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A reproductive mode so far unknown in African ranids: *Phrynobatrachus guineensis* GUIBÉ & LAMOTTE, 1961 breeds in tree holes
(Anura: Ranidae)

Eine bei afrikanischen Raniden bisher unbekannte Fortpflanzungsstrategie: *Phrynobatrachus guineensis* GUIBÉ & LAMOTTE, 1961, ein Baumhöhlenbrüter
(Anura: Ranidae)

MARK-OLIVER RÖDEL

KURZFASSUNG

Im Tai Nationalpark, Republik Elfenbeinküste, wurden Männchen und Kaulquappen von *Phrynobatrachus guineensis* GUIBÉ & LAMOTTE, 1961 gemeinsam in wassergefüllten Baumhöhlen angetroffen. Große, einzeln im Öffnungsbereich einer der Baumhöhlen über der Wasseroberfläche befestigte Eier gehörten zu dieser Art. Die Larve von *P. guineensis* wird erstmalig beschrieben. Darüberhinaus ist dies der erste Bericht über einen baumhöhlenbrütenden afrikanischen Raniden. Die Bedeutung der gemeinsamen Anwesenheit von bis zu fünf Männchen von *P. guineensis* in einer Baumhöhle bleibt unklar.

ABSTRACT

In Tai National Park, Ivory Coast, males and tadpoles of *Phrynobatrachus guineensis* GUIBÉ & LAMOTTE, 1961 were found together in water-filled tree holes. Large, macrolecithal eggs that were singly attached to the aperture of one of the tree holes, belonged to this species. The tadpole of *P. guineensis* is described for the first time. Furthermore, this is the first report on an African ranid species breeding in tree holes. The significance of the simultaneous presence of up to five male *P. guineensis* within a tree hole remains unresolved.

KEY WORDS

Amphibia, Anura, Ranidae; *Phrynobatrachus guineensis*, Ivory Coast, breeding biology, tree holes, reproductive mode, tadpole description

INTRODUCTION

In 1996, I investigated the herpetofauna of Tai National Park in south-western Ivory Coast which is the largest rainforest remainder of West Africa. The most abundant frogs on the forest floor belonged to various species of the genera *Phrynobatrachus* and *Arthroleptis*. While *Arthroleptis* is not dependent on open water due to 'direct' development (e.g. GUIBÉ & LAMOTTE 1958; BARBAULT & TREFAUT RODRIGUEZ 1979; WAGER 1986) all known *Phrynobatrachus* tadpoles live in ponds or streams until metamorphosis (e.g. WAGER 1986; RÖDEL 1996). There, *Phrynobatrachus* species lay single-layer egg films floating on the water surface. These films consist of hundreds to several thousands of small mesolecithal eggs. Due to this reproductive mode, most *Phrynobatrachus* species are supposed to live in the vicinity of open water. During my field work in Tai National Park, I collected a very small species of this genus, *P. guineensis*, in relatively dry parts of the rain forest which are mainly restricted to higher elevations. These areas generally lack open water on the forest floor.

Phrynobatrachus guineensis was described by GUIBÉ & LAMOTTE in 1961 from Mont Tonkoui, Ivory Coast. The species has been recorded from Sierra Leone to western Ivory Coast (GUIBÉ & LAMOTTE 1963; SCHIØTZ 1967; FROST 1985; BÖHME 1994). Most specimens were collected in forest habitats (GUIBÉ & LAMOTTE 1961, 1963; BÖHME 1994). Biological data have not been reported so far.

STUDY SITE AND METHODS

With its size of 3,300 km^2, Tai National Park (6°10'-5°10'N; 7°20'-6°50'W) is the largest rainforest remainder of West Africa. Annual precipitation reaches approximately 2,200 mm in the south-west and 1,300 in the north-east of the park (ROTH & MERZ 1986). Highest precipitation is measured from April / May to June / July and from September to October / November. The first dry period lasts from December to February, a second one typically occurs in August. Temperature varies between 20-33 °C, range of daily temperature variation is up to 10°C, mean annual temperature is around 25°C. Humidity fluctuates from 85 % during the day, to 90-100 % during the night. From its flora, the park belongs to the Guineo - Congolian Region (GUILLAUMET 1967; FGU-KRONBERG 1979). The vegetation in the southern part of the park is characterized by *Diospyros - Mapania* forest which houses many endemic plants and is the most diverse floral region of Ivory Coast. In this part the soils are slaty with high water capacity.

