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Meristic and morphometric characters of *Leptopelis natalensis* tadpoles (Amphibia: Anura: Arthroleptidae) from Entumeni Forest reveal variation and inconsistencies with previous descriptions

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Abstract. The tadpole of *Leptopelis natalensis* is described based on a series of 32 specimens from Entumeni Forest, KwaZulu-Natal, South Africa. Previous descriptions are brief, lack morphometric data, or are based on specimens of imprecise origin. The tadpole resembles other *Leptopelis* tadpoles and is generally in agreement with existing accounts, although some differences exist. Some of these differences seem to fall within the range of natural variation. Others, such as the presence of a fifth anterior row of keratodonts, might be indicative of variation at the population level and should be considered in future taxonomic revisions. *Leptopelis natalensis* tadpoles seem to be most readily distinguished by their more narrowly keratinized beaks from the geographically overlapping or adjacent *L. mossambicus* and *L. xenodactylus*.

Keywords. South Africa, KwaZulu-Natal, Eastern Cape, taxonomy, buccal morphology, ontogenetic variation.

INTRODUCTION

The genus *Leptopelis* currently comprises 53 described species (Frost, 2017) of medium to large tree frogs that are distributed throughout most of Sub-Saharan Africa (Schiøtz, 1999). The most southerly distributed species of the genus is *L. natalensis*, which is found in a variety of habitats along the eastern region of the South African provinces of KwaZulu-Natal and part of Eastern Cape (Schiøtz, 1999; Bishop, 2004; Venter and Conradie, 2015). Although some, mostly brief, descriptions and illustrations of *L. natalensis* tadpoles have been published (Wager, 1930, 1965; van Dijk, 1966; Lambiris, 1988; Channing, 2001; du Preez and Carruthers, 2009; Channing et al., 2012), Channing (2001) considered none of the South African *Leptopelis* tadpoles to have been adequately described. The various descriptions furthermore differ in a number of diagnostic characters, such as labial keratodont formula. These differences in the existing descriptions could be the result of variation or population-specific differences that might be significant in future taxonomic revisions (Penske et al., 2015). To differentiate between these options, it is important to provide detailed locality information, which is lacking in some works providing information on tadpole morphology of *L. natalensis* (e.g., du Preez and Carruthers, 2009). While detailed, or at least limited, locality data are provided by Wager (1930, 1965, 1986), Pickersgill (2007) and Channing et al. (2012), these accounts provide mostly meristic data but few or no morphometric data that would help in assessing subtle differences that might exist between populations. We here provide a description and measurements of an ontogenetic series of tadpoles of *L. natalensis* based on a series collected at Entumeni Forest,

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KwaZulu-Natal, assess variability and ontogenetic changes, and highlight differences between these and previous descriptions.

MATERIALS AND METHODS

A total of 32 tadpoles were collected at Entumeni Forest, KwaZulu-Natal, South Africa on 3 December 2014. The tadpoles were collected in a small forest stream (28.888334°S, 31.365928°E). Some tadpoles were preserved on the day of collection, while others were raised on a diet of commercial aquarium fish food and sampled in regular intervals to obtain different stages of development. Identification of the tadpoles was confirmed by raising some through metamorphosis. Specimens were euthanized in an aqueous solution of tricaine methanesulfonate (MS222; Fluka), fixed in 4% neutral buffered formalin, and transferred to 70% ethanol. Voucher specimens have been deposited in the herpetological collection of the Museum für Naturkunde Berlin, Germany (ZMB85717).

Staging followed Gosner (1960). Standard measurements and labial tooth row formula followed Altig and McDiarmid (1999) and description of buccopharyngeal morphology Wassersug (1976). Drawings were prepared with the aid of a camera lucida attached to a Zeiss SV12 stereomicroscope. For inspection of the buccopharyngeal morphology, one tadpole of stage 36 was dissected, postfixed with 1% osmium tetroxide, dehydrated and critical point dried in an Emitech K850 critical point dryer, sputter coated with gold-palladium using an Emitech K500 and investigated using a Phillips XL30 ESEM scanning electron microscope with a digital image capture system.

