Revue suisse de Zoologie 114 (4): 825-837; décembre 2007

Larval morphology of reed frogs, *Hyperolius kivuensis* and *H. viridiflavus*, from western Kenya (Amphibia, Hyperoliidae)

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Larval morphology of reed frogs, *Hyperolius kivuensis* and *H. viridiflavus*, from western Kenya (Amphibia, Hyperoliidae).- We describe external characters, oral disc and oral cavity structures of larval *Hyperolius kivuensis* and *H. viridiflavus,* i.e. exotrophous lentic benthic type IV tadpoles. External morphology of both is comparable and matches descriptions of other *Hyperolius* species. Differences among the two taxa were noted in the keratinized labial teeth. In *H. kivuensis*, the spoon-shaped cusped tooth type is frequent and represented by two different subtypes: (i) "cusped" with four cusps, the two distal of which only slightly larger than the lateral cusps; (ii) "pointed" with the two distal cusps larger than the two lateral cusps forming a bifurcation. The latter subtype is rare in *H. kivuensis*, while most frequent in *H. viridiflavus*. In this species, also another type occurs, characterized by two long distal cusps, forming a bifurcation, and two small lateral cusps; the cusped type with cusps of the same size as in *H. kivuensis* is rare. Both species show similar oral cavity structures except for the choanae position, i.e. arranged in a V that is opened posteriorly in *H. kivuensis* versus a V opened anteriorly in *H. viridiflavus*. Choanae position and keratinized labial teeth structure may provide diagnostic features for these and other species of *Hyperolius*.

Keywords: Anura - labial teeth - oral cavity - tadpoles.

INTRODUCTION

There are approximately 120 described species of Afrotropical reed frogs, genus *Hyperolius* (Schiøtz, 1999). However, detailed descriptions of the larvae exist for less than 20 of them (Rödel, 1999; Schiøtz, 1999; Channing, 2001; Channing & Howell, 2006). During field surveys in western Kenya, adults and larvae of five syntopic reed frog species were collected (Lötters *et al.,* 2004). The larvae of *Hyperolius kivuensis* Ahl, 1931 and *H. viridiflavus* (Duméril & Bibron, 1841), for which a large series of positive species allocation could be obtained (see below), are described here. The former species is known from eastern and central Africa, while the latter is distributed in eastern Africa. (Schiøtz, 1999; Lötters *et al.,* 2004).

Manuscript accepted 05.07.2007

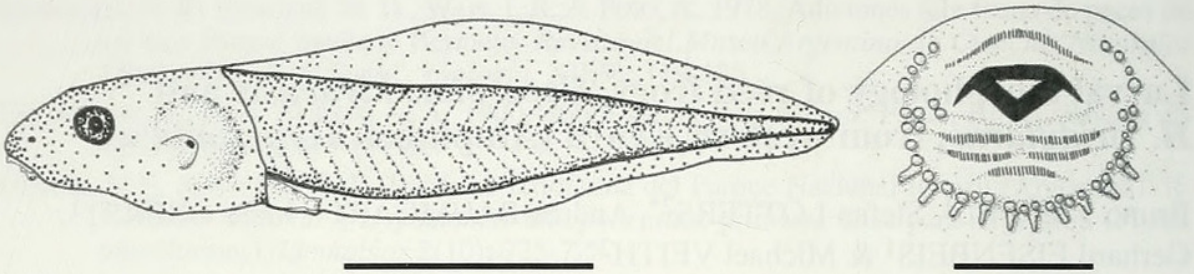


FIG. 1

Views of lateral body and oral disc of a *Hyperolius kivuensis* larva from western Kenya, stage 36 (MHNG 2661.31). Lines equal 1 cm and 1 mm, respectively. Illustration by A. and J. Channing.

Larval morphology may provide useful characters for species diagnoses and for assessment of phylogenetic relationships (Orton, 1953, 1957; Starrett, 1973). However, the known larvae of *Hyperolius* are similar in external morphology. Differences in size, body proportions, and colors between the species are apparently too minor for unambiguous identification or systematic purposes (e.g. Channing, 2001).

More than 100 years ago Heron-Royer & van Bambeke (1889) and Boulenger (1891) introduced the oral disc morphology including the oral teeth as diagnostic tadpole characters. The morphology of the oral cavity was also used by Wassersug (1980, 1984), Viertel (1982), and Wassersug & Heyer (1988) for the diagnosis of anuran larvae. Oral disc and oral cavity morphology has yet not been studied in *Hyperolius* larvae.

The goal of the present study is (i) to describe and to discuss the external, oral disc, and oral cavity morphology of *H. kivuensis* and *H. viridiflavus* larvae, and (ii) to discuss their utility for *Hyperolius* taxonomy.

