

A new species of *Mantidactylus* (subgenus *Guibemantis*) from Madagascar, with a comparative survey of internal femoral gland structure in the genus (Amphibia: Ranidae: Mantellinae)

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A new species of *Mantidactylus* (subgenus *Guibemantis*) from the rainforests of eastern Madagascar is described. The new species is sympatric with the closely related *M. depressiceps* (Boulenger, 1882) and *M. tornieri* (Ahl, 1929) but differs by larger size, a more strongly developed prepollex, and by advertisement calls. *Mantidactylus acuticeps* Ahl, 1929 and *Rhacophorus moquaardii* Boulenger, 1896 are confirmed to be junior synonyms of *M. depressiceps*.

The presence of distinct femoral glands in the new species was noted; a feature so far not reliably recognized in other members of the subgenus *Guibemantis*. Femoral gland structure was investigated in representatives of each of the subgenera included in *Mantidactylus* by dissecting and reflecting the femoral skin. Four femoral gland types were identified. Type 1: many small, single granules in an ill-delimited patch, grouped in rosettes at the patch edges; type 2: a group of moderately sized granules in a well-delimited patch; type 3: comprising two different structures: distal granules enclosing externally a distinct central depression, and smaller proximal granules or groups of granules; type 4: as type 3, but lacking the proximal granules.

Mantidactylus rivicola Vences, Glaw and Andreone, 1997, *M. cf. malagasius* (Methuen and Hewitt, 1913) and *M. ventrimaculatus* (Angel, 1935) differed from all other species examined; their femoral glands comprise a reduced number of large granules with an indistinct central depression in external view. The presence of a distal granule group with external central depression (types 3 and 4 above) provides a probable synapomorphy for the subgenera *Brygoomantis*, *Ochthomantis*, *Hylobatrachus*, *Chonomantis* and *Mantidactylus*. In females of these subgenera rudimentary femoral glands are present, but they lack completely in females of the other groups.

KEYWORDS: Anura, Ranidae, *Mantidactylus*, *Mantidactylus kathrinae* n. sp., femoral glands, Madagascar.

Introduction

Malagasy frogs of the genus *Mantidactylus* Boulenger, 1895 are classified, together with the genus *Mantella* Boulenger, 1882, in the endemic ranid subfamily

Mantellinae (Blommers-Schlösser, 1993). *Mantidactylus* is the most speciose anuran genus in Madagascar and was divided into 12 subgenera (Dubois, 1992; Glaw and Vences, 1994). Blommers-Schlösser (1979) first defined species groups within *Mantidactylus* and included *M. depressiceps* (Boulenger, 1882), *M. tornieri* (Ahl, 1929) and *M. peraccae* (Boulenger, 1896) in a *M. depressiceps* group. Blommers-Schlösser and Blanc (1991) added *M. elegans* (Guibé, 1974) to this group, and Glaw and Vences (1992b) transferred *M. liber* (Peracca, 1893) from the *M. bicalcaratus* group to the *M. depressiceps* group. Dubois (1992) elevated the *M. depressiceps* group to the subgenus *Guibemantis* Dubois, 1992. Glaw and Vences (1994) transferred *M. peraccae* from *Guibemantis* to the subgenus *Spinomantis*.

Blommers-Schlösser (1993) and Glaw *et al.* (1998) distinguished mantellines from other ranid frogs by two synapomorphies: Y-shaped terminal phalanges (shared with rhacophorines) and lack of a strong amplexus during mating. The monophyly of mantellines was recently corroborated by molecular data (Richards and Moore, 1998). Blommers-Schlösser (1993) used presence of femoral glands as a potential synapomorphy of the Mantellinae, Petropedetinae and Indiraninae. However, these glands are absent in most petropedetines (*sensu* Blommers-Schlösser, 1993), while their presence in some mantellines is uncertain (Daly *et al.*, 1996). Members of the subgenus *Guibemantis* and the genus *Mantella* lack obvious externally visible femoral glands (Blommers-Schlösser and Blanc, 1991). The structure of femoral glands is useful in distinguishing several subgenera within *Mantidactylus* and in assessing phylogenetic relationships within the genus (Blommers-Schlösser, 1979; Andreone *et al.*, 1998).

The aim of this paper is, first, to describe a new species of *Guibemantis* from the rainforests of eastern Madagascar and, second, to describe and discuss femoral gland structure in all *Mantidactylus* subgenera.

Material and methods

Calls were analysed with the MEDAV sound analysing system Spekro 3.2. The following morphological measurements were taken to the nearest 0.1 mm using callipers: SVL (snout–vent length), HW (head width), HL (head length), ED (horizontal eye diameter), END (eye–nostril distance), NSD (nostril–snout tip distance), IND (inter–narial distance), TD (tympanum diameter), HAL (hand length), FORL (forelimb length), HIL (hindlimb length), FL (foot length). Institutional abbreviations are as listed in Leviton *et al.* (1985). In addition, MRSN is used for Museo Regionale di Scienze Naturali, Torino. Webbing formula follows Blommers-Schlösser (1979).

Recognition of femoral glands is often difficult in preserved specimens by simple external examination. By dissecting and reflecting the skin around the femoral glands (turning the skin upside-down), the internal aspect of the whole gland was exposed to direct observation. The components of femoral glands were examined and photographed using a stereo microscope to the nearest 0.1 mm. Our descriptions refer to the macroscopic structure of the gland on the ventral thigh as visible from internal view.

Results

Mantidactylus kathrinae n. sp.

HOLOTYPE ZFMK 62264 (figures 1–2), adult male, collected in rainforest near An'Ala (18°56'S, 48°28'E, 840 m above sea level), eastern Madagascar, on 3 February 1996 by F. Glaw.

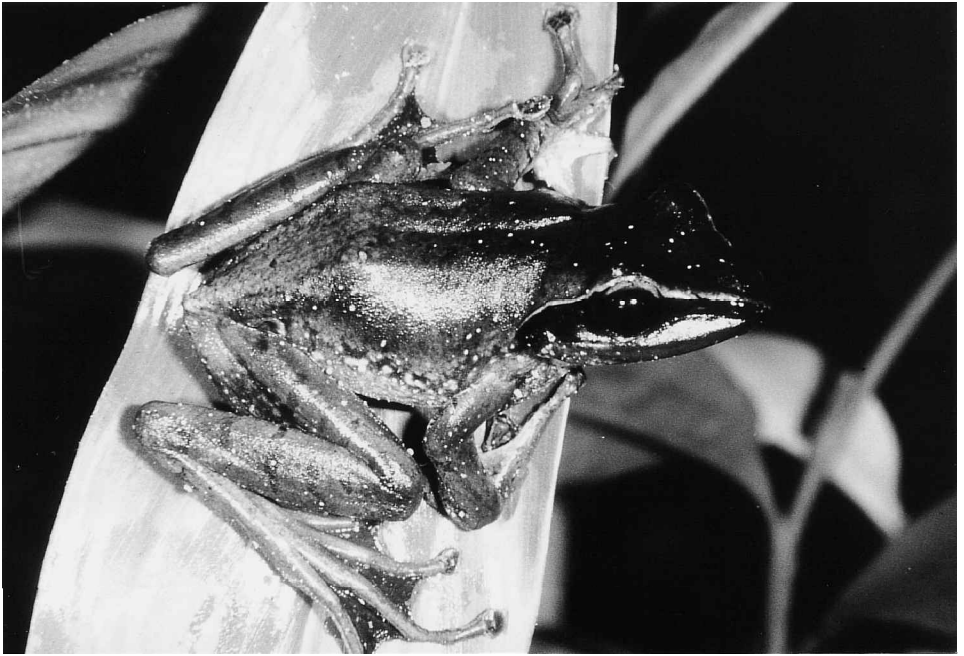


FIG. 1. Holotype of *Mantidactylus kathrinae* in life, ZFMK 62264.

