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A new species of *Mantidactylus* from northeastern Madagascar with resurrection of *Mantidactylus blanci* (Guibé, 1974)

(Amphibia, Anura, Ranidae)

Frank Glaw & Miguel Vences

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Mantidactylus schilfi, spec. nov. is described from the Marojezy massif in north-eastern Madagascar. Males of the new frog species are characterized by a distinct colouration of the head sides (a white band along the upper lip which is bordered by a black band), very long hindlegs, and a small snout-vent length (males 27–29 mm). In addition, *M. schilfi* differs from all similar *Mantidactylus* species by advertisement calls. The new species is tentatively included in the subgenus *Gephyromantis*. *Gephyromantis blanci* Guibé, 1974 is resurrected (as *Mantidactylus blanci*) from the synonymy of *Mantidactylus decaryi* (Angel, 1930). Both species are redefined and advertisement calls of *M. decaryi* are described.

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Introduction

Madagascar harbours an enormous diversity of amphibian species of which a large number still remains to be described. 182 valid species were scientifically named until the end of the 20th century, but a total of at least 224–250 species have already been discovered and identified (Glaw & Vences in press). The most speciose amphibian genus in Madagascar is *Mantidactylus* (Ranidae: Mantellinae), which is classified in 12 subgenera (Glaw & Vences 1994). Phylogenetic relationships between these subgenera are largely unknown. In the present paper we describe a new species of *Mantidactylus* from northeastern Madagascar and resurrect another one, which bears similarities to the new species in a number of characters.

Material and methods

Vocalizations were recorded using portable tape recorders with an external microphone (Vivanco EM 238) and were analyzed with the MEDAV sound analyzing system Spekro 3.2. Sonagrams were edited with high frequency resolution (FFT 512). Morphological measurements were taken by the same person (FG) with a calliper to the nearest 0.1 millimeter. For definition of external and internal views of femoral glands, see Glaw et al. (in press). Webbing formula is given according to Blommers-Schlösser (1979). Institutional abbreviations are as follows: MNHN (Muséum national d’Histoire naturelle, Paris); UADBA (University of Antananarivo, Departement de Biologie Animale); ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn); ZSM (Zoologische Staatssammlung, München). SVL is used to abbreviate snout-vent length.



Fig. 1a. Holotype of *Mantidactylus schilfi*, spec. nov. (ZFMK 59885) from the Marojezy massif in dorsolateral view.



Fig. 1b. Holotype of *Mantidactylus schilfi*, spec. nov. Drawing by R. Kühbandner (Photo: M. Müller).



Fig. 2. Holotype of *Mantidactylus schilfi*, spec. nov. in ventral view.



Fig. 3. Paratype of *Mantidactylus schilfi*, spec. nov. (ZSM 587/1999) in dorsolateral view.

Results and Discussion

Mantidactylus schilfi, spec. nov.

Figs 1-5

Types. Holotype: ZFMK 59885, adult male, collected in the “Réserve Naturelle Intégrale Marojezy”, Camp 4 (ca. 1250 m above sea level), northeastern Madagascar, on 28 February 1995 by F. Glaw & O. Ramilison. – Paratypes: 2 males: ZSM 587/1999 (originally ZFMK 59886) and UADBA (number unknown), both with same locality, date and collectors as holotype; 1 female: MNHN 1973.931 (with very small oocytes as ascertained by dissection) from Marojezy, 1300 m above sea level, collected by C. P. Blanc on 2 July 1972.

Diagnosis. *M. schilfi* is characterized as a member of the genus *Mantidactylus* by the lack of nuptial pads in males and by its general similarities to other species of the genus. Males differ from all other *Mantidactylus* by a combination of the following characters: (1) Colouration of the head sides (a distinct white band along the upper lip which is bordered by a black band from the snout tip to the insertion of hindlimbs, Fig 1); (2) very long hindlegs (when limbs are adpressed to the body, tibiotarsal articulation reaches far beyond the tip of snout); (3) small snout-vent length (males 27–29 mm); (4) virtually not recognizable femoral glands in calling males; (5) largely, but not completely connected lateral metatarsalia; (6) advertisement calls (see below). It differs from *M. granulatus* (which can have very similarly coloured head sides) by (1) largely connected metatarsalia, (2) less webbing between toes, (3) smaller SVL (males up to 29 mm in *M. schilfi* versus up to 42 mm in *M. granulatus*), (4) lack of black vocal sac folds along the lower jaw in males, (5) advertisement calls, and (6) by the calling habitat (along brooks in *M. granulatus* versus independent from water bodies in *M. schilfi*).