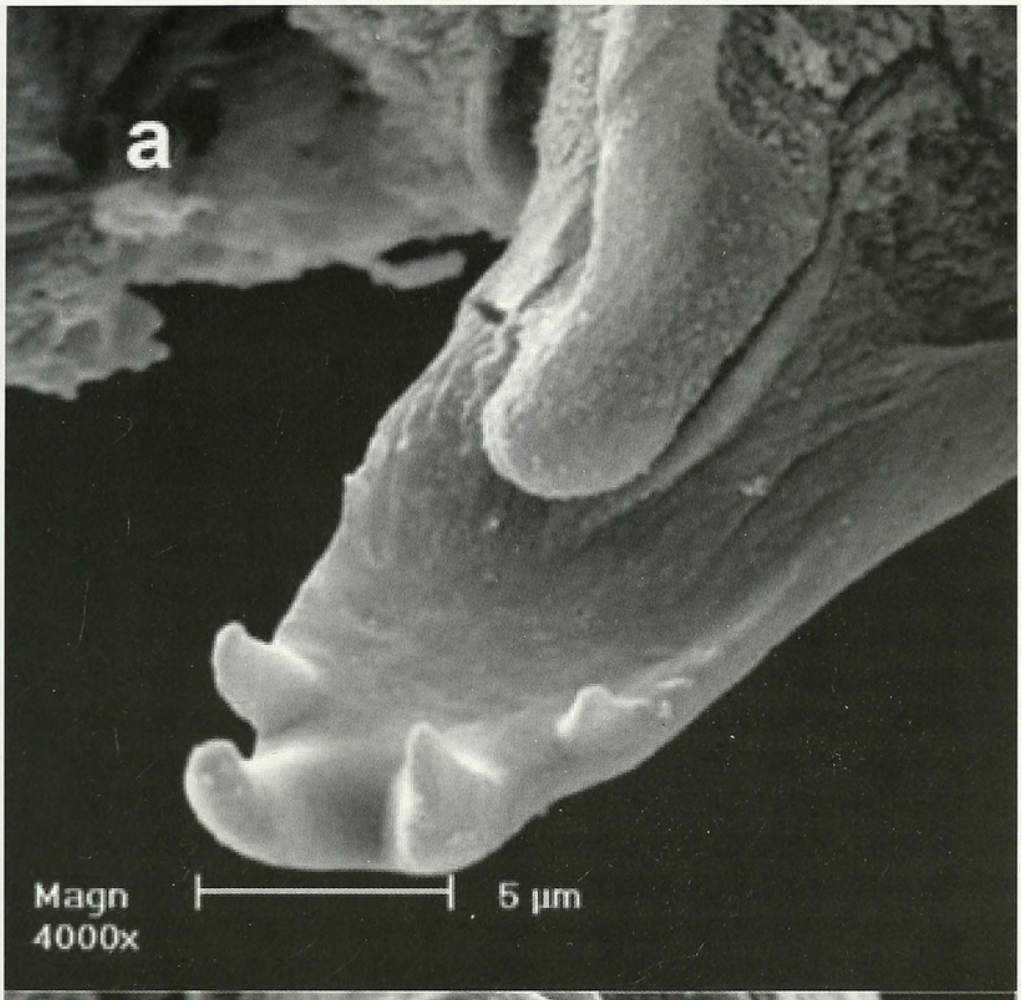
MATERIAL AND METHODS

Egg clutches were obtained from amplexed pairs collected in the field between 16 March and 5 April 2003 in the Kakamega Forest (0°21' N, 34°51' E; 1650 m above sea level), Western Province, Kenya. The adults were diagnosed according to Lötters *et al.* (2004). Their tadpoles were reared in captivity, and different developmental stages were fixed and stored in 4% formaldehyde. Voucher specimens have been deposited at the Muséum d'histoire naturelle, Geneva (*Hyperolius kivuensis:* MHNG 2661.31, N = 23; *H. viridiflavus:* MHNG 2661.42, N = 50).

Larval stages were diagnosed according to Gosner (1960). Body measurements were taken using the primary landmarks of Altig & McDiarmid (1999a). A W-PL 10x/23 ocular attached to a Zeiss Stemi 2000-C stereomicroscope was applied. The labial tooth row formula (LTRF) was defined by Altig & Johnston (1989). Photographs of live larvae were taken with a Contax Aria digital camera to obtain life color information.

FIG. 2

The labial teeth of *Hyperolius kivuensis* in stage 36: (a) cusped teeth of the anterior (upper) labium (posterior view). (b) non-cusped (pointed) teeth and cusped (bifurcated) teeth (at the bottom of the micrograph) of the posterior (lower) labium. LDC = long distal bifurcated cusps.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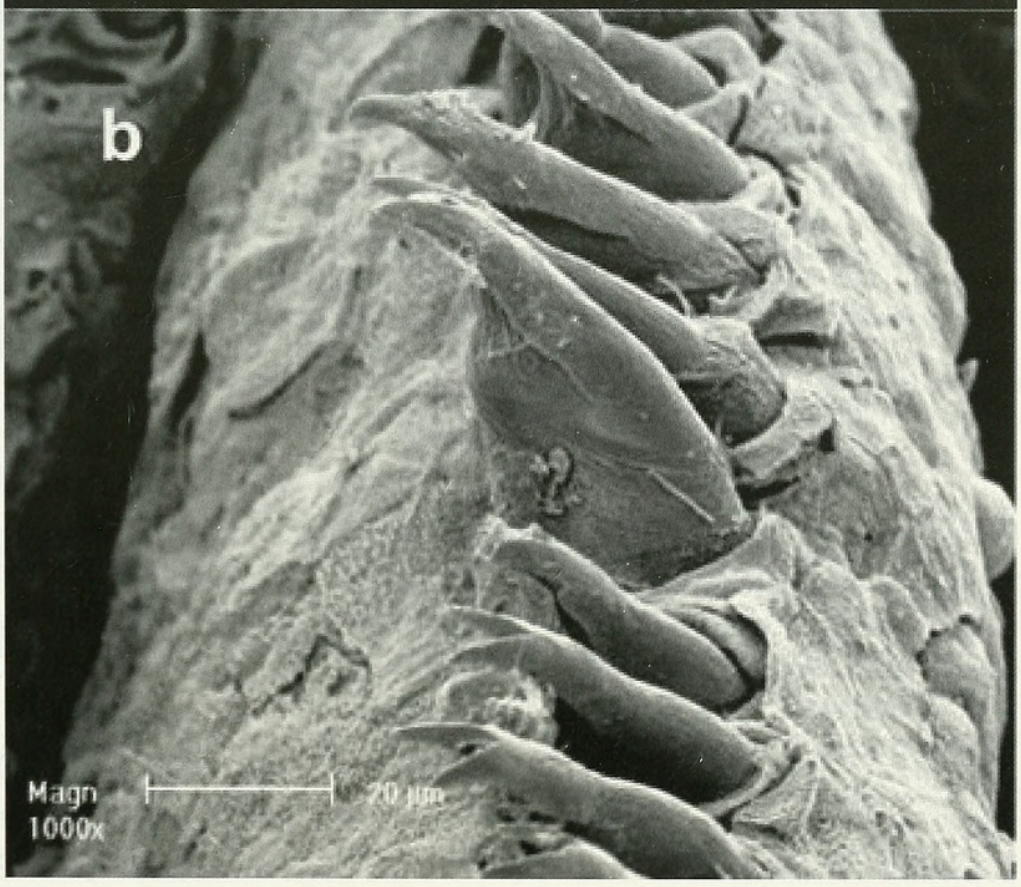
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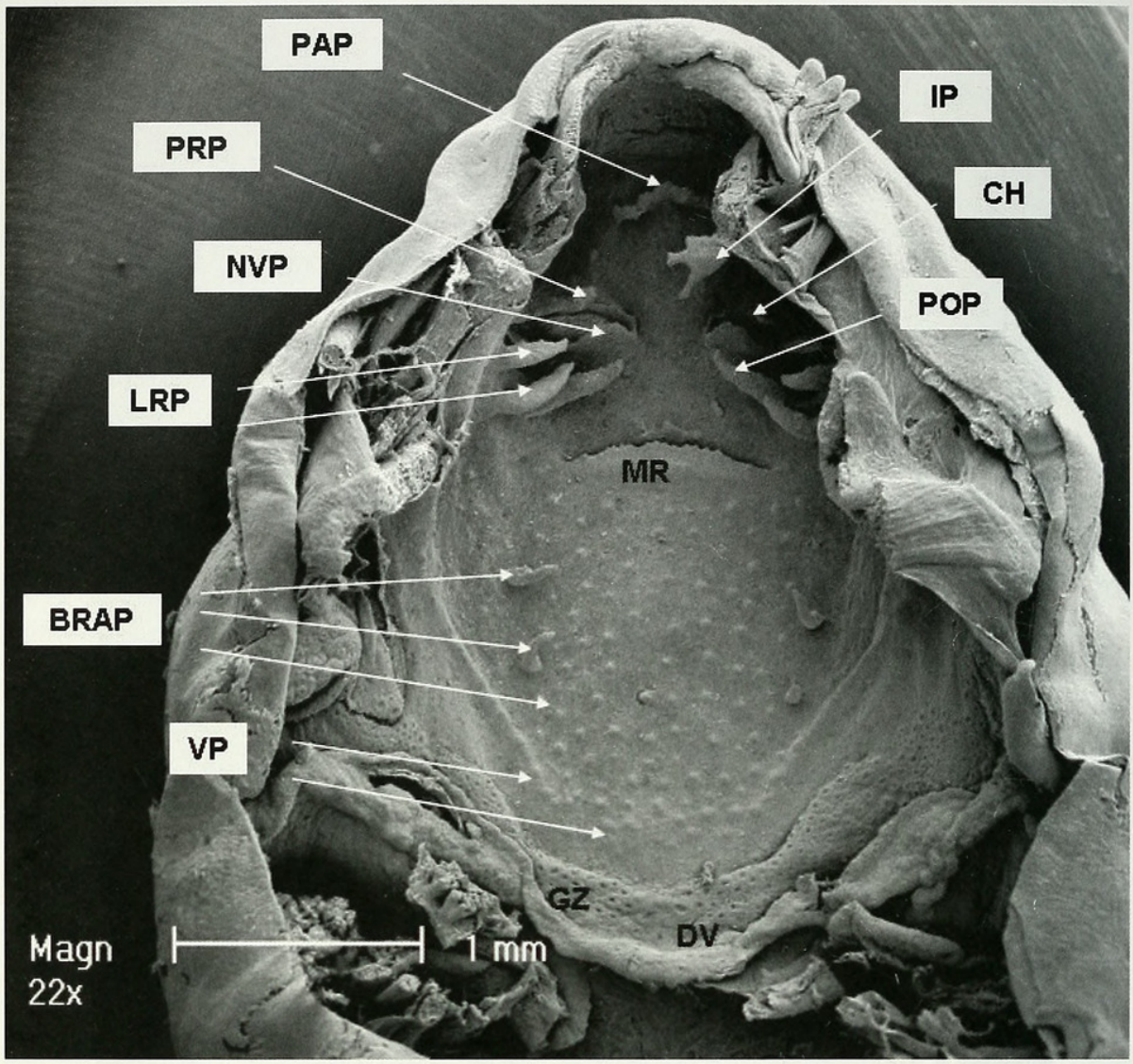