All adult *P. guineensis* collected were intended to be kept alive. Unfortunately, they all died during a bus trip. They were primarily preserved in 4 % formaldehyde. Later they were transferred into 70 % ethanol. Tadpoles and eggs were preserved in 4 % formaldehyde. The tadpole drawing was done with the aid of a camera lucida. The mouth parts of one tadpole were examined by means of scanning electron microscopy (SEM). Snout-vent length of adult frogs was measured with dial callipers, precision ± 0.1 mm. All other measurements of adults and tadpoles were taken with an ocular micrometer (precision ± 0.1 mm). Imagines were identified according to GUIBÉ & LAMOTTE (1961, 1963). Additionally, I compared the frogs to specimens of the type series and with ZFMK (Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn) 56335 from Guinea (BÖHME 1994). All specimens will be deposited in collections (Staatliches Museum für Naturkunde, Stuttgart and ZFMK).

Tadpole staging follows GOSNER (1960), descriptive characters and terminology are largely based on VANDIJK (1966) and the keratodont formula is in accordance with RÖDEL (1996).

RESULTS

Field observations

On September 13, 1996 I collected two male *P. guineensis* in a water-filled tree hole 1.5 m above the forest floor. The hole was 10 cm deep and measured 2.5 cm in diameter. Upon my approach, the frogs fled into the water. After several minutes during which I tried to capture them they jumped down to the forest floor. Both males had almost black backs; white bellies with large black spots, thighs that were yellow on the ventral side, and dark black throats. Neither tadpoles nor further adults were found in this tree hole.

On the same day, I discovered a second water-filled tree hole, approximately 200 m from the first site, which was also 1.5 m above the forest floor. It was 15 cm deep and measured 3 cm in diameter. Thirty five bluish grey and white macrolecithal eggs, approximately 3 mm in diameter each, were singly attached to the bark in the tree hole (fig. 1). In the water I observed some dozens of tadpoles which were rather difficult to capture. However, with a leave folded to a funnel, I succeeded in collecting three of them. The tadpoles continuously surfaced to breath. During my efforts in capturing tadpoles some of the eggs attached above the water surface dropped into the water. Several tadpoles immediately approached and fed on these eggs.

In this tree hole I also discovered five adult *P. guineensis*. Initially, when I sexed them according to the colour of their throats, I classified them as three males and two females. The "females" had a white throat with only a few spots and their dorsum was lighter in colour than in the other frogs. After dissection, however, I found well developed testes in all specimens. One of the 'typical' males had a nar-

Fig. 1: Clutch of *Phrynobatrachus guineensis* attached to the bark above the water surface of a tree hole.
Abb. 1. Gelege von *Phrynobatrachus guineensis* an der Borke über dem Wasserspiegel einer Baumhöhle.

Fig. 2: Male *Phrynobatrachus guineensis* from Tai National Park (Ivory Coast).
Abb. 2: Männlicher *Phrynobatrachus guineensis* aus dem Tai Nationalpark (Elfenbeinküste).

Table 1: Measurements (mm) of three *Phrynobatrachus guineensis* tadpoles.
Tab. 1 : Maße (mm) von drei *Phrynobatrachus guineensis* Kaulquappen.

Features measured (mm) / Meßstrecken (mm)	Tadpole / Kaulquappe I	II	III
GOSNER (1960) Stage / Stadium nach GOSNER (1960)	35	38	42
Snout vent-lenth / Kof-Rumpflänge	3.5	3.5	2.1
Trunk Width / Rumpfbreite	2.6	2.6	2.0
Length of Tail / Schwanzlänge	7.2	6.0	7.3
Length of Hind Leg / Hinterbeinlänge	1.9	3.8	3.8
Hight of Tail including Fin / Schwanzhöhe incl. Flossensaum	1.8	2.0	1.5
Hight of Base of Tail / Höhe der Schwanzbasis	1.0	1.0	1.4
Horizontal Diameter of Oral Disc / Horizontaldurchmesser des Mundfeldes	0.5	-	-
Interocular Distance / Abstand zwischen den Augen	0.6	0.6	0.6
Eye Diameter / Augendurchmesser	0.6	0.8	0.6
Distance: Eye - Nostril / Abstand: Auge - Nasenloch	0.4	-	0.3
Distance: Eye - Tip of Snout / Abstand: Auge - Schnauzenspitze	1.7	-	0.4

row red middorsal line. A second one had a large yellow spot on each side of the body (fig. 2).

The adult frogs measured between 15.8 and 17.3 mm in snout-vent length ($\bar{x}$ = 16.6 mm ±0.6; n=7). Length of thigh was $\bar{x}$ = 8.0 mm ±0.5, length of tibia $\bar{x}$ = 8.3 mm ±0.4, and length of foot including longest phalange was $\bar{x}$ = 12.1 mm ±0.4 mm.

