

Systematics of ‘Little Brown Frogs’ from East Africa: recognition of *Phrynobatrachus scheffleri* and description of a new species from the Kakamega Forest, Kenya (Amphibia: Phrynobatrachidae)

SUSANNE SCHICK¹, BRED A. M. ZIMKUS², ALAN CHANNING³, JÖRN KÖHLER⁴ & STEFAN LÖTTERS¹

¹ Trier University, Department of Biogeography, Am Wissenschaftspark 25-27, 54296 Trier, Germany

² Harvard University, Museum of Comparative Zoology, Cambridge, Massachusetts 02138, USA

³ The University of The Western Cape, Biodiversity and Conservation Biology Department, Private Bag X17, Bellville 7535, South Africa

⁴ Hessisches Landesmuseum Darmstadt, Department of Natural History – Zoology, Friedensplatz 1, 64283 Darmstadt, Germany

Corresponding author: STEFAN LÖTTERS, e-mail: loetters@uni-trier.de

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Abstract. We elucidate the status of some populations of small East African *Phrynobatrachus* frogs by an integrative approach, using morphology, bioacoustics and DNA barcoding. We redescribe *Phrynobatrachus scheffleri* from western Kenya, designate a lectotype and formally resurrect it from its current synonymy with *P. minutus*. Although molecular data suggest a close relationship of *P. scheffleri* and *P. minutus*, both taxa differ by 2.9% uncorrected pairwise distance in the 16S mitochondrial rRNA gene sequence and throat colouration of breeding males. *Phrynobatrachus scheffleri* apparently is widely distributed in semi-humid habitats from coastal Kenya and Tanzania northwest up to the Ugandan border and occurs from sea level up to elevations of 1650 m. In addition, a new species of *Phrynobatrachus* is described from the Kakamega Forest, Kenya, where it co-occurs with *P. scheffleri*. The new species is morphologically similar to *P. inexpectatus*, *P. mababiensis*, *P. minutus*, *P. parvulus* and *P. scheffleri* and can be best distinguished on the basis of advertisement calls and molecular genetics. Relatively low uncorrected pairwise distance in the 16S mitochondrial rRNA gene sequence (1.7%) is noted between the new species and an unidentified but apparently unnamed population of *Phrynobatrachus* from Tanzania. Relatively low values of uncorrected pairwise genetic distances, also recognized in other East African *Phrynobatrachus* species, may be the result of a recent radiation and colonisation of the Rift Valley.

Key words. Anura, *Phrynobatrachus kakamikro* new species, *P. scheffleri*, bioacoustics, molecular genetics, taxonomy, Afro-tropics.

Introduction

Tropical biodiversity in sub-Saharan Africa is rich but largely still poorly understood. In anuran amphibians, this includes species that are small in size, generally brown in colour and exhibiting inter- and intraspecific polymorphism (e.g. ZIMKUS & BLACKBURN 2008). As a result, numerous frog species are difficult to identify and herpetologists have come to refer to them as ‘Little Brown Frogs’ (LBFs). One example is the genus *Phrynobatrachus* GÜNTHER, 1862. Currently, more than 75 species are recognized and the majority of these nominal species include several junior synonyms (FROST 2008). Original descriptions often lack diagnostic details and/or type specimens are in poor condition, leading to difficulties in identification and recognition of new species. *Phrynobatrachus* taxonomy may therefore only be resolved, if modern systematic methods are used, including bioacoustics and molecular data (e.g., ZIMKUS 2009), along with traditional taxonomic studies of type material and large series of specimens.

Our on-going fieldwork at the Kakamega Forest, western Kenya (e.g., LÖTTERS et al. 2006), revealed that two diminutive *Phrynobatrachus* species co-occur there. Both are similar to each other and superficially resemble *P. mababiensis* FITZSIMONS, 1932, originally described from southern Africa. Based on morphological, molecular and bioacoustic studies, we identify one of the two *Phrynobatrachus* species from the Kakamega Forest as *P. scheffleri* (NIEDEN, 1911), which has been a junior synonym of *P. minutus* (BOULENGER, 1895) for many decades. The other cannot be allocated to any of the described species and is new to science. The purpose of this paper is (1) to formally revalidate and redescribe the East African *P. scheffleri* and (2) to describe the new species from the Kakamega Forest, Kenya.

Material and methods

The results of the morphological study are based on specimens from museum collections (Appendix 1). Museum ab-

abbreviations correspond to those of LEVITON et al. (1985), with the exception of AC, which refers to field numbers of A. CHANNING, and NMK (National Museums of Kenya, Nairobi). A diagnostic scheme was compiled to distinguish East African *Phrynobatrachus*, combining information from recent publications (LARGEN 2001, RÖDEL & ERNST 2002, CRUTSINGER et al. 2004, UYEDA et al. 2007, HILLERS et al. 2008, ZIMKUS & BLACKBURN 2008). Definitions of 14 morphological characters studied are as follows: (1) snout-vent length (SVL) of males and females; (2) tibia-fibula length (TIL)/SVL; (3) head width at angles of jaws (HW)/SVL; (4) dorsal skin texture, papilla on tongue present or absent; (5) dorsal and lateral snout shape and visibility of nostrils in dorsal view; (6) distance from anterior corner of eye to nostril (E-N)/horizontal eye diameter (EYE), shape of canthus rostralis, distance from anterior corner of eye to snout (E-ST); (7) width of interorbital space (IO); (8) (E-N)/width of the internarial space (INTERNARIAL), distance between the naris and the tip of the snout (N-ST); (9) tympanum free and distinct or covered by skin and indistinct, horizontal tympanum diameter (TYMP)/EYE (if

applicable); (10) tarsus length (TAL) from tibiotarsal articulation to tip of longest toe (TAL)/TIL, TAL/SVL, length of femur (FE); (11) pedal and manual webbing (if present) formula in the manner described by GLAW & VENCES (2007: 70); (12) toe and finger tips expanded to discs or not; (13) presence/absence of femoral glands; (14) dorsal and ventral colour pattern and eye colouration in life. Information was obtained from adult specimens only. The 14 characters mentioned are used to provide a standardized definition scheme for species.

Furthermore, we provide the GenBank accession number (<http://www.ncbi.nlm.nih.gov>; BENSON et al. 2004) of an approximately 550 base pairs (bp) sequence of the 16S mitochondrial rRNA gene as obtained by ZIMKUS & SCHICK (in press; Appendix 2). DNA Sequences were aligned using MEGA 3.1 (KUMAR et al. 2004); uncorrected p-distances were determined using PAUP*4b10 (SWOFFORD 2001).

Advertisement calls were recorded (see below for species and localities) with different equipment (A. CHANNING: Marantz PMD 660 digital recorder and an Audio Technica 350 mm directional microphone; S. SCHICK: Sony DPC, MZ-B10 minidisc player, Sony WM D6C tape recorder and a Sennheiser Me-80 directional microphone). Call recordings were sampled at a rate of 22.05 kHz and 16-bit resolution. They were analysed with Batsound 3.31 (Patterson Elektronik AB) and Cool Edit 96 (Syntrillium) on a PC. Frequency information was obtained through Fast Fourier Transformation (width 512 points). Time scales of the figured spectrograms and waveforms were chosen to allow for the best comparison of call characteristics. Spectral settings in figures are Hanning window functions with 256-band resolution.

Systematics

Phrynobatrachus scheffleri (NIEDEN, 1911) (Figs. 1, 2)

Arthroleptis scheffleri NIEDEN, 1911 "1910": 438. "Kibwesi in Britisch-Ostafrika", "Nairobi", "Zanzibar", "Mpapua".

Phrynobatrachus minutus (non BOULENGER) – LOVERIDGE 1929: 107 (partim), 1936: 421 (partim), PARKER et al. 1940: 309 (partim).

Pseudarthroleptis scheffleri – DECKERT 1938: 159.

Phrynobatrachus scheffleri – LARGEN 2001: 287, CHANNING & HOWELL 2006: 292, PICKERSGILL 2007: 187, FROST 2008.