FIG. 3

The oral cavity of *Hyperolius kivuensis* in stage 36: the roof of the mouth. PAP = prenarial arena pustulations, POP = postnarial papillae, PRP = prenarial papillae, IP = infralabial papillae, CH = choanae, internal nares, NVP = narial valve projection, LRP = lateral ridge papillae, MR = median ridge, BRAP = buccal roof arena papillae or pustulations (smaller than the height twice the diameter of the base), VP = prevelar pustulations, GZ = glandular zone, DV = dorsal velum (terminology according to Wassersug, 1980; Viertel, 1982).

The heads of 25 tadpoles (stage 36) from each species were dissected under the binocular microscope (carcasses were not maintained as vouchers) to describe the oral cavities. For scanning electron microscopy (SEM) twelve specimens from each species were dehydrated in 70%, 80%, 96%, and 100% acetone. After desiccation with liquid CO_2 in a critical-point drying apparatus (BAL-TEC CPD 030) the specimens were coated with gold (sputter coater BAL-TEC SPD 005). A Philips ESEM XL 30 scanning electron microscope was used.

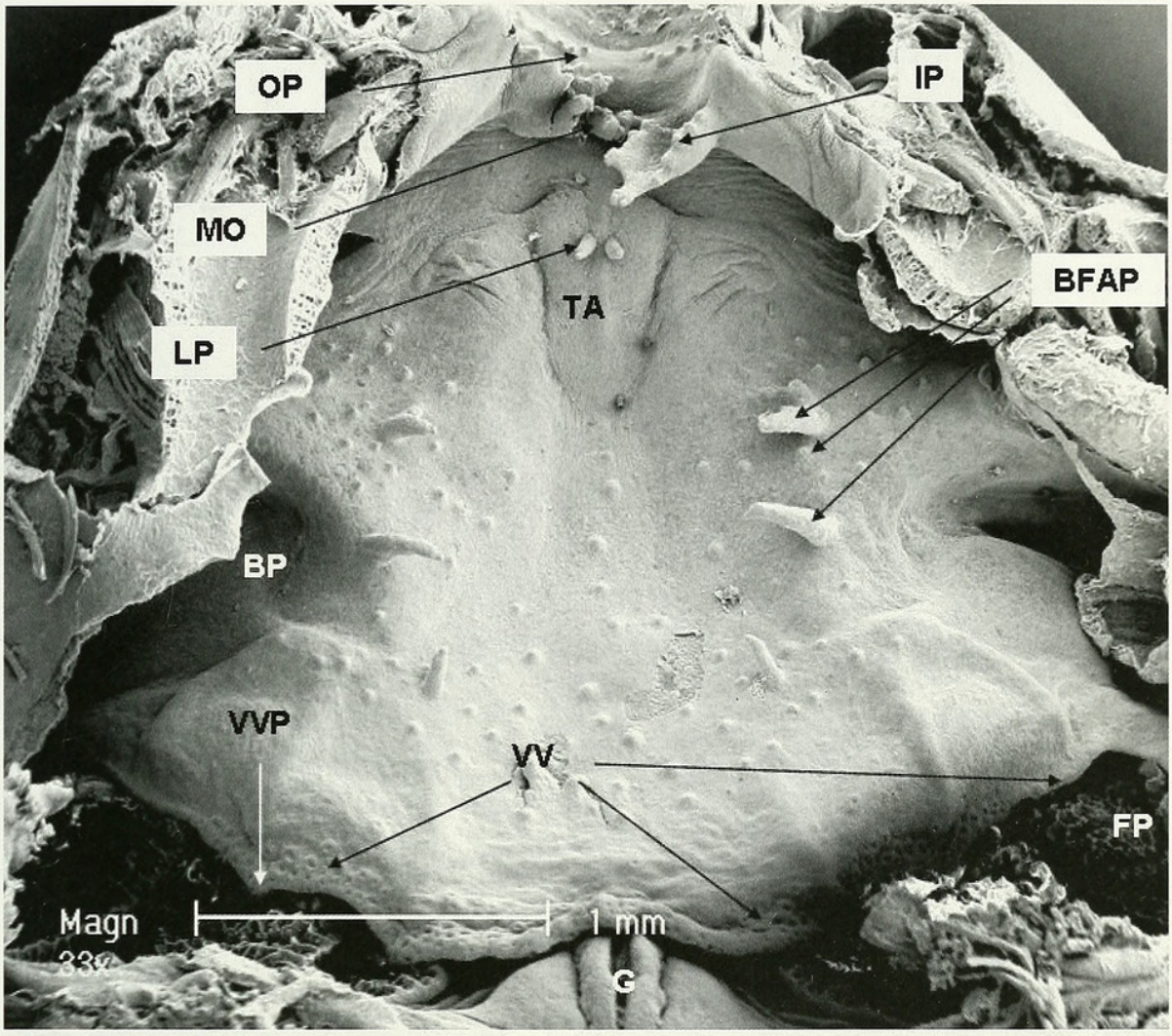


FIG. 4

The oral cavity of *Hyperolius kivuensis* in stage 36: the floor of the mouth. OP = pustulations in the oral orifice, MO = median papilla in the oral orifice, TA = tongue anlage, LP = lingual papilla, IP = infralabial papillae, BFAP = buccal floor arena papillae or pustulations (smaller than the height twice the diameter of the base), BP = buccal pocket, VV = ventral velum, VVP = velar papilla, FP = filter plate, G = glottis (terminology according to Wassersug, 1980; Viertel, 1982)

RESULTS

THE TADPOLE OF *HYPEROLIUS KIVUENSIS* AHL, 1931

External morphology: Measurements are as follows (mm): stage 36 (N = 14), total length (TL) = 34.9 (range 28.8-40.7), body length (BL) = 11.6 (range 10.6-13.1), BL/TL = 0.33 (range 0.31-0.38). The following description is based on a larva stage 36 as shown in Figure 1 (MHNG 2661.31, individual number W19). In dorsal view the body is elongated and ovoid and is widest at mid-body. The snout is rounded both in lateral and dorsal views. The eyes are relatively large, somewhat bulging, and not visible in ventral view. The interorbital distance is equal to the shortest distance to the tip of the snout. The eyes are positioned laterally and are directed dorsolaterally. The external nares are ovoid (horizontally elongated), small, and positioned laterally. They

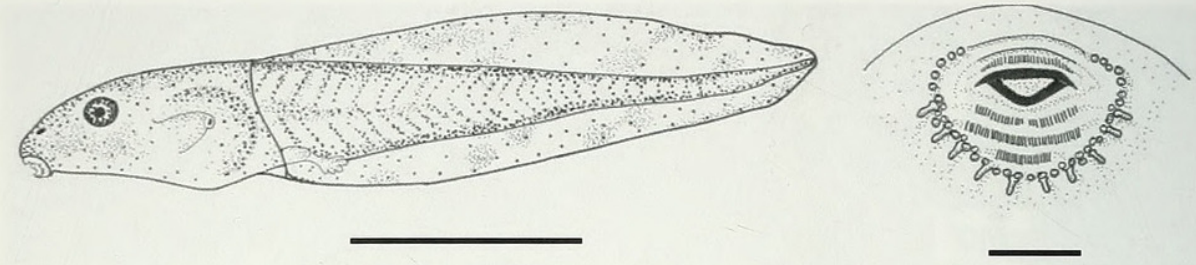


FIG. 5

Views of lateral body and oral disc of a *Hyperolius viridiflavus* larva from western Kenya, stage 36 (MHNG 2661.42). Lines equal 1 cm and 1 mm, respectively. Illustration by A. and J. Channing.

