Zootaxa 5584 (1): 026–046
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5584.1.2
http://zoobank.org/urn:lsid:zoobank.org:pub:E8DB2F4B-246B-4232-BB05-6559A69B1976

Digging out another cryptic species: A new sand frog (Anura: Pyxicephalidae: *Tomopterna*) from Mozambique

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Abstract

A new species of *Tomopterna* is described from Banhine National Park, southern Mozambique. It differs from all other sand frogs by an uncorrected p-distance of 4.9–8.7% for 16S rRNA. The new species can be distinguished from all other described species of sand frogs by: males 37 mm SVL or less, undivided subarticular tubercles, more than three phalanges free of webbing on the fourth toe, a continuous glandular ridge below the tympanum, a distinct tympanic membrane, the nostrils closer to the snout tip than the eye, the rounded canthus rostralis, a round tympanum, the absence of an outer metatarsal tubercle, an interrupted inter-orbital bar, small dorsal warts, the absence (or weakness) of vomerine teeth, the solid pigmented throat in mature males, the distinct palmar tubercles, the smooth ventral surface, and barring on the limbs. This description adds a further amphibian to the list of Mozambican frogs, which has increased significantly in recent years.

Key words: Banhine National Park, sand frogs, new species, distribution, advertisement call, DNA

Introduction

The genus nomen *Tomopterna* (Duméril & Bibron) was initially regarded as a subgenus of *Rana* Linnaeus. Van Dijk (1966) based on a study of southern African tadpoles, recognised *Tomopterna* as a genus distinct from other African ranids. There are presently 18 recognised species, of which seven were described in the genus *Tomopterna* (Frost 2024). The earlier species now placed in the genus *Tomopterna* include *Pyxicephalus Delalandii* Tschudi [= *T. delalandii*]; *Pyxicephalus natalensis* Smith [=*T. natalensis*]; *Pyxicephalus marmoratus* Peters [=*T. marmorata*]; *Rana tuberculosa* Boulenger (a replacement name for *Pyxicephalus rugosus* Günther) [=*T. tuberculosa*]; *Phrynobatrachus monticola* Fischer [=*T. monticola*]; *Rana pulchra* Boulenger [=*T. pulchra*]; *Chiromantis kachowskii* Nikolskii [=*T. kachowskii*] ; *Rana cryptotis* Boulenger [=*T. cryptotis*]; *Arthroleptis milleti-horsini* Angel [=*T. milletihorsini*]; *Arthroleptis elegans* Calabresi [=*T. elegans*]; and *Arthroleptella ahli* Deckert [=*T. ahli*].

Recent descriptions include *Tomopterna krugerensis* Passmore & Carruthers; *Tomopterna tandyi* Channing & Bogart; *Tomopterna luganga* Channing, Moyer & Dawood; *Tomopterna gallmanni* Wasonga & Channing; *Tomopterna wambensis* Wasonga & Channing; *Tomopterna branchi* Wilson & Channing; and *Tomopterna adiastola* Channing & Du Preez.

The species of sand frogs are very similar in overall morphology, no doubt the reason why so many cryptic species were unrecognised, or synonymised with *T. cryptotis* which was believed to be a single widespread taxon. The development of advertisement call analysis developed in the 1960s and later easy access to DNA sequencing, supported the ongoing description of sand frog species. Since 1975 a further seven species have been described (see above). There is no indication that all the sand frog species have been discovered yet.

 Accepted by W. Conradie: 20 Dec. 2024; published: 5 Feb. 2025

Sand frogs are widely distributed in sub-Saharan Africa, excluding the rainforests of central Africa. They are usually found on sandy soils, although *T. pulchra* has been found in more rocky habitats (Channing & Rödel 2019, Willems & Channing 2023).

A small collection of frogs from inland of Beira, Mozambique made in December 1991, included two specimens of *Tomopterna*. These were not identified to species level, and were later referred to as *Tomopterna* sp. Beira (Dawood *et al.* 2002). The recognition of these specimens as a distinct species of sand frog has been demonstrated in a series of published phylogenies, based on mitochondrial DNA sequences (Dawood *et al.* 2002; Dawood & Uqubay 2004; Zimkus & Larson 2011; Wasonga & Channing 2013).

In subsequent years a series of *Tomopterna* specimens was collected from Banhine National Park (Pietersen *et al.* 2013). The 16S rRNA gene sequences of the Banhine specimens (sequenced by AD, see Pietersen *et al.* 2013, but subsequently lost, along with the tissues) are identical to those of *Tomopterna* sp. Beira.