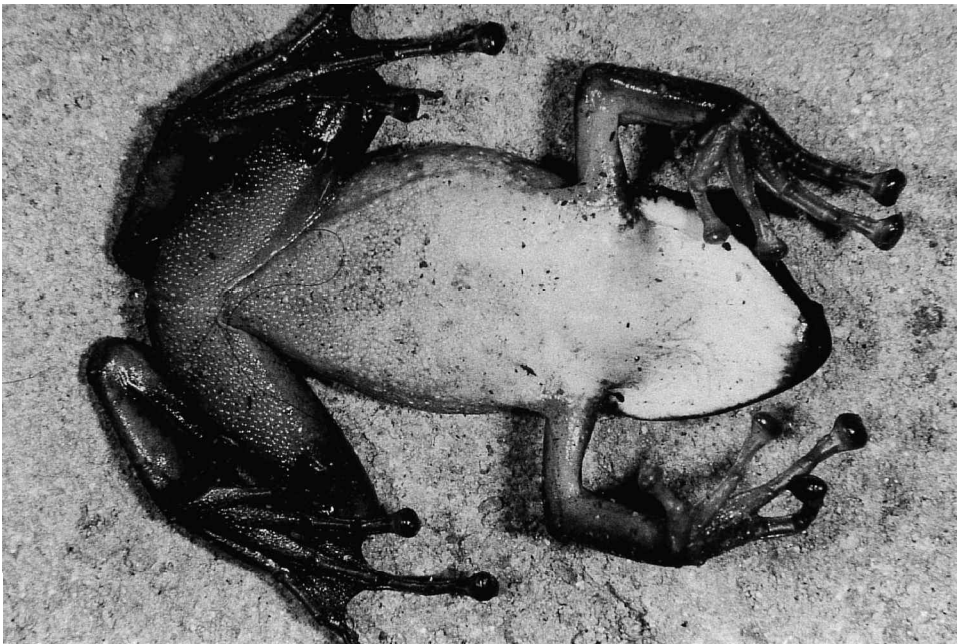


FIG. 2. Holotype of *Mantidactylus kathrinae* in life, ZFMK 62264, ventral view.

PARATYPES ZFMK 62263, adult male, same locality, date and collector as holotype; ZFMK 62266, same locality as holotype, collected on 30 January 1996 by D. Vallan.

Additional specimens. ZFMK 64543 and 64544 from Andapa (14°40'S,

49°39'E), north-eastern Madagascar, are attributed to the new species but not defined as paratypes due to their bad state of preservation.

Diagnosis. A species of the genus *Mantidactylus* as indicated by the lack of nuptial pads in breeding males and by the presence of femoral glands (recognizable from internal view). A member of the subgenus *Guibemantis* as indicated by large relative hand length (hand length/snout–vent length 0.32–0.35), a white vocal sac, femoral gland structure (table 2) and arboreal egg deposition site above stagnant water bodies. The new species is distinguished from all other valid species of the subgenus *Guibemantis* (*M. depressiceps*, *M. tornieri*, *M. liber*) by a more distinct prepollex and by advertisement calls (figures 3–6). It further differs from *M. tornieri* and *M. liber* by white eggs and white jelly of its clutches, from *M. liber* and *M. depressiceps* by its larger snout–vent length (adult males > 44 mm SVL) and from *M. depressiceps* by a more extended foot webbing (reaching further than last sub-articular tubercle on fifth toe), lower pulse repetition rate, longer note duration and lower dominant frequency (table 3). Specimens from a population sympatric (but not syntopic) with *M. depressiceps* and *M. tornieri* can be easily diagnosed by their much larger size (adult males > 55 mm SVL).

Description of holotype. Measurements of the holotype are included in table 1. Body relatively slender; head longer than wide, wider than body; snout rather pointed in dorsal and lateral views; nostrils directed laterally, not protuberant; canthus rostralis distinct, straight; loreal region concave; tympanum distinct, small, rounded, its diameter about one-half that of eye; distinct supratympanic fold, running straight for most of its length, curving towards the forelimb insertion; tongue ovoid, distinctly bifid posteriorly; vomerine teeth form a distinct, large, oblique group posterolateral to choanae; choanae medium-sized, rounded. Forelimbs slender; sub-articular tubercles single; inner and outer metacarpal tubercle present; a distinct prepollex (3 mm) of about one-third of the length of the inner finger. Fingers with

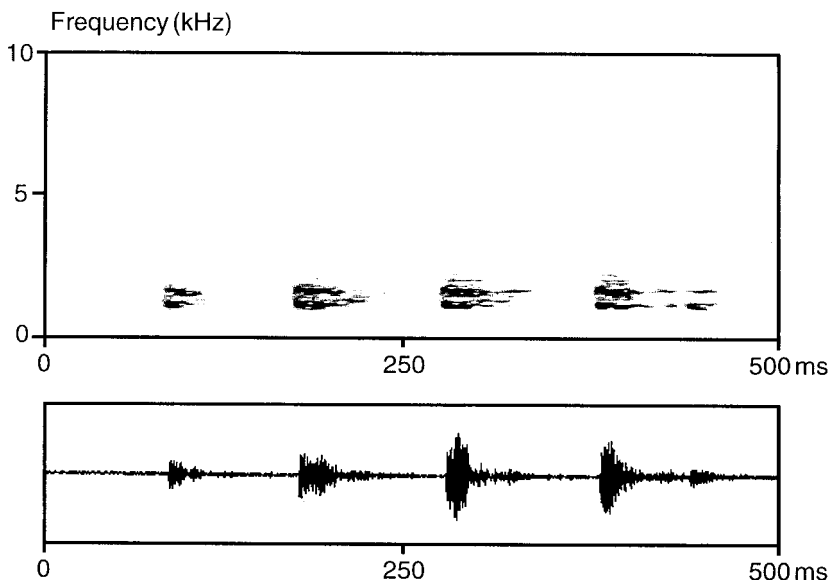


FIG. 3. Sonogram and oscillogram of one note (four pulses) of a call of *Mantidactylus kathrinae* from Andapa.

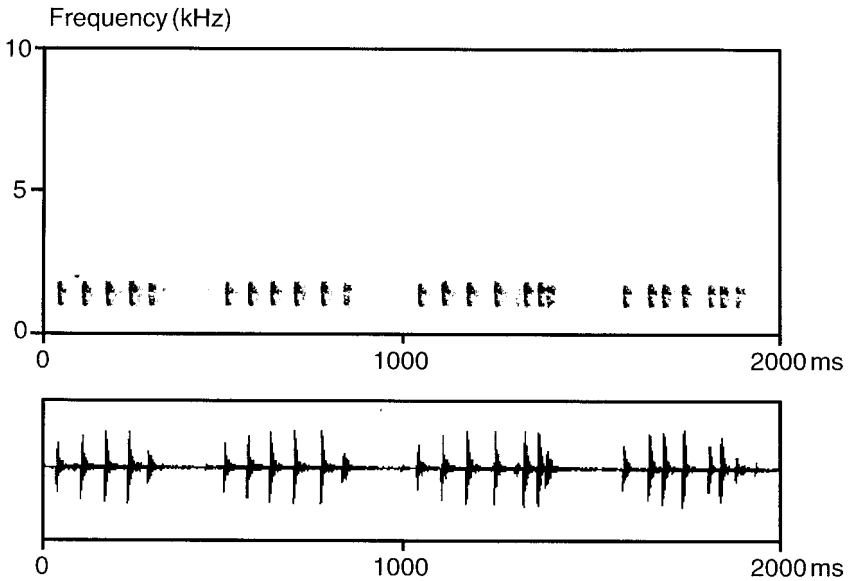


FIG. 4. Sonogram and oscillogram of a call (series of four notes with five to seven pulses each) of *Mantidactylus kathrinae* from An'Ala.