DESCRIPTION

Tadpole. The description is based on 32 tadpoles from Gosner (1960) stages 25 to 42 (see Table 1 for measurements and detailed information). The tadpole is slender overall, with a moderately elongated, slightly dorsoventrally flattened body (wider than deep) and a relatively long tail with low dorsal and ventral fins. The widest point of the body is just behind the eyes (Fig. 1). No nares are visible until stage 34. From stage 35 to 37, the nares are indicated as light coloured spots, but do not seem to be open until stage 38. When fully formed, the nares are positioned dorsolaterally, about twice as far from the eye than the tip of the snout in lateral view. The eyes are positioned dorsally. A small anlage of the developing eyelid is first visible at stage 40, anterior of the eye. The spiracle is sinistral, about as far from the snout as from the body-tail junction. The spiracular opening is an upright oval, slightly slanted forward; its largest diameter almost as large as the diameter of the eye lens. The spiracular tube is angled upwards at about 45°; the posterior end, including its inner wall, is free from the body. The tail is about 2.5 times as long as the body (see Table 1 for measurements) and very muscular. The myomeres are visible in the posterior half of the tail, but are otherwise indistinct or obscured by the dense pigmentation. The tailfins are very low, with the dorsal fin marginally deeper than the ventral fin. The dorsal fin has a low origin on the base of the tail, just behind the tail-body junction, and gradually rises towards the middle of the tail, where it reaches its maximum height. The ventral tailfin is very even, with the margin of the fin running more or less parallel to the ventral edge of the muscular tail. The overall deepest point of the tail is at about half its length. Tip of tail is pointed, with the muscular tail terminating some distance before the tail tip (Fig. 1B). The vent tube is attached to the right side of the ventral tailfin, with a very large opening forming a pointed arch. The coiled gut is well visible through the ventral body wall.

Oral Disc. The oral disc is positioned subterminally and is not visible in dorsal view. The oral disc is lightly emarginated and has a broad rostral gap. One row of globular marginal papillae is present anterolaterally and laterally; posteriorly, two rows of papillae are present. Papillae are largest anterolaterally and laterally, and smaller posteriorly. A few submarginal papillae are present laterally. Keratodont formula is 4(2-4)/3(1) in the majority of the examined specimens (see below for variation). Moving inwards, supralabial keratodont rows are progressively smaller (Fig. 1A), infralabial rows are of nearly equal length, with P3 being slightly shorter than P1 and P2. Interruption of P1, if present, is very narrow in some specimens (Fig. 1A) but more pronounced in others. Keratodonts are about equally sized in most rows, except in P3 where they get progressively smaller laterally. The individual keratodonts are spoon-shaped and have eight or nine cusps along their margins, with the apical cusps being larger than the more laterally positioned ones (see inset in Fig. 2A). The jaw sheaths are serrated but only narrowly keratinised (indicated by the dark pigmentation). By stage 42, the lower jaw sheath and all keratodonts are absent and the papillation is much reduced in extent.

Buccopharyngeal Morphology. The prenarial area of the buccal roof (Fig. 2A) is somewhat elongated and contains a few scattered pustules. In addition, a pair of short ridges is present and somewhat slanted laterally. The orientation of the choana is oblique to the midline (about 45 degrees) and both choanae form a forward-pointing angle of approximately 90 degrees. The jagged narial valves project deep into the buccal cavity and obscure the choanal openings. Anterolateral of each choana is a broad, flap-like papilla with a pustulate edge. Three to four thick, broad-based papillae are present posterolaterally to each

Table 1. Measurements of *Leptopelis natalensis*. All measurements in millimeters (arithmetic mean ± SD). * indicates a damaged tail in one of the specimens of the series, which was omitted from the calculations.

