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VARIATION IN *MANTIDACTYLUS MADECASSUS* MILLOT & GUIBÉ, 1950, A
LITTLE KNOWN MALAGASY FROG, WITH RESURRECTION OF
MANTIDACTYLUS PAULIANI GUIBÉ, 1974

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Based on morphological differences, specimens currently attributed to the Malagasy montane frog species *Mantidactylus madecassus* can be divided into two distinct groups, which correspond to the geographically separated populations from the mountain massifs of Ankaratra and Andringitra. The Ankaratra populations differ from the Andringitra populations by the lack of distinctly bilobed subarticular tubercles on the fingers; more extended webbing between the toes; and a less contrasting dorsal colour pattern. Furthermore, they are distinguished morphometrically. The name *Mantidactylus pauliani* Guibé, 1974 is available for the Ankaratra specimens and is hereby resurrected. A lectotype of *M. madecassus* is designated. The two species share a lack of vomerine teeth and both possess a very short snout, and should be considered as closely related allopatric sister taxa. So far as is known, they occur between 1500 and 2500 m altitude (mainly above 2000 m), in brooks and their tributaries in areas of ericoid vegetation or of rock formations with rupicolous plant communities. A short review of Malagasy montane amphibian species is provided, confirming that montane habitat in Madagascar harbours an important diversity of species specialized to high-altitudes.

Key words: Anura, Ranidae, Mantellinae, *Brygoomantis*, montane herpetofauna, Madagascar

INTRODUCTION

Madagascar contains a rich diversity of habitat types, mainly due to the variety of climates. The eastern rainforest belt is separated from the western arid regions by a high plateau on which special montane ecosystems are found. The three highest massifs are Tsaratanana in the north (2876 m), and Ankaratra (2642 m) and Andringitra (2658 m) in central Madagascar. The Malagasy montane herpetofauna is known from extensive collections, harboured mainly in the Museum National d'Histoire Naturelle (MNHN), Paris, but basic information on the biology and ecology of most species is still lacking.

Recently, Raxworthy & Nussbaum (1996a) reviewed the montane amphibian and reptile communities of the Malagasy massifs of Andringitra, Ankaratra, and Tsaratanana, based on their own surveys. They found that a relatively large number of species are restricted to the montane heathland, and rejected the hypothesis that this habitat is artificial and faunistically depauperate. In another publication (Raxworthy & Nussbaum, 1996b), the same authors emphasized the similarities in the montane herpetofauna between the Ankaratra and Andringitra massifs.

One frog species so far known only from high altitudes of these two massifs is *Mantidactylus madecassus*

(see Millot & Guibé, 1950; Blommers-Schlösser & Blanc, 1991), which was not collected in the survey of Raxworthy & Nussbaum (1996b), and thus not included in the list of montane amphibians from Madagascar published by Raxworthy & Nussbaum (1996a).

M. madecassus is a representative of the most speciose and heterogeneous anuran genus in Madagascar. According to the most recent descriptions (Vences *et al.*, 1997; Glaw & Vences, 1997; Andreone *et al.*, 1998), the endemic genus *Mantidactylus* currently contains 63 described species classified into 12 subgenera (Dubois, 1992; Glaw & Vences, 1994). *M. madecassus* is included in the subgenus *Brygoomantis* Dubois, 1992 (formerly *Mantidactylus ulcerosus* group) which currently consists of seven valid species (Blommers-Schlösser & Blanc, 1991, Glaw & Vences, 1994). *Brygoomantis* are distinguished from representatives of other subgenera of *Mantidactylus* by a derived karyotype (chromosome number $2n = 24$, see Blommers-Schlösser & Blanc, 1991; not known in *M. madecassus*) and a combination of femoral gland structure (glands including a prominent rounded structure with external median depression, rudimentary glands present in females), sexual dimorphism in tympanum size (males having a larger tympanum than females), slightly distensible single subgular vocal sac in males, slightly enlarged finger and toe discs, semiaquatic and partly diurnal habits, tadpoles with generalized mouthparts and distinct spiral-shaped intestine visible through ventral skin, and advertisement call structure (series of pulsed calls with low intensity).

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In the course of our ongoing revisions of the frog genera of Madagascar, we examined the type material of *Mantidactylus madecassus* and of its junior synonym *M. pauliani*. In the present paper, we give a detailed re-description of both taxa and revalidate *M. pauliani* based on several morphological and morphometric differences. We also provide an updated list of montane amphibians of Madagascar, and a comparison between the herpetofaunas of Andringitra and Ankaratra.

MATERIALS AND METHODS

The following morphological measurements were taken with a calliper to the nearest 0.1 millimeter: SVL (snout-vent length), HW (head width), HL (head length), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (tympanum diameter), HAL (hand length), FORL (forelimb length), HIL (hindlimb length), FOL (foot length), FOTL (foot length including tarsus). All available specimens of the taxon *pauliani* were measured, whereas in *M. madecassus* specimens measured were selected according to their state of fixation, in order to get a sample in a comparable state to the *pauliani* specimens. All measurements were taken by the same person (MV). Institutional abbreviations are as listed in Leviton *et al.* (1985). Webbing formula follows Savage & Heyer (1967) as modified by Myers & Duellman (1982) and Savage & Heyer (1997). To facilitate comparisons with other species of *Mantidactylus*, we also give the formula used by Blommers-Schlösser (1979) and most subsequent authors who have published accounts on Madagascan anurans.

Femoral glands were examined and photographed under a stereo-microscope. Our description refers to the macroscopic appearance of the gland on the ventral femur. In a few specimens, we also carefully removed the skin of the ventral femur and turned it upside down; by this procedure, the gland structures, which remain completely attached to the skin, could be examined in more detail and could easily be distinguished from simple granular thigh patches as present in many frogs.

