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 (including 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* Abl. 1929 (junior synonymy 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 rDNA gene supported monophyly of the *M. granulatus* group and of the *M. pseudoasper* group in the subgenus *Phylomedusa*, 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
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 (Brommer-Schlässer, 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 Blochmania, Guthorniana, Pandamysella, Spondylosoma). A second group consists of brood-clinging species, the larvae of which often show specialized mouthparts and similar species (subgenera Bryognathus, Chlamydactylus, Helobatrachus, Mantidactylus, Oberharmannia). The third assemblage contains three subgenera (Gephyromantis, Lauromantina, Pyhygomantis), while Phyllomedusa males usually call along brooks and at least some species have free-swimming larval stages, calling males of most Lauromantina 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. edwardsi (Brommer-Schlässer, 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 Brommer-Schlässer & 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 metatarsals, and black-pored subgular vocal sacs in males. We re-examined the material available to Brommer-Schlässer & Blanc (1991), and complemented this information by own field observations.

ABBREVIATIONS AND MEASUREMENTS

Vocalizations were recorded using portable tape recorders with an external microphone (Vivavox EM 238) and analyzed with the MEDAW sound analyzing system Spectro 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; EN, eye-nostril distance; NSD, nostril-snout tip distance; NND, nostril-nostril distance; TD, horizontal tympanum diameter; HAL, hand length; FOL, forelimb length; HIL, hindlimb length; HFL, foot length; FTOL, 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; IMTLSVL, and IMTH/SVL, relative size of inner metatarsal tubercle; FOL/SVL, and HFL/SVL, relative length of fore- and hindlimbs), and of interspecific differences in selected morphological variables and ratios. Measurements are given as range, with mean ± standard deviation in parentheses.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London (formerly British Museum of Natural History); MNNH, Musee National d'Histoire Naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; MSNG, Museo Civico "G. Doria" di Storia Naturale, Genova; M1KD, Museum für Tierkunde, Dresden; TM, Transvaal Museum, Pretoria; UABDA, Université d'Antananarivo, Département de Biologie Animale; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZMA, Zoologisches 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 four number followed by the field number of R. Brommer-Schlässer, since they bear no individual ZMA tag.

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'Ambari population previously considered as Mantidactylus plesioter by Brommer-Schlässer & 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 plesioter as a
species of usually rather large body size and with large and distinct femoral glands from south-eastern Madagascar; (2) the recognition of mid-altitude eastern populations previously assigned to M. leucorhinus by GLAW & VENCES (1994) as a distinct species M. scapulatus. 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 biocoustic differentiation and sympatric occurrence of M. scapulatus and M. ploski at Ranomafana. More detailed justifications are given in the respective Identity and Diagnosis sections below.

MORPHOLOGICAL TERMINOLOGY

Webbing formula is given according to BLUMMERS-SCHLOSTER (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 subspecies in the genus Mantidactylus. To refer unequivocally to these structures, we here define a number of terms (fig. 1).

1) Interocular 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 elevated black interocular spots as present in M. leucorhinus (Pyhilochnus). In several Phylchnus (M. cornutus, M. redunus, M. madagascariensis, M. tschenkii), one pair of rounded, black tubercles are present. On the contrary, in M. asper, M. ploski 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 always appear to be a discontinuous anterior continuation of the inner dorsolateral ridges; and sometimes, in M. ploski, 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 run above or up to 4 mm behind the eyes and run medially onto the anterior back. They either continue straight dorsolaterally onto the posterior fourth of the back, or curve slightly towards the flank and fade.

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

4) Connecting dorsal ridge. - In some M. ploski, 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 Phylchnus; e.g., M. cornutus, M. redunus, M. tschenkii), 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 asper (left), female MNHN 1972.1414. M. ploski (center), female MNHN 1972.1431, and M. leucorhinus (right), female MNHN 1985.245. The arrows mark dermal structures which are described in the text: CDR, connecting dorsal ridge; HSP, heel spine; IDR, inner dorsolateral ridge; EOT, inter-ocular tubercles; ODR, outer dorsolateral ridge; SOS, 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. Besides the M. asper group, it is also found in several Phylchnus and in species of the genus Boulengerina (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 prominence. - 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. laticeps, M. ploski, M. tschenkii), 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 prominence. It is best visible in
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 Venes 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, UADRA-EM26017, A131480, M. latans, ZMK 6675, A1215312, ZMK 622206, A1314834, ZMK 633304, A1314796, M. boulengeri, ZMK 66762, A1215312, M. carneus, ZMK 70494, A1215320, M. cf. pseudospadix, ZMK 49087, A1314807, M. m. latans, ZMK 645001, A1314794, M. sp. nov. (Tarratana; new species close to M. m. latans), ZMK 6272001, A1314795, M. braziliensis, ZMK 59593, A1314805, M. c. ZMK 3082000, A1314798, M. s. ZMK 62296, A1314806, M. tamarina, ZMK 59894, A1314803, Bophis xerophilus (ZMK 68055).

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 MODEST (Prado & Chander, 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)

Boulepetr (Boulenger, 1882) - Name-bearing type: lectotype, by present designation, BMNH 1882.3.16.80, adult male, collected by W. D. Oates, S.Y. 257.8 mm. Type locality: “Boulepetr” according to original description. Other types: paralectotypes, following present lectotype designation, BMNH 1882.3.16.80-90, same collecting data as lectotype.

Mantidactylus cruzi (Alv, 1929) - Name-bearing type: lectotype, by present designation, ZMB 10415, adult male, collected by J. M. Boulenger, according to original description. Type locality: “Bolivian” according to original description. Other types: paralectotypes, following present lectotype designation, ZMB 10414 and 10501-10502, 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. cruzi. Detailed morphological measurements of these lectotypes are given in tab. 1. (2) Boles & Boulenger (1914) listed the specimens “BMNH 1882.3.16.80-81” as syntypes of M. asper. The number “316” in this mention is certainly a typographic error for “316”. Beside BMNH 1882.3.16.80-81, all specimens of the
series BMNH 1882.3.16.83-90 are labeled as syntypes of the taxon in the London museum. We examined four species of this series which were not individually numbered. We could not locate the specimen BMNH 1882.3.16.32 in the London collection; it may have been exchanged or used for osteological examinations. It can be assumed that the series of paratypes (according to present lectotype designation) consists of at least nine, possibly ten specimens. - (3) BLOOMER-SCHLÖSSER & BAX (1991) stated that the type of *Montasalac-

*tylus ceratophyra* Abl. 1929 was lost. In the meantime, four original syntype specimens have been rediscovered in the ZMB collection (lectotype and paralecotypes according to present designation).

