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A preliminary review of cryptic diversity in frogs of the subgenus *Ochthomantis* based on mtDNA sequence data and morphology

(Anura, Mantellidae, *Mantidactylus*)

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Based on a fragment of the mitochondrial 16S rRNA gene, we discuss cryptic diversity in the anuran subgenus *Ochthomantis* Glaw & Vences (genus *Mantidactylus* Boulenger) from Madagascar and conclude that its species diversity is more than twice as high as hitherto recognized. A review of external morphology of the type specimens and additional material shows that a reliable definition of most existing taxa and their assignation to the genetic lineages is difficult. More field work and a comprehensive revision are necessary to clarify taxonomy and biogeography of the group. *Mantidactylus zolitschka*, spec. nov. is described from eastern Madagascar. Beside genetic differences it is distinguished from all other *Ochthomantis* species except *M. ambreensis* Mocquard by distinctly smaller snout-vent length. From *M. ambreensis* it differs by colouration, relative toe length, and relative tympanum size. Lectotypes are designated for *Rana femoralis* Boulenger, 1882 and *Mantidactylus majori* Boulenger, 1896.

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Introduction

The genus *Mantidactylus* Boulenger, 1895, endemic to the Malagasy region, contains currently more than 70 nominal species (Vences & Glaw 2001) and is a group of highly diversified frogs, ranging from the large, brook dwelling *M. guttulatus* (SVL up to 120 mm) to the minute species *M. madinika* (SVL of adult males 11-13 mm).

Mantidactylus is divided into 12 subgenera. The subgenus *Ochthomantis* Glaw & Vences, 1994 currently consists of four valid species: *M. femoralis* (Boulenger, 1882), *M. ambreensis* Mocquard, 1895, *M. majori* Boulenger, 1896, and *M. mocquardi* Angel, 1929. They are distinguished from other *Mantidactylus* by the combination of webbed feet, large tympanum size (larger than ½ eye diameter), sexual dimorphism in tympanum size (females having a smaller tympanum than males), femoral gland structure, moderate to large size (adult SVL 31-75 mm), usually a yellow streak in the inguinal region, distinctly dark brown tympanic region, and brook edge dwelling habits (Blommers-Schlösser & Blanc 1991, Glaw & Vences 1994). A possible synapomorphy of *Ochthomantis* is the specialized tadpole morphology (Blommers-Schlösser 1979) which, however, so far has only been verified in *M. femoralis*.

During surveys in the rainforests near An'Ala (eastern Madagascar) we found three species of *Ochthomantis* syntopically along a brook. One of these

differs from type material of all *Ochthomantis* species and is herein described as new species. We additionally present genetic data that indicate a surprisingly high cryptic diversity in this subgenus, emphasizing the need of a comprehensive taxonomic revision.

Materials and Methods

We took the following morphological measurements with a calliper 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 (tympanum diameter), HAL (hand length), FORL (forelimb length), HIL (hindlimb length), FL (foot length), FGL (femoral gland length), FGW (femoral gland width). Webbing formula follows Savage & Heyer (1967) as modified by Myers & Duellman (1982) and Savage & Heyer (1997). To facilitate comparisons with other species of *Mantidactylus*, we also give the formula used by Blommers-Schlösser (1979) and most subsequent authors who published accounts on Madagascan anurans. We here introduce the term inguinal streak for a light (mostly yellow) marking in the inguinal region which often is regular and of longitudinal shape, but can also be interrupted, and of more irregular shape. Institutional abbreviations used are BMNH (The Natural History Museum, London), MNHN (Muséum National d'Histoire Naturelle, Paris), UADBA (Université d'Antananarivo, Département de Biologie Animale), ZFMK (Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn), ZSM (Zoologische Staatssammlung München). Numbers for specimens deposited in UADBA are preliminary fieldnumbers of M. Vences (UADBA-MV). A further abbreviation used is FG/MV which indicates fieldnumbers of F. Glaw and M. Vences (specimens to be deposited in ZSM or UADBA).

