

- TARKHNISHVILI, D. N., AND R. GOKHELASHVILI. 1999. Spatial structure and regulation of a population of the brown frog *Rana macrocnemis* in Georgia. *Herpetological Journal* 9:169–145.
- TYLER, M. J. 1994. *Australian Frogs. A Natural History*. Reed Books, Sydney, New South Wales, Australia.
- TYLER, M. J., L. A. SMITH, AND R. E. JOHNSTONE. 2000. *Frogs of Western Australia*. West Australian Museum, Perth, Western Australia, Australia.
- VILLA, J., AND D. S. TOWNSEND. 1983. Viable frog eggs eaten by phorid fly larvae. *Journal of Herpetology* 17:278–281.
- VONESH, J. R. 2000. Dipteran predation on the arboreal eggs of four *Hyperolius* frog species in western Uganda. *Copeia* 2000:560–566.
- WALDMAN, B. 1982. Adaptive significance of communal oviposition in Wood Frogs (*Rana sylvatica*). *Behavioral Ecology and Sociobiology* 10:169–174.
- WARKENTIN, K. M., C. C. CURRIE, AND S. A. REHNER. 2001. Egg-killing fungus induces early hatching of Red-Eyed Treefrog eggs. *Ecology* 82:2860–2869.
- WATSON, G. F., AND A. A. MARTIN. 1968. Postmating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution* 22:664–666.
- WILLIAMSON, I., AND C. M. BULL. 1994. Population ecology of the Australian frog *Crinia signifera*: egg-laying patterns and egg mortality. *Wildlife Research* 21:621–632.
- WOODRUFF, D. S. 1976a. Courtship, reproductive rates, and mating system in three Australian *Pseudophryne* (Amphibia, Anura, Leptodactylidae). *Journal of Herpetology* 10:313–318.
- . 1976b. Embryonic mortality in *Pseudophryne* (Anura: Leptodactylidae). *Copeia* 1976:445–449.
- YORKE, C. D. 1983. Survival of embryos and larvae of the frog *Polypedates leucomystax* in Malaysia. *Journal of Herpetology* 17:235–241.

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Tadpole of *Bufo taitanus* (Anura: Bufonidae) with Notes on Its Systematic Significance and Life History

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ABSTRACT.—The tadpole of *Bufo taitanus* is described from material recently collected at the type locality. Tadpoles of *B. taitanus* possess a crownlike structure on top of the head. Observations suggest that the crown likely acts as an accessory respiratory organ. Development in *B. taitanus* is rapid with metamorphosis completed after just 13 days. Based on its similarity to tadpoles of *Stephopaedes anotis* and *Mertensophryne micranotis*, a close phylogenetic relationship between these three taxa is proposed.

Bufo taitanus is a small African toad species, described by Peters (1878) from Mt. Mbololo in the Taita Hills, Kenya. Its known range extends from Kenya through Tanzania to Northern Zambia, Southeastern Democratic Republic of Congo, Malawi and adjacent Mozambique (Channing, 2001; Frost, 2002). The phylogenetic relationships of small African toads are poorly understood (Clarke, 2001). Grandison (1981) placed *B. taitanus* in her *vertebralis* group, which includes most of the small African bufonids (but see Clarke, 2001). The tadpoles of many small African bufonids are unknown, but some species are characterized by tadpoles with unusual morphologies, in-

cluding *Schismaderma carens*, *Stephopaedes anotis*, and *Mertensophryne micranotis* (Channing, 2001; Grandison, 1980). Herein, we describe the tadpole of *B. taitanus* and present some observations on its life history.

MATERIALS AND METHODS

Mating pairs of *B. taitanus* were found in a puddle on Mt. Mbololo, Kenya, in November 2003. The adults are easily identifiable by the typical trident mark on the chest (Stewart, 1967) and comparison with museum material confirmed our initial identification (see Appendix 1). Strings of spawn and hatchlings were collected two days later and reared to metamorphosis in a plastic container. The container contained mud and debris from the collection site. No additional food was

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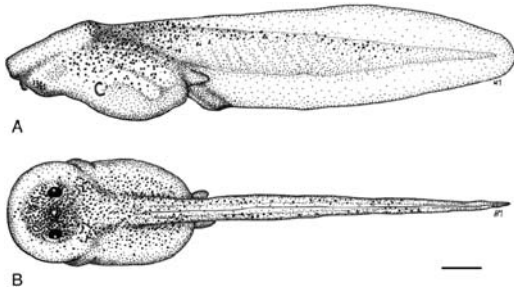


FIG. 1. Tadpole of *Bufo taitanus* at stage 28 (Gosner, 1960) in (A) lateral and (B) dorsal view. Scale bar equals 1 mm.

supplied, and water was replenished daily by fresh stream, rain, or tap water. Specimens were taken daily and fixed in Bouin's or 70% Ethanol. To confirm the conspecificity of the tadpoles with *B. taitanus*, we analyzed fragments of 12s mtDNA of one tadpole and one of the spawning toads collected earlier from the same puddle. The specimens were collected from a temporary puddle in a road passing through a blue gum (*Eucalyptus grandis*) plantation at 1410 m asl. The plantation had burnt some weeks earlier and, thus, lacked undergrowth. At the time of collection, the tadpoles of *B. taitanus* were the only amphibian species present in this puddle.

