

Systematic review and molecular phylogenetic relationships of the direct developing Malagasy anurans of the *Mantidactylus asper* group (Amphibia, Mantellidae)

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The taxonomy and distribution of Malagasy frogs of the *Mantidactylus asper* group (included in the subgenus *Gephyromantis*) is revised. The group is considered to include *Mantidactylus asper*, *M. spinifer*, *M. luteus*, *M. plicifer*, *M. sculpturatus* (which is resurrected from the synonymy of *M. luteus*) and a new species described herein. Lectotypes are designated for *Rana aspera* Boulenger, 1882 (*Mantidactylus asper*), *Mantidactylus ceratophrys* Ahl, 1929 (junior synonym of *M. asper*) and *Rana plicifera* Boulenger, 1882 (*Mantidactylus plicifer*). *M. asper* and *M. spinifer* are characterized, among other features, by a distinct black-brown contrasted ventral pattern, presence of an outer metatarsal tubercle, and a moderate amount of webbing. They are apparently allopatrically distributed, *M. spinifer* occurring in south-eastern Madagascar and *M. asper* inhabiting eastern and north-eastern rainforests. *M. luteus*, *M. plicifer* and *M. sculpturatus* have a largely uniform light venter, lack the outer metatarsal tubercle and have more extended webbing. A reliable distinction of these three species is only possible in adult males, and is based on differences in femoral gland size and advertisement calls. *M. luteus* is mainly distributed in lowlands along the Malagasy east coast, while *M. sculpturatus* appears to be restricted to mid-altitudes. *M. plicifer* has been found sympatrically with *M. sculpturatus* and *M. luteus*, and is known from the south-east. The new species described herein shares characters with *M. asper* and *M. spinifer* (presence of an outer metatarsal tubercle) and with *M. luteus*, *M. plicifer* and *M. sculpturatus* (uniform venter, extended webbing). It is only known from Montagne d'Ambre in far northern Madagascar.

A molecular phylogenetic analysis based on partial sequences of the mitochondrial 16S rRNA gene supported monophyly of the *M. granulatus* group and of the *M. pseudoasper* group in the subgenus *Phylacomantis*, and of a clade containing *M. luteus*, *M. plicifer* and *M. sculpturatus*. In contrast, the *M. asper* group and the subgenus *Gephyromantis* as a whole appeared to be paraphyletic. The obtained trees indicated a possible evolution of the direct-developing lineage from brook breeding ancestors, and a reversal from direct development in *M. granulatus*. Although these

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aspects received no relevant bootstrap support, they constitute hypotheses of great interest for general questions on amphibian evolution and should be tested with extended data sets.

INTRODUCTION

The Malagasy genus *Mantidactylus* currently contains more than 70 species which show a large diversity in morphology and reproductive biology. DUBOIS (1992) and GLAW & VENCES (1994) divided the genus into a total of 12 subgenera, reflecting this diversity. Major characteristics of all *Mantidactylus* include the absence of nuptial pads in males (and, as far as known, of a strong mating amplexus), and the deposition of eggs outside the water in all species studied so far (BLOMMERS-SCHLÖSSER, 1979). Most species additionally have specialized femoral glands on the ventral surface of thighs (GLAW et al., 2000), especially in males.

GLAW & VENCES (1994) distinguished three major clades within *Mantidactylus*. One group contains more or less arboreal species which mostly deposit their eggs on leaves above the water surface; their tadpoles are rather generalized (subgenera *Blommersia*, *Guibemantis*, *Pandanusicola*, *Spinomantis*). A second group consists of brook-edge-dwelling species, the larvae of which often show specialized mouthparts (subgenera *Brygomantis*, *Chonomantis*, *Hylobatrachus*, *Mantidactylus*, *Ochthomantis*). The third assemblage contains three subgenera (*Gephyromantis*, *Laurentomantis*, *Phylacomantis*): while *Phylacomantis* males usually call along brooks and at least some species have free-swimming larval stages, calling males of most *Laurentomantis* and *Gephyromantis* do not aggregate around water bodies, and direct development without free-swimming larval stages has been demonstrated in two species, *Mantidactylus asper* and *M. eiselti* (BLOMMERS-SCHLÖSSER, 1979; GLAW & VENCES, 1994). Due to this reproductive diversity, studies on these frogs have the potential to contribute to the understanding of the evolution of direct development and other specializations in anuran reproductive biology.

One basic pre-requisite for such studies, however, is a detailed basic knowledge on the species' taxonomy and distribution (GLAW & VENCES, 2000). Distributional data of Malagasy frogs are largely based on the monograph of BLOMMERS-SCHLÖSSER & BLANC (1991) who, however, mostly did not recognize sibling species and gave no voucher specimens for the localities plotted on their distribution maps. Apart from type specimens from other collections, their work was based almost exclusively on the collections housed at Amsterdam and Paris.

In the present paper, we review the *Mantidactylus asper* group, a phenetic species assemblage in the subgenus *Gephyromantis*, distinguished from other *Mantidactylus* by reproduction independent from water, mainly nocturnal calling behaviour, largely separated lateral metatarsalia, and black paired subgular vocal sacs in males. We re-examined the material available to BLOMMERS-SCHLÖSSER & BLANC (1991), and complemented this information by own field observations.