A fragment of the mitochondrial 16S rRNA gene (up to 529 nucleotides) was amplified and sequenced using primers and protocols of Vences et al. (2000). Sequences were analyzed using PAUP*, version 4b10 (Swofford 2002). They were deposited in public databases; Genbank accession numbers are: *Mantidactylus zolitschka*, from An'Ala (voucher ZSM 184/2003; AY324811); *Mantidactylus ambreensis*, Montagne d'Ambre (ZSM 492/2000; AY324822); *Mantidactylus* cf. *femoralis*, Andasibe (UADBA-MV 2001.1277, AY324812), Ranomafana (FG/MV 2002.155, AY324815), Antoetra (FG/MV 2002.56, AY324817), Isalo (FG/MV 2002.1415, AY324813), Andringitra (ZSM 746/2001, AY324814), Manongarivo (FG/MV 2002.825, AY324816), Montagne d'Ambre (FG/MV 2002.929, AY324818); *Mantidactylus* cf. *mocquardi*, Manongarivo (FG/MV 2002.824, AY324819), Tsaratanana (ZSM 643/2001, AY324820); Ambato, Masoala (ZFMK 66668, AF215317), Ranomafana (FG/MV 2002.173, AY 324821). *Mantidactylus* cf. *betsileanus* (Andranofotsy; ZSM 327/2000, AY324810) was used as the outgroup.

Results and Discussion

Genetic differentiation in the subgenus *Ochthomantis*

After exclusion of gaps the alignment consisted of 521 characters of which 408 were constant and 60 were parsimony-informative. Heuristic searches using TBR branch swapping and a random addition sequence with 10,000 replicates yielded 5 equally most parsimonious trees (215 steps; consistency index 0.651, retention index 0.617). A strict consensus of these is shown in fig. 1. The basal polytomy of this tree and the low bootstrap support of most nodes indicate that relationships between major lineages are not resolved.

Genetic divergences between most samples were surprisingly high. Eight clades had total pairwise divergences > 4% to all other specimens. Even within one major lineage assigned to *M. femoralis*, three secondary clades (divergences > 1.5%) were discernible.

According to available data, intraspecific sharing of haplotypes of more than 4% divergence in the 16S rRNA gene is unknown in frogs, and usually maximum divergences around 1-2% are found among conspecific populations of Malagasy frogs (Vences & Glaw 2002, Vences et al. 2002, 2003). In several cases (specimens from Montagne d'Ambre, Manongarivo, Ranomafana) syntopic representatives of different primary lineages were *a priori* identified as being morphologically divergent. We strongly suspect that all primary lineages in fig. 1 represent good biological species, which would rise the number of species in the subgenus *Ochthomantis* from four to nine (*M. majori* is not included in the cladogram).

Morphological review of *Ochthomantis* species and designation of lectotypes

Mantidactylus femoralis (Boulenger, 1882)

Type material. The definition of *Mantidactylus femoralis* is difficult because of the heterogeneity of the original syntype series. These are three large female specimens and one small specimen which may be a subadult or a male (Tab. 1). Boulenger (1882) listed four types in the original description of *Rana femoralis*: "a-d. Males & hgr.", which almost certainly means that he considered the large specimens as males and the small specimen as half-grown (hgr.). The size of the species is indicated as "50 mm" which corresponds to the SVL of the large specimens. The original description is therefore mainly based on these