Tadpole description

Measurements of three tadpoles are summarized in table 1. The description is based on a single tadpole of stage 35, 10.7 mm in total length (tadpole I in table 1; fig. 3A). The SEM micrographs were taken from tadpole II in table 1 (stage 38).

The tadpole body shape is ovoid in dorsal view; snout slightly pointed; tail length 67 % of total length.

The dorsal fin originates in the posterior end of the trunk; tail depth slightly exceeds trunk height; dorsal and ventral fins subequal in depth with barely curved margins; height of muscular portion of tail is 55 % of maximum depth of tail fin; dorsal fin depth is largest in the last third of tail; tip of tail rounded.

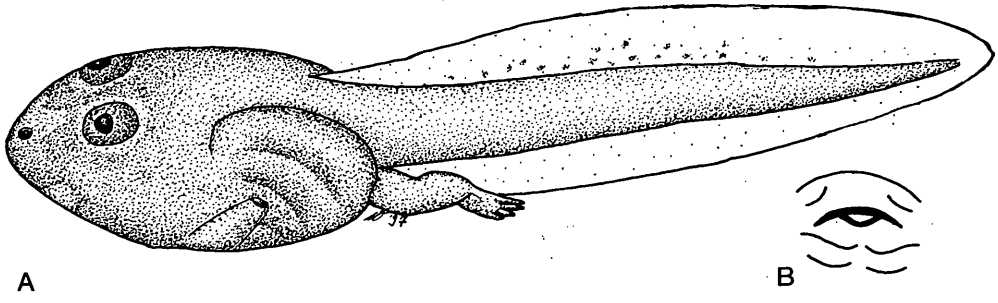

Fig. 3: Tadpole stage 35 (GOSNER 1960) of *Phrynobatrachus guineensis* (tadpole I in table 1).
A - Dorsolateral view; B - Arrangement of tooth rows on oral disc.
Abb. 3: Larvenstadium 35 (GOSNER 1960) von *Phrynobatrachus guineensis* (Larve I in Tab. 1).
A - Dorsolateralansicht; B - Anordnung der Zähnchenreihen des Mundfeldes.

The nostrils are very small, roundish and barely visible from dorsal, much closer to the tip of the snout than to the eye. The eyes are situated dorsolaterally; interocular distance is 23 % of head width. The spiracle is sinistral, visible from dorsal, originating in the middle of the trunk and directed posterodorsally. The aperture of the vent is directed posteroventrally and opens at the margin of the ventral fin, close to the trunk.

The oral disc (fig. 4A) is in subventral position, not visible from dorsal; its width is 19 % that of the trunk. A single row of marginal papillae is present laterally and ventrally while papillae are absent dorsally. Dorsal and ventral jaw sheaths are robust, uniformly curved and sharply serrated. Keratodont formula: 1 / 1+1 // 2 + 2 (fig. 3B). Kreatodonts are slender and multidenticulate (3-4 cusps; fig 4B).

Dorsally, the tadpole is of uniform brown color, the venter is lighter, the tail is evenly pigmented. In formaldehyde, the area around the eyes and the tip of the snout becomes lighter in colour. The fin is nearly hyaline, with a few small dots in its dorsal part.

Based on the body length of the tadpole stage 42 (tadpole III in table 1) which is 2.1 mm, the size of newly metamorphosed froglets is not supposed to exceed 2 mm markedly.

DISCUSSION

I observed *P. guineensis* exclusively in primary forest. Likewise, GUIBÉ & LAMOTTE (1961) collected the species in dense forest at Mont Tonkoui in Ivory Cost. Unfortunatley, they gave no habitat description for the paratypes captured at Mont Nimba in Guinea. In 1963, GUIBÉ & LAMOTTE published on additional specimens from the savannah. Both SCHIØTZ (1967) and BÖHME (1994) collected their frogs in primary forest. BÖHME (1994) mentioned the exceptionally high jumping capability of this frog. In my specimens I observed this as well.

While other members of the genus *Phrynobatrachus* breed in temporary ponds of variable size (e.g. WAGER 1986; RÖDEL 1996), *P. guineensis* seems to breed in tree holes. I cannot rule out other types of breeding sites since I discovered only two water-filled tree holes, though both occupied by this species.

