

A NEW *MANTIDACTYLUS* FROM SOUTH-EASTERN MADAGASCAR, WITH A REVIEW OF *MANTIDACTYLUS PERACCAE* (RANIDAE: MANTELLINAE)

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In the course of a herpetological survey in southern Malagasy rainforest, a new species of the endemic genus *Mantidactylus* was discovered and is here described as *M. brunae* n. sp. This frog is similar to *M. peraccae* for which a redescription, new locality records, and natural history notes are provided. The examined *M. peraccae* specimens are slightly warty dorsally, with small, dark protruding dots surrounding brown rounded patches on the light brown dorsum. *Mantidactylus peraccae* has a wide distribution in eastern Madagascar, occurring at elevations between 900 and 1800 m. *M. brunae* n. sp. inhabits the low-altitude rainforest of Andohahelo and differs from *M. peraccae* in its slender form and smoother skin. In contrast to *M. peraccae* (which is arboreal), *M. brunae* n. sp. was found on the ground in crevices along rocky forest brooks. Its acoustic repertoire consists of a rapid trill-like series of 3-4 click notes with a frequency ranging from about 1.4 to 6.7 kHz, whereas *M. peraccae* emits metallic sounds, single or in series, from elevated positions. Morphological and bioacoustic differences between populations attributed to *M. peraccae* indicate that they may constitute more than one species, but available data are insufficient to corroborate taxonomic conclusions. A redescription of *M. elegans*, phenetically similar to *M. brunae* n. sp. and *M. peraccae*, is provided based on specimens from Andringitra, together with a diagnostic key to the currently known species of the subgenus *Spinomantis*.

INTRODUCTION

The ranid subfamily Mantellinae currently contains two genera, *Mantella* and *Mantidactylus* (Glaw & Vences, 1994). The genus *Mantella* is phylogenetically a well defined unit which is characterized by several autapomorphies such as hyoid structure, presence of skin alkaloids and loss of maxillary teeth (pers. obs.; Daly *et al.* 1996). Some *Mantidactylus* of the subgenus *Chonomantis* (e.g. *M. opiparis* and *M. albofrenatus*) superficially resemble some *Mantella* (especially *M. betsileo*). However, this is probably due to convergence since these species are characterized by a derived femoral gland structure which is shared with other *Mantidactylus* (but not with *Mantella*), and by a unique tadpole morphology (Glaw & Vences, 1994; pers. obs.). At present, relationships between *Mantella* and *Mantidactylus* remain unresolved and no evidence is known to support the monophyly of *Mantidactylus*. Basic data on morphology, variability and natural history of many *Mantidactylus* are still unknown, even though the Malagasy herpetofauna has been intensively studied during recent years.

One of these poorly known species is *Mantidactylus peraccae*, which was originally described by G. A. Boulenger in 1896 as *Rhacophorus Peraccae*. Boulenger named this new frog based upon a single specimen (BM 1947.2.9.7) captured by C. J. Forsyth Major at "Ivohimanita", and he dedicated it to his Ital-

ian colleague M. G. Peracca. The type locality was located in NW Madagascar by Blommers-Schlösser (1985), but most likely it corresponds to Ivohimanitra (Tanala region, Fianarantsoa Province) in central-eastern Madagascar (Blommers-Schlösser & Blanc, 1991). The species was transferred to the genus *Mantidactylus* by Blommers-Schlösser (1978). This author examined two further specimens from "Tampoketsa d' Ankazobe" in central Madagascar. At least one of them was found within the axil of a *Pandanus* screw palm at an altitude of 1600 m, this representing the first information on *M. peraccae* ecology. The species was more formally transferred to the genus *Mantidactylus* by Blommers-Schlösser (1979) who, in her monographic contribution on mantellines, included *Mantidactylus peraccae* in the *Mantidactylus depressiceps* group together with *M. depressiceps* and *M. tornieri*.

In the first volume of "Faune de Madagascar" dedicated to the amphibians, Blommers-Schlösser & Blanc (1991) reported further localities for *M. peraccae*: Tsaratanana Massif (northern Madagascar) and Anosy Mountains (SE Madagascar). The *Mantidactylus depressiceps* group then increased by addition of *M. elegans*. The *depressiceps* group was later treated as a *Mantidactylus* subgenus, *Guibemantis*, by Dubois (1992).

In the second edition of their field guide, Glaw & Vences (1994) published a black-and-white photograph (Fig. 289, p. 142) and a colour plate (Pl. 84) of a

M. peraccae specimen from Ankeniheny (forest south of Moramanga, central-eastern Madagascar). The ecology and presence of distinct femoral glands, as well as morphochromatic and bioacoustic data led them to transfer the species to the subgenus *Spinomantis*, which presently includes *Mantidactylus aglavei*, *M. fimbriatus*, *M. massi*, *M. phantasticus* and *M. peraccae* (Glaw & Vences, 1997b).

Recent field observations of *Mantidactylus peraccae* have been carried out by F. Andreone on the western slopes of the Anjanaharibe chain (NE Madagascar), by F. Glaw at Vohiparara (Ranomafana National Park), and by D. Vallan in the rainforest of Ambohitantely, a locality which corresponds to Tampoketsa d'Ankazobe, already quoted by Blommers-Schlösser (1978). Our observations, together with the re-examination of all specimens previously attributed to *M. peraccae*, allows the clarification of some aspects of the ecology and distribution of this species. Furthermore, one specimen captured in a low-altitude rainforest in SE Madagascar which has been tentatively assigned to *M. peraccae*, turned out to be a new species. The aim of the present paper is therefore to describe this new taxon and to review *M. peraccae* based on our recent studies.

MATERIALS AND METHODS

Specimens were captured during the night with the aid of electric torches by locating calling males. Advertisement calls were recorded with a variety of tape recorders and microphones, and were analysed with the sound system Voxys 3.0. Specimens were fixed in 10% formalin or in 90% ethanol, with successive preservation in 65% ethanol. All morphological measurements were taken by the senior author to the nearest 0.1 mm on the following parameters (Table 1): A, snout vent length (SVL); B, head width at the maxillary commissure; C, head length from the maxillary commissure to the tip of the snout; D, eye commissure - nostril distance; E, nostril - tip of snout; F, horizontal eye diameter; G, horizontal tympanum diameter; H, forearm length to the tip of the longest finger; I, hand length to the tip of the longest finger; J, tibia length; K, foot length (including the tarsus) to the longest toe. Some other morphological data such as the tibiotarsal articulation extension, size of femoral glands and inner metatarsal tubercle length were also recorded. The webbing formula described by Blommers-Schlösser (1979) and Glaw & Vences (1994), provides the range of the free unwebbed phalanges at each side of the fingers and toes. Museum acronyms used are as follows: BM, Natural History Museum, London; MNHN, Muséum national d'Histoire naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; NMBE, Naturhistorisches Museum, Bern; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn. The location of the sites of *M. peraccae* and the new species is given in Fig. 1. Latitudes and longitudes were given according to GPS prospecting, bibliography analysis and IUCN/UNEP/WWF (1987).