**Material examined.** - BMNH 1882.3.16.80-81, 1882.3.16.83-86 (East Berbice, lectotype and paralectotypes); BMNH 1925.7.27 (Antsiranana); BMNH 1928.5.9.1 (Brickaville); MNHN 1972.557-558 (Taratanna); MNHN 1972.559-560 (Mandraka); MNHN 1972.574-576, 1972.578-583, 1972.586-591 (Taratanna); MNHN 1972.554-555 (Manampy, alt. 1500 m); MNHN 1972.51 (Manampy); MNHN 1975.531 (Manampy, alt. 1300 m); MNHN 1975.530 (Manampy, alt. 1500 m); MNHN 1975.529 (Manampy, alt. 1200 m); MNHN 1975.527 (Manampy, alt. 1300 m); MNHN 1975.526 (Manampy, alt. 1300 m); ZFMK 62534.62937, 62940 (Madagascar, ZBM 6895.480-481 and 6895.482-483 (Mandraka). ZMB 6895.500 and 6895.502 and 6895.504 (Madagascar). (4) Bax, lectotype and paralectotypes of *Montasalac-

*tylus ceratophyra* Abl. 1929 were collected in the ZMB collection (lectotype and paralectotypes according to present designation).

**Morphology and diagnosis.** - The following morphological description is based on the type series, and on specimens from central eastern Madagascar (Mandraka, Andasibe, Mantady, Antsiranana, Brickaville). Specimens from these localities form a well-delineated morphological group, although several characters (expression of dorsal tubercles and ridges, relative hindlimb 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 1-2 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 intertectal tubercles. Additional smaller tubercles and smaller ridges on the dorsum or most specimens. Distinct supracocular spines in all specimens, two of these being especially large. A distinct heel spine; tarsal spines generally reduced to smaller tubercles; sometimes not recognizable (e.g. in several specimens of this type series). Femoral glands usually visible in males, but not very distinct or prominent. Vocal sac paired subglular. No clearly recognizable humeral protrusion in either sex. Webbing in most specimens reaching slightly beyond the first subtibial tubercle of the fifth toe; webbing formula 5(0.5) to 5(0.5). One inner and two outer metatarsal 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 interspecific 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 preservative, 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 62393; 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 (supraspinous spines reduced to tubercles in most specimens), and a very weak ventral pattern. In part, they thus remain 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 more elongate 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) Antsahamaka; (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 arc at mid-elevations, ranging from ca. 700 to 1200 m. Marojejy specimens are catalogued as originating from an elevational range of 1200–2900 m.

**BLOMMESES-SCHÖSSER & BLANC (1991)** additionally recorded the species from Les Rousettes (Montagne d’Ambre) and Ambatoitoharanana. Specimens from the former locality are here attributed to the new species described below, while the voucher specimen from Ambatoitoharanana (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 30 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 5.1-3 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. Sonagram and oscillogram of a call (series of four notes) of Mantidactylus asper from Ankeniheny.**

Calls from Mandraka (recorded by R. Blommers-Schlässer in December 1972 at 17.01 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 322-494 ms (386 ± 69 ms, n = 5), duration of intervals between note groups was 626-735 ms (684 ± 44 ms, n = 4). Frequency was 1800-6000 Hz without recognizable dominant frequency.

**Mantidactylus spinifer** Blommers-Schlässer & Blanc, 1991

*Mantidactylus spinifer* Blommers-Schlässer & Blanc, 1991.—Same 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.** “Chaines Anosyennes” according to original description; “Camp IV, Chaines Anosyennes” according to MNHN catalogue. — *Paratypes*: MNHN 1972.1449 and 1972.1470, adult female and male.

**Material examined.**—(1) type and naprotypical material: MNHN 1972.1450 (holotype; Camp IV, Chaines Anosyennes); MNHN 1972.1449 (paratype; Camp IV, Chaines Anosyennes); MNHN 1972.1459, 1972.1443-1446 (Camp IV, Chaines Anosyennes); (2) further material: MNHN 1972.551-554 (Ihosy, Marovatsika forest).

**Morphology and diagnosis.**—Beside the three type specimens designated by BLOMMESES-SCHÖSSER & BLANC (1991), nine males, thirteen females and four juveniles from the same
series and general locality were available. Considering this material, the following updated description of *M. spiniger* (based on the toptype material only) can be provided. Identity of other specimens is discussed in the section on distribution.

Inner dorsolateral ridges prominent, starting 0.5-2 mm behind the eye. Dorsal connecting ridge present in some specimens and completely absent in others. Outer dorsolateral ridges generally present, but mostly not continuous and poorly defined, often appearing as an irregular series of short folds and tubercles. One pair of distinct and very prominent ridge-like interocular tubercles, a second, less distinct anterior pair often being also visible; the two pairs sometimes fusing to a single symmetrical structure (fig. 1). A large number of additional irregular tubercles and short ridges scattered on the dorsum. Distinct supraocular spines in all specimens, two of these being especially large. A distinct heel spine and a line of 2-7 distinct tarsal spines. Males with very distinct and rather prominent femoral glands. Vocal sac pair subgular. A weakly expressed humeral protuberance in both sexes (fig. 2). Webbing in most specimens reaching distinctly beyond last subarticular tubercle of fifth toe, but not reaching to disc. Webering formula 3(0,3) to 3(0,7). One inner and two outer metatarsal tubercles, the latter two in contact with each other. A large inner and a distinct, small to medium sized outer metatarsal tubercle.

Morphometric measurements are given in tab. 1-3. No significant sexual dimorphism was found in relative foardlength (P > 0.5), but the remaining variables tested showed significant differences between sexes: females were significantly larger (mean male/female size ratio 95.6; P < 0.05), had shorter relative hindlimbs (P < 0.05), and smaller relative tympanum sizes (P < 0.01). Relative length and height of the inner metatarsal tubercle were also distinctly smaller in females (P < 0.001).

**Coloration.** — The following description is based on preserved specimens only, no color pictures of living specimens were available. Dorsal coloration with various toptones of brown, generally arranged in longitudinal patterns. Narrow, or broad brown bands sometimes arranged dorsolaterally, following the dorsal ridges, on a beige or light brown dorsum (MNHN 1972:145, 1972:1459), or dark brown central dorsum with cream-beige flanks (MNHN 1972:1458, 1972:1461). In most specimens a rather distinct mixture of dark and light brown.

All specimens ventrally with a very distinct coloration, the dark flank color reaching onto the posterior ventre and ending abruptly, without any fading, bordering into the ventral color which (in preservatives) is bright white (fig. 2). Males with a brownish throat (laterally black, corresponding to the inflattable parts of the vocal sac) with a more or less distinct median white stripe. Females with a white throat and a brown border along the lower lip. Limbs ventrally more or less distinctly marbled with dark brown and white. This conspicuous ventral color pattern is already visible in juveniles (MNHN 1972:1452, 1972:1466-1468) of 14-18 mm SVL.

**Distribution.** — Beside the specimens from the type locality Châline Anosyrembe, Bloomer, Schlösser & Black (1993) included three additional localities of *M. spiniger* in their distribution map: Marojejy, Marovitsika and Andringitra. The MNHN vouchers from Marojejy were herein assigned to *M. asper* and we did not locate vouchers from Andringitra assignable to the species. However, a series from the Marovitsika forest (Pâ d'Ibible) could be included...
with some reservations in *M. spinifer* (MNHN 1972.351-554). It contains specimens larger than typical *M. asper*, with more distinctly expressed spines and tubercles (two tarsal spines clearly recognizable) and a more distinct venal pattern of white and dark coloration. These characters remark those of *M. spinifer* (see below). However, the specimens are still smaller than typical representatives of the species, and the ventral pattern contrast is less expressed. We here tentatively follow their assignation to *M. spinifer* as suggested by Bloomers-Schlosser & Blanc (1991), but it should be kept in mind that they are intermediate between *M. spinifer* and *M. asper* in size and expression of venal pattern contrast. The species is therefore known from (1) the Château Anosyennes (2) Ivolahy.

