length, from the axil to the tip of the longest finger), HIL (hindlimb length, from the cloaca to the tip of the longest toe), FOL (foot length, from the tarsal-metatarsal articulations to the tip of the longest toe), FOTL (foot length including tarsus, from the tibiotarsal articulation to the tip of the longest toe), IMTL and IMTH (maximum length and height of inner metatarsal tubercle), FD4 (maximum width of the terminal disc of fourth finger). The sex and maturity of preserved specimens were either determined by obvious secondary sexual characters of males in breeding conditions (vocal sac) or by dissection and gonad examination.

Advertisement calls were recorded in the wild or in captivity and were analysed on a PC using the software Cooledit (Syntrillium Corp.). Statistical analyses were carried out using SPSS for Windows, version 10. Measurements are given as range, with mean \pm standard deviation in parentheses. DNA sequences of a fragment (ca. 540 base pairs, depending on the number of indels) of the mitochondrial 16S rRNA gene were obtained using primers and protocols given in Vences *et al.* (2000b), and have been deposited in Genbank. Voucher specimens for sequences and Genbank accession numbers are as follows: *Scaphiophryne boribory* sp. n. (ZSM 644/2000, AJ314810), *S. marmorata* (ZSM 303/2000, AJ417567), *S. spinosa* (ZSM 1154/2001, AF215383).

RESULTS AND SPECIES ACCOUNTS

During the revision of the available material thus far attributed to *S. marmorata*, we noted the existence of two distinct species: a large species with a very granular and spiny dorsal skin, and a smaller, less granular species. Careful examination showed that the less granular species is distinguished from the spiny species by the following characters: (1) smaller body size (male SVL 32-49 mm vs. 40-48 mm; Table 1); (2) presence of a variable number of regular larger granules on head and body, usually including a symmetrical pair of elongated tubercles in the shoulder region and a smaller pair on the posterior dorsum, these tubercle pairs being especially distinct in subadults (vs. a large number of irregular dorsal tubercles of different size, and absence of elongated symmetrical tubercles in the shoulder region); (3) absence of large spiny tubercles above forelimb insertion, at posterior end of maxilla, and in tympanic region (vs. presence); (4) tympanum often faintly recognizable, its horizontal diameter larger than 50% of eye diameter (vs. tympanum usually totally concealed, smaller than 50% of eye diameter – if visible); (5) ventral pattern variable, but often (especially in juveniles) with contrasting dark-light marbling, the dark colour extending onto the posterior belly and the femur (vs. absence of contrasted marbling, usually dark on throat, chest and anterior belly, light on posterior belly and femur). These differences were already visible in juveniles of both species (e.g. UMMZ 191157; ZSM 303/2000). We also recognized a third larger species, with a smoother dorsal body surface and reddish discs on the fingers and toes. The three species showed a relevant molecular differentiation in the sequenced fragment of the 16S rRNA gene (see comments in the section of *S. boribory* below).

SCAPHIOPHRYNE MARMORATA BOULENGER, 1882 (FIG. 1-2)

Diagnosis. A *Scaphiophryne* with highly expanded terminal discs on the fingers; dorsally green with symmetrical dark markings, and lacking pink markings; adult SVL 32-49 mm; typically two symmetrical pairs of larger tubercles, an elongated pair in the shoulder region and a smaller pair on the posterior dorsum; absence of large spiny tubercles above forelimb insertion, at posterior end of maxilla, and in tympanic region; tympanum typically visible with a horizontal diameter > 50% of eye diameter; ventral pattern often with contrasted dark-light marbling, the dark colour extending onto the posterior belly and the femur.

Material examined. BMNH 1947.2.30.81 (holotype by monotypy; East Betsileo, collected by W. D. Cowan); MNHN 1883.581 (Madagascar); MNHN 1953.241 (large series of juveniles; Andasibe); MNHN 1962.923 (Andasibe, collected by E. R. Brygoo); MNHN 1962.924 (Andasibe, collected by J. Arnoult); MNHN 1965.315 (Andasibe); MNHN 1975.1569 (Andasibe); UMMZ 211504-211505 (Zahamena reserve, Volotsangana river, 850 m; collected by C. J.

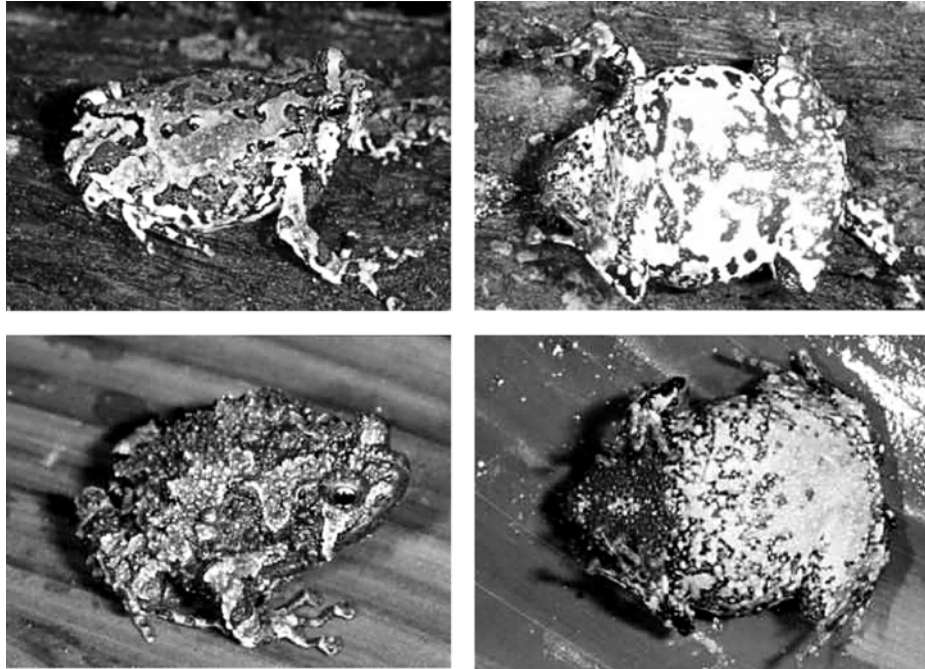


FIG. 1. Comparative dorsolateral and ventral views of *Scaphiophryne marmorata* (upper figures; Andasibe, 1995; specimen not collected) and *S. spinosa* (lower figures; An'Ala, close to Andasibe, 1996; specimen not collected).