MATERIALS AND METHODS

ABBREVIATIONS AND MEASUREMENTS

Vocalizations were recorded using portable tape recorders with an external microphone (Vivanco EM 238) and were analyzed with the MEDAV sound analyzing system Spektro 3.2. The following morphological measurements were taken with a caliper 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, horizontal tympanum diameter; HAL, hand length; FORL, forelimb length; HIL, hindlimb length; FOL, foot length; FOTL, foot length including tarsus; IMTL and IMTH, length and height of inner metatarsal tubercle; TL1, length of first toe. Statistical analyses were carried out using SPSS for Windows, version 10. We performed Mann-Whitney *U* tests to test significance of intersexual differences in size and morphometric ratios (TD/SVL, relative tympanum diameter; IMTL/SVL and IMTH/SVL, relative size of inner metatarsal tubercle; FORL/SVL and HIL/SVL, relative length of fore- and hindlimbs), and of interspecific differences in selected morphological variables and ratios. Measurements are given as range, with mean \pm standard deviation in parentheses.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London (formerly British Museum of Natural History); MNHN, Muséum National d'Histoire Naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; MSNG, Museo Civico "G. Doria" di Storia Naturale, Genova; MTKD, Museum für Tierkunde, Dresden; TM, Transvaal Museum, Pretoria; UADBA, Université d'Antananarivo, Département de Biologie Animale; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZMA, Zoologisch Museum, Amsterdam; ZMB, Museum für Naturkunde, Berlin; ZSM, Zoologische Staatssammlung, München. The catalogue numbers of voucher specimens housed in the ZMA are given as the jar number followed by the field number of R. Blommers-Schlösser, since they bear no individual ZMA tags.

TAXONOMY

To avoid confusion by introducing working definitions (operational taxonomic units) and assigning them to specific names in a second step, we decided to anticipate our taxonomic proposals and use consistent names throughout this paper. This mainly regards: (1) the recognition of the Montagne d'Ambre population previously considered as *Mantidactylus plicifer* by BLOMMERS-SCHLÖSSER & BLANC (1991) or as *M. cf. asper* by GLAW & VENCES (1994) as a new species which is described herein; (2) the re-definition of *Mantidactylus plicifer* as a

species of usually rather large body size and with large and distinct femoral glands from south-eastern Madagascar; (3) the recognition of mid-altitude eastern populations previously assigned to *M. luteus* by GLAW & VENCES (1994) as a distinct species *M. sculpturatus*. These decisions are largely corroborated by high genetic divergence levels between the species recognized, by the morphological differentiation of the new species from Montagne d'Ambre and by the morphological and bioacoustic differentiation and syntopic occurrence of *M. sculpturatus* and *M. plicifer* at Ranomafana. More detailed justifications are given in the respective *Identity* and *Diagnosis* sections below.

MORPHOLOGICAL TERMINOLOGY

Webbing formula is given according to BLÖMMERS-SCHLÖSSER (1979). Femoral gland morphology is described according to GLAW et al. (2000). Most *Gephyromantis* species are characterized by a number of dermal spines, tubercles and ridges. The arrangement and degree of expression of these structures is often important for species definitions and probably also bears relevance for the assessment of phylogenetic relationships among species and subgenera in the genus *Mantidactylus*. To refer unequivocally to these structures, we here define a number of terms (fig. 1):

(1) *Inter-ocular tubercles*. – On the upper surface of the head, between the eyes, a number of tubercles are present in many species. These are generally arranged symmetrically, either as one pair or as two pairs, and should not be mistaken with the unelevated black inter-ocular spots as present in *M. leucomaculatus* (*Phylacomantis*). In several *Phylacomantis* (*M. cornutus*, *M. redimitus*, *M. tandroka*, *M. tschenki*), one pair of rounded, black tubercles are generally present. On the contrary, in *M. asper*, *M. spinifer* and the new species described herein (*Gephyromantis*), the tubercles are generally not rounded but rather longitudinal and ridge-like; often, two pairs of such tubercles are present which sometimes appear to be a discontinuous anterior continuation of the inner dorsolateral ridges; and sometimes, in *M. spinifer*, these ridge-like tubercles are fused to form a symmetrical figure (fig. 1).

(2) *Inner dorsolateral ridges*. – As a constant state in all species of the *M. asper* group, two largely continuous ridges start above or up to 4 mm behind the eyes and run medially onto the anterior back. Here they either continue straight dorsolaterally onto the posterior fourth of the back, or curve slightly towards the flanks and fade.

(3) *Outer dorsolateral ridges*. – In all species of the *M. asper* group, a second pair of dorsolateral ridges runs laterally of the inner dorsolateral ridges. Often this second pair is not continuous and poorly defined.

(4) *Connecting dorsal ridge*. – In some *M. spinifer*, at the point of maximum convergence of the inner dorsolateral ridges on the anterior dorsum, these are connected by a short transversal ridge.

(5) *Supraocular spines*. – Above the eyes, distinct dermal spines are usually present in all species of the *M. asper* group (and in several *Phylacomantis*; e.g., *M. cornutus*, *M. redimitus*, *M. tschenki*), although they can be small and indistinct in the new species described herein. In contrast to the rather rigid dorsal ridges, these spines are flexible.

