

## **The tadpoles of *Scaphiophryne gottlebei* (Microhylidae: Scaphiophryninae) and *Mantella expectata* (Mantellidae: Mantellinae) from Isalo Massif, south-central Madagascar**

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The tadpoles of the microhylid *Scaphiophryne gottlebei* and of the mantellid *Mantella expectata* from the Isalo Massif (south-central Madagascar) are described and compared with already known tadpoles belonging to the same genera. The tadpole of *S. gottlebei* is peculiar in having the oral apparatus with a horny beak surrounded by dermal papillae, and a spiracle in intermediate position, between ventral and lateral. Furthermore, it shows unique feeding habits and a peculiar associated behaviour. During the day it stays close to the bottom and often burrows half of the body into the sand with the tail obliquely upwards; in this position it ingests organic material from among the substrate particles. During night time the tadpole leaves the bottom and swims throughout the water column. Since this tadpole cannot be included in any of the currently known ecomorphological categories we create a new category for this species, the “*psammonektonic*” tadpole. *Mantella expectata* was often found in the same environments, although it appears to prefer more open habitats. In some cases, tadpoles of both species were found together, although *M. expectata* usually prefers small and temporary streams for reproduction. The mantella tadpoles were also found in quite open savannah areas. The tadpole morphology agrees in general with that of other mantellas, mainly of the *M. betsileo* group, and is of the generalized ranoid type.

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## INTRODUCTION

Given the very high number of known species of amphibians in Madagascar (more than 220 according to ANDREONE & LUISELLI, 2003, ANDREONE et al., 2005, and subsequent updates), it is not surprising that for most of them the tadpole morphology and general larval ecology are not yet known. Nevertheless, it is clear that the knowledge of the tadpoles is a crucial step in the assessment of conservation priorities, as it allows understanding the ecological requirements of the species in its whole and not only during the adult stage. Besides, the analysis of anuran larvae may help in the clarification of enigmatic phylogenetic positions that are hardly to be unveiled by studying only the adult characters. Finally, it is interesting to understand how the adaptation to peculiar and local ecological conditions is reflected in the larval ecology.

The conservation status of all the Malagasy amphibians was recently evaluated during the Global Amphibian Assessment (ANDREONE et al., 2005), which led to the identification of nine critically endangered species. Since the majority of these species (five of the genus *Mantella* and *Scaphiophryne gottlebei*) are (or have been until recently) important items in the pet trade, and therefore quite regularly kept in captivity (ANDREONE & LUISELLI, 2003), it is surprising that the larval morphology is known for only one species, *Mantella aurantiaca* (ARNOULT, 1965; VENCES et al., 1999).

Thus, a series of surveys was recently carried out aimed at unveiling distribution and life history traits of these species. This was the case for *Scaphiophryne gottlebei* Busse & Böhme, 1992 and *Mantella expectata* Busse & Böhme, 1992, which are limited in distribution to the sandstone Isalo Massif, south-central Madagascar (GLAW & VENCES, 1994). Incidentally both these species were described upon specimens imported for the trade, and until recently little was known about their life history traits (BUSSE & BÖHME, 1992; GLAW & VENCES, 1994). During an inventory in the Isalo Massif we had the opportunity to find the tadpoles of these species, for which we provide here descriptions.

Since the tadpole of the enigmatic genus *Scaphiophryne* was stated to be intermediate between the microhylid and ranid forms (WASSERSUG, 1984), we also took the opportunity to compare the *S. gottlebei*'s tadpole with those of other allied species. Its peculiar behaviour and habits led us to create a new ecomorphological category, discussed in detail below. Since both species turned out to be syntopic, we also provide information on their larval ecology.

## MATERIAL AND METHODS

Tadpoles were captured with a handnet during day and night inspections of the pools and other water bodies present in the wet canyons (and nearby areas) of the Isalo Massif, south-central Madagascar (Fianarantosa Province). They were maintained alive in small aquaria and fed with fish food. This allowed us to obtain a complete development series and to confirm their natural history traits via observations in a controlled environment. Preserved tadpoles are now housed in the Museo Regionale di Scienze Naturali, Torino (MRSN; see Appendix).