Materials and methods

Sampling. Two specimens were collected from outside Beira, Mozambique (19.6466° S, 34.7666° E) by Alan Channing, 20 December 1991 (PEM A15572 and PEM A15573). An additional nine specimens were collected from Fish Eagle Research Camp, Banhine National Park, Mozambique (22.6328° S, 33.2673° E) by Errol W. Pietersen, 7 April 2007 and 26 November. These were deposited in the Ditsong National Museum of Natural History, and toe-clips were taken of an additional specimen that was not collected.

Phylogenetic analyses. DNA extraction and amplification of fragments of mitochondrial 16S rRNA followed standard protocols (Channing *et al*. 2016). 16S rRNA sequences of all *Tomopterna* species except *T. monticola* were downloaded from Genbank. In total 194 sequences from 19 species were available (Supplementary material Table S1), plus one sequence (MH115755) of the outgroup *Ptychadena anchietae* (Bocage)

Sequence divergences between species were determined as mean uncorrected p-distances using MEGA 11 (Stecher *et al*. 2020; Tamura *et al*. 2021) (Table 1). All ambiguous positions were removed for each sequence pair (pairwise deletion option), yielding a final dataset with a length of 433 base pairs.

TABLE 1. Mean uncorrected p-distances between *Tomopterna* species. KAC—*T. kachowski*, BAN—*T. banhinensis* **sp. nov**., NAT—*T. natalensis*, TAN—*T. tandyi*, DEL—*T. delalandii*, CRY—*T. cryptotis*, BRA—*T. branchi*, TUB—*T. tuberculosa*, WAM—*T. wambensis*, LUG—*T. luganga*, MAR—*T. marmorata*, PUL—*T. pulchra*, KRU—*T. krugerensis*, AHL—*T. ahli*, ADI—*T. adiastola*, MIL—*T. milletihorsini*, GAL—*T. gallmanni*, ELE—*T. elegans*.

	KAC	BAN	NAT	TAN	DEL	CRY	BRA	TUB	WAM	LUG	MAR	PUL	KRU	AHL	ADI	MIL	GAL
BAN	7.7																
NAT	7.3	8.7															
TAN	5.7	5.6	6.7														
DEL	5.1	4.9	6.2	3.4													
CRY	7.4	8.1	9.3	6.7	5.7												
BRA	4.5	5.4	5.9	3.3	2.6	5.3											
TUB	5.8	6.7	7.2	6.1	4.6	6.9	5.1										
WAM	4.0	5.4	7.1	3.8	3.8	6.7	3.1	5.3									
LUG	6.6	5.8	8.3	4.8	4.5	7.7	5.4	7.4	5.5								
MAR	7.1	7.1	8.6	6.0	5.1	6.8	5.0	7.6	5.3	4.4							
PUL	5.6	6.5	7.4	5.8	5.7	7.9	5.9	3.9	5.1	6.9	8.0						
KRU	6.2	6.3	7.1	4.8	3.9	6.1	3.9	6.0	4.3	5.7	5.1	6.0					
AHL	4.8	5.0	5.8	2.7	1.8	5.6	2.2	5.3	3.0	3.9	4.5	5.7	2.9				
ADI	5.4	5.0	6.2	1.5	3.0	6.4	2.8	5.8	3.7	4.9	5.4	5.3	3.7	2.2			
MIL	5.4	6.8	7.5	5.6	4.4	8.0	4.8	5.7	4.2	6.7	7.6	5.1	6.0	4.5	5.1		
GAL	4.7	6.0	5.9	4.0	3.0	6.0	4.0	4.3	3.7	5.1	5.9	5.0	4.2	3.0	3.3	4.1	
ELE	3.9	5.0	5.9	3.0	2.1	4.9	1.8	4.1	2.1	4.4	4.5	5.0	3.0	1.6	2.6	3.8	2.2

The phylogeny based on the aligned 16S sequences was determined using the Maximum Likelihood software IQ-TREE (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016) analysed on the W-IQ-TREE website (http://iqtree.cibiv.univie.ac.at). The ultrafast bootstrap UFBoot2 (Minh *et al.* 2013; Hoang *et al.* 2017) was calculated using 1000 replicates, with the appropriate model for the ML analysis automatically determined by the software. The best-fit model according to BIC was TIM2e+I+G4. Confidence values for the phylogeny were calculated as SH-aLRT (%) and the ultrafast bootstrap (%). *Ptychadena anchietae* was selected as the outgroup as the Ptychadenidae are basal to the Pyxicephalidae (Frost *et al*. 2006). The tree was rooted with the outgroup and drawn using FigTree 1.4.4 (Rambaut 2018).