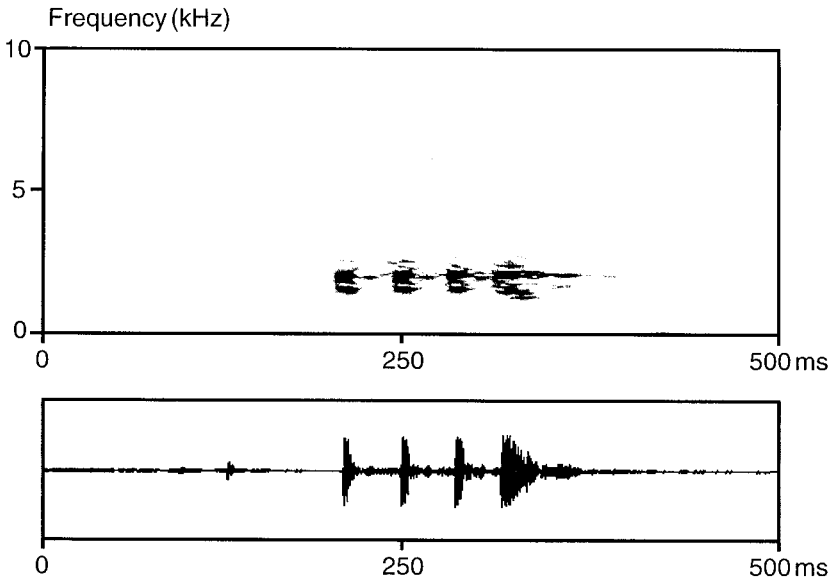


FIG. 5. Sonogram and oscillogram of a call (single note with four pulses) of *Mantidactylus depressiceps* from Andasibe.

very little rudiments of webbing; relative finger length $1 < 2 < 4 < 3$; finger discs strongly enlarged; nuptial pads absent; ventral circummarginal groove of fingers and toes complete, very distinct.

Legs slender; tibiotarsal articulation reaches between eye and nostril; lateral metatarsalia separated; inner metatarsal tubercle rather small; outer metatarsal tubercle present, distinct; webbing formula of the foot $1(1), 2i(1.5-2), 2e(0.75)$,

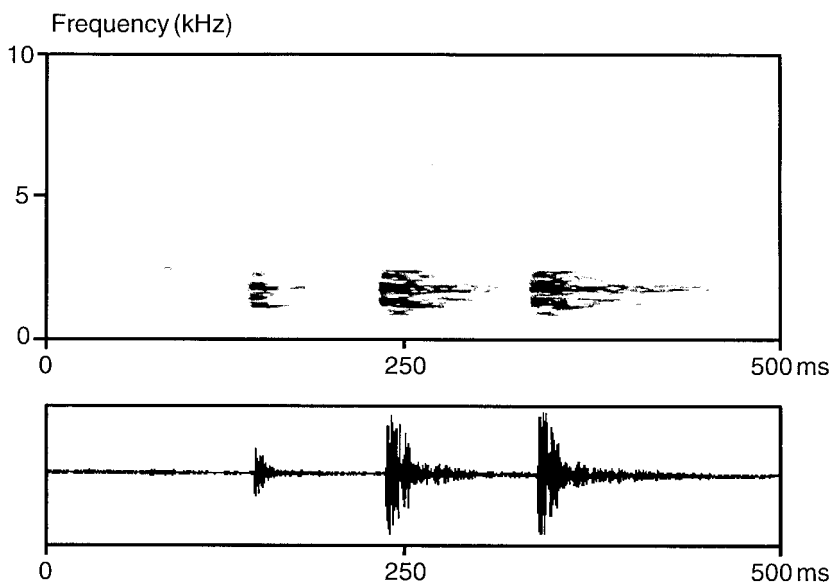


FIG. 6. Sonogram and oscillogram of a call (single note with three pulses) of *Mantidactylus tornieri* from Andasibe.

3i(1.75), 3e(0.75), 4i(2), 4e(1.75), 5(0.5) (since only one subarticular tubercle is recognizable on the second toe, the actual relative extension of the web can only be estimated on this toe); relative toe length $1 < 2 < 3 \leq 5 < 4$. Skin on the dorsum smooth; ventral skin smooth, but more granular posteriorly. Skin ventrally on thigh distinctly granular (glandular patch only slightly prominent). The gland extends over about three-quarters of the surface of the thigh and gland patches on opposite thighs are in contact in the anal region. There are no enlarged tubercles around the anus.

Colour of holotype in life. Dorsal colour fading from a lighter brown posteriorly to dark brown anteriorly, with a few very small scattered whitish spots. Head sides and tympanic region dark brown. Iris uniformly dark except a narrow copper streak along the upper margin. Webbing, posterodorsal part of thighs, arm insertions and lower flanks dark grey. On the flanks, the beige dorsal colour fades gradually into the more whitish ventral colour, with an irregular series of rather small light spots which are indistinctly bordered by darker pigment. Venter dirty white with some dark pigment, throat bright white, sharply bordering on the dark brown lower lip. Ventral side of fore-and hindlimbs greyish except the more yellowish thigh patch area.

Colour in preservative similar to that in life. Dorsum almost uniformly light brown to beige, dark colour of webbing less distinct.

Variation. The male paratypes are very similar to the holotype. The pattern of light spots (bordered by dark brown) on the flanks and the posterodorsal surface of the thigh is more contrasting in ZFMK 62266. Canthus rostralis and supratympanic fold are light beige in this specimen, emphasizing the contrast between dark head side and light dorsum. In life, this specimen had a lighter dorsal colour (back and upper head surface light brown). Nearly the upper third of the iris was light brown to copper. Webbing formula of the foot is 1(1), 2i(1.5–2), 2e(0), 3i(1.5), 3e(0.5), 4i(2), 4e(1.75), 5(0.5) in ZFMK 62263 and 1(1), 2i(1.5–2), 2e(0.5), 3i(1.75), 3e(0.75), 4i(2), 4e(2),

Table 1. Measurements (mm) of type specimens of *Mantidactylus kathrinae*, *M. depressiceps*, *M. tornieri*, *M. acuticeps* (junior synonym of *M. depressiceps*) and *Rhacophorus moequardii* (junior synonym of *M. depressiceps*). See *Material and methods* section for abbreviations of variables. HT = holotype, PT = paratype, LT = lectotype, PLT = paralectotype.

	<i>M. kathrinae</i>			<i>M. depressiceps</i>			<i>M. tornieri</i>		<i>M. acuticeps</i>		<i>R. moequardii</i>
	ZFMK	ZFMK	ZFMK	BMNH	BMNH	BMNH	BMNH	ZMB	ZMB	ZMB	BMNH
	62264	62263	62266	1947.2.27.50	1947.2.27.51	1947.2.27.52	1947.2.27.53	30533	30496	1947.2.8.62	
Status	HT	PT	PT	LT	PLT	PLT	PLT	HT	HT	HT	HT
Sex	M	M	M	M	M?	M?	?	?	M?	M?	?
SVL	56.7	58.6	57.4	39.6	36.7	34.5	32.5	47.9	35.1	35.1	33.0
HW	20.0	20.6	21.0	13.2	11.8	11.9	10.7	16.7	11.8	11.8	12.3
HL	22.4	23.3	23.4	13.7	12.2	12.7	11.2	18.6	12.6	12.6	13.6
TD	3.0	3.3	3.4	2.4	2.2	2.0	2.2	2.5	2.0	2.0	1.8
ED	5.6	5.8	6.5	4.2	4.0	4.0	3.6	5.3	4.0	4.0	3.7
END	6.1	6.8	6.7	3.7	3.2	3.3	3.0	5.2	3.2	3.2	3.4
NSD	4.1	4.2	4.0	2.4	2.2	2.2	2.3	3.3	2.4	2.4	2.1
IND	6.3	6.6	6.3	3.9	4.1	3.7	3.5	4.9	3.8	3.8	4.0
HAL	19.7	19.1	19.7	13.2	12.1	11.1	10.4	16.0	11.7	11.7	10.4
FORL	37.0	37.5	37.5	27.4	22.0	22.0	22.0	30.2	23.9	23.9	21.9
HIL	92.9	94.2	97.8	69.6	61.0	60.7	56.6	75.9	63.7	63.7	54.9
FOL	29.7	30.6	30.2	20.9	19.0	17.7	16.6	23.4	19.3	19.3	15.6

5(0.5) in ZFMK 62266. Of the additional specimens from Andapa, ZFMK 64543 (male) measures 44.4 mm SVL and ZFMK 64544 (female) 46.1 mm SVL.