Raxworthy, J. B. Ramanamanjato, A. Raselimanana, A. Razafimanantsoa and A. Razafimanantsoa on 26 February 1994); UMMZ 219487 (Kirindy forest, 20° 04.099'S, 44° 39.403'E; collected by C. J. Raxworthy, J. B. Ramanamanjato, A. Raselimanana, A. Razafimanantsoa and A. Razafimanantsoa on 31 January 1996); UMMZ 219488-219489 and 219491-219495 (Antranopasasy, 18° 42.481'S, 44° 42.981'E, Bemaraha reserve; collected by C. J. Raxworthy, J. B. Ramanamanjato, A. Raselimanana, A. Razafimanantsoa and A. Razafimanantsoa, 8-11 March 1996); UMMZ 225606 and UMMZ 225608-225613 (Ampahanana forest, near Fierenana, 18° 29.53'S, 48° 26.68'E, 1000-1200 m altitude; collected by O. Ramilison, N. Rabibisoa and D. Foley IV on 22-24 January 1998);



FIG. 2. *Scaphiophryne marmorata*, specimen from western Madagascar (Kirindy).

UMMZ 227489 (Isalo region; collected by local collectors); UMMZ 227499 (Namoroka reserve, 16° 28.189'S 45° 20.906'E; collected by C. J. Raxworthy, J. Rafanomesantsoa, J. B. Ramanamanjato, A. Razafimanantsoa and A. Razafimanantsoa on 6 December 1996); ZMA 6877 (1077 and 1121-1122) (Andasibe; collected by R. M. A. Blommers-Schlösser on 24 December 1972); ZFMK 52760 (Andasibe, collected by local collectors in 1991); ZSM 303/2000 (Andasibe, collected by F. Glaw on 10 April 2000).

Distribution. The type locality is the region of East Betsileo. Other precise and reliable localities are the following: (1) Zahamena, (2) Andasibe, (3) Fierenana, (4) Namoroka, (5) Bemaraha, (6) Kirindy, and (7) the Isalo region. The species is distributed in mid-altitude rain-forest localities of central eastern Madagascar, and is known from four sites in western Madagascar (Fig. 3). This combined humid and arid habitat distribution is highly unusual for an amphibian species in Madagascar. The localities Foizana, Ampasy and Ambana in Blommers-Schlösser & Blanc (1991) are here assigned to *S. spinosa* (see below).

Natural history. The dissected females UMMZ 227489 and UMMZ 225610 contained a large number of small oocytes (diameter 1.2 mm) which were yellowish with a large dark brown pole. Advertisement calls are unknown.

Comments. The holotype of *S. marmorata* (BMNH 1947.2.30.81) is a subadult specimen (see Table 1 for measurements). However, with the exception of SVL, the *marmorata* type agrees well with the diagnosis given above. Among the specimens examined, some variation in coloration is apparent: specimens from the east are

TABLE 1. Morphometric measurements (all in mm) of adult specimens of *Scaphiophryne marmorata*, *S. spinosa* and *S. boribory*, and of the subadult holotype of *S. marmorata*. For abbreviations of measured variables, see Materials and Methods; further abbreviations used: M (male); F (female); SA (subadult); HT (holotype); PT (paratype); RHL (relative hindlimb length: point reached by tibiotarsal articulation when the hindlimb is adpressed along the body). RHL is coded as follows: 0, the tibiotarsal articulation does not reach the forelimb insertion; 1, it reaches the forelimb insertion; 2, it reaches between forelimb and tympanic region; 3, it reaches tympanic region.

