



Additional diagnosis, observations of breeding biology and tadpole of a little known dwarf puddle frog, *Phrynobatrachus inexpectatus* (Anura: Phrynobatrachidae)

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Abstract. *Phrynobatrachus inexpectatus* and *P. minutus* are sister species of dwarf-size puddle frogs endemic to humid montane forests in the Ethiopian highlands. For almost two decades *P. inexpectatus* was officially known only from two populations, although a wider distribution was assumed. We confirm a population of this species in Harennna Forest (Bale Zone), at 1,400–2,400 m a.s.l. and report observations of its ecology and breeding biology, including descriptions of its advertisement call and tadpole. *Phrynobatrachus minutus* was long believed to be distributed east of the Great Rift Valley in the same forested area, but we did not find any evidence of this species in the area surveyed. We discuss the misidentification of these species by previous researchers and replace *P. minutus* with *P. inexpectatus* in the amphibian species list of the Harennna Forest. An additional diagnostic description of *P. inexpectatus* is provided that should help to distinguish this species from *P. minutus* and from the sympatric members of the *P. natalensis* complex.

Key words. Amphibia, Ethiopia, Harennna Forest, larva, taxonomy, reproduction, vocalisation.

Introduction

For more than 100 years the Ethiopian dwarf-sized members of the Afrotropical puddle frog genus *Phrynobatrachus* GÜNTHER, 1862 were thought to be just one species – *Phrynobatrachus minutus* (BOULENGER, 1895). LARGEN (2001) restricted the nominal species' range to Ethiopia and separated another species from *P. minutus*, which he named *P. inexpectatus*. Both these taxa are considered endemic to the Ethiopian highlands (LARGEN 2001). At the time of its description, *P. inexpectatus* was known from two localities: east of the Great Rift Valley (GRV) – near Bore at 2,650 m a.s.l., 70 km northwest of Kibre Mengist; in the west of the GRV – and at Dorze (also Dorse) at 2,600 m a.s.l., in vicinity of Arba Minch. More than ten years later, unpublished reports appeared in online sources (IUCN et al. 2013) that this species was present in the “Shawe Swamp, Bale Mountains National Park”, which probably referred to a marshy area somewhere at the river Shawe in the Harennna Forest. However, no further details of its distribution and habitats in this area followed, and to the best of our knowledge no voucher specimens from this locality were available. However, the recently published results of the surveys carried out in this area in 2008 and 2009 reported neither this nor any other *Phrynobatrachus* species (SABER et al. 2019).

In contrast to SABER et al. (2019), our own observations from the southern Harennna Forest confirm the presence of a viable population of *P. inexpectatus* in the Bale Zone, at a wider altitudinal range of 1,400–2,400 m a.s.l. than at the previously known localities. Although both, *P. minutus* and *P. inexpectatus*, have long been known and are locally common, their natural history is surprisingly poorly studied. We observed *P. inexpectatus* during field trips in 2016–2019. During our visit to the area in 2018 we had an opportunity to gain insights into the breeding biology of this species and could study its larvae. The results of this work are reported in this paper.

Material and methods

Identification

We identified 6 adult and 1 juvenile frogs collected in the Harennna Forest in October 2016 that are now housed in museum collections (KUMN Γ-1988, ZFMK 101035–36, ZSM 6–9/2017) by comparison of their 16S rRNA mitochondrial gene sequences with sequences of specimens from type locality of *P. inexpectatus* that were identified as this species and made available in the NCBI GenBank by previous authors (ZIMKUS & SCHICK 2010, ZIMKUS et al.

Table 1. Morphometrics of *Phrynobatrachus inexpectatus* from the Hareenna Forest (in millimetres); for abbreviations used see Material and methods. Barcoded specimens are marked with an asterisk.

Accession #	Sex	SVL	HW	ED	IOD	IND	DEN	DNS	TD	TL	FL	FLT	IMT	OMT	MD1	MD2	MD3	MD4	PD1	PD2	PD3	PD4	PD5
ZSM 7/2017*	m	14.0	5.0	1.8	1.1	1.0	0.6	0.7	0.5	6.7	6.6	12.7	0.2	0.6	1.6	1.9	2.8	0.7	1.3	2.8	4.0	7.0	5.1
ZSM 8/2017*	m	13.5	5.0	1.2	1.3	1.1	0.5	0.8	0.4	5.5	5.2	10.7	0.2	0.5	1.2	1.3	1.8	0.9	1.2	2.8	4.2	6.1	4.0
ZSM 9/2017*	(juv.)	9.7	4.5	1.0	1.2	0.7	0.4	0.2	0.2	3.5	3.7	6.0	0.0	0.2	0.4	0.3	0.9	0.3	0.2	0.4	1.4	3.1	1.4
ZSM 6/2017*	m	18.8	7.0	2.0	1.3	1.2	0.8	0.9	0.5	6.0	6.1	11.5	0.3	0.8	1.6	1.9	3.3	2.0	1.8	2.8	5.5	7.2	3.9
ZFMK 101035*	m	14.0	5.0	1.6	1.1	1.2	0.6	0.9	0.4	7.6	7.5	10.6	0.2	0.5	1.2	1.3	1.7	1.2	1.7	2.5	4.7	6.4	4.1
ZFMK 101036*	m	14.2	5.2	2.0	1.1	1.4	0.6	0.6	0.4	7.3	7.4	12.5	0.3	0.5	1.6	1.7	2.7	1.3	1.2	2.4	3.7	6.5	3.9
ZFMK 102214	m	17.9	6.8	2.1	1.6	1.2	1.1	0.9	0.6	7.3	7.9	13.8	0.6	0.7	1.4	1.6	3.0	1.0	2.3	3.6	4.2	6.6	4.1
ZFMK 102215	f	19.8	6.0	2.2	1.2	1.2	0.7	0.4	0.4	7.6	7.4	12.7	0.6	0.6	1.8	1.9	3.5	1.9	2.6	3.9	5.7	6.9	4.6
KUMN Γ-1988*	f	14.3	4.6	1.7	1.3	1.2	0.5	0.7	0.3	6.9	6.5	10.9	0.3	0.5	1.5	1.7	2.7	1.3	1.2	2.4	4.6	6.3	3.8
ZSM 90/2019	f	21.1	6.9	3.2	1.8	1.7	1.4	1.4	0.7	8.3	7.4	14.1	0.9	0.7	2.4	2.7	3.2	2.2	2.6	3.5	6.0	7.3	3.7
ZSM 86/2019	m	18.4	7.0	2.3	1.7	1.6	1.0	1.3	0.4	8.4	7.5	12.4	1.0	0.7	2.0	2.4	2.9	1.7	2.3	2.5	5.3	6.1	3.3
ZSM 87/2019	m	17.8	6.4	2.9	1.4	1.6	1.0	1.2	0.5	6.4	7.1	11.0	0.7	0.4	1.7	2.3	2.6	1.8	1.1	2.3	4.5	5.7	3.7
ZSM 85/2019	m	18.4	6.2	3.2	1.3	1.7	1.0	1.0	0.9	7.7	5.9	12.2	0.8	0.6	2.3	2.2	2.7	1.9	1.3	2.0	4.7	7.4	3.7
ZSM 92/2019	m	15.5	5.1	2.1	1.1	1.3	1.0	1.0	0.5	6.2	5.7	11.7	0.8	0.6	1.3	1.5	2.3	1.5	1.6	2.3	3.8	6.7	3.7
ZSM 91/2019	m	15.3	6.0	2.1	1.1	1.4	0.9	1.2	0.5	5.6	6.1	11.0	0.7	0.5	1.2	1.4	2.2	1.3	1.6	2.1	3.6	6.4	3.4
ZSM 93/2019	m	15.5	5.9	2.4	1.4	1.7	0.7	1.2	0.7	6.9	5.7	12.0	0.8	0.6	1.9	1.5	2.4	1.5	1.6	2.5	4.8	6.6	2.9
ZSM 88/2019	m	17.7	6.4	2.3	1.3	1.3	0.8	1.0	0.5	7.5	6.9	13.3	0.7	0.5	2.0	2.2	2.5	1.3	1.8	2.5	5.6	6.2	3.3
ZSM 89/2019	m	18.5	6.6	3.0	1.2	1.6	0.7	1.9	0.7	7.6	6.4	12.9	0.8	0.6	2.3	2.4	2.7	1.8	2.0	2.7	4.7	6.7	3.7