The similar SVL of both Andapa specimens of *M. kathrinae* is in accordance with Blommers-Schlösser's (1979) observation that in the subgenus *Guibemantis* sexual size dimorphism is very low. Although the available Andapa specimens are distinctly smaller than those from An'Ala, they still are larger than the available specimens of *M. depressiceps*. According to Blommers-Schlösser (1979), only one out of 11 examined *M. depressiceps* males, ZMA 6976, reached a SVL of 44 mm, the remaining ten specimens ranging from 34–41 mm.

Femoral glands. The structure of the femoral glands was studied in one paratype (ZFMK 62266). From internal view it is evident that the externally visible granular patch is composed of a very large number of single light small granules. In the centre of the gland, these granules are densely arranged next to each other, without further structure, whereas towards the edges of the gland patch they are increasingly arranged in small rosette-like groups (five to seven granules surrounding one central granule). In some of these rosette-like granule groups, the central granule is dark, giving the impression of a central porus-like structure. For measurements of the gland structures see table 2.

Advertisement call. Calls were recorded at An'Ala (on 3 February 1995, c.21:00 h) and at Andapa (by K. Schmidt on 18 March 1997, 18:00 h). Calls from both localities were rather similar and consisted of series of three to four pulsed notes (figures 3–4, table 3).

Natural history. About 20 whitish clutches, very probably laid by *M. kathrinae*, were seen on 3 February 1996 at An'Ala hanging from the vegetation above a pool at few metres distance from a forest brook. On this evening, however, very little calling activity of *M. kathrinae* was observed. K. Schmidt (personal communication) observed many whitish clutches being laid by a large breeding colony of the species near Andapa in 1996, but heard only weak calling and breeding activity at the same pool on 18 March 1997. The senior author observed white clutches on 30 March 1994 (with greenish tadpoles ready to hatch) and on 23 February 1995 above a pond near the edge of a river in the Marojezy Reserve (c.300 m above sea level) in north-eastern Madagascar; these clutches may also have belonged to *M. kathrinae*.

Distribution. The new species is so far only known from the type locality and from Andapa in north-eastern Madagascar.

Etymology. Dedicated to Kathrin Schmidt, Bonn, in recognition for her invaluable help with our research on Malagasy amphibians and reptiles; her call recordings from Andapa helped to clarify the relationships and distribution of the species of the *M. depressiceps* complex.

Available names in Guibemantis

Rhacophorus mocquardii Boulenger, 1896 and *Mantidactylus acuticeps* Ahl, 1929 were considered to be junior synonyms of *M. depressiceps* (Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1992b). A re-examination of the holotypes of both taxa confirmed the validity of these synonymizations (see below). We also re-examined the holotype of *Rhacophorus tornieri* Ahl, 1929 and the lectotype of *Rhacophorus depressiceps* Boulenger, 1882 to confirm that the names *Mantidactylus tornieri* and *M. depressiceps* were correctly applied and defined by Blommers-Schlösser (1979) who first noted the presence of two distinct biological species previously subsumed under the name *depressiceps*.

Table 2. Femoral gland measurements of studied males of *Mantidactylus* (all referring to internal view). See text for definition of gland types. Granule size is given as range, followed (in parentheses) by mean \pm standard deviation and number of measured granules. In species with gland types 3 (double glands), measurements and counts are given separately for A and B structures as defined in the text.

Species	Catalogue number	SVL [mm]	gland type	gland size [mm]	number of granules	granule size [mm]
<i>M. (Guibemantis) kathirinae</i> n. sp.	ZFMK 62266	57.4	1	19.8 \times 6.9	> 1000	0.23–0.33 (0.27 \pm 0.03, n = 10)
<i>M. (Guibemantis) depressiceps</i> (Boulenger, 1882)	ZMA 6972 (742)	39.2	1	14.9 \times 6.6	> 1150	0.18–0.35 (0.26 \pm 0.06, n = 10)
<i>M. (Guibemantis) liber</i> (Peracca, 1893)	MRSN A437.1	26.7	1	7.6 \times 3.0	c.380	0.18–0.33 (0.25 \pm 0.05, n = 10)
<i>M. (Spinomanantis) aglarei</i> (Methuen and Hewitt, 1913)	ZFMK 46021	46.5	2	9.0 \times 3.3	53	0.50–0.90 (0.75 \pm 0.14, n = 10)
<i>M. (Spinomanantis) finbriatus</i> Glaw and Vences, 1994	ZFMK 59900	33.5	2	5.4 \times 2.1	39	0.43–0.67 (0.57 \pm 0.08, n = 10)
<i>M. (Blommersia) cf. witrei</i> Guibé, 1974	ZMA 7058 (761)	—	2	4.0 \times 1.9	44	0.20–0.60 (0.39 \pm 0.13, n = 10)
<i>M. (Pondanusicola) bicaratus</i> (Boettger, 1913)	ZFMK 53702	20.6	2	4.5 \times 1.7	41	0.17–0.70 (0.43 \pm 0.19, n = 10)
<i>M. (Phylacomantis) pseudoasper</i> Guibé, 1974	ZFMK 53706	32.1	2	5.1 \times 1.9	36	0.30–0.63 (0.47 \pm 0.12, n = 10)
<i>M. (Gephyromantis) asper</i> (Boulenger, 1882)	ZFMK 62237	29.0	2	5.9 \times 1.7	39	0.30–0.80 (0.50 \pm 0.14, n = 10)
<i>M. (Gephyromantis) luteus</i> Methuen and Hewitt, 1913	MNHN 1972.1410	45.0	2	9.4 \times 3.8	72	0.40–0.85 (0.65 \pm 0.15, n = 10)
<i>M. (Gephyromantis) boulengeri</i> (Methuen, 1920)	MNHN 1972.1875	24.5	2	3.0 \times 1.6	19	0.40–0.58 (0.52 \pm 0.05, n = 10)
<i>M. (Gephyromantis?) rivicola</i> Vences, Glaw and Andreone, 1997	MRSN	24.0	?	2.6 \times 1.7	4	0.65–1.13 (0.93 \pm 0.19, n = 8)
<i>M. (Laurentomanitis) cf. malagasius</i> (Methuen and Hewitt, 1913)	ZFMK 59929	23.0	?	4.4 \times 2.2	2 \times 3–4	1.05–1.40 (1.23 \pm 0.13, n = 10)
<i>M. (Laurentomanitis) ventrimaculatus</i> (Angel, 1935)	ZFMK 62281	23.0	?	5.1 \times 1.7	9	0.80–1.20 (0.99 \pm 0.13, n = 9)
<i>M. (Brygoomanitis) ulcerosus</i> (Boettger, 1880)	MNHN 1975.632	34.0	3	A: 3.3 \times 3.3 B: 3.6 \times 3.3	A: 7 B: 238	A: 0.60–1.45 (1.04 \pm 0.27, n = 8) B: 0.13–0.30 (0.20 \pm 0.06, n = 10)
<i>M. (Hylobatrachus) lugubris</i> (Duméril, 1853)	MNHN 1973.886	27.8	3	A: 1.4 \times 1.4 B: 2.1 \times 1.4	A: 8 B: not counted	A: 0.48–0.63 (0.57 \pm 0.05, n = 10) B: 0.18–0.40 (0.32 \pm 0.07, n = 10)
<i>M. (Ochthomantis) cf. femoralis</i> (Boulenger, 1882)	MNHN 1973.853	48.6	3	A: 4.4 \times 4.1 B: 4.1 \times 4.1	A: 21 B: 168	A: 0.35–1.55 (1.01 \pm 0.38, n = 10) B: 0.15–0.68 (0.42 \pm 0.19, n = 10)
<i>M. (Chonomantis) brevipalmatus</i> Ahl, 1929	ZFMK 59853	32.0	3	A: 5.1 \times 3.1	A: c.10 B: few granules	A: 1.00–1.50 (1.25 \pm 0.16, n = 10) B: c.0.3
<i>M. (Mantidactylus) grandidieri</i> Mocquard, 1895	MRSN A1971.1	86.0	4	A: 12.4 \times 8.1	A: 24	A: 0.70–3.50 (1.97 \pm 1.04, n = 10)