**Natural history and advertisement call.** Unknown.

**Manitalectus ambolotra n. sp.**
(fig. 3c-e)

**Hologotype.** ZSM 1084-2001 (originally ZFMK 57418), adult male, Montagne d'Ambre, collected by Frank Glaw, Rudi Rahbison and Olivier Ramilison on 14-17 March 1994.

**Paratypes.** MNHN 1883.241-245 (two females) from Montagne d'Ambre, MNHN 1883.246 (female), 1893.249-250 (two females), 1893.252 (female), 1893.253 (juvenile) (previously 1893.246A; female), all from Maroano (Montagne d'Ambre), sent to the Paris museum by Alluaud and Bellocq in 1893; MNHN 1972.537 (female) from Montagne d'Ambre, MNHN 1973.314 (female), 1975.322 (female), 1975.325 (female), 1975.329 (female), 1975.330-331 (two males) from Les Rousettes (Montagne d'Ambre), all without precise collecting data; MTKD 37424 (male) from Montagne d'Ambre, ZFMK 57419 (female) from Montagne d'Ambre, with same collecting data as holotype, ZFMK 6204-62205 (two subadults), collected by J Steinbrecher on 26 November 1995 at Montagne d'Ambre.

**Diagnosis.** A member of the genus *Manitalectus* based on the presence of gonadal glands and absence of nuptial pads in males. Assignable to the *Manitalectus asper* group in the subgenus *Geophrynornate* based on: (1) blackish paired subgular vocal sacs in males; (2) inner and outer dorso-lateral ridges; (3) small heel spines; and (4) general similarity with other species of the group. The species is in several characters intermediate between *M. asper* and *M. spinifer* on the one hand, and *M. leucas* and *M. platyrhine* and *M. sculpator* on the other hand. It is distinguished from *M. asper* and *M. spinifer* by its largely uniformly colored ventral side, lower amount of dermal spines, less extended webbing and less prominent dorso-lateral ridges. It is distinguished from *M. leucas* and *M. platyrhine* and *M. sculpator* by its smaller body size (male SVL 34-37 mm vs. 36-48 mm), less prominent inner dorso-lateral ridges, smaller size of heel spines and supracleithral spines, presence of an outer metatarsal tubercle and occasional occurrence of interocular tubercles.

**Etymology.** Derived from *Ambolotra*, the Malagasy name for the Amber Mountain (Montagne d'Ambre), the type locality of the species. The name is used as invariable noun in apposition to the generic name.

**Description of the holotype.** Adult male, SVL 35.8 mm [fig. 3c-e]. For measurements, see tab. 1. Body slender, head slightly longer than wide, distinctly wider than body, snout rounded in dorsal and lateral views; nostrils directed laterally, slightly protruding, mouth nearly to tip of snout than to eye; canthus rostralis distinct, cuneate; loreal region concave, tympanum distinct, elliptical (slightly higher than wide), 67% of eye diameter; supratympanic fold very distinct, straight, tongue ovate, distinctly bifid posteriorly; vomerine teeth distinct, in two rounded aggregations, positioned postero-lateral to choanae; choanae rounded. Arms slender, subarticulate tubercles single; one outer, central, and inner metacarpal tubercles present; fingers without webbing; relative length of fingers 1 < 2 < 3 < 4 < 5, second finger distinctly shorter than fourth; finger disks distinctly enlarged; nuptial pads absent. Hindlimbs slender; tibiotarsal articulation reaching widely beyond snout tip when hindlimb is addorsed along body; lateral metatarsals separated by webbing; inner metatarsal tubercle distinct, outer metatarsal tubercle smaller but recognizable; webbing formula between toes I(1, 2(2), 2(2), 3(2), 3(2), 4(2), 4(2), 4(1), 7(5)), 5(1), 5(2), relative toe length 1 > 2 > 3 > 4 > 5, hind toe clearly shorter than fifth toe. Skin on the upper surface smooth; dorso-lateral folds present but weakly expressed and not very prominent; inner dorso-lateral folds present, starting ca. 25 mm behind the eyes and fading on the anterior back; outer dorso-lateral folds running ca. 4 mm posterior to the supratympanic fold in the inguinal region. Two distinct, longitudinal intertubercular tubercles, of same color as surrounding skin; supracleithral tubercles present; supracleithral spines and heel spine present but small. Ventral skin smooth on throat, slightly granular on posterior belly. Femoral glands very poorly delimited and very indistinct from both external and internal views; a patch of indistinct granules visible from internal view.

Dorsal coloration in preservative dark brown with a weakly defined vertebral region of lighter beige-brown color. Posterior fifth of the dorsum and dorsal surface of the hindlegs light brown. One distinct and four indistinct dark brown crossbands on femur, one indistinct and three distinct bands on tibia, and five indistinct bands on tarsus and foot. Dorsal color of
forelimbs irregularly dark and light brown. On the flanks, the dark dorsal color fading gradually into the light ventral color. Head sides dark brown except an ill-defined light band running from the anterior eye corner to the upper lip. Ventrally cream-white with some weak symmetrical brown markings in the chest region. Throat cream-white, the inflatible lateral parts of the vocal sac black. In life, color was similar to that in preservative, the iris being light brown in its upper part, reddish brown laterally, and greyish brown in its lower part.

Variation. — The available specimens are largely in mediocre state of preservation, especially the MHN specimens that were collected more than 100 years ago. Nevertheless, a relatively large variability of morphological (dorsal dermal structures) and coloration could be assessed. ZFMK 57419 (fig. 3c) has a strongly contrasted dorso lateral pattern of dark dorso lateral stripes on a light brown back. A further specimen (fig. 3d, not collected) had a light reddish brown head surface with a triangular posterior end. A pattern also known in Mantidactylus lutuus (GLAW & VENCES, 1994: color plate 93) and other representatives of the genus. Another specimen (not collected) had a broad and sharply delimited median light stripe on the dorsum. The inner and outer dorso lateral ridges are always present but usually weakly expressed and often discontinuous. The inner dorso lateral ridges generally begin 2.3 mm behind the eyes. In some specimens, one or two pairs of indistinct ridge-like intercubital tubercles are seen, but usually they are absent. Heel spine and supracubital spines are small, and often reduced to tubercles; tarsal spines are absent. Males have rather indistinct femoral glands. Humeral protrusions are not visible in the available material. Webbing in most specimens is rather undeveloped, reaching almost the fifth toe level, although it is less extended in other specimens (formula 6.5.5). The outer metatarsal tubercle is always visible though generally small. The three available juvenile paratypes already show some of the characteristics of M. ambotiana (e.g., not very prominent dorso lateral ridges, presence of ridge-like intercubital tubercles).