Developmental stages follow Gosner (1960). We obtained a developmental series of 83 specimens ranging from Gosner stage 18 to Gosner stage 44/45. The description of external morphology and illustrations are based on six tadpoles of Gosner stage 28, with remarks on ontogenetic variation. Standard measurements and labial tooth row formula follow Altig and McDiarmid (1999) except for body length and total length, which were measured from the base of the hind-limb bud, and body height, which was measured from the convergence of the tail with the crown. Interorbital and internarial distances and the distance between the naris and eye were measured from the inner margins of eye and/or naris. All measurements were made under a binocular microscope with an ocular micrometer. Drawings were done with the aid of a camera lucida. Specimens are deposited in the Natural History Museum, London and The National Museum of Kenya, Nairobi (for full details, see Appendix 1).

DESCRIPTION

Tadpole Description.—The most conspicuous feature of tadpoles of *B. taitanus* is a crownlike ring structure on top of the head (Fig. 1). In dorsal view, it appears as a raised ring enclosing the nostrils and eyes. At its posterior end, it is confluent with the base of the tail. In lateral view, the crown stretches from the tip of the snout to the level of the spiracle. At its ventral margin, it forms a groove with the body. The crown is present from stage 23 and starts regressing from stage 36 on. It is absent by stage 42. The body is elongated and, in dorsal view, elliptical. A bulge below the crown, behind the level of the eyes, is visible on each side in dorsal view. Eyes are positioned dorsally with their lower half overgrown by the crown. The nares are dorsally positioned and slightly raised. Narial openings are

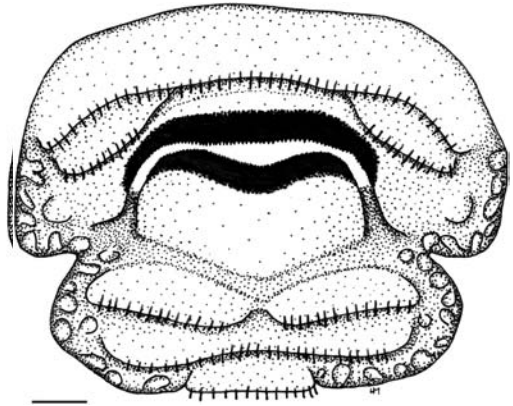


FIG. 2. Oral disc of *Bufo taitanus* at stage 28 (Gosner, 1960). Scale bar equals 0.1 mm.

oval to kidney shaped with a well-defined rim. The spiracle is sinistral and opens dorsoposteriorly. It has no inner wall at stage 28, but a low inner wall is present from stage 32 on. The muscular tail does not extend to the rounded tail tip. Its myotomes are not well defined and are difficult to trace, especially at the cranial end. Tail fins are low, dorsal and ventral fins being about equal in height. The height of the dorsal fin increases from the base of the tail to just past the midpoint of the tail, from where the margin of the fin runs almost parallel to the tail musculature. The margin of the ventral fin runs parallel to the muscular tail over its entire length. The dorsal fin originates at the tail body junction just behind the crown, whereas the ventral fin originates at the posterior ventral terminus of the body. The vent tube is medial with respect to the ventral fin, long, and directed ventroposteriorly. Its opening is usually medial but appears slightly dextral in some specimens. At stage 28 the gut forms three coils.

Measurements.—The given values are means ($N = 6$) for tadpoles of Gosner stage 28, with standard deviation (SD) in parenthesis. All measurements are given in millimeters: total length: $13.32 (\pm 1.02)$; body length: $4.71 (\pm 0.46)$; body width: $2.78 (\pm 0.35)$; body height: $2.26 (\pm 0.31)$; tail length: $8.72 (\pm 0.63)$; tail muscle height: $1.1 (\pm 0.07)$; tail height: $2.78 (\pm 0.21)$; interorbital distance: $0.73 (\pm 0.04)$; internarial distance: $0.54 (\pm 0.05)$; distance eye–naris: $0.21 (\pm 0.03)$; distance naris–snout: $0.68 (\pm 0.09)$; eye diameter: $0.38 (\pm 0.05)$; crown length: $2.61 (\pm 0.1)$; crown width: $2.65 (\pm 0.05)$; crown wall width: $0.58 (\pm 0.05)$; crown height: $0.51 (\pm 0.05)$. Except for the transformations occurring during early tadpole development and metamorphosis, body proportions do not markedly change during larval development.