For *S. gottlebei*, the species identification was based on rearing the tadpoles until metamorphosis and on comparing the mitochondrial DNA of larvae (voucher specimen MRSN A2618) and of adults. For DNA study, we used standard extraction methods. A fragment of the mitochondrial 16S rRNA gene was amplified using the primers 16Sa-L and 16Sb-H of PALUMBI et al. (1991). Sequences were validated and aligned with the software Sequence Navigator (Applied Biosystems), and deposited in Genbank (accession numbers of newly obtained sequences from the tadpole: DQ078784). For *Mantella expectata*, the tadpoles were collected in a temporary pool and were reared until metamorphosis.

Tadpoles were photographed at different stages. A small number was euthanized by immersion in chlorobutanol, and successively fixed in 4 % formalin for morphological measurements. A few individuals were fixed and preserved in 90 % ethanol for genetical analyses. The remnant part was released at the capture site.

Terminology of measurements follows ALTIG & MCDIARMID (1999), whereas the labial tooth formula is given according to ALTIG (1970). Measurements were made at 0.01 mm under stereoscope, and are respectively based on 10 specimens at GOSNER's (1960) stages 25-44 for *S. gottlebei*, and on 20 specimens at stages 25-37 for *M. expectata*. Mean values and standard deviations are given in the descriptions (see tab. 1-2). We measured the following physicochemical parameters at two sites: pH (with Extech Extik PH100), conductivity (Extech Extick EC400) and oxygen (Extech D0407510).

## RESULTS

### TADPOLES' DESCRIPTIONS

#### Scaphiophryne gottlebei Busse & Böhme, 1992 (fig. 1-3)

The tadpole of this species exhibits a mosaic of different ecomorphological traits (MCDIARMID & ALTIG, 1999), and we propose for it a new ecomorphological category (see *Discussion*).

The body is stout and elliptical, flattened below, ovoid above. The snout is trapezoidal in dorsal view. The eyes are medium-sized, positioned dorso-laterally. The external nares are located dorsally, closer to eyes than to snout tip. They are visible and positioned in a slight light-coloured furrow. In tadpoles at advanced development stages (from 25 to 38), the narial apertures are apparently not open; they become clearly open at stage 41.

Tail fins are rather high. The dorsal fin is parallel to tail musculature, the ventral fin is higher than the dorsal, with its maximum height at about two-thirds of tail length. The dorsal fin originates at the tail-body junction and the ventral fin at the postero-ventral end of the body.

The spiracle is latero-ventral with a posterior opening. The inner wall of spiracle is absent. The vent tube is medial, ventrally directed, with a medial aperture.

Table 1. – Measurements (at 0.1 mm) of 10 tadpoles of *Scaphiophryne gottlebei*. GS, Gosner stage; *n*, number of specimens; TL, total length; TAL, tail length; BL, body length; BW, body width; E, eye diameter; IOD, inter-orbital distance; TMW, tail muscle width; TMH, tail muscle height; MTH, maximum tail height. Values are given as mean ± standard deviation. See the Appendix for locality references.