Diagnosis: A species of the genus *Phrynobatrachus* sensu ZIMKUS & BLACKBURN (2008) defined by the following combination of characters: (1) SVL: mean males 12.92 mm, females 15.06 mm; (2) TIL/SVL: mean males 0.54, females 0.54; (3) HW/SVL: mean males 0.34, females 0.33; (4) dorsal surface finely coarse; papilla on tongue present; (5) snout shape dorsally subovoid, laterally rounded, nostrils visible from above; (6) E-N/EYE: mean males 0.76, females 0.93, canthus rostralis slightly concave from tip of snout to nostril and straight from nostril to eye, E-ST: mean males 2.20, females 2.31; (7) IO: mean males 2.37 mm, females 2.66 mm; (8) E-N/INTERNARIAL: mean males 0.72, females 0.65, N-ST: mean males 1.05, females 1.18; (9)

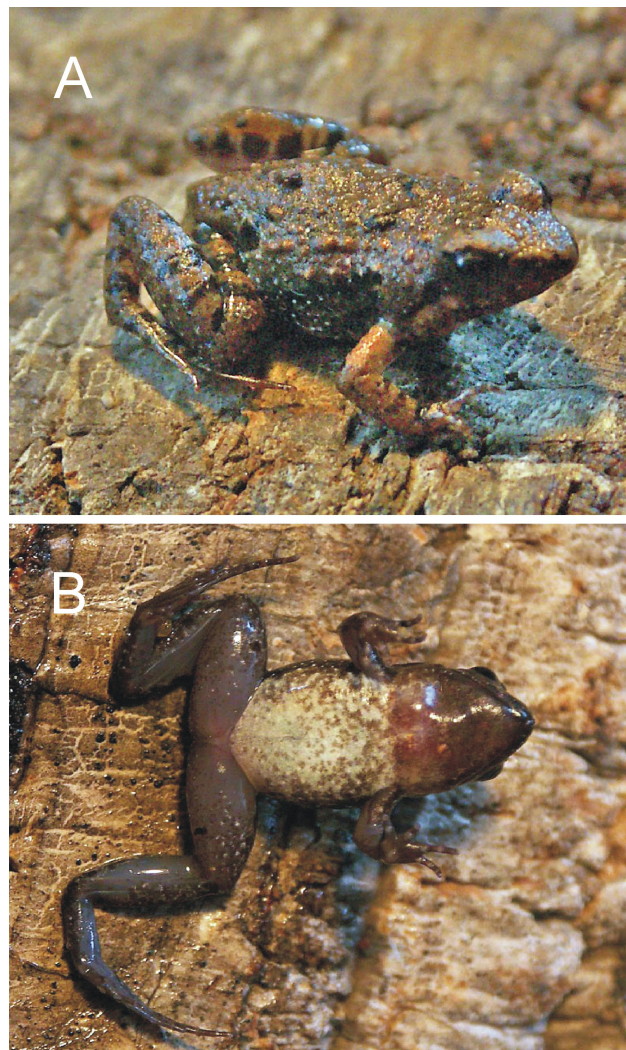


Figure 1. Dorsolateral (A) and ventral (B) views of *Phrynobatrachus scheffleri* in life from Nairobi (specimens not collected).

tympanum not visible; (10) TAL/TIL: mean males 1.55, females 1.51, TAL/SVL: mean males 0.84, females 0.81, FE: mean males 6.19 mm, females 6.88 mm; (11) pedal webbing formula I ($\frac{1}{2}$), Ili (1) IJe (1), IIIi (2) IIIe ($1\frac{1}{2}$ –2), IVi ($2\frac{1}{2}$ –3) IVe (3), V ($1\frac{1}{2}$ –2); (12) toe and finger tips may be slightly swollen but not expanded to digital discs; (13) small femoral glands present; (14) in life, dorsum brown with unregular dark brown markings on each side, with a thin, light vertebral line; back of thighs banded; venter cream to translucent, with dark marks in the pectoral region; males with a light grey throat; a brownish golden ring around the pupil; (15) for sequence of a 550 bp fragment of the 16S mitochondrial rRNA gene see GenBank (accession number FJ889497).

Based on this definition, *Phrynobatrachus scheffleri* can be distinguished from all other species in the genus. Among the East African congeners, the following can be distinguished from *P. scheffleri* (SVL < 20 mm) by having larger adult SVLs: *Phrynobatrachus acridoides* (COPE, 1867) (ca. 25 mm), *P. auritus* BOULENGER, 1900 (> 35 mm), *P. bullans* CRUTSINGER, PICKERSGILL, CHANNING & MOYER, 2004 (ca. 25 mm), *P. dendrobates* (BOULENGER, 1919) (> 30 mm), *P. irangi* DREWES & PERRET, 2000 (> 50 mm), *P. krefftii* BOULENGER, 1909 (> 35 mm), *P. natalensis* (SMITH,

1849) (> 24 mm), *P. packenhami* LOVERIDGE, 1941 (> 25 mm) and *P. versicolor* AHL, 1924 (> 25 mm). The East African *Phrynobatrachus graueri* (NIEDEN, 1911), *P. kinangopensis* ANGEL, 1924, *P. perpalmatus* BOULENGER, 1898 and *P. rouxi* (NIEDEN, 1912) are of similar SVL to *P. scheffleri*, but have digital discs and a visible tympanum (both absent in *P. scheffleri*). In addition, the foot of *P. kinangopensis* and *P. perpalmatus* is well-webbed (versus rudimentary webbing in *P. scheffleri*). *Phrynobatrachus pallidus* PICKERSGILL, 2007, *P. rungwensis* (LOVERIDGE, 1932), *P. ukingensis* (LOVERIDGE, 1932), *P. ungujae* PICKERSGILL, 2007 and *P. uzungwensis* GRANDISON & HOWELL, 1983, all from East Africa, share similar SVLs with *P. scheffleri* and exhibit an indistinct tympanum, but differ through presence of well developed digital discs (versus absence in *P. scheffleri*). In addition, the throat is heavily pigmented in *P. ukingensis*, and *P. uzungwensis* exhibits extensive pedal webbing (versus rudimentary webbing in *P. scheffleri*). *Phrynobatrachus breviceps* PICKERSGILL, 2007, *P. keniensis* BARBOUR & LOVERIDGE, 1928, *P. stewartae* POYNTON & BROADLEY, 1985 and *Phrynobatrachus* sp. of PICKERSGILL (2007:275) from East Africa exhibit more extensive pedal webbing (at maximum two and a half phalanges of fourth toe free of webbing versus three free of webbing in *P. scheffleri*). The East African *Phrynobatrachus inexpectatus* LARGEN, 2001, *P. mababienensis* (including its junior synonyms *P. vanrooyeni* HOFFMAN, 1940, *P. chitilaensis* HOFFMAN, 1944, *P. broomi* FITZSIMONS, 1948), *P. minutus* (for discussion of the name *P. albiifer* AHL, 1924 see Remarks), *P. parvulus* (BOULENGER, 1905) (including its junior synonyms *P. schoutedeni* DE WITTE, 1921, *P. ukingensis nyikae* LOVERIDGE, 1953) and the new species described below are morphologically most similar to *P. scheffleri*. Pedal webbing in *P. inexpectatus* is almost absent (toe IV with 3–4 phalanges free) and the throat of males is strongly suffused with dark grey pigment (LARGEN 2001). *Phrynobatrachus minutus* and *P. parvulus* males in breeding condition can be distinguished by their throat colour, yellowish and dark grey, respectively (versus light grey in *P. scheffleri*). As shown below, these species can be best distinguished by comparisons of molecular data or advertisement calls (see also ZIMKUS & SCHICK in press). For a diagnosis of *P. scheffleri* relative to the new species described in this paper see below.

Description: Body slender, head narrower than body; snout in dorsal view subovoid, in lateral view rounded. Maxillary teeth present, vomerine teeth absent; choanae rounded; tongue as long as wide, free for about two thirds of its length, tip bifurcated; papilla on tongue present. In external morphology, mature sexes differ in size and proportions (Table 1) and the presence of a vocal sac or transverse gular folds in males only. Nostrils visible from above, closer to tip of snout than to anterior corner of eye; canthus rostralis slightly concave from tip of snout to nostril and straight from nostril to eye; horizontal eye diameter larger than distance from nostril to anterior corner of eye; tympanum invisible. Dorsal skin finely coarse, ventrally smooth, small femoral glands present. Pedal webbing formula Ie ($\frac{1}{2}$), Ili (1) IJe (1), IIIi (2) IIIe ($1\frac{1}{2}$ –2), IVi ($2\frac{1}{2}$ –3) IVe (3), Vi ($1\frac{1}{2}$ –2); relative toe length: I < II < III < IV > V. Tarsal tubercle and metatarsal tubercles well developed; rest of sole smooth; well-developed subarticular tubercles