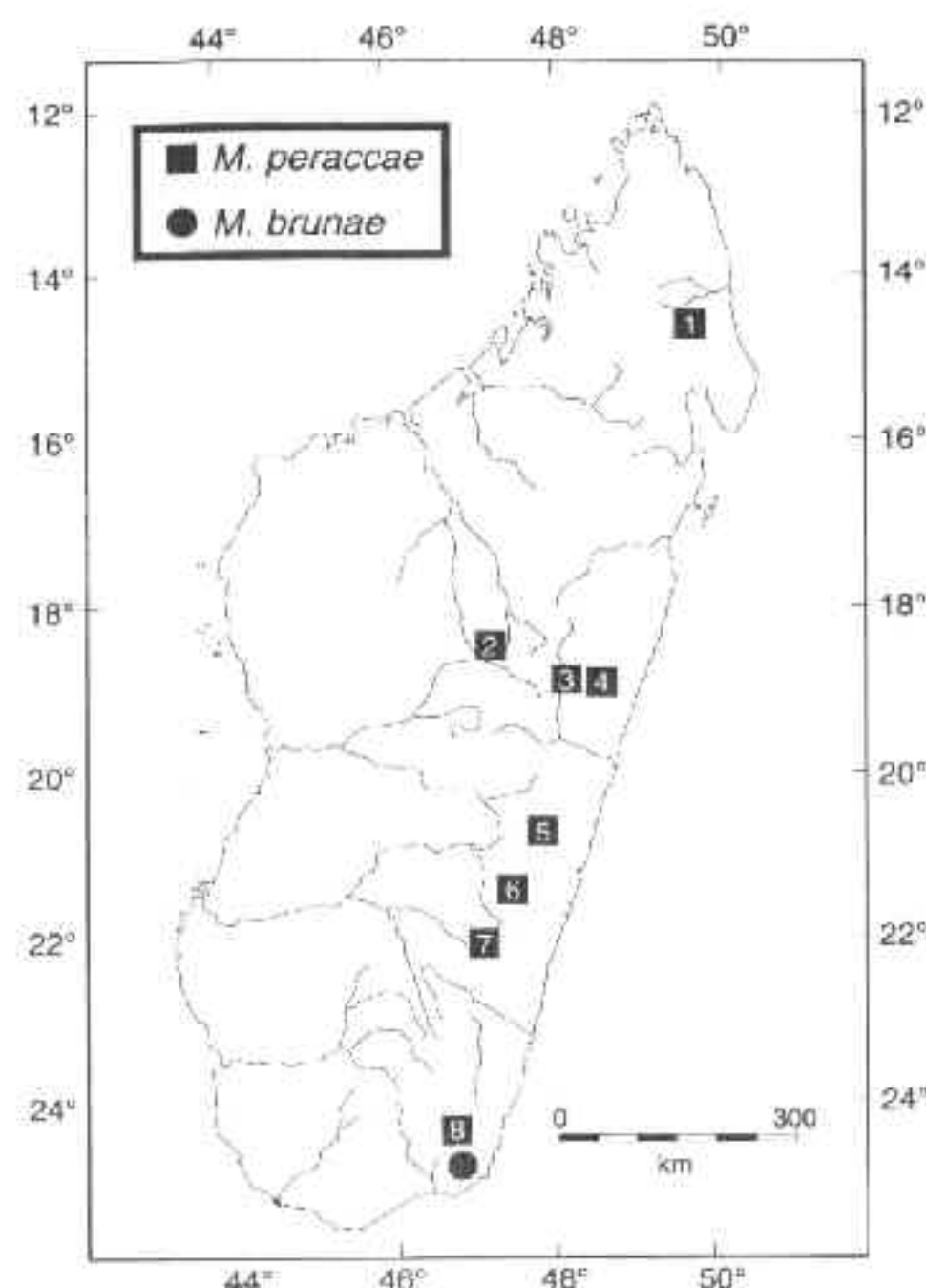


FIG. 1. Provenance localities of *Mantidactylus peraccae* [1, Anjanaharibe-Sud; 2, Tampoketsa d'Ankazobe (= Ambohitantely); 3, Ankeniheny; 4, Andasihe; 5, Ivohimanitra; 6, Vohiparara; 7, Andringitra (after Raxworthy & Nussbaum, 1996); 8, Anosy Chain], and *M. brunae* n. sp. between Eminiminy and Isaka-Ivondro (Andohahelo Strict Nature Reserve).

RESULTS

REVIEW OF MANTIDACTYLUS PERACCAE

Mantidactylus peraccae (Boulenger, 1896) [Figs. 2-4]
Rhacophorus peraccae - Boulenger, 1896: 420-421.
Rhacophorus peraccae - Mocquard, 1909: 60; Ahl, 1931: 191; Guibé, 1978: 67
Mantidactylus peraccae - Blommers-Schlösser, 1978: 32, Fig. 14; Blommers-Schlösser, 1979: 43; Blommers-Schlösser, 1985: 438; Blommers-Schlösser & Blanc, 1991: 153-154; Glaw & Vences, 1992 a: 108-109, 117, Figs. 135-136; Blommers-Schlösser & Blanc, 1993: Pl. 15 (Fig. 53); Raxworthy & Nussbaum, 1996: 162, 169.
Mantidactylus (Guibemantis) peraccae - Dubois, 1992: 312
Mantidactylus (Spinomantis) peraccae - Glaw & Vences, 1994: 124-125, 144.
Mantidactylus (Spinomantis) cf. peraccae - Glaw & Vences, 1997b: 243-258.

Diagnosis. A medium-sized arboreal and nocturnal *Mantidactylus* (SVL 30-45 mm). Dorsally brownish-greenish with darker blotches; dorsum rather warty with small dark protruding dots. Measurements of the

TABLE 1. Biometric measurements (to the nearest 0.1 mm) of the specimens analysed in the present paper and belonging to *Mantidactylus brunae* n. sp. and to *M. peraccae*. Holotypes are marked with an asterisk. M, males; F, females; Locality, capture locality of the specimens (1, d'Ankazobe = Tampoketsa d'Ankazobe); A, snout-vent length; B, head width at the maxillary commissure; C, head length from the maxillary commissure to the tip of the snout; D, eye - nostril distance; E, nostril - tip of snout distance; F, eye diameter; G, horizontal tympanum diameter; H, forearm length at the tip of the longest finger; I, hand length at the tip of the longest finger; J, tibia length; K, foot length (including the tarsus) at the longest toe; L, length of the femoral gland; M, width of the femoral gland; N, tibiotarsal articulation reaching (1) eye, (2) beyond eye, (3) nostrils, (4) snout tip. Range and mean of females was calculated from the positively sexed specimens (ZFMK 62270 and ZMA 6869/704) whereas possibly immature individuals (ZMA 6869/703 and BM 1947.2.9.7) were not included.

Species	Sex	Locality	A	B	C	D	E	F	G	H	I	J	K	L	M	N
<i>Mantidactylus brunae</i> n. sp.																
MRSN A1649*	M	Andohahelo	32.3	11.5	13.4	2.5	3.8	5.4	2.8	17.2	10.5	18.0	23.6	8.6	3.2	(4)
<i>Mantidactylus peraccae</i> (males)																
MRSN A1861	M	Anjanaharibe (Analabe Valley)	43.9	15.9	17.1	4.4	3.3	6.2	3.3	22.9	16.0	23.6	35.9	10.5	4.0	(2)
MRSN A1862	M	Anjanaharibe (Analabe Valley)	44.3	17.3	17.2	4.3	3.1	5.8	3.4	23.6	15.3	23.0	34.8	9.7	3.8	(3)
MRSN A1863	M	Anjanaharibe (Analabe Valley)	40.9	16.1	16.9	4.5	3.9	5.6	3.1	25.2	16.1	24.2	33.9	9.0	3.3	(3)
MRSN A1864	M	Anjanaharibe (Analabe Valley)	34.1	13.2	14.4	3.1	3.3	5.5	2.4	20.1	14.9	19.2	25.9	8.8	3.5	(3)
NMHE 10151/96	M	Ambohitantely	41.3	16.2	17.1	4.4	3.8	5.2	2.8	22.8	15.0	19.9	32.6	9.3	4.2	(2)
ZFMK 57452	M	Ankeniheny	37.7	14.2	14.7	2.9	3.6	4.6	2.5	20.1	12.5	17.9	26.9	10.0	4.0	(2)
ZFMK 62269	M	Vohiparara	38.7	14.9	15.4	3.7	4.8	5.7	3.0	22.1	13.3	20.4	29.8	9.8	4.9	(4)
MNHN 1975-753	M	Anosy Chain	43.1	16.6	18.1	3.6	3.9	6.5	2.8	23.1	14.9	22.4	32.7	7.5	3.2	(4)
Range																
			34.1 - 43.9	13.2 - 17.3	14.4 - 18.1	2.9 - 4.5	3.1 - 4.8	4.6 - 6.5	2.4 - 3.4	20.1 - 25.2	12.5 - 16.1	17.9 - 24.2	25.9 - 35.9	7.5 - 10.5	3.2 - 4.9	
Mean																
			40.5	15.6	16.4	3.9	3.7	5.6	2.9	22.5	14.8	21.3	31.6	9.3	3.9	
<i>Mantidactylus peraccae</i> (females)																
ZFMK 62270	F	Vohiparara	39.4	15.6	16.5	3.7	3.5	5.5	3.1	23.2	14.3	20.9	31.2	/	/	(3)
ZMA 6869/704	F	T. d'Ankazobe	45.0	15.4	17.7	3.5	4.5	5.6	2.7	23.2	14.7	23.3	33.5	/	/	(1)
ZMA 6869/703	F?	T. d'Ankazobe	34.7	12.9	14.9	3.2	2.9	5.2	2.5	18.6	12.5	18.5	25.2	/	/	(1)
BM 1947.2.9.7*	F?	Ivohimanitra	31.9	12.1	13.4	3.7	3.2	5.4	2.4	18.1	10.8	12.0	23.9	/	/	(2)
Range																
			39.4 - 45.0	15.4 - 15.6	16.5 - 17.7	3.5 - 3.7	3.5 - 4.5	5.5 - 5.6	2.7 - 3.1	23.2 - 25.2	14.3 - 14.7	20.9 - 25.3	31.2 - 33.5	/	/	
Mean																
			42.2	15.5	17.1	3.6	4.0	5.6	2.9	23.2	14.5	22.1	32.4	/	/	