Gosner Stage	25 (n=3)	31 (n=1)	34 (n=1)	35 (n=2)	36 (n=14)	37 (n=2)	38 (n=2)	39 (n=1)	40 (n=1)	41 (n=1)	42 (n=4)
Total length	32.1 ± 2.3*	29.7	34.9	34.1 ± 1.2	36.5 ± 2.7*	35.3*	37.9 ± 0.8	41.7	39.1	37.2	36.2 ± 2.3
Body length	7.1 ± 0.6	8.2	9.5	9.2 ± 0.8	10.2 ± 0.8	10.7 ± 0.0	10.7 ± 0.8	11.8	11.2	11.0	10.9 ± 0.3
Body width	3.8 ± 0.2	4.0	4.9	4.5 ± 0.3	5.2 ± 0.6	5.9 ± 0.1	5.9 ± 0.1	6.0	6.1	5.5	4.3 ± 0.6
Body height	2.9 ± 0.1	3.6	4.2	3.4 ± 0.4	4.3 ± 0.4	4.8 ± 0.1	4.9 ± 0.1	5.3	4.4	5.0	4.2 ± 0.2
Tail length	16.7 ± 1.6*	21.2	25.2	24.9 ± 0.1	26.4 ± 2.3*	24.5*	27.1 ± 0.4	30.0	27.6	27.0	26.1 ± 1.8
Tail height	3.3 ± 0.3	3.6	4.2	4.1 ± 0.4	4.6 ± 0.3	4.4 ± 0.6	5.1 ± 0.4	5.0	4.9	5.0	4.1 ± 0.5
Tail muscle height	1.9 ± 0.3	2.3	3.0	2.8 ± 0.2	3.2 ± 0.4	3.2 ± 0.1	3.1 ± 0.1	3.5	3.0	2.9	2.8 ± 0.3
Width of oral disc	1.2 ± 0.2	1.4	1.6	1.6 ± 0.1	1.9 ± 0.2	1.9 ± 0.1	2.0 ± 0.1	2.4	2.2	2.0	1.6 ± 0.2
Interorbital distance	2.7 ± 0.3	3.3	3.9	3.5 ± 0.8	4.1 ± 0.3	4.4 ± 0.1	4.3 ± 0.1	4.6	4.3	4.7	4.7 ± 0.4
Internarial distance	-	-	-	-	-	-	1.9 ± 0.9	2.0	1.9	1.7	1.4 ± 0.2
Snout-naris distance	-	-	-	-	-	-	1.6 ± 0.1	1.6	1.7	1.6	1.2 ± 0.3
Snout-eye distance	2.5 ± 2.6	2.9	3.3	3.4 ± 0.1	3.3 ± 0.2	3.5 ± 0.2	3.4 ± 0.1	3.9	4.0	3.8	3.1 ± 0.1
Snout-spiracle distance	4.9 ± 0.5	5.4	6.1	6.3 ± 0.4	6.7 ± 0.4	27.1 ± 0.3	7.1 ± 0.2	8.1	7.4	7.2	-
Naris-eye distance	-	-	-	-	-	-	1.9 ± 0.1	2.1	2.0	2.1	2.2 ± 0.1
Eye diameter	0.6 ± 0.1	0.8	1.1	1.0 ± 0.0	1.2 ± 0.1	1.2 ± 0.1	1.2 ± 0.1	1.5	1.5	1.5	1.4 ± 0.1