Advertisement calls. Recordings were made in the field using a Sony TC-D5M recorder with a directional microphone. Recordings were made of the Beira specimens (PEM A15572 and PEM A15573), after dark, alongside a small stream, at an air temperature of 24°C. Calls were analysed using Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics 2022). We used a call centered approach (Köhler et al 2017) for the analysis. The calls were compared to those of *T. krugerensis*, *T. gallmanni*, *T. tuberculosa*, *T. pulchra*, *T. adiastola*, *T. ahli*, *T. branchi*, *T. cryptotis*, *T. marmorata*, *T. natalensis, T. wambensis*, *T. luganga*, *T. delalandii* and *T. tandyi*.

Adult morphology. Morphological comparisons were made with reference to Dawood & Channing (2002), Rödel & Hallermann (2006), Zimkus & Larson (2011), Wasonga & Channing (2013), Channing & Rödel (2019), Wilson & Channing (2019), Channing & Du Preez (2020). Additional comparative material was examined from the following collections: SAIAB—South African Institute for Aquatic Biodiversity, Makhanda, South Africa; TM—Ditsong National Museum of Natural History, Pretoria, South Africa; AD—private collection of A. Dawood; BMNH—Natural History Museum, London, UK; PEM—Bayworld (Port Elizabeth Museum), Gqeberha, South Africa.

Measurements were made with an electronic calliper accurate to 0.01 mm, rounded to 0.1 mm. The following measurements were taken: SVL—snout-vent length; SUL—snout-urostyle length; HW—head width at the angle of the jaw; HL—head length, from behind lower jaw to tip of snout; HND—length of hand from basal tubercle to tip of third finger; IOS—interorbital space, measured across the top of the head; DAE—distance between anterior corners of eyes; IND—internarial distance; END—eye to nostril distance; SL—snout length, measured from the anterior corner of the eye to the snout tip; TYM—width of tympanum; ED—horizontal eye diameter; ETD—eye to tympanum distance; EL—upper eyelid length; CRU—length of flexed crus; IMT—length of inner metatarsal tubercle; FOT—length of foot to include inner metatarsal tubercle to tip of fourth toe.

Body proportions were calculated as the following ratios: SUL/HW, HW/HL, SUL/HND, DAE/IOS, SL/END, ED/TYM, TYM/ETD, IMT/TYM, SUL/CRU.

In addition, the presence of tarsal and outer metatarsal tubercles, the visibility of the tympanum, and the amount of webbing between the toes was noted. Webbing was recorded as phalanges of fourth toe free of webbing. Colour patterns were based on preserved material and photographs of the specimens in life.

The morphological characters of *Tomopterna* sp. Beira and all other *Tomopterna* species are compared in Table 2. The characters are coded as follows (based on Wasonga & Channing 2013):

1. Snout vent length, adult male: (1) <37 mm, (2) 38–44 mm, (3) >44 mm.
2. Subarticular tubercles: (1) single, (2) completely or partially divided.
3. Webbing, phalanges free on toe 4: (1) 1, (2) 2–3, (3) >3.
4. Glandular ridge below the tympanum: (1) absent, (2) continuous, (3) interrupted, (4) isolated glands.
5. Tympanic membrane: (1) hidden, (2) scarcely visible, (3) distinct.
6. Nostril position: (1) closer to snout tip, (2) mid-way, (3) closer to eye.
7. Canthus rostralis: (1) rounded, (2) moderately angled, (3) sharply angled.
8. Tympanum: (1) absent, (2) round, (3) ovoid.
9. Outer metatarsal tubercle: (1) absent, or just a bump, (2) present.
10. Inter-orbital bar: (1) absent, (2) interrupted, (3) complete.
11. Dorsal warts: (1) absent), (2) small, (3) distinct and prominent.
12. Vertebral line: (1) absent, (2) present.
13. Vomerine teeth: (1) absent or weak, (2) present.
14. Gular colouration in sexually mature males: (1) immaculate, (2) sparsely mottled, (3) densely mottled, (4) solid, dark.
15. Palmar tubercles: (1) absent, (2) slightly raised, (3) distinct.
16. Ventral surface: (1) smooth, (2) granular near vent and thighs.
17. Barring on limbs: (1) absent), (2) present.
18. Asperities surrounding vent: (1) absent, (2) present.