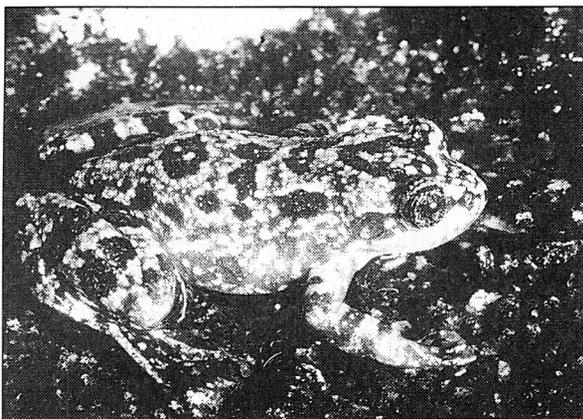


FIG. 1. *Mantidactylus madecassus* (ZFMK 57416 from Cuvette Boby, Andringitra) in life.

Morphometric data were processed statistically with the software package SPSS for Windows, version 6.1.2. Samples were compared for representative ratios by non-parametric Mann-Whitney *U*-tests. Data were transformed logarithmically (\log_{10}) to render relationships between them linear. A Principal Component Analysis (PCA) was carried out using the \log_{10} -transformed data (three factors extracted).

RESULTS

VARIATION IN *M. MADECASSUS*

According to Blommers-Schlösser & Blanc (1991), *M. madecassus* is known from seven localities: Ankaratra, Nosiarivo, Ivangomena, Andohariana, Ambalamarovandana, and Anjavidilava. The first two localities are located in the Ankaratra massif and refer to the type series of the taxon *Mantidactylus pauliani* Guibé, 1974 (which was synonymized with *M. madecassus* by Blommers-Schlösser & Blanc, 1991), and to several ZMA specimens previously also referred to *M. pauliani* (see Blommers-Schlösser, 1979). All other localities are located in the Andringitra massif according to the map in Blommers-Schlösser & Blanc (1991), which did not include information on voucher specimens. We found MNHN vouchers for all mentioned sites except Ambalamarovandana. Several other localities are corroborated by MNHN specimens and by one ZFMK specimen (Fig. 1); all these sites are located close to each other within the Andringitra massif.

Detailed examination and direct comparison of all available specimens demonstrated that they can be classified into two distinct groups, corresponding to the Andringitra and Ankaratra samples, respectively. Differences are (a) subarticular tubercles on fingers (very prominent, mostly bilobed in Andringitra specimens, but single and indistinct in those from Ankaratra; Fig. 2); (b) webbing (more extended in Ankaratra, generally reaching the disc of the fifth toe); and (d) colouration (darker and more uniform in Ankaratra).

Additionally, distinct morphometric differences between both samples were found. Measurements of all available Ankaratra specimens and of a representative

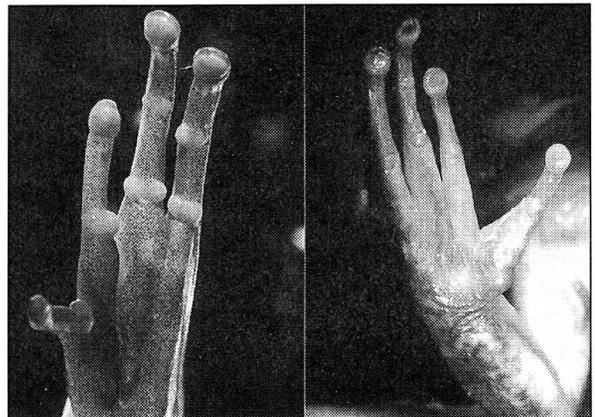


FIG. 2. Ventral side of hands of type specimens of *M. madecassus* (MNHN 1953.246; left) and *M. pauliani* (MNHN 1972.1508, right). Not to scale. Note difference in shape of subarticular tubercles.

TABLE 1. Measurements (in mm) of adult specimens of *Mantidactylus madecassus* and *M. pauliani*. See Materials and Methods section for abbreviations of characters. LT = lectotype, PLT = paralectotype, HT = holotype, PT = paratype.

	Status	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	FOTL	HAL	HIL	FL
<i>M. madecassus</i>															
MNHN 1953.246	LT	F?	27.5	9.6	9.7	1.9	3.1	1.8	2.2	3.0	16.6	22.4	7.9	47.0	15.3
MNHN 1989.3591	PLT	M?	25.4	8.0	8.6	1.6	2.2	1.7	1.8	3.0	12.7	21.3	6.2	36.1	12.0
MNHN 1989.3592	PLT	F?	31.0	9.6	10.2	2.3	3.0	1.8	2.0	3.0	16.7	21.0	7.6	43.1	14.5
MNHN 1989.3594	PLT	F?	29.2	10.6	10.3	2.9	3.2	2.0	2.2	3.3	16.3	17.2	7.7	43.7	14.7
MNHN 1972.1182	-	F	32.0	10.8	11.1	2.3	3.5	1.9	2.6	3.2	17.2	24.8	8.5	51.0	18.3
MNHN 1972.1185	-	F	32.4	10.9	11.0	2.2	3.3	2.1	2.7	3.1	17.1	25.2	8.7	50.5	17.7
MNHN 1972.1190	-	M?	27.0	9.2	9.9	1.7	3.1	2.0	2.2	2.8	15.3	21.1	7.0	42.4	14.2
MNHN 1972.1192	-	F	33.7	10.9	11.2	2.6	3.5	2.0	2.5	3.4	18.0	25.1	8.4	49.6	16.7
MNHN 1972.1198	-	M	27.0	9.4	9.9	2.0	3.3	1.7	2.4	3.0	15.5	20.1	7.8	45.4	15.0
MNHN 1972.1199	-	M	29.8	9.9	10.7	2.9	3.4	2.0	2.1	3.3	17.6	23.7	8.8	48.6	16.8
MNHN 1972.1204	-	F	29.3	9.5	10.0	2.0	3.1	1.8	2.2	3.3	16.2	25.3	7.7	44.7	13.1
MNHN 1972.1206	-	F	31.4	10.5	10.2	2.1	3.5	2.1	2.3	3.4	19.0	21.4	8.5	51.4	17.2
<i>M. pauliani</i>															
MNHN 1972.1508	HT	M	31.0	11.0	11.0	2.5	3.1	1.8	2.3	2.6	18.0	25.7	8.9	50.4	17.2
MNHN 1972.1509	PT	F?	29.7	11.2	11.7	2.8	3.1	1.9	2.1	3.1	17.4	24.4	9.0	47.5	17.0
MNHN 1972.1510	PT	F	33.7	11.5	10.8	2.2	4.0	1.6	2.2	3.1	18.7	24.2	8.9	48.7	17.0
MNHN 1972.1511	PT	F	31.1	10.7	10.8	2.0	3.3	1.5	2.1	2.7	17.6	23.8	8.3	47.1	16.0
MNHN 1972.1512	PT	F?	27.7	10.0	10.5	2.2	3.4	1.5	2.1	3.0	17.5	24.2	8.7	42.1	17.0
MNHN 1972.1513	PT	F?	25.8	9.6	9.7	2.1	3.4	1.7	1.9	2.7	16.6	23.1	8.4	44.9	15.8
MNHN 1972.1514	PT	M	29.5	11.0	11.3	2.7	3.3	1.6	2.1	3.0	17.7	24.5	9.0	47.4	16.7
MNHN 1972.1515	PT	F	32.9	10.6	11.1	2.2	3.4	1.6	2.0	3.1	18.2	23.8	9.6	49.1	16.7
MNHN 1972.1516	PT	M?	31.6	11.5	11.9	3.1	3.5	1.7	2.3	3.0	18.9	25.5	8.9	50.1	17.3
ZMA 6803 (1184)		F	31.6	10.1	10.4	2.0	3.4	1.4	2.3	3.0	16.5	22.1	8.1	45.5	15.6
ZMA 6803 (1185)		F?	27.5	9.2	9.3	2.3	3.4	1.4	1.7	3.1	15.7	21.8	7.8	42.8	15.2
ZMA 6803 (1186)		F?	26.9	8.8	9.2	1.6	3.2	1.4	1.8	2.7	16.0	21.4	8.6	44.8	14.7
ZMA 6803 (1187)		F?	24.4	8.6	9.1	1.6	3.1	1.3	1.7	2.8	15.0	20.2	7.4	41.6	14.0
ZMA 6803 (1188)		M?	24.8	8.8	9.1	1.8	3.2	1.5	1.8	2.7	15.4	20.5	8.0	41.1	14.0