Description

Holotype (Figs 1-2). SVL 29.0 mm. Body slender; head longer than wide, slightly wider than body; snout pointed in dorsal and lateral views; nostrils directed laterally, slightly protuberant, nearer to snout tip than to eye; canthus rostralis distinct, slightly concave; loreal region weakly concave; tympanum distinct, rounded, horizontal tympanum diameter (1.9 mm) is 50 % of eye diameter (3.8 mm); supratympanic fold recognizable (appears distinct by the strong colour border), rather straight; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct, positioned posterolateral to choanae; choanae rounded. Arms slender; subarticular tubercles single; outer metacarpal tubercle not recognizable, inner metacarpal tubercle indistinct; fingers without webbing; relative length of fingers: $1 < 2 < 4 < 3$; finger disks distinctly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaches far beyond snout tip; lateral metatarsalia largely, but not completely connected; inner metatarsal tubercle small but distinct; outer metatarsal tubercle rudimentary and indistinct; webbing formula between toes: 1(1), 2i(1.5), 2e(1), 3i(2.25), 3e(1.5), 4i(3), 4e(2.5), 5(1); relative length of toes: $1 < 2 < 3 < 5 < 4$. Skin on the upper surface smooth, back with rather indistinct dorsolateral folds; ventral side largely smooth, slightly granular on the venter. No distinct tubercles in the anal region. Femoral glands (in life and in preservative) very poorly delimited and very indistinct from both external and internal view (not referable to the gland types defined in Glaw et al. in press). After more than four years in alcohol, dorsum grey-brown, more beige posteriorly. A brown band between eyes, bordering a more or less triangular beige patch which covers the head surface. Arms light brown without distinct dark crossbands. Hindlimbs light brown with indistinct dark crossbands. Head colouration very characteristic: a highly distinct white band along the upper lip from snout tip to the insertion of arms, sharply bordered by a black band from snout tip to the insertion of arms which is interrupted by the eye. Venter beige to yellowish, with small dark spots on the venter and a more reticulated pattern on the shanks. Brown mottling on the throat, with a thin blackish band along the lower jaw. Colouration in life (Figs 1-2) generally similar to that in preservative. However, the dorsal surface is more colourful in life, being more orange-brown. The ventral surface is more yellowish than in alcohol.

Paratypes. ZSM 587/1999 is morphologically very similar to the holotype. SVL 27.1 mm. Tympanum diameter (2.0 mm) is 51 % of eye diameter (3.9 mm). The dorsolateral folds are more distinct than in the holotype. Femoral glands very poorly delimited and very indistinct from both external and internal view. Webbing formula is identical to the holotype. The paratype from UADBA was not available for morphological comparison. The life colouration of the two male paratypes is shown in Figs 3-5. Morphology and colouration of MNHN 1973.931 is largely similar to ZFMK 59885 and ZSM

587/1999, except for its distinctly larger size (SVL 34.5 mm) and the fact that the head is as wide as the body (which may be due to a different mode of fixation). The skin in the femoral gland region of the shanks is similar to the male paratypes. Vomerine teeth present; tympanum diameter (2.3 mm) is 58 % of eye diameter (4.0 mm); dorsolateral folds distinct; tibiotarsal articulation reaches much beyond snout tip, webbing formula of the foot: 1(1), 2i(1.75), 2e(1), 3i(2.5), 3e(1.75), 4i(3), 4e(2.5), 5(1); lateral metatarsalia partially connected. Dorsal colouration light brown with black head sides and distinct white lips. Two very small black dots between the eyes. Ventral colouration whitish with vermiculated markings. The stomach contained one beetle of about 3 mm length. The dorsal colouration of MNHN 1973.931 closely resembles that of *Mantidactylus granulatus* and it was considered as such in Vences et al. (1999). However, a careful re-examination of this specimen revealed that it has much less webbing between the toes and partially connected lateral metatarsalia and therefore can not be a subadult *M. granulatus*. It is very probably a female of *M. schilfi* because of its general similarities in colouration and external morphology with the other type specimens and the fact that it was collected in the same area at virtually the same altitude as the other *schilfi* types. It must be emphasized, however, that the available *schilfi* males are distinctly smaller than MNHN 1973.931 (79-84 % of the female SVL) and that such distinct sexual size dimorphism is unusual in both the *M. granulatus* group and the *M. boulengeri* group (see "Relationships" below).