| GS | <i>n</i> | TL         | TAL        | BL         | BW        | E         | IOD       | TMW       | TMH       | MTH       |
|----|----------|------------|------------|------------|-----------|-----------|-----------|-----------|-----------|-----------|
| 25 |          | 12.7 ± 1.9 | 25.3 ± 0.4 | 14.6 ± 5.1 | 4.8 ± 1.1 | 0.2 ± 0.1 | 2.5 ± 1.1 | 1.0 ± 0.0 | 1.7 ± 0.2 | 4.6 ± 1.6 |
| 26 |          | 14.3       | 26.1       | 11.8       | 4.8       | 0.2       | 3.0       | 1.2       | 2.0       | 4.5       |
| 27 | 1        | 21.0       | 37.0       | 15.5       | 18.0      | 0.3       | 5.0       | 1.2       | 3.0       | 7.0       |
| 33 | 1        | 23.5       | 40.8       | 17.3       | 10.0      | 0.4       | 5.7       | 2.0       | 3.5       | 8.0       |
| 34 | 1        | 25.0       | 41.5       | 16.5       | 8.5       | 0.3       | 6.0       | 1.3       | 3.1       | 8.2       |
| 38 | 1        | 29.1       | 48.2       | 19.1       | 11.0      | 1.6       | 8.0       | 2.6       | 5.0       | –         |
| 41 |          | 25.7 ± 3.2 | 41.3 ± 3.2 | 16.0 ± 0.0 | 9.3 ± 0.4 | 0.4 ± 0.1 | 5.3 ± 0.4 | 1.8 ± 0.4 | 3.6 ± 0.4 | 7.0 ± 1.3 |
| 44 | 1        | 13.6       | 26.6       | 13.0       | 6.0       | 0.4       | 3.7       | 1.2       | 2.1       | 2.3       |

Table 2. – Measurements (at 0.1 mm) of 20 tadpoles of *Mantella expectata*. GS, Gosner stage; *n*, number of specimens; TL, total length; TAL, tail length; BL, body length; BW, body width; E, eye diameter; IOD, inter-orbital distance; TMW, tail muscle width; TMH, tail muscle height; MTH, maximum tail height. Values are given as mean ± standard deviation. See the Appendix for locality references.

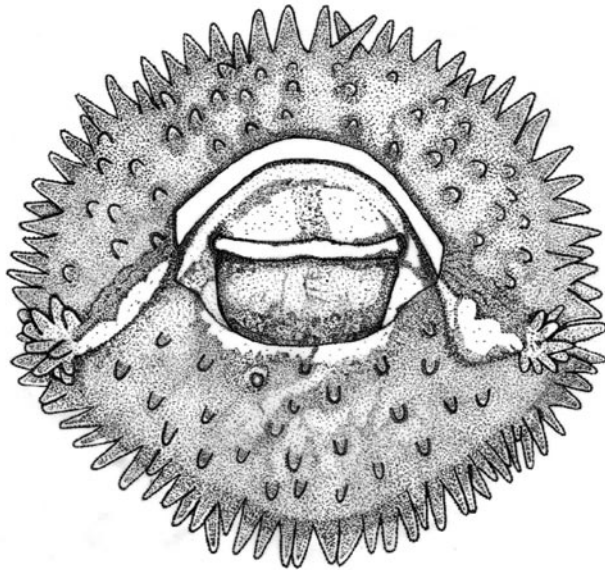
| GS | <i>n</i> | TL         | TAL        | BL        | BW        | E         | IOD       | TMW       | TMH       | MTH       |
|----|----------|------------|------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| 25 | 2        | 15.6 ± 3.4 | 9.4 ± 2.1  | 6.2 ± 1.3 | 4.0 ± 0.9 | 0.5 ± 0.1 | 1.3 ± 0.3 | 0.9 ± 0.3 | 1.1 ± 0.3 | 2.6 ± 0.6 |
| 26 |          | 19.7 ± 0.1 | 12.4 ± 1.8 | 7.3 ± 0.5 | 3.6 ± 0.3 | 0.6 ± 0.1 | 1.2 ± 0.2 | 0.9 ± 0.1 | 1.1 ± 0.3 | 2.4 ± 0.3 |
| 27 |          | 18.8 ± 4.9 | 11.0 ± 4.2 | 7.8 ± 0.7 | 3.8 ± 0.2 | 0.7 ± 0.1 | 1.3 ± 0.1 | 1.1 ± 0.2 | 1.1 ± 0.2 | 2.5 ± 0.2 |
| 28 |          | 20.0       | 12.0       | 8.0       | 4.0       | 0.7       | 1.5       | 0.9       | 1.1       | 1.3       |
| 35 |          | 25.1       | 14.8       | 10.3      | 5.7       | 0.9       | 1.5       | 1.7       | 1.7       | 4.0       |
| 37 |          | 28.6       | 17.8       | 10.8      | 6.2       | 1.1       | 1.8       | 1.8       | 2.6       | 4.6       |

The oral disc is roundish, not emarginated, with marginal and submarginal papillae tidily arranged all over the disc. The papillae are conical with rounded tips, sometimes with brownish pigment except at tips. Labial teeth are absent. Jaw sheaths are well developed. The inferior part of the lower jaw sheath is partially pigmented.