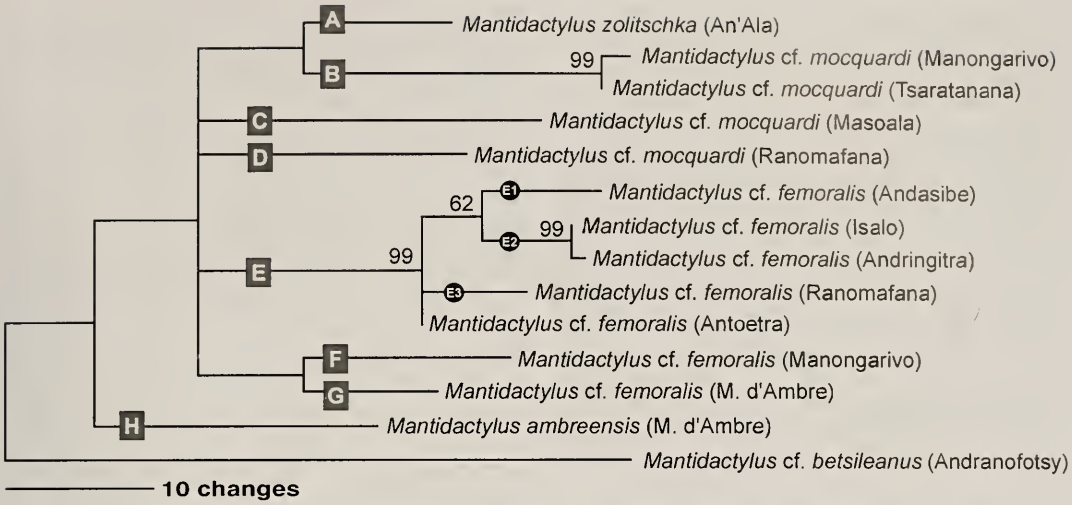

Fig. 1. Maximum Parsimony phylogram (strict consensus of five equally parsimonious trees) of *Ochthomantis* specimens analyzed. Numbers above branches are bootstrap support values in percent (2000 replicates; values <50% not shown). Letters in grey boxes indicate primary lineages of pairwise genetic divergences >4% to all other specimens; black circles indicate secondary lineages of pairwise genetic divergences >1.5% to all other specimens.

specimens which are females according to external morphology (gonads not examined).

Although it is generally preferable to designate males as lectotypes because their secondary sexual characters are often important for species diagnosis, we believe that in this particular case taxonomical stability and comparability is best served by designating one of the females as lectotype, since the name-bearing types of the other taxa most similar to *M. femoralis (mocquardi, flavicrus, catalai, poissoni)* are females as well. The original description of "loins marbled with black and bright yellow" (Boulenger 1882) further corresponds well with the distinct inguinal streak of specimens usually assigned to *M. femoralis* (e.g. Glaw & Vences 1994). Therefore, we hereby designate the female BMNH 1947.2.22.65 as lectotype of *Rana femoralis* Boulenger, 1888. The size and morphology of this specimen agree with other female specimens assigned to *M. femoralis* and characterized by a white frenal stripe and a distinct inguinal streak (e.g. ZFMK 59871 from Andasibe and ZFMK 59937 from Marojejy; SVL 49.2 mm and 51.8 mm).

Synonyms. Several available names are currently considered as junior synonyms of *Mantidactylus femoralis* or as dubious species (Blommers-Schlösser & Blanc 1991): *Rana flavicrus* Boulenger, 1889 (currently considered as synonym of *M. femoralis*), *Mantidactylus catalai* Angel, 1935 (currently considered as synonym of *M. femoralis*), and *Mantidactylus poissoni* Angel, 1937 (currently considered as dubious species, possibly conspecific with *M. femoralis*). A reliable attribution of these names to the lineages identified by molecular analysis is currently not possible.

Description and identity. According to the above lectotype designation, we consider specimens as belonging to *M. femoralis* which are characterized by a moderate size (male SVL 32.9-41.7 mm; female SVL 43.7-55.2), a relatively granular dorsal skin, a distinct light inguinal streak (yellow in life), a usually distinct and continuous whitish frenal stripe, a fifth toe that is longer than the third toe, and relatively long hindlimbs (usually reaching between eye and nostril). Specimens from the south (Chaînes Anosyennes, Nahampoana) are slightly larger than those from central eastern Madagascar, but otherwise agree in morphology and colouration. Also one specimen from Isalo and two specimens from Antsingy can be assigned to *M. femoralis* by morphology in a preliminary way.

In the molecular cladogram, this definition of *M. femoralis* applies to the lineages F and G and to the specimen from Antoetra, indicating that probably at least three different species are subsumed under the name *M. femoralis* at present.

While the description given above does apply to some specimens from mid-altitudes in the Chaînes Anosyennes in south-eastern Madagascar, other individuals from this area show morphological differences and rather agree with the type of *Mantidactylus catalai* Angel, 1935 which has been described from Isaka-Ivondro in the south-east. The main dif-

ference is the lack of a distinct inguinal streak and of a frenal stripe. Colouration of the *catalai* holotype has largely faded, but the original description (Angel 1935) informs about a spotted region below the tympanum (thus no frenal stripe) and contains no mention of an inguinal streak which is a conspicuous character unlikely to be overlooked. A similar colouration is also observed in specimens from Itremo (lineage E in the cladogram). Further material and studies are necessary before a formal revalidation as distinct species seems justified.

