Alytes, 1997, **14** (4): 130-146.

Description of two new frogs of the genus *Mantidactylus* from Madagascar, with notes on *Mantidactylus klemmeri* (Guibé, 1974) and *Mantidactylus webbi* (Grandison, 1953) (Amphibia, Ranidae, Mantellinae)

Miguel VENCES *, Frank GLAW * & Franco ANDREONE **

* Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany

** Museo Regionale di Scienze Naturali, Sezione di Zoologia, Via G. Giolitti 36, 10123 Torino, Italy

Two new species of the endemic Malagasy frog genus *Mantidactylus* were discovered during recent fieldwork in northeastern Madagascar, and these are formally named and described in this paper. The first one inhabits mossy stone habitats in the Marojezy massif and is mainly characterized by its olive-greenish coloration and a short snout. The second new species is similar but larger and has a copper red iris. It is characterized by a very distinctly protruding inner metatarsal tubercle which is less developed in other known *Mantidactylus*. Both new species are tentatively included in the subgenus *Gephyromantis*, but their relationships with other *Mantidactylus* remain obscure. Morphologically they are most similar to *M. klemmeri* and *M. webbi*; we therefore provide an updated diagnosis of these two species and a detailed description of the call of *M. klemmeri*, as well as first data on its ecology and coloration in life.

INTRODUCTION

The systematics of the frog genus *Mantidactylus* Boulenger, 1895, endemic to Madagascar, has been the subject of several studies during the last 20 years. The biosystematic investigations of BLOMMERS-SCHLÖSSER (1979) showed that the distinction between the genera *Gephyromantis* and *Mantidactylus*, as made by GUIBÉ (1978) and previous workers, was largely artificial. As a conclusion, BLOMMERS-SCHLÖSSER (1979) considered *Gephyromantis* as a junior synonym of *Mantidactylus*. She also described two new species of the genus and assigned 31 *Mantidactylus* species to 10 phenetic species groups. BLOMMERS-SCHLÖSSER & BLANC (1991) assigned all *Mantidactylus* species to these groups and analysed phylogenetic relationships within *Mantidactylus*. The cladogram presented by these authors characterized the species groups by assumed synapomorphies,

and thus suggested that each represents a monophyletic unit. DUBOIS (1992) elevated some of these groups to subgeneric rank. Based on new biosystematic data, GLAW & VENCES (1994) argued that the monophyly of the subgenera within *Mantidactylus* would be more convincing recognizing four additional subgenera. They also noted that no phylogenetic arguments remain to regard *Laurentomantis* Dubois, 1980 as a genus separate of *Mantidactylus*, and thus considered it as a subgenus, transferring the three *Laurentomantis* species to *Mantidactylus*. Following GLAW & VENCES (1994), 12 subgenera within *Mantidactylus* are presently accepted: *Mantidactylus* Boulenger, 1895; *Gephyromantis* Methuen, 1920; *Hylobatrachus* Laurent, 1943; *Laurentomantis* Dubois, 1980; *Blommersia* Dubois, 1992; *Brygoomantis* Dubois, 1992; *Guibemantis* Dubois, 1992; *Spinomantis* Dubois, 1992; *Chonomantis* Glaw & Vences, 1994; *Ochthomantis* Glaw & Vences, 1994; *Pandanusicola* Glaw & Vences, 1994; *Phylacomantis* Glaw & Vences 1994.

Since 1990, eight new *Mantidactylus* species have been described (BLOMMERS-SCHLÖSSER & BLANC, 1991; GLAW & VENCES, 1992*b*, 1994), one species was transferred to this genus from the genus *Boophis* (GLAW & VENCES, 1992*a*) and three species were resurrected from synonymy (BLOMMERS-SCHLÖSSER & BLANC, 1991; RAXWORTHY & NUSSBAUM, 1994; ANDREONE & GAVETTI, 1994). Despite this intensive work on the genus, the species inventory of *Mantidactylus* is far from being complete. The continued discovery of new species even in well studied areas shows that the genus is much more speciose than presently recognized (59 named species according to GLAW & VENCES, 1994).

The subgenus *Gephyromantis* currently contains 10 species which are arranged in two species groups according to GLAW & VENCES (1994): the *M. asper* group with four scansorial primary forest species, which can be found during the day on the forest floor and which call predominantly at night from leaves and branches; and the *M. boulengeri* group with six rather small ground-dwelling frogs which call mainly during the day. Probably closely related subgenera are *Laurentomantis* with three species and *Phylacomantis* with six species. The monophyly of these taxonomic units (subgenera and species groups) must still be verified since the attribution of species to subgenera within *Mantidactylus* is often only based on phenetic similarity, the diagnostic synapomorphies of the groups generally being derived from studies of only a few species.

Two species of the subgenus *Gephyromantis* differ from other species of this subgenus mainly in terms of their coloration which is partly greenish, and their ecology which is associated with mossy rocks along forest brooks. These species are *M. webbi*, and one species which up to now was regarded as *M. klemmeri* (GLAW & VENCES, 1994).

Fieldwork conducted during 1994 and 1995 yielded new data on these two forms, and resulted in the discovery of two additional species which are morphologically similar to *M. webbi* and to the species previously regarded as *M. klemmeri*. After examination of the types of *Mantidactylus klemmeri* and *M. webbi* in the context of the two similar, newly discovered species, we conclude that the four forms studied by us are *M. klemmeri*, *M. webbi*, and two unnamed forms which we will here describe as new species.

MATERIAL AND METHODS

Specimens were captured by hand both during the day and at night with the aid of flashlights. They were fixed for a few minutes in 96 % ethyle alcohol, and stored in 70 % ethyle alcohol. Live animals were photographed to document color and pattern variation. Morphometric measurements were taken by the first author with a ruler to the nearest 0.5 mm or with a precision calliper to the nearest 0.1 mm. Abbreviations used are SVL (snout-vent length) and HW (head width). Tympanum and eye diameter were measured along a horizontal plane.

Calls of *M. klemmeri* were recorded with a Tensai portable tape recorder and an external VIVANCO EM 238 microphone. These were analysed with the sound analyzing system "MEDAV Spektro 3.2".

Type material was examined both in the Natural History Museum, London, United Kingdom (BM) and the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Other abbreviations used in this paper are as follow: MRSN, Museo Regionale di Scienze Naturali, Torino, Italy; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

RESULTS

THE IDENTITY OF *MANTIDACTYLUS KLEMMERI*

In 1994, GLAW & VENCES (color plate 101) showed a picture of a brook-dwelling frog from the Marojezy mountains which they considered to be *Mantidactylus klemmeri*. The pictured species occurred along brooks near the *M. klemmeri* type locality and was morphologically similar to that species. Furthermore, its unique character combination separated it clearly from any other described *Mantidactylus*. In 1995, however, F. GLAW collected a second frog species in Marojezy which inhabited the forest floor and showed some important morphological and ecological differences from the species previously assigned to *M. klemmeri*. These differences are summarized in tab. 2, whereas tab. 1 shows the absolute measurements of all specimens considered in the present publication. A direct comparison with the types of *Mantidactylus klemmeri* showed that the species inhabiting the forest-floor should be assigned to this taxon. An updated diagnosis of *M. klemmeri* together with first data on its advertisement call is presented below. The brook-dwelling form is consequently described as a new species.