In life, the tadpoles are light greyish-brownish at night, shading to black during day, with sparse dark melanophores, denser in the dorsal and lateral posterior part of the body. A diamond-shaped translucent area is present between the eyes. Tail fins are transparent with a darker pigmented border on external edges, broader in the posterior end of ventral fin. Above the darker border, the tail is lightly scattered with dark spots. In preservative, the specimens become darker but maintain the natural pattern. Tadpoles near metamorphosis begin to acquire the adult pattern. Tadpoles in formalin kept the overall natural colour pattern, whereas tadpole in ethanol showed a general shrinkage and loss of colour. Metamorphosing toadlets are 10-15 mm long, with an overall coloration (white, red and black) similar to that of the adults, although apparently less contrasted.



Fig. 1. – Lateral view of a tadpole of *Scaphiophryne gottlebei*. MRSN A4961, Gosner stage 38 (total length 29.1 mm), from Zahavola, Isalo Massif.



**1 mm**

Fig. 2. – Oral disc of *Scaphiophryne gottlebei* (based upon MRSN A2618) at Gosner stage 38.



Fig. 3. – Tadpole of *Scaphiophryne gottlebei* half-buried in the sand, a typical position assumed during the day.

Observations in captivity and in nature confirmed that during the day the tadpoles stay close to the bottom and often burrow within the bottom's substrate with half the body embedded in the sand and mud and with the tail projecting obliquely upwards at an angle of about 30-45°. In this position, the tadpoles ingest particles of the substratum. At night they leave the bottom and swim throughout the water column, often reaching the surface where they ingest air.

*Mantella expectata* Busse & Böhme, 1992 (fig. 4-5)

These tadpoles are of the benthic type (McDIARMID & ALTIG, 1999).

The body is elliptical in lateral view and ovoid in dorsal view. The snout is dorsally rounded, whereas in lateral view it slopes gently to the oral region and then turns strongly. External nares are located dorso-laterally, almost half way from eyes to snout tip. The eyes are small and directed dorsally.

Tail fins are low and of about equal height, the dorsal fin being lower than the ventral at the level of the vent tube. The dorsal fin originates near the tail-body junction, and the ventral fin at the posterior ventral end of the body. The maximum tail height is at the middle of the tail. The tail tip is rounded with the tail muscle almost reaching the end of the tail.

The spiracle is sinistral with a mid-lateral opening directed posteriorly. The inner wall of the spiracle is present and free from the body. The vent tube is parallel with the ventral margin of the fin, tubular in shape and displaced dextrally, with a medial aperture.

The oral disc is antero-ventral, elliptical, emarginated, with a uniserial row of marginal papillae in the lower labium and on the lateral side of the upper labium. Few submarginal papillae are present in the lateral portions of the upper labium. The papillae are conical, with rounded tips, unpigmented and translucent. The labial tooth row formula is 5(2-5)/3(1). The upper jaw sheath is flat on its large medial part with a median concavity, the lower jaw sheath is V-shaped; both are finely serrated and entirely pigmented in black.

In life, these tadpoles are uniformly brownish and speckled with sparse melanophores, denser in the dorsal and lateral posterior part of the body. Tail fins are mainly transparent, slightly scattered with dark spots, especially the dorsal fin. In preservative, the specimens maintained the natural colour pattern.