TABLE 2. Comparison of the morphological characters of the species of *Tomopterna*. See Material and methods for character coding.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. *T. adiastola*	1	1	3	2	1	2	1	1	1	2	1	1,2	2	1	1	1	2	1,2
2. *T. ahli*	2	1	3	2	3	1	1	2	1	1	1	1	2	4	2	1	2	1
3. *T. banhinensis* **sp. nov.**	1	1	3	2	3	1	1	2	1	1,2,3	2	1,2	1	4	3	1	1	1
4. *T. branchi*	2	1	3	4	3	3	1	2	1	3	2	1,2	1	4	3	1	2	1
5. *T. cryptotis*	1	1	2	2	1	2	1	1,2	2	1,2	1	1,2	2	1	1	1	1	1,2
6. *T. delalandii*	2	1	3	4	3	1	3	3	2	3	1	1	1	4	2	1	2	1
7. *T. elegans*	2	1	2	1,2,3	3	1	3	2	2	1,3	2	1,2	2	3	3	1	2	1,2
8. *T. gallmanni*	2	2	2	2,3	3	2	2	3	1	2,3	3	1,2	2	2	2	1	2	2
9. *T. kachowskii*	2	1	3	2,3	3	1	1,2,3	2	2	1,3	2	1,2	2	4	3	2	2	2
10. *T. krugerensis*	2	2	3	2	2	1	3	3	1	3	1	1	2	4	3	2	2	1
11. *T. luganga*	2	1	2	3	2	1	2	3	1	1	2	1	1	4	3	1	2	1
12. *T. marmorata*	2	1	2	4	3	3	1	2	1	3	1	2	1	3	2	1	2	1
13. *T. milletihorsini*	1	1	2	3	1	1	1	1	2	3	2	1					1	1
14. *T. monticola*	2	1	2	3	2	1	1	3	1	2	2	1	2	3	3	1	2	1
15. *T. natalensis*	1	1	3	2	3	1	1	2	1	1	1	1	2	4	1	1	2	2
16. *T. pulchra*	1	1	3	1,3	2	3	1	2,3	1	3	3	1,2	1	4	3	1	2	2
17. *T. tandyi*	2	1	2	2	1	1	2	1	2	1,2,3	2	1	2	3	2	2	2	2
18. *T. tuberculosa*	2	1	3	1,3	2	3	1	2,3	1	3	3	1,2	1	4	3	1	2	2
19. *T. wambensis*	2	2	2	3	3	1	2	2	1	3	2	1,2	2	3	3	1	2	1

Nomenclatural acts. The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new name contained herein is available under that code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is urn:lsid:zoobank.org:pub: E8DB2F4B-246B-4232-BB05-6559A69B1976, and the new name is registered under urn:lsid:zoobank.org:act: 71490F4F-381C-4765-AB62-82695545CFE1. The electronic edition of this article was published in a journal with an ISSN, and has been archived and is available from the following digital repository: www.mapress.com/zootaxa.

Results

Phylogenetic analysis. The phylogeny based on 16S rRNA (Fig. 1) places *Tomopterna* sp. Beira in a clade basal to *T. luganga* from Tanzania, and *T. marmorata* which ranges from northern South Africa to Kenya. Many of the clades had SH-aLRT values >80%, and ultrafast bootstrap support >95%, levels deemed to show confidence in the clades.

Intra-specific uncorrected p-distances ranged from 0.0–0.1%, while the mean inter-specific p-distances ranged from 1.5–9.3% (Table 1). *Tomopterna* sp. Beira shows a mean p-distance of 4.9–8.7% from all other *Tomopterna* species. The new species has an uncorrected p-distance of 5.8% from *T. luganga*, and 7.1% from *T. marmorata*. These are within the ranges of differences for 16S rRNA detected in other pyxicephalid frogs (*Amietia* 1.3–10.0%, Channing *et al*. 2016; *Strongylopus* 2.8–7.7%, Channing *et al*. 2022; *Pyxicephalus* 2.3–10.0%, Du Preez *et al*. 2024). The lowest p-distances observed are between the tetraploid *T. tandyi* and its maternal diploid species *T. adiastola* (1.5%), reflecting the relatively recent (5.2 mya) split between these two species (Bogart *et al*. 2022). This was followed by *T. elegans* from northern Somalia and *T. ahli* from northern Namibia and southern Angola (1.6%), *T. elegans* from northern Somalia and *T. branchi* from South Africa (1.8%) and *T. ahli* from Namibia and *T. delalandii* from South Africa (1.8%).