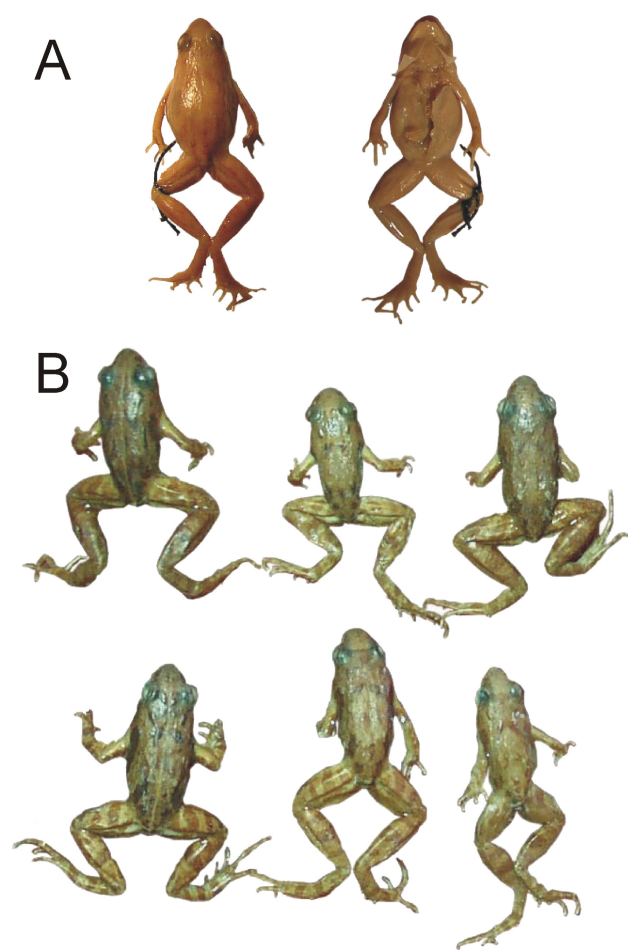


Figure 2. Part of the type series of *Phrynobatrachus scheffleri* including dorsal and ventral views of the female lectotype ZMB 21783 (A; SVL 17.4 mm).

Table 1. Measurements (mm) and proportions of *Phrynobatrachus scheffleri* and *P. kakamikro* sp. n. The mean is followed by one standard deviation and the range in parentheses. For abbreviations see text; for specimens examined see Appendix 1.

	<i>Phrynobatrachus scheffleri</i>		<i>Phrynobatrachus kakamikro</i>	
	females (n = 18)	males (n = 49)	females (n = 3)	male (n = 1)
SVL	15.1 ± 1.7 (13.0–19.1)	12.9 ± 1.4 (10.0–16.4)	18.0 ± 0.8 (17.5–19.0)	16.2
TIL	8.0 ± 0.6 (7.0–9.1)	7.0 ± 0.8 (5.5–8.8)	8.5 ± 0.3 (8.2–8.8)	7.3
HW	4.9 ± 0.4 (4–5.5)	4.3 ± 0.5 (3.3–5.3)	5.1 ± 0.2 (4.9–5.3)	4.8
E–N	1.1 ± 0.2 (1.0–1.5)	1.0 ± 0.1 (0.9–1.3)	1.4 ± 0.2 (1.4–1.6)	1.3
INTERNARIAL	1.8 ± 0.3 (1.0–2.2)	1.5 ± 0.3 (1.0–2.0)	1.8 ± 0.1 (1.7–1.9)	2.2
I–O	2.7 ± 0.4 (2.0–3.0, n = 16)	2.4 ± 0.5 (1.5–3.0, n = 30)	3.2 ± 0.1 (3.0–3.2)	2.6
EYE	1.3 ± 0.5 (1.0–2.3)	1.5 ± 0.4 (1.0–2.0)	1.4 ± 0.1 (1.3–1.6)	1.9
N–ST	1.2 ± 0.1 (1.0–1.4, n = 16)	1.1 ± 0.1 (0.9–1.2, n = 17)	1.4 ± 0.2 (1.1–1.5)	1.3
E–ST	2.3 ± 0.3 (2.0–3.0, n = 16)	2.2 ± 0.3 (1.8–3.0, n = 30)	2.9 ± 0.2 (2.7–3.1)	2.5
FEL	6.9 ± 0.8 (5.8–9.1, n = 16)	6.2 ± 0.7 (5.0–8.5, n = 28)	7.6 ± 1.2 (6.3–8.8)	6.6
TAL	12.1 ± 1.1 (10.0–14.4)	10.8 ± 1.3 (8.0–13.7)	13.6 ± 0.3 (13.4–13.9)	11.5
TIL/SVL	0.5–0.6	0.4–0.7	0.4–0.5	0.5
HW/SVL	0.3–0.4	0.3–0.4	0.2–0.3	0.3
E–N/EYE	0.5–1.5	0.5–1.0	0.8–1.2	0.7
E–N/INTERNARIAL	0.5–1.0	0.5–1.0	0.7–0.9	1.0
TAL/TIL	1.3–1.7	1.3–1.8	1.5–1.7	1.6
TAL/SVL	0.7–1.0	0.7–1.2	0.7–0.8	0.7

at joints of all phalanges of foot. Toe tips may be slightly swollen but not expanded to digital discs. Hand webbing absent; relative finger length: I = II < III > IV; outer metacarpal tubercle well-developed, inner one weak; rest of palm smooth; well-developed subarticular tubercles at joints of all phalanges of hand. Fingertips may be slightly swollen but not expanded to digital discs.

Life colouration is dorsally brown with semi-regular dark brown markings on each side. Like in many leaf litter species a thin, light vertebral line may be present or absent. The upper arm is of lighter colour, the back of thighs is banded. Ventral colouration is translucent to cream, with dark marks in the pectoral region. In males the throat is light grey and light femoral glands are present. The iris is brownish golden. In preservative, the brown fades to grey, the dark brown dorsal and dorsolateral markings are darker than the rest of the body colouration; ventrally, cream and translucent fade to greyish white.

Molecular genetics: Uncorrected p-distances of the ca. 550 bp fragment of the 16S mitochondrial rRNA gene are generally high between *P. scheffleri* and morphologically similar species and vary between 2.86 and 18.01% (Table 2). The p-distance is smallest to *P. minutus* (2.86%) and *P. inexpectatus* (3.60%). For a discussion see the description of the new species below.

Distribution and life history: According to our study of type material and additional collections, in part supported by molecular data (see below), *Phrynobatrachus scheffleri* is widely distributed in semi-humid eastern Africa from coastal Kenya and Tanzania (including Zanzibar) northwest up to the Ugandan border (Kakamega Forest), i.e., from sea level up to at least 1650 m (Fig. 3). According to CHANNING & HOWELL (2006), this species' range

may extend into Uganda. *Phrynobatrachus scheffleri* is associated with both open land (savannah or farm land) and secondary forest margins. Climate in the distribution area of this species shows bimodal rainfall, i.e., May to June (Kakamega) and September to October (Kibwezi, Nairobi). The species is nocturnal and ground-dwelling and occurs in mud or leaf litter, often near water bodies.

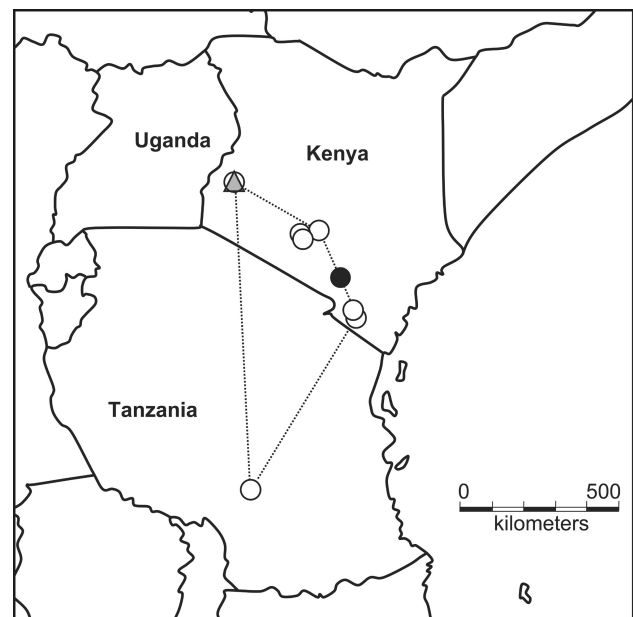


Figure 3. Schematic map with known distribution ranges of *Phrynobatrachus scheffleri* and *P. kakamikro* sp. n. generated from specimens used in this study. Localities of *P. scheffleri* are indicated by circles (black: type locality, white: additional localities) and that of *P. kakamikro* sp. n. by a grey triangle.

Table 2. Pairwise genetic distances (uncorrected) of *Phrynobatrachus scheffleri* (NMK A/4737/4) and *P. kakamikro* sp. n. (NMK A/3924/2) compared to other East African *Phrynobatrachus* species using the 16S mitochondrial rRNA gene. For localities and GenBank accession numbers of samples studied see Appendix 2.