Tab. 1. - Measurements (all in mm) of the *Mantidactylus* specimens considered in the present study. Number: abbreviation of museum where specimen is held, and its collection number. Holotypes are marked with a * behind the number, paratypes with a + behind the number. Other abbreviations used are: M, male; F, female; J, juvenile; SVL, snout-vent length; HW, head width; Eye, horizontal eye diameter; Tym, horizontal tympanum diameter; E-N, distance between anterior eye margin and nostril; N-ST, distance between nostril and snout tip; HL, hand length; FLiT, foot length including tarsus; TibT, tibiotarsal articulation reaching (1) eye, (2) beyond eye, (3) nostrils, (4) snout tip, (5) slightly beyond snout tip, (6) clearly beyond snout tip; ToeL, relative length of third toe compared with fifth toe; FGS, size of femoral glands, given as length × width; FGD, distance between inner margins of glands on opposite femurs. All specimens are from the type localities of the respective species, except for MNHN 1975.781 (*M. klemmeri*; female from the Chaînes Anosyennes) and MNHN 1975.951-952 (male and female of *M. webbi* from Andohahela).

Species and number	Sex	SVL	HW	Eye	Tym	E-N	N-ST	HL	FLiT	TibT	ToeL	FGS	FGD
Mantidactylus klemmeri													
MNHN 1973.960+	M	20.8	7.3	3.0	1.2	2.0	1.2	6.9	16.5	(5)	3=5	1.5×1.5	2.7
MNHN 1973.959+	M	20.8	7.2	2.6	1.1	2.3	1.5	6.2	17.1	–	3=5	1.7×1.4	2.6
MNHN 1973.957+	M	20.0	6.9	3.0	0.9	2.2	1.3	6.6	17.5	(4)	3=5	1.9×1.2	2.4
MNHN 1973.958+	M	21.2	6.6	2.8	0.9	2.2	1.3	6.5	16.0	(5)	3=5	-	-
ZFMK 59944	M	20.5	7.0	2.7	0.9	2.2	1.5	7.0	16.2	(6)	3=5	2.0×1.4	1.5
ZFMK 59943	M	19.5	6.5	2.5	0.9	2.2	1.5	6.2	15.6	(5)	3=5	2.4×1.7	2.2
ZFMK 59942	M	20.5	6.6	2.5	1.0	2.2	1.5	6.4	17.3	(5)	3=5	1.8×1.3	2.7
MNHN 1973.962+	F	20.8	6.5	2.7	0.9	2.2	1.2	6.5	17.2	(5)	3≤5		
MNHN 1973.961+	F	24.0	7.3	3.3	1.2	2.5	1.5	7.7	18.4	(4)	3=5		
MNHN 1973.956+	F	24.0	7.2	3.1	1.0	2.5	1.4	7.0	18.5	-	3=5		
MNHN 1973.955*	F	24.0	7.5	2.8	1.1	2.6	1.4	8.0	18.9	(5)	3=5		
MNHN 1973.963+	J	16.8	-	-	-	-	-	-	-	-	-		
MNHN 1975.781	F	26	8	3.2	1.4	2.5	2.2	8.2	-	(4)	3=5		
Mantidactylus rivicola													
ZFMK 57428*	M	22.5	7.5	2.6	1.0	2.0	1.4	7.8	16.7	(4)	3≤5	1.5×1.3	0.8
ZFMK 59898+	M	24.3	8.8	3.4	1.7	2.5	1.7	8.0	18.0	(5)	3=5		
ZFMK 57429+	F	23.8	7.8	3.2	1.2	2.0	1.6	7.5	16.3	(2)	3=5		
ZFMK 59946+	F	24.3	7.7	2.9	1.4	1.9	1.4	7.0	16.5	(4)	-		
ZFMK 59945+	F	24.2	7.5	3.0	1.1	1.9	1.5	7.1	15.5	(2)	3=5		
ZFMK 59947–	J	19.4	5.9	2.5	0.9	1.6	1.1	5.6	14.4	(5)	3=5		
Mantidactylus silvanus													
MRSN A1661*	M	30.5	10.5	3.9	2.2	2.9	2.0	9.5	21.0	(3)	3≤5	2.2×1.5	ca. 1.0
Mantidactylus webbi													
MNHN 1975.951	M	22.5	8.0	2.2	1.0	2.3	1.4	7.3	16.0	(3)	3=5	3.7×2.0	1.0
MNHN 1975.952	F	24.9	8.5	2.9	1.3	2.4	1.8	8.8	20.0	(6)	3=5		
ZFMK 52725	M	24.9	8.7	3.0	1.8	2.5	1.5	7.8	19.0	(5)	3=5	3.6×1.5	2.3
ZFMK 52726	F	30.5	10.5	2.7	1.6	3.5	1.7	9.8	22.2	(4)	3=5		

Tab. 2. - Comparison between the four *Mantidactylus* species treated in the present study. Morphometric data from tab. 1. IMT: inner metatarsal tubercle. Other abbreviations as in tab. 1. Values are given as range; mean ± standard deviation is given in brackets. Significant differences (Mann-Whitney *U* test) were detected between value pairs marked with stars (* $P < 0.05$; ** $P < 0.005$). Values for snout-vent length are given separately for males (M) and females (F). For snout-vent length only specimens from the type localities were considered; other values are based on all specimens listed in tab. 1.

	M. klemmeri	*M. rivicola*	*M. silvanus*	*M. webbi*
SVL (M) [mm]	19.5 - 21.2	22.5 - 24.3	30.5	24.9
SVL (F) [mm]	20.8 - 24.0	23.8 - 24.3	–	30.5
HW:SVL	0.30 - 0.35 (0.32±0.02)	0.30 - 0.36 (0.33±0.02)	0.34	0.34 - 0.36 (0.35±0.01)
HL:SVL	0.29 - 0.34 (0.32±0.02)	0.29 - 0.35 (0.31±0.02)	0.31	0.31 - 0.35 (0.33±0.02)
FLiT:SVL	0.40 - 0.88 (0.77±0.12)	0.64 - 0.74 (0.71±0.04)	0.69	0.71 - 0.80 (0.75±0.04)
Tym:Eye	**0.30 - 0.44 (0.37±0.05)	0.36 - 0.50 (0.41±0.06)	0.56	**0.45 - 0.60 (0.52±0.08)
(Eye-N + N-ST):SVL	*0.14 - 0.19 (0.17±0.01)	*0.14 - 0.17 (0.15±0.01)	0.16	0.16 - 0.17 (0.17±0.004)
Eye-N : N-ST	**0.48 - 0.68 (0.60±0.07)	**0.68 - 0.80 (0.73±0.05)	0.69	0.49 - 0.75 (0.61±0.1)
General habitat	forest floor	forest brooks	forest brooks?	forest brooks
Micro-habitat	on leaf litter/roots	on mossy rocks	at night on leaves	on mossy rocks
Habitus	very slender	slender	less slender	less slender
Dorsal skin	finely granular	some large granules	finely granular	coarsely granular
Snout	long, pointed	short	long	long
IMT	small	protruding	strongly protruding	reduced
Color	brownish	olive greenish	olive greenish/brown	olive greenish

Tab. 3. - Parameters of six notes from calls of *Mantidactylus klemmeri*, recorded in the Marojezy Strict Nature Reserve. Notes 1-3 from Camp 3 (26.02.1995; air temperature 23.8°C), notes 4-6 from Camp 4 (28.02.1995; air temperature 22.5°C). All temporal measurements are given in milliseconds (ms).