TABLE 2. Principal component loadings (PCL) of the first three principal components from a principal component analysis of data in Table 1 (log-transformed), given separately for analyses of male and female data. The five most influential PCLs for each principal component are marked by a superscript ranking.

Variable	PCA of males			PCA of females		
	PCL1	PCL2	PCL3	PCL1	PCL2	PCL3
SVL	0.107	0.170 ⁵	-0.077	0.094	0.093	0.122
HL	0.115 ²	0.037	-0.040	0.102 ⁴⁻⁵	0.024	0.268
HW	0.110 ⁴⁻⁵	0.033	-0.076	0.107 ¹	-0.016	0.123
END	0.005	0.406 ¹	-0.059	0.060	0.419 ¹	-0.278 ⁵
NND	0.015	0.293 ³	0.547 ¹	0.062	0.363 ²	0.292 ⁴
NSD	0.071	0.301 ²	-0.316	0.083	0.238 ⁵	-0.623 ²
ED	0.077	-0.010	0.461 ²	0.085	-0.288 ³	-0.106
TD	0.105	0.062	0.262 ³	0.086	0.113	0.811 ¹
FORL	0.117 ¹	-0.050	0.011	0.102 ⁴⁻⁵	-0.149	0.033
HAL	0.099	-0.214 ⁴	0.097	0.092	-0.263 ⁴	0.032
HIL	0.114 ³	-0.001	-0.108 ⁵	0.102	-0.029	-0.458 ³
FOL	0.108	-0.118	-0.065	0.106 ²⁻³	-0.087	-0.100
FOTL	0.110 ⁴⁻⁵	-0.115	-0.170 ⁴	0.106 ²⁻³	-0.099	-0.114

sample of *Andringitra* specimens are given in Table 1. We performed a statistical comparison of both samples using Mann-Whitney *U*-tests on the ratios in Table 3; males and females were tested separately. Males and females from Ankaratra had relatively longer hands ($P < 0.05$ in females; $P < 0.1$ in males), shorter eye-nostril distances (relative to head length; $P < 0.05$ in males; $P < 0.001$ in females), shorter nostril-snout tip distances (relative to head length; significant only in females; $P < 0.005$), and shorter nostril-nostril distances (relative to head width; $P < 0.05$ in males and females). In both samples, relative tympanum width was larger in males than in females (ratios TD/ED and TD/SVL), but these differences were not statistically significant.

A multivariate PCA resulted in a clear separation of the two samples both in separate and combined analy-

ses of males and females. After removal of the first factor (equivalent to the size or growth effect), the second and third factors (equivalent to the most important shape factors) were plotted in Fig. 3. Both samples were mainly separated along the second principal component. The most influential loadings of the second principal component (Table 2) corresponded largely to those variables previously identified as significantly different between the samples: END, NSD, NND, HAL and SVL in males; END, NND, ED, HAL and NSD in females.

Table 3 summarizes the most important morphological and morphometric differences between the Ankaratra and *Andringitra* samples. A discriminant analysis using the data in Table 1 predicted correctly group membership of all specimens with $P < 0.0001$.