ZNHM = Zoological Natural History Museum of Addis Ababa University, Ethiopia; ZSM = Zoologische Staatssammlung München, Germany.

To review the morphological characters, we examined the following 33 specimens of *P. inexpectatus* from the Hareenna Forest found in collections: KUMN Γ-1988 (1 male – vicinity of Chaffadhera village, 2016, 6°30'03.5" N, 39°44'43.8" E, 1,567 m a.s.l.); LIV 1986.212.228–241 (13 specimens – vicinity of river Shawe, 6°40'04.8" N, 39°43'58.8" E, 1,980 m a.s.l., 19.8.1986, catalogued as "*P. minutus*"); ZFMK 101035–36 (2 males – vicinity of Chaffadhera village, 10.2016, 6°30'01.4" N, 39°44'41.9" E / 6°30'08.6" N, 39°45'08.2" E, 1,500 m a.s.l.); ZFMK 102214–15 (1 male, 1 female – Haro Alati glade, ca. 2 km north of Cirri village, 12.11.2018, 6°26'08.1" N, 39°45'59.9" E, 1,434 m a.s.l.); ZNHM not accessioned (1 male, 1 female, without exact locality information and date – labelled as "*P. minutus*, Bale, BMNP, 2015"); ZSM 6–9/2017 (2 males, 1 female, 1 juvenile – vicinity of Chaffadhera village, 10.2016, 6°29'58.5" N, 39°44'59.0" E / 6°30'00.1" N, 39°44'46.4" E / 6°29'59.1" N, 39°44'46.5" E / 6°30'09.0" N, 39°45'08.1" E, 1,503–1,569 m a.s.l.); ZSM 85/2019 (1 male – Manyate, flooded grass area in the village, 31.5.2019, 6°29'18.8" N, 39°44'44.1" E, 1,520 m a.s.l.); ZSM 86–88/2019 (3 males – Segoba glade, north side, 1.6.2019, 6°35'14.0" N, 39°44'41.1" E / 6°35'10.3" N, 39°44'31.0" E, 1,770–1,780 m a.s.l.); ZSM 90/2019 (1 female – 1 km north-west of Katcha, 8.6.2019, 6°41'20.7" N, 39°39'20.4" E, 2,378 m a.s.l.); ZSM 91/2019 (1 male – Kaffa Guasaa glade, 6.6.2019, 6°41'20.7" N, 39°39'20.4" E, 1,885 m a.s.l.); ZSM 89/2019 (2 males – Woraba glade, 5.6.2019, 6°35'39.0" N, 39°45'14.6" E, 1,800 m a.s.l.); ZSM 93/2019 (1 male – Hacho glade, 6.6.2019, 6°43'17.5" N, 39°43'02.8" E, 1,908 m a.s.l.). We also verified our identification with

the type series of *P. inexpectatus* housed in the NHMUK: BM 1975.1711 (holotype: male) and BM 1975.1684, 1689, 1691, 1695–1698, 1702, 1712–1714, 1716–1735 (31 paratypes: 16 males, 11 females, 4 immature – 70 km north-west of Kibre Mengist, near Bore, 06°23' N, 38°35' E, 2,650 m a.s.l.); BM 1979.1781–1787 (7 paratypes: 6 males, 1 female – 4 km north of Dorse, 06°16' N, 37°40' E, 2,600 m a.s.l.).

In situ measurements

GPS coordinates and distances were taken with a Garmin Oregon 450t. Values of water temperature were recorded with a Garmin tactix GPS watch submerged in water near eggs or tadpoles for 10 min. The advertisement call of a male was recorded in situ with a ZOOM H8 recorder. The recordings, edited with Adobe Audition CC, were analysed and visualised with a Sonic Visualiser (Release 3.2.1, University of London). In our description of the call we follow the terminology and methods used by other authors in similar cases (CRUTSINGER et al. 2004, SCHICK et al. 2010, TABOUE & FOKAM 2016, KÖHLER et al. 2017).

We identified the vegetation zones of the Hareenna Forest according to the classification by FRIIS (1986).