Material examined. BMNH 1947.2.22.65 (lectotype by present designation) and 1947.2.22.66-68 (paralectotypes by present designation) (East Besileo); MNHN 1953.49-49A (Antsingy); MNHN 1953.55 (Morafenobe); MNHN 1972.562-563 (Ivohibe); MNHN 1972.564 (Ambalamarovandana); MNHN 1972.565 (Ambohitantely); MNHN 1972.1517-1521 (Ambana, Chaînes Anosyennes); MNHN 1975.705 (Andasibe); MNHN 1975.707 (Marolafa); ZFMK 52683 and 53671 (Nahampoana); ZFMK 59937 (Marojezy); ZFMK 59871, 60043, 60071 (Andasibe); ZFMK 59858 (Isalo); ZFMK 60107-60109 (An'Ala); ZFMK 60139, (Ambohitantely); ZFMK 62277 (Ranomafana). Specimens without distinct inguinal streak and frenal stripe: MNHN 1972.1523, 1527-1533 (Camp V, Chaînes Anosyennes); MNHN 1972.1534, 1538-1554, 1556 (Camp IV and Camp IIIbis, Chaînes Anosyennes); MNHN 1973. 832-833, 835, 837, 839-843, 846-850 (Ambatomenaloha, Itremo).

Mantidactylus mocquardi Angel, 1929

Type material and identity. As with *M. femoralis*, the identity of *M. mocquardi* is disputable. The holotype (MNHN 1929.207) is a female of 62.9 mm SVL. Such a large size is found in only two clusters of specimens: in specimens from the north (Marojejy and Tsaratanana) with a usually uniform cream ventral colour, and in specimens from several localities in north-eastern, central eastern and south-eastern Madagascar which are characterized by a distinct silvery-white belly colouration (uniform or with contrasted dark marbling). At Marojejy, both forms occur sympatrically: from 1300 m altitude, only the cream-bellied form is known, while at 600 m altitude the silver-bellied form has been collected. As these records are based on reasonably large series of specimens, it can be stated that the differences are relatively constant and probably refer to two separate species. This is also corroborated by our molecular analysis, in which the northern specimens from Tsaratanana and Manongarivo formed a separate clade (Fig. 1B). We believe that most probably the type of *mocquardi* belongs to the silver-bellied form, based on the following rationale: (a) The type of *mocquardi* was collected in the "région de Rogez", which is close to An'Ala where the silver-bellied form has been collected; (b) there are no reliable records of cream-bellied specimens from this region in central eastern Madagascar.

Description. Characterized by rather large size, especially of females. Male SVL is 38.0-44.7 mm, female SVL is 52.8-66.7 mm. The inguinal streak can be absent; if present, it is narrow or interrupted. The third toe can be longer than the fifth toe in some specimens (e.g. those from An'Ala), although it is shorter than the fifth toe in other individuals, including the holotype. The hindlimbs are relatively short, the tibiotarsal articulation reaching to the anterior eye corner. The dorsal skin is relatively smooth. A frenal stripe can be present but is often interrupted and faintly expressed. The throat and chest usually have silvery white colour, partly marbled with black.

The northern cream-bellied specimens are characterized by a large body size (male SVL 43.0-50.4 mm; female SVL 53.3-66.6 mm), a fifth toe that is slightly longer or of similar length as the third toe, a usually uniform, light ventral side, sometimes with a rather weakly expressed wedge-shaped marking and without silvery white colour on throat and chest, and without or with a rudimentary light inguinal streak. The ventral side of the limbs is often marbled brown. The dark dorsal pigment reaches rather far ventrally and borders relatively sharply to the light ventral colour. Most specimens have a distinct light frenal stripe, the skin is rather smooth.

Material examined. (1) silver-bellied form: MNHN 1929.207 (holotype; région de Rogez); MNHN 1933.93-94 (Betampona); MNHN 1953.52 (Ivohibe, 1400 m altitude); 1953.53-53c (Andringitra); MNHN 1972.561 (Ivohibe); MNHN 1973.873-876 (Marojejy, 600 m); ZFMK 52684 (Andasibe); ZFMK 60104-60106 (An'Ala); ZFMK 62314 (Ranomafana); ZFMK 66668 (Ambato). (2) cream-bellied form: MNHN 1973.851-856, 1973.859, 1973.861-869 (Marojejy, 1300 m altitude). ZSM 634/2001-635/2001 and 643/2001 (Antsahamanara, Manarikoba forest, Tsaratanana).