Significant intersexual differences (Mann-Whitney U tests) were detected in relative length of forelimb (P < 0.05) and hindlimb (P < 0.005) and in relative length (P < 0.05) and height (P < 0.005) of the inner metatarsal tubercle, but not in relative tympanum diameter or SVL. Limbs are longer in males than in females, which is a rather uncommon state in Madagascan frogs; the inner metatarsal tubercle is longer and higher in males. Male/female size ratio is 102%.

Further material. MHN 1893.243 (Montagne d’Ambre) is a large male specimen which reminds Mantidactylus plinius by size (SVL 48.8 mm) and by its large, distinct femoral glands. The probably subadult female MHN 1875.324 (La Ressouze) reminds M. lutuus rather than M. ambotiana. As both specimens are in poor state of preservation, it is not possible to make a definitive statement on their identity. It is possible, however, that more than one representative of the M. ambotiana group occurs at Montagne d’Ambre.

Three further specimens agree morphologically with M. ambotiana but are not included in the type series due to dubious or lacking information on their local identity. The male MHN 1875.326 is labeled as originating from “Flaty” but we consider it as very improbable that this refers to Flaty in extremely west south-western Madagascar close to Toamasina. The female MHN 1875.323 has no locality information. Both these specimens bear numbers subsequent to small series originating from the Montagne d’Ambre region. The female MHN 1873.896 was collected, according to the MHN catalogue, by C. P. Blanc on 16 July 1972 at Marojejy (300 m elevation); however, its “hard” state of fixation is similar to that of specimens from Montagne d’Ambre (e.g., MNHN 1875.322) rather than to the more flexible, obviously formal-fixed M. lutuus specimens from Marojejy, collected also by C. P. Blanc in July 1972 (MNHN 1873.897-902).

Distribution. — The species is so far reliably known only from (1) its type locality, Montagne d’Ambre in far northern Madagascar.

Natural history. — We observed specimens during the day on the forest floor. F. Kohler (pers. comm.) observed calling males in November in the evening (19-22 h) and later during light rain, calling from bushes at the forest edge, ca. 60-150 cm above the ground. Inflated vocal sacs were paired subaural (fig. 3f).

Advertisement call. — Unknown.

Mantidactylus lutuus (Methuen & Hewitt, 1913)

(fig. 5a-b)

Mantidactylus lutuus Methuen & Hewitt, 1913. Nona-bearing type; holotype, by original designation, TM 10097; adult male collected by Herschel-Chauvin. — Type locality: Folody. — Other types: paratypes, TM 10095-1010, two adult males, two adult females and three juveniles, and TM 10084 (exchanged with another collection according to TM catalogue).

Identity. — The type series, as examined by us in 1998, agrees morphologically with the populations attributed to M. lutuus and inhabiting the low-elevation areas of the Marojejy east coast. This form is morphologically recognizable by: (1) rather small size; (2) distinct but rather small femoral glands in males; and (3) generally uniformly whitish ventral without distinct dark chest markings. The holotype has a SVL of 41.3 mm, FGFL of 6.4-6.8 mm and FGW of 1.6-1.9 mm (W. Hauke, pers. comm. 2001), thus within the range of other male specimens herein assigned to the species (tab. 2). We will, in the following, provide a detailed morphological description of M. lutuus, and only mention differences from this pattern in the subsequent sections on M. plinius and M. sculpturatus.

Material examined. MNHN 1873.323 (Kianjavato); MNHN 1872.1435 (Ambasa-Sovaha, Chatras Antsiny); MNHN 1872.1418 (Camp V, Chatras Antsiny); MNHN 1873.897-902, 907, 908, 910 (Marojejy, alt. 300 m); MNHN 1873.906 (Marojejy, alt. 1300 m); MNHN 1873.909 (Marojejy, alt. 600 m); TM 10077, 10089-1010 (holotype and paratypes; Folody; ZFMK 47222, 47290-47291, 52711, 52713-52714 (Nosy Boraha); ZFMK 52713, 66674 (Nosy Mangabe).

Morphology. — The description provided here refers to male specimens from Marojejy (MNHN 1873.897, 1873.899-902, 1873.908-909). Nosy Mangabe (ZFMK 66674) and Nosy Boraha (ZFMK 52714) which form a morphologically homogeneous group. Morphology and attribution of other specimens is discussed in the section on distribution. Inner and outer dorso lateral ridges present and usually continuous, the inner ridge being more prominent than the outer ridge. Inner dorso lateral ridges generally beginning above the eye and running onto the central dorsum, ending in various modes, either fading or curving medially or laterally, sometimes continued as indistinct undulations structures towards the inguinal region. Outer dorso lateral ridges generally beginning in the shoulder region where the inner ridges end (fig. 1). No connecting dorsal ridge, no intercubital tubercles. Supracubital tubercles and a
few small supracocular spines present. Usually one distinct supracocular spine coinciding with the origin of the inner dorsolateral ridge. A distinct heel spine; no dorsal spines. Males with small but distinct ventral glands (see fig. 24). In MNHN 1973.899 (Marojejy), the gland on the forefoot is material view, composed of 16 granules of 0.6-0.9 mm diameter each in ZFMK 66674 (Nosi Bay) and 15 granules of 0.8-0.8 mm (Vocal sac paired sublingual. A strongly expressed hemeral proterandric males, lacking in females. Webbing in most specimens reaching the disc of the fifth toe, resulting in webbing formula of 5(0) or 5(0.25). One inner and two outer metatarsal tubercles, the latter two in contact with each other. A distinct inner but no outer metatarsal tubercle.

Significant intersexual differences in the whole sample attributed to M. batesii were found in SVL and in relative length (Mann-Whitney U test, P < 0.05) and height (P < 0.005) of the inner metatarsal tubercle (longer and higher in males), but not in relative tympanic diameter or relative length of limbs. Male/female size ratio is 89.5%.

Coloration. - Dorsally generally uniformly greyish brown, sometimes with some shades and indistinct markings of lighter or darker brown. Usually with at least a partial black bordering of the inner dorsolateral ridges towards the flanks. Two further black spots often present at the origin of the outer dorsolateral ridges. Indistinct but often well-defined crossbands on the hindlimbs (5-7 on femur, 5-7 on tibia, 4-10 on tarsus and foot). Ventral color uniformly creamy, including the limbs. Only some specimens with faint brownish markings on chest and (in males) on throat. Lateral, infaust parts of the paired sublinguals are black.

Distribution. - Beside male specimens from Marojejy, Nosy Mangabe and Nosy Boutha, we also attribute several vouchers to M. batesii. Two males from the Chaînes Anosyennes (MNHN 1972.1418 and 1972.1435), which were collected sympatrically with M. plicifer (see below), differ from that species by their completely uniform chest, smaller size and smaller femoral glands (consisting of 24 granules of 0.4-0.6 mm diameter in MNHN 1972.1435). The male MNHN 1975.325 (Knajvangi) also agrees in having distinct femoral glands with 21 granules. The females ZFMK 52711 (Nosy Boutha) and ZFMK 52715 (Nosy Mangabe) are rather large (SVL 45.0 and 37.5 mm, respectively), and would therefore agree better with M. plicifer by size. However, the almost uniform whitish ventral of ZFMK 52711 and the very faint chest motting of ZFMK 52715 agree with the state in M. batesii. As so far no records of M. plicifer exist for central-eastern or north-eastern Madagascar, we assign these female specimens to M. batesii. We attribute also the juveniles MNHN 1972.509 and 910 (Marojejy) to this species, as neither M. plicifer nor M. sculpturatus are known from this region. A further locality is Foulpointe which is based on a single voucher (ZMA 6725) which agrees with M. batesii in body size and femoral gland proportions according to a personal communication of F. Andreone. Summarizing, specimens attributable to M. batesii are from: (1) Marojejy; (2) Nosy Mangabe; (3) Nosy Boutha; (4) Foulpointe; (5) Foholoty (type locality); (6) Knajvangi; and (7) the Chaînes Anosyennes (including Ambaena and Camp V). All these localities are at low elevations along the Malagasy coast; only one specimen (MNHN 1973.906) is catalogued as originating from 1300 m on the Marojejy massif, while the other specimens from this locality were collected at 300-600 m elevation.