The morphology of *Mantella expectata* tadpoles is similar to that of other mantellas of the *M. betsileo* group, being of a generalized ranoid type. Tadpoles close to metamorphosis begin to acquire the coloration typical of most of *Mantella* species: the back is brownish-yellowish, and the flanks blackish. At metamorphosis the froglets measure about 10 mm.

#### HABITAT DESCRIPTION

The sandstone Isalo Massif is located within the Central Ecoregion (ANONYMOUS, 2003). At the closest town, Ranohira, the mean monthly temperature is 25.1° C, with an absolute minimum of 3.4° C (June); precipitation is concentrated in the rainy season from late October to February (ANONYMOUS, 1999).



Fig. 4. – Lateral view of a tadpole of *Mantella expectata*. MRSN A3435, Gosner stage 37 (total length 28.5 mm) from Zahavola 1, Isalo Massif.

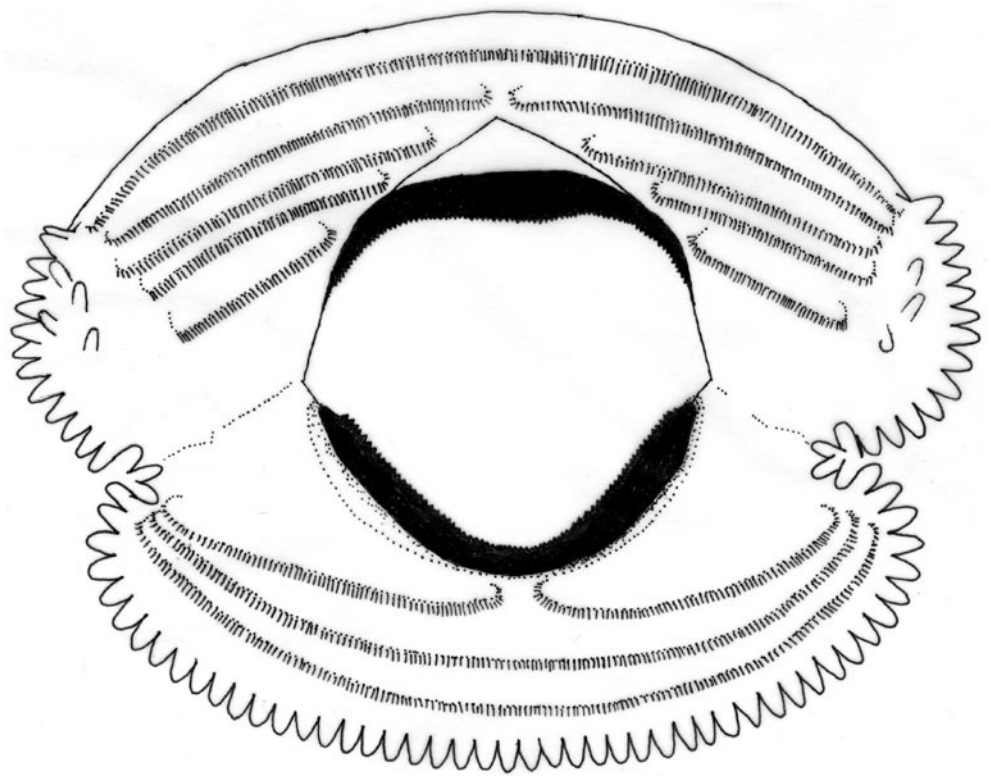


Fig. 5. – Oral disc of *Mantella expectata* (MRSN A3435) at Gosner stage 37.



To provide indications about the ecological preferences in adults and tadpoles of *S. gottlebei* and *M. expectata*, it is necessary to give an overall description of the Isalo Massif in terms of habitat availability.

The three main habitat types recognised within the Isalo Massif are related to the peculiar topography: (1) the savannahs, (2) open valleys, and (3) narrow canyons.