Species	Mean uncorrected pairwise distance (%) to <i>P. scheffleri</i>	Standard deviation	Mean uncorrected pairwise distance (%) to <i>P. kakamikro</i>	Standard deviation	Number of samples
<i>P. acridoides</i>	14.30	0.19	13.08	0.22	6
<i>P. acutirostris</i>	16.34	0.09	13.88	0.11	3
<i>P. auritus</i>	18.01	0.00	16.78	0.00	1
<i>P. bullans</i>	16.72	1.00	15.67	1.36	4
<i>P. dendrobates</i>	14.75	0.14	14.23	0.13	3
<i>P. graueri</i>	14.31	0.10	12.39	0.45	6
<i>P. inexpectatus</i>	3.60	0.28	5.40	0.28	3
<i>P. kakamikro</i>	5.24	0.06	—	—	3
<i>P. keniensis</i>	4.55	0.50	4.91	0.24	3
<i>P. kinangopensis</i>	14.49	0.00	13.11	0.00	1
<i>P. krefftii</i>	14.73	0.30	13.70	0.44	6
<i>P. mababiensis</i> A	5.10	0.00	5.20	0.00	1
<i>P. mababiensis</i> B	10.07	0.47	9.49	0.22	4
<i>P. mababiensis</i> C	5.59	0.18	1.65	0.17	4
<i>P. minutus</i>	2.86	0.17	4.19	0.10	5
<i>P. natalensis</i>	17.06	0.39	15.57	0.47	18
<i>P. pakenhami</i>	14.59	0.00	13.28	0.00	2
<i>P. pallidus</i>	9.93	0.00	8.81	0.00	1
<i>P. parvulus</i>	4.56	0.46	6.28	0.38	12
<i>P. rungwensis</i>	4.96	0.20	6.54	0.12	3
<i>P. scheffleri</i>	—	—	4.81	0.38	37
<i>P. ukingensis</i>	9.85	0.00	9.20	0.00	1
<i>P. unguae</i>	10.24	0.23	9.51	0.11	2
<i>P. uzungwensis</i>	5.37	0.00	6.27	0.00	1
<i>P. versicolor</i>	15.06	0.00	13.83	0.00	1

Bioacoustics: Advertisement calls of *Phrynobatrachus scheffleri* were recorded close to Nairobi, Kenya (01°19'55.0" S, 36°48'8.0" E, 1650 m a.s.l., on 18 October 2006; air temperature unknown; voucher NMK/A 4740/8), and at Luisenga Dam, Mufindi Highlands, Tanzania (08°36'51.2" S, 35°20'22.8" E, 1858 m a.s.l., on 8 November 1999; air temperature 24°C; voucher AC 1954). At the former site, calling and non-calling frogs were sitting on floating vegetation and at the edge of ponds or freely floating in small water bodies. Other calling anurans included *Phrynobatrachus natalensis*, *Amietophrynus maculatus* (HALLOWELL, 1854), *Kassina senegalensis* (DUMÉRIL & BIBRON, 1841) and *Hyperolius glandicolor* PETERS, 1878. At Luisenga Dam, *Phlyctimantis keithae* SCHIÖTZ, 1975, *Amietophrynus regularis* (REUSS, 1833) and *Hyperolius pictus* AHL, 1931 were heard calling.

Advertisement calls from both sites largely agree with each other and can be described as a long 'trill', consisting of a single note. *Phrynobatrachus mababiensis*, *P. parvulus* and the new species described below produce advertisement calls of more than one note and have lower pulse rate and higher dominant frequencies (Fig. 4A–D, Table 3; for *P. parvulus* see CHANNING & HOWELL 2006). The advertisement calls of *P. inexpectatus* and *P. minutus* are unknown. PICKERSGILL (2007) described and illustrated an advertise-

ment call for *P. scheffleri* from Bermi, Tanzania (1900 m a.s.l.), which is very similar to calls from the Nairobi and Luisenga Dam populations.

Threat status: The IUCN Red List of Threatened Species (IUCN 2008) considers this taxon as being of 'Least Concern' given its relatively large distribution and apparent tolerance to habitat change (i.e., occurrence in farm land), which is supported by our observations.

Remarks: As small species in the genus *Phrynobatrachus* species are difficult to distinguish and because cryptic diversity is involved (see below), we here designate ZMB 21783 (Fig. 2) from "Kibwesi" (= Kibwezi, Makueni District, Eastern Province, Kenya, 2° 25' S, 37° 58' E, 913 m above sea level) of the original type series (168 syntypes) as the lectotype of *Arthroleptis scheffleri* NIEDEN, 1911. This specimen agrees well with the original description. Individual characters are: SVL 17.4 mm; HW 5.4 mm; HW/SVL 0.31; E–N 1.2 mm; EYE 2.1 mm; INTERNARIAL 1.5 mm; TIL 8.5 mm; TIL/SVL 0.49; TAL 13.4 mm; TAL/SVL 0.77; TAL/TIL 1.58; pedal webbing formula Ie (½), Ili (1) IIe (1), IIIi (2) IIIe (½), IVi (2½) IVe (3) V(½). As a consequence of this action, the remaining 167 type specimens (see Appendix 1) become paralectotypes.

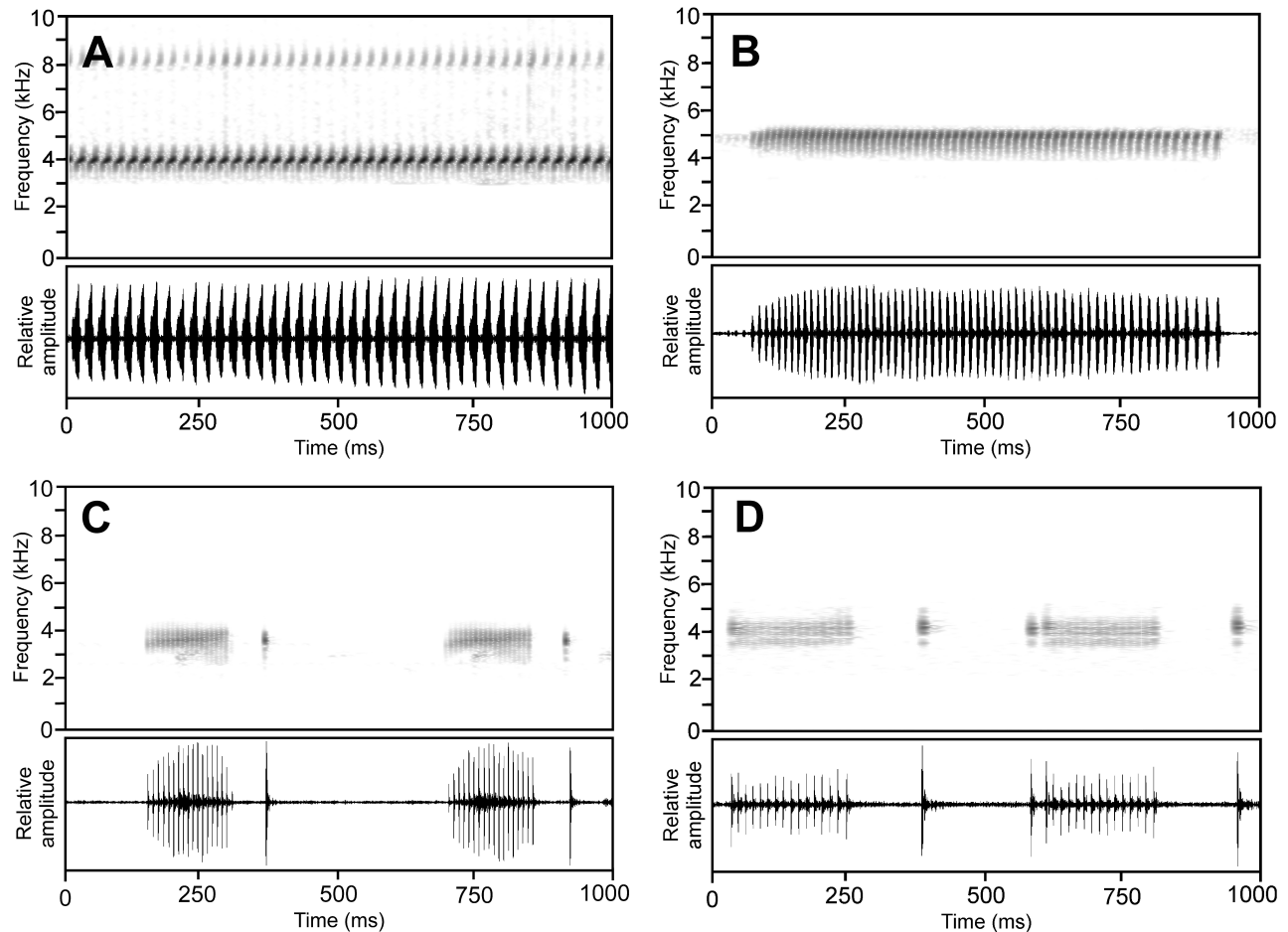


Figure 4. Oscillograms and sound spectrograms of advertisement calls of *Phrynobatrachus scheffleri* (A) from Luisenga Dam, Tanzania, and (B) near Nairobi, Kenya, (C) of *P. kakamikro* sp. n. from the type locality, (D) of *P. mababiensis* from Lake Liambezi, Namibia. See text and Table 3 for recording and call details.