Specimen	Sex	Status	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FOTL	FOL	IMTL	IMTW	FD4	RHL
<i>S. marmorata</i>																			
BMNH 1947.2.30.81	SA	HT	29.1	10.0	8.9	(1.8)	3.0	1.7	1.6	2.5	10.0	20.5	41.8	20.6	14.3	2.9	2.0	—	2
UMMZ 219487	M	—	41.6	13.9	11.8	(2.3)	3.5	2.9	1.1	2.9	14.8	31.2	56.9	26.3	18.5	3.7	2.6	2.2	1
UMMZ 219489	M	—	39.9	13.2	11.0	—	3.2	2.3	1.5	2.2	14.1	28.3	51.4	25.1	17.9	2.9	2.3	2.5	1
UMMZ 225606	M	—	35.8	13.1	10.5	(1.8)	3.5	2.3	1.3	2.8	12.4	25.5	49.0	23.5	17.0	2.6	2.3	2.0	1
UMMZ 225608	M	—	32.4	11.5	9.6	—	3.5	2.0	1.3	2.2	11.4	21.8	45.1	20.7	15.4	3.2	2.3	1.6	1
UMMZ 225612	M	—	33.0	11.7	8.8	—	3.1	2.0	1.4	2.4	11.7	23.9	43.3	21.6	15.2	2.7	2.3	1.9	1
ZMA 6877 (1077)	M	—	35.9	11.8	9.9	—	3.8	2.5	1.4	2.6	12.6	25.5	50.0	23.7	17.4	3.4	2.4	2.2	1
ZMA 6877 (1121)	M	—	35.6	13.3	10.8	(2.0)	4.0	2.2	1.6	2.7	12.8	26.6	46.4	23.3	16.5	3.3	2.2	2.1	1
ZMA 6877 (1122)	M	—	36.2	12.0	10.8	(2.0)	3.7	2.0	1.2	3.0	13.2	26.4	51.1	24.1	17.6	3.1	2.4	2.0	2
UMMZ 211504	F	—	37.5	12.7	11.0	—	3.5	2.4	1.5	3.0	11.6	26.0	49.1	24.2	16.7	3.0	2.3	2.0	1
UMMZ 211505	F	—	43.5	13.3	11.3	(2.0)	3.7	2.5	1.5	2.8	14.3	28.2	57.0	27.4	19.7	3.3	2.4	2.0	1
UMMZ 225609	F	—	34.9	12.2	10.4	—	2.7	2.2	1.3	2.5	12.2	24.6	50.3	23.8	17.0	3.3	2.5	2.1	1
UMMZ 225610	F	—	40.4	12.6	10.6	—	3.0	2.6	1.1	2.9	13.8	27.5	56.0	26.9	19.1	3.3	2.5	2.4	1
UMMZ 225611	F	—	36.6	13.5	11.1	—	3.8	2.3	1.3	3.3	14.0	27.3	54.2	26.1	18.9	3.2	2.8	2.2	3
UMMZ 225613	F	—	39.9	13.9	11.1	—	3.6	2.7	1.2	3.2	13.2	26.7	51.1	25.5	17.9	3.2	2.6	2.1	1
UMMZ 227489	F	—	48.5	17.1	13.6	(2.5)	4.3	3.0	1.8	3.5	(13.0)	30.9	59.5	28.8	20.4	3.9	2.8	3.4	1
<i>S. spinosa</i>																			
UMMZ 191154	M	—	40.4	13.7	12.0	—	3.6	2.7	1.5	2.8	13.9	27.9	58.0	27.6	19.9	3.6	2.5	2.2	2
UMMZ 191155	M	—	39.7	12.5	11.4	—	3.6	2.4	1.9	2.7	13.3	26.4	55.1	26.2	19.0	3.4	2.5	2.3	1
UMMZ 191158	M	—	42.1	14.1	12.3	—	3.7	3.0	1.9	2.5	13.8	31.1	57.5	28.8	20.3	3.0	2.3	2.4	3
UMMZ 198870	M	—	48.3	16.0	13.3	—	4.6	3.4	1.7	3.1	16.5	34.0	66.0	32.3	22.6	3.3	3.0	2.6	2
UMMZ 198871	M	—	46.5	15.8	14.1	(1.6)	4.1	3.1	2.0	3.0	16.4	35.1	65.3	31.3	22.3	4.0	3.0	2.6	3
UMMZ 198872	M	—	48.0	14.9	13.3	(1.7)	4.4	3.3	1.9	3.1	15.7	34.0	66.7	31.3	22.4	3.8	2.8	2.5	1
UMMZ 198873	M	—	46.9	15.8	13.8	(1.4)	4.9	3.0	1.8	3.2	17.2	34.4	64.9	31.5	22.6	3.8	2.7	3.0	2
UMMZ 198874	M	—	45.0	14.3	12.4	—	3.7	2.9	1.7	3.1	16.5	32.4	62.0	31.0	22.1	3.6	2.7	2.5	3
UMMZ 198875	M	—	45.4	14.8	12.2	—	4.1	3.1	1.7	3.0	16.6	32.7	65.3	31.0	22.3	3.6	3.0	3.0	3

UMMZ 211487	M	—	45.3	14.3	12.6	—	4.6	3.1	1.7	2.5	16.0	31.9	64.0	28.9	20.1	3.2	2.8	2.3	3
UMMZ 211489	M	—	45.7	14.5	12.3	—	4.1	3.3	1.7	2.6	16.1	30.7	64.5	29.4	21.4	3.3	2.6	2.7	2
UMMZ 211490	M	—	44.7	14.4	12.6	(1.9)	4.7	2.8	1.9	2.9	15.5	31.4	64.3	29.9	21.5	3.6	2.5	2.7	2
UMMZ 211491	M	—	44.3	14.6	12.0	—	4.6	2.9	1.6	3.0	16.3	31.5	64.0	30.6	22.7	3.0	2.7	2.5	3
UMMZ 211492	M	—	46.0	14.8	12.4	—	4.8	2.9	1.6	2.7	16.5	31.5	61.2	31.0	22.6	3.4	2.9	2.6	2
UMMZ 227498	M	—	41.0	13.4	11.8	—	3.3	2.7	1.5	2.8	13.8	30.1	57.3	26.1	19.1	3.5	2.5	2.3	2
MNHN 1973.575	F	—	43.0	14.2	12.1	—	4.4	3.0	1.6	3.0	14.6	31.1	58.7	28.3	20.1	2.9	2.2	2.4	2
NMW 3919	F	HT	43.6	14.5	12.8	—	4.5	2.9	1.8	3.5	14.7	31.1	61.3	28.0	19.6	3.3	2.5	2.4	1
UMMZ 191156	F	—	47.2	14.0	13.0	—	4.0	2.8	1.6	3.3	15.9	32.6	63.6	30.9	21.9	3.7	2.6	2.2	2
UMMZ 211493	F	—	48.2	17.0	13.5	—	4.5	2.9	1.7	3.4	17.0	34.3	68.9	32.8	24.4	3.6	3.0	2.7	3
<i>S. boribory</i>																			
UMMZ 225614	M	HT	56.3	17.9	14.1	—	4.6	3.2	2.0	3.7	19.4	36.8	71.9	36.2	25.0	3.8	3.0	3.2	0
UMMZ 225615	M	PT	57.4	17.6	13.7	—	4.8	3.0	2.2	4.0	20.5	36.6	76.1	38.6	27.5	4.5	3.5	3.4	0
UMMZ 225617	M	PT	53.3	17.2	13.2	—	4.5	3.6	1.9	2.2	20.1	36.1	74.7	38.2	26.6	3.7	3.2	2.7	1
UMMZ 225618	M	PT	50.8	16.7	13.9	—	5.0	3.2	2.2	3.8	19.5	37.2	75.0	37.0	26.4	4.5	3.4	3.0	1
UMMZ 227490	M	PT	55.2	17.0	13.1	—	4.5	3.1	2.2	3.4	20.5	36.9	74.6	37.9	27.8	4.0	3.1	2.8	1
UMMZ 227492	M	PT	57.0	16.7	13.0	—	4.7	3.3	2.1	3.6	19.2	34.6	74.7	37.9	27.0	4.6	3.2	2.6	1
UMMZ 227494	M	PT	59.1	17.9	13.8	—	4.5	3.2	2.1	3.6	20.1	36.4	80.8	40.8	28.6	4.7	3.4	3.1	1
UMMZ 227495	M	PT	59.8	18.8	14.5	—	5.3	3.2	1.8	3.2	20.0	37.9	77.4	37.8	27.0	4.6	3.5	2.7	1
UMMZ 227496	M	PT	58.5	18.6	14.7	—	4.7	3.3	2.0	3.6	20.8	36.9	78.1	38.7	27.6	4.1	3.6	3.2	1
UMMZ 227497	M	PT	57.5	17.0	13.3	—	4.6	3.1	1.7	3.3	19.4	36.4	80.9	37.6	26.6	4.3	3.0	2.8	1
ZSM 644/2000	M	PT	49.0	16.0	13.3	—	4.2	2.9	1.7	3.1	18.7	37.2	68.4	33.4	24.2	4.0	3.1	2.6	2
ZSM 8/2000	M	PT	54.2	17.7	13.6	—	4.3	3.6	1.8	3.5	20.0	35.8	74.8	36.5	25.8	4.7	3.4	2.7	1
UMMZ 225616	F	PT	56.6	17.4	13.8	—	4.8	3.0	2.0	3.4	19.9	34.6	74.3	37.0	26.3	4.2	3.3	3.4	0
UMMZ 227491	F	PT	59.4	18.2	15.0	—	5.0	3.3	2.0	3.4	20.1	39.4	79.7	39.2	27.1	4.6	3.7	3.2	1
UMMZ 227493	F	PT	55.3	15.9	13.3	—	4.0	3.1	2.0	3.9	19.3	35.7	73.7	35.8	25.9	3.9	3.3	3.1	0
ZSM 7/2000	F	PT	55.8	17.2	13.8	—	4.4	3.5	1.6	3.3	19.9	42.7	79.5	39.0	26.5	3.7	3.1	2.2	2
ZFMK 76102	F	PT	52.6	17.6	14.0	—	5.0	3.5	1.9	3.4	20.7	35.3	76.8	38.1	26.1	4.4	3.0	2.6	1