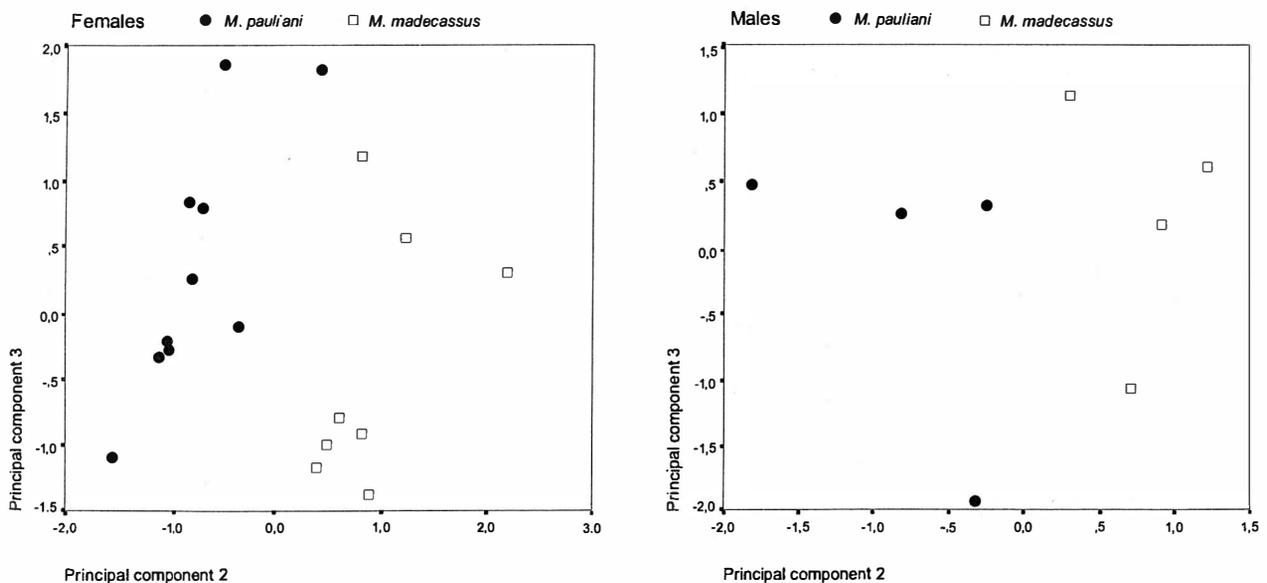


FIG. 3. Scatterplots of second and third principal components of a PCA of log-transformed data in Table 1, analyzed separately for males and females.

TABLE 3. Differential characters between *Mantidactylus madecassus* and *M. pauliani*. Variable ratios are given as mean \pm SD (minimum and maximum values in parentheses). Data were compared using Mann-Whitney *U*-Tests. Significant differences between data pairs are marked with asterisks: * $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$.

Species	<i>M. madecassus</i> (Andringitra)	<i>M. pauliani</i> (Ankaratra)
SVL (males)	27.0-29.8 mm	24.8-31.6 mm
SVL (females)	25.4-33.7 mm	24.4-33.7 mm
HAL/SVL (males)	0.27 \pm 0.02 (0.26-0.30)	0.30 \pm 0.02 (0.28-0.32)
HAL/SVL (females)	0.26 \pm 0.02 (0.24-0.29) *	0.29 \pm 0.02 (0.26-0.33) *
FOTL/HIL (males)	0.48 \pm 0.02 (0.45-0.50) *	0.51 \pm 0.01 (0.50-0.52) *
FOTL/HIL (females)	0.49 \pm 0.01 (0.47-0.50)	0.50 \pm 0.03 (0.48-0.57)
END/HL (males)	0.19 \pm 0.01 (0.18-0.20) *	0.15 \pm 0.01 (0.14-0.17) *
END/HL (females)	0.18 \pm 0.01 (0.17-0.21) ***	0.15 \pm 0.01 (0.13-0.18) ***
NSD/HL (males)	0.21 \pm 0.01 (0.20-0.22)	0.20 \pm 0.01 (0.19-0.21)
NSD/HL (females)	0.23 \pm 0.02 (0.20-0.25) **	0.19 \pm 0.01 (0.18-0.22) **
NND/HL (males)	0.31 \pm 0.02 (0.28-0.33) *	0.26 \pm 0.03 (0.24-0.30) *
NND/HL (females)	0.31 \pm 0.02 (0.28-0.35) *	0.29 \pm 0.02 (0.25-0.33) *
HL/SVL (males)	0.36 \pm 0.01 (0.34-0.37)	0.37 \pm 0.01 (0.36-0.38)
HL/SVL (females)	0.34 \pm 0.01 (0.32-0.37)	0.35 \pm 0.02 (0.32-0.39)
HW/SVL (males)	0.34 \pm 0.02 (0.34-0.36)	0.36 \pm 0.01 (0.36-0.37)
HW/SVL (females)	0.33 \pm 0.01 (0.31-0.35)	0.35 \pm 0.02 (0.32-0.38)
TD/ED (males)	0.74 \pm 0.17 (0.55-0.91)	0.77 \pm 0.14 (0.56-0.89)
TD/ED (females)	0.67 \pm 0.07 (0.60-0.77)	0.63 \pm 0.11 (0.50-0.90)
Colour in preservative	mostly beige with dark markings.	mostly uniformly dark with indistinct darker markings
Subarticular finger tubercles	distinct, bilobed.	indistinct, not bilobed.
Foot webbing	ends just below disc on toe 5.	reaches disc on toe 5.

Within the genus *Mantidactylus* (and also other Malagasy anurans), there is no other example of such important morphological differences (especially in the shape of the subarticular tubercles) between populations included in a single species. Generally, even slight morphological differences between populations are paralleled by bioacoustic (see data in Glaw & Vences, 1994) or, as in the genus *Mantella*, by genetic differentiation (Vences *et al.*, 1998). Sometimes, bioacoustically well differentiated *Mantidactylus* species are even virtually indistinguishable by morphology (Glaw & Vences, 1994).

We consider the differences found between the Andringitra and Ankaratra populations attributed to *Mantidactylus madecassus* as sufficient support for a distinction at the specific level. Because the name *Mantidactylus pauliani* is available for the Ankaratra populations, we resurrect this name from the synonymy of *M. madecassus*.

REDESCRIPTION OF *M. MADECASSUS* AND *M. PAULIANI*

MANTIDACTYLUS MADECASSUS MILLOT & GUIBÉ, 1950

Diagnosis. A species of the genus *Mantidactylus* as indicated by the lack of nuptial pads in males and the presence of femoral glands (verified in ZFMK 57416).

A member of the subgenus *Brygoomantis* as indicated by (a) sexual dimorphism in tympanum size (males having a relatively slightly larger tympanum than females); (b) only slightly enlarged finger and toe discs; (c) well developed webbing between toes; and (d) presence of femoral glands including a rounded structure with external median depression, and of rudimentary femoral glands in females (verified in ZFMK 57416).