BLOMBERGS-SCHÖSSEL & BLANC (1991) additionally recorded the species from a number of further localities, namely Les Rousses (Montagne d'Ambre), Ambalamamorondava, Morovitsika and Antsalova. The available Montagned'Ambre specimens are here all referred to the new species M. amboliatra, although at least two of these are actually morphologically similar to M. batesii, and the possible occurrence of this or a similar species at Montagne d'Ambre warrants further research (see section on M. amboliatra). The available material from Ambalamamorondava may be attributable to M. sculpturatus or M. batesii (see below). The locality Morovitsika forest (Pic Ivohibe) is based on juvenile specimens only. The locality Antsalova (Antsirabe) is corroborated by one MNHN voucher from this site catalogued as M. batesii. This specimen (MNHN 1975.327), however, has no dorsolateral ridges and clearly agrees in general morphology with Mantidactylus carinatus and M. pseudosporus (subgenus Physiocomys), two morphologically similar species of which one (M. carinatus) has been...
described from western Madagascar (Isole). Occurrence of *M. cf. pseudoaxilis* in the Antsingy forest is also corroborated by MSNG 40087 which was the origin of the tissue samples used for DNA analyses herein.

**Natural history.**—Calling activity was mainly nocturnal but sometimes started before dusk. In such cases, the calls were emitted from the ground. Calling activity increased with progress of dusk, and at night specimens generally called from leaves 1-2 m above the ground. We never observed calling specimens gathering at or close to water bodies.

**Advertisement call.**—Calls were series of short, relatively melodious notes (fig. 6). Each note did correspond to one expiration. Between notes, the vocal sac did not remain distinctly inflated, although a slight inflation was noted when a call series was about to start. Calls from Marojejy (Camp 1) were recorded on 27 March 1994, 17:30 h, at 22°C air temperature. They consisted up to 21 notes. Note duration was 22-24 ms (23 ± 1 ms, n = 5), duration of intervals between notes was 170-180 ms (173 ± 5 ms, n = 4). Note repetition rate was 5.0-5.5 ms. Calls from Nosy Boraha as described by GLÄW & VINCÉS (1992) were similar and are here re-described. They were recorded on 8 March 1991 at ca. 22°C air temperature. Note duration was 44-59 ms (51 ± 5 ms, n = 8), interval duration 127-230 s (136 ± 40 ms, n = 7), and note repetition rate 4.3-5.0 second.

On 28 March 1994, distress calls were emitted by a specimen from Marojejy when handled. Two calls had a duration of 1600 ms and 1663 ms. Frequency was 1630-1000 Hz, respectively 0-1000 Hz, and showed the frequency band pattern typical for anuran distress calls.

**Mantidactylus plicifer** (Boulenger, 1882)

(fig. 5c-d)

*Rana plicifer* Boulenger, 1882. — *Nose-bearing* type; lectotype: by present designation, BMNH 1882.3.16.55, adult male collected by W. D. Cowan. Type locality: "Last betsileo" according to the original description. — *Parexophyllum*; BMNH 1882.3.16.57, female and 1882.3.16.56 and 59; two subadult specimens, with same collecting data as lectotype.

**Comment.**—The current re-definition of the species *M. plicifer* is based on characters (size and structure of femoral glands) recognizable in males only. As only one of the original syntypes of *Rana plicifera* is a male, its present designation as lectotype is necessary to reach taxonomic stability in a group of extremely similar species (*M. latens*, *M. plicifer*, *M. sculpturatus*).

**Identity.**—Our field observations demonstrated syntopic occurrence of a smaller and a larger *M. latens*-like species in Ramomana, males of the larger species reaching 44.2-44.4 mm SVL. Also in the MNHN sample from the Chaînes Anosyennes, a larger and a smaller form could be distinguished, males of the larger form ranging from 43.6 to 48.3 mm SVL. One distinctive character of the large form at both sites were its consistently large and distinct femoral glands. Based on this character, we consider the large specimens as *Mantidactylus plicifer*, fig. 7 shows that they agree with the lectotype of *Rana plicifer* in relative femoral gland size, although the type is distinctly smaller (38.8 mm SVL; see tab. 1-2). The difference both in SVL and in relative length and width of femoral glands (ratio FG/L SVL and FGW/SVL) was highly significant between *M. plicifer* and *M. latens* (P < 0.005).


**Morphology and diagnosis.**—Beside the larger size of most specimens as compared to *M. latens*, the most important morphological character to identify *M. plicifer* is the large size of its femoral glands (see *Identity* section). In internal view, a gland of the lectotype contained about 45 granules. In one specimen from Ramomana (ZFMK 62206), a gland was composed of 47 granules of 0.5-0.7 mm in diameter. In one specimen from the Chaînes Anosyennes, a gland was composed of 55 granules of 0.4-0.8 mm in diameter.

Beside this character, the morphology of *M. plicifer* is extremely similar to *M. latens*. The differences mentioned by BRAMMERS-SCHLÖSSER & BLANC (1991) in their key to *Mantidactylus*, namely webbing less developed in *M. plicifer* and heel spine (only a tubercle present in *M. plicifer*) are not suited to distinguish both species. The webbing is variable in *M. plicifer*. For instance, it reaches the disk of the fifth toe in ZFMK 62306, but only between the disk and the external subarticular tubercle in ZFMK 62305, resulting in webbing formulas for the fifth toe of 5(0) vs. 5(0.5). And the presence of a heel spine appears to be highly dependent on
Fig. 7. Scatterplot of snout-vent length (SVL) and relative femoral gland length (ratio FGL/SVL) in Madidactylus luteus, M. plicifer, and M. sculpturatus. Note the clear distinction of Madidactylus plicifer from the other two species by its larger femoral gland size. Most M. plicifer can also be distinguished by their larger SVL; the lectotype of M. plicifer (marked by an arrow), which is not well sized, shares with the other specimens its large femoral glands.

the state of fixation and preservation of the specimens. So, a fixed spine is clearly visible in the formalin-fixed M. plicifer from Chames Anosyennes, but this structure is only rudimentary and faintly recognizable in the ethanol-fixed specimens from Ranomafana. The outer metatarsal tubercle, absent in M. luteus, is sometimes visible as small rudiment in formalin-fixed M. plicifer. The pair of outer metatarsal tubercles are often indistinct in M. plicifer as in M. luteus, but when recognizable, the outermost tubercle is distinctly smaller and more elongate.