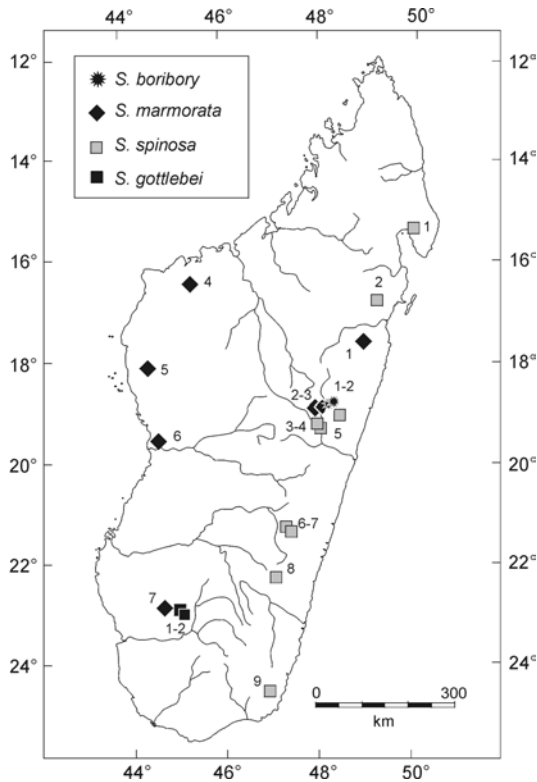


FIG. 3. Distribution map of species of *Scaphiophryne* with expanded finger discs (*S. boribory*, *S. gottlebei*, *S. marmorata*, *S. spinosa*). The only known localities for *S. gottlebei* are in the Isalo region: (1) Vallée (or Canyon) des Singes within the Isalo Reserve (Busse & Böhme, 1992; and Raxworthy, unpublished); and (2) 2 km from Ilakaka (28° 45'29"S, 45° 15'17"E) according to a personal observation by K. Schmidt in 1999. Localities of the other three species are listed in the respective species accounts; locality numbers in the map correspond to those in the text.

usually green, while those from the west often have a largely brown pattern. This variation in coloration and the unusual distribution of this species may suggest that two or more taxa are involved. However, an assessment of the genetic differentiation is necessary before the taxonomic status of the western populations can be reliably determined.

SCAPHIOPHRYNE SPINOSA STEINDACHNER, 1882 (FIG. 1, 4)

Diagnosis. A *Scaphiophryne* with highly expanded terminal discs on the fingers; dorsally green with symmetrical dark markings, and lacking pink markings; adult SVL 40–48 mm; presence of a large number of irregular dorsal tubercles of different size, and absence of elongated symmetrical tubercles in the shoulder region; presence of large spiny tubercles above forelimb insertion, at posterior end of maxilla, and in tympanic region; tympanum typically not visible, or if visible, with a horizontal diameter < 50% of eye diameter; ventral pattern usually lacking contrasting marbling (especially on the belly), and typically dark on throat, chest and anterior belly, light on posterior belly and femur.

Material examined. MNHN 1953.243 (2 juveniles; Moramanga); MNHN 1975.1567 (Ampasy forest, Ivohibe); MNHN 1973.575 (Ambana, Chaînes Anosyennes; collected by C. P. Blanc on 3 December 1971); MRSN A2018 and A2019 (Andasibe region; collected by local collectors in 2001); NMW 3919 (holotype by monotypy; collected at Foizona according to original description, changed to Foizana by Blommers-Schlösser & Blanc (1991) and probably referring to Fizoana near Maroantsetra); UMMZ 191154–191158 (Ambatovaky, 16° 51'S, 49° 08'E, 600–650 m elevation; collected by C. J. Raxworthy, J. B. Ramanamanjato, A. Raselimanana on 8–19 February 1990); UMMZ 198870–198875 (Vatoharanana, Ranomafana National Park, 21° 17'E, 47° 25.5'E, 950 m elevation; collected by C. J. Raxworthy on 31 January 1991); UMMZ 211487 and 211489–211493 (Sahavatoy River, Andringitra National Park, 22° 13'44"S, 47° 01'29"E, 820 m elevation; collected by C. J. Raxworthy, A. Razafimanantsoa and N. Rabibisoa on 26–27 November 1993); UMMZ 227498 (Andasibe region; collected by local collectors). ZFMK 62217 (An'Ala; collected by F. Glaw on 3 February 1996); ZSM 1154/2001 (locality unknown; obtained through the pet trade in 1999).