M. madecassus is distinguished from all other species of *Mantidactylus* by the presence of distinct, bilobed subarticular tubercles on the fingers (never bilobed in other *Mantidactylus*); further from all other *Mantidactylus* except *M. pauliani* by the unique head shape, with a broadly rounded, very short snout; from other species of the subgenus *Brygoomantis* except *M. pauliani* by the lack of vomerine teeth; and, additionally, from *M. betsileamus*, *M. biporus* and *M. alutus* by the great extent of the webbing between the toes. For further distinction from *Mantidactylus pauliani*, see below.

Name bearing type. Lectotype (hereby designated) MNHN 1953.246 (Fig. 4). Collected by J. Millot at Cirque Boby, Andringitra massif. Specimen in mediocre state of preservation. Colour patterns well preserved, dorsally beige with irregular large dark brown markings, ventrally uniformly light. Fingertips slightly enlarged. Fingers with very distinct bilobed

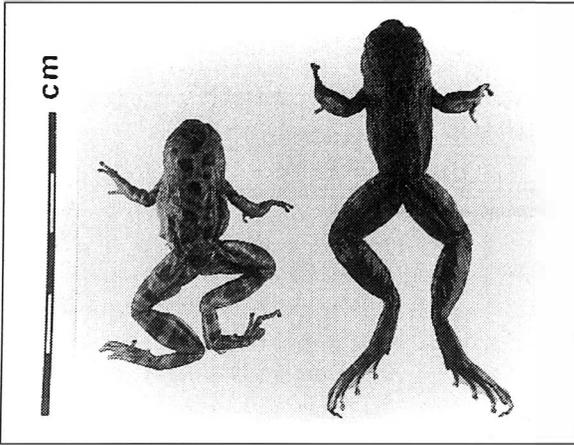


FIG. 4. Lectotype of *M. madecassus* (MNHN 1953.246, left) and holotype of *M. pauliani* (MNHN 1972.1508) in dorsal view.

subarticular tubercles. No femoral glands visible (possibly due to poor fixation). Webbing formula of foot: I $1^+ - 2^-$ II $1 - 2$ III $1^+ - 2^+$ IV $2^+ - 1$ V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0.25), 2i(0.75), 2e(0), 3i(1), 3e(0.25), 4i(1.5), 4e(1.25), 5(0). Toe 5 of same length as toe 3. Foot longer than tibia. Tibiotarsal articulation reaches the centre of the eye.

Other types. Eight paralectotypes (MNHN 1989.3590-3597; originally all subsumed under MNHN 1953.246) in a mediocre state of preservation, partly in worse state than the lectotype, all with the same collection dates and locality as the lectotype. The original catalogue entry reads 10 specimens under MNHN 1953.246, but only eight specimens (beside the lectotype, which retained the original number) were given new numbers in 1989. The missing specimen is probably BMNH 1950.1.2.80, which is labeled as co-type and was received in 1950 from J. Guibé. This specimen, in a better state of preservation than the MNHN specimens, must therefore also be regarded as paralectotype.

All paralectotypes agree morphologically with the lectotype. The following data refer to variation in three specimens (MNHN 1989.3591-3592, 1989.3594). Webbing formula I $(1 - 1^+) - (1^+ - 2)$ II $(1 - 1^+) - (2 - 2^+)$ III $1^+ - (2 - 3)$ IV $(2 - 3^-) - (1 - 1^+)$ V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0-0.25), 2i(0.5-1), 2e(0-0.5), 3i(1-1.5), 3e(0.25), 4i(1-2), 4e(1-1.75), 5(0-0.5). Toe 5 of same length as toe 3. Foot longer than tibia. Tibiotarsal articulation reaches posterior eye margin in MNHN 1989.3591 and 3594, tympanum in MNHN 1972.3592.

The prominent bilobed subarticular tubercles on the fingers are visible in all specimens. Femoral glands are not clearly recognizable in any paralectotype, probably due to their poor state of preservation.

Additional material examined. ZFMK 57416 (Cuvette Boby, Andringitra, collected by F. Glaw and M. Vences on 18 January 1994) and 26 specimens from the MNHN, all collected by C. P. Blanc and co-workers

during their 1970/71 expedition to the Andringitra massif: MNHN 1972.1181 (Cuvette Boby, 28.11.1970), 1182-3 (Marositry), 1184-5 (Andohabatomana, Varavarana, ruisseau, 18.11.1970), 1186 (Plateau Andohariana, riv. Riambavy, ca. 2030 m altitude, 6.12.1970), 1189 (Cuvette Boby, 25.11.1970), 1190 (Ibory face ouest, 17.12.1970), 1191 (Cuvette Boby), 1192 (Ibory face ouest, 25.11.1970), 1193-5 (Cuvette Boby), 1196-7 (Ibory face nord, ruisseau, 16.12.1970), 1198-9 (Antsifotra, 4.12.1970), 1200-1 (plateau Andohariana, riv. Riambavy, 2.12.1970), 1202-3 (Anjavidilava, 9.1.1971), 1204-5 (Ibory face sud, 16.12.1970), 1206 (Cirque Boby, 26.11.1970). MNHN 1972.1187 (Ibory, 16.12.1970) and 1188 (Ivangomena) were not examined; in the MNHN catalogue, they are provided with the comment "échangé Duellman 1977" and almost certainly they correspond to the specimens KU 173060-61 (L. Trueb, *pers. comm.*).

All examined specimens correspond well with the type series. Femoral glands (a small, rudimentary structure with median depression and additional irregular structures towards the anal region) are recognizable in ZFMK 57416 (probably a female), but are not evident in MNHN specimens, probably due to poor fixation and preservation.