Distribution. *Mantidactylus schilfi* is only known from 1250-1300 m altitude of the Marojezy Reserve in northeastern Madagascar. Numerous amphibian and reptile species appear to be endemic to this massif, and the same may be true for the new species. Except for MNHN 1973.931, no additional voucher specimens of *M. schilfi* were found in the MNHN collection which harbours a large collection from the Marojezy mountains. This may indicate that *M. schilfi* is a rare species. However, it appears more likely that it is simply difficult to discover by opportunistic searching, since all recently collected specimens were found only by locating calling males.

Habitat. Calling males were sitting at mid-day in bushes ca. 1-1.5 m above the bottom. No water body was recognized in the vicinity of the calling males. Therefore, it appears likely that *M. schilfi* has a reproductive mode which is independent from water bodies. It probably has direct development (without free swimming tadpoles) as is known for several species of the subgenus *Gephyromantis* (Blommers-Schlösser 1979, Glaw & Vences 1994).

Advertisement calls (Fig. 10. Vocalizations were recorded at the type locality in the Marojezy Reserve on 28 February 1995, 11:30 h, at 22.5 °C air temperature: Notes are unharmonious, distinctly pulsed and (generally) emitted in regular series. One completely analyzed note series consisted of 21 notes and had a duration of about 40 seconds. Temporal parameters (given as range, followed by mean \pm standard deviation and number of measurements) are as follows: Note duration is 326-428 ms (404 ± 27 ms, $n=22$), interval duration 974-3607 ms (1625 ± 743 ms, $n=21$). Intervals between the first notes of a note series are the longest and become successively shorter until they reach a constant value (about 1000-1500 ms). Notes consist of 48-61 pulses (56 ± 4 , $n=8$), the pulse rate is 136-155/s (142 ± 7 /s, $n=7$). Frequency range is 2400-3900 Hz (dominant frequency 2800-3300 Hz).

Etymology. *Mantidactylus schilfi*, spec. nov. is dedicated from Mrs. Margot Schilf (Augsburg) to her son Prof. Dr. Wolfgang Schilf on the occasion of his 50th birthday.

Relationships. The relationships of *M. schilfi* are of special interest, because it shows a mosaic of characters which are typical either for the *Mantidactylus granulatus* group of the subgenus *Phylacomantis* or for the *Mantidactylus boulengeri* group of the subgenus *Gephyromantis*. Other characters are intermediate between both groups. *M. schilfi* therefore seems to represent a connecting link between both species groups that may indicate close phylogenetic relationships between them.

- The contrasting colouration of the head sides with a distinct white band along the upper lip and a black band from the snout tip to the insertion of arms is very typical for *Mantidactylus* (*Phylacomantis*) *granulatus*. However, most species of the *Mantidactylus boulengeri* group (subgenus *Gephyromantis*) can also have a blackish temporal region and a light band along the upper lip, although this band is less distinct and often disrupted by small dark spots.
- The lateral metatarsalia are largely or completely connected in all species of the *Mantidactylus boulengeri* group and partially or completely separated in the species of *Phylacomantis*.



Fig. 4. Paratype of *Mantidactylus schilfi*, spec. nov. (ZSM 587/1999) in ventral view.



Fig. 5. Paratype of *Mantidactylus schilfi*, spec. nov. (UADBA) in dorsolateral view.



Fig. 6. *Mantidactylus blanci* (Guibé) from the Andringitra massif (male in dorsolateral view).



Fig. 7. *Mantidactylus blanci* (Guibé) from the Andringitra massif (male in ventral view).