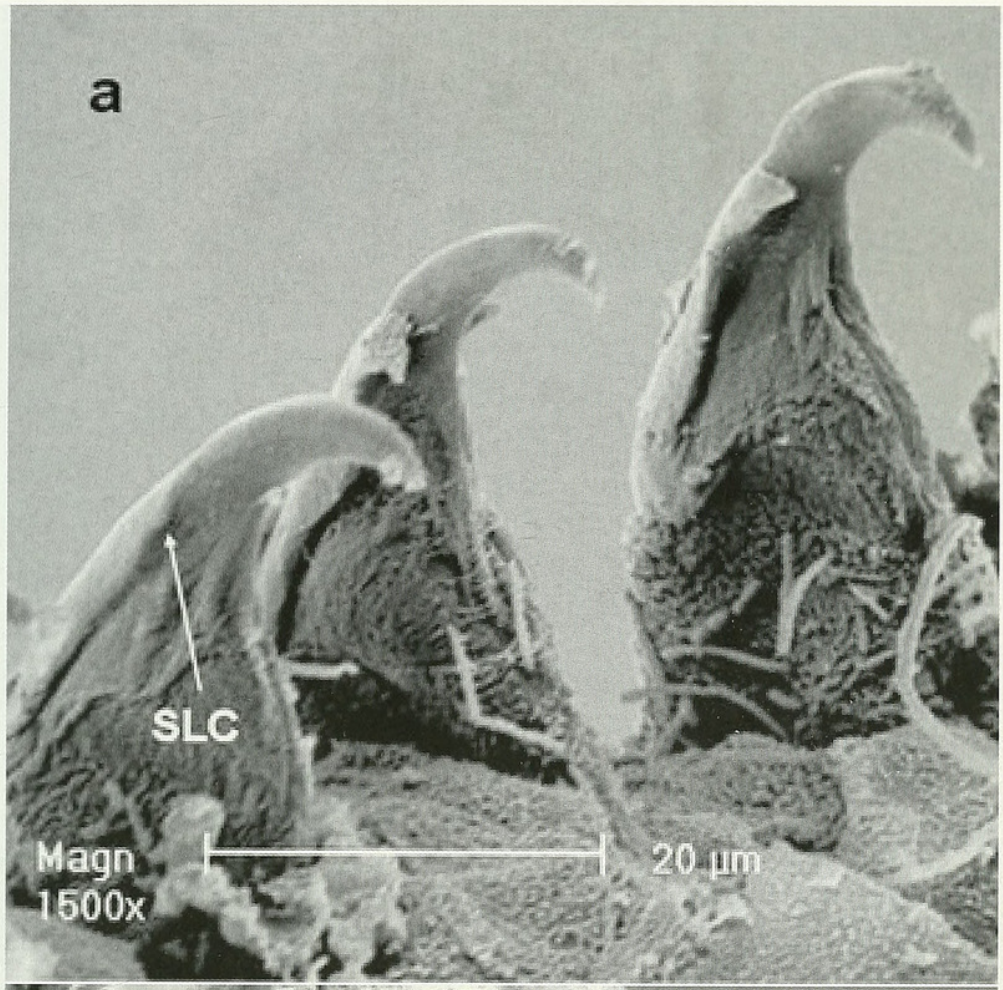
are more closely positioned to the snout than to the eyes. In lateral view the body is highest at the posterior half. The height is about one half of the body length. The spiracle is single, sinistral, and attached to the body wall. Its shape is cylindrical and in length it equals half eye diameter to eye diameter. The spiracle opening is rounded, directed posteriorly, and located slightly anterior to the mid-axis of eye and vent tube. The length of the tail represents approximately two thirds of the total length and is highest at about mid-tail. The total tail height is about three quarters of the body length. The tail fin height is greater than that of the body. The upper tail fin is larger in height than the lower. The dorsal fin is highest from mid tail to the posterior quarter of the tail. The ventral fin is almost as high just before the rounded tip of the tail. The height of the tail musculature is about half of the maximum tail height. The dorsal fin does not extend onto the body. The vent tube is short, dextral, posteriorly directed, and linked to the tail musculature. The oral disc is anteroventral, not emarginated, and entirely bordered by a row of short round papillae. Few submarginal papillae are present. The LTRF is 1/3(1, 2). The tooth rows are equal in length, occupying nearly the entire width of the oral disc except the shorter, most posterior one. Jaw sheaths are finely serrated. The upper jaw sheath is inversely U-shaped and the lower V-shaped and shorter.

The variation in external morphology of 23 larvae between stages 32 and 40 is limited to size (Table 1) and LTRF including 1/3, 1/3(1), 1/3(1, 2), 1/3(2), 1/3(1, 3), and 1/3(3). LTRF observed in specimens in stages 25 and 26 (tadpoles not preserved) was 1/2, 1/2(1), 1/2(1, 2), and 1/2(2). Gaps occurred in the centers or more to the periphery of tooth rows.

Two different types of keratinized labial tooth are found. The spoon-shaped cusped type is often seen and is represented in two different morphological subtypes. One has four cusps and the two distal cusps were only slightly larger than the lateral cusps (Fig. 2a). In the other subtype, the two distal cusps are clearly larger than the one or two lateral cusps (Fig. 2b) and form a bifurcated fork. The non-cusped (pointed) type is rarely found.