	1	2	3	4	5	6
Note duration	648	662	769	731	718	626
Number of primary pulses	4	4	4	1	2	1
Duration of primary pulses (range)	17 - 22	16 - 26	20 - 25	-	-	-
Duration of primary pulses (mean)	19.5	20.5	21.5	-	-	-
Interval between primary pulses (range)	24 - 43	25 - 41	19 - 36	-	-	-
Interval between primary pulses (mean)	32	31	28.3	-	-	-
Number of double clicks	1	1	2	0	0	0
Duration of double clicks	20	17	18 - 20	-	-	-
Duration of secondary pulse series	406	419	507	684	575	534
Number of secondary pulses	23	25	31	18	17	17
Repetition rate of secondary pulses	56.7	59.7	61.1	26.3	29.6	31.8

Mantidactylus klemmeri (Guibé, 1974)

Gephyromantis klemmeri Guibé, 1974; Guibé, 1978.
Mantidactylus klemmeri: Blommers-Schlösser & Blanc, 1991; Glaw & Vences, 1992*b*, 1994 (partim).
Mantidactylus (Gephyromantis) klemmeri: Dubois, 1992.

Diagnosis. – A small, extremely slender, brownish frog, belonging to the genus *Mantidactylus* as is evident from the presence of femoral glands in males (not recognizable in females). The absence of webbing between the toes, in combination with the small size, connected lateral metatarsalia, and the presence of a subgular vocal sac (laterally blackish) in males allow a distinction to be made from most other *Mantidactylus*. *M. eiselti* and *M. thelenae* are morphologically very similar but their advertisement calls differ distinctly. *M. webbi* and the two new species described below have a different coloration (partly greenish). Additionally, *M. webbi* males can be recognized by the white vocal sac, and the two new species have distinct, protruding inner metatarsal tubercles (small and not protruding in *M. klemmeri*).

The tibiotarsal articulation of *M. klemmeri* reaches at least the tip of snout or beyond as was noted by Guibé (1974) in the original description, not between nostrils and tip of snout as was first stated by Blommers-Schlösser & Blanc (1991) and subsequently quoted by Glaw & Vences (1992*b*, 1994).

Type material. – Holotype MNHN 1973.955, adult female, and paratypes MNHN 1973.956-963, four adult males, three adult females and one juvenile specimen, all collected by C.-P. Blanc in December 1972 in the "Massif du Marojezy" at an altitude of 600 m. Measurements of the types and of three additional ZFMK specimens from the type locality are given in tab. 1.

Color in life. – Based on color slides of ZFMK specimens, the dorsum and flanks are marbled grey or brownish without distinct transversal markings. No specimens with a light median dorsal stripe were found at Marojezy. Indistinct dark crossbands are present on fore- and hindlegs. The lower lip is dark with some rather regularly spaced light spots. Sometimes this pattern also occurs on the upper lip, resulting in transverse dark and light bands. In other specimens a light frenal stripe is faintly recognizable. The tympanic area is brown. This brown patch runs from the eye to the insertion of forelegs. The thorax and throat are marbled brown and white, the marbling on the venter and ventral limb surfaces being lighter and less contrasting. A light median line is sometimes present on the throat. Males have a distinct subgular vocal sac which is laterally blackish, indicating a possible paired or bilobate shape of the inflated sac.

Distribution. – Apart from the type material and our specimens, which were all collected in the Marojezy Strict Nature Reserve (Réserve Naturelle Intégrale) in northeastern Madagascar, one additional specimen from the Anosy mountains ("Chaînes Anosyennes") in southeastern Madagascar is available in the MNHN. This female (MNHN 1975.781) is somewhat larger than the other specimens and has a light median dorsal stripe, but shows no other morphological differences (tab. 1) from the types. We therefore consider it as belonging to the species *M. klemmeri* pending the obtention of more data.

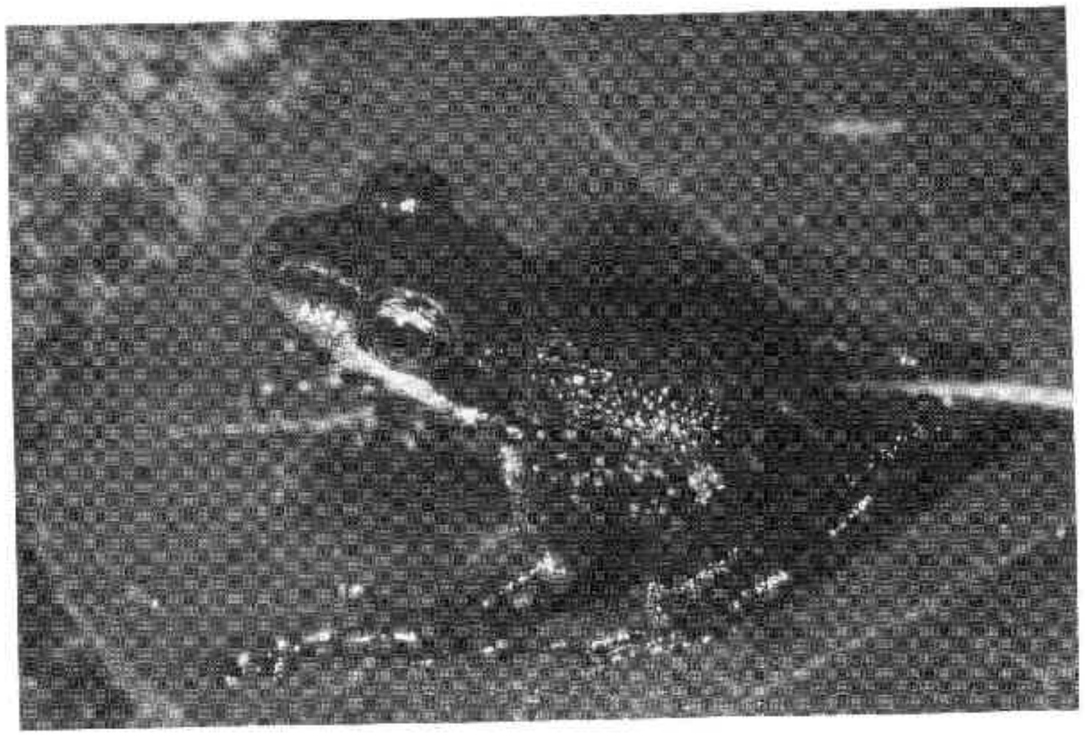

Fig. 1. – Specimen of *Mantidactylus klemmeri* from Marojezy Strict Nature Reserve, Camp 3, 26.02.1995.

Habitat and habits. – Specimens were found in 1995 at Marojezy between 600 and 1300 m elevation (up to above Camp 4). Males call during the day from the ground, mostly from between tree roots where specimens hide when disturbed. Calling males occur in small groups clustered in certain areas, but do not form dense choruses. They are not confined to the vicinity of water bodies. No activity was observed at night.