Distribution. Reliable localities are the following: (1) Foizona (type locality), (2) Ambatovaky, (3) Moramanga; (4) Ankeniheny (photographic record in Glaw & Vences 1994), (5) An'Ala, (6) Ambatolahy (call recordings and photographs of F. Andreone), (7) Vatoharanana (Ranomafana), (8) Ampasy, (9) Ambana, and (10) Andringitra. Except for the type locality, which seems to be at low altitude, the species is known from mid-altitude localities along the Malagasy east coast (Fig. 3).

Natural history. Dissected females (e.g., UMMZ 211493 and 191156) contained a large number of yellowish oocytes with a large dark brown pole of 1.4–1.7 mm diameter. Males at Ranomafana were found calling during the day, in a flooded marsh in rainforest between 09.00 and 17.00 hr (Andreone, pers. com.). Males at Andringitra were heard calling at night, at 20.00 hr, in a small (1 x 3 m) temporary pool of water in rainforest.

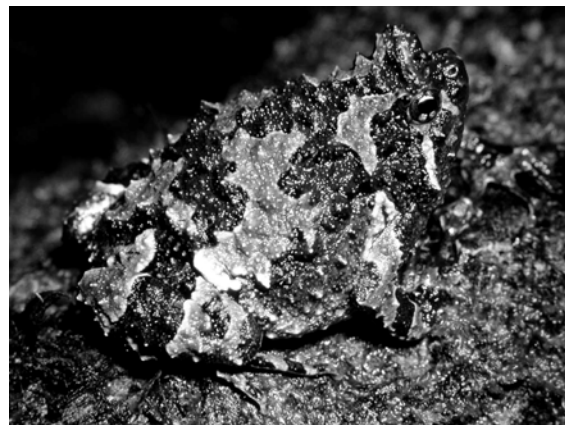


FIG. 4. Adult specimen of *Scaphiophryne spinosa* from Vatoharanana (Ranomafana).

Advertisement call. Recordings of the specimen ZSM 1154/2001 were taken by K. Schmidt in captivity at unknown temperature (about 25°C). The call was a long series of short harmonious notes (Fig. 5). Call duration was 3539–9117 ms (7214 ± 3183 ms, $n=3$). Calls contained 83–200 notes (157 ± 64 , $n=3$). Note duration was 25–34 ms (28.6 ± 2.9 ms, $n=10$), and duration of intervals between notes was 9–18 ms (12.3 ± 3.2 ms, $n=10$). Intensity of notes increased from the first to the last notes of the call, the first notes had especially very low intensities. Note repetition rate was 21–23/s. Frequency was 600–1000 Hz.

These calls were similar to those recorded by F. Andreone at Ranomafana (next to Ambatolahy village) on 14 December 1991, ca. 21.00 hr, at 19–20°C air temperature. At least 5–10 specimens called in a chorus in the water, and identification of single calls and notes was therefore very difficult on the sonagrams (not shown). Frequency was 600–1050 Hz, note duration was 21–35 ms, duration of intervals between notes was about 10 ms.

Comments. According to several authors (e. g. Guibé, 1978; Blommers-Schlösser & Blanc, 1991) the holotype of *Scaphiophryne spinosa* is deposited in the NMW, but the specimen has not been so far identified (see Häupl *et al.* 1994, Tiedemann & Grillitsch 1999). However, the original description (Steindachner 1882) is relatively detailed and complete. Some relevant parts of the description are quoted in the following: “*Haftscheiben an den Fingern stark entwickelt, am vorderen Ende breit und in der Mitte des Vorderrandes seicht eingebuchtet. ... Zahllose kleine, mehr oder minder dornenähnliche Wärzchen an der Rückenseite des Körpers, zwischen denen insbesondere an der Oberseite des Kopfes, in der Ohrgegend und an den Seiten des Rumpfes bedeutend grössere konische Wärzchen zerstreut liegen. ... Ein Exemplar, c. 4 1/2 Cm. lang, von Foizona auf Madagascar. ... Kopfänge 14 Mm. Kopfbreite nahezu 20 Mm. Länge der vorderen Extremitäten c. 32 Mm., der hinteren Extremitäten 59 Mm.*” This information, in combination with the excellent drawings of the holotype given in the original description, leave no doubts about the correct assignation of the name *Scaphiophryne*

spinosa to the spiny species previously attributed to *S. marmorata* (see above). We also consider that the female NMW 3919 agrees very well with this description and therefore very probably is the holotype of *Scaphiophryne spinosa*, although it bears no label indicating its type status. The colour of NMW 3919 has largely faded to a uniform beige; however, its general appearance agrees with the drawing in Steindachner (1882), and most of its measurements (Table 1) agree with the values given in the original description as quoted above. Differences in head width and hindlimb length values are probably explained by different landmarks of measurements: head width at the level of the maxillary rictus measured herein, maximum head width probably measured by Steindachner (1882); hindlimb length of totally outstretched limbs to the tip of longest toe measured herein, possibly not to the longest toe or not totally outstretched limbs measured by Steindachner (1882). Boulenger (1883) considered *S. spinosa* a junior synonym of *S. marmorata* without stating specific justifications, but he appears to have been influenced by the deposition of an additional adult specimen at the British Museum (the *S. marmorata* holotype is a juvenile).

SCAPHIOPHRYNE BORIBORY SP. N. (FIGS. 6-7)

Diagnosis. A *Scaphiophryne* with highly expanded terminal discs on the fingers that are reddish in life; dorsally green with symmetrical dark markings, and lacking pink markings; adult SVL 47–60 mm; total absence of dorsal tubercles on body in preservation; absence of large spiny tubercles above forelimb insertion, at posterior end of maxilla, and in tympanic region; tympanum not visible; ventral pattern black with white spots.

Distinguished from *Scaphiophryne brevis*, *S. calcarata* and *S. madagascariensis* by the highly expanded terminal discs on the fingers (vs. absent, or only slightly expanded); from *S. gottlebei* by a much larger size (SVL 47–60 vs. 36 mm) and a different coloration (dorsally green with symmetrical dark markings vs. white with green, black and pink markings); from *S. spinosa* by larger adult size (SVL 47–60 mm vs. 40–48 mm), total absence of dorsal tubercles on body in preservation (vs. presence of tubercles), and ventral colour (black with white spotted pattern vs. irregular dark on throat, chest and anterior belly and light on posterior belly and femur); and from *S. marmorata* by larger adult size (SVL 47–60 mm vs. 32–49 mm) and total absence of dorsal tubercles in preservation (vs. presence of at least some large regular tubercles in the head and shoulder region). In life, *S. boribory* is further recognizable by the reddish discs on fingers and toes (not reddish in the other species).