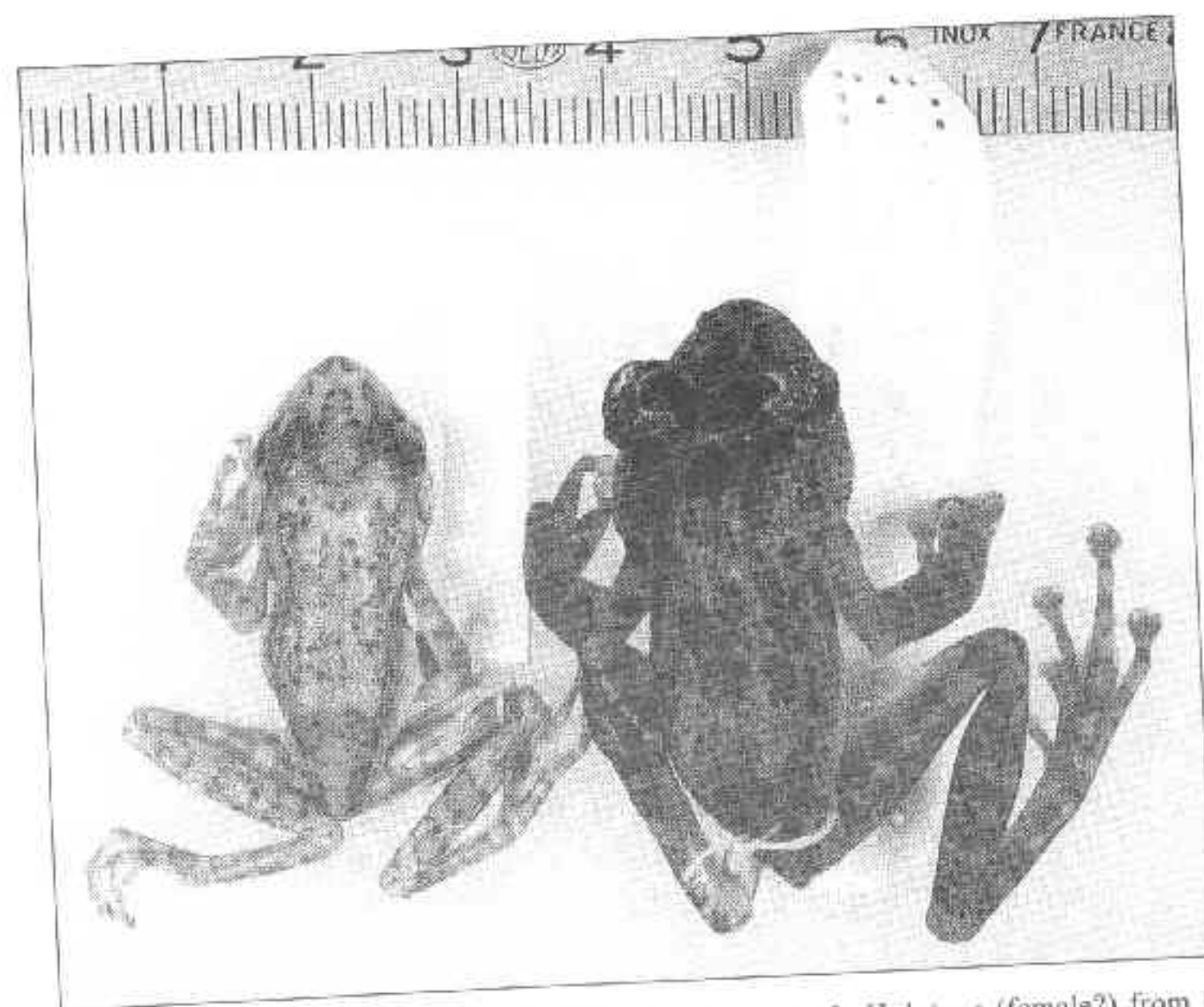


FIG. 2. Dorsal view of preserved specimens of *Mantidactylus peraccae*. Left: Holotype (female?) from Ivohimanitra (BM 1947.2.9.7). Right: comparative specimen (male) from Anosy Chain (MNHN 1975-753).

holotype and comparative specimens are given in Table 1. Distinguishable from the other species of the subgenus *Spinomantis* (*M. aglabei*, *M. fimbriatus*, *M. massi* and *M. phantasticus*) by the absence of dermal flaps and fringes on the legs; from *M. elegans* by the presence of an outer metatarsal tubercle and large femoral glands, and by the relative length of the 3rd toe. Quite similar to *M. brunae* n. sp.: for distinctive characters see the diagnosis of this new species.

Redescription of the holotype. BM 1947.2.9.7, Ivohimanitra, Tanala region, Fianarantsoa Province, collected by C. J. Forsyth Major. Specimen in rather good condition, with a longitudinal cut on the belly. As indicated by the lack of femoral glands, the specimen is not an adult male; it may be a female or a subadult specimen. Head slightly longer than wide; snout rounded, not projecting and as long as the diameter of the orbit. Canthus rostralis obtuse, loreal region concave; nostrils interposed midway between the eye and the tip of the snout. Interorbital space as broad as the upper eyelid; tympanum distinct, about half the diameter of the eye. Vomerine teeth in two slightly oblique oval groups just behind choanae. Hind legs overlap about 3 mm when curved at right angle; tibiotarsal articulation reaches the nostril when appressed to the body. Finger length: $1 < 2 < 4 < 3$. Fingers without webbing; finger tips with well developed expansions about half of the tympanum diameter. Subarticular tubercles and the tubercle at the basis of the pollex are visible. Toe length: $1 < 2 < 5 < 3 < 4$. Foot webbing: 1(1), 2i(1), 2e(0.5), 3i(1), 3e(0.5), 4i(2), 4e(2), 5(1). Inner metatarsal tubercle 1.3 mm long; outer metatarsal tubercle reduced. Lateral metatarsalia separated. Expansions of

toes smaller than those of fingers. Small warts on the head, dorsum and upper surface of tibiae. Foreleg and upper femur surfaces rather smooth. A prominent fold extends above the tympanum. Throat smooth; belly and ventral side of thighs slightly warty. Femoral glands absent. The colouration is still in accordance with the original description i.e. pale brown above with dark brown, light-edged markings forming a cross on the head, the horizontal branches on the upper eyelids, and regular bars on the limbs (see Fig. 2). Small protruding blackish dots on the dorsum, especially at the borders of the dark markings. The belly and lower parts of the body are whitish except for a few dark spots on the throat.

Comparative specimens. MNHN 1975.753, Anosy Chain, Toliara (Tuléar) Province, Camp VI, approximately $24^{\circ}25'S / 47^{\circ}00'E$, 1800 m, 12 December 1971, Ch.P. Blanc leg.; ZMA 6869/703, Tampoketsa d'Ankazobe, Antananarivo (Tanararive) Province, approximately $18^{\circ}08'-18^{\circ}13'S / 47^{\circ}18'-47^{\circ}21'E$, 1500-1600 m, 9 April 1972, A. Peyrieras leg.; ZMA 6869/704, Tampoketsa d'Ankazobe, Antananarivo (Tanararive) Province, approximately $18^{\circ}08'-18^{\circ}13'S / 47^{\circ}18'-47^{\circ}21'E$, 1500-1600 m, 9 April 1972, A. Peyrieras leg.; ZFMK 57452, Ankeniheny, Toamasina (Tamatave) Province, $19^{\circ}10'S / 48^{\circ}2'E$, about 1000 m, 20 February 1994, F. Glaw, N. Rabibisoa and O. Ramilison leg.; NMBE 1035196, Ambohitantely (Ankazobe), Antananarivo (Tanararive) Province, $18^{\circ}06.4'S / 47^{\circ}15.0'E$, 1475 m, 7 February 1996, D. Vallan leg.; MRSN A1861, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 1, $14^{\circ}47'S / 49^{\circ}27'E$, 1050 m, 25 January 1996,

