Alytes, submitted

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

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The tadpoles of the microhylid *Scaphiophryne gottlebei* and of the mantellid *Mantella expectata* (Isalo Massif, central-southern Madagascar) are described and compared to already known species of the same genera. The tadpole of *S. gottlebei* is peculiar in having the oral apparatus with a horny beak surrounded by dermal papillae, and has a spiracle in intermediate position, between ventral and lateral. Furthermore, the tadpole shows unique feeding habits and peculiar associated behaviour: during the day it stays close to the bottom and often borrow within the substrate with half body dug inside the sand and with the tail obliquely upwards. In this position it ingests particles of the substratum. During the night time the tadpole leaves the bottom, and move within the whole water column. This tadpole is difficult to be included in any of the currently known ecomorphological categories. Therefore, we create a new category, the "psammonektonic" tadpole. *Mantella expectata* was sometimes found in the same environments, although it appears to prefer more open habitats. In some cases tadpoles of both the species were found together, although *M. expectata* usually prefers for reproduction small and temporary streams. The tadpoles were found in the also 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.

INTRODUCTION

Seen the very high number of known species of amphibians in Madagascar (more than 220 according to Andreone et al., 2005) it is not strange that for most of them the tadpole morphology and general larval ecology are not yet known. Notwithstanding, it is clear that the knowledge of the tadpoles is a crucial step in the assessment of conservation priorities, understanding the ecological requirements of the species in its whole and not only for the adult stage. Then, the analysis of larvae may help in the clarification of enigmatic phylogenetic positions that are hardly to be unveiled by basing only upon the adult characters. Finally, it is

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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 program (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 (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 to unveil 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, southcentral Madagascar (Glaw & Vences, 1994). Incidentally both these species were described upon specimens imported for the trade, and little was until 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, that are here described in detail.

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

MATERIAL AND METHODS

Tadpoles were captured with a handnet during 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.

For *S. gottlebei* the species identification was based on comparison of the mitochondrial DNA of larvae (voucher specimen MRSN A2618) and adults, using standard extraction methods and 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), and rearing the tadpoles until metamorphosis. For *Mantella expectata* the tadpoles were collected in a temporary pool and were reared until metamorphosis.

Tadpoles were then 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. Preserved tadpoles are now housed in the Museo Regionale di Scienze Naturali, Torino (MRSN; see the Appendix).

Terminology of measurements usually follows Altig & McDiarmid (1999), while the labial tooth formula is given according to Altig (1970). Measurements were made at 0,01 mm under stereoscope magnification 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 description (see tab. 1). We measured the 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

(Figs. 1-3)

The tadpole of this species exhibits a mosaic of different ecomorphological traits (McDiarmid & Altig, 1999), and we propose for it the new ecomorphological category: "psammonektonic" (see discussion).

Stout and elliptical body flattened below, ovoid above. The snout is trapezoidal in dorsal view. Medium-sized eyes positioned dorsolaterally. External nares located dorsally, closer to eyes than to snout tip. They are visible and positioned in a slight light-coloured furrow. In spite of the fact that the tadpoles are in advanced development stages (from 25 to 38), the narial aperture is apparently not open. They become clearly open from stage 41.

Tail fins comparatively high. Dorsal fin parallel to tail musculature, ventral fin higher than dorsal with maximum height at about two-thirds of the tail length. Origin of dorsal fin at the tail-body junction and origin of the ventral fin at the posteroventral terminus of the body.

Spiracle lateroventral with a posterior opening. Inner wall of spiracle absent. Vent tube medial, ventrally directed with a medial aperture.

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

In life, the tadpoles are greyish-brownish at night, shading to black during the day, with sparse dark melanophores, more dense in the dorsal and lateral posterior part of the body. Diamond-shaped translucent area 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 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 maintained the overall natural colour pattern, while tadpole in ethanol showed a general shrinkage and loss of colour. Metamorphosing toadlets are 10-15 mm long, with an overall colouration similar to that of the adults -. white, red and black, although apparently less contrasted.

Observations in captivity and in nature confirmed that during the days the tadpoles stay close to the bottom and often borrow 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

(Figs 4-5)

Tadpoles of the benthic type (McDiarmid & Altig, 1999).

Body elliptical in lateral and ovoid in dorsal view. Snout dorsally rounded, while in lateral view it slopes gently to the oral region and then turns strongly. External nares located dorsolaterally, almost half way from eyes to snout tip. Eyes small and directed dorsally.