Measurements of the respective type specimens (*tornieri*: holotype ZMB 30533 (figure 7); *depressiceps*: lectotype BMNH 1947.2.27.50 (figure 8), paralectotypes BMNH 1947.2.27.51–53; *acuticeps*: holotype ZMB 30496 (figure 9); *mocquardii*: holotype BMNH 1947.2.8.62 (figure 10)) are included in table 1. Webbing formulae of the name-bearing types (holotypes of *tornieri*, *acuticeps* and *mocquardii* lectotype of *depressiceps*) are 1(1), 2i(1), 2e(0.5), 3i(1.75), 3e(1), 4i(2), 4e(2), 5(0.5) in *tornieri*; 1(1), 2i(1.75), 2e(1), 3i(2), 3e(1), 4i(2.25), 4e(2.25), 5(1) in *depressiceps*; 1(1), 2i(1.75), 2e(0.5), 3i(2), 3e(1), 4i(2.25), 4e(2.25), 5(1) in *acuticeps*; 1(1), 2i(1.25), 2e(0.75), 3i(2), 3e(1), 4i(2.25), 4e(2), 5(0.75–1) in *mocquardii*.

The type specimens of *acuticeps* and *depressiceps* show reduced webbing and a small SVL compared with *tornieri* and *kathrinae*, confirming the attribution of *acuticeps* as junior synonym of *depressiceps*. The holotype of *mocquardii* (maybe an immature specimen) is in a rather bad state of preservation and has slightly more webbing than generally present in *depressiceps*. We here consider it to be a junior synonym of *M. depressiceps* since the extent of webbing in *mocquardi* is less than in *tornieri* and its small size is a further difference to that species. All four name bearing type specimens (*tornieri*, *depressiceps*, *acuticeps*, *mocquardii*) have a rather small and indistinct prepollex differentiating them from *M. kathrinae*.

Advertisement calls in *Mantidactylus depressiceps* and *M. tornieri*

Calls of *M. depressiceps*, consisting of a single pulsed note, were recorded at Andasibe on 1 April 1995 at 21:00 h. Sonogram and oscillogram of one call are



FIG. 7. Preserved holotype of *Mantidactylus tornieri*, ZMB 30533. Scale: 20 mm.



FIG. 8. Preserved lectotype of *Mantidactylus depressiceps*, BMNH 1947.2.27.50. Scale: 20 mm.



FIG. 9. Preserved holotype of *Mantidactylus acuticeps*, ZMB 30496, junior synonym of *Mantidactylus depressiceps*. Scale: 20 mm.



FIG. 10. Preserved holotype of *Rhacophorus mocquardii*, BMNH 1947.2.8.62, junior synonym of *Mantidactylus depressiceps*. Scale: 20 mm.

shown in figure 5. Calls of *M. tornieri* were recorded simultaneously and syntopically with *M. depressiceps* (figure 6). Their temporal and spectral characters largely agree with the data given by Glaw and Vences (1992a). In both species, each note corresponds to one expiration.

The calls of *M. depressiceps*, *M. tornieri* and *M. kathrinae* bear strong structural similarities but are different to the human ear. The call of *M. depressiceps* differs from that of *M. tornieri* by a faster pulse repetition rate (table 3). The call of *M. kathrinae* has a pulse repetition rate intermediate between *M. tornieri* and *M. depressiceps* and an intermediate duration of intervals between pulses (table 3). Although the ranges of both values overlap between species, there is a clear difference in pulse repetition rate in most calls. Calls of *M. kathrinae* from Andapa differ from the An'Ala calls by a lower pulse repetition rate and a lower duration of intervals between pulses. One important distinctive character of *M. kathrinae* calls from both localities is the arrangement of notes into regular series as shown in figure 4. Calls of *M. depressiceps* and *M. tornieri*, on the contrary, generally consist of only a single note and are repeated after longer and often irregular intervals.

Presence and morphology of femoral glands in *Mantidactylus* subgenera

The presence of femoral glands in the subgenus *Guibemantis* has been the subject of continued discussion (Blommers-Schlösser, 1979; Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994; Daly *et al.*, 1996). Discovery of femoral glands in *M. kathrinae*, which can be observed clearly in internal view (figures 11–12), led the investigation the internal macroscopic femoral gland structure in *Mantidactylus* subgenera. Femoral glands were found in males of all known *Mantidactylus* species

Table 3. Temporal and spectral call parameters in *Mantidactylus kathrinae*, *M. depressiceps* and *M. tornieri*. Temporal data are given as range, followed (in parentheses) by mean \pm standard deviation and number of measured elements.

	<i>M. kathrinae</i>	<i>M. kathrinae</i>	<i>M. depressiceps</i>	<i>M. tornieri</i>
Locality	An'Ala	Andapa	Andasibe	Andasibe
Air temperature	21°C	unknown	19°C	19°C
Note duration [ms]	268–372 (329 \pm 44, n = 4)	172–455 (286 \pm 82, n = 20)	22–333 (188 \pm 57, n = 49)	213–247 (n = 2)
Intervals between notes [ms]	185–195 (189 \pm 5, n = 3)	125–200 (161 \pm 22, n = 9)	2252–4771 (2858 \pm 616, n = 14)	several seconds
Pulses per note	5–7 (6.2 \pm 0.9, n = 11)	3–7 (4.0 \pm 1.0, n = 20)	1–7 (4.9 \pm 1.5, n = 49)	2–6
Pulse duration [ms]	9–22 (17 \pm 3, n = 31)	9–46 (28 \pm 7, n = 83)	4–36 (17 \pm 7, n = 56)	17–27 (24 \pm 4, n = 6)
Intervals between pulses [ms]	7–63 (41 \pm 15, n = 26)	10–98 (6 \pm 10, n = 62)	12–91 (28 \pm 18, n = 45)	65–81 (73 \pm 4, n = 4)
Pulse repetition rate [1/s]	17.3–21.1 (19.0 \pm 1.6, n = 4)	11.0–17.4 (14.0 \pm 1.5, n = 20)	17.5–35.7 (26.3 \pm 4.0, n = 45)	12.1–14.1 (n = 2)
Frequency [Hz]	850–1700 (– 2800)	850–2400	1200–2400	1600–2100
Dominant frequency [Hz]	1250–1550	1450–1900	1700–2200	1600–2100
Notes per call	3–4	3–4	1	1

except two: *M. elegans* (of which possibly no adult males have so far been collected) and *M. microtypanum* (personal observation).

Femoral gland is here defined as the whole unpigmented prominent glandular tissue on the ventral side of the thigh which becomes visible when the skin is carefully reflexed. The glands of the examined *Mantidactylus* species (see detailed data in table 2 and figures 11–12) could be classified into four main gland types (all data referring to femoral gland structures of adult male specimens examined in internal view).

Type 1. A large number (380 up to more than 1150) of small granules (maximum diameter 0.35 mm) which are arranged in a patch without sharp borders; granules are densely packed centrally and generally arranged in more isolated, often rosette-like groups towards the edges of the gland patch. This type is only found in the four *Guibemantis* species (*M. kathrinae*, *M. depressiceps*, *M. tornieri*, *M. liber*). *M. liber* is somewhat deviant, with better defined gland edges and less distinct rosette-like granule groups.

Type 2. A single sharply delimited granule group, generally consisting of a moderate number (19–72) of moderately sized granules (up to 0.90 mm diameter). Externally, the gland is visible as an ovoid patch. Differences in granule size exist but are generally randomly distributed, giving the overall impression of a regular arrangement of the granules which are in contact with neighbouring granules in the whole gland patch. Only in *M. asper* and (to a lesser degree) *M. luteus* we observed poorly defined subgroups of granules, sometimes rosette-like, within the gland patch. Found in the subgenera *Blommersia*, *Pandanusicola*, *Spinomantis*, *Gephyromantis* and *Phylacomantis*.