(1) The savannahs are subject to repeated fires and are covered with extensive meadows with scattered trees and isolated forest parcels. The night-day temperature difference is high, and the humidity is usually very low. Aquatic habitats are represented by temporary pools (often used for cattle), streams and rivers. The temporary rivers are filled by seasonal rains, and are dry for most of the year. A few permanent or semi-permanent rivers are present and may be accompanied by gallery forests. At these habitats we found species which breed in temporary waters (e.g., *Boophis occidentalis*, *Laliostoma labrosum*, *Ptychadena mascareniensis*, *Scaphiophryne brevis* and *Dyscophus insularis*).

(2) The open valleys are usually crossed by permanent or semi-permanent torrents with quite wide water beds, cascades and pools, and gallery forests of various sizes. We found frog species that usually need permanent water to breed, such as *Mantidactylus cf. femoralis*, *Boophis goudoti* and also *Boophis occidentalis*.

(3) The rocky and montane part is crossed by canyons of various lengths, widths and depths, and with a variable water presence. Some canyons are very narrow with a sandy bed delimited by vertical rock walls. The habitat is dark and sometimes quite similar to a cave, with a rather low and constant temperature (19-22°C) and high humidity (about 100 %). Within these close canyons, vegetation is absent (due to scarcity of light) or limited to a few isolated trees. Typical species of this habitat are *Scaphiophryne gottlebei*, *Mantidactylus corvus* and *Mantella expectata*.

The canyons can be ideally divided in four tracts, although not all of them are always present: (a) savannah tract, with absent to low walls (0.5-1.5 m high), grass vegetation, sandstone soil substratum with cobbles, small pools (0.1-0.2 m deep) with little or no water, exposed to sunlight and subject to strong evaporation; (b) initial tract with medium-high walls (1.5-5.0 m), if present high arboreal or shrub-like vegetation in the floodwater bed, thin sandstone substratum with cobbles or isolated stones, and deep water-filled pools (0.5-1,5 m), sometimes exposed to sunlight; (c) gully tract, with high to very high vertical walls (5.0 m and more), no vegetation, thin sandstone soil or rocky substratum, very deep water-filled pools (1.5 m and more), generally no sunlight exposure (in some cases this tract may have a cave-like aspect); (d) terminal tract, with high to very high vertical or concave walls directly in contact with the watershed, possibly temporary waterfalls, absent or scarce flood-water bed vegetation, water-filled pools of different depths, temporarily exposed to sunlight.

Adults of *S. gottlebei* were usually found within the canyons, where they burrow in the sandy substrate or hide in cavities in the walls. In rare cases we found them outside the canyons. As a consequence, the tadpoles were usually found in temporary pools excavated by running water in the rocks within the narrow canyons, gully and terminal tracts (fig. 6). In some cases, especially after heavy rainfalls, tadpoles were found in the initial tract. In December 2004, we found tadpoles that had likely hatched at the beginning of October: after



Fig. 6. – Habitat of *Scaphiophryne gottlebei* at Malaso, Isalo Massif. Gully tract of the canyon, with deep and semi-permanent water pools.

more than two months, they were still without hind legs. For this reason, we suspect that metamorphosis in this species takes 2-3 months, according to the local climatic conditions.

Adult individuals of *M. expectata* were found in open areas along the small streams quite exposed to the sun. We usually did not observe the mantellas within the real canyons, although in some occasions they were seen at the initial tract. The tadpoles were found in the small pools in open areas, only rarely within the canyons. Tadpoles of *M. expectata* were generally found in the savannah and initial tract of canyons, quite exposed to the sunlight, although in some cases they could be present in the other tracts (fig. 7). *M. expectata* breeds and completes its larval development in about 1-2 months.

We also measured the chemical water parameters at two of the studied sites: (1) "Zahavola 2" (presence of *S. gottlebei* tadpoles): water temperature 24°C, pH 5.23, conductivity 10.04  $\mu\text{S}/\text{cm}$ ,  $\text{O}_2$  8.8 mg/l; (2) "Zahavola 3" (presence of *M. expectata* tadpoles), water temperature 26.6°C, pH 7.25, conductivity 8.07  $\mu\text{S}/\text{cm}$ ,  $\text{O}_2$  2.7 mg/l.