Morphological measurements and assessments

All measurements were taken with an accuracy of ± 0.1 mm by one person (AT). Measurements of adult specimens were taken with electronic callipers and a micrometrical ocular and comply with the morphometry schemes used by other authors (BLACKBURN & RÖDEL 2011, RÖDEL et al.

2012, RÖDEL et al. 2015, WATTERS et al. 2016). Webbing formulae are after RÖDEL et al. (2012, 2015). The following abbreviations are used for morphometric parameters: SVL = snout–vent length, HW = head width, ED = horizontal eye diameter, IO = interorbital distance (minimum distance between eyelids), IN = internarial distance, DEN = distance from anterior corner of eye to naris, DNS = distance from naris to snout tip, TD = horizontal tympanum diameter, FL = femur length, TL = tibia length, FLT = foot length including toe IV, IMT = length of inner metatarsal tubercle, OMT = outer metatarsal length, MD1–4 = manus digit length, PD1–5 = pedal digit length.

Tadpoles were measured with a 10x micrometrical ocular, and the parameters follow those used in other tadpole descriptions of this genus (PFALZGRAFF et al. 2015): SVL = snout–vent length, BW = body width, BH = body height, AH = tail axis height at base, VF = ventral fin height, DF = dorsal fin height, AW = maximum tail axis width, IOD = interorbital distance, SND = direct snout-to-naris distance, SED = direct snout-to-eye distance, ED = eye diameter, SSD = spiracle-to-snout distance, ODW = oral disc width, SL = spiracle length.

The sizes of eggs were estimated in situ with a ruler placed at the clutch.

Illustrations were drawn by one of the authors (AT) from specimen ZFMK 102216/2 and verified by comparison with other specimens before final preservation in ethanol as well as with photographs in life of the same tadpoles.

Results

The 16S gene sequences of our specimens from the Haremma Forest (Table 1) matched the sequences ($p = 0.0$) of topotypic specimens of *P. inexpectatus* (GenBank # EU075290–292). These results match the identification of another *P. inexpectatus* specimen (SB143) from the Haremma Forest (Manyate village) recently published by GOUTTE et al. (2019). Our specimens differed from superficially similar species in this group distributed in nearby geographic areas: *P. keniensis* BARBOUR & LOVERIDGE, 1928 – $p = 0.045 \pm 0.001$ (GenBank # EU075293, FJ889459, FJ829270, JX564885); *P. minutus* – $p = 0.035$ (GenBank # FJ829284–288); *P. scheffleri* (NIEDEN, 1911) – $p = 0.039 \pm 0.001$ (GenBank # FJ889469–500); and *P. parvulus* (BOULENGER, 1905) – $p = 0.053 \pm 0.006$ (GenBank # GQ183588–591, FJ829306–310, FJ889465–467, EU075295–297). The distance from the unnamed sympatric species in the *P. natalensis* complex (that we here refer to as ‘*P. cf. natalensis*’) was more significant: $p = 0.193$ (ZFMK 101146, ZSM 17/2017). From the other three, even more distantly related species of *Phrynobatrachus* that were recorded at the Horn of Africa – *P. acridoides* (COPE, 1867), *P. bibita* GOUTTE, REYES-VELASCO, BOISSINOT, 2019, *P. bullans* CRUTSINGER, PICKERSGILL, CHANNING, MOYER, 2004 – the population of *P. inexpectatus* in the Haremma Forest is very strongly separated ecologically and geographically. Therefore we did not include these species in our study and in further discussion here.

Additional diagnosis

Adult males and females of *P. inexpectatus* are similar in size, but males are generally slightly smaller, although this is not statistically significant (Table 1). The largest female we measured (ZSM 90/2019) had SVL 21.1 mm while the largest males (ZSM 85/2019, 86/2019) were 18.8 mm in size. Terminal phalanges are not expanded. Most measured specimens (Table 1) had the same webbing formula: I(1), II(1), III(1), IV(1), V(1): Pedal webbing is very limited; a broad webbing does not extend beyond phalanx 1 on all toes, but may be present on phalanx 2 of toe IV as a feeble fringe. However, in the largest specimen (ZSM 90/2019) 1.3 phalanges on toe II, 1.2 on toes III and IV had broad webbing. On toe V the broad webbing extended almost to the middle of phalange 2.

Tympanum present but indistinct; supratympanal fold barely visible (usually present only as a small streak); naris at almost equal distance between orbit and rostrum. Femoral pores visible in breeding males, but feeble and barely recognisable in preservative.

Skin on dorsum generally smooth or finely granular, with some enlarged warts; occipital and scapular glands usually enlarged and darker colored, arranged as an ‘X’. No gular pattern in either sex; gular region in both males and females pale cream or rose, posteriorly darker rose or reddish; in breeding males, the entire throat is more uniformly rose. Dorsal coloration red-brown or copper-red, with some darker brown blotches. Cream or yellowish longitudinal vertebral stripe absent or present. Forelimbs are gold or orange dorsally. Dark crossbands on tibia, thighs and forearms. Shoulders dorsally free of this pattern; ventrally with dark spots that merge on the front side of the shoulder to a dark longitudinal band. Large dark brown or grey patches on flanks: one, reaching from hind limb approximately to the level of the sacral vertebra on the back, and another one starts just above the shoulder and extends all over the flank to the insertion of the thigh. There is a band of the same colour between eye and shoulder. Venter pale or cream-colored, often with a light grey mottled pattern that turns darker towards the flanks. Canthus rostralis not outlined or feebly outlined with the same dark colour as the rest of markings. Live photographs in Figure 2 show a *P. inexpectatus* specimen from the Haremma Forest with a coloration that is typical for this species. A thin pale mid-dorsal stripe is present in some individuals.

Aberrant individuals with a dorsally red-brown body and head occur. The aforementioned pattern of blotches and bands will then be usually indistinct, and the animal will appear more or less bicolored – with brown flanks and limbs, and reddish dorsum.