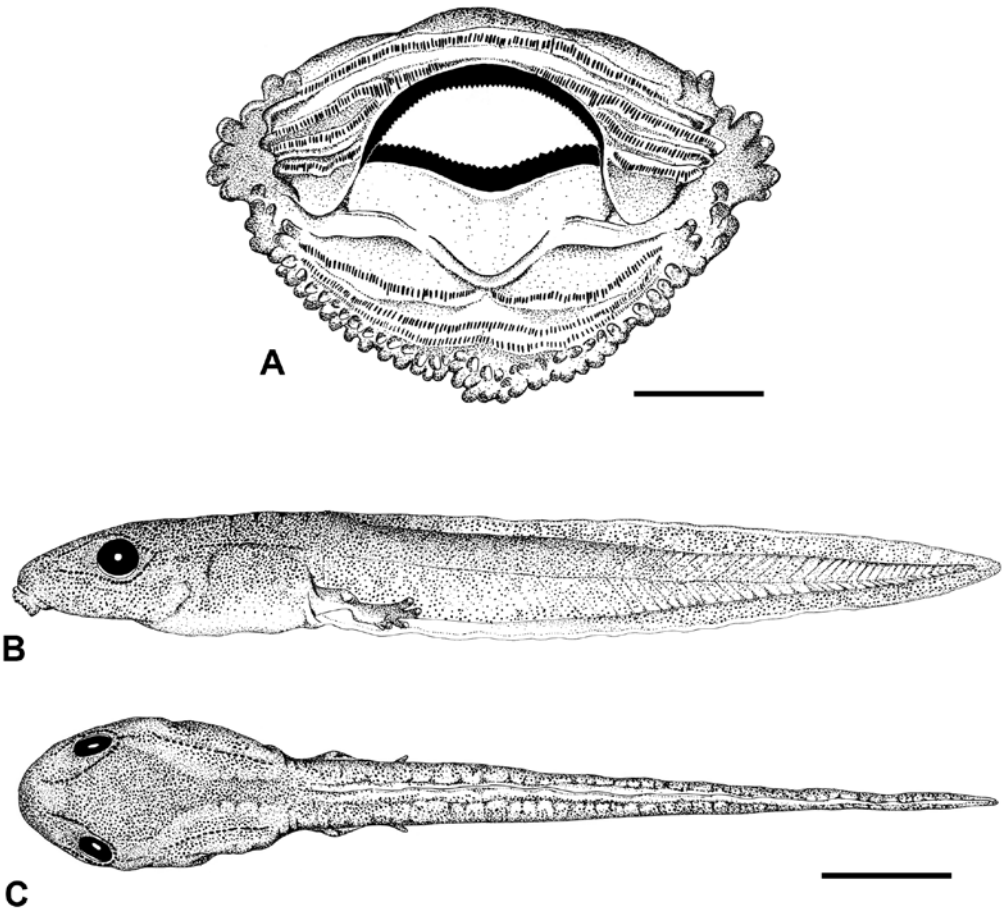

Fig. 1. Oral disc (A), lateral (B) and dorsal (C) view of a Gosner stage 36 tadpole of *Leptopelis natalensis* from Entumeni Forest, KwaZulu Natal, South Africa. Scale bar equals 0.5 mm in (A) and 5 mm in (B) and (C).