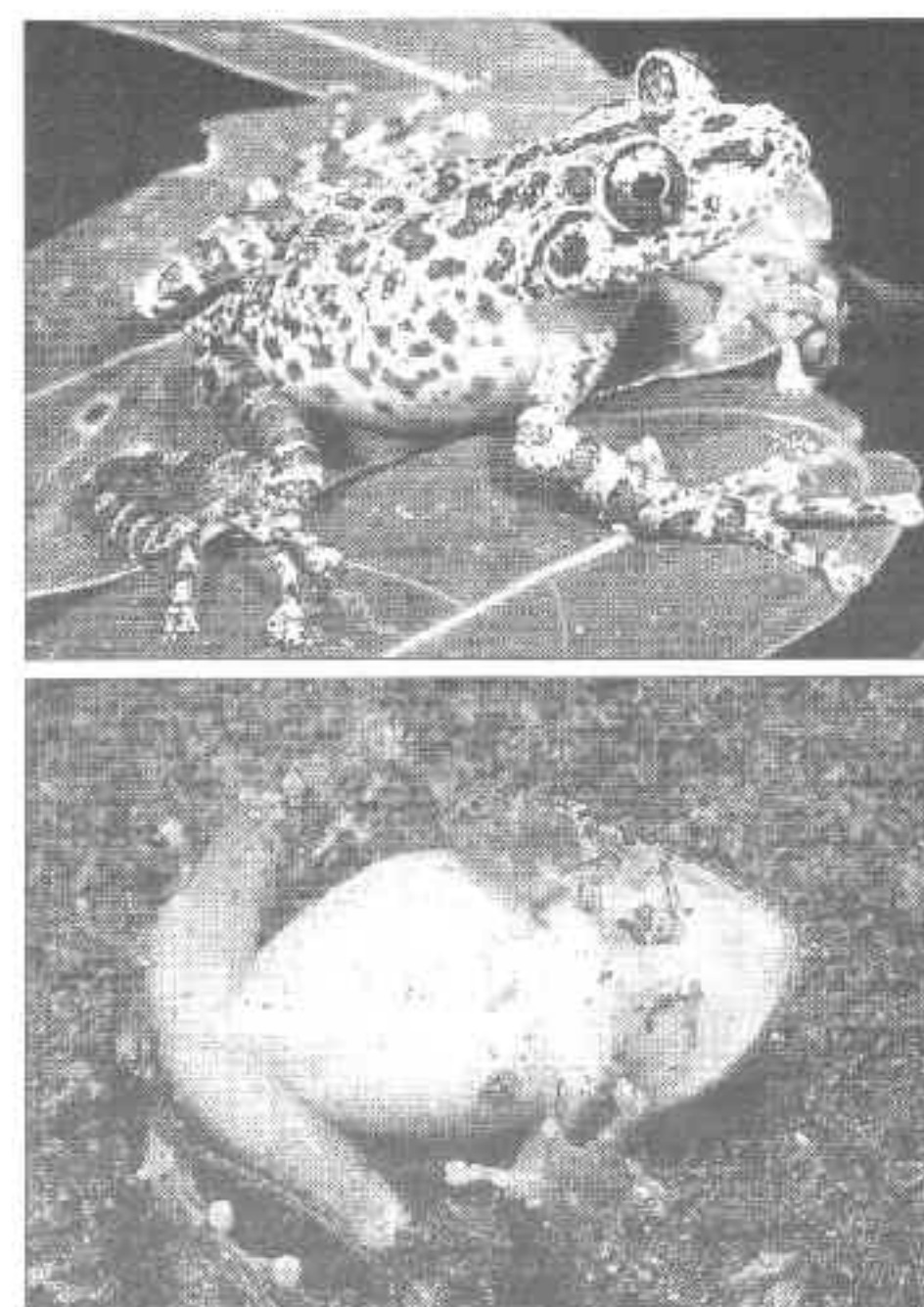


FIG. 3. *Mantidactylus peraccae*. MRSN A1862, live male from Analabe Valley, Anjanaharibe Chain. Dorsal (a) and ventral (b) views.

F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; MRSN A1862, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 1, $14^{\circ}47'S / 49^{\circ}27'E$, 1050 m, 26 January 1996, F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; MRSN A1863, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 2, $14^{\circ}46'S / 49^{\circ}26'E$, 1200 m, 5 February 1996, F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; MRSN A1864, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 2, $14^{\circ}46'S / 49^{\circ}26'E$, 1200 m, 6 February 1996, F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; ZFMK 62269 and 62270, Vohiparara Forest, Ranomafana National Park, Fianarantsoa Province, $21^{\circ}13'S / 47^{\circ}22'E$, 1000 m, 27 February 1996, F. Glaw, D. Rakotomalala and F. Ranaivojaona leg.

Compared to the holotype, the male MNHN 1975.753 (Anosy Chain) is larger, with nostrils protruding, equidistant between the tip of snout and the eye commissure. The finger tip expansions are of about the same size of the tympanum. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1). The femoral glands are ovoidal, whitish, their internal distance being 3.2 mm. Dorsal colouration brownish with irregular darker spots. Small protruding warts are distributed almost uniformly on the upper surfaces of the dorsum as well as on the femurs and the forelegs. They are blackish when within the dark markings,

lighter in the areas between them. The belly is whitish with scattered dark spots on the anterior chest.

ZMA 6869/704 (Tampoketsa d'Ankazobe) is probably an adult female. Foot webbing: 1(1), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1). The other specimen from the same locality (ZMA 6869/703) is similar, but smaller. Both the specimens are beige with dark spots and small warts. NMBE 1035196, a male captured from the same area, has well developed femoral glands. Its dorsum is rather smooth while the belly is warty. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(2), 4e(1.5), 5(1).

ZFMK 57452 (Ankeniheny) is a male with a blunted, non-projecting, snout. Nostrils situated nearer to the tip of the snout than to the eye. Tibiotarsal articulation reaches between the eye and the nostril. Foot webbing: 1(1), 2i(1.5), 2e(0.5), 3i(2), 3e(1), 4i(2), 4e(2), 5(0.5). Small dark spots (not visible in life) are present in the areas between the larger dark blotches of the dorsum. The belly is almost completely white. Head and dorsum do not show warts, but these were recognizable in the live specimen.

ZFMK 62269 (Vohiparara) is a male with a rather contrasting dorsal colouration and large, brownish spots. Foot webbing: 1(1), 2i(1), 2e(0), 3i(1), 3e(1), 4i(2), 4e(2), 5(1). The whitish-yellow belly has a few scattered dark dots on the chest. ZFMK 62270 from the same locality is a female of 39.4 mm. The colouration and general morphology is as in the male. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(2), 4e(2), 5(0.5).

The specimens from Analabe Valley, western slope of the Anjanaharibe Massif, are rather homogeneous in morphology and colouration. MRSN A1861 (male) has large femoral glands, but these are not pronounced and not protruding in preservative. Its dorsum is slightly granular with blackish warts. The finger tips are large, about the same size as the tympanum. The throat is immaculate, while the thorax has some isolated black spots. The lower surfaces of thighs are brownish. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1.5), 3e(0), 4i(1.5), 4e(1.5), 5(1). MRSN A1862 (male) has a warty dorsum and a rather enlarged head (Fig. 3a). The finger-tips expansions are smaller than the tympanum. The head is rather flattened, and the throat is smooth, while the belly is relatively warty. The femoral glands are visible and well developed. The belly is whitish with some dark spots (Fig. 3b). Foot webbing: 1(1), 2i(1.5), 2e(0.5), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1.5). MRSN A1863 (male) has a warty dorsum, the belly is rather smooth and the femoral glands are large. The finger-tips are enlarged and of the same size as the tympanum diameter. The dorsum is rather dark with large dark spots. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1), 3e(1), 4i(2), 4e(2), 5(1). MRSN A1864 (most likely a subadult male) is rather small. Its body, compared to that of the other examined specimens from the same locality, is also less flattened. The snout is rather pointed. The eyes are large. The dorsum, belly and throat are smooth.