## DISCUSSION

The discovery and description of the tadpole of *Scaphiophryne gottlebei* allows us to make some preliminary comparisons with the general morphology of tadpoles of other species belonging to the genus *Scaphiophryne*. At present only the tadpoles of *S. calcarata* and of the recently described *S. menabensis* are sufficiently known (BLOMMERS-SCHLÖSSER, 1975; BLOMMERS-SCHLÖSSER & BLANC, 1991; GLOS et al., 2005).

Concerning *S. calcarata*, the line drawing and the written description of the tadpoles suggested that they were nektonic. The text also indicated that their beak was not keratinised. As stressed in WASSERSUG's (1984) study of the internal anatomy, this statement was wrong, since these mouthparts are keratinised. Apart from this, the description of this tadpole does not differ much from what we report for *S. gottlebei*. Both species have a terminal mouth surrounded by dermal papillae. Possible differences concern the lack of the extended flap on the lower lip and the narial position, which appears nearer to the tip of the snout in *S. calcarata* and nearer to the eye in *S. gottlebei*.

The tadpole of *Scaphiophryne gottlebei* differs from that of *S. menabensis* by body shape, by narial distances (nearer to the eye vs. same distance to snout tip and to eye). Similarities are shared in the morphology of the oral disc with unpigmented jaw sheaths and marginal conical papillae, and on the displacement of the spiracle (GLOS et al., 2005).

The tadpoles of *Scaphiophryne gottlebei* also show unique feeding habits and an associated particular swimming behaviour. During the day they usually stay close to the bottom and burrow within the substrate, propelled by intermittent movements of tail and body, with half the body dug into the sand and with the tail obliquely upwards (at an angle of 35-40°). In this half-buried position they ingest particles from the mud and sand substratum. In fact, in all collected tadpoles the intestine was completely filled with detritus. During night time the tadpoles leave the bottom and swim throughout the water column while apparently filtering suspended particles. As far as known the only other tadpoles that show somewhat similar habits belong to the microhylid *Otophryne robusta*. This tadpole is a passive filter-feeder in a



Fig. 7. – Habitat of *Mantella expectata* at Lola, Isalo Massif. It is represented by a temporary stream at the beginning of the initial tract of the typical montane canyons.

full fossorial habitat with related unique morphological features (WASSERSUG & PYBURN, 1987).

The odd feeding habits make it hard to place the *S. gottlebei* tadpole in the ecomorphological categories of McDIARMIG & ALTIG (1999). If forced into this classification, it should be considered as intermediate between “suspension feeder type 2” and “suspension rasper” and between “benthic” and “psammonic”. For this reason we coined the name “*psammonektonic*” for a new ecomorphological category. This category describes a tadpole with keratinised mouthparts and papillae, ventro-lateral spiracle, dorso-lateral eyes, feeding partially by filtering suspended particles within the water column and by direct ingestion of substratum through active burrowing, and active day and night.

Four other *Scaphiophryne* species (*S. brevis*, *S. sp.* from Andringitra [formerly attributed to *S. madagascariensis*], *S. madagascariensis* from Ankaratra, and *S. marmorata* from Andasibe area) were cursorily described by GLAW & VENCES (1994), VENCES et al. (2002) and BIGGI (2002), but none of these data allows any detailed comparison. Anyhow, from the observations and photographs in these publications, we presume that the tadpoles of these species are similar to that of *S. gottlebei* in having: (1) a ventro-lateral spiracle, (2) keratinized jaw sheaths, (3) an absence of teeth, (4) dorso-lateral eyes, (5) a general robust body shape, and (6) suspension and/or macrophagous feeding habits. Furthermore, these tadpoles are also transitional between benthic and nektonic morphotypes and feed on small particles. The general morphological similarity is also confirmed by the photograph of *S. madagascariensis* from Ankaratra (VENCES et al., 2002), that shows a tadpole very similar to that of *S. gottlebei* herein described.