Arthroleptis albifer AHL, 1924 from “Usaramo, Deutsch-Ost-Afrika”, i.e., coastal Tanzania, is currently considered a junior synonym of *P. minutus* (FROST 2008). Since LARSEN (2001) restricted the range of nominal *P. minutus* to Ethiopia and the type locality of *P. albifer* falls within the distribution of *P. scheffleri*, we directly compared the holotype of *P. albifer* (ZMB 26865; Fig. 5) to the types of *P. scheffleri*. Due to the rather poor condition of the former, a final judgement is not possible. However, we are inclined to consider *P. albifer* a junior synonym of *P. scheffleri*.

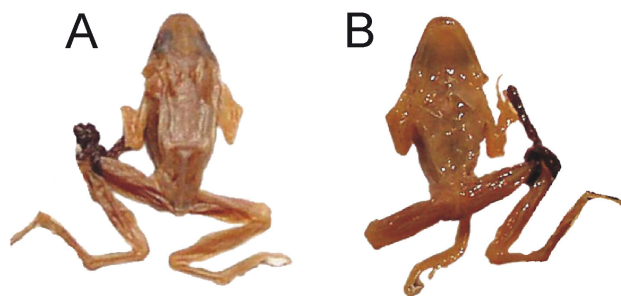


Figure 5. Dorsal (A) and ventral (B) views of the holotype of *Phrynobatrachus albifer* (ZMB 26865). SVL 12.3 mm.

Phrynobatrachus kakamikro sp. n. (Fig. 6)

Phrynobatrachus sp. – SCHICK et al. 2005: 186; LÖTTERS et al. 2006: 171.

Holotype: NMK A/3924/2 (SL 02/34), adult female, from a temporary puddle at the border of the Kakamega Forest (0°21' N, 34°51' E; 1650 m a.s.l.), Western Province, Kenya, collected on 2 May 2002 by S. LÖTTERS, K. SCHEELKE, S. SCHICK and P. TEEGE.

Paratypes: NMK A/3924/1 (SL 02/33), adult male, A/3924/3 (SL 02/29), MHNG 2709.89, adult females, same data as holotype.

Diagnosis: A species of the genus *Phrynobatrachus* sensu ZIMKUS & BLACKBURN (2008) defined through the following combination of characters: (1) SVL: single male 16.2 mm, mean females 18.04 mm; (2) TIL/SVL: male 0.45, mean females 0.47; (3) HW/SVL: male 0.3, mean females 0.28; (4) dorsal surface finely coarse; papilla on tongue absent; (5) snout shape dorsally subovoid, laterally rounded, nostrils visible from above; (6) E–N/EYE: male 0.68, mean females 1.09, canthus rostralis slightly concave from tip

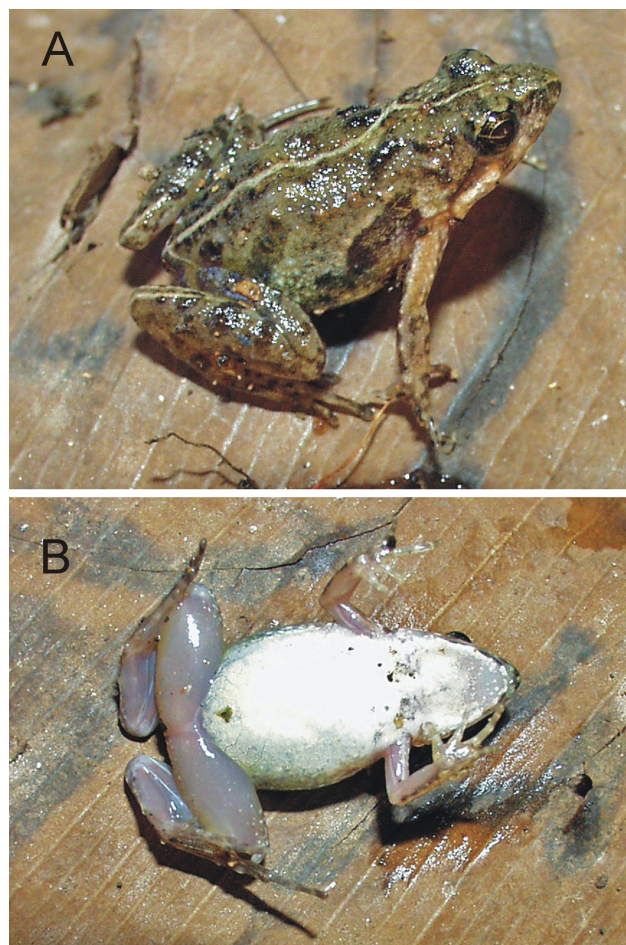


Figure 6. Dorsolateral (A) and ventral (B) views of the female holotype of *Phrynobatrachus kakamikro* sp. n. in life.

of snout to nostril and straight from nostril to eye, E–ST: male 2.51, mean females 2.94; (7) IO: male 2.58 mm, mean females 3.15 mm; (8) E–N/INTERNARIAL: male 1.0, mean females 0.84, N–ST: male 1.29 mm, mean females 1.36 mm; (9) tympanum invisible; (10) TAL/TIL: male 1.57, mean females 1.61, TAL/SVL: male 0.71, mean females 0.75, FE: male 6.58 mm, mean females 7.58 mm; (11) pedal webbing formula I (1), Ili (1), Ile (1), IIIi (2–2½), IIIe (2), IVi (2½–3), IVe (2¾–3), V (1½–2); (12) toe and finger tips may be slightly swollen but not expanded to digital discs; (13) femoral glands absent; (14) in life, dorsally light brown with unregular dark brown dorsal to dorsolateral markings each side, with a thin light vertebral line; ventrally cream to translucent, occasionally with few dark marks in the pectoral region; male with greyish throat; a brownish golden ring around the pupil; (15) for the sequence of a 550 bp fragment of the 16S mitochondrial rRNA gene see GenBank (accession number FJ889458).

Based on this definition, *Phrynobatrachus kakamikro* can be distinguished from all other species in the genus. Among the East African congeners, the following can be distinguished from *P. kakamikro* (SVL < 20 mm) by having larger adult SVLs: *Phrynobatrachus acridoides* (ca. 25 mm), *P. auritus* (> 35 mm), *P. bullans* (ca. 25 mm), *P. dendrobates* (> 30 mm), *P. irangi* (> 50 mm), *P. krefftii* (> 35

mm), *P. natalensis* (> 24 mm), *P. packenhami* (> 25 mm) and *P. versicolor* (> 25 mm). The East African *Phrynobatrachus graueri*, *P. kinangopensis*, *P. perpalmatus* and *P. rouxi* have similar SVLs compared to *P. kakamikro*, but display expanded digital discs and a visible tympanum (both absent in *P. kakamikro*). In addition, the feet of *P. kinangopensis* and *P. perpalmatus* are well webbed (versus rudimentary webbing in *P. kakamikro*). *Phrynobatrachus pallidus*, *P. rungwenensis*, *P. ukingensis*, *P. ungujae* and *P. uzungwenensis* from East Africa are similar in SVL to *P. kakamikro* and also have an indistinct tympanum, but differ by the presence of well-developed digital discs (versus absence in *P. kakamikro*). In addition, the throat is heavily pigmented in *P. ukingensis*, and *P. uzungwenensis* has extensive webbing (versus rudimentary webbing in *P. kakamikro*). *Phrynobatrachus breviceps*, *P. keniensis*, *P. stewartae* and *Phrynobatrachus* sp. (PICKERSGILL 2007:275) from East Africa exhibit more extensive pedal webbing (at maximum two and a half phalanges of the fourth toe free of webbing versus three free of webbing in *P. kakamikro*). *Phrynobatrachus kakamikro* is morphologically most similar to the East African *P. inexpectatus*, *P. mababiensis* (including its junior synonyms *P. vanrooyeni*, *P. chitilaensis*, *P. broomi*), *P. minutus* (for a discussion of the name *P. albifer* see Remarks under *P. scheffleri*), *P. parvulus* (including its junior synonyms *P. schoutedeni*, *P. ukingensis nyikae*) and *P. scheffleri*. *Phrynobatrachus inexpectatus* is slightly smaller than the new species (mean SVL 14.5 and 16.4 mm in males and females versus 16.2 and 18.0 mm for male and females in *P. kakamikro*, respectively). *Phrynobatrachus minutus* and *P. parvulus* males in breeding condition can be distinguished from the new species by their throat colours, i.e., yellowish and dark grey, respectively, versus greyish in *P. kakamikro*. *Phrynobatrachus scheffleri* possesses a papilla on the tongue (absent in *P. kakamikro*) and femoral glands, which seem to be absent in *P. kakamikro* (however, given the fact that femoral glands are only present in males, it may be too early to use the absence of femoral glands as a diagnostic character on the basis of a single male specimen). Femoral glands are also present in *P. inexpectatus*, *P. minutus* and *P. parvulus*. As shown below, these species can be best distinguished by comparisons of molecular data and advertisement calls (ZIMKUS & SCHICK in press; see below).