- Accordingly, webbing on the fourth toe is generally absent in the *Mantidactylus boulengeri* group, but present in all *Phylacomantis* species.
- The range of SVL is 20-33 mm in the *Mantidactylus boulengeri* group and 31-50 mm in the subgenus *Phylacomantis*. The size of *M. schilfi* (27-34.5 mm) is therefore intermediate between the *M. boulengeri* group and the subgenus *Phylacomantis*.
- Black spots between the eyes occur in species of both the *M. boulengeri* group (*M. boulengeri*) and the subgenus *Phylacomantis* (*M. redimitus*, *M. cornutus*).
- Indistinct femoral glands of males (from external view) occur in species of the *M. boulengeri* group (*M. eiselti*, *M. thelenae*) and the subgenus *Phylacomantis* (*M. granulatus*).
- The distinct sexual size dimorphism of *M. schilfi* is neither typical for the *Mantidactylus boulengeri* group nor for *Phylacomantis* species.
- Diurnal calling activity far away from water bodies is typical for the species of the *M. boulengeri* group, whereas calling activity is mainly nocturnal in *Phylacomantis* and – if diurnal – concentrated along brooks. The calling activity of *M. schilfi* is therefore in agreement with the *M. boulengeri* group.
- A limited series of regularly repeated notes is a typical call structure of numerous *Mantidactylus* species with diurnal calling activity (including the species of the *M. boulengeri* group) whereas *Phylacomantis* species tend to produce long series of notes.

Summarizing, the available data do not allow an unambiguous attribution of *Mantidactylus schilfi* either to *Gephyromantis* or *Phylacomantis*. The main argument to erect the subgenus *Phylacomantis* was the observation of free-swimming and feeding tadpoles in *Mantidactylus corvus* and *M. pseudoasper*, whereas *Gephyromantis* was thought to have direct development (Glaw & Vences 1994). Unfortunately, nothing is known about the reproduction of *M. schilfi*. However, the calling activity far away from water bodies may indicate that direct development is much more likely in this species than reproduction with free swimming larvae. We therefore consider *Mantidactylus schilfi* tentatively as a member of the *Mantidactylus boulengeri* group (sensu Vences et al. 1997) in the subgenus *Gephyromantis*.

Available names. All valid *Mantidactylus* species can be clearly distinguished from *M. schilfi* by the character combination given in the diagnosis. However, synonyms of valid taxa are to be excluded as earlier available names. Among others, *M. schilfi* is characterized by a small SVL, by very long hindlegs, and by largely, but not completely connected lateral metatarsalia. Two available names which may fit into the description of *M. schilfi* are *M. decaryi* and *M. blanci*, the latter being considered as a junior synonym of the former. However, as will be demonstrated below, both taxa are referable to valid species which are clearly different from *M. schilfi*.

Identity of *Mantidactylus blanci* (Guibé, 1974) and *M. decaryi* (Angel, 1930)

Mantidactylus blanci was originally described as *Gephyromantis blanci* from the Andringitra mountains without providing any explicit characters to distinguish it from other *Mantidactylus* species. In his monograph on Madagascan frogs, Guibé (1978) considered the species again, largely repeating the original description, but provided an identification key. In 1991 Blommers-Schlösser & Blanc designated a lectotype of *Gephyromantis decaryi* and synonymized *G. blanci* with *Mantidactylus decaryi* without any discussion, although these authors obviously studied the type material of both taxa.

In his identification key Guibé (1978: 46) characterized *M. blanci* by: "(1) Une barre sombre entre les yeux. (2) Lèvre supérieure nettement marquée de blanc. (3) Un fin repli dorso-latéral. (4) Face ventrale blanche avec un semi plus ou moins dense de petites taches sombres." *M. decaryi* was characterized by: "(1) Pas de barre sombre entre les yeux. (2) Lèvre supérieure sans marque blanche. (3) Pas trace de repli dorso-latéral. (4) Téguments irrégulièrement granuleux, surtout sur l'abdomen. (5) Canthus net. (6) Dents vomériennes en deux groupes distincts. (7) Deux barres sombres sous l'oeil. (8) Dessous du corps clair, légèrement ponctué de sombre." Characters 1-3 to identify *M. blanci* agree with our material from near Ambalamarina in the Andringitra mountains (ZFMK 57426, 57427, 59829, 59830, see also Figs 6-7) whereas character 4 is less well recognizable. Characters 1, 2, 4, 5, 7 and 8 to identify *M. decaryi* agree well with our material of an unidentified and recently collected species from the Ranomafana region (ZFMK 62294 and 62279, see also Figs 8-9), although character 1 approaches the state of *M. blanci* in ZFMK 62294. Character 3 is less clear since partial dorso-lateral folds are recognizable in both specimens. Character 6 can not be confirmed at all since vomerine teeth are virtually absent in ZFMK