Mantidactylus ambreensis Mocquard, 1895

Identity. This species is well-defined by its small size and its usually continuous white band along the flanks, running from the groin to the forelimb, and continued as frenal stripe until the snout tip. Although the holotype is in rather bad state of preservation, the colour border along the flanks is still recognizable.

Description. Based on one topotypic male specimen (ZFMK 57417). SVL 32.2 mm. The dorsal skin is

only slightly granular. The tibiotarsal articulation reaches between eye and nostril. The third and fifth toes are of similar length. The lateral white band and frenal stripe are very distinct and sharply delimited both against the dorsal and ventral colours. The ventral side is brownish with some light markings.

Material examined. MNHN 1893.241 (holotype; Montagne d'Ambre); MNHN 1953.51-51A (Tsaratanana); ZFMK 57417 (Montagne d'Ambre); ZSM 634/2001-635/2001 (Andampy, Manarikoba forest, Tsaratanana).

Mantidactylus majori Boulenger, 1896

Identity and description. This species is well defined by its strongly pointed snout, usually sharp colour border between whitish-cream ventral and brown dorsal colour along the flanks, absence of an inguinal streak, rather uniform ventral side with a few dark spots and sometimes brown marbling on the throat, and smooth dorsal skin. Nevertheless, the available sample does not appear to be homogeneous; specimens from the Chaînes Anosyennes are much larger (male SVL up to 44.0 mm) than the remaining sample, while those from Andasibe, Maroantsetra region and Marojejy are in mediocre state of preservation only, and more data are necessary to clarify their identity. To stabilize the name *Mantidactylus majori* and facilitate future revisions of *Ochthomantis*, we hereby designate the male specimen BMNH 1947.2.10.27 as lectotype. Measurements of lectotype and paralectotype (both in good state of preservation) are given in tab. 1.

Material examined. BMNH 1947.2.10.26-27 (paralectotype and lectotype of *Mantidactylus majori* according to present designation; Ivohimanitra); MNHN 1972.1321-1327 (Ambana-Soavala, Chaînes Anosyennes); MNHN 1936.31 (Tsianovoha); MNHN 1975.389 (Ivoloina road, Maroantsetra region), MNHN 1975.390 (Marojejy, 300 m); MNHN 1975.391 (Andasibe); MNHN 1953.58 and MNHN 1989.3573-3575 (ex 1953.58a-c) (Col d'Ivohibe, 1200 m); ZFMK 59958 (Andapa).

A new species of *Mantidactylus (Ochthomantis)*

During our fieldwork at An'Ala, we collected three syntopic species of the subgenus *Ochthomantis*. By a preliminary morphological diagnosis, two of these could be assigned to *Mantidactylus femoralis* and *M. mocquardi*. In contrast, the third species showed distinct morphological differences to the type material of these two species as well as to all other valid names and synonyms in *Ochthomantis*. This species is described in the following.

Mantidactylus zolitschka, spec. nov.
Figs 2-4

Types. Holotype: ZFMK 60110, adult male, collected in rainforest near An'Ala (18°56' S / 48°28' E, 840 m above sea level), eastern Madagascar, on 21 March 1995 by F. Glaw and D. Vallan. – Paratypes: ZSM 939/2000 (originally ZFMK 60111), ZFMK 60112-60114, four adult males, and ZFMK 60115-60116, two adult females, same locality, date and collectors as holotype, ZSM 184/2003, female, same locality, but collected on 2 March 2003 by G. Aprea, F. Glaw, M. Puente, L. Raharivololoniaina, R. D. Randrianiaina & M. Thomas.

Additional specimens. Several specimens (same locality, date and collectors as holotype) were deposited in the herpetological collection of the University of Antananarivo, Madagascar.

Diagnosis and comparison with other species. A species of the genus *Mantidactylus* as indicated by the presence of distinct femoral glands and absence of nuptial pads in males. A member of the subgenus *Ochthomantis* as indicated by webbed feet, separated lateral metatarsalia, sexual dimorphism in tympanum size, femoral gland structure (glands with distinct central porus in males, rudimentary glands present in females), presence of an inguinal streak, distinctly dark brown tympanic region, presence of two dark oblique markings on the throat (typical for all known *Ochthomantis* except *M. majori*), brook edge dwelling habits, and overall phenetic similarity to other representatives of the subgenus.