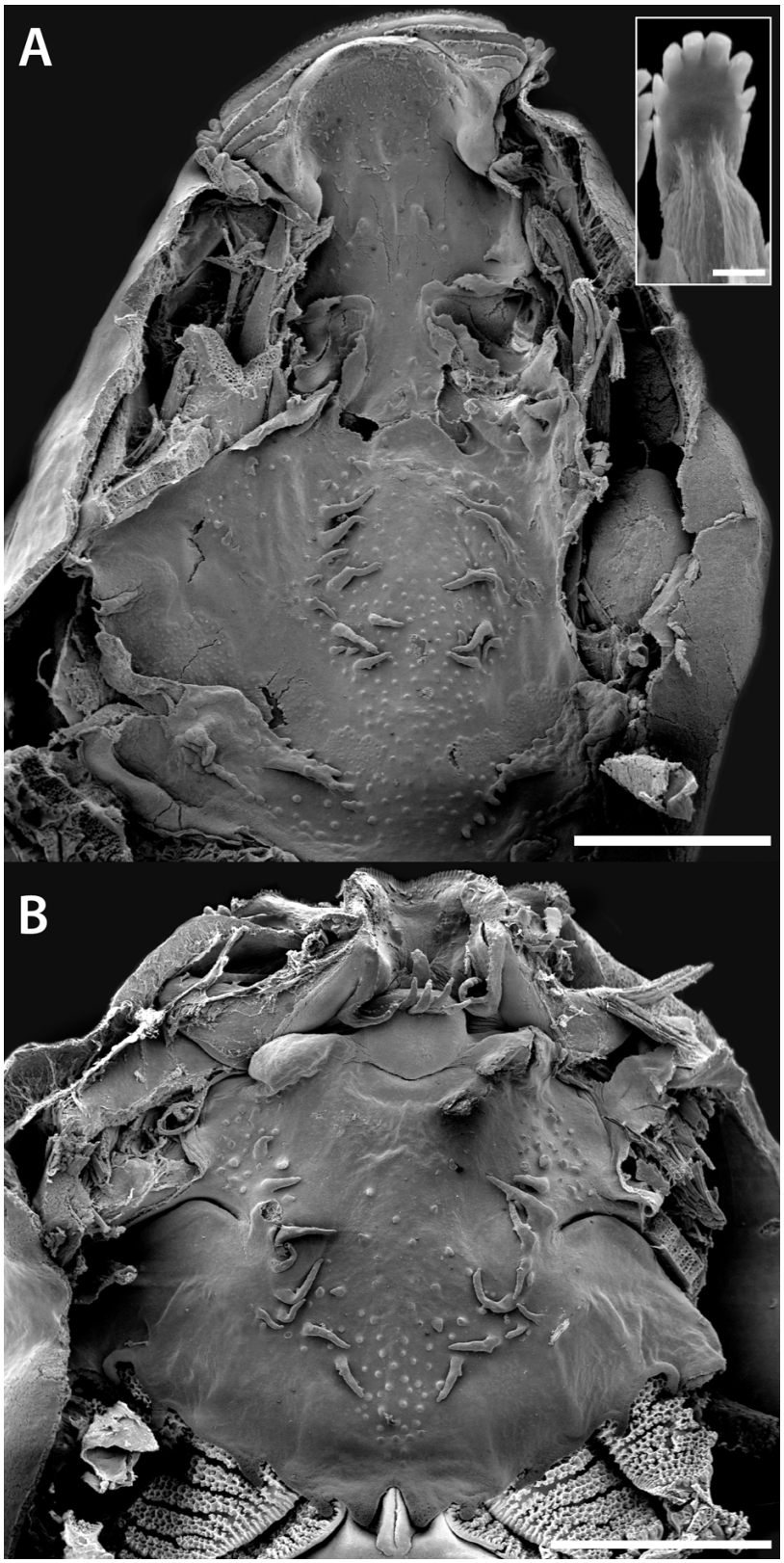

Fig. 2. Scanning electron microscope images of the (A) buccal roof and (B) buccal floor of a Gosner stage 36 tadpole of *Leptopelis natalensis*. Inset in (A) shows a close-up of a keratodont. Scale bars in (A) and (B) equal 1 mm, and 5 µm in the inset.

Table 2. Ontogenetic variation in labial keratodont formula. Number in brackets indicates number of specimens exhibiting the labial keratodont formula; asterisk (*) indicates asymmetry in the last (innermost) anterior keratodont row, with keratodonts present on one side only; keratodont data were only taken for 13 of the 14 investigated specimens of stage 36.

Stage	Labial keratodont formula
25	4(2-4)/3(1) [2]; 4(2-4*)/3 [1]
31	5(2-5)/3(1) [1]
34	5(2-5*)/3(1) [1]
35	4(2-4)/3(1) [2]
36	4(2-4)/3(1) [6]; 4(2-4)/3 [1]; 5(2-5*)/3(1) [1]; 5(2-5)/3(1) [5]
37	5(2-5)/3(1) [2]
38	4(2-4)/3(1) [2]
39	5(2-5)/3(1) [1]
40	5(2-5*)/3(1) [1]
41	5(2-5*)/3(1) [1]

choana, and about six small pustules are present in the area between them. The median ridge separating postnarial arena and buccal roof arena is very prominent and forms an almost semi-circular flap. The buccal roof arena is fringed by eight pairs of medium to large papillae of similar sizes as in the buccal floor arena. An additional three to four pairs of smaller papillae are present in second row towards the posterior part of the buccal roof arena. There is furthermore a group of three to four short lateral roof papillae at each side of the arena. Within the buccal roof arena and posterior to it are ca. 100 pustules. A well-defined glandular zone with numerous secretory pits is present; it is broader laterally and has a relatively narrow medial gap. The dorsal velum has a broad medial gap and number of smaller papillae and pustules along its edge and sides. Additional pustules are present posterior to the dorsal velum and within its median gap.

In the buccal floor (Fig. 2B), a pair of large, flap-like infralabial papillae, with smaller pustules along their margins, is present immediately inside the oral cavity on each side. An additional large, flap-like infralabial papilla is present medially just behind the lower jaw sheath. Four large lingual papillae are present on the tongue anlage. The area immediately behind the lingual papillae is marked by a transverse groove. To the left and right of this grove is a fairly large, bulbous structure. The buccal floor arena is fringed by nine to ten pairs of medium to large buccal floor papillae, all curved towards the buccal floor arena, except for the posteriormost pair of papillae, which point backwards (possibly an artefact of preservation). Around 60 pustules cover the posterior two thirds

Table 3. Summary of published information on *Leptopelis natalensis* tadpoles. EC – Eastern Cape Province, KZN – KwaZulu-Natal Province, G – Gosner (1960) stage.