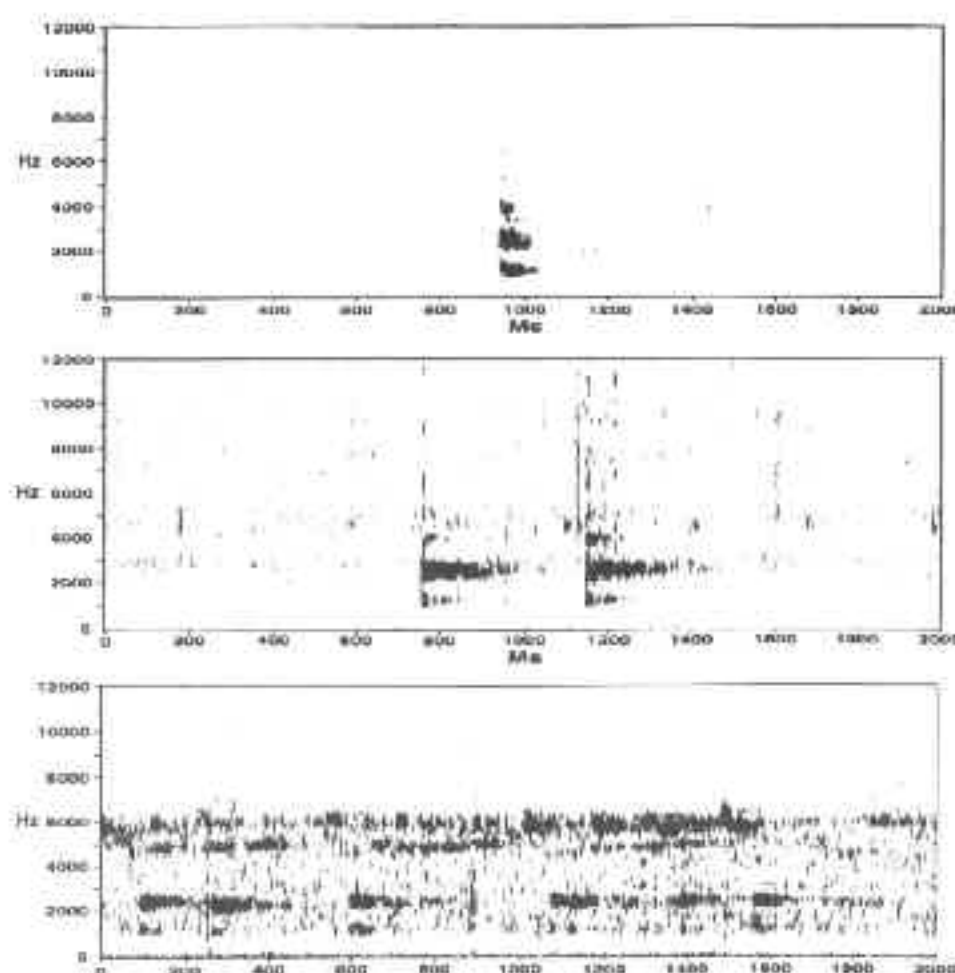


FIG. 4. Sonograms of *Mantidactylus peraccae*: (a) isolated note from Ankeniheny, central-eastern Madagascar; temperature, 19°C; (b) note pair from Vohiparara, Ranomafana National Park, central-eastern Madagascar; temperature, 21°C; (c) note series from Analabe Valley, Anjanaharibe Chain, north-eastern Madagascar; temperature, 20°C.

Femoral glands are pronounced and whitish. A few large and contrasting spots are present on the dorsum. Belly whitish, without dark spots. Foot webbing: 1(1), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1).

Colouration in life. Data are available for specimens from Ankeniheny, Vohiparara, Anjanaharibe, and Ambohitantely. These had a similar dorsal colour pattern, i.e. light brown with large irregular brown markings. The markings were oblong at the centre of the dorsum, becoming more rounded dorsolaterally. In ZFMK 57452 from Ankeniheny (colour photograph in Glaw & Vences, 1994), greenish shading was present as a thin line around the dark markings; the flanks were whitish to green; the throat and anterior part of belly were white; the posterior part of the belly and the ventral side of the arms and legs were translucent green; the femoral glands were bright yellow and the bones were greenish; the tympanum was brownish and the iris yellowish with an irregular brownish outer border. Specimens from Vohiparara corresponded well with the above description, also sharing the greenish shade of the ventral side, and the bright yellow of the femoral glands in the males. In MRSN A1862 from Analabe Valley (Anjanaharibe), the greenish colour was less developed when compared to the Ankeniheny specimen. The posterior part of the belly and the femoral glands were more whitish.

Habitat and habits. The studied specimens of *M. peraccae* were found in mid-altitude rainforests. At Anjanaharibe (Analabe Valley) the habitat is a patchwork of pristine and altered forest, with most of the unaltered forest occurring on the ridges and steepest slopes. In the degraded patches, the original vegetation

has been replaced by ferns and grasses. Trunks along the forests streams are usually covered by lichens and mosses. *Mantidactylus peraccae* appears to be mainly an arboreal species. A high density of males was usually observed overnight at Campsite 1 (altitude of about 1050 m) on the mossy trees at an elevation of 2–4 m. At Vohiparara one male was found in February at night, 2–3 m high on a tree. A fresh clutch of eggs, possibly belonging to *M. peraccae* and similar to clutches of *M. aglavei* as described in Glaw & Vences (1992), was hanging from a leaf near the female.

Acoustic repertoire. The advertisement call of *M. peraccae* is composed of one note type which often has a rather "metallic" sound. Some differences regarding note arrangements exist in the different tape recordings which may be ascribed to intraspecific geographical variation or to the varied motivational states of the calling specimens.

At Ankeniheny (Fig. 4a), only single, explosive and isolated notes were noticed (see also Glaw & Vences, 1994). Note duration (recorded 20 February 1994, 21:30, 19°C) was 132–273 ms (mean 212 ± 51 ms, $n = 5$). Intervals between two notes were 20–70 s (mean 37 ± 20 s, $n = 5$). Fundamental frequency was between 1.05 and 1.45 kHz, dominant frequency 2.25–2.85 kHz, additional (lower emphasized) frequency bands at 3.80–4.20, 4.95–5.50, 6.25–6.55 and 7.65–7.80 kHz.

At Vohiparara (Fig. 4b), calls consisted mostly of note pairs (temperature = 21°C). Note duration was 195–250 ms (mean 221 ± 17 ms, $n = 10$), and duration of intervals between the notes of a note pair was 248–336 ms (mean 278 ± 30 ms, $n = 10$). To guard against presenting subjective measurements, we also state the period from the start of the first note until the start of the second note. This time period, which could be accurately measured, was 340–360 ms (mean 352 ± 9 ms, $n = 5$). Two dominant frequency bands were present at 1.2–1.5 kHz and 2.4–2.9 kHz, and an additional low intensity frequency band is present at 3.9–4.2 kHz. Besides the note pairs, several isolated notes were recorded which were similar to those from Ankeniheny. Duration of these notes was 52–85 ms (mean 69 ± 14 ms, $n = 4$). Two three-note calls were also recorded. These resemble note pairs but contain an additional short note (duration 9 and 22 ms).

At Anjanaharibe, Analabe Valley, calls usually consisted of note pairs. Sometimes the call series was followed by a "croaking" note. This additional note has a frequency ranging from 1.1–1.9 kHz. In a few cases the calls were repeated in a series of up to 5 notes (Fig. 4c). Temperature during time of recording was 20°C. Frequency ranged between about 0.9–9.0 kHz, with a maximum of emission at 2.5–2.8 kHz. Note duration was 53–349 ms (mean 140 ± 76 ms, $n = 27$) and duration of intervals between the starts of notes within one series was 419–727 ms (mean 624 ± 98 ms, $n = 7$).