Call. – The calls were recorded on 26.02.1995 and 28.02.1995 in the Marojezy reserve (near Camp 3, about 700 m elevation, at 23.8°C, and at Camp 4, 1250 m, at 22.5°C). The first locality is very near to the type locality of *M. klemmeri*: "Massif du Marojezy (600 m)" (GUIBÉ, 1974: 1175).

As in some other members of the *M. boulengeri* group (*M. boulengeri, M. decaryi, M. eiselti, M. thelenae*), the general structure of a call can be described as a series of notes. In *M. klemmeri* a call consists of up to 6 notes. Note duration ranges from 626 to 982 ms; the duration of intervals between two notes of a series is about 2 s (measured minimum 1709 ms).

The general structure of a note is often quite complex and can be described as a series of 1-5 primary pulses, followed by 0-2 double-clicks, followed by a series of 17-31 secondary pulses. The pulse repetition rate of the secondary pulses is 56.7-61.1/s at a temperature of 23.8°C (recorded at Camp 3). The notes recorded at higher altitude (Camp 4) had a much lower pulse repetition rate (26.3-33.9/s) which may only partly be explained

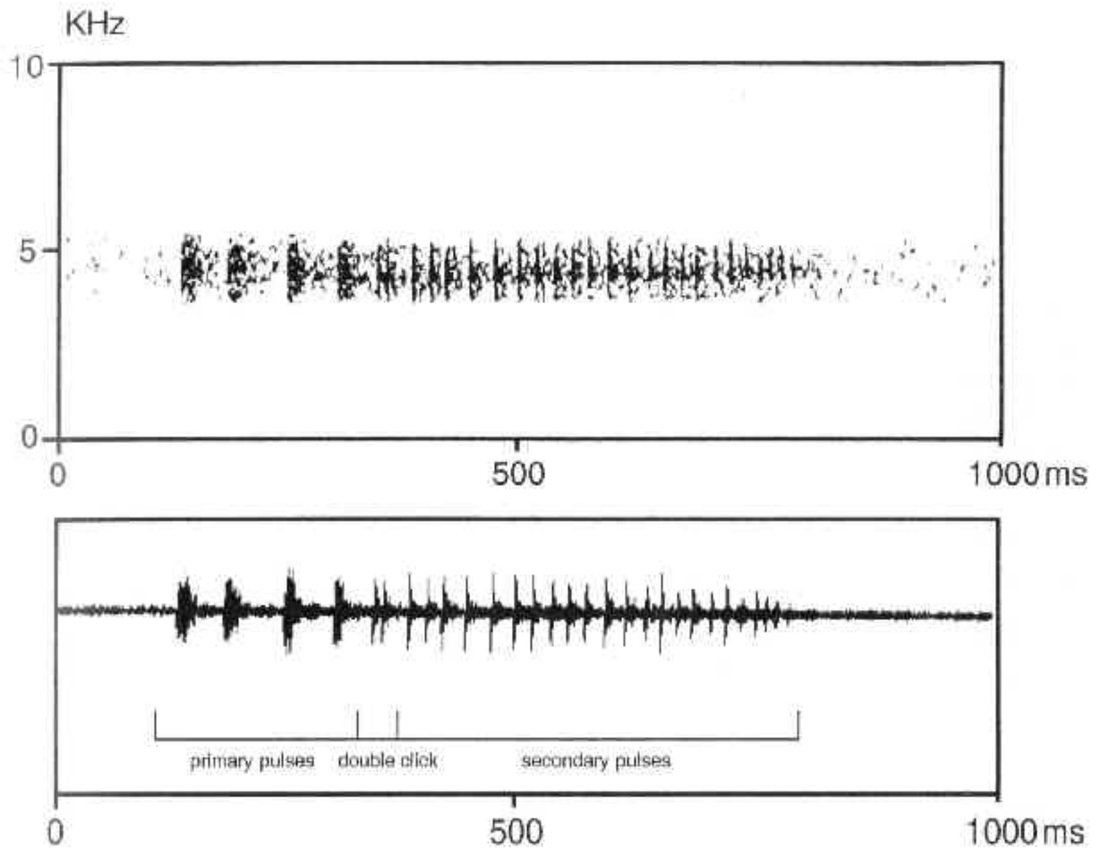

Fig. 2. – Sonagram and oscillogram of the call of *Mantidactylus klemmeri*, recorded in the Marojezy Strict Nature Reserve, Camp 3, on 26.02.1995 (air temperature 23.8°C).

by the slightly lower temperature (22.5°C). The frequency of all call components range from 3700 to 5100 Hz. Detailed data of six notes are summarized in tab. 3.

The structure of the call of *M. klemmeri* is similar to that of *Mantidactylus thelenae*. However, the call of the latter species is characterized by a shorter note duration (540-650 ms) and shorter intervals between notes (1140-1480 ms). A striking difference is the much higher pulse repetition rate (about 250/s) in the call of *M. thelenae*.

Subgeneric attribution. – As indicated by its morphology (subgular vocal sac laterally blackish, connected lateral metatarsalia, femoral glands present only in males) and especially natural history (calling not concentrated around water, therefore probably direct development), this species belongs to the subgenus *Gephyromantis*, *M. boulengeri* group. It is probably closely related to *M. eiselti* and *M. thelenae*.

Mantidactylus rivicola sp. nov.

Diagnosis. – A rather small olive-greenish frog belonging to the genus *Mantidactylus* as is evident from the presence of femoral glands in the males (absent in females). The character combination of small size, connected lateral metatarsalia, scarcely webbed feet, and presence of a protruding inner metatarsal tubercle is diagnostic for this species. Other riparian *Mantidactylus* with partly greenish dorsal coloration are *Mantidactylus lugubris* (subgenus *Hylobatrachus*) and young *Mantidactylus microtympanum* (subgenus *Mantidactylus*) which have strongly webbed feet and separated lateral metatarsalia, and *M. webbi* which has only rudimentary metatarsal tubercles and a laterally white vocal sac. Members of the subgenus *Laurentomantis* generally have a coarse granular skin and a very broad head; however, the species *Mantidactylus* cf. *malagasius* which occurs sympatrically with *M. rivicola* is morphologically rather similar to the latter. It can be distinguished by the more granular skin, different coloration (not greenish), absence of recognizable vocal sac in males, and slightly longer hindlimbs (tibiotarsal articulations reaching distinctly beyond snout tip).

M. rivicola is most similar to the second new species described below: for distinctive characters see the diagnosis of that species.

Derivatio nominis. – From the Latin *rivus* (brook) and *colere* (to inhabit). This species typically is an inhabitant of brook edges.

Holotype. – ZFMK 57428, adult male, from near Camp 1, Marojezy Strict Nature Reserve (Réserve Naturelle Intégrale), northeastern Madagascar, altitude about 300 m above sea level, collected by F. Glaw, N. Rabibisoa and O. Ramilison on 27.03.1994.