Color and pattern variation is as follows. Many specimens with a tendency of a lighter lateral coloration and a darker dorsal coloration, more or less sharply separated by the dorsolateral ridges; this contrasted pattern very distinct in a few specimens (e.g., MNHN 1972.1427) which have light brown to beige flanks and dark brown central dorsum and head surfaces, both colors sharply separated by the dorsolateral ridges. In this specimen, head also laterally beige, with a broad vertical band running from the eye to the upper lip. In some specimens, head laterally with a broad light beige band along the upper lip, bordered sharply by a dark brown band along the canthus rostralis. Venter cream whitish, with a few brownish markings usually present in the chest region. Throat largely covered by faint brown pigment in many males (except a longitudinal light median band). Vocal sacs blackish.

Interspecific differences in SVL and relative tympanum size are close to significance (Mann-Whitney U test, P < 0.07), males being smaller and having relatively larger relative tympanum sizes than females. Highly significant differences were found in relative length and height of the inner metatarsal tubercle (P < 0.001; longer and higher in males), while relative limb length did not differ significantly between sexes. Mean male/female size ratio is 96%.

Distribution. - Beside the imprecise type locality East Betsileo, the species is reliably known from (1) Ranomafana and (2) the Chames Anosyennes (BLOOMSCHLÖSSER & BLANC 1991) listed six additional localities for the species: Tsaratanana, Marojejy, Ambalakante, Mandraka, Amelametamana, Manarivatra. We could not locate any voucher for the Ambalakante locality in the MNHN or ZMA collections. The specimens from Tsaratanana, Marojejy and Mandraka, determined as M. plicifer by R. Blommers-Schloesser according to the MNHN catalogue, are here all referred to M. ayer (see also GIAX & VENCE, 1994, for the Tsaratanana vouchers). The specimens from Manarivatra are juveniles that cannot be reliably determined, while those from Amelametamana are here assigned to M. sculpturatus in a preliminary way (see below).

Natural history. - Calls were heard during dusk from the vegetation in rainforest. Calling males were sitting ca. 50 cm above the ground. No water bodies were observed in the surroundings.

Advertisement call. - Recordings were done on 2 March 1996, 18:15 h, at 23°C air temperature in the Ranomafana National Park. Single notes as well as short series of up to five notes (fig. 8) were emitted. Note duration was 121-148 ms (34 ± 10 ms, n = 5), duration of intervals between notes was 492-559 ms (535 ± 31 ms, n = 4). Since intensity faded continuously at the end of each note, measuring of note duration was difficult, and it would also be possible to consider note durations as longer (and, correspondingly, interval durations as shorter). Frequency was 1200-4000 Hz, dominant frequency 2700-3300 Hz.

Mandidactylus sculpturatus Abl., 1929
(fig. 5a-c)

Mandidactylus sculpturatus Abl., 1929. - Name-bearing type holotype, by monotypy, ZMB 30515. - Type locality: "Northeast-Madagascar" according to original description (probably erroneous). - Other types known.

Identity. - At mid-altitude localities of eastern Madagascar, a species occurs which is extremely similar to M. luteus by morphology. It is, however, distinguished by its unlevelname (vs melodious) advertisement calls, its indistinct femoral glands, and a relatively high genetic divergence (see below). We here validate the name Mandidactylus sculpturatus for this species based on the following rationale. (1) The type of M. sculpturatus is a female of 37.5 mm SVL; its morphology totally corresponds to species previously assigned to M. luteus,
and its size agrees with the mid-altitude lutens-like species but not with the larger species *M. pilifer* (2). (2) ANT. (1929) described *M. sculpturatus* from a specimen that was collected by J. M. Hildebrandt, and that was reported to originate from northwestern Madagascar. However, no species close to *M. lutens* is so far known from this region, except an undescribed species from the Manongarivo Reserve collected by C. J. Raxworthy (deposited in the London museum) and by D. Rakotomalala (pers. comm.). These Manongarivo specimens, however, have distinct interocular tubercles in males and females which are absent in the type of *M. sculpturatus*. As with other anuran species collected by J. M. Hildebrandt in this region, it is probable that some labeling errors occurred either by Hildebrandt himself or when the specimens were entered in the Berlin Museum after Hildebrandt’s death in Madagascar in 1888 (VENICE & GLAV, submitted). (3) Beside localities in northwestern Madagascar, Hildebrandt collected at sites in central eastern Madagascar but apparently not at low altitudes along the east coast (BRENNER, 1998). It is therefore probable that the *M. sculpturatus* type was collected at a mid-altitude eastern locality. We are aware that these arguments do not suffice to fully clarify the identity of *M. sculpturatus*, but its present re-definition appears as most parsimonious solution and avoids the description of the mid-altitude lutens-like form as a new species.

Note. - BLOOMER & SCHOFER (1991) stated that the “type” of *M. sculpturatus* was lost. In the meantime, the holotype has been rediscovered in the Berlin museum.

**Material examined.** - ZFMK 53688-53689 (Andasibe); ZFMK 62304 (Ramcoalana); ZMB 36515 (holotype).

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**Morphology and diagnosis.** - By size and general morphology, this species is similar to *M. lutens*. Temporal glands are indistinct in most specimens; in ZFMK 62304 (Ramcoalana), an adult male collected while calling and therefore in sexually mature and active state; no temporal glands at all were recognizable in external or internal view. The male ZFMK 53688 (Andasibe) had 36 scattered granules visible in internal view of a gland. These granules, however, were smaller than in *M. lutens* (0.3-0.4 mm in diameter).

In the available material, no recognizable outer metatarsal tubercle. Webbing reaching the disk of the fifth toe or slightly below, resulting in a webbing formula of 5(0)-5(0.25). A small heel spine, and two external metacarpal tubercles of approximately similar size. General coloration as in *M. lutens*, the specimen ZFMK 62304 from Ramcoalana having a broad white streak along the upper lip bordered by a blackish streak running under the canthus rostralis. This specimen additionally with a curved white streak running transversally above the clavicle region. Venter uniformly light, with very faint brownish pigment on the chest in some specimens.

**Distribution.** - The species is reliably known from: (1) Andasibe; (2) Ankarafantsika (no voucher specimens collected); and (3) Ramcoalana.

**Natural history.** - Calling males were observed at night, not concentrated around water bodies, 1-2 m high in the vegetation, in rainforest.

**Advertisement call.** - Calls from Ankarafantsika were recorded on 18 December 1994, 21:45 h, at ca 22°C air temperature. They consisted of up to 22 unharmonious notes, but at the beginning...
of calling activity single-note calls were common. Following several of these, note-series were successively composed of an increasing number of notes. After such a call series, calling activity was often interrupted for some minutes; one call series from Andasibe lasted 20 s and showed the following pattern: 1-1-2-3-15 (numbers referring to notes per call). However, multi-note calls were emitted spontaneously as well. Note duration at Aukéeny was 154-180 ms (168 ± 13 ms, n = 5); duration of intervals between notes was 126-163 ms (143 ± 18 ms, n = 4). Note repetition rate was 3.0-3.3 per second. Calls from Andasibe (recorded on 12 January 1992 at 22°C air temperature) were similar, with a note duration of 90-120 ms, an interval duration of 250-260 ms, and a note repetition rate of 2.8/s (GLAW & VENCES, 1994).