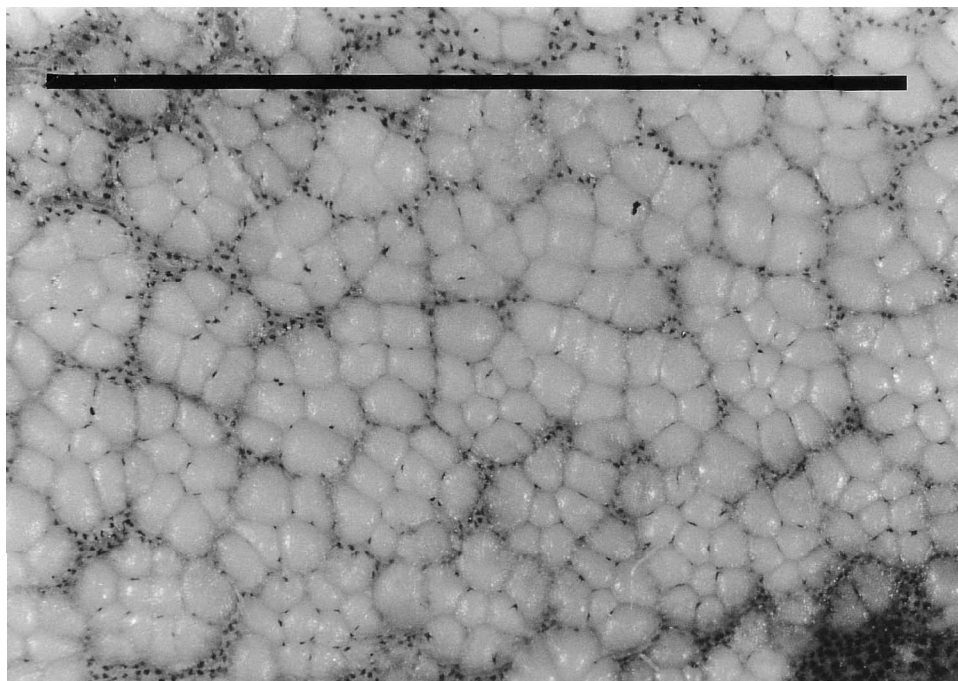


FIG. 11. Femoral gland (type 1) of *Mantidactylus depressiceps*, ZFMK 59870 (adult male), internal view. Scale: 5 mm.

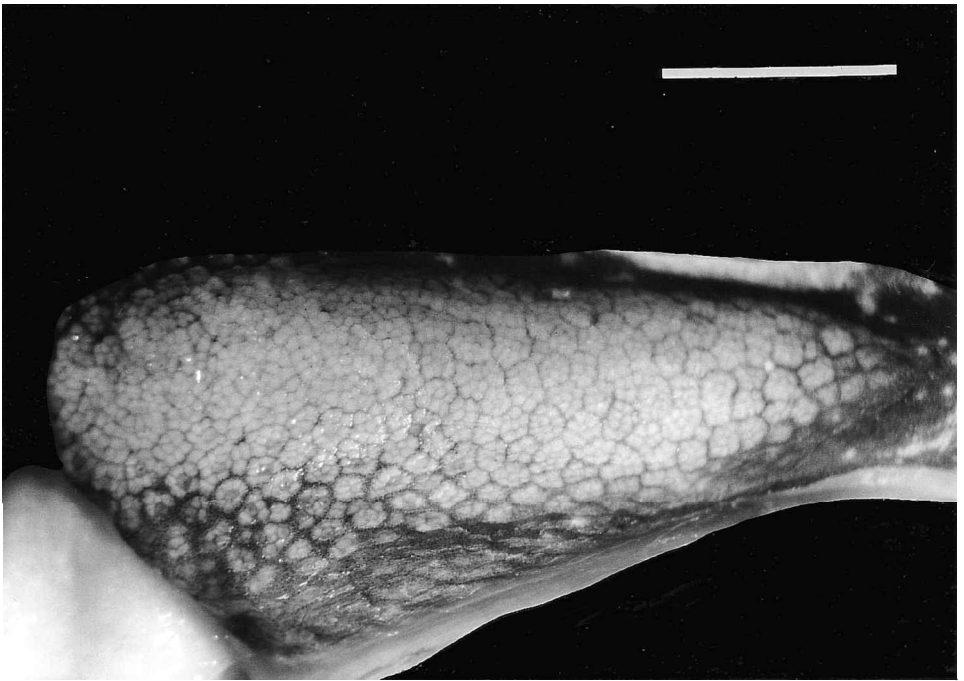


FIG. 12. Femoral gland (type 1) of *Mantidactylus kathrinae*, ZFMK 62266 (adult male), internal view. Scale: 5 mm.

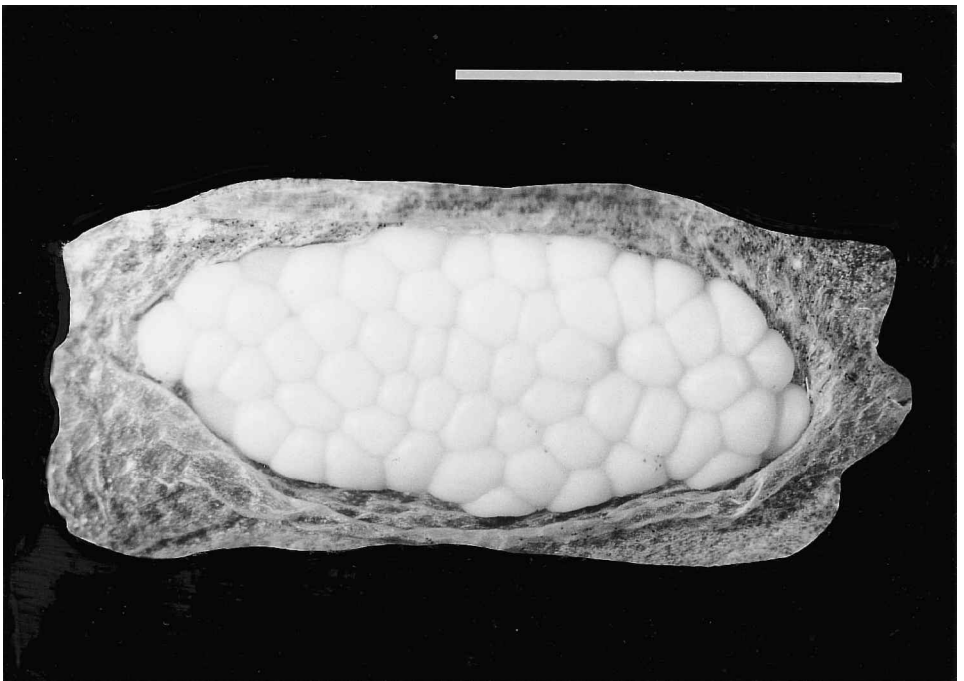


FIG. 13. Femoral gland (type 2) of *Mantidactylus aglavei*, ZFMK 60002 (adult male), internal view. Scale: 5 mm.