Distribution. Locality coordinates and altitudes are given according to Paulian *et al.* (1971) and Goodman (1996a,b). The species is only known from the Andringitra massif and was found at 9-10 localities between ca. 1500 and 2500 m altitude (most localities higher than 2000 m): (1) Cirque Boby, 2520 m (see Blommers-Schlösser & Blanc 1991: 254), probably $22^\circ 11'S/46^\circ 53'E$; (2) Cuvette Boby, ca. 2470 m, $22^\circ 11'S/46^\circ 53'E$; (3) Andohariana plateau, ca. 2030 m, $22^\circ 09'S/46^\circ 54'E$; (4) Anjavidilava, 1800-2100 m, $22^\circ 09'S/46^\circ 57'E$; (5) Marositry, ca. 2000 m, $22^\circ 10'S/46^\circ 56'E$; (6) Varavarana 1500-1850 m, $22^\circ 08'S/46^\circ 57'E$; (7) Antsifotra, ca. 2000 m, $22^\circ 10'S/46^\circ 56'E$ (altitudes and coordinates referring to Antsifotra River); (8) Ivangomena, 2100-2500 m, $22^\circ 09'S/46^\circ 53'E$; (9) Ibory (north, west and south slope), probably referring to Pic Bory, up to 2630 m, $22^\circ 12'S/46^\circ 55'E$; possibly also (10) Ambalamarovandana, altitude ca. 1530 m, $22^\circ 08'S/46^\circ 57'E$ (locality in Blommers-Schlösser & Blanc 1991, possibly referring to a personal observation of C. P. Blanc).

Natural history. MNHN 1989.3593 (SVL 31.3 mm) contained 10 very large (diameter 3.8 mm) uniformly yellowish oocytes. MNHN 1972.1206 (SVL 31.4 mm) contained 28 yellowish to light brown oocytes of 2-2.3 mm diameter. We found two specimens in a stagnant tributary of a brook, surrounded by ericoid vegetation (Glaw & Vences, 1994). Specimens were sitting in or near water, and readily dived when disturbed.

MANTIDACTYLUS PAULIANI GUIBÉ, 1974

Diagnosis. A species of the genus *Mantidactylus* as indicated by the lack of nuptial pads in males and the presence of femoral glands. A member of the subgenus

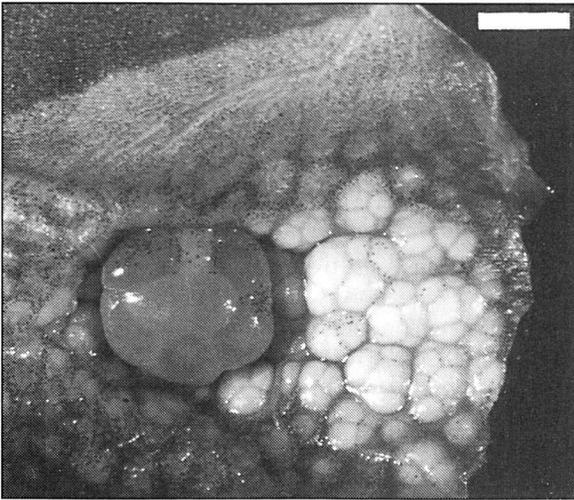


FIG. 5. Femoral gland of *Mantidactylus pauliani* (MNHN 1972.1514, male) in internal view (on the underside of ventral femur skin after dissection). Scale = 1 mm.

Brygoomantis as indicated by (a) sexual dimorphism in tympanum size (males having a relatively slightly larger tympanum than females); (b) only slightly enlarged finger and toe discs; (c) well developed toe webbing; and (d) presence of femoral glands including a prominent rounded structure with external median depression, and of rudimentary femoral glands in females.

M. pauliani is distinguished from all other *Mantidactylus* except *M. madecassus* by the unique head shape, with a broadly rounded, very short snout; from other species of the subgenus *Brygoomantis* except *M. madecassus* by the lack of vomerine teeth; and, additionally, from *M. betsileanus*, *M. biporus* and *M. alutus* by the great extent of the foot webbing. *M. pauliani* is distinguished from *M. madecassus* by the single and indistinct subarticular tubercles on the fingers, by the great extent of the webbing between the toes (webbing extending onto disc of fifth toe), and by a less distinct dorsal pattern.

Name bearing type. Holotype MNHN 1972.1508 (Fig. 4). Collected by C. P. Blanc at Nosiarivo, Ankaratra massif. Adult male in excellent state of preservation. Dorsal colour uniformly dark brown, with a few light elements on femur resulting in slight crossband pattern. Ventrally uniformly cream with a slight fading from ventral to dorsal colour along the flanks. Finger tips barely enlarged. Greyish outer metatarsal tubercle present, rather large and distinct, slim (2.2 x 0.9 mm).

Webbing formula I 1 – 1⁺ II 1 – 2 III 1⁺ – 2 IV 1⁺ – 0⁺ V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0), 2i(0.5), 2e(0), 3i(1), 3e(0.25), 4i(1), 4e(0.25), 5(0). Toe 5 of same length as toe 3. Foot longer than tibia. Tibiotarsal articulation reaches the tympanum.

Femoral glands present, consisting of one larger, rounded externally prominent structure with a median depression, and irregular, less prominent groups of granules proximally. A rosette-like structure of several of these small granule groups is recognizable.

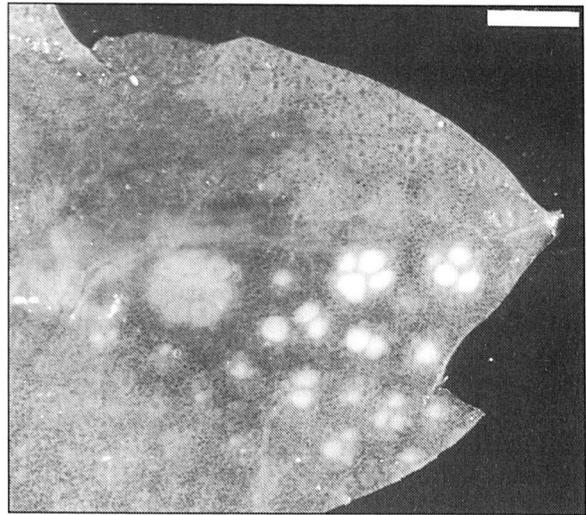


FIG. 6. Femoral gland of *Mantidactylus pauliani*, MNHN 1972.1511, female, in internal view (on the underside of ventral femur skin after dissection). Scale = 1 mm.