Holotype. UMMZ 225614, adult male, from Ampahanana forest, near Fierenana, 18° 29.53'S, 48° 26.68'E, 1000–1200 m altitude; collected by O. Ramilison, N. Rabibisoa and D. Foley IV on 25 January 1998.

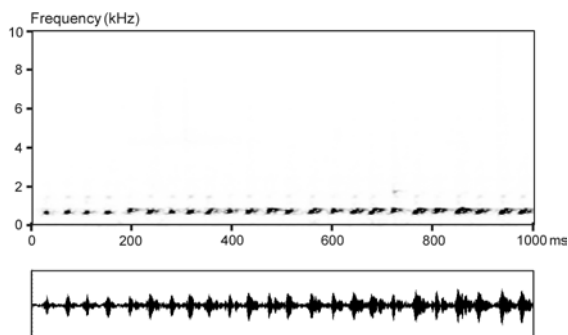


FIG. 5. Sonagram and oscillogram of part of an advertisement call (start of call with first 24 notes) of *Scaphiophryne spinosa* (ZSM 1154/2001), recorded in captivity.



FIG. 6. Adult male specimen of *Scaphiophryne boribory* (ZSM 153/2002) in dorsolateral view.

Paratypes. UMMZ 225615-225616 (one male and one female, same collecting dates as holotype); UMMZ 225617-225618 (two males, Sahanomana, near Fierenana river, 18° 29.82'S, 48° 28.21'E; collected by O. Ramilison, N. Rabibisoa and D. Foley IV on 27 January 1998); UMMZ 227490-227497 (six males and two females, Andasibe region; collected by local collectors, December 1996); ZSM 7/2000-8/2000, 644/2000-645/2000, MRSN A2016 and A2017, and ZFMK 76102 (two males, three females and two unsexed adult specimens, Fierenana region; collected by local collectors in 2000). ZSM 153/2002 (adult male, Fierenana region, collected by local collectors in January 2002).

Description of the holotype. Specimen in good state of preservation. For measurements, see Table 1. Body stout; head wider than long, less wide than body; snout rounded in dorsal view, truncate in lateral view; nostrils directed dorsolaterally, not protuberant, nearer to tip of snout than to eye; canthus rostralis indistinct; loreal region flat; tympanum not visible; supratympanic fold rudimentary; tongue ovoid and broad, posteriorly free and not bifid; maxillary teeth rudimentary; vomerine teeth absent; choanae ovoid. Arms moderately slender, faintly marked single subarticular tubercles; indistinct outer and distinct inner metacarpal tubercle; fingers without webbing; relative length of fingers $1 < 2 < 4 < 3$, fourth finger clearly longer than second finger; finger discs greatly expanded; nuptial pads absent. Hindlimbs short and rather stout; tibiotarsal articulation does not reach forelimb insertion when hindlimb is adpressed along body; lateral metatarsalia strongly connected; large and sharp inner metatarsal tubercle present, outer metatarsal tubercle not recognizable; a further distinct tubercle present on tarsus (tarsal tubercle); traces of webbing between toes; relative length of toes $1 < 2 < 5 < 3 < 4$; third toe distinctly longer than fifth toe; terminal discs of toes only slightly expanded.

Skin on dorsal surface smooth, with only a few small tubercles on head. Ventral skin smooth except on throat (vocal sac), which appears to be slightly granular. The skin gives an impression that it is oversized, giving a loose and baggy fit on the body.



FIG. 7. Adult male specimen of *Scaphiophryne boribory* (ZSM 153/2002) in ventral view.

In preservative, dorsally bluish grey with symmetrical, sharply delimited dark brown to black markings. Ventral side dark brown with small, sharply delimited creamy-white spots and vermiculations. Throat blackish. Tips of fingers and toes beige ventrally and beige with dark markings dorsally.

Variation. The available material is very homogeneous. Size is similar between males (SVL 49.0-59.8 mm; 55.7 ± 3.3 mm) and females (47.4-59.4 mm; 54.5 ± 4.1 mm) (Table 1). Males are characterized by a vocal sac which appears to be highly distensible, and which is blackish in specimens from Fierenana (probably captured in breeding condition). In life, some large tubercles were visible on the head and shoulders, but these are not recognizable in preserved specimens which all have smooth dorsal skin. The tympanum is totally concealed in all specimens.

Colour in life. The dorsal colour was a vivid green. The dorsal markings were centrally brown and are surrounded by black. Fingers and toes were largely brown, and their terminal discs were light brown to reddish. Ventrally, black with white spots on the belly; dark brown with green spots on the chest and with three more or less continuous greenish longitudinal bands on the throat. The fingers and toes were ventrally black to dark brown, while their terminal discs were distinctly reddish.

Etymology. The specific name is an unlatinized epithet derived from the Malagasy adjective boribory (= rounded), and refers to the stout and rounded body shape of this species.

Natural history. Dissected females (e.g. UMMZ 227493) contained a large number of light brown oocytes with a dark brown pole (diameter 1.7 mm).

Advertisement call. Recordings were taken in captivity by P. Klaas from specimens of unknown origin (no vouchers preserved; living specimens determined by F. Glaw). Quality of recordings was poor due to echo effects in the aquarium. However, it could be ascertained that the general call structure was similar to that of *S. spinosa*. Call duration was between 1799 ms and 12 492 ms, and calls were composed of 45-317 notes ($n=7$).

Some of the calls with the longer duration were interrupted by 1-2 short pauses of 258-326 ms. Note duration was ca. 35-38 ms, duration of intervals between notes 7-19 ms. Note repetition rate was 25/s. Frequency was 400-1000 Hz; a number of irregular harmonics were visible on the sonagram but were probably artifacts caused by the recording conditions.

Distribution. Only known from two specific sites in the Fierenana region, central eastern Madagascar (Fig. 3): (1) Ampahanana, and (2) Sahanomanana.

