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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 *Brygoomantis*, *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 ± 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, Zoölogisch 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 BLOMMERS-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.

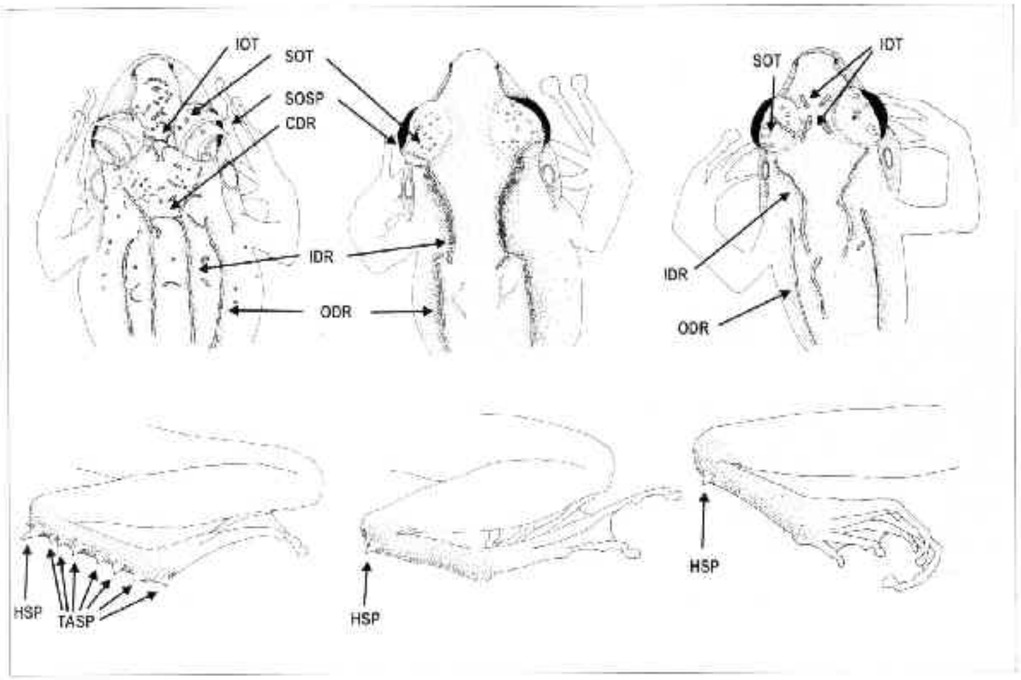

Fig. 1. Partial dorsal views (head and anterior body and hindlimb) of three representative species of the *Mantidactylus asper* group: *Mantidactylus spinifer* (left), female MNHN 1972.1444; *M. plicifer* (center), female MNHN 1972.1431; and *M. ambohitra* (right), female MNHN 1893.245. The arrows mark 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, suprocular 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