The name-bearing types of *M. femoralis* (and its junior synonyms *Rana flavicrus*, *Mantidactylus catalai* and *Mantidactylus poissoni*, which additionally have a much more developed webbing between toes according to the original descriptions) and *M. mocquardi* measure 48-63 mm and are therefore far outside the size range of *M. zolitschka* females (Table 1). Furthermore, specimens assigned to *M. mocquardi* generally have silvery-white colour on throat and chest that lacks in *M. zolitschka*; and specimens assigned to *M. femoralis* have a continuous and distinct inguinal streak which often is narrow or interrupted in *M. zolitschka*. *Mantidactylus majori* also differs by its larger size (see tab. 1 for measurements of syntypes) and, additionally, has more extensive webbing, a continuous light lateral band and a more pointed snout. *M. ambreensis* (SVL of holotype 42 mm) is only slightly larger than *M. zolitschka*, but differs by a larger tympanum (tympanum diameter larger than eye diameter in males), by the presence of a distinct continuous light lateral band, and by comparative toe length (third and fifth toe of similar length).

Fig. 2. *Mantidactylus zolitschka*, spec. nov. Female paratype (ZFMK 60116) in life.

Two further *Ochthomantis* species occur syntopically with *M. zolitschka* at An'Ala which we here assign to *M. femoralis* and *M. mocquardi* in a preliminary way. At this locality, a total of 11 *M.* cf. *mocquardi* (4 males, 5 females), 2 *M.* cf. *femoralis* (1 male, 1 female), and 12 *M. zolitschka* (3 females, 9 males) were compared directly in the field. Consistent differences were found in size (male *M. zolitschka* measuring 29-32 mm, *M.* cf. *femoralis* 38 mm, *M.* cf. *mocquardi* 39-45 mm SVL), in tympanum size (TD about $^4/_5$ of ED in *M. zolitschka*, $^9/_{10}$-$^1/_1$ in *M.* cf. *femoralis* and *M.* cf. *mocquardi*), and in relative toe length (third toe shorter than fifth toe in all *M. zolitschka*, of similar length or longer in *M.* cf. *mocquardi* and *M.* cf. *femoralis*).

By genetic data (Fig. 1) *M. zolitschka* was distinct from all other *Ochthomantis* specimens examined. Pairwise genetic divergences were 5.5-6.7 % to specimens assigned to *M. mocquardi*, 4.6-6.1 % to specimens assigned to *M. femoralis*, and 6.3 % to *M. ambreensis*.

Description of holotype

Measurements of the holotype are included in Tab. 1. Body relatively slender; head clearly longer than wide, as wide as body; snout pointed in dorsal and lateral view; nostrils directed laterally, not protuberant; canthus rostralis distinct, straight; loreal region weakly concave; tympanum very distinct, large, rounded, its diameter about $^4/_5$ of eye diameter; distinct supratympanic fold, beginning straight, with a rather distinct bend midway towards the forelimb insertion; tongue ovoid, distinctly bifid posteriorly; vomerine teeth arranged as distinct, rather small and rounded group posterolaterally of choanae; choanae small, rounded. Forelimbs slender; subarticular tubercles single; inner and outer metacarpal tubercle present; fingers without webbing; comparative finger length 1<2<4<3; finger disks moderately enlarged; nuptial pads absent. Legs slender; tibiotarsal articulation reaches the nostril; lateral metatarsalia separated; inner metatarsal tubercle rather small; outer metatarsal tubercle present, distinct. Webbing formula of the foot: I 2–2$^+$ II 2–2$^+$ III 2–3 IV 3–2 V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(1), 2i(1.25), 2e(1), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1). Comparative toe length 1<2<3<5<4. Skin on the upper surface rather smooth, slightly granular on the flanks; ventral side smooth. Distinct, prominent femoral glands, not consisting of single, sharply delimited granules but having a rather irregular tubercular surface with median porus. Femoral glands of opposite femurs

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Figs 3, 4. *Mantidactylus zolitschka*, spec. nov. Preserved male holotype (ZFMK 60110). **3.** Dorsal view. **4.** Ventral view.

in contact in the anal region.