Tail fins low and of about equal height; the dorsal fin lower than the ventral at the plane of the vent tube. Origin of dorsal fin near at the tail-body junction and origin of ventral fin at the posterior ventral terminus of the body. Maximum tail height in the middle of the tail. Tail tip rounded with the tail muscle almost reaching the tip of the fins.

Spiracle sinistral with a midlateral opening directed posteriorly. Inner wall of spiracle present and free from the body. Vent tube parallel with the ventral margin of the fin, tubular in shape, and displaced dextrally with a medial aperture.

Oral disc anteroventral, 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 present in the lateral portions of upper labium. The papillae are conical, with rounded tips, nonpigmented and translucent. Labial tooth row formula 5(2-5)/3(1). Upper jaw sheath flat on its large medial part with a median concavity, lower jaw sheath V-shaped, both finely serrated and entirely pigmented black.

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

The morphology of *Mantella expectata* tadpoles agree with that of other mantellas of the *M. betsileo* group, and are 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 with the flanks blackish. At metamorphosis the froglets measure about 10 mm.

HABITAT DESCRIPTION

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

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

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

(1) The savannahs are subject to repeated fires and are represented by extensive meadows with scattered trees and isolated forest parcels. The night-day temperature excursion 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 a gallery forest. 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 a quite wide water bed, 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 *B. 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), sometime 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. In some cases, especially after heavy rainfalls, tadpoles were found in the initial tract. In December 2004 we found tadpoles that were likely hatched at the beginning of October, and after more than two months, they still were without hind legs. For this 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 more open areas along the small streams quite exposed to the sun. We usually did not observe the mantellas within the 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. *M. expectata* breeds and completes its larval development in about 1 month.

We also measured the chemical water parameters at two of the studied sites, which are: (1) "Zahavola 2" (presence of *S. gottlebei* tadpoles): water temperature 24°C, pH 5.23, conductivity 10.04 µS/cm, O_2 8.8 mg/l; (2) "Zahavola 3", (presence of *M. expectata* tadpoles), water temperature 26.6 °C, pH 7.25, conductivity8.07 µS /cm, O_2 2.7 mg/l.

DISCUSSION

The discovery and description of the tadpole of *Scaphiophryne gottlebei* allows us to make a preliminary comparison with the general morphology 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 (see Blommers-Schlösser, 1975; Blommers-Schlösser & Blanc, 1991; Glos et al., 2005).

Concerning *S. calcarata* the line drawing and the written description of tadpoles indicated that they are nektonic. The text provided the information that its beak was not keratinised. This affirmation, as stressed by Wassersug's (1984) study of the internal anatomy, was wrongly diagnosed, and 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 deal with the narial position, which is likely nearer to the tip of the snout in *S. calcarata* and nearer to the eyes in *S. gottlebei,* together with the lack of the extended flap on the lower lip.

The tadpole of *Scaphiophryne gottlebei* differs from that of *S. menabensis* by body shape (without a visible gap between the outer integument and the body vs. presence of a gap), by narial distances (nearer to the eyes vs. same distance to snout tip and to eyes); similarities are shared in the morphology of oral disc with unpigmented jaw sheaths and marginal conical papillae and on the displacement of spiracle (Glos et al., 2005).

Scaphiophryne gottlebei's tadpoles also show unique feeding habits and an associated particular swimming behaviour. During the day the tadpoles stay close to the bottom and usually borrow within the substrate, propelled by intermittent movements of tail and body, with half body dug inside the sand and with the tail obliquely upwards (35-40°). In this position they ingest particles of the substratum (represented by mud or sand). In fact, in all collected tadpoles the intestine was complete detritus filled. During the night time the tadpoles leave the bottom and the half-dug position, and swim within the whole water column apparently by filtering suspended particles. As far as known the only other tadpoles that show a somewhat similar habits belong to the microhylid *Otophryne robusta*. This species is also unique having tadpoles that shows an aquatic passively filter-feed in a full fossorial habitat with relating unique morphological features (Wassersug & Pyburn, 1987).

The odd feeding habits make difficult the insertion of *S. gottlebei* tadpole inside the ecomorphological categories proposed in McDiarmig & Altig (1999). Forced to 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 here coin the name "psammonektonic" for a new ecomorphological category. This category describes a tadpole with keratinised mouthparts and papillae, ventrolateral spiracle, dorsolateral eyes, feeding partially by filtering suspended particles within the water column and by direct ingestion of substratum through active burrowing, active day and night.