At Ambohitantely (temperature = 19°C) the recorded calls ranged from typical double notes up to five notes. The spectral structure is very similar to that of other localities: the maximum intensity of emission is at

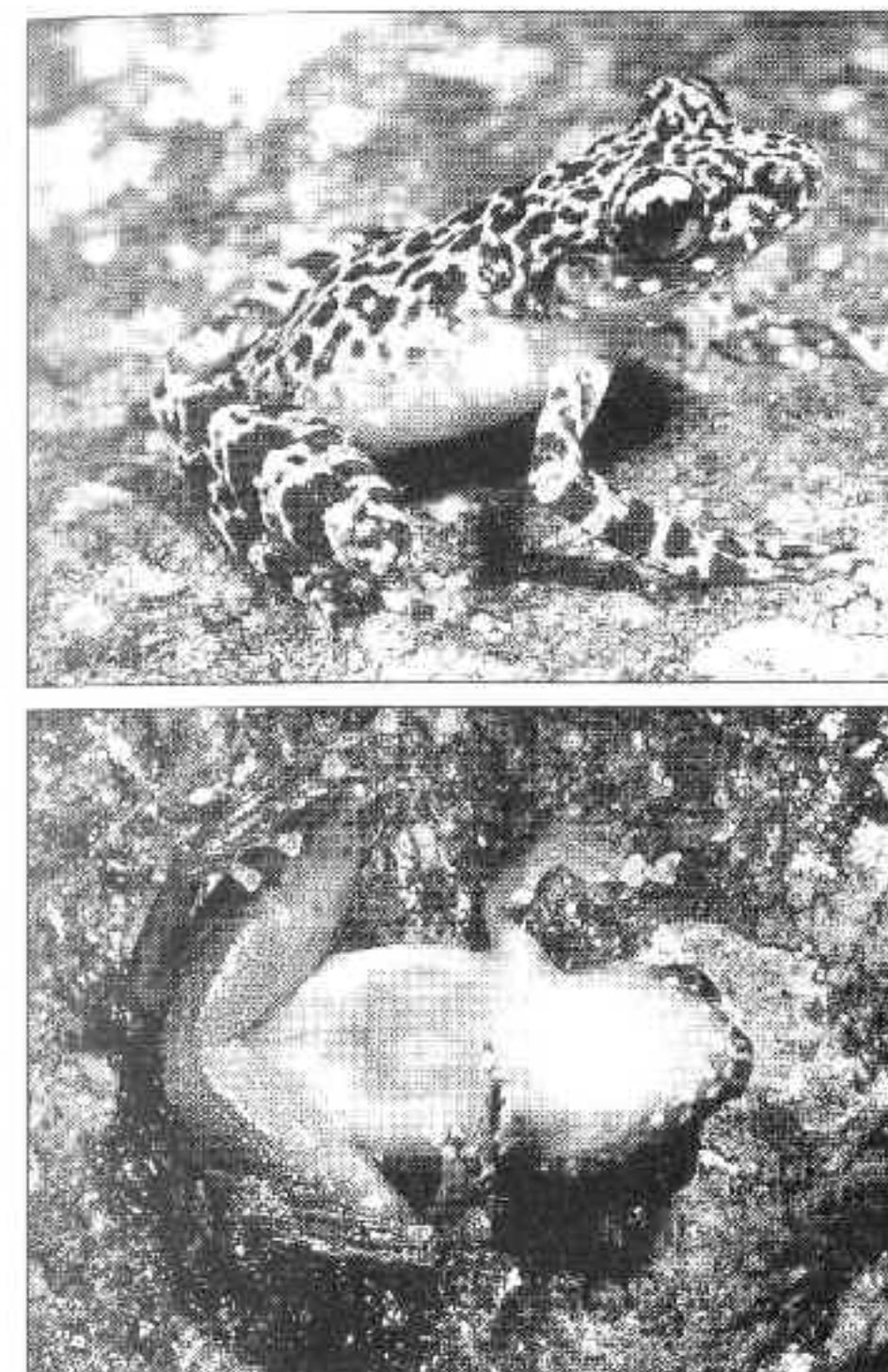


FIG. 5. *Mantidactylus brunae* n. sp. MRSN A1649, live holotype (male) from Andohahela low altitude rainforest, southern Madagascar. Dorsal (a) and ventral (b) views.

about 2.2–3.0 kHz, with other components at 1.2 and 4.0 kHz and highest frequency at 9.0 kHz. Note duration was 137–228 ms (mean 175 ± 28 ms, $n = 10$), duration of intervals between the starts of notes within one series was 376–544 ms (mean 458 ± 61 ms, $n = 8$).

Remarks. ZMA 6869/703 was identified as a male by Blommers-Schlösser (1979). Femoral glands are not evident in this specimen, whereas they are visible in MNHN 1975-753 (Fig. 2; also depicted by Blommers-Schlösser & Blanc, 1991 and by Glaw & Vences, 1992a: Figs. 135–136, p. 116). Gonads are not recognizable, but the presence of eggs can be excluded. For this reason it might be an immature individual; it was probably upon the analysis of this specimen that Blommers-Schlösser & Blanc (1991) concluded that the femoral glands of *Mantidactylus peraccae* males are not visible.

Other specimens held at Paris were attributed to *M. peraccae*, but most likely do not belong to this species: they all have the fifth toe longer than the third, a feature distinctive of *M. elegans* and *M. brunae* n. sp. (see below). MNHN 1975.752 (from Anjaridilava, Andringitra, Fianarantsoa Province; presumably collected by Ch.P. Blanc, 15 January 1971), SVL 37.9 mm, colouration similar to that of *M. peraccae*: the dorsum is brownish with irregular darker spots, not large as

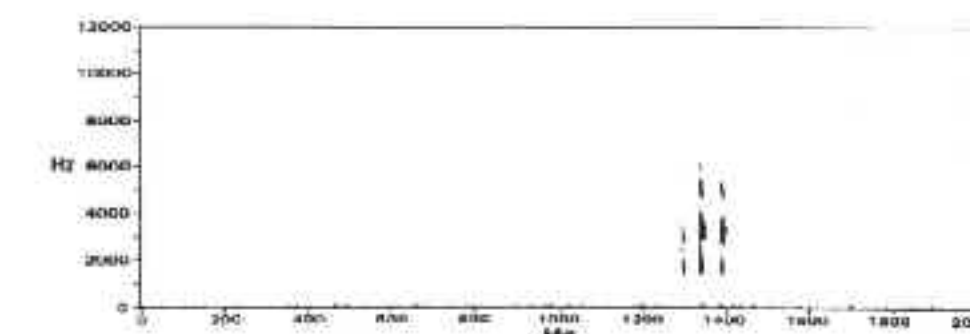


FIG. 6. Sonogram of the advertisement call of *Mantidactylus brunae* n. sp. from Andohahela low altitude rainforest; temperature, 18°C.

in other *M. elegans* specimens (e.g. Fig. 268 and plate 85 in Glaw & Vences, 1994). The belly is whitish with blackish spots on the chest forming a network on the throat. The dorsum and throat are smooth while the belly and under-surface of hindlegs are slightly granular. The snout is rather rounded and the nostrils do not protrude. An inner metatarsal tubercle is present (length = 1.5 mm) as well as a small wart-like protuberance similar to the external tubercles observed in the "typical" *M. peraccae*.

MNIIN 1975.754 (same collecting data as MNHN 1975.752) lacks the outer metatarsal tubercle (inner metatarsal tubercle length = 1.9 mm). The tibiotarsal articulation reaches beyond the tip of snout. Femoral glands are absent. The dorsum colouration is greyish with large dark spots, the throat is dark. The SVL of 33.1 mm is comparable to that of a newly metamorphosed *M. elegans* found at Andringitra (shown by Glaw & Vences, 1994, plate 85) which measured 34 mm.

MNHN 1975.751, from Andilabe, Tsaratanana Massif, Antsiranana (Diégo-Suarez) Province, 1700 m, approximately 13°49'–14°05'S / 48°44'–59' E, February 1951, unknown collector, labelled as "Rhacophorinae sp.", is here tentatively regarded as a juvenile of *M. elegans*, as already noted in the old catalogues. Snout-vent length is 23.5 mm. The preservation conditions are poor, but it is still possible to discern a dorsum colour patterning very similar to that of *M. elegans*. The belly is "dirty" and dark spots are not visible, neither are femoral glands. The inner metatarsal tubercle is evident (length = 1.1 mm), while the outer one is lacking.

A NEW MANTIDACTYLUS FROM SOUTHERN MADAGASCAR

Mantidactylus brunae new species [Figs. 5–6]

Mantidactylus cf. *peraccae* - Andreone, 1995: 35; Andreone, 1996a: 307, 402; Andreone & Randriamahazo, 1997: 112–113, 126, Figs. 51–52.

Holotype. MRSN A1649, adult male from the low altitude rainforest between the villages of Isakavondro and Eminiminy, Andohahela Strict Nature Reserve, Toliara (Tuléar) Province, 24°45'30"S / 46°51'15"E, elevation of about 600 m, 17 November 1994, F. Andreone & D. Vallan leg.

Diagnosis. A medium-sized slender frog belonging to the genus *Mantidactylus* as is evident from the presence of femoral glands in the male (females unknown).