62294 and 62279. Summarizing, according to the key of Guibé (1978), there remains little doubt that our material from the Ranomafana region is referable to *M. decaryi*, whereas the specimens from Andringitra belong to the taxon *M. blanci*.

Mantidactylus blanci (Guibé, 1974), bona species

Figs 6-7

Identity. A recent re-examination of the *M. blanci* type specimens confirmed that this taxon is referable to specimens collected in the Andringitra mountains which were described and figured under the name *M. decaryi* (Glaw & Vences 1994). On the other hand, the type material of *M. decaryi* closely resembles the species from the Ranomafana region, which is clearly different from *M. blanci* in morphology, colouration and advertisement calls. *Mantidactylus blanci* must therefore be considered as a valid species.

Diagnosis. *M. blanci* is characterized as a species of the subgenus *Gephyromantis* by completely connected lateral metatarsalia, virtually no webbing between toes, rather smooth skin, small snout-vent length, calling habitat (independent from water bodies), and its similarity with the other species of the *Mantidactylus boulengeri* group. It differs from the other species of this group as follows: From *M. boulengeri*, *M. silvanus*, *M. eiselti*, and *M. thelenae* by longer hindlegs (tibiotarsal-articulation reaches beyond snout tip); from *M. decaryi*, *M. boulengeri*, *M. eiselti*, *M. thelenae*, *M. klemmeri*, *M. webbi* and *M. schilfi* by advertisement calls and colouration; and from *M. rivicola* by colouration and terrestrial habits. Males of *M. blanci* differ from those of *M. eiselti*, *M. thelenae*, and *M. schilfi* by the presence of distinct and well delimited femoral glands which are easily visible from external view. *M. blanci* differs from *M. decaryi* by the characters mentioned in the key of Guibé (1978) as discussed above, and in addition by smaller snout-vent length (males 21.9-22.8 mm versus 26.3-26.5 mm in the ZFMK material), shorter hindlimbs (tibiotarsal articulation reaches slightly beyond snout tip versus far beyond snout tip), life colouration (see Figs. 6-9) and by advertisement calls (see Figs. 11-12). The only available female of *M. blanci* (ZFMK 57427) is similar to the three males, but slightly larger (SVL 24.5 mm) and without blackish vocal sac folds.

Distribution. *M. blanci* is known from two localities in the Andringitra mountains, the forest of Ambalamarovandana at 1500 m altitude (Guibé 1974) and the rain forest around Ambalamarina at similar altitude (Glaw & Vences 1994). In addition, a specimen from the Ranomafana area (photographed by J. Köhler in 1995) should be considered as *M. blanci* as well, since it has distinct femoral glands and recognizable blackish vocal sac folds. The calls here referred to *M. blanci* were recorded at Vohiparara (ca. 1000 m altitude). The four localities (1) Iorantjatsy, (2) Andrianony, (3) Fivahona, and (4) Chaines Anosyennes, listed in Blommers-Schlösser & Blanc (1991), may refer either to *M. decaryi* or to *M. blanci*.

Habitat. Calling males were found during the day on the ground in primary rainforest of the Andringitra massif (in January) and heard in secondary fern scrub at Vohiparara (in February). In both cases, calling males were not found around water bodies.