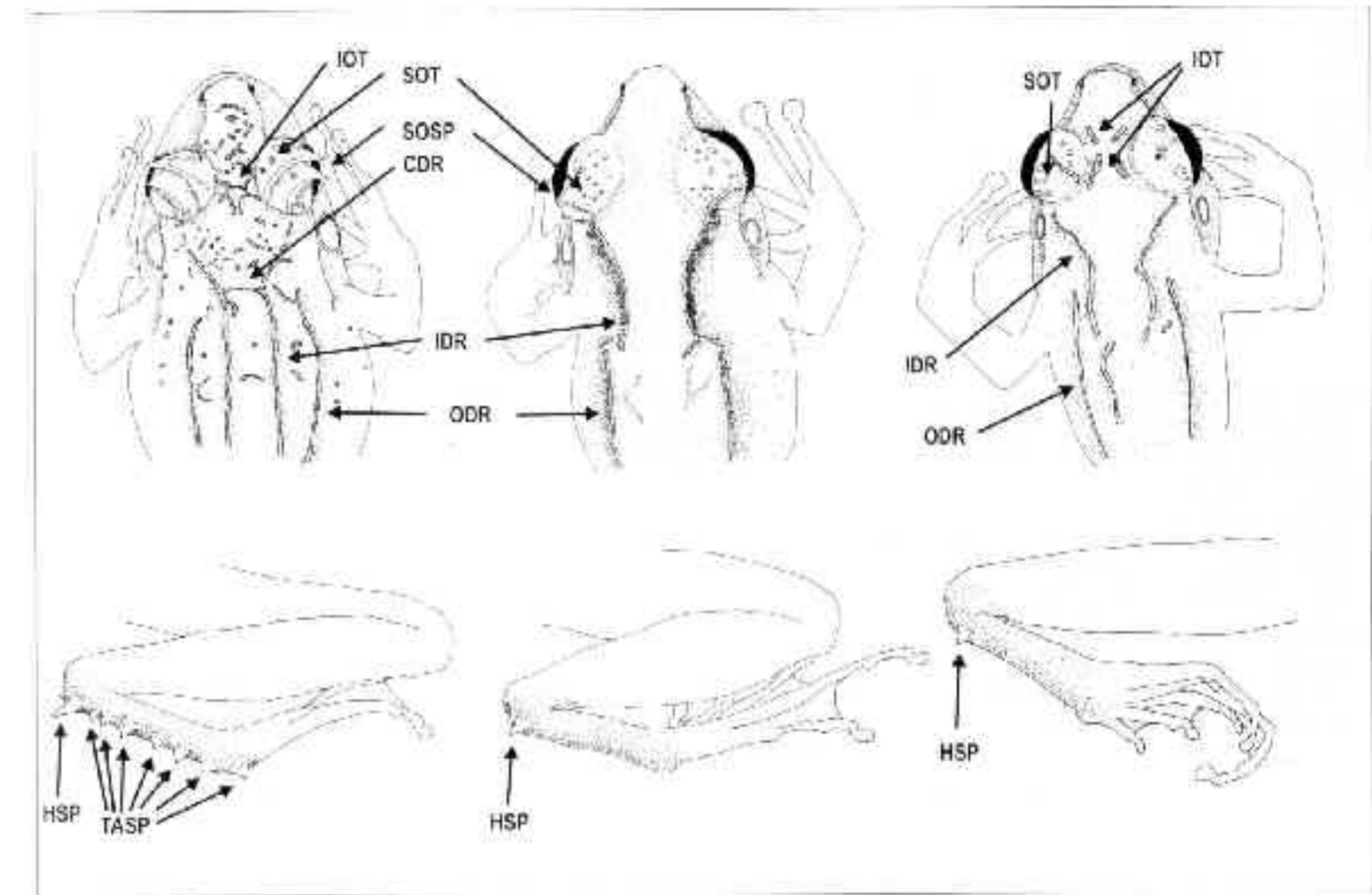


Fig. 1. Partial dorsal views (head and anterior body and hindlimb) of three representative species of the *Mantidactylus asper* group: *Mantidactylus spinifer* (left), female MNHN 1972.1444; *M. plicifer* (center), female MNHN 1972.1431; and *M. ambohitra* (right), female MNHN 1893.245. The arrows mark dermal structures which are described in the text: CDR, connecting dorsal ridge; HSP, heel spine; IDR, inner dorsolateral ridge; IOT, inter-ocular tubercles; ODR, outer dorsolateral ridge; SOSP, supraocular spines; SOT, supraocular tubercles; TASP, tarsal spines. Not to scale.

(6) *Supraocular tubercles*. – These are homologous to supraocular spines but less elevated and not pointed.

(7) *Heel spine*. – A long or short spine may be present on the heel. Similar to the supraocular spines, the heel spine is a dermal, flexible structure. Beside the *M. asper* group, it is also found in several *Phylacomantis* and in species of the genus *Boophis* (e.g., *B. madagascariensis*).

(8) *Tarsal spines*. – A number of smaller dermal spines are sometimes arranged at the posterior edge of tarsus. Species with tarsal spines always bear also a distinct heel spine.