Of the above mentioned characters, the presence in *S. madagascariensis* of keratinised jaw sheaths, described by GLAW & VENCES (1994), has been recently confirmed by HAAS (2003). Maybe, as observed also in the tadpole description of *S. calcarata*, the presence of unpigmented but keratinised jaw sheaths lead previous authors to mistake as they assumed that keratinized tissue has to be black.

A more detailed comparative analysis of the *Scaphiophryne* tadpoles is much needed because the scaphiophrynines have so far been alternatively included in the Ranidae, Microhylidae or Hyperoliidae families (WASSERSUG, 1984) or even in a separate family (DUBOIS, 1992). The type 2 larva of ORTON (1953, 1957) was generally considered diagnostic of the Microhylidae, but indeed larvae of scaphiophrynines and many other microhylids remain unknown. As shown by BLOMMERS-SCHLÖSSER's and WASSERSUG's works, now confirmed by the description of the *S. gottlebei* tadpole, the tadpole groups after ORTON often appear inadequate to provide clear phylogenetic information. Furthermore, the inclusion the genus *Paradoxophyla* within the Scaphiophryninae should be re-investigated, as this genus has a specialised filtering tadpole (ANDREONE et al., 2006). So far, the information available does not provide an unequivocal indication.

Finally, tadpoles of the genus *Mantella* are less crucial in determining phylogenetic allocation because they belong to the typical ranoid morph. Moreover, the genus *Mantella* appears very homogeneous in terms of morphology and ecology. The only detailed data were reported for *M. aurantiaca* by ARNOULT (1965) and later summarised by BLOMMERS-SCHLÖSSER & BLANC (1991). Indeed, both species share a labial tooth row formula of 5(2-5)/3(1) and have an emarginated oral disc with papillae on the lower labium. Papillae in *M.*

*expectata* are displaced in a uniserial row whereas in *M. aurantiaca* they are apparently biserial. In contrast, *M. laevigata* differs in having a reduced labial formula of 3(2-3)/3 or 4(2-3)/3(1-3) and a stronger and more notched horny beak (GLAW & VENCES, 1994). Further comparisons with other species are not possible because of lack of information.

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## APPENDIX

### LIST OF EXAMINED SPECIMENS

All the collecting sites are within Ranohira Fivondrononana, Fianarantsoa Faritany, Madagascar. An asterisk (\*) indicates ethanol fixed specimens.

*Scaphiophryne gottlebei* Busse & Böhme, 1992: MRSN A2618 ( $n = 1$ ) and A2619\* ( $n = 1$ ), Isalo Massif, Parc National de l'Isalo, Vallée du Petit Nazareth, 22°32.91'S, 45°21.72'E, 890 m, leg. V. Mercurio, 2.II.2004; MRSN A4961 ( $n = 3$ ), Isalo Massif, Parc National de l'Isalo, Marojana River, 22°27.43'S, 45°22.40'E, 867 m, leg. V. Mercurio, 15.XI.2004; MRSN A4962 ( $n = 6$ ), Isalo Massif, Zahavola 2, 22°37.38'S, 45°21.52'N, 825 m, leg. F. Andreone, F. Mattioli & V. Mercurio, 20.XI.2004.

*Mantella expectata* Busse & Böhme, 1992: MRSN A3432 ( $n = 22$ ) and MRSN A3433 ( $n = 23$ ), Isalo Massif, Andranomena, 45°18.86'E, 22°45.71'S, 786 m, leg. F. Andreone, V. Mercurio & J. E. Randrianirina, 28.I.2004; MRSN A3434, ( $n = 2$ ), Isalo Massif, Parc National de l'Isalo, Zahavola 3, 45°21.48'E, 22°37.51'S, 835 m, leg. V. Mercurio, 2.II.2004; MRSN A3435 ( $n = 2$ ), Isalo Massif, Parc National de l'Isalo, Andohasahenina, 45°17.28'E, 22°49.79'S, 630-680 m, leg. F. Andreone, G. Aprea, V. Mercurio & J. E. Randrianirina, 15.I.2004.