FIG. 6

The labial teeth of *Hyperolius viridiflavus* in stage 36: (a) pointed teeth with small lateral cusps in the anterior (upper) labium. (b) bifurcated type of the anterior (upper) labium. LDC = long distal bifurcated cusps, SLC = small lateral cusp.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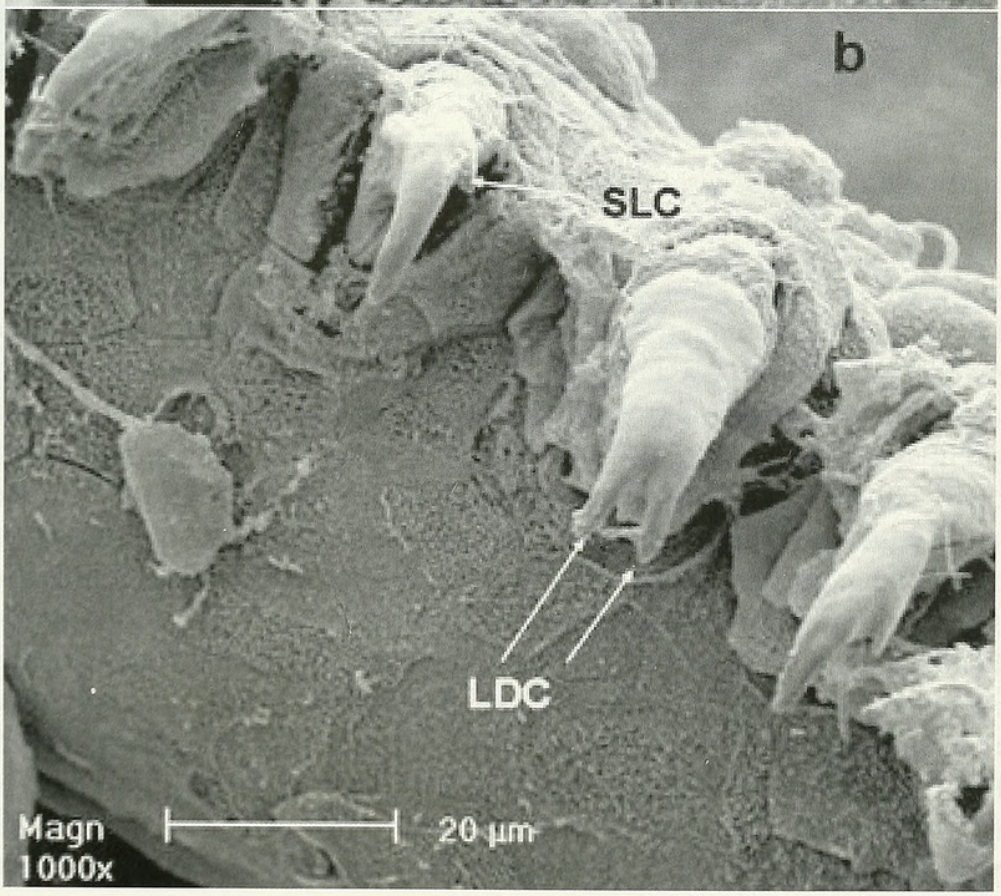
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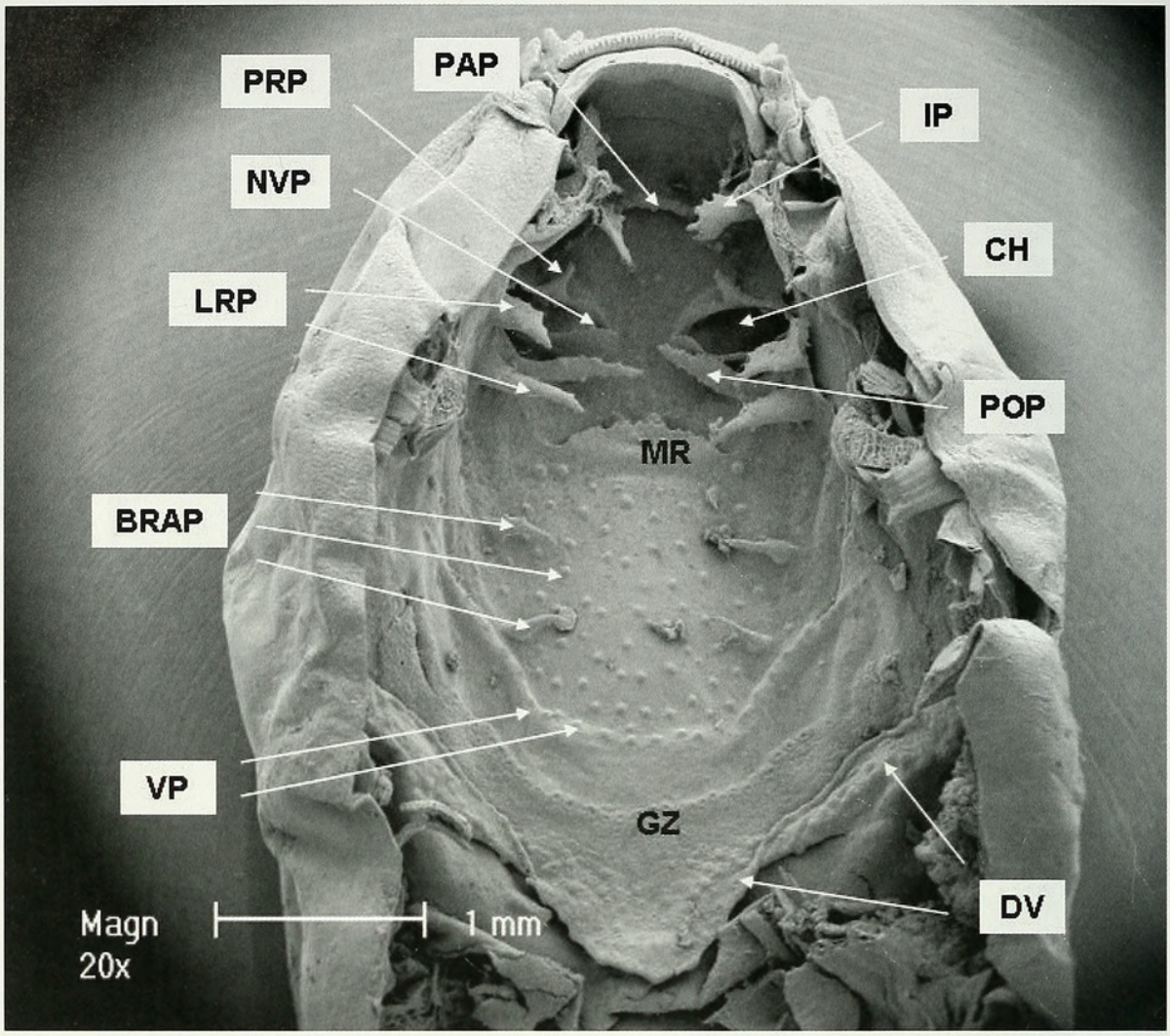

FIG. 7
The oral cavity of *Hyperolius viridiflavus* in stage 36: the roof of the mouth. For abbreviations see Figure 3.

In preservative, the larvae are entirely light gray to tan. They are darker on the dorsal body from dense scattered melanophores and are translucent on the posterior venter. Melanophores on the tail musculature and the fins are almost uniformly arranged. The margins of the fins are dark gray and melanophores are observed on the spiracle. The coloration in life of the body was dorsally tan and ventrally translucent whitish. The tail musculature was tan and the fins were translucent tan with irregular dark marbling. A dark line occurred on the tail musculature along one third of tail length beginning at the base of the tail. The pupil coloration was black and the iris was bronze with a bright ring around the pupil.

Oral cavity: The description of the roof and floor of the mouth is based on Figures 3 and 4, respectively. The buccal roof is divided into three areas. The prenarial arena is positioned in the anterior region of the upper beak. The small prenarial arena postulations (PAP) are arranged in a horseshoe shape, sometimes in a V. The central PAP are fused at their base, the lateral PAP are not. The prenarial arena is bordered caudally by the choanae (CH) or internal nares. They are arranged in a posteriorly open