Reference	Locality	Keratodont formula	Oral disc characters	Maximum length /tail length as multiple of body length
this study	Entumeni Forest (KZN)	4(2-4)/3(1) or 5(2-5)/3(1), rarely 4(2-4)/3	double row of marginal papillae posteriorly, single row of slightly larger papillae laterally; jaw sheaths delicate and narrowly keratinized; disc emarginated	42mm (G39)/2.5x
Wager (1930)	Port St. Johns (EC)	4(2-4)/3	double row of marginal papillae posteriorly, single row laterally; disc emarginated	51mm/2.5x
Wager (1965)	Port St. Johns (EC)	4(2-4)/3	double row of marginal papillae posteriorly, single row laterally; disc emarginated	49mm/2.75x
	Durban (KZN)	4(2-4)/3		35mm/2.5x
	Nkandla (KZN)	5(2-5)/3		50mm/2.3x
Lambiris (1988)	-	4(2-4)/3	double row of marginal papillae posteriorly, single row laterally	50mm (G38)/-
Pickersgill (2007)	Hillcrest (KZN)	4(2-4)/3, sometimes 4(2-4)/3(1)	double row of marginal papillae posteriorly, single row laterally; jaw sheaths narrowly keratinized; disc not emarginated	49mm (G37?)/2.5x
du Preez and Carruthers (2009)	-	4(2-4)/3, sometimes 4(2-4)/3(1)	double row of marginal papillae posteriorly, single row laterally; jaw sheaths delicate	50mm/2.6x (figured tadpole)
Channing et al. (2012)	KZN	4(2-4)/3	double row of marginal papillae posteriorly, single row of slightly larger papillae laterally; jaw sheaths delicate and keratinized along margins; disc emarginated	35mm/2.2x

of the buccal floor arena, as well as the area immediately posterior to it. In addition, ca. 15 pustules are present anterolaterally of the buccal floor arena, just in front of the buccal pockets. The buccal pockets are simple, narrow but deep, curved slits, with no associated papillae or pustules. It is unclear whether the buccal pockets are perforated to provide a bypass to the atrial chamber (Wassersug, 1976) or whether these end blind. The ventral velum is wide, with four marginal projections on each side, and a deep medial notch that exposes the glottis. The ventral velum contains secretory pits along its margin.

Coloration in life. A nearly uniform dark olive, with a scatter of iridiophores across the entire dorsal and lateral sides of body and tail. Ventral side more sparsely pigmented anteriorly, but skin above the abdominal cavity completely unpigmented and translucent in younger stages but becoming somewhat more opaque in older specimens.

Coloration in preservative. Dorsal body densely pigmented and overall homogenously dark brown in colour. Lateral line system very well visible as pigment-free spots in clearly defined lines along the body. Ventral body sparsely pigmented anteriorly but pigment-free above the abdominal cavity, with the coiled gut clearly visible. Pigmentation becomes somewhat less dense on tail and individual melanophores more easily discernible. Pigmentation on the dorsal tail-fin similar to the muscular tail, but distalmost edge pigment-free. Ventral fin free of pigment and translucent, with only some scattered melanophores present along the basal edge and towards the posterior end.

Variation. Overall, little variation is present within the examined material. Specimens differ slightly in the distribution of melanophores on the tail-fins, with some specimens having a ventral tailfin that is almost entirely free of pigmentation except for the very tip of the tail, whereas others show scattered pigment to a various extent within the posterior half of the fin. Pigmentation of the dorsal fin also slightly less or more dense in some specimens. The most variation is seen in the oral disc, in particular the number and arrangement of keratodont rows. Slightly more than half of the specimens (14 of 27; see Table 2) have four anterior rows of keratodonts, with the first always undivided, and the remainder divided. The rest of the specimens have an additional, innermost fifth keratodont row (A5). In all specimens, the last anterior row is usually rather short and in a number of specimens present on one side only (Table 2). The first posterior row is usually divided by a small gap of variable width, but undivided in two of the 27 specimens examined that have an oral apparatus.

DISCUSSION

Overall, the tadpole of *L. natalensis* resembles other *Leptopelis* tadpoles in general shape and appearance (see Channing et al., 2012, and Barej et al., 2015, for most recent and comprehensive treatments of the group). In South Africa, the range of *L. natalensis* is close to or overlaps with the ranges of *L. xenodactylus* and *L. mossambicus* (Channing, 2001; Minter et al., 2004). Based on the available information, the tadpole of *L. mossambicus* appears to be somewhat larger and proportionally shorter-tailed than that of *L. natalensis*, and overall darker in colouration, being more brown than olive (du Preez and Carruthers, 2009). *Leptopelis mossambicus* further appears to differ from *L. natalensis* by having slightly higher tailfins, a very broad rostral gap in the papillation of the oral disc that is almost as broad as the disc itself, and somewhat more robust jaw sheaths that are keratinized for about half their width (du Preez and Carruthers, 2009; Channing et al., 2012). The tadpole of *L. xenodactylus* is very similar to *L. natalensis* and these species appear to be indistinguishable by overall shape and colouration alone. However, in contrast to *L. natalensis*, *L. xenodactylus* tadpoles do seem to have a more robustly keratinized jaw (Channing, 2008; du Preez and Carruthers, 2009; Channing et al., 2012), which should help facilitate a correct identification. In addition there are differences in papillation, with more submarginal papillae being present in *L. xenodactyloides* and the posterior papillae differing in size (inner row of shorter, more globular papillae and outer row of relatively long papillae; Channing 2008). The two species have so far not been found in sympatry, although they occur in close proximity to each other in central KwaZulu-Natal.