Habitat and distribution in the Haremma Forest

Phrynobatrachus inexpectatus is fairly common in the *Podocarpus-Felicium* forest at an altitude of 1,400–1,600 m a.s.l. In the rainy season of 2016, about 5 individuals per hour

could be encountered during a normal forest walk, i.e., not by dedicated search. We first observed the frogs in October in the area between the villages of Manyate and Chaffadhera. Unlike *P. cf. natalensis* that are frequently found at riverbanks and in villages, *P. inexpectatus* occurs only on the forest floor, under trees (Figs 3A, B). During the next field trip in November 2018, we observed *P. inexpectatus* in similar habitats as before, north of the Harena Buluk road, about 5 km west of the previous locality. At that time they were not as common on the forest floor. Instead we found more of them in puddles in a glade (Figs 3C, D). The vegetation in this zone of the Harena Forest is dominated by large trees, such as *Afrocarpus (Podocarpus) gracilior*, *Celtis africana*, *Cassipourea malosana*, *Croton macrostachyus*, etc. The undergrowth is formed by wild coffee (*Coffea arabica*), young trees of the above-mentioned species, and various species of vines.

In 2019, we frequently observed and recorded vocalisations of *P. inexpectatus* at many localities in the *Podocarpus-Felicium* and *Aningeria-Olea-Ocotea* vegetation zones between approximately 1,600 and 2,000 m a.s.l. (Fig. 1).

P. inexpectatus occurs also at higher altitudes in this area: In collections there are vouchers from the *Schefflera-Syzygium* vegetation zone, which begins at about 2,000 m a.s.l., where the climatic conditions and the flora community are radically different. Our highest record of this species is at 2,370 m a.s.l. – ca. 1 km north-west of Katcha (ZSM 90/2019). This species seems to be absent from the higher altitudes of the *Hagenia-Hypericum* vegetation zone (above 2,800 m a.s.l.), as well as from the heather (*Erica* sp.) vegetation zone that begins at approximately 3,250 m a.s.l. and extends to the high plateau of the Bale Mountains.

Glades that could serve *P. inexpectatus* as breeding sites are absent in these areas.

Phrynobatrachus inexpectatus appears to be diurnal: Although frequently encountered during the day, we did not see these frogs during night excursions, while toads (*Sclerophrys*) and ridged frogs (*Ptychadena*) were normally active.

Breeding biology

We made our observations in November 2018, close to the end of the main rainy season, which lasted longer than usual in that year. The breeding activity of *P. inexpectatus* appears to be induced by strong rains. On the days we spent in the study area it rained briefly several times every day and night, but long torrential rains were experienced only during two nights – on 11 and 16 November 2018. On 12 November, between noon and 2 p.m., we found males calling and a couple in amplexus. Amplexus was axillary and performed in water (Fig. 4A). The weather on that day was a mix of periods with clear skies and bright sunshine, and those with overclouding and a little rain. On other days (with normal, short rainfalls) the frogs were absent from the puddles. We did not observe further calling males in the puddles after eggs had been laid there. However, we noticed shorter and less intensive vocalisations from nearby puddles on 17 November 2018, and, again, it had rained very heavily in the night before.

Although these frogs spend most of their life in shaded environments, inhabiting grass and leaf-litter on the forest floor, during breeding, *P. inexpectatus* prefers places with



Figure 2. Photographs of *Phrynobatrachus inexpectatus* in life (ZSM 6/2017, female) from the vicinity of the village of Chaffadhera, Harena Forest: lateral and dorsal aspects.

strong insolation, such as large glades with low grass. At our study locality, they were using temporary puddles with approximately 50 m² in surface area and a maximum depth of 20 cm. The frogs were spawning in about 10-cm deep places where during the day the water temperature remained around 25–26°C when it was cloudy or even close to 30–31°C on sunny days. Evaporation was compensated by short rainfalls several times a day. Most puddles were connected with each other after rains via slow-flowing runnels. Those small streams were merging at the south end of the glade and running off into larger streams outside the forest within agricultural area. In the dry season, such shallow waterbodies will certainly dry up, leaving very little time for metamorphosis when eggs are laid late.

On this single glade, an area of approximately 500 × 150 m, we counted more than 100 puddles of various sizes and shapes. Although the majority were of similar size and depth, the males were calling only from a few (not more than a dozen) of them that were situated in the southwest of the glade. We observed amplexus only in one such puddle at noon on 12 November.

We presume that the main spawning event from this amplexus took place later, after we had left this area – most

probably in the evening or in the night. Then, other couples also attended this single pool: When we visited this puddle the next day, 13 November, we found 17 clutches, situated in a small, 18-cm deep area, close to the middle of it, but none in the puddles nearby. Each clutch contained around 30 eggs that were ca. 1 mm in diameter. The clutches were attached to thin leaves and stalks of grass just below the water surface (Fig. 4B), with some of them sticking together in aggregations of two or more. On the subsequent day, 14 November (Fig. 4C), the embryos were at stage 19–20 (GOSNER 1960). When we visited the site three days later, all clutches had disappeared, and we found swimming tadpoles that were already at stage 24–25 (Fig. 4D).

Advertisement call

The vocal sac is subgular. When inflated, it has a diameter of approximately 1.7 of the head width. Males call from the water or from low grass near it, and we observed that they generally do so only in bright sunshine. We heard no or fewer and shorter calls when a cloud obscured the sun or when it was raining. The calls are not loud – in normal conditions