Paratypes. – ZFMK 57429, adult female, same collection data as the holotype; ZFMK 59945-59946, two adult females, ZFMK 59898, adult male, and ZFMK 59947, juvenile, from same locality as holotype, collected by F. Glaw and O. Ramilison from 25 to 28.02.1995.

Description of the holotype. – See tab. 1 for measurements. Body slender. Widest part of head slightly wider than widest part of body. Dorsal outline of head triangular, snout rather short. Snout protruding over upper jaw in lateral view. Nostrils not distinctly protruding, with lateral openings. Loreal region slightly concave. Tympanum distinct, rather small, slightly larger than 1/3 of eye diameter. Distinct supratympanic fold above the tympanum, which does not distinctly continue posterior to the tympanum. Forelegs and hindlegs slender. Outer metacarpal tubercle present. Finger discs enlarged, semicircular. No webbing between fingers. Comparative finger length $1 < 2 < 4 < 3$. Toe discs slightly enlarged, smaller than finger discs. Traces of webbing between toes. Comparative toe length $1 < 2 < 3 \leq 5 < 4$. Inner metatarsal tubercle rather large (length about 1 mm), protruding forewards. Lateral metatarsalia largely connected. Dorsal skin rough, with longitudinal tubercles in two rows bordering the median line. Some larger tubercles on the flanks. Small, oblique femoral glands with rather indistinct borders. Vomerine teeth rudimentary, hardly recognizable. Subgular vocal sac structure distinctly recognizable. Greyish lateral color on the sac surface possibly indicates that the (subgular) vocal sac may have a paired or bilobate shape when inflated.

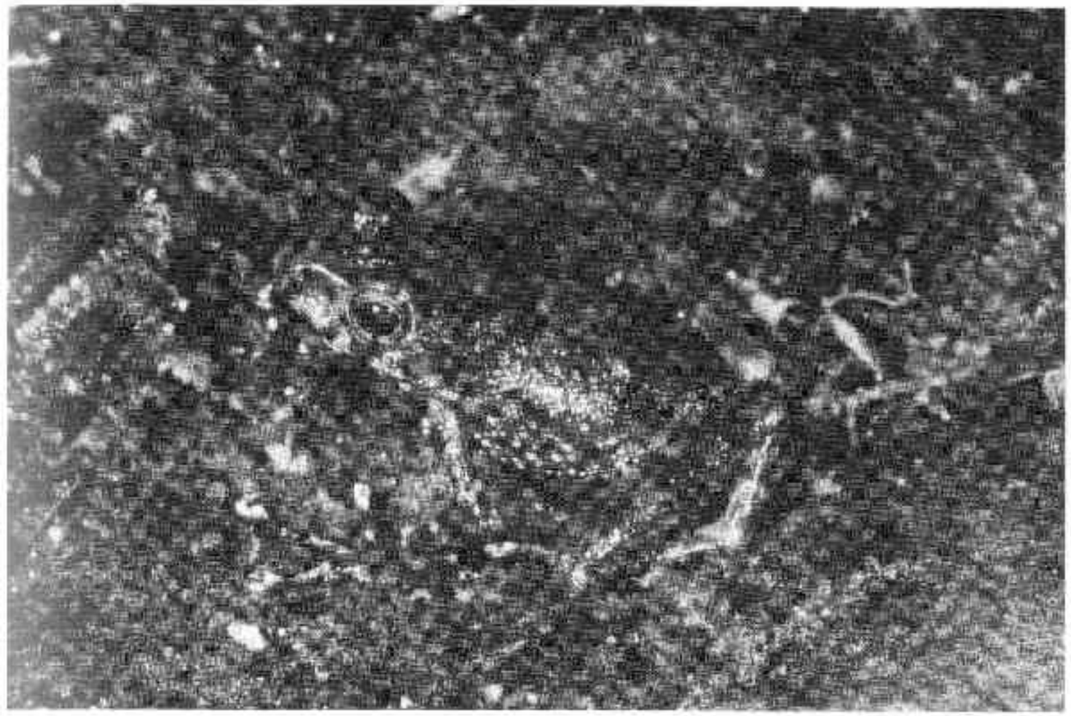

Fig. 3. – Paratype of *Mantidactylus rivicola*, ZFMK 57429, from Marojezy Strict Nature Reserve, Camp 1, 27.03.1994.

Coloration of the holotype. – After 1.5 year in alcohol, the head, dorsum and flanks are mossy olive greenish with two indistinct dark transversal markings. A light median line runs from tip of snout to the anus. In the middle of the dorsum to the left and the right of this line there are very thin dark and discontinuous folds; on the anterior dorsum these folds run laterally towards the eyes. Fore- and hindlimbs as well as hands and feet have distinct dark crossbands. The tips of the fingers are white. The eyes are completely white. The lower lip is dark, broken by some alternating light spots, which do slightly correspond to the markings on the upper lip. The tympanum is brownish and lighter than the skin surrounding it. There is no distinct brown spot from the eye through the tympanum to the insertion of the foreleg and no light stripe along the upper lip. Throat and venter are grey with no distinct spots. A distinct white stripe extends from the tip of snout to the thorax. In the thorax area this stripe is surrounded by brown. The ventral surface of the limbs is greyish.

Description of paratypes. – Morphological features of the paratypes are consistent with those of the holotype. See tab. 1 for measurements. The supratympanic folds are quite irregular, often nearly unrecognizable behind the tympanum or fusing with large lateral tubercles. Coloration of the paratypes is similar to that of the holotype. A median dorsal stripe is absent in all paratypes except ZFMK 59947. The dark transverse markings on the

dorsum are more distinct in ZFMK 57429 and 59945, the dark bands on hands and feet are very distinct in ZFMK 59898. The latter specimen also has some white tubercles on the flanks which are less distinct in the other specimens. The light stripe on throat and thorax is broken in most paratypes (complete only in the dorsally striped paratype ZFMK 59947), whereas it is reduced to a light spot on the thorax in ZFMK 59946. None of the paratypes has a distinct brown spot in the tympanic region or a light stripe on the upper lip.

ZFMK 57429 was pictured in life by GLAW & VENCES (1994) as color photo 101. The iris was golden, the pupil probably of horizontal shape. Dorsum was olive greenish with dark grey-brown markings. Patterns were similar to those in preservative. Distinct white tubercles were present on the flanks. The fingertips were white.

Other specimens. – Additional specimens are kept in the herpetological collection of the University of Antananarivo, Madagascar. Collection data are the same as for the type material.

Distribution. – Only known from the type locality.

Habitat and habits. – Males and females were found during day and night along stony brooks in the rain forest. No calling activity could be observed. Specimens were mostly sitting on mossy stones in the brooks.

Subgeneric attribution. – Tentatively placed in the subgenus *Gephyromantis*, *Mantidactylus boulengeri* group.

A NEW SPECIES FROM NOSY MANGABE

In 1953, A. GRANDISON described *Rhacophorus webbi* which had been collected by C. S. WEBB in the small Malagasy offshore island Nosy Mangabe. GUIBÉ (1978) transferred the species to the genus *Gephyromantis*. BLOMMERS-SCHLÖSSER & BLANC (1991) included the species in *Mantidactylus*. The presence of a paired subgular vocal sac in combination with connected lateral metatarsalia were the main characters used by GLAW & VENCES (1994) to group *Mantidactylus webbi* within the subgenus *Gephyromantis*. However, it differs from all other members of this taxonomic group by the laterally white (not blackish) vocal sac (GLAW & VENCES, 1992*a*).