It differs from the other known *Mantidactylus* species as follows: from the species of the subgenera *Mantidactylus*, *Brygomantis*, *Chonomantis*, *Ochthomantis*, and *Hylobatrachus* by the lack of a visible porus in the femoral glands; from the species of the subgenera *Laurentomantis* and *Pandanusicola*, as well as the species of the *M. boulengeri* group (subgenus *Gephyromantis*), by separated lateral metatarsalia; from the *M. asper* group (subgenus *Gephyromantis*) by the lack of distinct folds on the shoulder region and shorter hindlimbs; from most species of the subgenus *Phylacomantis* (*M. pseudoasper*, *M. corvus*, *M. granulatus*, *M. leucomaculatus*) by the lack of a paired vocal sac; from *M. redimitus* and *M. cornutus* (subgenus *Phylacomantis*) by the lack of two tubercles between the eyes; from the subgenus *Guibemantis* (*M. depressiceps*, *M. tornieri*, *M. liberi*) by the presence of distinctly visible femoral glands; from the *M. wittei* complex (subgenus *Blommersia*) by the larger size; from *M. argenteus* (subgenus *Blommersia*) by the smaller tympanum; from *M. guibei* and *M. bertini* (subgenus *Blommersia*) by separated metatarsalia; from *M. aglavei*, *M. fimbriatus*, *M. massi*, and *M. phantasticus* (subgenus *Spinomantis*) by the complete lack of dermal flaps and fringes, and relative toe lengths. Externally *M. brunae* mostly resembles *M. peraccae*, from which it differs in the relative third and fifth toe length, trilled calls, terrestrial/scansorial habits, slender form, rather pointed snout, lack of dorsal warts, and the dorsal pattern arranged to form a dark reticulation. Another *Mantidactylus* of uncertain subgeneric attribution, the high-mountain species *M. elegans*, has a similar relative toe length, colour pattern, and, according to Glaw & Vences (1994), also habitat preferences. However, it differs by larger size, lack of outer metatarsal tubercle, and, as far as is known, by lack of femoral glands. A re-description of this species is given later (see *Remarks*).

Subgeneric attribution. The species cannot unequivocally be assigned to any subgenus. Based on its phenetic similarity with *Mantidactylus peraccae* it is tentatively included in the subgenus *Spinomantis*.

DESCRIPTION OF THE HOLOTYPE

Morphology. Male in excellent preservative condition. SVL 32.3 mm. Snout pointed, head longer than wide. Loreal region rather concave, nostrils not distinctly projecting, situated nearer to the eyes than to the tip of snout. Tympanum distinct, half the diameter of the eye. Vomerine teeth arranged in two slightly oblique oval groups behind the choanae. Hind legs overlap about 2 mm when curved at right angles; the tibiotarsal articulation reaches the tip of the snout. Finger length: $1 < 2 < 4 < 3$. Unwebbed fingers with digital expansions about the same size as the tympanum. Subarticular tubercles, as well as the tubercle at the basis of the pollex, visible. Lateral metatarsalia separated. Toe length: $1 < 2 < 3 < 5 < 4$. Foot webbing: 1(1),

2i(0.75), 2e(0), 3i(1), 3e(0.75), 4i(2), 4e(2), 5(0.5). Inner metatarsal tubercle length = 1.7 mm; wart-like outer metatarsal tubercle. Dorsum and belly rather smooth. Femoral glands distinct, 8.6*3.2 mm, distance between inner margins of glands on opposite femurs = 1.5 mm.

Colouration in life. The dorsum has a yellowish-light brownish ground colour. Several black blotches are present on the dorsum, coalescing to form a reticulation on the head and loreal region. Upper surface of humerus and forearm smooth, of the same colouration of the dorsum with dark transverse bands. Fingers and toes with dark and whitish transverse bands; fingertips whitish. Flanks, as well as the area between the foreleg insertion and the jaw, are pink; the yellowish dorsum colouration continues onto the pink flanks with isolated yellowish spots. Upper jaw dark with yellow spots. Iris yellowish: lower part darker; upper part lighter; dark outer ring encircling the eye. Belly pink and throat brownish. A few light spots were visible on the dark area of throat, especially at its anterior part. Femoral glands reddish.

Colouration in preservative. The dorsum colour has changed from yellowish to greyish. The eyes are greyish-blackish. The belly is whitish and the throat greyish with some whitish spots. Femoral glands are greyish, having lost their reddish colouration.

Etymology. The specific name is a personal noun in the genitive case. F. Andreone wishes to dedicate this new species to his mother Bruna Cugnetto, for her enthusiastic support and continuous help.

Habitat and habits. The holotype was found in a small shaded spring, a tributary of the Ampasy stream, within the primary low altitude rainforest of Andohahela. The water source was covered by large rocks which constituted a cave-like formation. The specimen vocalized in these crevices at about 18.00 hr whilst clinging onto a wet rock a few centimetres above the water flow. Thus it appears to be a terrestrial-scansorial species, although it is also possible that it may be arboreal or semi-arboreal during certain periods.

Acoustic repertoire. The analysis of nine calls (temperature, 19–20°C) is presented in Table 2. The call is a trill consisting of 3–4 click notes; the duration of each note series ranges from 106–155 ms. The duration of single notes ranges from 4–25 ms, the first note being distinctly shorter than the successive ones. Inter-note intervals (within a note series) vary from 17–38 ms, being longest between the first two notes. The frequency (Fig. 6) ranges from 1.4–6.7 kHz, dominant frequency is 3.1–3.6 kHz. Other components are visible at about 1.5–1.7 and 5.0–5.2 kHz. Usually the beginning and end of the calls are less intense.

Remarks. Since the new species *M. brunae* is rather similar to *M. elegans*, we here give a detailed description of specimens attributed to *M. elegans* collected at Andringitra. It must be stated, however, that specimens currently considered as *M. elegans* may in fact belong to different species. The most problematic point is that

TABLE 2. Analysis of nine calls of *Mantidactylus brunae* n. sp. Each call consists of 3–4 short clicks, here called notes. Note duration and duration of intervals between notes is given separately for successive notes of a call. Recording temperature, 19–20°C.

Call number	N	range	mean	SD
Number of notes	9	3–4	3.4	0.5
Call duration (ms)	9	106–155	125.1	20.3
Note duration (1) (ms)	9	4–19	10.0	4.7
Note duration (2) (ms)	9	14–25	19.2	4.1
Note duration (3) (ms)	9	12–23	18.6	4.3
Note duration (4) (ms)	4	14–19	16.5	2.4
Interval duration 1 (ms)	9	31–38	34.3	2.3
Interval duration 2 (ms)	9	25–34	28.9	3.7
Interval duration 3 (ms)	4	17–30	22.0	5.9

up to now no reproducing specimens of *M. elegans* have been found; it is therefore not possible to draw definite conclusions on the adult morphology of the species. Lack of femoral glands in *M. elegans* is probable (despite the contrary mention in Guibé, 1978:31 which probably referred to *M. peraccae* specimens), but not yet definitely ascertained in live adult males. Specimens of the type series of *M. elegans*, however, are distinctly larger than *M. brunae* (52–60 mm SVL; Blommers-Schlösser & Blanc, 1991), and easily distinguished from that species by a number of external features.

ZFMK 57453 (Fig. 7) is a specimen in good state of preservation coming from Pic Boby (Andringitra Massif, Fianarantsoa Province, approximately 22°07'–21°S / 46°47'–47°02'E, 18 January 1994, F. Glaw & M. Vences leg. SVL of 34.7 mm. Snout rather rounded, head clearly longer than wide. Loreal region rather straight, nostrils not projecting, situated nearer to tip of snout than to eye. Tympanum rather indistinct, about half the diameter of the eye. Vomerine teeth arranged in two small, indistinct groups between the choanae. Hind legs overlap about 2 mm when curved at right angles; the tibiotarsal articulation reaches nearly the tip of the snout. Finger length: $1 < 2 < 4 < 3$. Unwebbed fingers with digital expansions slightly larger than tympanum diameter. Subarticular tubercles visible. Lateral metatarsalia more or less separated. Toe length: $1 < 2 < 3 < 5 < 4$. Foot webbing: 1(0.5), 2i(1), 2e(0.5), 3i(1.25), 3e(1), 4i(2), 4e(2), 5(0.5). Inner metatarsal tubercle length = 1 mm; no distinct outer metatarsal tubercle. Dorsum smooth, venter slightly granular. No distinct, prominent femoral glands visible; a granular thigh patch (see Daly et al. 1996) extends from the anus onto about 2/3 of the ventral femur surface.