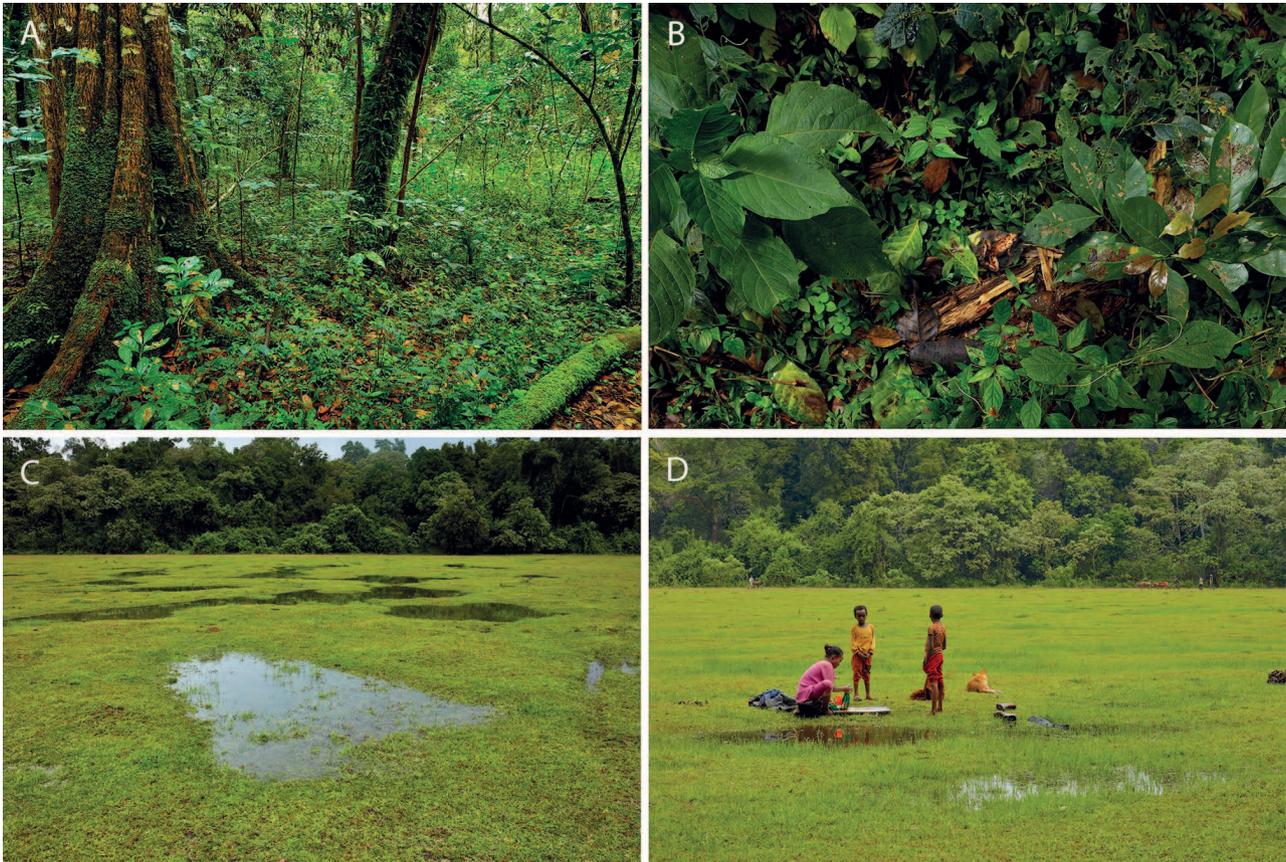


Figure 3. A – Typical habitat of *Phrynobatrachus inexpectatus* in the south of the Harena Forest, vicinity of the village of Chaffadhera; B – *P. inexpectatus* in its microhabitat on the forest floor; C – breeding site in the Haro Alati glade, in the vicinity of Cirri village; D – the Haro Alati glade with the studied breeding site is extensively used by local people as pasture, for laundry, but also for recreation and social events, such as community meetings and wedding parties.

Table 2. Morphometrics of *Phrynobatrachus inexpectatus* tadpoles (in mm); for abbreviations used see Material and methods.

Accession #	SVL	TL	BW	BH	AH	VF	DF	AW	IOD	SND	SED	ED	SSD	ODW	SL
ZFMK 102216/1	3.9	6.4	2.6	2.2	1.0	0.9	1.2	0.4	1.3	0.3	1.3	0.4	2.1	0.8	0.3
ZFMK 102216/2	4.1	5.5	2.4	2.0	0.9	0.9	1.1	0.4	1.1	0.2	1.1	0.5	2.0	0.9	0.2
ZSM 276/2018/1	4.0	5.6	2.4	2.3	0.8	0.8	1.0	0.5	1.1	0.3	1.2	0.6	2.1	0.8	0.3
ZSM 276/2018/2	3.8	5.3	2.6	2.0	0.9	0.9	1.1	0.3	1.2	0.2	1.2	0.5	1.9	0.7	0.3

(with usual background noise) they are barely audible as a rather high-pitched rattle from 100–150 m away. The frogs become silent upon approach at a distance of 5–7 m from the puddle. It seems likely that people that frequently pass through the glade during the sunny hours of the day disturb the frogs. Due to consistent disturbances of this kind we managed only one successful recording. The call that we recorded on 12 November at about 25°C (water temperature) lasted for 15–16 seconds and consisted of two or more longer notes of 4–9 seconds that were interrupted by short notes of less than 1 second and by a couple of singleton clicks (Fig. 5). Several similar clicks precede and follow the call. The pulse rate is about 112 pulses per second, with intervals of ca. 9 ms between pulses. Longer notes consist of 1000

pulses or more. The tone frequency is 3,700–4,700 Hz. Another call follows after a few seconds of silence. The pause may be longer if something disturbs the caller.

Description of tadpole

Our description is based on four tadpoles at development stages 24 and 25 (GOSNER 1960): ZFMK 102216 (2 specimens) and ZSM 276/2018 (2 specimens), all collected from a temporary shallow puddle on a glade in *Podocarpus-Felicionum* zone of the Harena Forest, 6°26'08.1" N, 39°45'59.9" E, 1,470 m a.s.l., on 17 November 2018. Measurements are provided in Table 2.



Figure 4. A – Pair of *Phrynobatrachus inexpectatus* in amplexus (the same animals as shown in Fig. 6); B – eggs on Day 1; C – eggs on Day 2, with embryos at stage 19–20; D – tadpole in development stage 24 on Day 5.