In preservative, dorsum gray-brownish with irregular dark and especially light marblings. One light longitudinal stripe runs from the inguinal region along the dark brown flanks, fading towards the forelimb insertion. Sharp border between dark flanks and light ventral colouration, giving an overall impression of an irregularly striped flank pattern. Forelimbs, hands, hindlimbs and feet light brown with dark crossbands (about six crossbands on forelimb and hand including third finger, four on femur, three on tibia, and five on tarsus and foot). Tympanic region dark brown, upper lip and loreal region whitish. Ventrally whitish on the throat, becoming more yellowish on venter and hindlimbs, with irregular dark mottling. On the throat, two longitudinal brown markings running from the lips obliquely to the thorax. Both markings fuse at the height of the shoulder girdle, forming an Y-shaped marking. Lower lip with rather indistinct alternating white and brown spots.

Variation. The male paratypes correspond morphologically very well to the holotype. The female paratypes are distinctly larger than the males. Their tympanum is relatively smaller. Femoral glands are distinct and of similar size in all male specimens, recognizable only as rudiments in the females. Toe 5 is longer than toe 3 in all paratypes. Webbing formula of the foot: I (1^+-2)–($2-2^+$) II (1^+-2^-)–(2^+-3) III 2 – 3 IV 3 – (1^+-2^-) V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0.5-1), 2i(1-1.5), 2e(0.5-0.75), 3i(1.5-2), 3e(1), 4i(2), 4e(2), 5(0.5-0.75). No variation in webbing between males and females was noted.

ZFMK 60112 has a dorsal pattern similar to the holotype, but in the remaining paratypes, colouration is more uniform, with less dorsal marbling and with less pronounced striped flank pattern. ZSM 939/2000 is dorsally rather uniform light brown with a cream longitudinal vertebral band. The dark markings on the throat are present in ZFMK 60112 and 60114, but do not form a Y-shaped marking; they are absent or very indistinct in the remaining specimens.

In life, specimens generally had a more vivid colouration than in preservative, but the observed patterns were similar. The light stripe on the dorsum and a small and patch-like inguinal streak were bright yellow.

Habitat and habits. The new species was found in rainforest around An'Ala at the edge of a large brook. No calls of *M. zolitschka* could be heard, confirming that species of this subgenus of *Mantidactylus* call rather secretively and probably not very continuously. The female paratype ZFMK 60116 was dissected; it contained 49 eggs with a yellowish and dark brown pole, measuring about 2 mm in diameter.

Distribution. The new species is so far only known from the type locality.

Etymology. This species is dedicated to the family of Joachim Zolitschka, in recognition to their contribution to nature conservation and biodiversity research through the BIOPAT programme. The name is defined as an invariable noun in apposition to the generic name. For the sake of brevity of the specific name we consider this short nominative variant as most appropriate in this particular case.

Discussion

As formerly noted in many other amphibian groups from Madagascar, there is a remarkable but largely unstudied cryptic diversity in the subgenus *Ochthomantis* as well. Beside the morphological similarity of several species, two main reasons might be responsible for the poor taxonomic knowledge of this group: advertisement calls which are a powerful tool to detect cryptic diversity of anurans are low-voiced and rarely heard in *Ochthomantis* species and accordingly, call recordings are rather difficult to obtain. These are available for only three taxa (*M.* cf. *femoralis*, *M. majori* and *M. ambreensis*) and from very few localities, and therefore do not allow for comprehensive comparisons. Furthermore, there is a remarkable sexual dimorphism in the group that makes an unequivocal attribution of males and females of the same taxon difficult, especially when two or more species occur syntopically. Comparisons of DNA sequence data are therefore the most powerful tool to identify the cryptic diversity in this amphibian group. We expect that species diversity in *Ochthomantis* is still higher than indicated in fig. 1. However, a reliable non-molecular delimitation of species boundaries requires much more field work and a comprehensive revision.

Tab. 1. Measurements (in mm) of holotype and paratypes of *Mantidactylus zolitschka* and comparative specimens and types of other species in the subgenus *Ochthomantis*. See Materials and Methods section for abbreviations of characters. HT = holotype, PT = paratype, LT = lectotype, PLT = paralectotype, nm = not measured. Asterisks mark holotypes of junior synonyms of *M. femoralis*: * *Rana flavicrus* Boulenger, 1889; ** *Mantidactylus catalai* Angel, 1935; *** *Mantidactylus poissoni* Angel, 1937.