Advertisement calls (Fig 11). Vocalizations from Andringitra have been shortly described by Glaw & Vences (1994) under the name *M. decaryi*. New recordings from Vohiparara (Ranomafana region), recorded 28 February 1996 at 18:15 h were similar to those from Andringitra, but unfortunately the calling specimens could not be located in the dense fern scrub. Since *M. blanci* was already recorded from the Ranomafana region by photographs (see above) it is nevertheless likely that the following description refers to the calls of *M. blanci*: Vocalizations were emitted in series of 11-14 (12.7 ± 1.0 , $n=7$) melodious notes. Interval duration between two note series was up to several minutes. The duration of note series was 1034-1325 ms (1215 ± 99.9 , $n=7$), the note repetition rate 9.8-11.1/s. Note duration was 21-28 ms (24 ± 2 ms, $n=13$), duration of intervals between two notes 58-103 ms (73 ± 11 ms, $n=12$). The interval between the two last notes of a series was longer than between the other notes. Fundamental frequency was between 2000-2300 Hz and dominant frequency between 4150-4700 Hz. The note series from Vohiparara are similar to *M. boulengeri* (especially in the number of notes per series) but the note repetition rate is higher in *M. blanci*. The note series from Vohiparara differ from those of Andringitra by a higher number of notes.



Fig. 8. *Mantidactylus decaryi* (Angel) from Ranomafana (male in dorsolateral view).



Fig. 9. *Mantidactylus decaryi* (Angel) from Ranomafana (male in ventral view).

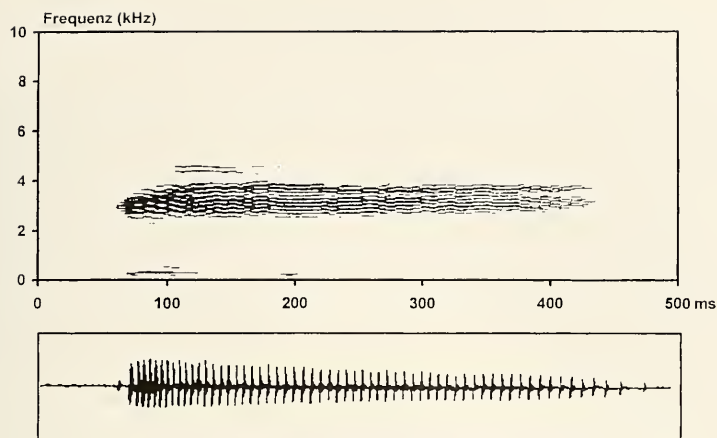


Fig. 10. Sonogram and oscillogram of one note of *Mantidactylus schilfi*, spec. nov. from the type locality.

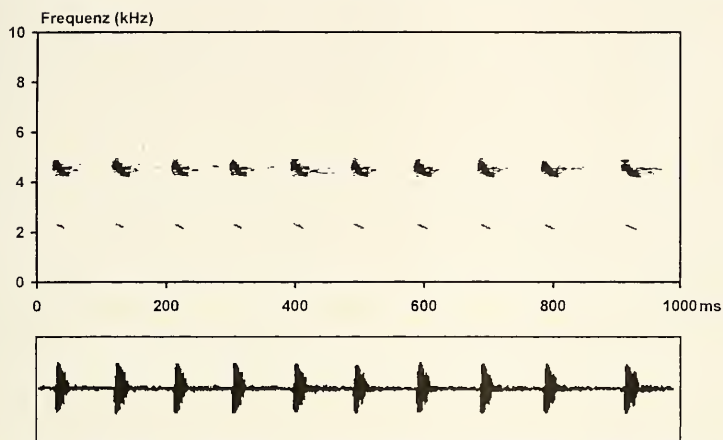


Fig. 11. Sonogram and oscillogram of a section of a note series of *Mantidactylus blanci* (Guibé) from Vohiparara.

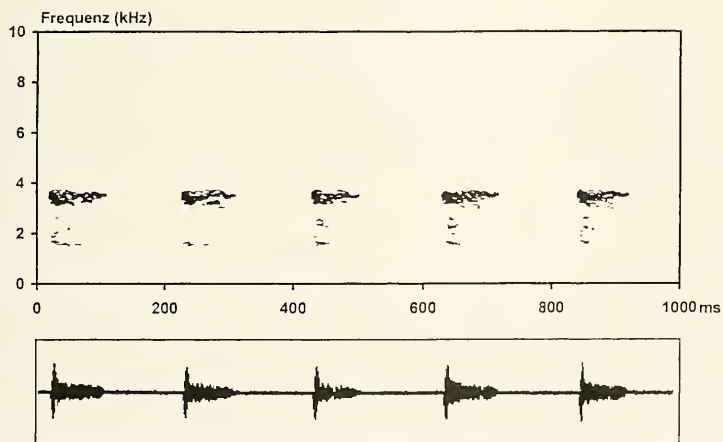


Fig. 12. Sonogram and oscillogram of a section of a note series of *Mantidactylus decaryi* (Angel) from Ranomafana.