(9) *Humeral protuberance*. – A well known synapomorphy of *Mantidactylus* species are the femoral glands on the ventral surface of the femur (GLAW et al., 2000). In several species of the *M. asper* group (*M. luteus*, *M. plicifer*, *M. spinifer*), we observed a prominent structure on the ventral side of the humerus, too (fig. 2). By dissection (internal view; GLAW et al., 2000), we noted that this prominence was not caused by enlargement of skeletal or muscular tissues but largely dermal, and sometimes contained a gland-like element at its most prominent part. Without further histological analyses we are unable to state whether this structure is actually a gland, and thus here refer to it as humeral protuberance. It is best visible in

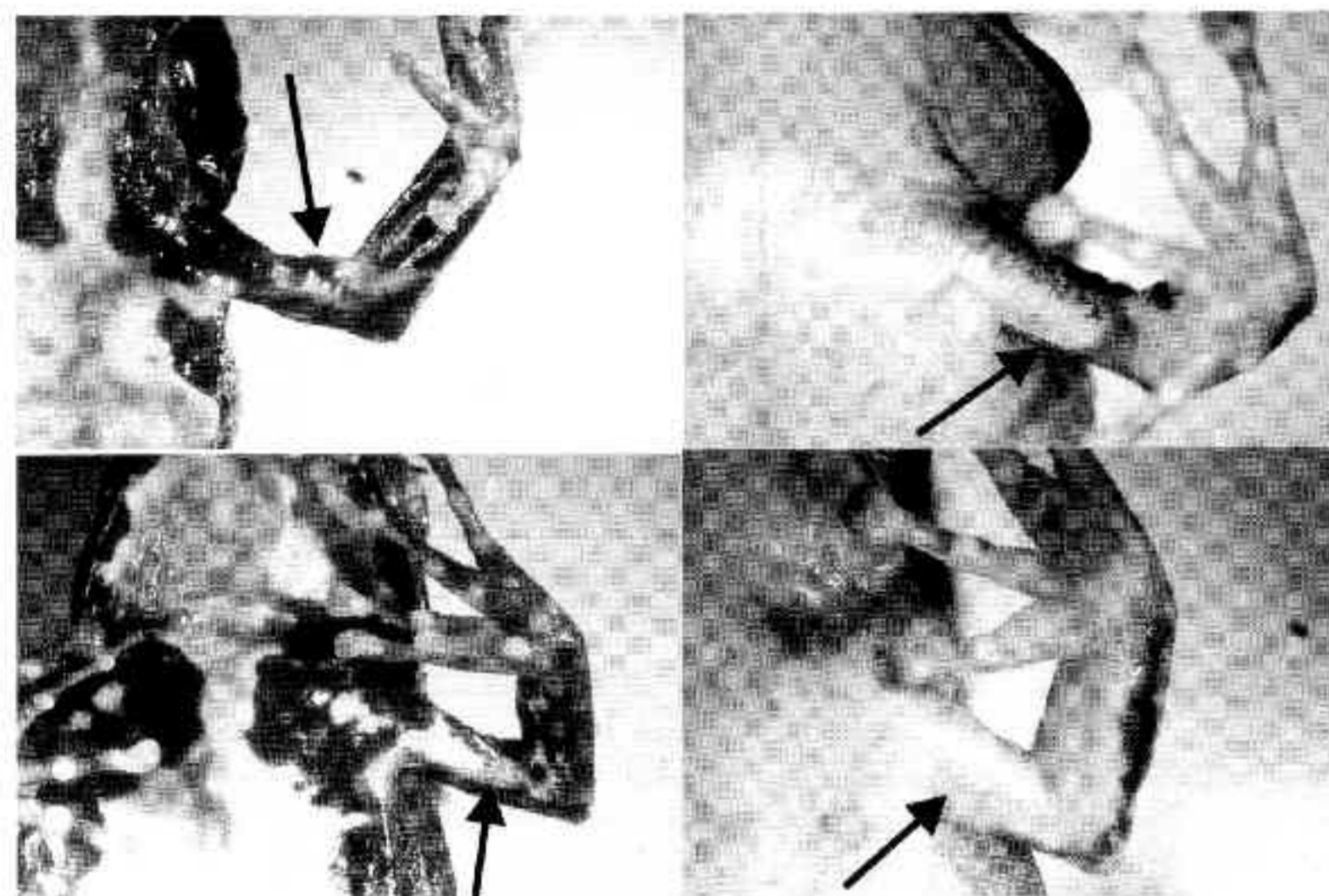


Fig. 2. – Left: ventral views of a male (above; MNHN 1972.1462) and a female (below; MNHN 1972.1443) of the forelimb of *Mantidactylus spinifer*. The arrows mark the humeral protuberances. Note also the strongly contrasted ventral pattern in both sexes. Right: ventral views of a male (above; MNHN 1972.1436) and a female (below; MNHN 1972.1431) of the forelimb of *M. plicifer*. In this species, the humeral protuberance is very distinct in males but apparently absent in females.

Mantidactylus plicifer and *M. luteus*, where a clear sexual dimorphism exists (no protuberance recognizable in females; fig. 2). In other species, e.g. *M. spinifer*, a weakly expressed humeral protuberance appears to be present in males and females (fig. 2).