ANDREONE (1993) made reference to an unidentified *Mantidactylus* species of which two specimens had been photographed at Nosy Mangabe. It was similar to *M. webbi* by general habitus but differed by the more finely granular skin (coarsely granular in *M. webbi*) and by body and iris coloration. During a second visit of F. ANDREONE to Nosy Mangabe, a third specimen of this form was seen and collected. Further study has confirmed that it belongs to an undescribed species of *Mantidactylus* which is superficially similar to *M. webbi*. Before the formal description of the new species, we present here a short diagnosis and a review of biology and distribution of *M. webbi*.

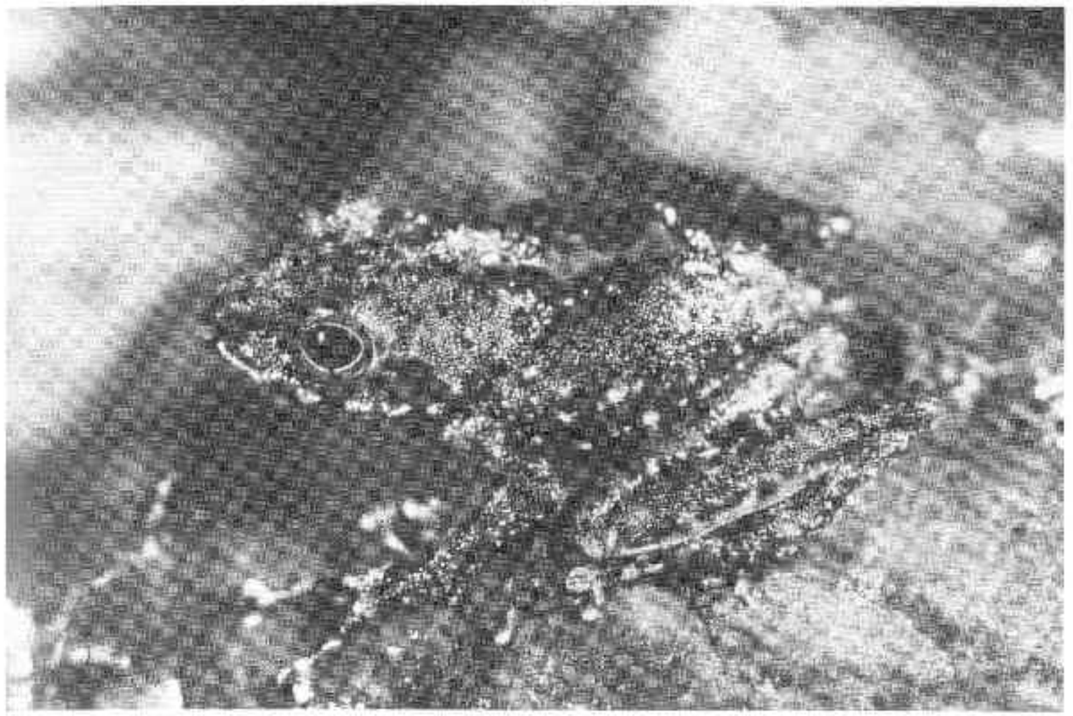

Fig. 4. – Specimen of *Mantidactylus webbi* from Nosy Mangabe, January 1991 (not preserved).

Mantidactylus webbi (Grandison, 1953)

Rhacophorus webbi Grandison, 1953.
Gephyromantis webbi: GUIBÉ, 1978.
Mantidactylus webbi: BLOMMERS-SCHLÖSSER & BLANC, 1991; GLAW & VENCES 1992*a-b*, 1994; ANDREONE, 1993.
Mantidactylus (Gephyromantis) webbi: DUBOIS, 1992.

Diagnosis. – A small olive-greenish frog which belongs to the genus *Mantidactylus* as is evident from the presence of femoral glands in the males. Metatarsal tubercles are rudimentary. Nostrils are situated dorsolaterally. The paired subgular vocal sac of the male is characteristic for most species of the subgenera *Phylacomantis* and *Gephyromantis*. The connected lateral metatarsalia in combination with the small size and greenish coloration allow a distinction from all *Phylacomantis*, whereas the presence of a laterally white (instead of blackish) vocal sac in males is a unique feature of *M. webbi* and can serve as an immediate recognition character.

Holotype. – BM 1953.1.2.34, adult female, SVL 33.3 mm. The original description (GRANDISON, 1953) included a picture of this specimen.

Distribution. – The type locality is the small Malagasy offshore island Nosy Mangabe. On the mainland near Nosy Mangabe we found this species at Voloina and Navana (GLAW & VENCES, 1992*a*) and at Ambanizana (ANDREONE, unpublished). Specimens from Andohahela

in south-eastern Madagascar (MNHN 1975.951-952) were tentatively excluded from *M. webbi* by GLAW & VENCES (1994); however, after detailed measurements of these specimens (see tab. 1), we consider them as *M. webbi* pending further study.

Habitat and habits. – Activity and calls were noticed only during the day. The species lives and calls on big mossy stones along brooks in primary forest and was never found at distances of more than 20 m from the water (GLAW & VENCES, 1992*a*; ANDREONE, 1993). Two egg clumps (one found in March, one in August), each with 7 yellowish eggs (diameter 4 mm), were found on rocks in the brooks (GLAW & VENCES, 1992*a*; ANDREONE, 1993). One of the egg clumps was guarded by a male during the night (ANDREONE, 1993). Four additional clumps of similar size were observed by F. ANDREONE in August 1994 at Nosy Mangabe.

Calls. – The advertisement call has been described by GLAW & VENCES (1992*a*). It is a series of up to 10 unharmonious notes (note repetition rate 6.25/s). Note duration is 26-46 ms, duration of intervals between notes is 122-168 ms, and frequency ranges from 0.5 to 5 kHz.

Subgeneric attribution. – Presently placed in the subgenus *Gephyromantis*, *Mantidactylus boulengeri* group (GLAW & VENCES, 1994).

Mantidactylus silvanus sp. nov.

Diagnosis. – A medium-sized member of the genus *Mantidactylus* as is evident from the presence of distinct femoral glands and lack of nuptial pads in males (females unknown). General color olive-greenish to light brown. The most distinctive character is the highly protruding inner metatarsal tubercle which allows a distinction from all other *Mantidactylus* thus far known. Additionally, *M. silvanus* can be distinguished from the superficially similar *M. lugubris*, young *M. microtympanum*, and *M. webbi* by the same character combinations specified above in the diagnosis of *M. rivicola*. A distinction from *M.* cf. *malagasius* (from Marojezy) can easily be made by the smaller size and the granular skin of that species.

M. silvanus is most similar and probably closely related to *M. rivicola*. Besides the size differences between both species, the following distinctive characters can be used for diagnosis: *M. rivicola* has a more granular skin on the dorsum, a larger distance between the femoral glands, a less developed metatarsal tubercle, and a more granular tympanic region with a more curved and rather discontinuous and irregular supratympanic fold (smooth, with a regular fold which is curved only partly, in *M. silvanus*).