Only a few African anurans are known to breed in tree holes. According to PERRET (1961) some *Hyperolius* species deposit their egg masses there. In his paper he describes the biology of the hyperoliid *Acanthixalus spinosus* (BUCHHOLZ & PETERS, 1875), that arranges its eggs (clutch size about 10 eggs) in a hemispheric gelatinous mass in tree holes above the phytotelm water surface. The bufonids *Nectophryne afra* (BUCHHOLZ & PETERS, 1875) and *Mertensophryne micranotis* (LOVERIDGE, 1925), lay their egg strings into the water bodies of tree holes (GRANDISON 1980; SCHEEL 1970; AMIET 1991; POYNTON 1996). NOBLE (1929) described arboreal tadpoles from two microhylid species, genus *Hoplophryne*, occurring in Tanzania. At least one of these species attaches its unpigmented eggs (4.5-5 mm in diameter) in a single layer to the inner walls of bamboo. As all known terrestrial breeding *Hyperolius* species deposit egg masses (e.g. SCHIØTZ 1967; RÖDEL 1996), all bufonids lay egg strings and no arboreal microhylid has ever been reported from West Africa, it is very likely that the observed eggs, singly attached to the bark, belong to the tree hole dwelling ranid *P. guineensis*.

Thirty-five eggs is rather low a number of eggs compared to other *Phrynobatrachus* species (e.g. WAGER 1986; RÖDEL 1996). The large egg size (3mm) observed compared to the small frog size of *P. guineensis* (females exceed male size only slightly), however, suggests the possibility that more than one female was involved in spawning at that site. Unfortunately, I have not obtained females to investigate ovarian egg numbers.

The specific identity of the tadpoles was assured by tadpole III (table 1) that already showed typical characters of the genus *Phrynobatrachus* as well as for the species *guineensis*.