Mantidactylus decaryi (Angel, 1930)

Figs 8-9

Identity. The type material of *M. decaryi* is in a bad state of conservation. In the lectotype MNHN 1930.435 (designated by Blommers-Schlösser & Blanc 1991) the left hindleg is completely separated from the body and the right hindleg is only loosely linked with the body (foot and tarsus are completely lacking from the right limb). The SVL is 22.5 mm. Although the original colouration is largely faded and the condition of the lectotype is very bad, several characters agree with that of the unidentified species from the Ranomafana region. (1) There is a slightly converging, dark-bordered ridge on each side of the neck, that is followed dorsolaterally by a further ridge. (2) A brown spot is present below the canthus rostralis between eye and nostril. (3) Two further brown spots are present between eye and nostril. About four brown irregularly dispersed spots on a light background are recognizable on each side of the lower jaw. A brown bar is present between the eyes. (4) In contrast to the original description (Angel 1930) vomerine teeth are rather indistinct. These characters of the lectotype are nearly identical in our specimens from the Ranomafana region, except that the colour of the spots in life is black instead of brown. Only the black tympanic region of the living specimens is not (no longer?) recognizable in the lectotype. Paralectotype MNHN 1930.438 is a juvenile of about 14.5 mm SVL. Paralectotype MNHN 1930.437 is an adult male of 23.4 mm SVL with very long limbs (exact measurements were not taken because of the poor conservational state), with distinct elongated femoral glands (5.0-5.5 mm × 1.5 mm), and with distinct skin folds along the lower jaw (vocal sac). In contrast to the lectotype brown spots on the head or folds on the back are less or not recognizable. Paralectotype MNHN 1930.436 was not received from the MNHN. It may represent the specimen that was exchanged with the Museum of Comparative Zoology in 1932 and probably corresponds to MCZ 17459 (Barbour & Loveridge 1946).

Angel (1930) mentioned four specimens collected 500-1100 m above sea level. Our records are virtually in the same altitudinal range and from the same region (southern half of eastern Madagascar). Regarding the amount of morphological similarity between the type material of *M. decaryi* and our specimens from the Ranomafana region we conclude that both are conspecific.

Distribution. Reliable records of *M. decaryi* sensu stricto are Midongy du Sud, 500-700 m altitude (lectotype MNHN 1930.435) and Pic d'Ivohibe, 1100 m altitude (MNHN 1930.436 to 438, paralectotypes). Personal records are from Ranomafana (21°14'S, 47°26'E, 500-600 m alt., ZFMK 62294), from above Vohiparara (ca. 1050 m alt., ZFMK 62279), and from several places along the street between both localities (no voucher specimens). The four localities (1) Iorantjatsy, (2) Andrianony, (3) Fivahona, and (4) Chaines Anosyennes, listed in Blommers-Schlösser & Blanc (1991), may refer either to *M. decaryi* or to *M. blanci*. Near Vohiparara *M. decaryi* apparently occurs in sympatry with *M. blanci*.

Habitat. Calling males were found in February and March during the day. They were sitting on or near the ground in primary rain forest and in secondary vegetation, far away from water bodies.

Advertisement calls (Fig 12). Calls were recorded on 26 February 1996 at Ranomafana during the day. The frogs emitted rather long series of notes. The duration of a note series with 44 notes was 9470 ms. Note duration was 65-120 ms (85 ± 14 ms, $n=44$), interval duration 114-178 ms (131 ± 13 ms, $n=43$). Both note duration and interval duration did tend to become shorter from the first to the last note of a series. Fundamental frequency was 1450-1650 Hz, dominant frequency 2950-3600 Hz. The intensity of each note had a peak at its beginning, decreasing toward its end.

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