MOLECULAR AND PHYLOGENETIC METHODS

To sample data on genetic differentiation and phylogenetic relationships, we sequenced fragments of the mitochondrial 16S rRNA gene of up to 567 base pairs (bp), using primers and protocols given by VENCES et al. (2000), in species of the *M. asper* group and of related taxa. The corresponding voucher specimens and EMBL/Genbank accession numbers are: *Mantidactylus asper*, UADBA-FG/MV 2000.17, AJ314802; *M. luteus*, ZFMK 66674, AF215313; *M. plicifer*, ZFMK 62306, AJ314800; *M. sculpturatus*, ZFMK 62304, AJ314799; *M. boulengeri*, ZFMK 66672, AF215318; *M. corvus*, ZFMK 70494, AF215320; *M. cf. pseudoasper*, MSNG 49087, AJ314803; *M. malagasius*, MRSN A1991, AJ314797; *M. aff. malagasius*, MRSN A1938, AJ314796; *M. granulatus*, ZSM 645.2001, AJ314794; *M. sp. n.* (Tsaratanana; new species close to *M. granulatus*), ZSM 627.2001, AJ314795; *M. leucomaculatus*, ZFMK 59953, AJ314805; *M. cornutus*, ZSM 308.2000, AJ314798; *M. tschenkii*, ZFMK 62296, AJ314806; *M. tandroka*, ZFMK 59894, AJ314803. *Boophis xerophilus* (ZFMK 66705,

AF215335) and *Mantidactylus liber* (subgenus *Guibemantis*; ZSM 491.2000, AJ314801) were used as outgroups. Sequences of the new species described below were obtained from the specimen MTKD 37424 and have the Genbank accession number AF215327.

Sequences were aligned using the CLUSTAL algorithm in SEQUENCE NAVIGATOR (Applied Biosystems); subsequently, the alignment was adjusted by eye. A total of 33 base pairs of the hypervariable region could not be reliably aligned and were excluded from further analysis. The aligned sequences were submitted to analysis using PAUP*, version 4.0 (SWOFFORD, 2001). We used MODELTEST (POSADA & CRANDALL, 1998) to estimate the model of sequence evolution for a Maximum Likelihood (ML) phylogenetic reconstruction. We additionally performed Maximum Parsimony (MP) analyses, using the heuristic search option with tree-bisection reconnection branch-swapping, and Neighbor-joining (NJ) analyses, with LogDet distances which are robust against possible variation of sequence evolution among lineages (LOCKHART et al., 1994). In the MP analyses, we coded gaps as fifth state, but also performed additional searches excluding all characters with gaps in one or more species. We used PAUP* to test for the presence of a significant phylogenetic signal by a permutation-tailed-probability (PTP) test with 100 replicates, and for homogeneity of base frequencies across sequences.

RESULTS

SPECIES ACCOUNTS

Mantidactylus asper (Boulenger, 1882)

(fig. 3a-b)

Rana aspera Boulenger, 1882. – *Name-bearing type*: lectotype, by present designation, BMNH 1882.3.16.80, adult male collected by W. D. Cowan, SVL 27.8 mm. – *Type locality*: “East Betsileo” according to original description. – *Other types*: paralectotypes, following present lectotype designation, BMNH 1882.3.16.81-90, same collecting data as lectotype.

Mantidactylus veratophrys Ahl, 1929. – *Name-bearing type*: lectotype, by present designation, ZMB 10443, adult female, collected by J. M. Hildebrandt according to original description. – *Type locality*: “Betsileo” according to original description. – *Other types*: paralectotypes, following present lectotype designation, ZMB 10444 and 50501-50502, three adult females with same collecting data as lectotype.

Comments. – (1) Considering the existence of at least one new species in the *M. asper* group as described below it appears important for taxonomic stability to define single name-bearing types for all taxa in the group. Following this rationale, we here designate lectotypes for *M. asper* and its junior synonym *M. veratophrys*. Detailed morphological measurements of these lectotypes are given in tab. 1. – (2) BLOMMERS-SCHLÖSSER & BLANC (1991) listed the specimens “BMNH 1882.316.80-82, 83-86” as syntypes of *M. asper*. The number “316” in this mention is certainly a typing error for “3.16”. Beside BMNH 1882.3.16.80-81, all specimens of the