Four other *Scaphiophryne* species (*S. brevis*, *S.* sp. from Andringitra and formerly attributed to *S. madagascariensis*, *S. madagascariensis* from Ankaratra, and *S. marmorata*) cursory descriptions were given by Glaw & Vences (1994), Vences et al. (2002 a), 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 latero-ventral spiracle, (2) keratinized jaw sheaths, (3) absence of teeth, (4) dorsolateral 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., 2002a),that shows a tadpole very similar to that herein described of *S. gottlebei*.

Of the above mentioned characters the presence in *S. madagascariernsis* of keratinised jaw sheaths has been recently confirmed in Haas (2003). As described by Glaw & Vences (1994) the absence was wrongly diagnosed. Maybe, as observed also in *S. calcarata* tadpole's description, the presence of unpigmented but keratinised jaw sheaths leads to mistake while to assume that keratinized tissue has to be black.

A more detailed analysis of the *Scaphiophryne* tadpoles is urgently 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 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 Orton's tadpole groups often appear inadequate to provide clear phylogenetic information. Furthermore, the inclusion the genus *Paradoxophyla* within Scaphiophryninae is still a matter of debate; whether this genus is correctly assigned to Scaphiophryninae should be investigated as it is a specialised filtering tadpole (Andreone et al., in press) derived from that of *Scaphiophryne*. So far, the information does not provide an unequivocal indication.

Finally, tadpoles of the genus *Mantella* are less crucial in determining phylogenetic assessment because they belong to the typical ranoid morph. Moreover, the genus *Mantella* appears very homogeneous in terms of morphology and ecology, and there is no evidence of a great divergence in tadpole morphology. The only detailed data are reported for *M. aurantiaca* by Arnoult (1965) and later summarised by Blommers–Schlösser & Blanc (1991). Indeed, both species share a labial tooth row formula 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 while in *M. aurantiaca* they are apparently biserial. In contrast, *M. laevigata* differs by having a reduced labial formula 3(2-3)/3 or 4(2-2)/3(1-3) and a stronger and more notched horny beak (Glaw & Vences, 1994). Further comparison with other species are not possible because the lack of information.

ACKNOWLEDGMENTS

This work was supported by the Nando Peretti Foundation, the National Amphibian Conservation Center, the Declining Amphibian Population Task Force / IUCN Madagascar, the Madagascar Fauna Group, Conservation International, and Wildlife Conservation Society. Thanks also to the Malagasy authorities for collection and export permits. G. Aprea, F. Mattioli, J. E. Randrianirina, and T. J. Razafindrabe assisted in the field. M. Vences helped with the genetic confirmation and with critical comments on an earlier draft of this paper. We are also greatly grateful to Ronald Altig to have improved the manuscript with his critical comments, and to Richard J. Wassersug for bibliography.

APPENDIX

LIST OF EXAMINED SPECIMENS

All the sites included within Ranohira Fivondrononana, Fianarantsoa Faritany). The asterisk (*) indicates the ethanol fixed specimens.

Scaphiophryne gottlebei

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 a.s.l., leg. V. Mercurio, 2.II.2004; MRSN A4961 (n = 3), Isalo Massif, Parc National de l'Isalo, "Marojana River", 867 m a.s.l., leg. V. Mercurio, 15.XI.2004, 22°27.43'S, 45°22.40'E; MRSN A4962 (n = 6), Isalo Massif, "Zahavola 2", 22°37.38'S, 45°21.52'N., 825 m a.s.l., leg. F. Andreone, F. Mattioli & V. Mercurio, 20.XI.2004.

Mantella expectata

MRSN A3432 (n = 22) and MRSN A3433, (n = 23), Isalo Massif, "Andranomena", 45°18.86'E, 22°45.71'S, 786 m a.s.l., 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 a.s.l., 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 a.s.l., leg. F. Andreone, G. Aprea, V. Mercurio & J. E. Randrianirina, 15.I.2004.

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CAPTIONS FOR FIGURES

Fig. 1. Lateral view of a tadpole of *Scaphiophryne gottlebei*. MRSN A4961, Gosner's stage 38, from Zahavola, Isalo Massif.

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

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

Fig. 4. Lateral view of the tadpole of *Mantella expectata*. MRSN A3435 on specimens at Gosner's stage 37 the most advanced stadium in our sample from Isalo Massif.