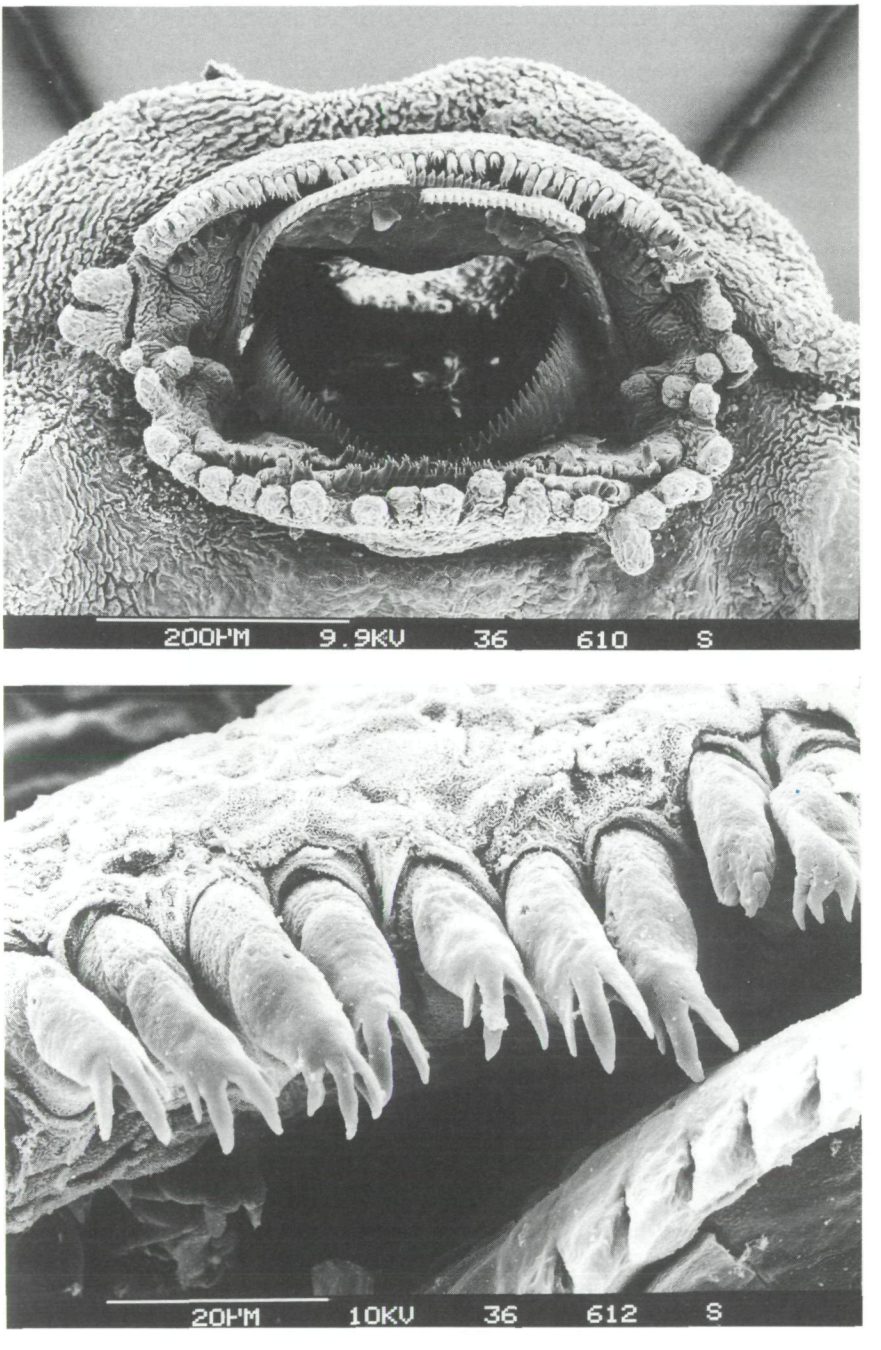

Fig. 4: SEM micrographs of oral disc (A, top) and keratodonts (B, bottom) of *Phrynobatrachus guineensis* tadpole stage 38 (GOSNER 1960) (tadpole II in table 1).

Abb. 4: Rasterelektronenmikroskopische Aufnahmen des Mundfeldes (A, oben) und der Hornzähnchen (B, unten) einer *Phrynobatrachus guineensis* Larve im Stadium 38 (GOSNER 1960) (Larve II in Tab. 1).

Many of the phytotelm dwelling tadpoles described so far show specific adaptations to their constrained habitat (WASSERSUG & al. 1981; LANNOO & al. 1986; ALTIG & JOHNSTON 1989) which have evolved to cope with the restrictions of confined space, food, and oxygen. In many cases adaptations refer to buccopharyngeal morphology, behaviour, and physiology, while external morphology is not strikingly affected. Hence, it is not surprising that external morphology of the tadpole of *P. guineensis* is of generalized ranoid type. Nevertheless, the tadpoles demonstrate some peculiarities which can be found in typical phytotelm dwellers: The spatulate, barely curved tail fin may be considered an adaptation to spatial restriction, the robust jaw sheaths as an adaptation to macrophagous feeding (as was obseved indeed), and frequent surfacing as an indication for aereal breathing.

As the frog's habitat lacked other bodies of open water it might be assumed that the males only searched for sufficient humidity. Since I observed the frogs during the rainy season, the aggregation of up to five males in a small water-filled tree hole is surely not a response to the dry environment. Further males of this species were frequently collected on the forest floor (pers. observation).

Why tiny and rare habitats (which provided space and food for a limited number of tadpoles only) were occupied by more than one male has to remain unresolved until further research will be done.

NOTE ADDED IN PROOF

I collected further data on *P. guineensis* during a field trip to Tai National Park from 24. November to 12. December 1997. On 25. Nov. I observed a male frog within a water filled tree hole. No frogs could be found in 12 additional tree holes in the vicinity (all within a distance of 25 m). On the respective day I discovered a further tree hole (No. 2), 1 km from the first, with two newly metamorphosed frogs (~3 mm SVL) inside. The opening of that hole, 70 cm above the forest floor measured 60 x 63 x 65 mm (width, height, depth). Water level was 67 mm including a detritus layer with a depth of 52 mm. Two egg clutches (egg diameter 3 - 3.5 mm), comprising 11 and 12 eggs, respectively, were attached to the ceiling of the hole. The tadpoles were close to the hatchling stage. Within the water body I observed at least 15 equally sized tadpoles (approx. stage 35-38). They gnawed on the bark as well as on the jelly envelopes of eggs which I had incidentally detached. Within 30 m diameter I found no further tree hole. On 26. November I observed four metamorphosed frogs in No. 2. On 28. November all tadpoles in No. 2 were hatched. Two size groups of tadpoles were now observed in the water body without any obvious interactions. On that day I collected an adult female in No. 2; after dissection it was found that the ovary contained five eggs (~3 mm diameter). On 4. December I found a tree hole with tadpoles, approximately 2 km from No. 2. In that forest part I additionally found tadpoles and new metamorphosed *P. guineensis* in a large, hollow, water field fruit capsule (resembling a coconut) on the forest floor. All breeding sites have been observed within forest parts lacking any bodies of open water. The species identification of eggs and tadpoles is confirmed by these additional observations.

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AUTHOR: Dipl.-Biol. MARK-OLIVER RÖDEL, Theodor-Boveri-Institut für Biowissenschaften, Lehrstuhl für Tierökologie und Tropenbiologie der Universität, Am Hubland, D-97074 Würzburg, BR-Deutschland. [roedel@biozentrum.uni-wuerzburg.de]