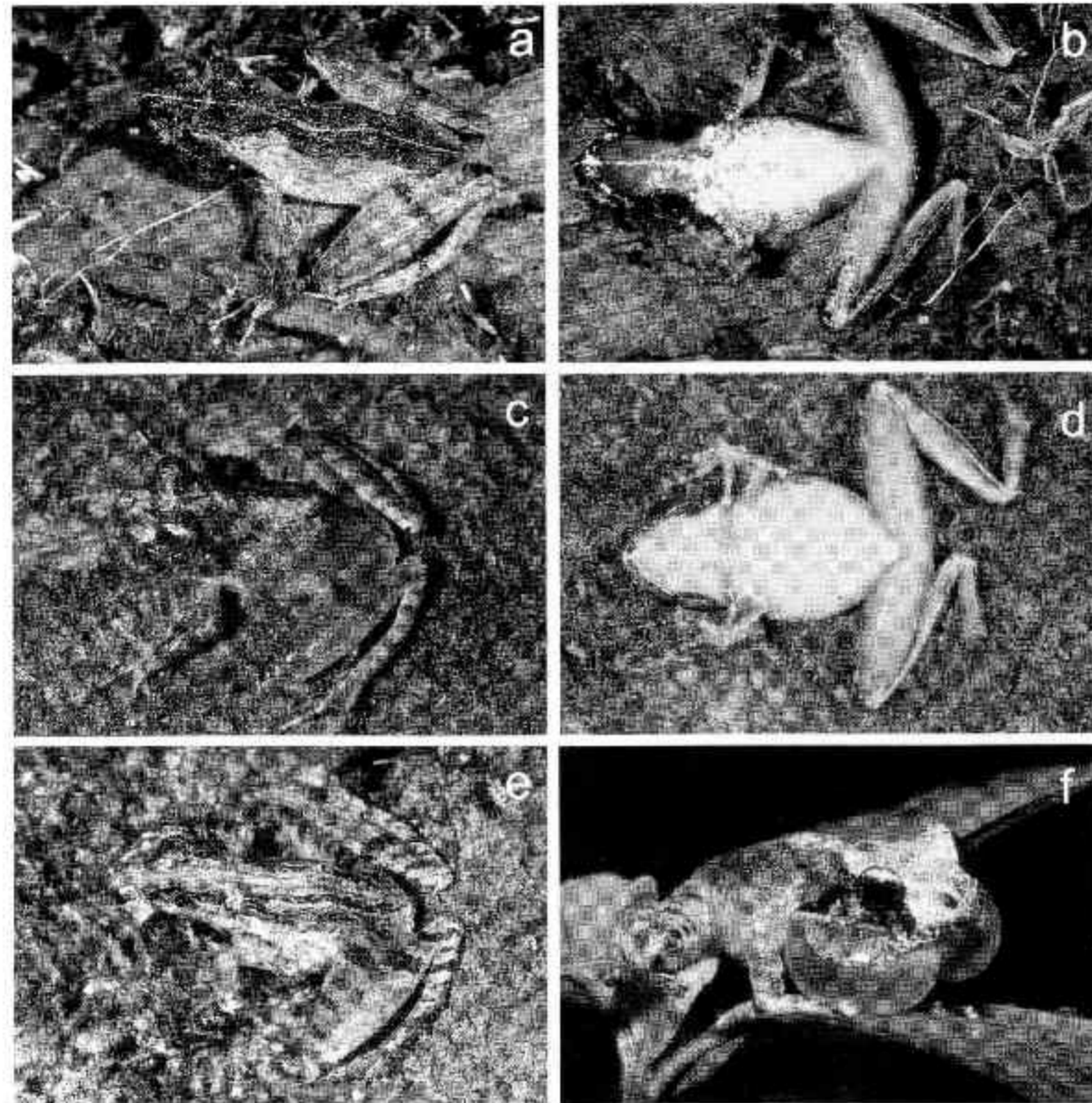


Fig. 3. – Photographs of *Mantidactylus asper*, male from Ankeniheny (ZFMK 60789), in dorsolateral and ventral views (a-b); of *Mantidactylus ambohitra*, male holotype from Montagne d'Ambre (ZSM 1084.2001) in dorsolateral and ventral views (c-d); and of two additional specimens of *M. ambohitra*: female ZFMK 57419 (e) and a calling male specimen (not collected), photographed by J. Köhler (f), both from Montagne d'Ambre.

series BMNH 1882.3.16.83-90 are labeled as syntypes of the taxon in the London museum. We examined four specimens of this series which were not individually numbered. We could not locate the specimen BMNH 1882.3.16.82 in the London collection; it may have been exchanged or used for osteological examinations. It can be assumed that the series of paralectotypes (according to present lectotype designation) consists of at least nine, possibly ten specimens. – (3) BLÖMMERS-SCHLÖSSER & BLANC (1991) stated that the type of *Mantidac-*

tylus ceratophrys Ahl, 1929 was lost. In the meantime, four original syntype specimens have been rediscovered in the ZMB collection (lectotype and paralectotypes according to present designation).

Material examined. – BMNH 1882.3.16.80-81, 1882.3.16.83-86 (East Betsileo, lectotype and paralectotypes); BMNH 1925.7.2.29 (Antsihanaka); BMNH 1928.5.9.1 (Brickaville); MNIIN 1972.557-558 (Tsaratanana); MNIIN 1972.559-560 (Mandraka); MNIIN 1972.574-576, 1972.578-583, 1972.586-591 (Tsaratanana); MNHN 1972.584-585 (locality uncertain); MNHN 1973.905 (Marojejy, alt. 1300 m); MNHN 1975.313 (Marojejy); MNHN 1975.317 (no precise locality); MNHN 1975.318 (Marojejy, alt. 1300 m); MNHN 1975.319-320 (Marojejy, alt. 2000 m); MNHN 1975.321 (Mandraka); ZFMK 62236-62237, 62240 (Manrady); ZFMK 62303 (Ranomafana); ZFMK 60789 (Ankeniheny); ZMA 6867.988-990 and 6868.470 (Andasibe); ZMA 6894.36, 6895.376-383 and 6895.480-482 (Mandraka); ZMA 6897.906 (Andasibe); ZMB 50501-50502 and 10443-10444 (Betsileo, lectotype and paralectotypes of *Mantidactylus ceratophrys*); ZSM 401.2000 and UADBA-FG/MV 2000.17 (Mandraka).

Morphology and diagnosis. – The following morphological description is based on the type series, and on specimens from central eastern Madagascar (Mandraka, Andasibe, Mantady, Antsihanaka, Brickaville). Specimens from these localities form a well-defined homogeneous cluster, although several characters (expression of dorsal tubercles and ridges, relative hind-limb length) are subject to considerable individual variation. Other attributed specimens are discussed in the section on distribution.