A number of descriptions of the tadpole of *L. natalensis* have been provided before (summarized in Table 3), but most of them are brief, lack measurements, or do not provide precise locality information. All previous accounts and our observations agree on the overall shape and colouration of the tadpoles, but some differences especially in total length, oral disc morphology, and keratodont formula exist. While most accounts provide a maximum length of around 50 mm, Wager (1965) and Channing et al. (2012) reported 35 mm as total length, at least for some populations, but did not indicate what stage the examined specimens were at. Furthermore, there is some variation regarding the length of the tail, but all of this seems to be within the limit of normal variation, given that maximum length is largely dependent on condition. While most previous investigators reported or figured a slightly emarginated oral disc, which matches our own observations, Pickersgill (2007) illustrated a disc

that is not emarginated. Assuming all observations to be correct, this would indicate a more substantial difference between that population and others. Both van Dijk (1966) and du Preez and Carruthers (2009) reported the presence of an elygium in the eye of *L. natalensis* tadpoles, although van Dijk (1966) indicated that an ocular elygium might not generally be present and is not easily detected. In our specimens, an ocular elygium is not present, but dorsally the pigmented skin seems to somewhat extend onto the eyeball, which may represent an epidermal elygium (see Kruger et al., 2013).

Most previous descriptions gave the keratodont formula of *L. natalensis* tadpoles as 4(2-4)/3, indicating an undivided P1 (Wager, 1930, 1986; Lambiris, 1988; Pickersgill, 2007; du Preez and Carruthers, 2009; Channing et al., 2012), but Pickersgill (2007) and du Preez and Carruthers (2009) also stated that P1 can sometimes be divided. In our series, only two specimens had an undivided P1, the rest all had a divided P1 although the gap was very slight in some specimens. While this may be an indication of interpopulational variation, it seems possible that previous reports might have simply overlooked a narrow gap in P1. Similar variations in the presence of a divided vs. undivided P1 have been reported by Penske et al. (2015) for *Leptopelis* cf. *grandiceps*. Furthermore, only slightly more than half of the specimens (14, see Table 2) of our ontogenetic series of *L. natalensis* tadpoles had four anterior rows of keratodonts. Almost as many (13 specimens) had an additional, divided A5 and a resulting keratodont formula of 5(2-5)/3(1). Although also present in some younger specimens, the presence of an A5 seemed to be more pronounced in older tadpoles (Table 2).

Variation in the number of keratodont rows has been reported for a number of species, including *L. calcaratus*, *L. gramineus*, *L. vannutelli* and *L. yaldeni* (see Channing et al., 2012). An ontogenetic increase has further been reported for *L. aubryoides* (Barej et al., 2015), *L. calcaratus* (Lamotte and Perret, 1961) and *L. viridis* (Rödel 2000), and specimens with an additional A5 have been reported for *L. modestus*, *L. spiritusnoctis* and *L. rufus* (Barej et al., 2015). In many anuran tadpoles, anterior keratodont rows are added during ontogeny and the presence of an A5 in some *Leptopelis* might be related to overall tadpole size. It is therefore possible that previous investigations did not examine specimens of a sufficient age for an A5 to be expressed. At the same time, the maximum length of 50 mm reported by several authors for *L. natalensis* (e.g., Wager, 1930; Lambiris, 1988; see Table 2 for full list), which substantially exceeds the 42 mm of the largest specimen in our sample, would argue against this. Only Wager (1965) reported tadpoles with an A5 from Nkandla Forest, KwaZulu-Natal. Entumeni Forest, the origin of the specimens examined here and only other reported population of *L. natalensis* tadpoles with a fifth anterior row of keratodonts, is less than 30 km away from Nkandla Forest. Given the current state of knowledge, these two populations seem diagnosably different from other *L. natalensis* populations at the level of tadpole morphology. Future studies of phylogeography of *L. natalensis* should include these populations and investigate their degree of differentiation compared to others.

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