	Status	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	HAL	FORL	HIL	FL	FGL	FGW
M. zolitschka																
ZFMK 60110	HT	M	30.6	10.5	12.0	3.0	3.7	2.7	1.8	3.3	10.0	20.2	52.1	16.9	4.7	2.4
ZFMK 60112	PT	M	28.8	9.9	11.3	3.2	3.7	2.5	1.8	3.0	10.0	20.1	50.7	15.2	4.8	2.3
ZFMK 60113	PT	M	29.8	10.0	11.7	3.1	3.3	2.7	2.0	3.1	9.9	19.6	52.3	16.2	4.6	2.4
ZFMK 60114	PT	M	30.6	10.0	11.6	3.0	3.3	2.5	1.8	2.8	9.6	19.6	53.8	16.7	5.1	2.5
ZSM 939/2000	PT	M	29.6	10.0	11.4	3.2	3.4	2.4	1.8	2.6	10.2	20.8	53.7	17.2	5.0	2.3
ZFMK 60115	PT	F	37.7	12.8	15.0	2.8	4.5	3.5	2.2	3.7	11.9	24.3	68.3	20.9	–	–
ZFMK 60116	PT	F	37.6	12.8	14.3	3.0	4.3	3.3	2.4	3.6	12.0	23.6	69.4	20.8	–	–
ZSM 184/2003	PT	F	33.6	11.3	14.0	2.5	4.2	3.4	2.3	2.9	10.6	21.0	63.0	19.5	1.8	1.0
M. ambreensis																
MNHN 1893.241	HT	F	42.2	12.3	14.4	3.4	4.6	3.3	1.5	3.2	11.7	26.0	69.6	20.0	–	–
ZFMK 57417	–	M	32.1	11.6	13.0	5.0	4.1	3.2	2.4	4.0	11.1	21.3	55.3	17.0	6.2	3.7
M. femoralis																
BMNH 1947.2.22.65	LT	F	51.2	16.4	17.8	3.7	5.6	4.2	2.4	4.3	13.5	30.5	85.5	26.8	–	–
BMNH 1947.2.22.66	PLT	F	51.0	17.0	18.5	3.6	6.1	5.0	3.0	4.5	13.7	29.5	86.2	26.4	–	–
BMNH 1947.2.22.67	PLT	F	44.7	14.2	16.0	3.6	5.0	4.0	2.2	3.7	13.5	30.0	82.0	25.0	–	–
BMNH 1947.2.22.68	PLT	M?	31.0	11.0	12.8	3.0	4.5	2.7	1.8	3.1	10.4	22.2	61.2	19.2	nm	nm
BMNH 1947.2.26.53*	HT	F	54.1	19.5	21.1	3.8	6.3	5.3	3.4	4.4	18.0	36.5	113.4	31.4	–	–
MNHN 1935.153**	HT	F	47.9	15.9	18.4	3.8	5.0	4.7	3.4	4.5	13.7	29.6	78.0	23.8	–	–
MNHN 1937.1***	HT	F	53.5	17.3	21.1	4.2	6.0	5.3	3.5	5.1	nm	nm	ca. 94	28.3	–	–
ZFMK 60109	–	M	37.2	11.9	13.3	4.7	4.3	3.6	2.6	4.2	10.9	24.0	65.2	19.8	5.9	2.6
M. mocquardi																
MNHN 1929.207	HT	F	62.9	21.3	22.7	4.2	6.4	5.4	3.9	6.2	17.9	38.9	100.6	29.6	–	–
ZFMK 60105	–	M	41.0	13.2	15.4	5.5	5.0	3.8	2.5	4.4	12.8	27.0	67.3	21.5	6.9	4.1
M. majori																
BMNH 1947.2.10.27	LT	M	38.7	12.3	14.3	3.6	4.4	3.3	2.4	4.0	12.0	24.1	61.2	18.5		
BMNH 1947.2.10.26	PLT	F	44.8	13.8	16.1	4.1	4.8	3.4	2.9	3.6	12.9	25.3	67.0	19.6	–	–

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