Derivatio nominis. – Classical Latin *Silvanus* (name of the God of forests). This species lives in lowland forest.

Holotype. – MRSN A1661, adult male, from Nosy Mangabe Special Reserve, northeastern Madagascar, collected by F. ANDREONE on 27.06.1995.

Description of the holotype. – See tab. 1 for measurements. Body more or less slender. Widest part of head clearly wider than widest part of body. Dorsal outline of head triangular, snout rather long. Snout protruding over upper jaw in lateral view. Nostrils

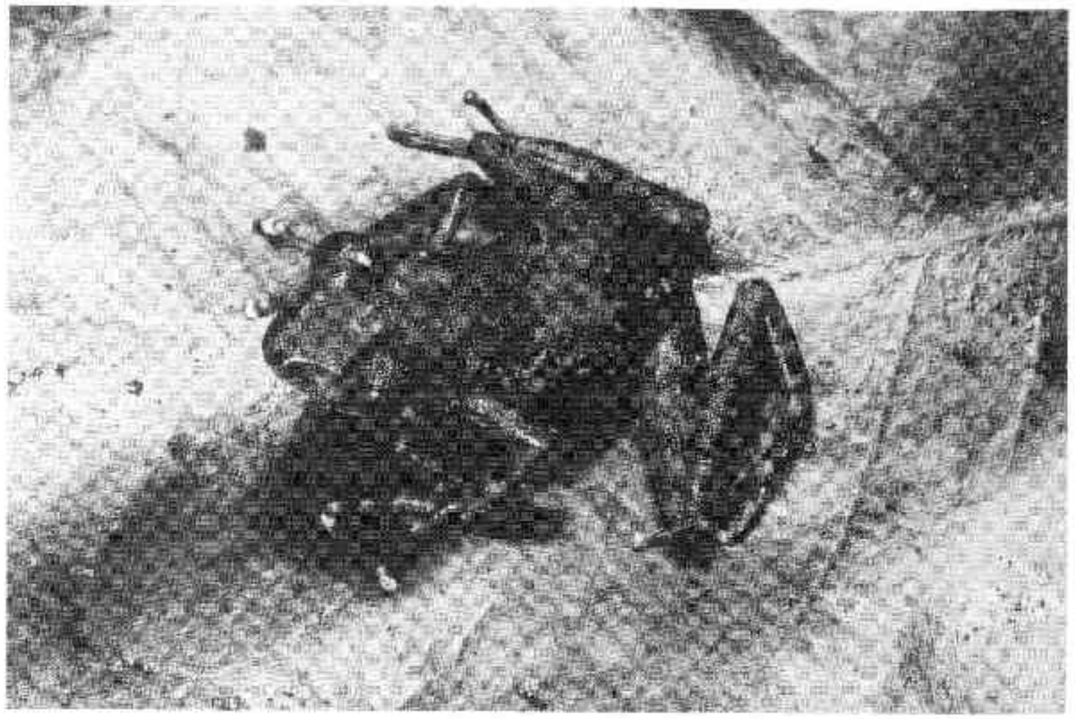

Fig. 5. – Holotype of *Mantidactylus silvanus*, MRSN A1661, adult male, Nosy Mangabe Special Reserve, 27.06.1995.

protruding with lateral openings. Loreal region slightly concave. Tympanum distinct, its diameter accounting for about 3/5 of eye diameter. Tympanic region without granules. Distinct and continuous supratympanic fold which runs rather straight and curves downwards only at a certain point behind the tympanum, near the foreleg insertion. Forelegs and hindlegs slender. Finger discs enlarged, semicircular to triangular. No webbing between fingers. Comparative finger length: $1 < 2 < 4 < 3$. Toe discs enlarged, smaller than finger discs. Traces of webbing between toes. Comparative toe length: $1 < 2 < 3 \leq 5 < 4$. Inner metatarsal tubercle large, protruding, resembling a "sixth toe", its size 1.8 × 0.5 mm. Outer metatarsal tubercle not recognizable. Foot length (not including tarsus) 13.5 mm. Lateral metatarsalia connected. Dorsal skin rugged to finely granular with few small dispersed tubercles. Oblique femoral glands, nearly touching each other, their diameter 2.2 × 1.5 mm. Small but distinct vomerine teeth. No externally recognizable vocal sac (neither distinct dark color in the angle of the lower jaw nor a skin fold is visible).

Coloration of the holotype. – After one month in alcohol, the head, dorsum and flanks are marbled brownish and light grey. Fore- and hindlimbs show distinct brown crossbands which extend to the fingers and toes. The tips of the fingers are grey. The eyes are dark. The lower lip is dark, broken by some alternating light spots, resulting in a pattern which partly corresponds to the markings on the upper lip. The tympanum is light brown. There is no distinct brown spot from the eye through tympanum to the insertion of foreleg and no light stripe along the upper lip. Throat, venter and the anterior ventral

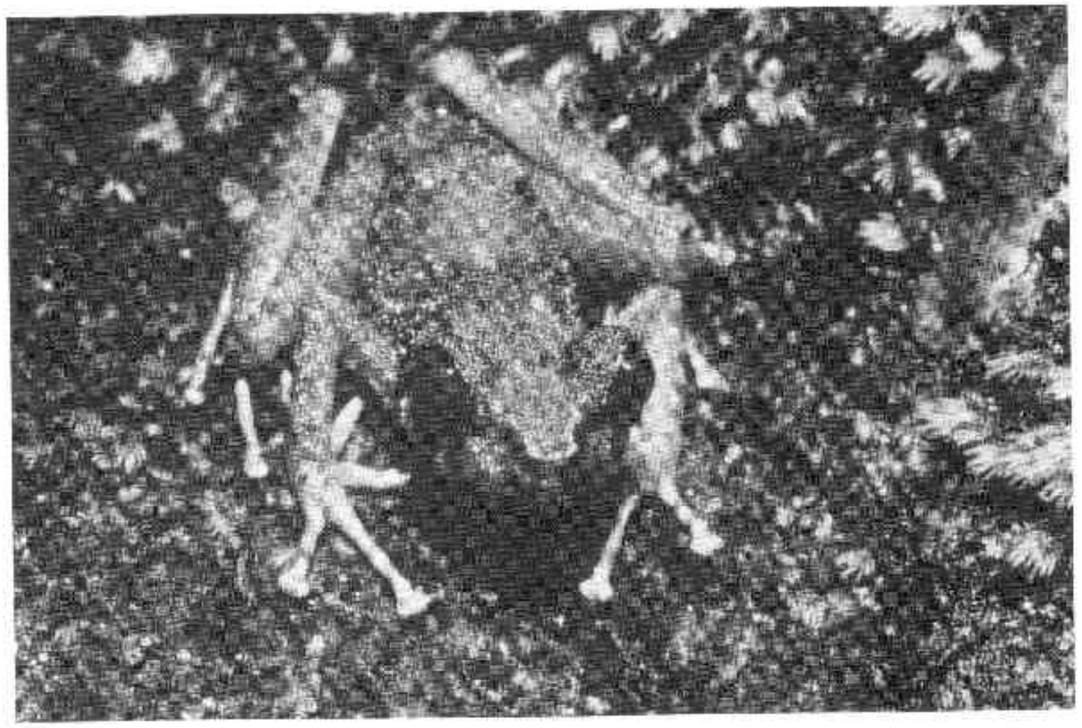

Fig. 6. – Specimen of *Mantidactylus silvanus* from Nosy Mangabe, August 1988 (not preserved).

region of the femur are light grey without distinct spots. The posterior region of the femur, i.e. between the femoral glands and anus, as well as the other ventral parts of the limbs, are more dark grey. An indistinct and incomplete white stripe runs ventrally from the tip of snout to the thorax.