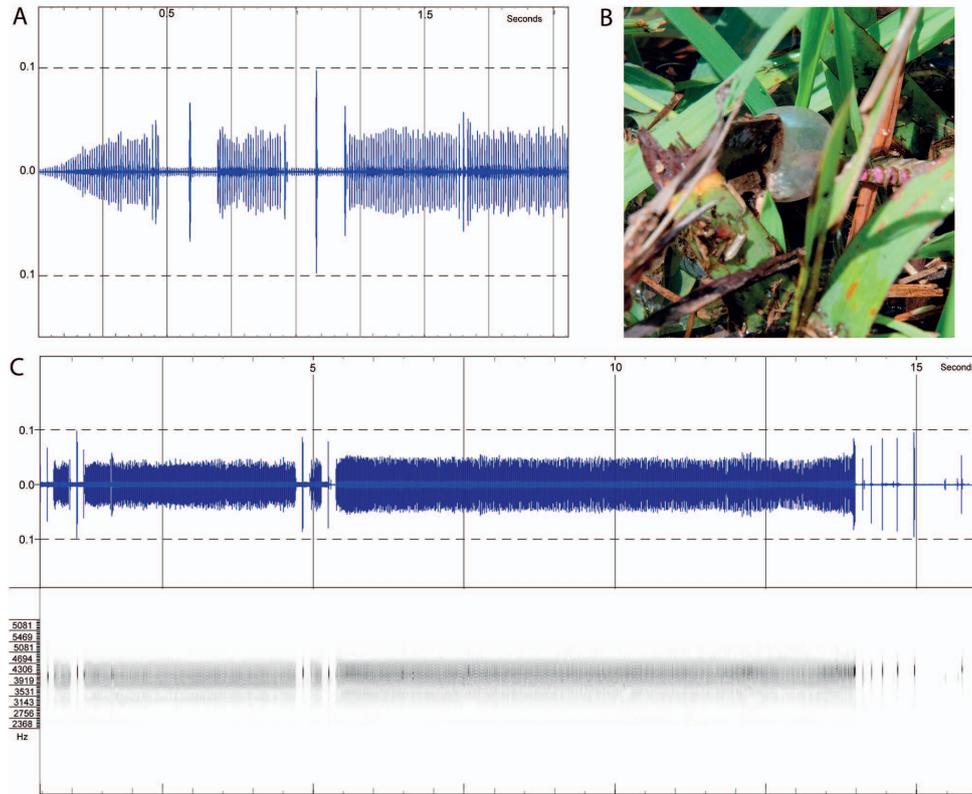


Figure 5. A – Oscillogram of the first two seconds of an advertisement call, enlarged; B – male *Phrynobatrachus inexpectatus* calling in situ; C – oscillogram and spectrogram of the entire advertisement call.

Body morphology (Fig. 6, left): Body ovoid, with width and height almost equal. SVL/TL 0.60–0.71; BH/SVL 0.56–0.57; BW/SVL 0.7; maximum body width is reached slightly posterior to the insertion of the spiracle. Snout rounded in dorsal view. Mouth near ventral face, not visible in dorsal view. Nostrils widely spaced, situated dorsolaterally, only slightly closer to snout tip than to eyes (SND/SED = 0.16–0.23); SND = 0.07 SVL. Spiracle sinistral, well below the median body axis, not visible in dorsal view. Eyes positioned dorsolaterally; ED/SVL 0.12.

Maximum height and width of tail are at its base; AH/BH 1.45; AW/BW 0.19; tail is narrower in dorsal view. Fins moderately developed. Dorsal fin emerges at tail–body junction, is slightly curved; its maximum height is approximately at 1/3 of tail length. Ventral fin emerges at the ventral terminus of the body and is lower than the dorsal. Tail tip pointed. Maximum tail height is lower than body height. Vent tube dextral.

Oral morphology (Fig. 7, right): Oral disc is 0.7–0.9 mm wide; relatively small at ODW/BW 0.27–0.33; oval in shape, posterior labium not emarginated. One outer posterolateral row of conical papillae is visible. No filamentous papillae present. Inner formations of papillae are indistinct (at least at this development stage). There are one anterior and two posterior continuous keratodont rows; labial tooth row formula: 1 / 2. Jaw sheaths moderately strong. Anterior

jaw very widely U-shaped, posterior jaw U-shaped with a median convexity.

Coloration in life: The tadpole is brown in general appearance. Body and tail translucent, with dense aggregations of melanophores on dorsum, snout and around eyes; very small golden spots on dorsum noticeable in strong light. Venter translucent; intestines well visible.

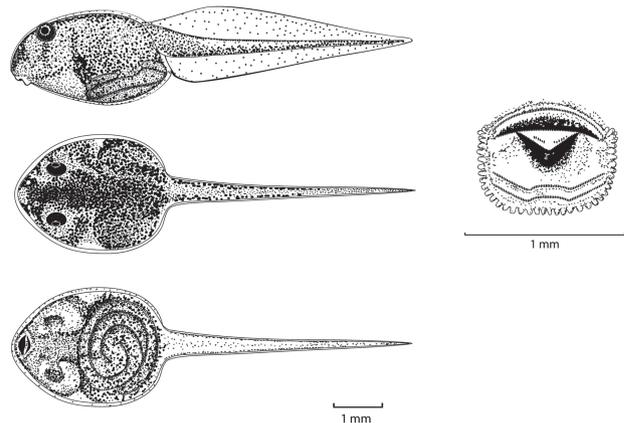


Figure 6. Tadpole of *Phrynobatrachus inexpectatus* in lateral, dorsal and ventral aspects, and its mouthparts.

Coloration in preservative: Body and tail axis irregularly speckled dark on pale ground; dorsal face predominantly translucent with dense dark speckles; ventral face translucent without spots; spiracle and vent tube translucent; intestines clearly visible.

Discussion

Contrary to the original description of this species (LARGEN 2001), none of our preserved specimens exhibited a gular region that was darkly pigmented even if the animal was in breeding condition at time of collection. The throat and ventral faces of the limbs of a breeding male, which are reddish in life (Fig. 7A), will become light yellow in ethanol (Fig. 7B). Preserved non-breeding males and females look alike. We did not observe the 'darker upper lip' in *P. inexpectatus* that was described by LARGEN (2001), and we noticed 'spinules on skin' in both sexes, rather than just males. These sharp apices of small skin glands disappear very quickly after the animal is captured and thus do not seem to be of any help as a diagnostic character.

We found one aberrant individual (ZFMK 101035) with a uniformly orange back. Amongst the specimens in the World Museum (Liverpool), which were collected by a British expedition to the Haremma Forest in 1986, are three frogs with such a pattern: LIV 1986.212.230, LIV 1986.212.231, and LIV 1986.212.233. Furthermore, in this series from the vicinity of Katcha (ca. 2,200 m a.s.l.), there is one specimen, LIV 1986.212.241, that has a thin vertebral stripe. During our next field season we found more such individuals in other glades in the Haremma Forest. This pattern seems to occur in about one third of all individuals at higher altitudes, i.e., above 1,700 m a.s.l.