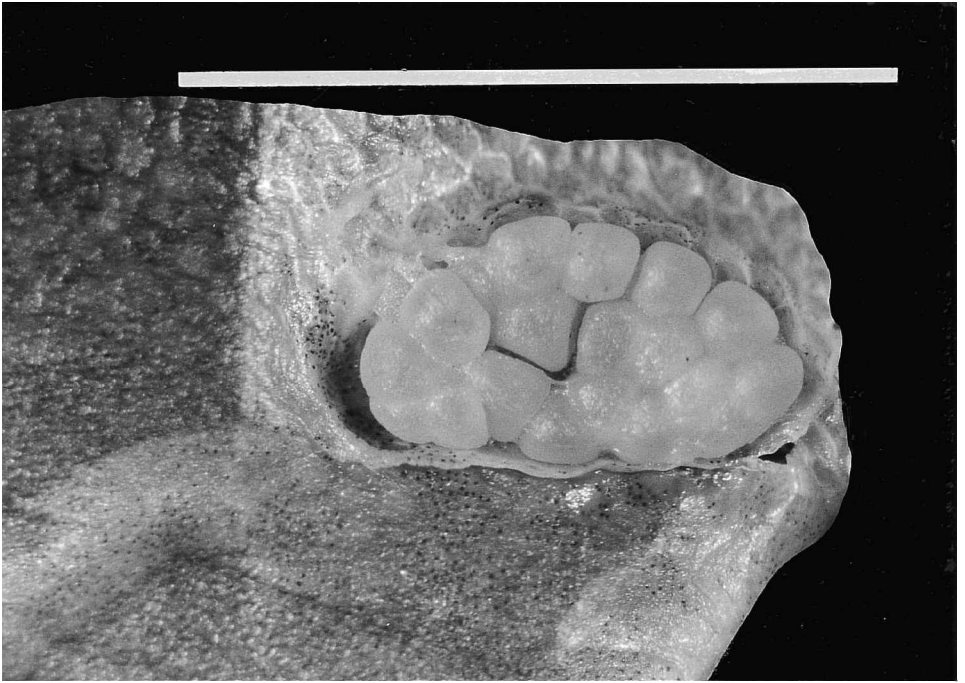


FIG. 14. Femoral gland (type 2) of *Mantidactylus boulengeri*, MNHN 1972.1875 (adult male), internal view. Scale: 5 mm.

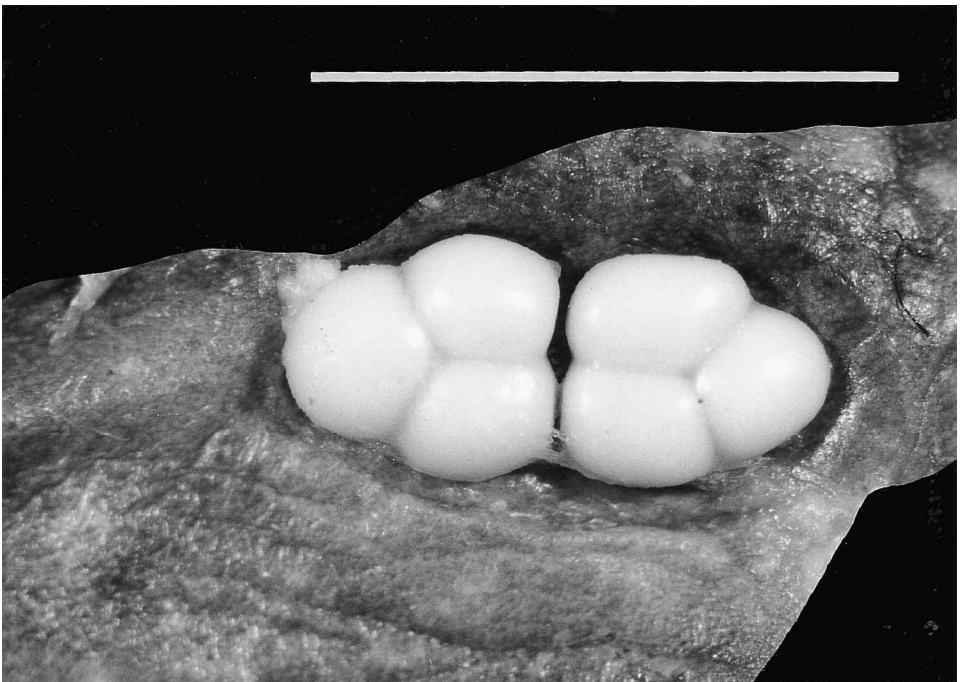


FIG. 15. Femoral gland of *Mantidactylus cf. malagasius*, ZFMK 59929 (adult male), internal view. Scale: 5 mm.

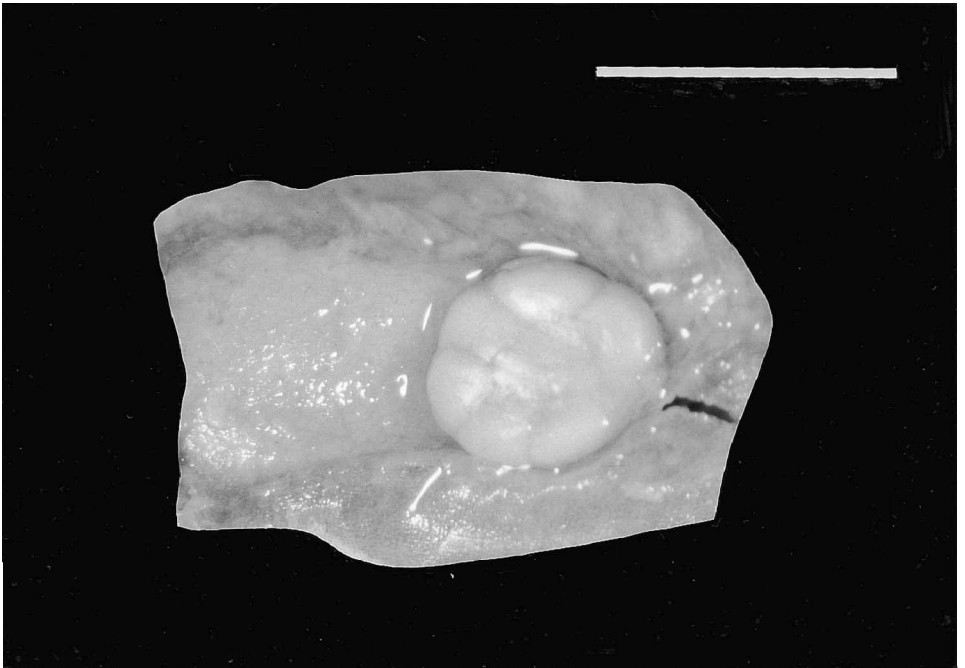


FIG. 16. Femoral gland (type 3) of *Mantidactylus ulcerosus*, MNHN 1975.632 (adult male), internal view. Scale: 5 mm. The 'B' structure is recognizable on the left, the enlarged granule group ('A' structure) on the right.

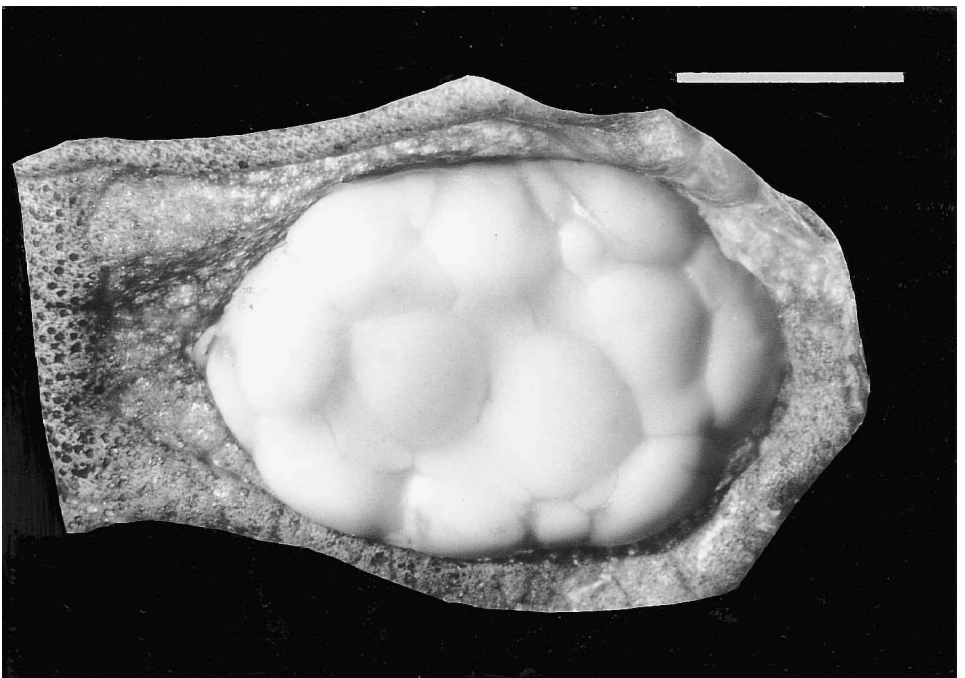


FIG. 17. Femoral gland (type 4) of *Mantidactylus grandidieri*, MRSN A1971.1 (adult male), internal view. Scale: 5 mm.