Calls from Ranomafana (fig. 9) were similar, too. Two analysed calls consisted of 15-17 notes and had a duration of 446-5127 ms. Note repetition rate was 3.3-3.4/s. Note duration was 150-196 ms (173 ± 13 ms, n = 10), inter-note interval duration was 122-155 ms (139 ± 12 ms, n = 10). Frequency bands were recognizable between 1500 and 2000 Hz, 2800 and 4000 Hz, and 4800 and 5200 Hz. Dominant frequency was between 3200 and 3400 Hz.

FURTHER SPECIMENS OF UNCERTAIN ATTESTATION

While the specimens listed in the respective sections above could be attributed to the recognized species with a certain reliability and were used to delimit distribution patterns (fig. 10), the following juvenile specimens (and thus the localities Vondrozo, Ivoloha, Sanga Sanga forest and Tolongonina) could be assigned to the complex of the three species *M. lineatus*, *M. phifer* or *M. sculpturatus*, but a specific determination was not possible: MNHN 1990-414 and MNHN 1991-3140-3150 (previously 1930.4.14A-B) (Vondrozo); MNHN 1972-556 (Ivoloha, Marovitsika forest); MNHN 1972-1434 (Ambalavao Valley); MNHN 1972-1406, 1972-1409, 1972-1411, 1972-1415-1417, 1972-1424, 1972-1426, 1972-1428, 1972-1431, 1972-1432-1433 (Camp V, Chiana Anezyzanes); MNHN 1972-1469 (Ambalavao-Camp IV, Chiana Anezyzanes); MNHN 1975-328 (Sanga Sanga forest); ZFMK 47252-47253 (Tolongonina). The same applies to an adult female (MNHN 1930.413) from Fort Carnot, (SVI, 42.1 mm) which is in poor state of preservation and with largely faded pattern.

A series from Ambalamarovana (Andringitra, at 1530 m elevation; MNHN 1972-595-599) consists of two juveniles, one subadult, and two adult females with immature oocytes. By the size of the females (SVI 40.8 mm, MNHN 1972-595; 40.6 mm, MNHN 1972-596) and complete lack of dark pattern on throat and chest, they can be assigned to either *M. lineatus* or *M. sculpturatus* rather than to *M. phifer*.

Three examined specimens probably belong to the *Mantisclactus asper* group but cannot be determined further at present. (1) MNHN 1975.315 (Ambalotsobonana) is a rather large female (SVI 42.9 mm) reminding *Mantisclactus asper* and *M. amabilis*. It has very weakly expressed, straight dorsolateral ridges and apparently no markings on the vent. The locality Ambalotsobonana is located close to Fianarantsoa, at a rather high altitude of ca. 1600 m. The specimen may represent a hitherto unknown species. (2) MNHN 1975.316 (Moamby, no elevational information), an adult female (SVI 31.3 mm) with maturing oocytes recognizable by dissection, has two distinct pairs of ridge-like interocular tubercles, but only rudiments of dorsolateral ridges; instead, the dorsum is covered with irregular small tubercles. The vent is uniformly light except two faint symmetrical brownish markings on the chest. This individual may represent a new species of *Mantisclactus* (Gephyromantis), but a description does not seem justified until further collections yield also male specimens. (3) MNHN 1895.257 is a juvenile specimen in poor state of preservation that reminds *M. asper*. It is remarkable because according to the MNHN catalogue it was collected on the west coast ("Côte Ouest"). However, we consider this locality information as dubious until the occurrence of the group at western localities is confirmed.

KEY TO SPECIES IN THE *MANTISCLACTUS ASPER* GROUP

The following key allows identification of most specimens belonging to the *Mantisclactus asper* group. However, in some taxa (e.g., *M. lineatus*, *M. phifer*, *M. sculpturatus*), reliable determination is only possible in adult males (after examination of femoral glands or advertisement calls). Considering the important variability of characters such as dorsolateral ridges within populations (e.g., of *M. asper* or *M. phifer*), determinations based on single specimens should be always considered with caution.

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Fig. 10. Distribution maps of species within the *Mantisclactus asper* group. Locality numbers refer to those used in the text.
1a. Moderately sized to large species (SVL 32-50 mm); ventrally uniformly cream-whitish, sometimes with brown motting on chest and throat; tarsal spines and connecting dorsal ridge absent; interocular tubercles usually absent; outer metatarsal tubercle present or absent; webbing generally reaching closer to the disk of the fifth toe than in the first subarticular tubercle; webbing formula 5(0.5) to 5(0.75), rarely 5(0.25). ........................................ 2
1b. Moderately sized species (SVL 27-38 mm); ventrally usually with distinct dark brown pattern (laterally defining a central white area on chest and sometimes belly; throat in males brown with a light median stripe); tarsal spines sometimes present; interocular tubercles generally present; outer metatarsal tubercle present; webbing generally closer to the first subarticular tubercle than to the disk of the fifth toe; webbing formula 5(0.75) to 5(0.85), rarely 5(0.25). ........................................ 4

2a. Moderately sized species (SVL 32-39 mm); interocular tubercles sometimes present; supraocular spines small or in the form of tubercles only; dorsolateral ridges relatively irregular and indistinct; heel spine small and indistinct; outer metatarsal tubercle present; only known from far northern Madagascar (Montagne d'Amble). .................................\textit{Manitidactylus antohiana} ........................................ 3
2b. Larger species (SVL 36-50 mm); interocular tubercles always absent; supraocular spines distinct, with one relatively large spine at the beginning of the inner dorsolateral ridge; inner dorsolateral ridge always distinct; heel spine distinct; outer metatarsal tubercle absent or rudimentary. ........................................ \textit{Manitidactylus sylvaticus} ........................................ 3
3a. SVL 39-50 mm; femoral glands distinct, composed of 47-55 granules; calls composed of a slow series of unharmonious notes. \textit{Manitidactylus pleifer} 3b. SVL 36-47 mm; femoral glands small but distinct, composed of 16-29 granules; calls composed of a rapid series of melodious notes; known from eastern lowlands. \textit{Manitidactylus basus} ........................................ 3
3c. SVL 38-43 mm; femoral glands small and indistinct or not recognizable, composed of 25 granules (if visible); calls composed of a rapid series of unharmonious notes; known from eastern lowlands. \textit{Manitidactylus cartusianus} ........................................ 4a. Very granular dorsum with highly elevated and sharp ridges; connecting dorsal ridge often present; tarsal spines present and distinct; very distinct sharp brown-white contrast in the ventral pattern, extending onto the belly. \textit{Manitidactylus spiniger} 4b. Less granular dorsum; no connecting dorsal ridge; tarsal spines usually reduced to tubercles or absent; sharp brown-white contrast in the ventral pattern usually restricted to chest and/or throat. \textit{Manitidactylus asper} ........................................ 4