Phrynobatrachus inexpectatus can be distinguished from *P. minutus* (sensu LARGEN 2001) by its pedal webbing, although not reliably so: In *P. inexpectatus* the broad webbing more usually does not reach past the joint of phalanges 1 on all toes, while in *P. minutus*, it extends beyond this point at least on toes III and VI, and is present as a distinct fringe up to the terminal phalanges on all toes. However, this difference is evident only when large series of specimens are compared. Both these species can be readily separated from *P. cf. natalensis* by their pedal webbing as well, which



Figure 7. Colorations of breeding male (left) and female (right) *Phrynobatrachus inexpectatus*: A – in life, B – in preservative (after 3 weeks of preservation in 70% ethanol, ZFMK 102214 and 102215).

is much more expansive in the latter, reaching to the joints of the terminal phalanges (Fig. 8). The nares are closer to the tip of the snout in *P. cf. natalensis* while they are at equal distances between orbit and snout tip in *P. minutus* and *P. inexpectatus*. The tympanum is always indistinct in *P. minutus* and *P. inexpectatus*, usually indistinct in young *P. cf. natalensis*, but quite well visible in adult *P. cf. natalensis*, being larger in males than in females (Fig. 9).

All three species are well distinguishable by their colour patterns. *Phrynobatrachus cf. natalensis* never has dark patches on its flanks and behind the eyes like *P. inexpectatus* has. These markings are usually much smaller in *P. minutus* or absent, whereas it appears to be a more regular colour pattern in *P. inexpectatus*. Male *P. cf. natalensis* in breeding condition have grey or dark grey throats in the breeding season. The gular coloration of breeding *P. minu-*



Figure 8. Examples of pedal webbing: A – *Phrynobatrachus inexpectatus*, Harena Forest (ZSM 90/2019); B – *P. inexpectatus*, vicinity of Bore (BM 1975.1691, paratype); C – *P. minutus*, Debre Markos (BM 1969.1102); D – *P. cf. natalensis*, Harena Forest (LIV 1986.212.226).

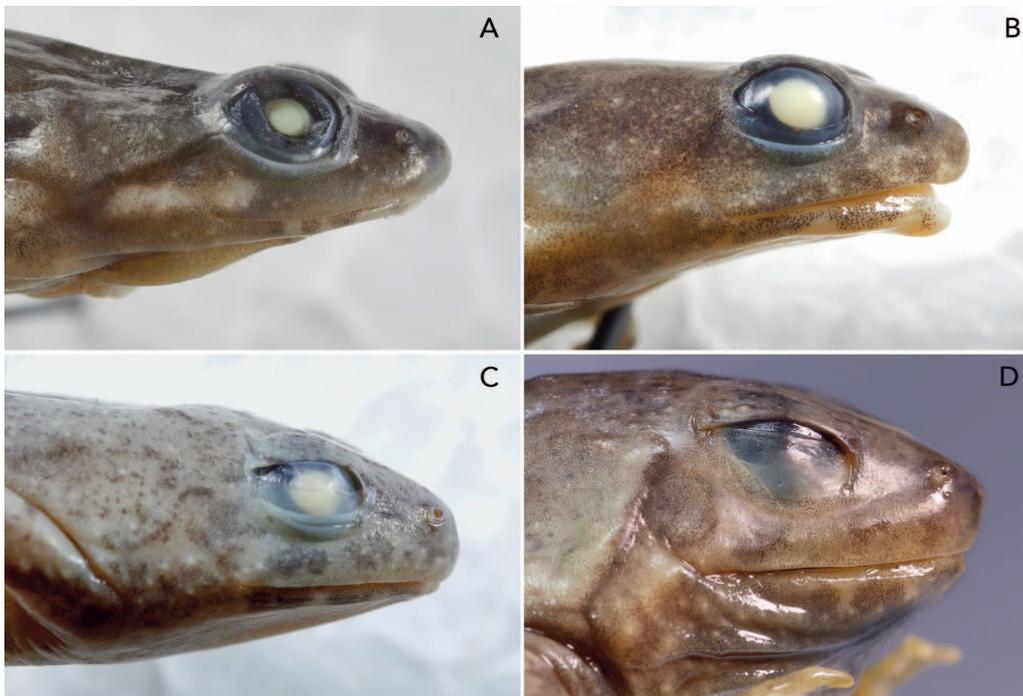


Figure 9. Comparison of head morphology in lateral view: A – *Phrynobatrachus inexpectatus*, mature male (ZSM 86/2019); B – *P. minutus*, mature male (BM 1969.894); C – *P. cf. natalensis*, immature (ZFMK 102232); D – *P. cf. natalensis*, mature male (LIV 1986.212.223). Note nostril position, snout shape, visible tympanum, and supratympanal skin fold.

tus males is bright yellow, and in *P. inexpectatus* males it is rose to reddish. The ventral colour patterns of females and non-breeding males also differ in all three species. In *P. inexpectatus* it is pale and mottled with light grey; in *P. minutus* there are irregular larger black or dark grey spots on a bright white background all over the belly (Fig. 10); in *P. cf. natalensis* the entire ventral face is pale – whitish or light grey, laterally with indistinct darker spots that gradually transition into the dorsolateral ground colour.

The size difference between mature individuals of *P. inexpectatus/minutus* and *P. cf. natalensis* is quite obvious: The latter are much larger, reaching well over 30 mm. *Phrynobatrachus inexpectatus* and *P. minutus* do not have SVL greater than 20–21 mm. In the field, this size difference is not useable as a diagnostic character because mature individuals can be reliably recognised only during breeding. Over the rest of the year, at altitudes around 1,500 m a.s.l., small individuals of *P. cf. natalensis* are more common. There is no recognisable size difference between *P. minutus* (sensu LARGEN 2001) and *P. inexpectatus*.