Comments. This species is assigned to the genus *Scaphiophryne* based on absence of vomerine teeth, rudimentary maxillary teeth, clavícula, small cartilaginous sternum, large cartilaginous omosternum (verified in ZSM 645/2000 by dissection), tarsal tubercle, widely distensible single subgular vocal sac, and high overall phenetic similarity to *Scaphiophryne spinosa* and *S. marmorata*. The pairwise genetic divergences, in a portion of the 16S rRNA gene, of *Scaphiophryne boribory* compared with the other two species of the *Scaphiophryne marmorata* complex were: 3.1% (17 substitutions) in comparison to *S. marmorata*, 2.4% (13 substitutions) in comparison to *S. spinosa*. The lowest differentiation was found in comparison with a fourth green-coloured species, *S. madagascariensis* (1.8%; 10 substitutions). Differentiation with the remaining species of *Scaphiophryne* was 1.8-4.4% (20-24 substitutions; Table 2). No phylogenetic analysis was performed because of the low amount of informative sites (see Vences et al., 2002b).

KEY TO ADULT SCAPHIOPHRYNE
WITH EXPANDED TERMINAL FINGER DISCS

- 1a. Dorsal colouration white with green, black and pink markings; ventral surface uniformly whitish; only known from the Isalo region — *Scaphiophryne gottlebei*
- 1b. Dorsal colouration always without pink, ventral surface with black or brown — 2
- 2a. Large species (SVL 47-60 mm); dorsal skin with few large tubercles in life, usually smooth in preservative; tympanum always concealed; ventral surface black with white spots — *Scaphiophryne boribory*

2b. Usually smaller (SVL 32-49 mm); dorsal skin with distinct tubercles in life and in preservative; tympanum concealed or visible; ventral surface light with dark marbling or with dark markings at least on the chest — 3

3a. SVL up to 49 mm, but often smaller than 40 mm; dorsal skin with tubercles of relatively regular size; no large and spiny tubercles above forelimbs and in tympanic region; tympanum, if visible, larger than 50% of eye diameter; posterior belly usually light with dark marbling — *Scaphiophryne marmorata*

3b. SVL 40-48 mm; dorsal skin with a large number of irregularly sized spines and tubercles; large spiny tubercles above forelimbs, at maxilla commissure, and in the tympanic region; tympanum, if visible, smaller than 50% of eye diameter; posterior belly usually uniformly light — *Scaphiophryne spinosa*

DISCUSSION

Previous workers (e.g. Noble & Parker, 1926; Guibé, 1978) considered *Scaphiophryne marmorata* to belong to a genus different from *Pseudohemisus*, which included the taxa *madagascariensis*, *brevis* and *calcarata* (and their synonyms). Blommers-Schlösser & Blanc (1991) noted that other than the expanded finger discs of *S. marmorata*, there were no characters to maintain this classification, and they lumped all species in the genus *Scaphiophryne*. Busse & Böhme (1992), describing a second species with expanded finger disks (*S. gottlebei*), proposed that the taxa sharing this character be considered as the subgenus *Scaphiophryne*, and the species with non-expanded disc as the subgenus *Pseudohemisus*. Until the phylogenetic relationships of these frogs are better clarified, we do not consider a subgeneric division to be useful.

The genus *Scaphiophryne* was listed by Vences et al. (2000a) as a relict genus of low species diversity having a reproductive mode adapted to savanna areas of western Madagascar. At this time, a total of six nominal species of *Scaphiophryne* were known, three of which were endemic to arid western Madagascar, two to high-altitudes, and only one (*S. marmorata*) known from the rainforests of eastern Madagascar.

TABLE 2. Pairwise distances (total number of substitutions; indels not counted) of species of *Scaphiophryne* in a fragment of c. 540 base pairs of the mitochondrial 16S rRNA gene.

	1	2	3	4	5	6	7
1 <i>S. calcarata</i>	-						
2 <i>S. brevis</i> (Kirindy)	24	-					
3 <i>S. brevis</i> (Ifaty)	23	1	-				
4 <i>S. gottlebei</i>	24	25	24	-			
5 <i>S. madagascariensis</i>	22	22	23	17	-		
6 <i>S. spinosa</i>	23	18	17	15	12	-	
7 <i>S. marmorata</i>	26	20	20	20	15	18	-
8 <i>S. boribory</i>	24	21	21	20	10	13	17

The present review implies some modifications to this view. The recognition of *Scaphiophryne boribory* and *S. spinosa* as distinct species elevates the number of species known from eastern rainforests to three. Not counting the dubious names *S. obscura* and *S. verrucosa*, the genus *Scaphiophryne* currently contains a total of seven nominal species, but this does not reflect adequately its diversity. At least three additional species have already been identified by us. Nevertheless, the actual diversity of *Scaphiophryne* is distinctly lower than that of the most diverse endemic Malagasy frog radiations. If the three taxonomically unrecognized species are taken into account, currently three species of *Scaphiophryne* appear to be endemic to eastern rainforests, four species to western Madagascar, two species to high elevations, and one species (*S. marmorata*) is distributed in the east as well as in the west. In contrast to the mantellid and cophyline radiations, which clearly have their maximum diversity in humid eastern Madagascar, *Scaphiophryne* appears to have diversified to an equal extent in the eastern, central and western biogeographic regions of the island.

An important feature of *Scaphiophryne* appears to be their low differentiation in advertisement calls and reproductive biology. We herein provide evidence that the general temporal and spectral pattern of the calls of *S. spinosa* and *S. boribory* – which are sympatric in the Fierenana region – are similar. The call of *S. madagascariensis* from the Ankaratra Massif as described by Vences *et al.* (2002b) also shows the same structure, while the calls of *S. brevis*, *S. calcarata* and *S. sp.* from the Kirindy forest differ from this pattern and from each other (F. Glaw, unpublished). However, the reproductive biology of all these species appears to be similar (Blommers-Schlösser, 1975; Glaw & Vences, 1994; Vences *et al.*, 2002b): a short and explosive bout of reproductive activity follows heavy rainfall; specimens forming extremely loud choruses in stagnant, mostly temporary waters, into which the many small eggs with dark pigment are laid. The fact that partly sympatric species of low differentiation in reproductive mode do not show distinct differences in advertisement calls is exceptional among Malagasy amphibians, and will certainly deserve further investigation in the future.