No definite conclusion as to the sex of this specimen is possible; it is most probably a subadult, since a specimen of similar size (ZFMK 57454; SVL 34.3 mm) is newly metamorphosed, as indicated by presence of a tail remnant. ZFMK 57453, together with other individuals of similar size, was collected under stones on rocky ground in high-mountain habitat, together with

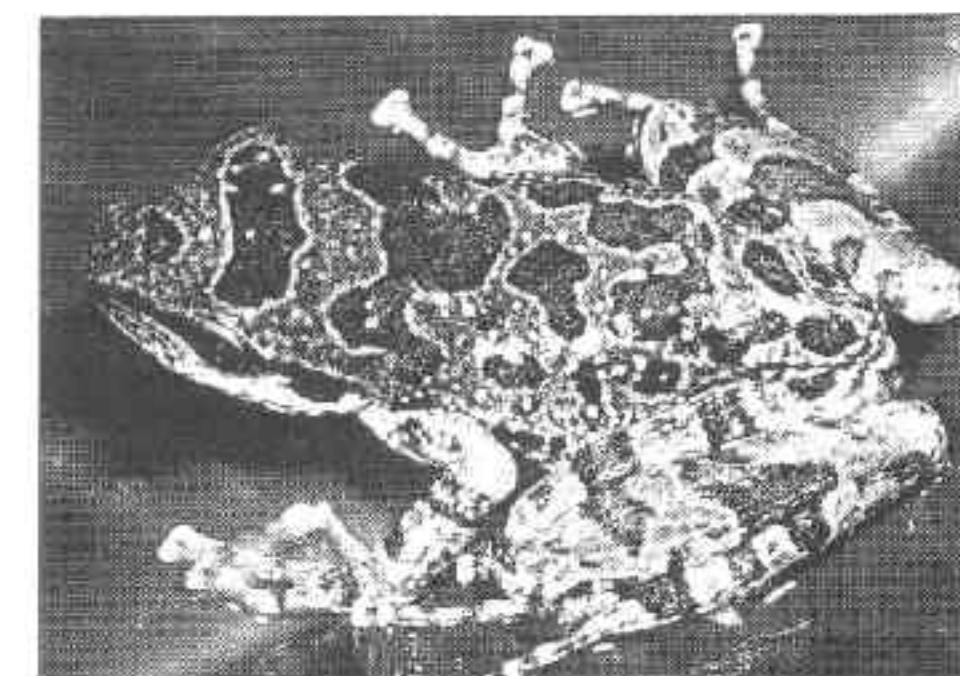


FIG. 7. *Mantidactylus elegans*. ZFMK 57453, live subadult from Pic Boby (Andringitra Massif). Dorsal view.

specimens of *Anodonthyla montana* (see Glaw & Vences, 1994). This indicates that the species is largely not arboreal.

DISCUSSION

According to present knowledge, *M. peraccae* has a wide distribution which extends from northern Madagascar (Anjanaharibe Chain), through the central-eastern escarpment (Vohiparara, Andasibe, Ankeniheny), Andringitra Massif (Raxworthy & Nussbaum, 1996), to the Anosy Chain in the south. It appears to be a mid-high altitude rainforest species, the lowest records being Andasibe (about 900 m), Ankeniheny (about 1000 m) and Analabe, Anjanaharibe Chain, Camp 1 (about 1050 m), whereas the highest locality is the Anosy Chain at 1800 m. Since this species is present on some high altitude massifs (e.g. Andringitra, Anosy Chain) which may constitute biogeographic refuges (Raxworthy & Nussbaum, 1996), it is quite likely that some of the populations presently included in *M. peraccae* may in fact belong to different taxa. If so, this might explain the observed variability in morpho-chromatic and acoustic traits. The existence of previously unrecognised cryptic species which differ bioacoustically has already been pointed out for other Malagasy frogs, e.g. those belonging to the *Boophis luteus* group (Andreone, 1996b), *B. goudoti* group (Glaw & Vences, 1997a) and some recently described *Mantidactylus* species (*M. fimbriatus*, *M. phantasticus*) of the subgenus *Spinomantis* which resemble *M. aglavei* (Glaw & Vences, 1994; 1997b). However, the small number of analysed *M. peraccae* specimens and populations, as well as the lack of knowledge of the extent of motivational call differences, currently do not allow for further statements on a possible taxonomic differentiation.

The new species herein described, *Mantidactylus brunae*, may represent a southern relative of *M. peraccae*, being currently known only from the Andohahela rainforests. Its tentative inclusion within the subgenus *Spinomantis* makes it necessary to provide a new diagnosis of this subgenus. The following

TABLE 3. Key to the *Mantidactylus* species currently included in the subgenus *Spinomantis*, and to *Mantidactylus elegans*.

- 1a. Large inner and distinct outer metatarsal tubercle present. One distinct femoral gland on each femur in males (ovoid, well defined and generally prominent, without median porus, each gland consisting of generally more than 60 single granules of similar size) subgenus *Spinomantis* 2
- 1b. Small inner metatarsal tubercle present; no distinct outer metatarsal tubercle. Prominent femoral glands probably absent in males and females *Mantidactylus elegans*
- 2a. Dermal tubercles and fringes present, especially on hindleg; Ratio tympanum diameter/eye diameter < 0.5 3
- 2b. Dermal tubercles and fringes absent; Ratio tympanum diameter/eye diameter 0.5 6
- 3a. Small dermal tubercles on hindleg; belly greenish *Mantidactylus massi*
- 3b. Larger dermal extensions and fringes, some of which generally reach a length of 1 mm; venter white or greenish 4
- 4a. Distinct tubercles and fringes on head and dorsum; belly greenish; call consisting of double-click series *Mantidactylus phantasticus*
- 4b. No fringes on head and dorsum; belly whitish; calls without double-click series 5
- 5a. SVL < 40 mm; generally one single (sometimes incomplete) row of lateral dermal fringes on foot and tarsus *Mantidactylus fimbriatus*
- 5b. SVL > 40 mm; generally smaller tubercles or fringes interposed between row of primary lateral dermal fringes on foot and tarsus *Mantidactylus aglavei*
- 6a. SVL of adult male 32 mm; head narrow; toe 3 < toe 5; belly pinkish; terrestrial habits; trill call *Mantidactylus brunae*
- 6b. SVL of adult males generally > 34 mm; head broad; toe 5 < toe 3; belly greenish or whitish-pinkish; arboreal habits; no trill call *Mantidactylus peraccae*

characters seem to apply to *Spinomantis* species, and their combination allows for a distinction from all other *Mantidactylus*: medium sized frogs (SVL 31-52 mm), tympanum diameter less than 2/3 of eye diameter, tympanum not distinctly larger in males than in females (known only in *M. aglavei*, *M. fimbriatus* and *M. peraccae*), lateral metatarsalia separated, inner and outer metatarsal tubercle present, finger disks distinctly enlarged, dorsum often with large, rounded, dark brown markings, femoral glands distinct and prominent in males, ovoid and well defined without median pores, consisting of a large number (generally > 60) of densely arranged, clearly discernible small granules of similar size which often (except *M. aglavei* and *M. fimbriatus*) are of different colour to the surrounding integument, absent in females. Since none of these

characters is an exclusive feature of the subgenus, its monophyly can not be currently ascertained.

The morphochromatic similarity of *M. brunae* with other representatives of *Spinomantis* in relation to its alternative ecology raises interesting questions regarding the subgeneric attribution and relationships within *Mantidactylus*. If *M. brunae* is really closely related to the other *Spinomantis* species it would be the first scansorial representative of this otherwise strictly arboreal subgenus, although it cannot be excluded (since only one specimen is known thus far) that it is at least partially arboreal. Another *Mantidactylus* species which may have relationships with *M. brunae* is *M. elegans*. The few available observations (e.g., Glaw & Vences, 1994) suggest that it is a terrestrial-scansorial frog living in high-mountain rocky habitats. In general appearance and ecology it is similar to *M. brunae*, differing in larger size, absence of an outer metatarsal tubercle and probably absence of femoral glands. Although little is known on morphological variation between the populations of Malagasy anuran species, we provide an updated diagnostic key which summarizes current knowledge on morphological differentiation within the subgenus *Spinomantis* (Table 3).

Considering the incomplete knowledge about Malagasy herpetofauna, it is likely that *M. brunae* and *M. elegans* represent key species in the understanding of relationships within *Mantidactylus* and between the subgenera as currently defined. Further data are therefore needed to determine the distribution and ecology of *M. brunae* and *M. elegans*, as well as to establish the variability within *M. peraccae*.

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