The acoustic characteristics of the *P. inexpectatus* call appear to be close to that of *P. keniensis* (PICKERSGILL 2007) and of Kenyan *P. scheffleri* (PICKERSGILL 2007, SCHICK et al. 2010). This is not surprising since it is known that these species belong to sister clades and differ genetically by less than 4% (ZIMKUS & SCHICK 2010, ZIMKUS et al. 2010). Surprisingly, the vocalisation of *P. inexpectatus* appears to differ more distinctly from that of *P. minutus* (recorded in a local-

ity between Bonga and Jimma; 7°32'06.0" N, 36°33'38.2" E, 2,216 m a.s.l.) as reported by GOUTTE et al. (2019). It consists of a series of shorter pulses that have, however, similar amplitude and frequency as that of *P. inexpectatus*.

The larvae of closely related species belonging to this group of taxa are not yet described, thus we cannot compare them here with those of *P. inexpectatus*. The tadpole of *P. inexpectatus* resembles that of *P. natalensis* (see CHANNING et al. 2010: 280) in body shape, but differs in its layout of keratodonts that follows the formula 1 1+ 1 / 1+1 2 whereas our four *P. inexpectatus* had the same formula: 1 / 2. The yet unnamed species of *Phrynobatrachus* within the *natalensis* complex is sympatric with *P. inexpectatus*, but uses different breeding habitats. In the Haremma Forest it breeds in flooded areas inside the forest and in deeper puddles near permanent streams. Its tadpoles and neometamorphs are generally larger than those of *P. inexpectatus*. According to POWER (1927), *P. natalensis* tadpoles grow up to 35 mm. Our observations also indicate that metamorphosis is substantially faster in *P. inexpectatus* than in *P. natalensis*, for which up to 49 days have been reported (WARBURG 1997: 115) or, according to other authors, even twice as long – 14 weeks (POWER 1927; CHANNING et al. 2012).

We did not have sufficient time in the field to observe the entire development of the tadpoles through their metamorphosis. The dry season in this region usually begins in November, and the small puddles in fully insolated places in this low-altitude area would normally be dry by Decem-



Figure 10. Coloration of breeding male and female *Phrynobatrachus minutus* after about two years of preservation in 70% ethanol (ZFMK 102232-102334). See photograph in NABU (2017: 203) for the coloration of these specimens in life.

ber. Therefore, if new clutches are laid after every heavy rainfall until the onset of the dry season, development must take no longer than 3–4 weeks.

We observed that all the puddles in the study site had a rich invertebrate fauna, including potential predators, such as Odonata larvae, water beetles and Nepomorpha bugs. Collective spawning in a single short event and in a single puddle may contribute to increased survival chances of eggs, tadpoles and frogs, as predator impacts are diluted by large numbers of prey animals in a limited area. It is not entirely clear how the frogs are brought together in just one single puddle when they are surrounded by many similar puddles. We assume that the first caller in a suitable puddle is heard by others and attracts further individuals. Other males may then prefer to join the caller instead of calling from their own puddles. We witnessed this on the first day, hearing further males calling from our study puddle. Once spawning has started, more and more males and females presumably join the same puddle.

The absence of *Phrynobatrachus* in some puddles could also be explained by excessive pollution with dung and urine of livestock grazing in the glade, as well as by soap from people washing laundry daily in some of the larger and deeper puddles. Of course, direct disturbances by people (mainly children) walking through the water and the resultant destruction of clutches may also play a role. In some puddles and in places free of grass, we noticed large deposits of iron ore grit. However, frequent and heavy rainfall may compensate for the excessive mineralisation and alkalinity of the water.

This part of the Hareenna Forest is extensively exploited by the local human population. Even the areas included in the national park are very weakly protected and used by people for wild coffee cultivation, wild beekeeping, timber harvesting, as pastures, and, near the fast-growing settlements, also for other agricultural and household purposes. A dense and regularly used network of paths and roads exists even in the remote parts of the forest. Glades that serve *P. inexpectatus* as breeding sites are used daily as pasture for livestock, for recreation and, during the rainy season, also for laundry. This seems not to have had a significant impact on the population of this frog thus far. According to our observations, *P. inexpectatus* is still the most common amphibian species in the Hareenna Forest.

This is the third officially known population of *P. inexpectatus*. A report (MILTO et al. 2016) about this species from the vicinity of Boka village, Kaffa province (see live photograph in NABU 2017: 203), is based on the misidentification of a juvenile *P. cf. natalensis* specimen. Similar cases of *P. cf. natalensis* mistaken for *P. inexpectatus* or *P. inexpectatus* for *P. minutus* are still very common, and the revision of Ethiopian *Phrynobatrachus* by LARGEN (2001) has caused only more confusion. This author's conclusions were based solely on a systematisation and comparison of the external morphology of various museum specimens tagged as '*P. minutus*' that had been preserved for more than 20 years and no live animals were examined. LARGEN (2001) only speculated about their appearance in life

and differences from each other using museum specimens. Specimens from the Hareenna Forest that LARGEN (2001) acquired for the Liverpool Museum (LIV 1986.212.228–241) were in fact *P. inexpectatus*, the species that he described, and not *P. minutus*, as he identified them on the specimen tags. We found these specimens morphologically identical to *P. inexpectatus* from other collections, including those that were confirmed by genetic barcoding (ZIMKUS et al. 2010). At the same time, they differ from the specimens from localities west of the GRV that very well agree with the definition of *P. minutus* by LARGEN (2001) and are currently treated as such (NHMUK: BM 1969.1100–1102, BM 1969.893, BM 1969.894–895, BM 1976.2026–2027; ZFMK: 102232–102268; ZNHM: A2008-078, A2008-101, A2008-103, A2008-104).

Phrynobatrachus minutus has been routinely included by various authors amongst the amphibian species of this area (KASSAHUN 2009, LARGEN & SPAWLS 2011, GOWER et al. 2012), which is likely because of ongoing taxonomic confusion between two similar-looking species. We did not identify any vouchers of *P. minutus* (sensu LARGEN 2001) collected in the Bale Zone. All *Phrynobatrachus* specimens from this area were identified either as *P. inexpectatus* or as *P. cf. natalensis*. The latter was, for instance, the case with 2 specimens in ZNHM with field numbers TJC 1343 and 1344 that are tagged as *P. minutes*, but clearly are members of the *P. natalensis* complex. Also, in our five field trips between 2012 and 2019, despite thorough search, we did not observe any other *Phrynobatrachus* than *P. inexpectatus* and *P. cf. natalensis* in the Hareenna Forest.

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