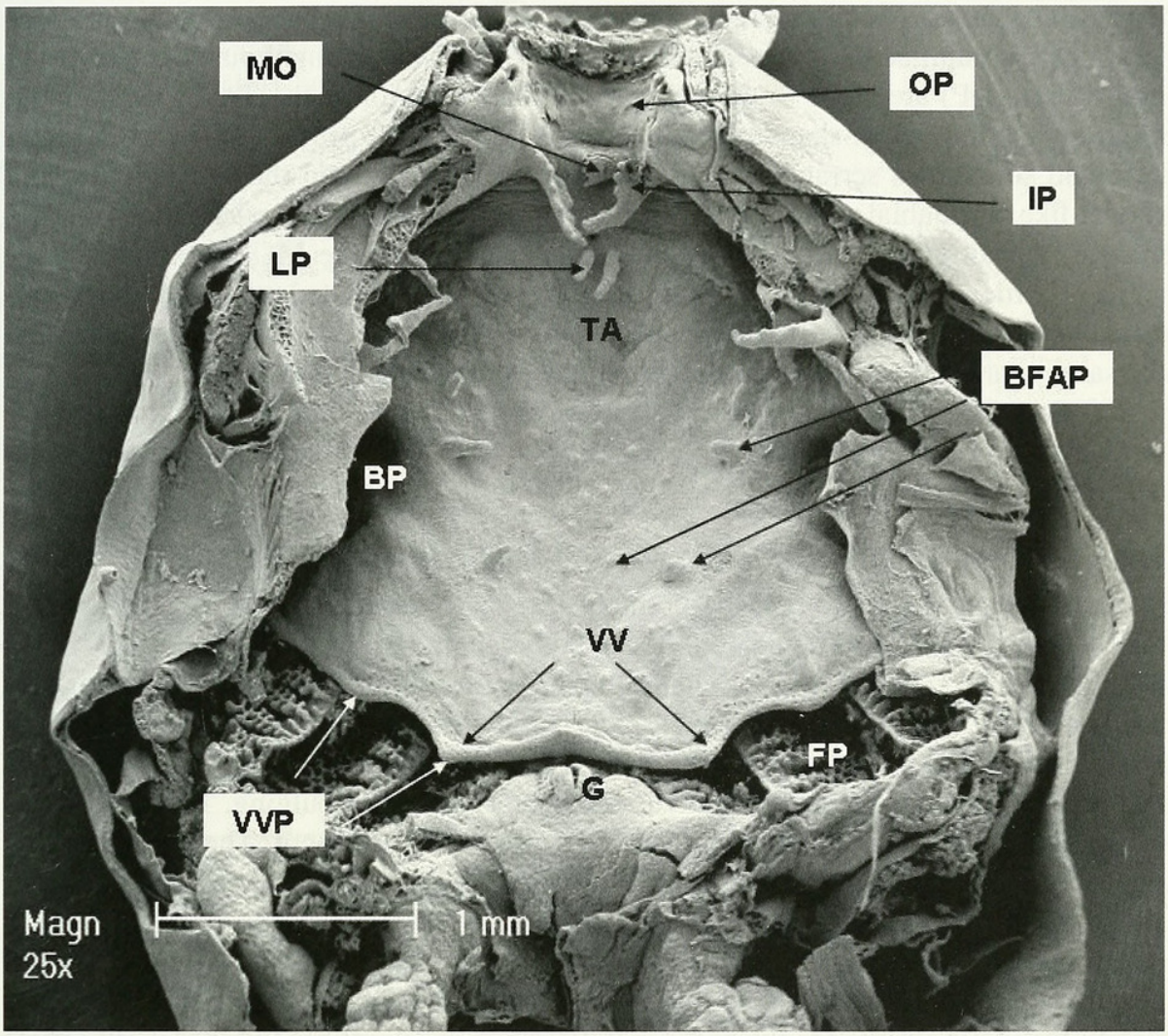

FIG. 8

The oral cavity of *Hyperolius viridiflavus* in stage 36: the floor of the mouth. For abbreviations see Figure 4.

V forming an obtuse angle. The CH is surrounded anteriorly by the PAP and posteriorly by the narial valve projection (NVP). There is one large prenarial papillae (PRP) per CH which is flanked by one or two small pustulations and also one small and lobed NVP on the median margin of each CH. The CH are joined caudally to the postnarial arena with the single large postnarial papilla (POP) positioned dorsolaterally on each side. Close to the POP but more laterally are two large lateral ridge papillae (LRP) equal in size with a separated base, found on each side. The largest of the arenas is the buccal roof arena which is bordered anteriorly by the flat and broadly based median ridge (MR) with a serrated margin, and laterally by two buccal roof arena papillae (BRAP). Around 50 small pustulations are on the buccal roof arena. The buccal roof arena is bordered caudally by the glandular zone (GZ) and the dorsal velum (DV) with 15-20 small pustulations (VP).

The buccal floor arena is the largest region of the buccal floor. It is bordered laterally by the buccal pockets (BP) and anteriorly by the tongue anlage (TA). Three large buccal floor arena papillae (BFAP) on each side are arranged in the form of an

anteriorly open horseshoe and around 60 pustulations cover the buccal floor arena. Two large lingual papillae (LP) are positioned on the TA. The ten small pustulations of the oral orifice (OP) are close to the ventral oral beak anterior to the TA. A single large blunt or pointed lancet-shaped median papilla of the oral orifice (MO) with a broad base and sometimes serrated apex is seen between the OP and the TA. One flat and shovel-like infralabial papilla (IP) with large surface and small pustulations on the margin is positioned laterally on each side in the level of the MO. The buccal floor arena is bordered caudally by the ventral velum (VV) of the pitted type with two broad-based velar papillae (VVP) on each side. Spot-tests with larval stage 32 demonstrated the same arrangement of oral cavity structures as described for stage 36.

Remarks: Wild-caught larvae attributed to *H. kivuensis* from the same pond at the Kakamega Forest (MHNG 2661.32-41, N = 60) well coincide with the external description given above.

THE TADPOLE OF *HYPEROLIUS VIRIDIFLAVUS* (DUMÉRIL & BIBRON, 1841)

External morphology: Measurements are as follows (mm): stage 36 (N = 38), total length (TL) = 35.4 (range 30.0-39.6), body length (BL) = 11.5 (range 10.3-12.9), BL/TL = 0.33 (range 0.31-0.36). The following description is based on a larva stage 36 as shown in Figure 5 (MHNG 2661.42, individual number D14): In dorsal view the body is elongated, ovoid, and widest behind the eyes. The snout is rounded in dorsal and ventral view. The eyes are relatively large and somewhat bulging. The interorbital distance is larger than the shortest distance to the tip of the snout. The eyes are positioned laterally, directed dorsolaterally, and not visible in ventral view. The nares are slit-like (horizontally), small, and positioned dorsolaterally. They are more closely positioned to the snout than to the eyes. In lateral view the body is highest at the posterior half. The height is about one half of the body length. The spiracle is single, sinistral, and not attached to the body wall. Its shape is cylindrical and the length equals the eye diameter. The spiracle opening is rounded, directed posteriorly, and located on the mid-axis of eye and vent tube. The length of the tail represents about two thirds of the total length and is highest at the anterior half. The total tail height is about two thirds of the body length. The tail fin height is greater than that of the body. The upper tail fin is taller than the lower. The dorsal fin is highest from mid tail to the posterior quarter of the tail. The ventral fin is almost as high just before the rounded tip of the tail. The height of the tail musculature is less than half of the maximum tail height. The dorsal fin does not extend onto the body. The vent tube is short, dextral, posteriorly directed, and linked to the tail musculature. The oral disc is anteroventral, not emarginated, and entirely bordered by a row of short round papillae. Submarginal papillae are absent. The LTRF is 1/3(1). The tooth rows are equal in length occupying nearly the entire width of the oral disc except for the shorter, most posterior one. Jaw sheaths are finely serrated. The upper jaw sheath has an arched, inverted U-shape, the lower is V-shaped and is shorter.