Description of type series: Body slender, head narrower than body; snout in dorsal view subovoid, in lateral view rounded. In external morphology, mature sexes differ in size and proportions (Table 1) and the presence of a vocal sac or transverse gular folds in males only. Maxillary teeth present, vomerine teeth absent; choanae rounded; tongue as long as wide, free for about two thirds of its length, tip bifurcated; papilla on tongue absent. Nostrils visible from above, closer to tip of snout than to anterior corner of eye; canthus rostralis slightly concave from tip of snout to nostril and straight from nostril to eye; horizontal eye diameter smaller than distance from nostril to anterior corner of eye; tympanum invisible. Dorsal skin finely coarse, ventrally smooth, femoral glands absent. Pedal webbing formula I (1), Ili (1), Ile (1), IIIi (2–2½), IIIe (2), IVi (2½–3), IVe (2¾–3), V (1½–2); relative toe length: I < II < III < IV > V. Tarsal tubercle and metatarsal tubercles well-developed; rest of sole smooth; well-developed subarticular tubercles

Table 3. Numerical parameters of advertisement calls of *Phrynobatrachus* populations analysed.

	<i>P. scheffleri</i> from Luisenga Dam (Fig. 4A)	<i>P. scheffleri</i> from outside Nairobi (Fig. 4B)	<i>P. kakamikro</i> from Kakamega Forest (Fig. 4C)	<i>P. mababiensis</i> from Lake Liambezi (Fig. 4D)
Number of calls analysed	1	19	23	1
Call length [s]	2.2	0.86 ± 0.25 (0.31–1.3)	0.54 ± 0.05 (0.40–0.62)	0.36–0.39
Number of notes per call [n]	1	1	2	2
Note length [s]	as of call	as of call	first: 0.42 ± 0.03 (0.37–0.5) second: 0.015 ± 0.010 (0.013–0.030)	first: 0.21–0.23 second: 0.01
Number of pulses per note [n]	91	46.3 ± 13.3 (17–67)	first: 22.6 ± 1.3 (20–26) second: 1	first: 16 second: 1
Dominant frequency [kHz]	4.1	3.58 ± 0.03	3.8	4.3
Lowest frequency [kHz]	3.5	22.9 ± 0.17	first: 3.55 ± 0.12 (3.47–3.62) second: 3.54 ± 0.14 (3.13–3.70)	3.2
Highest frequency [kHz]	5.2	3.95 ± 0.07	first: 4.04 ± 0.08 (3.99–4.09) second: 4.01 ± 0.09 (3.65–4.11)	5.2

at joints of all phalanges of foot. Toe tips may be slightly swollen but not expanded to digital discs. Hand webbing absent; relative finger length: I = II < III > IV; outer metacarpal tubercle well developed, inner one weak; rest of palm smooth; well-developed subarticular tubercles at joints of all phalanges of hand. Finger tips may be slightly swollen but not expanded to digital discs.

Life colouration is dorsally brown with unregular dark brown markings on each side and a thin, light vertebral line may be present or absent. The back of the thighs is banded. Ventral colouration is translucent to cream, occasionally with dark marks in the pectoral region. In males the throat is greyish. The iris is brownish golden. In preservative, the brown colour fades to grey, the dark brown dorsal and dorsolateral markings are darker than the rest of the body colouration; ventrally, cream and translucent fade to greyish white.

The female holotype (Fig. 6) agrees with the above given description. Where variation is mentioned, holotype conditions are as follows: pedal webbing formula I (1), IIi (1), IIe (1), IIIi (2½), IIIe (2), IVi (2½), IVe (3), V (1½); toe and finger tips not slightly swollen. Measurements (in mm): SVL: 19.0; HW: 5.0; E–N 1.5; EYE: 1.6; E–S: 3.1; IO: 3.2; N–ST: 1.5; INTERNARIAL: 1.8; TAL: 13.4; TIL: 8.8; FE: 8.8. Proportions: HW/SVL: 0.26; TIL/SVL: 0.46; TAL/SVL: 0.70; TAL/TIL: 1.53.

Molecular genetics: Of the species morphologically similar to the new species, an identified but unnamed population from central Tanzania (Tabora and Iringa regions; Appendix 2), called '*Phrynobatrachus mababiensis* clade C' by ZIMKUS & SCHICK (in press), is most similar according to uncorrected p-distances of a 550 bp (including gaps) fragment of the 16S mitochondrial rRNA gene (Table 2). In their phylogeny, ZIMKUS & SCHICK (in press) showed *P. kakamikro* and the mentioned populations to represent closely related sister taxa. The genetic divergence of only 1.7% between these two is low compared to other *Phrynobatrachus* species (Table 2; see also HILLERS et al. 2008) and

for the recognition of anuran species in general (VENCES et al. 2005, FOUQUET et al. 2007). Consequently, we should not rule out that *P. kakamikro* and the frogs here called '*Phrynobatrachus mababiensis* clade C' are conspecific. However, even in this case, this does not imply that the new species is synonymous to *P. mababiensis*. Indeed, the name *P. mababiensis* comprises a complex of species, and the form referable to *P. mababiensis* sensu stricto with its type locality in southern Africa ('clade A' of ZIMKUS & SCHICK in press) is genetically highly divergent from *P. kakamikro* (Table 2). The genetic distances between *P. kakamikro* and other close congeners, i.e., *P. keniensis*, *P. minutus*, *P. scheffleri*, support its specific status (see Table 2).

With regard to the relatively low genetic divergence between *P. scheffleri* and *P. minutus*, ZIMKUS & SCHICK (in press) suggested that such values do occur among East African *Phrynobatrachus* species, which are considered as distinct species based on other characters than molecular markers (e.g., *P. inexpectatus* and *P. minutus* differ by 3.0%, *P. inexpectatus* and *P. scheffleri* by 3.6%, *P. rungwenensis* and *P. uzungwenensis* by 1.7%). This phenomenon may be explained with a relatively recent colonisation of the Rift Valley and subsequent radiation of these frogs.

Distribution and life history: *Phrynobatrachus kakamikro* is only known from the type locality in semi-humid western Kenya, 1650 m above sea level (Fig. 3). In addition to *Leptopelis mackayi* KÖHLER, BWONG, SCHICK, VEITH & LÖTTERS, 2006 and *Petropedetes dutoiti* LOVERIDGE, 1935, this is the third anuran species currently known only from western Kenya. It remains to be studied, if these species actually do represent endemics or whether their restricted known ranges are the result of insufficient sampling efforts. *Phrynobatrachus kakamikro* was found active at night at a small temporary pond in anthropogenic grass land on the forest edge (Fig. 7) during the rainy season (May–June) along with *Hyperolius acuticeps* AHL, 1931, *H. ituriensis* LAURENT, 1940, *H. kivuensis* AHL, 1931, *H. lateralis* LAURENT, 1940, *H. viridiflavus* (DUMÉRIE & BIBRON, 1841),

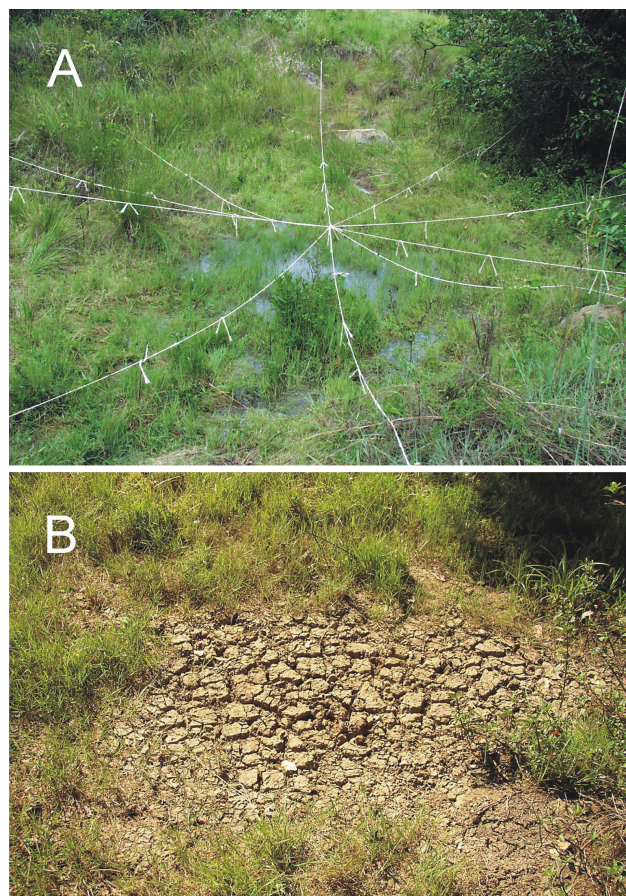


Figure 7. Pond at the type locality of *Phrynobatrachus kakamikro* sp. n. during the rainy season in April 2002 (A) and during the dry season in October 2003 (B). The visible rope was used for an ecological study.