Other types. Eight paratypes. Four males (MNHN 1972.1509, 1972.1512, 1972.1514, 1972.1516), three females (MNHN 1972.1510, 1972.1511, 1972.1515), and one possibly subadult male (MNHN 1972.1513). MNHN 1972.1509-1513 with the same collecting dates and locality as the holotype; MNHN 1972.1514-1516 collected by C. P. Blanc at Betay forest, Ankaratra massif. All in excellent state of preservation. Dorsal colour rather uniform, but lighter with large dark brown markings in a few specimens (e. g. MNHN 1972.1509).

The following data refer to variation in three paratype specimens (MNHN 1972.1510, 1972.1514-1515). Webbing formula I 1 – 1⁺ II 1 – 2 III 1⁺ – 2 IV (1⁺ – 2) – 0⁺ V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0), 2i(0.5), 2e(0), 3i(1), 3e(0.25-0.5), 4i(1), 4e(0.25-1), 5(0). Toe 5 of same length as toe 3. Foot longer than tibia. Tibiotarsal articulation reaches the posterior eye margin in MNHN 1972.1514, the tympanum in the other two specimens.

Femoral glands are visible in all specimens, also in females (although clearly smaller). The gland section with external median depression is small in the males as compared with other *Brygoomantis*. The smaller, proximal groups of granules are also present in females, but rosette-like structures are less distinct in most females. It is not easy to distinguish externally between male and female glands. Females are therefore only tentatively sexed except MNHN 1972.1511 which was dissected (see below).

After dissection of one male (MNHN 1972.1514), it could be recognized that the gland section externally showing the median depression consists of two median granules surrounded circularly by seven slightly smaller granules, and the proximal smaller irregular structures are groups of several much smaller granules (Fig. 5). In a female (MNHN 1972.1511), the rudimentary median depression section was a central granule surrounded by seven granules of similar size, and the proximal irregular groups of granules were smaller and more widely spaced (Fig. 6).

Additional material examined. ZMA 6803, five specimens individually labeled with the field numbers 1184-1188, collected by R. Blommers-Schlösser on 21.3.1973 at Nosiarivo, Ankaratra massif, 2200 m altitude.

Distribution. Known from two collecting sites, located close to each other in the Ankaratra massif at altitudes above 2000 m: (1) Nosiarivo, 2200 m (see Blommers-Schlösser 1979); (2) Betay forest (according to Viette 1991: Ambohimirandrana, 2100/2200 m).

Natural history. One female (MNHN 1972.1511) contained 16 mature uniformly yellowish oocytes of 3.5 mm diameter. According to Blommers-Schlösser (1979), specimens were found under boulders in rapids.

DISCUSSION

RELATIONSHIPS OF *MANTIDACTYLUS MADECASSUS* AND *M. PAULIANI*

Mantidactylus madecassus and *M. pauliani* can be considered as strictly montane amphibian species, occurring between 1500 and 2500 m altitude, mainly above 2000 m. Habitats, so far as is known, are brooks and their tributaries in areas of ericoid vegetation or of rock formations with rupicolous plant communities (compare locality lists with site descriptions in Paulian *et al.*, 1971; Blommers-Schlösser, 1979; Glaw & Vences, 1994; Goodman 1996a).

The distinguishing features between *M. madecassus* and *M. pauliani* have already been shown by Guibé (1978) in his drawings of the hands and feet of both species (figs. 14-15 versus 72-73; *M. madecassus* having bilobed to paired subarticular tubercles on fingers, and its webbing not reaching the disc of the fifth toe). Guibé (1978) also mentioned the special subarticular tubercles of *M. madecassus* as "élargis transversalement, ceux du doigt 3 parfois doubles". However, neither in the original description of *Mantidactylus pauliani* (Guibé, 1974) nor in his monograph (Guibe, 1978) did he mention the obvious external resemblance of *pauliani* and *madecassus*. Their similarity was seemingly first noted by Blommers-Schlösser & Blanc (1991). These authors, however, did not recognize the differences between the taxa (characterizing the subarticular tubercles as "peu saillants", probably based on examination of *pauliani* specimens only) and synonymized them without any discussion.

The head shape shared by *Mantidactylus madecassus* and *M. pauliani* is unique among Malagasy frogs and may be regarded as a derived state. The rounded, short snout strongly resembles that of European newts, genus *Triturus*, in their aquatic phase, and may be a morphological adaptation to largely aquatic habits.

Attribution of the two species to the subgenus *Brygoomantis* is mainly based on femoral gland morphology, because the other main synapomorphies of the subgenus (reduced chromosome number and spiral-shaped intestine of tadpole) are unknown. However, the

similarity of the structure of the femoral glands to certain species of *Brygoomantis*, such as *Mantidactylus curtus*, is striking (*pers. obs.*), and the subgeneric attribution of *M. madecassus* and *M. pauliani* is therefore rather certain.

RELATIONSHIPS OF THE MONTANE AMPHIBIAN FAUNA OF ANKARATRA AND ANDRINGITRA MASSIFS

A recent analysis of montane herpetofaunas in Madagascar (Raxworthy & Nussbaum, 1996a) compared the high mountain communities endemic to altitudes higher than 1500 m of the three highest massifs in Madagascar: Andringitra, Ankaratra and Tsaratanana. As these authors found no additional species of amphibians and reptiles during the final 3-5 survey days at each site, they considered the species lists compiled during their surveys as "nearly complete". Their reptile data actually appear to be relatively complete, in comparison with available literature. According to Raxworthy & Nussbaum's (1996a) list, however, they only recorded the amphibians *Anodonthyla montana*, *Plethodontohyla tuberculata*, *Boophis microtympanum*, *Mantidactylus aerumnalis*, *M. alutus*, and *M. domerguei* as high mountain species of the Ankaratra and Andringitra massifs. At least half of the mentioned species also occur lower than 1500 m altitude and therefore cannot be viewed as high mountain endemics in the sense defined by Raxworthy & Nussbaum (1996a). *M. domerguei* is known between 900-1800 m altitude (Glaw & Vences, 1994), and *M. alutus* occurs at least down to 1200 m altitude. *M. aerumnalis* sensu Andreone & Gavetti (1994) is only known from the type locality Andrangoloaka (1389 m according to Viette, 1991) and An'Ala (ca. 850 m, *pers. obs.*) and therefore is clearly not a montane species. The records of *M. aerumnalis* of Raxworthy & Nussbaum (1996a) may actually refer to *M. brevipalmatus* (which in the past was considered as a synonym of *M. aerumnalis*; see Blommers-Schlösser & Blanc, 1991), but even this species is possibly not a high mountain endemic. According to Blommers-Schlösser & Blanc (1991) it is known from Mandraka, which lies at about 1200 m altitude. Equally, *Boophis microtympanum* is possibly not a high mountain endemic, but the taxonomy of populations from the lower altitudes of Andringitra needs further study (see Glaw & Vences, 1994). Although *Plethodontohyla tuberculata* has been recorded from Angavokely (Blommers-Schlösser & Blanc, 1991) which is at 1400 m (Viette, 1991), this species and *Anodonthyla montana* can be considered as high mountain endemics, at least in a less strict sense, according to current knowledge.