Inner dorsolateral ridges prominent; either continuous (e.g. in ZMA 6867.990) or discontinuous (e.g. in ZMA 6867.989), starting 1-3 mm behind eyes. No connecting dorsal ridge in the specimens examined by us. Outer dorsolateral ridges generally present, but often not continuous, appearing as an irregular series of short folds and tubercles. One or two pairs of distinct more or less prominent ridge-like interocular tubercles. Additional smaller tubercles and short ridges on the dorsum of most specimens. Distinct supraocular spines in all specimens, two of these being especially large. A distinct heel spine; tarsal spines generally reduced to small tubercles, sometimes not recognizable (e.g. in several specimens of the type series). Femoral glands usually visible in males, but not very distinct or prominent. Vocal sac paired subgular. No clearly recognizable humeral protuberance in either sex. Webbing in most specimens reaching slightly beyond the first subarticular tubercle of the fifth toe; webbing formula 5(0.5) to 5(0.75). One inner and two outer metacarpal tubercles, the latter in contact with each other. A large (males) or medium-sized (females) inner metatarsal tubercle and a distinct, small to medium-sized outer metatarsal tubercle.

Significant or near-significant intersexual differences were found in SVL (Mann-Whitney *U* test, $P < 0.06$), in relative length of the inner metatarsal tubercle ($P < 0.005$), and in relative tympanum diameter ($P < 0.05$), but not in relative height of the inner metatarsal tubercle or limb length. Males had larger relative tympanum sizes and longer inner metatarsal tubercles than females. Male/female size ratio was 97%.

Coloration. – In-preserved, dorsal coloration generally brown, with more or less symmetrical light brown or dark brown markings. In ZMA 6867.988, dark brown vertebral area enclosed between inner (anterior dorsum) and outer (posterior dorsum) dorsolateral ridges, and beige flanks and areas lateral to the ridges, the beige color starting as narrow dorsolateral bands above the eyes. Hindlimbs brown with dark brown crossbands. A thin light vertebral line in ZFMK 62236. Head laterally brown, including the lips, with some rather indistinct

dark brown markings. Ventral side white on the chest and, in females, on the throat, more cream on the posterior belly. Throat in males light brown with a distinct central white longitudinal stripe, and with black lateral color coinciding with the inflatable parts of the vocal sac. In females, indistinct but sharply delimited brown vermiculations on throat and chest. Limbs ventrally light brown, with some darker pattern at the edges.

Distribution. – Beside the specimens from central eastern Madagascar, we also assign to *M. asper* rather than to *M. spinifer* one subadult male from Ranomafana (ZFMK 62303; vocal sac not visible, but throat laterally already slightly black colored) based on its smaller size, ventral pattern, and expression of ridges and tubercles. The situation is more difficult for the available material from the Marojejy and Tsaratanana massifs in northern Madagascar. These specimens are larger than typical *M. asper*, have more weakly expressed spines and ridges (supraocular spines reduced to tubercles in most specimens), and a very weak ventral pattern. In part, they thus remind specimens from Montagne d'Ambre which are described below as a new species. However, the low amount of webbing (at fifth toe consistently 0.75-1), as well as other characters constitute a distinct difference to that species, and support the tentative inclusion of the Tsaratanana and Marojejy populations in *M. asper*. Despite low number of females in this sample (only two specimens), the inner metatarsal tubercle is significantly relatively longer in males ($P < 0.05$; tab. 2-3). Male/female size ratio is 99 %.

Summarizing, the species is known from the following precise localities: (1) Tsaratanana; (2) Marojejy; (3) Antsihanaka; (4) Brickaville; (5) Mantady; (6) Andasibe; (7) Ankeniheny; (8) Mandraka; (9) Ranomafana. Except for Brickaville, which is located close to sea level at the east coast, all localities in the central east are at mid-elevations, ranging from ca. 700 to 1200 m. Marojejy specimens are catalogued as originating from an elevational range of 1300-2000 m.

BLOMMERS-SCHLÖSSER & BLANC (1991) additionally recorded the species from Les Roussettes (Montagne d'Ambre) and Ambatofitoharanana. Specimens from the former locality are here attributed to the new species described below, while the voucher specimen from Ambatofitoharanana (MNHN 1975.315) cannot be reliably attributed to any described species (see section at the end of the species accounts).

Natural history. – Calling males were observed during the day on the ground (at Ankeniheny) and after dusk from branches about 50 cm above the ground (at Mantady and Mandraka). At Ankeniheny, they were mainly found close to a swampy brook, while they called far from water bodies at Mantady, and close to a tiny brook at Mandraka. Vocal sacs did not remain inflated between notes. Each note was one expiration.

Advertisement call. – Calls were recorded at Ankeniheny on 18 February 1994, 17.15 h, at 23.5°C air temperature. They consisted of series of single notes or series of note groups of 2-4 notes each (fig. 4). Note duration was 5-13 ms (10 ± 3 ms, $n = 8$), duration of intervals between notes was 56-80 ms (66 ± 11 ms, $n = 6$). Frequency was 1700-7700 Hz, dominant frequency 3200-4200 Hz.

Similar calls were heard after dusk on 10 February 1996 at Mantady. Only series of single notes were heard (note repetition rate 1.3-1.4 per second). Frequency was about 2000-5000 Hz, dominant frequency 3500-4500 Hz.