Oral Disc.—The oral disc is positioned subterminally and is emarginated. It has a single row of rounded marginal papillae (Fig. 2). The row of marginal papillae is interrupted on the upper labium by a large gap, comprising its upper half. On the lower labium, the row of marginal papillae is interrupted by the third row of labial teeth. A pair of large submarginal papillae is present on the upper labium. Two pairs of submarginal papillae are found on the lower labium, laterally above P1 and between P1 and P2. In the specimens examined,

the occurrence of submarginal papillae on the lower labium is variable, ranging from duplication to absence including right-left asymmetry. The tooth row formula is 2(2)/3(1), P3 being the shortest. Labial teeth are similar in length in all rows. The jaw sheets are wide and well pigmented. The upper sheet is concave and the lower sheet V-shaped. Both jaw sheets have finely serrated edges, the serrations being slightly larger on the upper sheet.

Coloration.—The color in preservative is a light yellowish-brown. Melanophores are evenly scattered over the dorsal side of the body, extending down the sides to the level of the spiracle. The highest concentration of melanophores is found on the dorsal side of the head, on the area enclosed by the crown. Here, melanophores are more or less evenly distributed, except for a pineal spot medially between the eyes and a round, pigment free, windowlike area in front of each eye. The crown is relatively free of melanophores except on its caudal rim, where they form a reticulate pattern. On the tail, melanophores are mostly restricted to the anteriormost part of the tail, but some stretch along the dorsal margin of the tail musculature. The fins lack pigment almost completely. The color in life is similar.

Life-History Notes.—The occurrence of *B. taitanus* in the blue-gum plantation appears rather exceptional. According to Channing (2001), it occurs in sandy habitats in savanna and open grassland. *Bufo taitanus* appears to be an opportunistic breeder. Three pairs of *B. taitanus* were observed mating in axillary amplexus in a puddle formed after heavy rainfall at the onset of the so-called vuli short rainy season. All pairs mated and spawned in the water. Fertilization of the eggs is, thus, presumably external. Channing (2001) reported the clutch size to be 125 eggs. We observed short strings of spawn of 10–15. Eggs of *M. micranotis* are laid in similarly short strings of 8–12 eggs (R. Drewes, pers. comm.). Development in *B. taitanus* is rapid. Embryonic development was completed after about two days. The first toadlets left the water after 11 days of larval life. The newly metamorphosed toads had a snout-vent length of 5 mm. A total developmental time of just 13 days is one of the most rapid developments reported for anurans (Duellman and Trueb, 1986; Spieler, 1997).

During periods of high water temperatures (30°C and beyond) tadpoles attached themselves with their crown to the water surface but descended to the bottom of the container as soon as the water was replaced by fresh and cooler, presumably more oxygenated water.

DISCUSSION

The only other known toad species whose tadpoles possess a crown are *Stephopaedes anotis* and *Mertensophryne micranotis*. In overall morphology, *B. taitanus* is similar to tadpoles of these two species, although some differences are readily discernible. *Bufo taitanus* is most easily distinguished from *S. anotis* and *M. micranotis* by its labial tooth row formula, having three infralabial rows of teeth as opposed to only two in the other two species. The crown of *B. taitanus* is not as prominent as in *S. anotis*, where it appears as a very superficial attachment to the larval head (Channing, 1978) but resembles the crown of *M. micranotis* in being more

shallow and confluent with the base of the tail (Grandison, 1980). The angle of the crown with the body axis is smaller in *S. anotis* and *M. micranotis*, as compared to *B. taitanus*, and probably reflects an adaptation to small breeding habitats like water-filled tree holes and other small water bodies, where the surface space is limited (Grandison, 1983; Channing, 1993). *Mertensophryne micranotis* differs from *B. taitanus* and *S. anotis* tadpoles by its slender tail with a greatly reduced dorsal fin (Grandison, 1983).

Channing (1978) suggested that the crown might act as an accessory respiratory surface in *S. anotis*. This was further corroborated by Channing (1993) and Grandison (1983) who observed tadpoles of *S. anotis* and *M. micranotis*, respectively, clinging to the water surface whenever the water temperature was high and oxygen levels therefore presumably low. Our observations suggest that the crown of *B. taitanus* tadpoles serves a similar function.