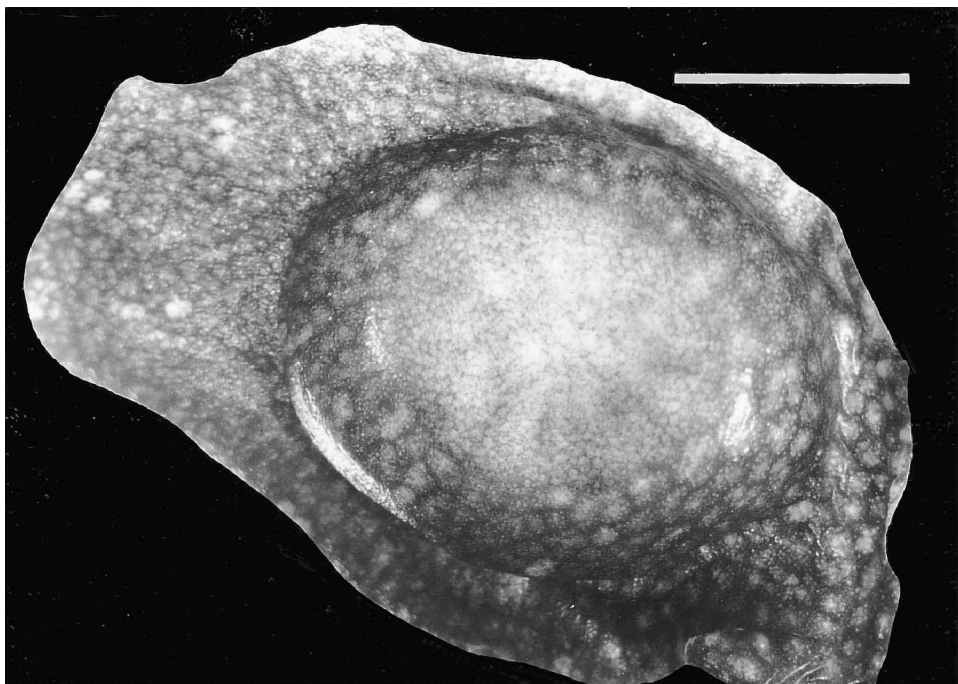


FIG. 18. Femoral gland (type 4) of *Mantidactylus grandidieri*, MRSN A1971.1 (adult male), external view. Scale: 5 mm.

Type 3 (found in the subgenera *Brygoomantis*, *Ochthomantis*, *Hylobatrachus* and *Chonomantis*). Consists of two different elements: Structure 'A' is a distal, very prominent and well defined rounded structure with an external central depression. It consists of a limited number (7–21) of enlarged granules (maximum diameter mostly > 1 mm) which are often arranged concentrically around one central granule. Structure 'B' is a patch with a variable number of smaller granules proximally towards the anus. In *M. brevipalmatus* (subgenus *Chonomantis*), the number of smaller granules in B was largely reduced. The same was found in two additionally studied *Chonomantis* (*M. albofrenatus*, ZFMK 59918; *M. aerumnalis*, ZFMK 62248).

Type 4. Like type 3, but no traces of B structure. Found in the subgenus *Mantidactylus*.

All examined species could be clearly assigned to one of these gland types, except for *M. rivicola* and species of the subgenus *Laurentomantis*, which had a reduced number of large granules (arranged in two groups of three to four granules on each thigh in the examined *M. cf. malagasius*; size of each group 2.2×2.2 mm). Their glands externally showed indistinct central depressions, possibly representing a trend from a gland of type 2 towards glands of type 3 or 4. Further studies are necessary to clarify the homology of the glands of these species with one of the major gland types as defined above.

Females of *Mantidactylus* generally had no large femoral glands and the female structures (if present) were always less developed than in conspecific males. Female gland rudiments, as far as known, only occur in species with gland types 3 and 4 as described above and the rudiments are generally miniature copies of the A structure. We observed such rudiments in the subgenera *Brygoomantis* (*M. ulcerosus*,

M. betsileanus, *M. biporus*, *M. ambohitombi*, *M. alutus*, *M. curtus*), *Ochthomantis* (*M. femoralis*) and *Mantidactylus* (*M. grandidieri*). In *M. biporus* (subgenus *Brygoomantis*) the female glands consist of rudiments both of the A and the B structure, which are not in contact with each other and thus give the impression of two porous structures ('*biporus*'). In one female of *M. tornieri*, ZMA 7110 (708), no gland rudiments could reliably be seen, although possibly one or two very small gland granules were present.

Discussion

The presented subdivision of femoral gland types is entirely based on macroscopically recognizable internal structures and partly different from that of Blommers-Schlösser (1979) which was based on external views. Forthcoming histological studies may reveal more detailed structural patterns and may also allow first statements on the secreting physiology of the glands as well as on their possible functions. Species of *Mantidactylus*, as far as known, do not display amplexus but a specialized mating behaviour in which the ventral thigh of the male comes into direct contact with the back of the female (Blommers-Schlösser, 1975). It is therefore likely that the glands are related to mating behaviour.

In glands of type 2 sometimes a small black central spot is visible in each granule, indicating that each granule may represent a single secreting unit. In the gland structures with central external depression, on the contrary, it is probable that all single granules secrete via elongated secretory channels into this depression, as indicated by a macroscopic inspection of the very large gland of *Mantidactylus grandidieri*.

Phylogenetically, it can be assumed that the glands of types 3 and 4, with their probable specialized secreting mode and gland rudiments present in females, represent a derived state and that the subgenera sharing these types are a monophyletic group. In this scheme, glands of type 4 evolved by reduction of the smaller granules from type 3 glands. On the other hand, since no outgroup data exist (the most suited outgroups, species of the ranid subfamily Rhacophorinae do not have femoral glands at all; see Blommers-Schlösser, 1993), it is difficult to decide whether type 1 (more likely) or type 2 represents the ancestral state.

Data given in the present paper support the transfer of *Mantidactylus peraccae* from the subgenus *Guibemantis* to *Spinomantis* as suggested by Glaw and Vences (1994) and confirmed by Andreone *et al.* (1998). The prominent femoral glands in male *M. peraccae* (type 2) are distinctly different from the externally indistinct type 1 glands typical for *Guibemantis*. On the other hand, the inclusion of *Mantidactylus elegans* in *Guibemantis* needs further comment. Available specimens of *M. elegans* lack femoral glands, but these may be present in adult males which possibly are not yet known. Its partly terrestrial, rock-dwelling habits indicate that it may occupy an isolated position within *Mantidactylus* rather than being closely related to species classified in the subgenus *Guibemantis*.

Mantidactylus depressiceps, *M. kathrinae* and *M. tornieri* share a similar habitus and femoral gland morphology, large relative hand length, separated lateral metatarsalia, an arboreal egg deposition site above stagnant water bodies, a white vocal sac in males and a similar call structure (a single note type which is composed of distinct pulses). These similarities indicate close relationships and the common call structure can be considered as a potential synapomorphy of the three species. Within this group, the white clutches (eggs and jelly) of *M. depressiceps* and *M. kathrinae*

(not known in any other *Mantidactylus*) are an obvious synapomorphy of these two species.

The generalized tadpole morphology of *M. liber* has similarities to *M. depressiceps* and *M. tornieri* (Glaw and Vences, 1992b). The femoral gland morphology of *M. liber*, described for the first time herein, is basically similar to *M. depressiceps*, *M. kathrinae* and *M. tornieri*, confirming its relationships to these species. However, *M. liber* differs from the three species by smaller size, connected lateral metatarsalia and a different call structure. Summarizing, the available data suggest the following phylogenetic relationships between the *Guibemantis* species: (((*M. depressiceps*–*M. kathrinae*) *M. tornieri*) *M. liber*).

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