The variation in external morphology of 50 larvae between stages 30 and 40 is limited to size (Table 1) and LTRF including 1/3, 1/3(1), 1/3(1, 2), 1/3 (1, 2, 3), 1/3(1, 3), 1/3(2), and 1/3(3). LTRF observed in specimens in stages 25 and 26 (tadpoles not preserved) is 1/2, 1/2(1), 1/2 (1, 2), and 1/2(2). Gaps are observed in the centers or more to the periphery of tooth rows.

TABLE 1. Measurements (mm) and ratios of 23 larvae of *Hyperolius kivuensis* and 50 larvae of *H. viridiflavus* from western Kenya in different stages. In N > 2, the mean is given, followed by one standard deviation, and the range in parentheses.

stage	N	total length	body length	body length/total length
Hyperolius kivuensis				
32	1	32.5	11.1	0.34
34	2	31.0, 32.4	10.6, 11.2	0.34, 0.35
35	1	33.5	11.4	0.34
36	14	34.9 ± 3.1 (28.8-40.7)	11.6 ± 0.6 (10.6-13.1)	0.33 ± 0.1 (0.31-0.38)
37	2	36.1, 36.6	12.0, 12.7	0.33, 0.35
38	1	38.2	12.2	0.32
39	1	38.6	13.7	0.36
40	1	40.4	13.4	0.33
Hyperolius viridiflavus				
30	1	27.1	9.4	0.35
33	1	32.9	10.2	0.31
34	1	30.8	11.1	0.36
35	2	35.4, 36.8	10.5, 11.5	0.30, 0.31
36	38	35.4 ± 2.2 (30-39.6)	11.5 ± 0.6 (10.3-12.9)	0.33 ± 0.01 (0.31-0.36)
37	3	36.2 ± 2.5 (33.5-38.4)	11.7 ± 0.3 (11.5-12.0)	0.30 ± 0.1 (0.30-0.34)
38	2	33.4, 40.0	12.7, 13.3	0.33, 0.38
39	1	40.6	12.8	0.31

Two different types of keratinized labial tooth are found. A pointed type with small lateral cusps (Figs 6a, b) is the most common type. The second type is characterized by two long distal cusps forming a bifurcated fork and two small lateral cusps (Fig. 6b). The cusped type with cusps of the same size as seen in *H. kivuensis* is rare. All these types are seen in one individual tadpole. There is no difference between stages 32 and 36.

In preservative, larvae are entirely translucent gray. They are darker on the dorsal body from dense scattered melanophores. Melanophores on the tail musculature are almost uniformly arranged while on the fins they are arranged in patches. On the spiracle the melanophores are distally missing. The coloration in life of the body was dorsally brownish with tiny dark brown and occasionally cream spots and ventrally translucent cream. The tail musculature was tan and the fins were translucent tan with dark blotches. The pupil coloration was black and the iris was bronze with a bright ring around the pupil.

Oral cavity: The description of the roof and floor of the mouth is based on Figures 7 and 8, respectively. The structures and their number are the same as in *H. kivuensis* with the exception of the choanae. These are arranged in an anteriorly open V forming an obtuse angle, in contrast to the latter species with a posteriorly open V. There is no difference between stages 32 and 36.

Remarks: Wild-caught larvae attributed to *H. viridiflavus* from the same pond at the Kakamega Forest (MHNG 2661.43-51, N = 54) well coincide with the external description given above.

DISCUSSION

External features in the two species are similar and both are comparable with other *Hyperolius* (Rödel, 1999; Schiøtz, 1999; Channing, 2001; Channing & Howell, 2006). *Hyperolius kivuensis* and *H. viridiflavus* differ in the frequency of occurrence of the two morphological types of teeth. The main type in the former is the cusped type with four cusps of nearly the same size. This type is rare in *H. viridiflavus*, while in larvae of this species the pointed type with or without small lateral cusps is the main type. Oral cavity structures of the two species are similar. Only the position of the choanae shows a clear difference. In *H. kivuensis*, they are arranged in a V which is opened posteriorly forming an obtuse angle, while in *H. viridiflavus* the V is open anteriorly in an obtuse angle. In some larvae of the latter species, the choanae do not form an angle.

The external morphology, including the oral disc, the keratinized labial teeth, and the oral cavity structures characterize both *H. kivuensis* and *H. viridiflavus* as exotrophous lentic benthic generalized tadpoles (Altig & McDiarmid, 1999a, b). The ventral velum of the pitted type and the oral disc are in connection with the sinistral position of the spiracle criteria of the larval type IV (Starrett, 1973). This is corroborated by the repertoire of structures in the oral cavity that are comparable to those from European larvae of *Bufo bufo*, *Epidalea calamita*, and *Rana temporaria* of the same larval type (Viertel, 1985, 1987). These tadpoles are known to filter suspended particles such as phytoplankton and detritus from the water (Viertel, 1990, 1992). They also scrape food off the substrate with the keratinized labial teeth in connection with the oral disc, suspend it in the water current and filter it. We expect larvae of both *Hyperolius* species to share this generalized feeding behavior.

Our analyses clearly show that morphological differences between tadpoles of theses two syntopic *Hyperolius* species are restricted to a few characters only and at best visible when applying REM technology. We expect many ecologically equivalent *Hyperolius* species to have ecologically – and hence morphologically – similar tadpoles. This casts doubts that external larval morphology will enable field researchers to discriminate between all ca. 120 *Hyperolius* species, even though only a few always occur sympatrically (e.g. Schiøtz, 1999; Channing, 2001; Channing & Howell, 2006). DNA barcoding may therefore become the future method of choice to identify *Hyperolius* tadpoles, although inevitably after fieldwork.

ACKNOWLEDGEMENTS

We are grateful to staff at the Herpetology Department of the National Museums of Kenya, Nairobi, for logistic support. Fieldwork was sponsored by the Federal Ministry of Education and Research, Germany (BMB+F) through BIOLOG-BIOTA to MV and SL (FZ 01LC0025). The Kenya Wildlife Service (KWS) kindly granted permissions. We are indebted to E. Sehn (Mainz) for her kind help preparing the larvae for scanning electron microscopy. A. and J. Channing, Stellenbosch, kindly contributed the drawings.

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