The genus *Stephopaedes* was erected by Channing (1978) to accommodate *B. anotis* for its unique crown-bearing tadpole. Grandison (1980) discovered a similar morphology in tadpoles of *M. micranotis* but took no taxonomic action, although she believed *Mertensophryne* and *Stephopaedes* form part of a group of small African bufonids (her *vertebralis* group, Grandison [1981]), which also included *B. taitanus*. Subsequent works (Poynton, 1991; Poynton and Clarke, 1999) maintained the generic separation of *Stephopaedes* and *M. micranotis* because of substantial differences in adult features and the current lack of life-history data for many African Dwarf Toads. However, we suggest that the characteristic crown possessed by the tadpoles of all three taxa indicates a close phylogenetic relationship of *Stephopaedes*, *Mertensophryne*, and *B. taitanus*. A close phylogenetic relationship was also suggested by Graybeal (1997) in her analysis of adult morphology. It is evident that the taxonomic assignment of *B. taitanus* to the genus *Bufo* needs to be reconsidered, preferably together with a revision of *Stephopaedes* and *Mertensophryne*. The data presented here for *B. taitanus* demonstrate the importance of larval characters for assessing phylogenetic relationships, especially in taxonomically difficult groups like African bufonids (Clarke, 2001).

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LITERATURE CITED

ALTIG, R. AND R. W. McDIARMID. 1999. Body plan—development and morphology. In R. W. McDiarmid and R. Altig (eds.), *Tadpoles—The Biology*

- of Anuran Larvae, pp. 24–51. Chicago Univ. Press, Chicago.
- CHANNING, A. 1978. A new bufonid genus (Amphibia: Anura) from Rhodesia. *Herpetologica* 34:394–397.
- . 1993. Observations on the Natural History of *Stephopaedes anotis* (Bufonidae). *Journal of Herpetology* 27:213–214.
- . 2001. Amphibians of Central and Southern Africa. Cornell Univ. Press, Ithaca, NY.
- CLARKE, B. T. 2001. Towards a natural classification of African toads (Anura, Bufonidae): past progress and future prospects. *African Journal of Herpetology* 50:19–30.
- DUELLMANN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. McGraw-Hill Book Co., New York.
- FROST, D. R. 2002. *Amphibian Species of the World: an online reference*. V2.21 (15 July 2002). Electronic database available at <http://research.amnh.org/cgi-bin/herpetology/amphibia>.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- GRANDISON, A. G. C. 1980. Aspects of breeding morphology in *Mertensophryne micranotis* (Anura: Bufonidae): secondary sexual characters, eggs and tadpole. *Bulletin of the British Museum (Natural History)*, Zoology 39:299–304.
- . 1981. Morphology and phylogenetic position of the West African *Didynamipus djoestedti* Anderson, 1903 (Anura Bufonidae). *Monitore zoologico italiano (N.S.) Supplement* 15:187–215.
- . 1983. The distribution, behavioural ecology and breeding strategy of the Pygmy Toad, *Mertensophryne micranotis* (Lov.). *Bulletin of the British Museum (Natural History)*, Zoology 45: 85–93.
- GRAYBEAL, A. 1997. Phylogenetic relationships of bufonid frogs and tests of alternate macroevolutionary hypotheses characterizing their radiation. *Zoological Journal of the Linnean Society* 119:297–338.
- PETERS, W. H. C. 1878. Über die von Hr. J. M. Hildebrandt während seiner letzten ostafrikanischen Reise gesammelten Säugethiere und Amphibien. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften Berlin* 1878:194–209.
- POYNTON, J. C. 1991. Amphibians of Southeastern Tanzania, with special reference to *Stephopaedes* and *Mertensophryne* (Bufonidae). *Bulletin of the Museum of Comparative Zoology* 152:451–473.
- POYNTON, J. C., AND B. T. CLARKE. 1999. Two new species of *Stephopaedes* (Anura: Bufonidae) from Tanzania, with a review of the genus. *African Journal of Herpetology* 48:1–14.
- SPIELER, M. 1997. Anpassungen westafrikanischer Froschlurche an Trockenstress und Räuberdruck in einer westafrikanischen Savanne. *Salamandra* 33: 133–152.
- STEWART, M. M. 1967. *The Amphibians of Malawi*. State Univ. Press, New York.

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APPENDIX 1

Material Examined

Bufo taitanus, BMNH 1978.1031–1040, collected at Lilongwe; Malawi; BMNH 1986.1527, collected at Morduli, Tanzania; NMK-A/4240 (two adults) and BMNH 2000.219 (one adult), collected by G. J. Measey and H. Müller at Mt. Mbololo, Taita Hills, Coastal Province, Kenya (03°20'58.2"S, 38°26'24.8"E), on 14 November 2003. NMK-A/4241 (52 embryos and tadpoles) and BMNH 2000.220 (31 tadpoles) raised from spawn collected by H. Müller and G. J. Measey from same locality on 16 November 2003.