Species which are more likely to be true high mountain endemics were apparently not found in the surveys of Raxworthy & Nussbaum (1996a,b), and thus not included in their accounts. *Boophis williamsi* is only known from 2200 m altitude (Guibé 1974, Blommers-Schlösser, 1979), whereas *B. laurenti* occurs 1500-2650 m above sea level (Guibé, 1974). The few

exactly known localities for *Scaphiophryne madagascariensis* are between 1530 m (Ambalamarovandana) and 2030 m (Andohariana), and *Scaphiophryne pustulosa* occurs at similar altitudes. Finally, *Mantidactylus madecassus* and *M. pauliani* appear to be confined to areas above 1500 m and can therefore be regarded as high mountain endemics.

An updated list of the montane amphibians (defined by a general restriction to altitudes of ca. 1500 m or higher) occurring on the three Malagasy massifs of Andringitra, Ankaratra, and Tsaratanana (and partly at other localities of high altitude; see Glaw & Vences 1994) is therefore as follows (data from Raxworthy & Nussbaum, 1996a; Andreone *et al.*, 1998; and as discussed above): *Boophis laurenti* (Andringitra), *B. williamsi* (Ankaratra), *B. ankaratra* (Andringitra, Ankaratra), *Mantidactylus madecassus* (Andringitra), *M. pauliani* (Ankaratra), *Anodonthyla montana* (Andringitra), *Plethodontohyla tuberata* (Ankaratra), *P. guentherpetersi* (Tsaratanana), *P. sp. A* (Tsaratanana), *P. sp. B* (Tsaratanana), *P. sp. C* (Tsaratanana), *Platyplelis tsaratananaensis* (Tsaratanana), *P. sp. A* (Tsaratanana), *Stumpffia sp. A* (Tsaratanana), *Scaphiophryne madagascariensis* (Andringitra), *S. pustulosa* (Ankaratra), and *S. sp. A* (Tsaratanana). Additional species which may be montane endemics but which need taxonomic revision are *Boophis microtympanium* (Andringitra, Ankaratra), *Mantidactylus brevipalmatus* (Andringitra, Ankaratra), and *Mantidactylus elegans* (Andringitra, Tsaratanana). This list contains up to 17, possibly 20 species, whereas Raxworthy & Nussbaum (1996a) listed 14 montane amphibian species. The general conclusion drawn by these authors – that the montane heathlands of Madagascar harbour a relatively diverse endemic amphibian fauna – is therefore strongly confirmed.

Three species pairs of montane amphibians may be examples of vicariant speciation between the Andringitra and Ankaratra massifs. *Mantidactylus madecassus* (Andringitra) and *M. pauliani* (Ankaratra) appear to be sister species due to the probably synapomorphic head shape and lack of vomerine teeth. *Scaphiophryne madagascariensis* (Andringitra) and *S. pustulosa* (Ankaratra) share a greenish colouration with sharply bordered brown markings which are not known in other *Scaphiophryne* (see illustrations in Glaw & Vences, 1994). *Boophis laurenti* (Andringitra) and *B. williamsi* (Ankaratra) share a large relative foot length and probably large blackish tadpoles (data in Blommers Schlösser & Blanc, 1991; Glaw & Vences, 1994). An additional example is found in reptiles: the geckos *Lygodactylus intermedius* (Andringitra, 1700–2600 m, see Pasteur, 1995) and *L. mirabilis* (Ankaratra, 2300–2640 m). Andringitra and Ankaratra populations of all other amphibian and reptile species which can be considered as mountain endemics (*Boophis ankaratra*, *Phelsuma barbouri*, *Calumma hilleniusi*, *Furcifer campani*, *Amphiglossus sp.*, *Mabuya boettgeri*, *Mabuya madagascariensis*) appear to be conspecific on

both massifs (data from Glaw & Vences, 1994; Raxworthy & Nussbaum, 1996a). Other species such as *Plethodontohyla tuberata* and *Anodonthyla montana* are known only from one of the two massifs and have no closely related sister species in the other massif. These species are therefore not helpful in indicating any vicariant speciation events between Ankaratra and Andringitra. The same is true for *Mantidactylus elegans* which occurs in Andringitra up to 2500 m, but is not known from Ankaratra.

The climatic history of the Quaternary in Madagascar included dynamic shifts between drier and more humid periods (Battistini, 1996). According to the data summarized in Burney (1996), ericoid vegetation of Madagascar's highest mountain ranges may have flourished at times during the Pleistocene down to elevations of ca. 1000 m. This continuous montane habitat was probably populated by the ancestor of the *M. madecassus/pauliani* clade, as well as by the ancestors of the other allopatric sister species. Due to a period of warmer climate, it is possible that such high mountain habitats and their associated amphibian fauna became restricted to the high altitude refuges of Ankaratra and Andringitra. In this scenario, the subsequent temperature decreases were not intense enough to allow the montane habitats of both massifs to get into long-term contact at lower altitudes again; hence, montane endemics of both massifs, such as the *Mantidactylus madecassus* and *M. pauliani* ancestor, remained isolated and several of them evolved into separate species.

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