The conservation of *Scaphiophryne marmorata*, *spinosa* and *boribory* will probably depend on the protection of suitable primary habitat. Their ability to survive in degraded habitats is uncertain (unlike other species such as *S. brevis* and *S. calcarata*). Both *S. spinosa* and *S. marmorata* occur in protected areas in Madagascar. However, *S. boribory* is known only from specific sites in the Fierenana region, outside the protected area network, in areas of highly active ongoing deforestation. Possibly this species also occurs in the Mantadia (= Mantady) or Perinet (= Analamazaotra) reserves in the Andasibe region, but herpetological surveys have yet to confirm this. More survey effort in these regions, and more generally in the forest corridor between Mantadia and Zahamena, would be especially

valuable for better determining the distribution limits of this species.

ACKNOWLEDGEMENTS

We are grateful to F. Andreone, D. Foley IV, S. Höß, P. Klaas, A. Peyrieras, O. Pronk, N. Rabibisoa, J. Rafanomesantsoa, J. B. Ramanamanjato, O. Ramilison, A. Raselimanana, A. and A. Razafimanantsoa, and K. Schmidt who assisted to this study. C. McCarthy and B. Clarke (BMNH), A. Dubois and A. Ohler (MNHN), R. Gemel, H. Grillitsch, F. Tiedemann (NMW), W. Böhme (ZFMK), and B. van Tuijl (ZMA) made possible the examination of specimens held in their care. We are grateful to the Malagasy authorities for permits to collect and export specimens. The work of MV and FG was financially supported by the “Deutscher Akademischer Austauschdienst” (DAAD). The work of CJR and RAN was supported in part by grants from the National Science Foundation (DEB 90-24505, DEB 93 22600, and DEB 96-25873) and the National Geographic Society (5396-94).

REFERENCES

- Blommers-Schlösser, R. M. A. (1975). Observations on the larval development of some Malagasy frogs, with notes on their ecology and biology (Anura: Discophinae, Scaphiophryninae and Cophylinae). *Beaufortia* **24** (309), 7-26
- Blommers-Schlösser, R. M. A. & Blanc, C. P. (1991). Amphibiens (première partie). *Faune de Madagascar* **75** (1), 1-379.
- Boulenger, G. A. (1883). II. Notes on little known species of frogs. *Ann. Mag. nat. Hist.* (5), **11**, 16-19
- Busse, K. & Böhme, W. (1992). Two remarkable frog discoveries of the genera *Mantella* (Ranidae: Mantellinae) and *Scaphiophryne* (Microhylidae: Scaphiophryninae) from the west coast of Madagascar. *Revue fr. Aquariol.* **19**, 57-64.
- Dubois, A. (1992). Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. mens. Soc. linn. Lyon* **61**, 305-352.
- Glaw, F. & Vences, M. (1994). *A fieldguide to the amphibians and reptiles of Madagascar. 2nd edition, including mammals and freshwater fish.* Köln: Vences & Glaw Verlag.
- Guibé, J. (1978). Les Batraciens de Madagascar. *Bonn. zool. Monographien* **11**, 1-140
- Häupl, M., Tiedemann, F. & Grillitsch, H. (1994). *Katalog der Typen der Herpetologischen Sammlung nach dem Stand vom 1. Jänner 1994. Teil I: Amphibia.* Kataloge der wissenschaftlichen Sammlungen des Naturhistorischen Museums in Wien, Vertebrata, 9 (3). Wien: Naturhistorisches Museum Wien.
- Noble, G. K. & Parker, H. W. (1926). A synopsis of the brevicipitid toads of Madagascar. *Amer. Mus. Novit.* **232**, 1-21
- Rödel, M. O. (2000). *Amphibians of the West African savanna - Herpetofauna of West Africa. Vol. 1.* Frankfurt: Chimaira.

- Steindachner, F. (1882). Batrachologische Mittheilungen. *Verh. Zool. Bot. Ges. Wien* **14**, 266-269.
- Tiedemann, F. & Grillitsch, H. (1999). Ergänzungen zu den Katalogen der Typusexemplare der Herpetologischen Sammlung des Naturhistorischen Museums in Wien (Amphibia, Reptilia). *Herpetozoa* **12**, 147-156.
- Vences, M., Andreone, F., Glaw, F., Raminosoa, N., Randrianirina, J. E., & Vieites, D. R. (2002a). Amphibians and reptiles of the Ankaratra Massif: reproductive diversity, biogeography and conservation of a montane fauna in Madagascar. *Ital. J. Zool.* **69** (in press)
- Vences, M., Aprea, G., Capriglione, T., Andreone, F. & Odierna, G. (2002b). Ancient tetraploidy and slow molecular evolution in *Scaphiophryne*: ecological correlates of speciation mode in Malagasy relict amphibians. *Chromosome Res.* **10**, 127-136.
- Vences, M. & Glaw, F. (2001). When molecules claim for taxonomic change: New proposals on the classification of Old World treefrogs. *Spixiana* **24**, 85-92.
- Vences, M., Glaw, F., Kosuch, J., Das, I. & Veith, M. (2000a). Polyphyly of *Tomopterna* (Amphibia: Ranidae) based on sequences of the mitochondrial 16S and 12S rRNA genes, and ecological biogeography of Malagasy relict amphibian groups. In *Diversité et endémisme a Madagascar*, 229-242. Lourenço, W. R. & Goodman, S. M. (Eds.). Paris: Mémoires de la Société de Biogéographie, Paris.
- Vences, M., Kosuch, J., Lötters, S., Widmer, A., Jungfer, K. H., Köhler, J. & Veith, M. (2000b). Phylogeny and classification of poison frogs (Amphibia: Dendrobatidae), based on mitochondrial 16S and 12S ribosomal RNA gene sequences. *Mol. Phyl. Evol.* **14**, 34-40.
- Wassersug, R. (1984). The *Pseudohemismus* tadpole: a morphological link between microhylid (Orton Type 2) and ranoid (Orton type 4) larvae. *Herpetologica* **40**, 138-149.

Accepted: 8.11.02