\textbf{Analysis of DNA Sequences}

A chi-square test did not contradict homogeneity of base frequencies across taxa ($\chi^2 = 51; P > 0.05$). The PTP test resulted in a significant difference ($P = 0.01$) between the most parsimonious tree and trees generated from random permutations of the data matrix, demonstrating presence of significant phylogenetic signal. Of the total of 556 included characters, 358 were constant, 59 variable but parsimony-uninformative, and 139 variable and parsimony-informative. MODESTTEST proposed a Tamura-Nei substitution model (TRN + 1 + G) as best fitting the data, with a proportion of invariable sites of 0.4764, a gamma shape distribution parameter of 0.0064, and empirical base frequencies (A: 0.3370; C: 0.2002; G: 0.1765; T: 0.3252) and substitution rates (A-G: 5.3886; C-G: 0.8536; T-G: 0.0036; all other rates: 1). The Maximum Parsimony analysis resulted in eight equally most parsimonious trees (505 steps; consistency index 0.54, retention index 0.48). A strict consensus of these is shown in fig. 11. Most splits in the topology were unresolved, resulting in several polytomies. The following clades were resolved: (1) a lineage containing the species of the \textit{Manitidactylus grandidrakensis} group in the subgenus \textit{Phyllocomantis} (sensu GLAW & VENCES, 1994); (2) within the \textit{M.}}
The distinctive Gephyromantis species that segregate along elevational gradients in Madagascar are phylogenetically younger than those which occur in close sympatry (as *M. piérier* - *M. laticeps* or *M. piérier* - *M. sculpturatus*).

The presence of a new species, *Mantidactylus anokihiata*, at Montagne d'Ambre in far northern Madagascar has already been suspected by Glaw & Vences (1994), who figured a specimen from this locality as "*Mantidactylus cf. asper*". The isolated Montagne d'Ambre rainforest shares a rather large number of species with the eastern and north-eastern rainforests which, on the contrary, are not present in the north-western (Sambirano) region (Rainey & Nussbaum, 1994; Raselimanana et al., 2000), but the taxonomy of the Ambre populations has so far not been studied in detail. Our amplified biocoustic and genetic data indicate substantial differentiation of the Ambre populations of at least three other species shared with the east, namely *Heterixalus herosele*, *Mantidactylus curvis* and *Mantidactylus liber*. At least some of these populations possibly merit a status as separate species, and may have originated by allopatric speciation in the isolated rainforest patch of the Ambre massif.

As the occurrence of *Mantidactylus laticeps* in Antsalova was based on a misidentification of MNHN 1975.327 (actually belonging to *M. pseudepudfer* or *M. corensis*), no reliable records of any species of the *M. asper* group and of the whole subgenus *Gephyromantis* exist at present from western Madagascar. Similarly, the record of *M. granulatus* from Antsiriny (Blommers-Schlosser & Blanc, 1991) in need of confirmation as we did not find any voucher specimen in the MNHN and ZMA collections on which the distribution data of these authors were largely based. Esselzen & Jesc (1995) did not record *M. granulatus* from this area. The only records of the whole *Gephyromantis-Laurentanomantis* assemblage occurring in western Madagascar refer, therefore to *M. corensis* and possibly *M. pseudepider*. This pattern correlates with reproductive modes, *M. corensis* and *M. pseudepider* have tadpoles developing normally in brooks through of derived morphology. See Glaw & Vences, 1994); *Gephyromantis* have direct development (Blommers-Schlosser, 1979; Glaw & Vences, 1995); direct development is also probable in some *Laurentanomantis* (Glaw & Vences, 1994); and the species of the *M. granulatus* group may have either direct development (e.g. *M. leucomelanus*) or non-feeding tadpoles (*M. granulatus*), although no detailed observations have so far been published. The absence of species with direct development and similarly derived reproductive modes from western Madagascar is probably a consequence of the need of sustained humidity for the development of terrestrial nests. The seasonal environments in western Madagascar possibly do not provide the climatic conditions for successful reproduction of direct-developing anurans or for the survival of their diminutive juveniles. This may also be the reason for the absence of cophyline microhyliids of the genus *Plethodontosphenia* (with non-feeding tadpoles developing in terrestrial nests) from western Madagascar.

In the molecular analyses, the subgenus *Gephyromantis* (including the *Mantidactylus asper* group) was a paraphyletic assemblage along the branch leading towards the subgenus *Laurentanomantis* and partly *Physaloesimus* (the *M. granulatus* group), while another section of *Physaloesimus* was placed basal to all these taxa (*M. corensis* and *M. pseudepider*). Relationships of *Laurentanomantis* to *M. granulatus* were also obvious from the cladograms of Richards et al. (2000). This topology was confirmed by further molecular or morphological data, it would indicate (beside the obvious diphyly of *Physaloesimus*) that the assemblage of

**ALYTES 19 (2-4)**

The distinctiveness of the three species *M. laticeps*, *M. piérier* and *M. sculpturatus* as re-defined here is well corroborated by their biocoustic and genetic differentiation. Previous works (e.g., Blommers-Schlosser & Blanc, 1991) also recognized two of these species (*M. laticeps* and *M. piérier*), but their concept of *M. piérieri* was equivocal, and in large part based on specimens attributable to *M. asper*. We observed syntopic occurrence of two species (*M. piérier* and *M. sculpturatus*) in the field at one site (Ranomafana), and preserved material provided evidence for syntopic occurrence of *M. piérier* and *M. laticeps* at the Chaudes Aneuses. On the other hand, the morphological differences between these species are extremely faint, and at present no reliable characters are known which could diagnose their females or juveniles. This is in agreement with the situation in almost all groups of anurans in Madagascar: the emerging picture indicates that all forms which differ biocoustically have a high genetic differentiation and must be regarded as valid species both under evolutionary and biological species concepts. Among *M. laticeps*, *M. piérier* and *M. sculpturatus*, the lowest genetic differences are found between *M. laticeps* and *M. sculpturatus*, which were reliably grouped as sister taxa by the phylogenetic analysis. The apparent allopatric distribution of these species indicates an altitudinal segregation. *M. sculpturatus* inhabiting mid-elevations and *M. laticeps* low-elevations along the eastern coast. This example may indicate that sibling
direct-developing *Mantidactylus* species evolved from brook-breeding ancestors such as *M. cervus* and *M. pseudosagrei*. If new field data confirm that *M. granulatus* has (possibly non-fertilizing) tadpoles rather than true direct development, the phylogenetic topology would furthermore suggest reversal of the reproductive mode (from direct development back to tadpoles) in this species. Such a (multiple) reversal has also been suggested for Neotropical hybrid frogs of the genus *Gaurodactylus* (e.g., Scanlan et al., 1980; Deloso & Escobar, 1981; Delfino & Hillis, 1987; see also discussion in Dubois, 1987), in this genus, direct development appears to be the ancestral state, and montane species from the Andes are hypothesized to have re-acquired a free-swimming tadpole stage through developmental arrest in the course of their evolution. However, some Andean species of direct development may have returned to this reproductive mode (Delfino & Hillis, 1987), which would indicate a high plasticity of this trait in this frog group. The testing of these hypotheses appears highly attractive to address general questions of amphibian evolution, and may qualify *Gaurodactylus* the *Geophrynontus-Lucentomontis-Phyllomedusa* lineage as a suited model group for such studies.

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**LITERATURE CITED**