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

Fig. 5. Habitats of *Scaphiophryne gottlebei* and *Mantella expectata* in the surroundings of Ilakaka, Isalo Massif. (A) narrow canyon; (B) temporary pool.

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

GS	N	TL	TAL	BL	BW	E	IOD	TMW	TMH	MTH
25	2	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	1	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	2	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; BL, body length; TAL, tail length; BW, body width; E, eyes diameter; IOD, inter-orbital distance; TMW, tail muscle width; TMH, tail muscle height; MTH, maximum tail height. Values are given as means ± standard deviations. See the appendix for locality references.

GS	N	TL	TAL	BL	BW	E	IOD	TMW	TMH	MTH
25	12	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	3	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	2	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	1	20.0	12.0	8.0	4.0	0.7	1.5	0.9	1.1	1.3
35	1	25.1	14.8	10.3	5.7	0.9	1.5	1.7	1.7	4.0
37	1	28.6	17.8	10.8	6.2	1.1	1.8	1.8	2.6	4.6

FIGURE 1

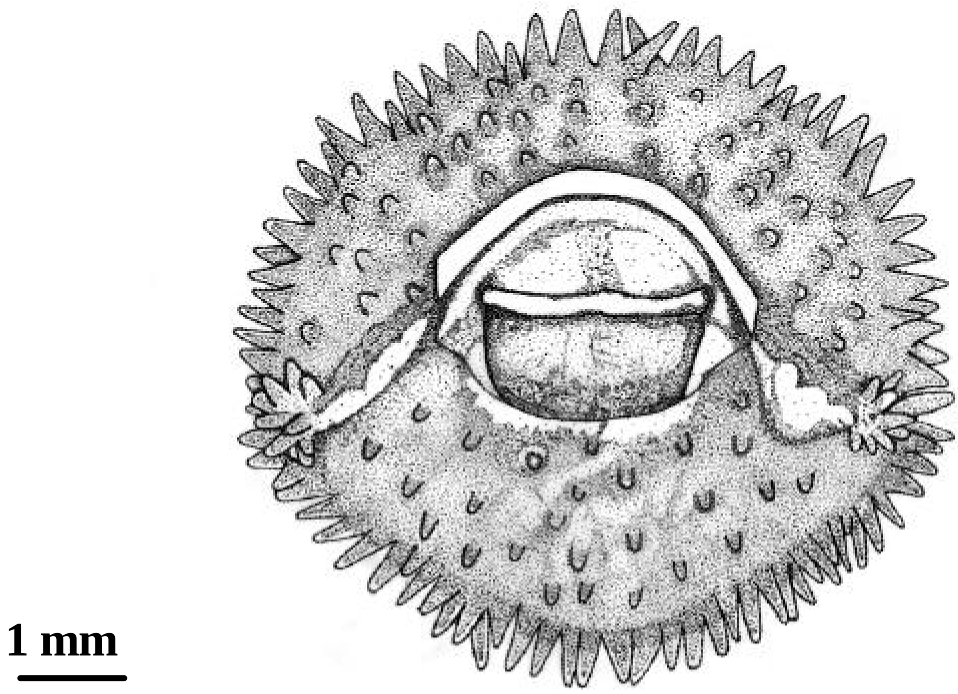

FIGURE 2

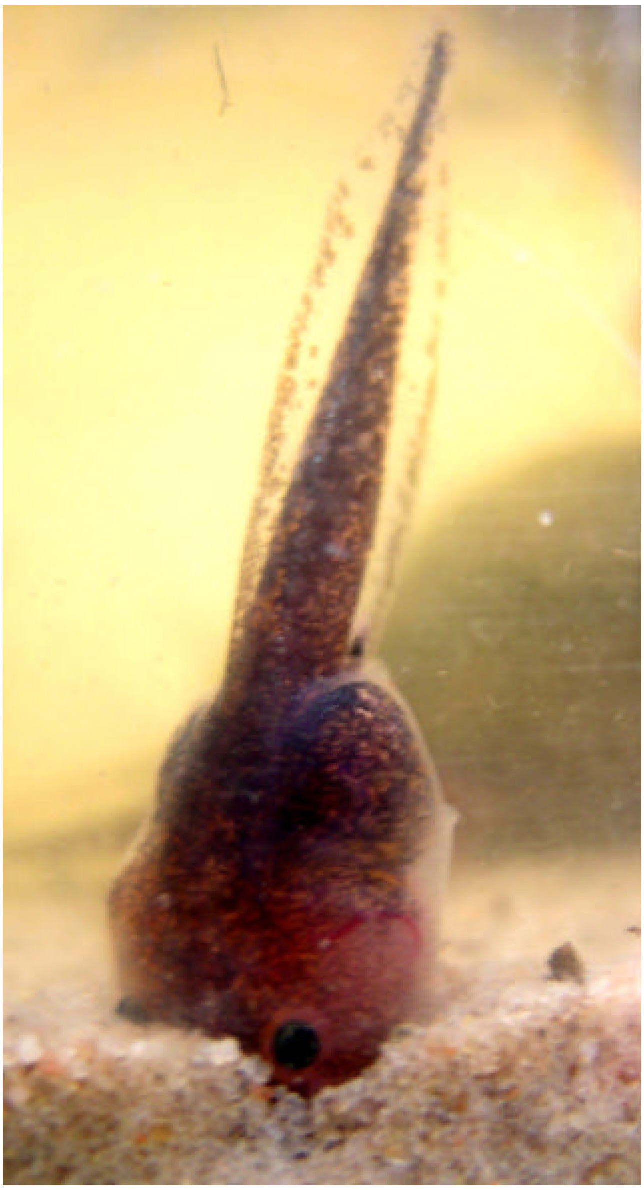

FIGURE 3

FIGURE 4

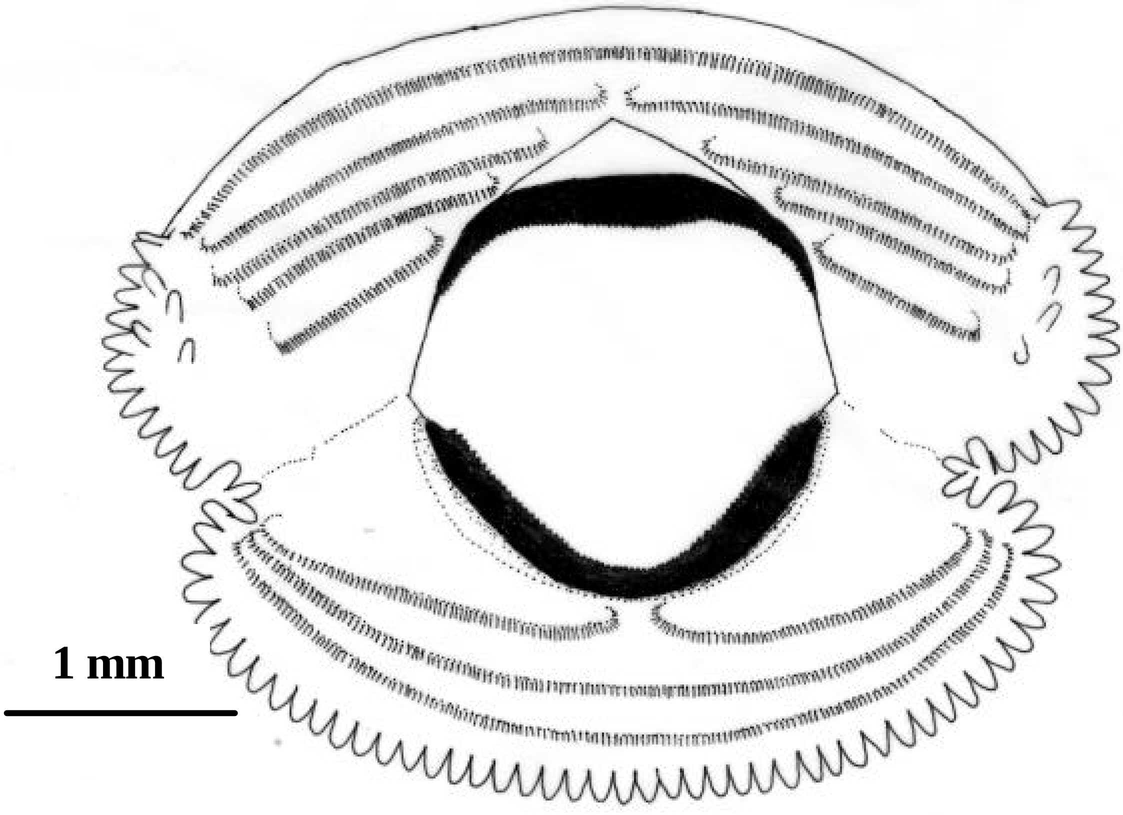

FIGURE 5

A **B**

FIGURE 6 (DA SOSTITUIRE)