Kassina senegalensis, *Xenopus victorinus* AHL, 1924, *Ptychadena* cf. *mascareniensis* (DUMÉRIL & BIBRON, 1841), *P. taenioscelis* LAURENT, 1954 and *Phrynobatrachus scheffleri*.

Bioacoustics: The advertisement call of *Phrynobatrachus kakamikro* was recorded at the type locality from a non-collected specimen (9 June 2002, 22:50 h; air temperature during recording 14.7°C). The call consists of two notes, the first being a 'buzz', followed by a single 'click' (Fig. 4C; Table 3). Individuals were observed calling while sitting on flooded vegetation in swampy areas. Syntopic *P. scheffleri* were not heard calling. *Phrynobatrachus kakamikro* advertisement calls differ from those of *P. scheffleri* by having two notes (versus one) and a lower pulse rate (Fig. 4A–C, Table 3). *Phrynobatrachus mababiensis* has a higher dominant frequency and *P. parvulus* a lower pulse rate than the new species (Fig. 4C–D, Table 3; for *P. parvulus* see CHANNING & HOWELL 2006). The advertisement calls of *P. inexpectatus* and *P. minutus* are unknown.

Threat status: Due to the sparse information available and according to the criteria of the IUCN Red List (IUCN 2008), we propose the threat status 'Data Deficient' for the species.

Etymology: The specific name is a free neologism that reflects the type locality and size of the new species (kaka + Greek mikro(s) = small). It is used as an invariable noun in apposition.

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Appendix 1

Material examined for morphological comparisons

Phrynobatrachus albifer: Usaramo, Tanzania: ZMB 26865 (holotype). *Phrynobatrachus graueri*: Rugege Forest, Rwanda: ZMB 21782 (holotype). *Phrynobatrachus inexpectatus*: 70 km NW of Kebre Mengist, Ethiopia: BM 1975.1684, 1689, 1691, 1695–1698, 1702, 1714, 1716–1735 (paratypes). *Phrynobatrachus kakamikro*: Kakamega Forest, Kenya: NMK A/3924/1–3, MHNG 2709.89. *Phrynobatrachus keniensis*: Northeast slope of Mt. Kenya, Kenya: A–MCZ 3479 (holotype). *Phrynobatrachus kinangopensis*: Mt. Kenya, Kenya: BM 1911.7.7.1–3, BM 1950.1.2.18–43, ZFMK 83497–501; Aberdares, Kinangop plateau, Kenya: NMK/A/3622/1–2, 4–7, MNHNP 1924.16 (holotype). *Phrynobatrachus minutus*: Kebre Mengist near Bore, Ethiopia: Durro, Ethiopia: BM 1947.2.30.51 (holotype): BM 1947.2.30.5; 70 km NW of Kebre Mengist, Ethiopia: BM 1975.1679–83, 1685–1688, 1690, 1692–1694, 1699–1701, 1703–1720, 1715; Bonga, Ethiopia: NMK/A/1450/1–2, NMK/A/415/1–3, ZFMK 15787. *Phrynobatrachus parvulus*: Bundibuyo, Uganda: MHNG 2711.51–54. *Phrynobatrachus perpalmatus*: Lake Mweru, DRC: BM 1947.2.4.34–35 (syntypes). *Phrynobatrachus rouxi*: Buddu Forest, Uganda: ZMB 23102 (holotype). *Phrynobatrachus scheffleri*: Kibwezi, Kenya: ZMB 21783 (lectotype), ZMB 25273, ZMB 64968–70 and 16 additional specimens without museum numbers (paralectotypes), NMK A/4737/6,7 +9 and 26 additional specimens without museum numbers (to be deposited at NMK); NMK A/3923, A/4740/1–6, 8–14; Kakamega Forest, Kenya: NMK A/3924/4–6; Taita Hills, Kenya: A/4358/1–3. *Phrynobatrachus ukingensis*: Kisumu, Kenya: NMK/A/2066/1–5; Taita Hills, Kenya: A/3705; Matipa, Zambia: BM 1954.113.85–86. *Phrynobatrachus uzungwensis*: Uzungwe Mountains, Tanzania: BM 1982.553 (holotype).

Appendix 2

Locality information and GenBank accession numbers of *Phrynobatrachus* species included in the molecular study (see Table 2) as processed by ZIMKUS & SCHICK (in press); for voucher specimens see there.

Species	Locality	GenBank accession number (16S rRNA)
<i>P. acridoides</i>	Tanzania: East Usambara Mountains, Kwamgumi Forest Reserve	FJ829253
<i>P. acridoides</i>	Tanzania: East Usambara Mountains, Mlinga Forest Reserve	FJ829255
<i>P. acridoides</i>	Tanzania: Pwani Region: Ruvu South Forest Reserve	FJ829254
<i>P. acridoides</i>	Tanzania: Dar es Salaam, University of Dar es Salaam	FJ829256
<i>P. acridoides</i>	Kenya: Coast Province: Arabuko Sokoke Forest	FJ829257
<i>P. acridoides</i>	Malawi: Mangochi District: Palm Forest Mangochi	FJ889453
<i>P. acutirostris</i>	Democratic Republic of Congo: South Kivu Province: Irangi	FJ829258
<i>P. acutirostris</i>	Democratic Republic of Congo: South Kivu Province: Irangi	FJ829259
<i>P. acutirostris</i>	Democratic Republic of Congo: South Kivu Province: Irangi	FJ829260
<i>P. auritus</i>	Uganda: Masindi District: Budongo Forest Reserve	FJ889454
<i>P. bullans</i>	Ethiopia: Southern Nations, Nationalities and People's Region: eastern shore of Lake Awassa	FJ829261
<i>P. bullans</i>	Tanzania: Tabora Region: Malagarasi River	FJ829264
<i>P. bullans</i>	Tanzania: Mwanza Region: Lamadi, near Lake Victoria	FJ829262
<i>P. bullans</i>	Kenya: Nyanza Province: Homa Bay	FJ829263
<i>P. dendrobates</i>	Uganda: Rukungiri District: Bwindi Impenetrable National Park	DQ283228
<i>P. dendrobates</i>	Uganda: Rukungiri District: Bwindi Impenetrable National Park	EU075286
<i>P. dendrobates</i>	Uganda: Rukungiri District: Bwindi Impenetrable National Park, Munyaga River	EU075287
<i>P. graueri</i>	Kenya: Trans-Nzoia District: Rift Valley Province: Mount Elgon	FJ889455
<i>P. graueri</i>	Rwanda: Northern Territory: between Mount Muhabura and Mount Gahinga on Uganda border	FJ829269
<i>P. graueri</i>	Rwanda: Northern Territory: Mudeni 1 TA Waypoint	FJ829265
<i>P. graueri</i>	Rwanda: Northern Territory: Sandi Waypoint	FJ829266
<i>P. graueri</i>	Rwanda: Northern Territory: Sandi Waypoint	FJ829267
<i>P. graueri</i>	Rwanda: Northern Territory: between Mount Muhabura and Mount Gahinga on Uganda border	FJ829268
<i>P. inexpectatus</i>	Ethiopia: Oromia Region: Bore, Ana-Kernessa	EU075290
<i>P. inexpectatus</i>	Ethiopia: Oromia Region: Bore, Ana-Kernessa	EU075291
<i>P. inexpectatus</i>	Ethiopia: Oromia Region: Bore, Ana-Kernessa	EU075292
<i>P. kakamikro</i>	Kenya: Western Province: Kakamega Forest	FJ889456
<i>P. kakamikro</i>	Kenya: Western Province: Kakamega Forest	FJ889457
<i>P. kakamikro</i>	Kenya: Western Province: Kakamega Forest	FJ889458
<i>P. keniensis</i>	Kenya: Rift Valley Province: Thompson Falls	FJ889459
<i>P. keniensis</i>	Kenya: south of Nakuru	EU075293
<i>P. keniensis</i>	Kenya: south of Nakuru	FJ829270
<i>P. kinangopensis</i>	Kenya: Central Province: southern flank of Mount Kenya	FJ889460
<i>P. krefftii</i>	Tanzania: Tanga Region: East Usambara Mountains, Mlinga Forest Reserve	FJ829271
<i>P. krefftii</i>	Tanzania: Tanga Region: East Usambara Mountains, Mlinga Forest Reserve	FJ829272
<i>P. krefftii</i>	Tanzania: Tanga Region: West Usambara Mountains, Ambangulu Tea Estate	FJ829273
<i>P. krefftii</i>	Tanzania: Tanga Region: East Usambara Mountains, Amani Nature Reserve	FJ829276
<i>P. krefftii</i>	Tanzania: Tanga Region: East Usambara Mountains, Amani Nature Reserve	FJ829274
<i>P. krefftii</i>	Tanzania: Tanga Region: East Usambara Mountains, Amani Nature Reserve	FJ829275
<i>P. mababiensis</i> clade A	Namibia: Rundu	AF215399; FJ829277
<i>P. mababiensis</i> clade B	Tanzania: Pwani Region: Zaraninge	FJ829278
<i>P. mababiensis</i> clade B	Mozambique: Niassa Game Reserve	FJ829279
<i>P. mababiensis</i> clade B	Mozambique: Niassa Game Reserve	FJ829280
<i>P. mababiensis</i> clade B	Zambia: Eastern Province: Luambe National Park	FJ889461
<i>P. mababiensis</i> clade C	Tanzania: Tabora Region: Malagarasi River	FJ829283
<i>P. mababiensis</i> clade C	Tanzania: Iringa Region: Udzungwa Mountains, Bomalang'ombe	FJ829281