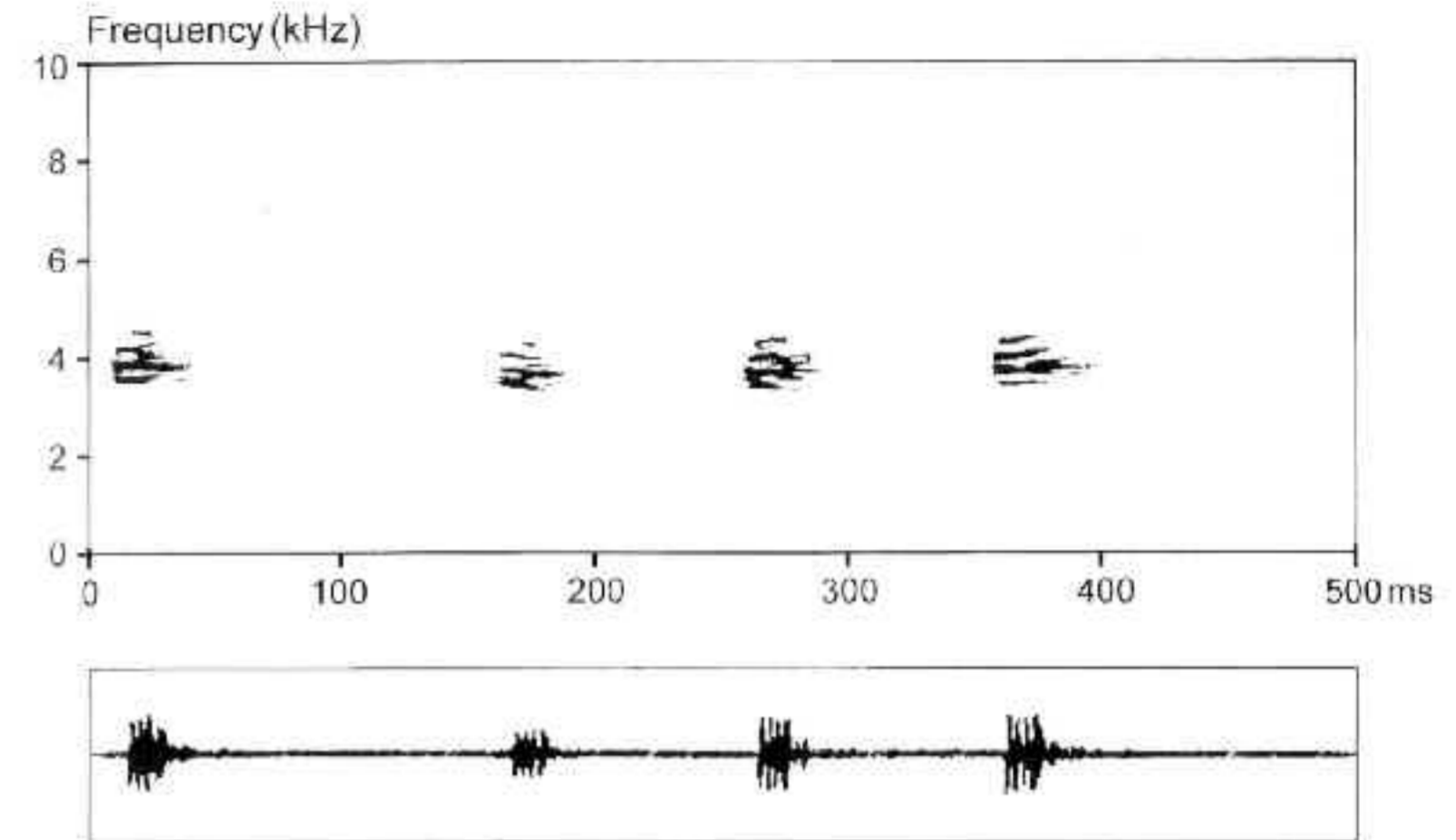


Fig. 4. Sonogram and oscillogram of a call (series of four notes) of *Mantidactylus asper* from Ankeniheny.

Calls from Mandraka (recorded by R. Blommers-Schlösser in December 1972 at 17.00 h) were series of note groups (up to 7 notes per group). Note duration was 13-20 ms (16 ± 2 ms, $n = 9$), duration of intervals between notes 72-80 ms (75 ± 2 ms, $n = 7$). Note groups with 4-7 notes had a duration of 323-494 ms (386 ± 69 ms, $n = 5$), duration of intervals between note groups was 626-733 ms (684 ± 44 ms, $n = 4$). Frequency was 1800-6000 Hz without recognizable dominant frequency.

Mantidactylus spinifer Blommers-Schlösser & Blanc, 1991

Mantidactylus spiniferus Blommers-Schlösser & Blanc, 1991. – *Name-bearing type*: holotype, by original designation, MNHN 1972.1450, adult male collected by C. P. Blanc in November-December 1971 according to MNHN catalogue. – *Type locality*: "Chaînes Anosyennes" according to original description; "Camp IV, Chaînes Anosyennes" according to MNHN catalogue. – *Paratypes*: MNHN 1972.1440 and 1972.1470, adult female and male.

Material examined. – (1) types and topotypical material: MNHN 1972.1450 (holotype, Camp IV, Chaînes Anosyennes); MNHN 1972.1440 (paratype, Camp IV, Chaînes Anosyennes); MNHN 1972.1470 (paratype, Ambana-Camp IV, Chaînes Anosyennes); MNHN 1972.1439, 1972.1443-1468 (Camp IV, Chaînes Anosyennes); (2) further material: MNHN 1972.551-554 (Ivohibe, Marovitsika forest).

Morphology and diagnosis. – Beside the three type specimens designated by BLOMMERS-SCHLÖSSER & BLANC (1991), nine males, thirteen females and four juveniles from the same