Coloration in life was yellowish-beige marbled with olive grey and with two dark transverse markings. The hindlegs were also beige with crossbands which were less distinct than after preservation. The toes and fingers, especially the fingertips, were white. The pupil was horizontal, the iris had copper-red coloration. The venter and ventral aspect of femurs were pinkish translucent, with some silvery white color on the belly.

Other specimens. – Photographs of two specimens from Nosy Mangabe which were not collected are available. Coloration patterns are in agreement with those of the holotype.

Distribution. – Only known from the type locality.

Habitat and habits. – The limited available data refer to the three specimens observed by F. ANDREONE. The holotype was collected at night (about 21 h 00) whilst perched on a leaf of a small tree, about 1 m above the water level of a very small brook flowing through large stones in primary forest. In sympatry a larger group of calling males of *Mantidactylus redimitus* were observed. The second and third specimens were photographed at night along a forest brook near a small cascade.

Subgeneric attribution. – We tentatively include this species in the subgenus *Gephyromantis*, *Mantidactylus boulengeri* group.

DISCUSSION

The divergence of the different *Mantidactylus* groups is evident in terms of the synapomorphies in tadpole morphology, but is much less obvious in adult morphology (GLAW & VENCES, 1994). *Mantidactylus rivicola* and *M. silvanus* show clear affinities to members of the subgenus *Gephyromantis* sensu GLAW & VENCES (1994), especially to *M. webbi*. However, reproductive biology of none of these three species is sufficiently understood. The reproductive mode of only two species of the subgenus, *M. eiselti* (*M. boulengeri* group) and *M. asper* (*M. asper* group), are known. Both undergo direct development in terrestrial eggs (BLOMMERS-SCHLÖSSER, 1979; GLAW & VENCES, 1994). Little doubt remains that *M. boulengeri*, the subgeneric type species, has a similar breeding biology, and that direct development is typical for *Gephyromantis*.

Egg clutches attributed to *M. webbi* were found overhanging brooks, thus not independent from water (GLAW & VENCES, 1992*a*; ANDREONE, 1993). It can be assumed that this species has a different breeding biology, with more or less developed tadpoles dropping into the brook. A similar reproductive mode may exist in *M. rivicola* and *M. silvanus*, which also live along brooks, but is very unlikely for *M. klemmeri*, which, like *M. eiselti*, calls far from any water body.

The lack of available information points to the fact that new data on the subgenera *Gephyromantis*, *Laurentomantis* and *Phylacomantis* are needed. The phylogenetic relationships between the various species of these groups, some of which are probably paraphyletic, need to be resolved as well as their status within the genus *Mantidactylus*.

Such a revision would also be useful for conservation purposes. Many species of the subgenera *Gephyromantis*, *Phylacomantis* and *Laurentomantis* are confined to primary rainforest habitats. Exceptions are *M. eiselti* and *M. thelenae*, which also inhabit secondary fern scrub at the forest edge or in clearings, *M. b. boulengeri*, which also lives in wood patches along brooks or in secondary eucalyptus forest, and *M. granulatus*, which can live in degraded forest along brooks and small streams. Nevertheless, these frogs are one of the Malagasy anuran groups which are mostly restricted to little disturbed habitat. Therefore they may be useful as indicator taxa for the assessment of the status and degree of forest habitat degradation. Since many of these species are active during the day and may easily be located by means of their characteristic calls, their presence can be established even by little experienced researchers. Detailed knowledge of the systematic status, distribution range and habitat preferences of each species are basic requirements if they are to be used as habitat indicators.

ACKNOWLEDGEMENTS

We thank Annemarie OHLER and Alain DUBOIS for their assistance during our visits to the Paris Museum (MNHN). Nirhy RABIBISOA and Olivier RAMILISON helped during fieldwork. The work of Frank GLAW was made possible by cooperation between the Zoological Institute of Antananarivo and the Zoologisches Forschungsinstitut und Museum A. Koenig (ZFMK), and financially supported by the "Deutscher Akademischer Austauschdienst" (DAAD), that of Franco ANDREONE by coope-

ration between the Parc de Tsimbazaza (Antananarivo) and the Museo Regionale di Scienze Naturali (Torino) and financially supported by Zoo-Project s.r.l. (Perugia). We are also indebted to two anonymous referees, and especially to Marius BURGER and Catherine PRICE (Grahamstown), who helped improving earlier manuscript versions.

LITERATURE CITED

ANDREONE, F., 1993. – Kommentierte Liste von Amphibienfunden auf Madagaskar. *Salamandra*, **29** (3/4): 200-211.

ANDREONE, F. & GAVETTI, E., 1994. – On the identity of *Mantidactylus aerumnalis* (Peracca, 1893) (Anura: Mantellidae). *Boll. Mus. reg. Sci. nat. Torino*, **12** (1): 57-71.

BLOMMERS-SCHLÖSSER, R. M. A., 1979. – Biosystematics of the Malagasy frogs. I. Mantellinae (Ranidae). *Beaufortia*, **29** (352): 1-77.

BLOMMERS-SCHLÖSSER, R. M. A. & BLANC, C. P., 1991. – Amphibiens (première partie). *Faune de Madagascar*, **75** (1): 1-379, pl. 1-12.

DUBOIS, A., 1992. – Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. Soc. linn. Lyon*, **61** (10): 305-352.

GLAW, F. & VENCES, M., 1992*a*. – Zur Kenntnis der Gattungen *Boophis*, *Aglyptodactylus* und *Mantidactylus* (Amphibia: Anura) aus Madagaskar, mit Beschreibung einer neuen Art. *Bonn. zool. Beitr.*, **43** (1): 45-77.

---- 1992*b*. – *A fieldguide to the amphibians and reptiles of Madagascar*. Köln, Vences & Glaw: 1-331.

---- 1994. – *A fieldguide to the amphibians and reptiles of Madagascar*. Second edition, including mammals and freshwater fish. Köln, Vences & Glaw: 1-480.

GRANDISON, A. G. C., 1953. – A new species of rhacophorid frog from Madagascar. *Ann. Mag. nat. Hist.*, (12), **6**: 855-856.

GUIBÉ, J., 1974. – Batraciens nouveaux de Madagascar. *Bull. Mus. natn. Hist. nat.*, (3), **171** (Zool. 116): 1169-1192.

---- 1978. – Les batraciens de Madagascar. *Bonner zool. Monogr.*, **11**: 1-140.

RAXWORTHY, C. J. & NUSSBAUM, R. A., 1994. – A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biol. Conserv.*, **69**: 65-73.

Corresponding editor: Alain DUBOIS.