Systematics of ‘Little Brown Frogs’ and description of a new species

Species	Locality	GenBank accession number (16S rRNA)
<i>P. mababiensis</i> clade C	Tanzania: Iriga Region: Udzungwa Mountains, Bomalang'ombe	FJ829282
<i>P. mababiensis</i> clade C	Tanzania: Iringa: Kibebe Farm, Netting Pond	DQ283424
<i>P. minutus</i>	Ethiopia: Oromia Region: Bore, Bore Bidika	FJ829284
<i>P. minutus</i>	Ethiopia: Oromia Region: Bore, Enshido Aliyo	FJ829285
<i>P. minutus</i>	Ethiopia: Oromia Region: Bore, Enshido Aliyo	FJ829286
<i>P. minutus</i>	Ethiopia: Oromia Region: Bore, Enshido Aliyo	FJ829287
<i>P. minutus</i>	Ethiopia: Oromia Region: Bore, Enshido Aliyo	FJ829288
<i>P. natalensis</i>	Ethiopia: Oromia Region: Yadot River, vicinity of Dola Mena	FJ829295
<i>P. natalensis</i>	Ethiopia: Oromia Region: Yadot River, vicinity of Dola Mena	FJ829296
<i>P. natalensis</i>	Ethiopia: Oromia Region: Yadot River, vicinity of Dola Mena	FJ829297
<i>P. natalensis</i>	Ethiopia: Oromia Region: Tributary to Yadot River, vicinity of Dola Mena	FJ829292
<i>P. natalensis</i>	Tanzania: Kigoma Region: Lugufu	FJ829299
<i>P. natalensis</i>	Tanzania: Kigoma Region: Lugufu	FJ829300
<i>P. natalensis</i>	Tanzania: Iringa, Mufindi, Sao Hill	FJ829293
<i>P. natalensis</i>	Tanzania: Morogoro Region: Mvomero District, Nguru Mountain, Pemba Village	FJ829294
<i>P. natalensis</i>	Uganda: Central Region: Kampala District	FJ829298
<i>P. natalensis</i>	Kenya: Western Province: Kakamega Forest	FJ889464
<i>P. natalensis</i>	Kenya: Western Province: Kakamega Forest	FJ889463
<i>P. natalensis</i>	Mozambique: Niassa Game Reserve	FJ829301
<i>P. natalensis</i>	Mozambique: Niassa Game Reserve	FJ829302
<i>P. natalensis</i>	Mozambique: Niassa Game Reserve	FJ829303
<i>P. natalensis</i>	Tanzania: Tatanda Village	DQ283414
<i>P. natalensis</i>	Rwanda: Northern Territory: Mukungwe Waypoint	FJ829290
<i>P. natalensis</i>	Rwanda: Northern Territory: Mukungwe Waypoint	FJ829291
<i>P. natalensis</i>	Malawi: Mangochi District: Southern Region: Lake Malawi National Park	FJ889462
<i>P. natalensis</i>	Tanzania	FJ829289
<i>P. pakenhami</i>	Tanzania: Pemba Island (Zanzibar): Machengwe Swamp (4 km south of Wete)	FJ829304
<i>P. pakenhami</i>	Tanzania: Pemba Island (Zanzibar): Machengwe Swamp (4 km south of Wete)	FJ829305
<i>P. pallidus</i>	Kenya: Coast Province: Kakoneni	EU075294
<i>P. parvulus</i>	Malawi: Nyika Plateau	FJ829306
<i>P. parvulus</i>	Tanzania: Rubeho Mangalisa Forest Reserve	FJ829309
<i>P. parvulus</i>	Tanzania: Rubeho Mangalisa Forest Reserve	FJ829310
<i>P. parvulus</i>	Tanzania: West Kilombero Scarp Forest Reserve, Udzungwa Mountains	FJ829307
<i>P. parvulus</i>	Tanzania: West Kilombero Scarp Forest Reserve, Udzungwa Mountains	FJ829308
<i>P. parvulus</i>	Uganda: Bundibugyo District: Bundibugyo	FJ889465
<i>P. parvulus</i>	Uganda: Bundibugyo District: Bundibugyo	FJ889466
<i>P. parvulus</i>	Uganda: Bundibugyo District: Bundibugyo	FJ889467
<i>P. parvulus</i>	Uganda: Bundibugyo District: Bundibugyo	FJ889468
<i>P. parvulus</i>	Malawi: Nyika Plateau, Chelinda Camp, vicinity of Dam 1	EU075295
<i>P. parvulus</i>	Malawi: Nyika Plateau, Chelinda Camp, vicinity of Dam 1	EU075296
<i>P. parvulus</i>	Malawi: Nyika Plateau, Chelinda Camp, vicinity of Dam 1	EU075297
<i>P. rungwensis</i>	Tanzania: Morogoro Region: Uluguru Mountains, Shikurufumi	EU075298
<i>P. rungwensis</i>	Tanzania: West Kilombero Scarp Forest Reserve, Udzungwa Mountains	EU075299
<i>P. rungwensis</i>	Tanzania: West Kilombero Scarp Forest Reserve, Udzungwa Mountains	EU075300
<i>P. scheffleri</i>	Kenya: Coast Province: Mwatate Dam, Taita Hills	EU075288
<i>P. scheffleri</i>	Kenya: Eastern Province: Lake Paradise, Marsabit National Reserve	EU075289
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889469
<i>P. scheffleri</i>	Kenya: Western Province: Kakamega Forest	FJ889484
<i>P. scheffleri</i>	Kenya: Western Province: Kakamega Forest	FJ889485
<i>P. scheffleri</i>	Kenya: Western Province: Kakamega Forest	FJ889483
<i>P. scheffleri</i>	Kenya: Coast Province: Taita Hills, Mghambonyi	FJ889480
<i>P. scheffleri</i>	Kenya: Coast Province: Taita Hills, Mghambonyi	FJ889481
<i>P. scheffleri</i>	Kenya: Coast Province: Taita Hills, Mghambonyi	FJ889482
<i>P. scheffleri</i>	Kenya: Central Province: Kakuzi	FJ889490

Species	Locality	GenBank accession number (16S rRNA)
<i>P. scheffleri</i>	Kenya: Central Province: Kakuzi	FJ889491
<i>P. scheffleri</i>	Kenya: Central Province: Kakuzi	FJ889492
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889497
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889498
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889499
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889500
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889501
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889502
<i>P. scheffleri</i>	Kenya: Eastern Province: Makueni District, Kibwezi	FJ889503
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889486
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889487
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889488
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889489
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889493
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889494
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889495
<i>P. scheffleri</i>	Kenya: Nairobi, Runda	FJ889496
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889470
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889471
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889472
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889473
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889474
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889475
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889476
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889477
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889478
<i>P. scheffleri</i>	Kenya: Nairobi, Karens	FJ889479
<i>P. ukingensis</i>	Tanzania: Morogoro Region: Uluguru Mountains, Ruvu	EU075301
<i>P. ungujae</i>	Tanzania: Unguja Island (Zanzibar): Jozani Chwaka Bay National Park	FJ829315
<i>P. ungujae</i>	Tanzania: Unguja Island (Zanzibar): Jozani Chwaka Bay National Park	FJ829316
<i>P. uzungwensis</i>	Tanzania: Morogoro Region: Uluguru Mountains, Tegetero	FJ829317
<i>P. versicolor</i>	Uganda: Rukungiri District: Bwindi Impenetrable National Park	FJ829318