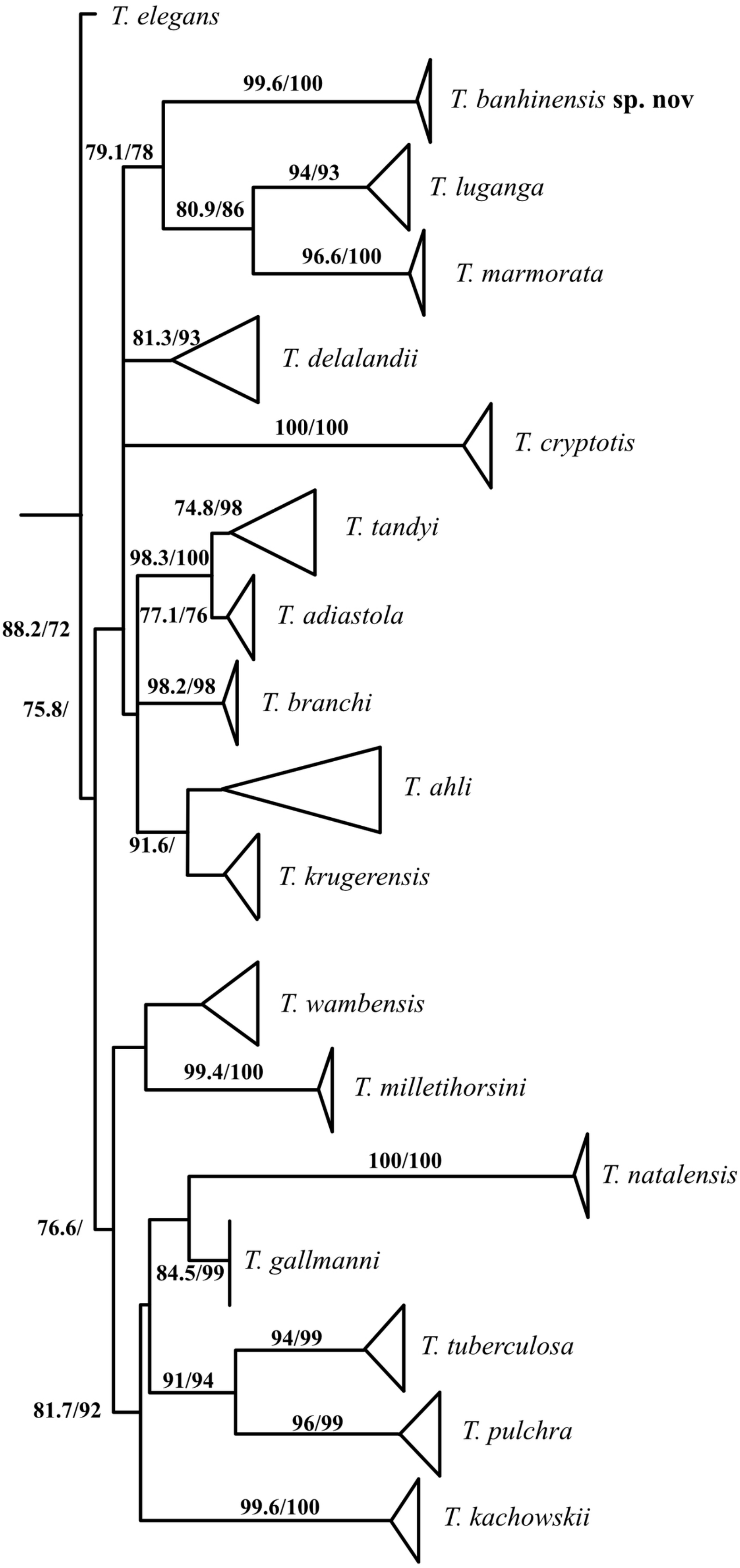

FIGURE 1. Phylogeny based on 16S rRNA, with the terminals collapsed. See Supplementary Table S1 for material included in the terminals. Support shown as SH-aLRT (%) / ultrafast bootstrap (%).

Advertisement call. The call is a rapid series of high-pitched notes (Fig. 2), and is compared with other species in Table 3. The fundamental frequency is emphasised (mean 1581 Hz, range 1559–1636 Hz); with two harmonics visible (mean 3133 and 4746 Hz). There are 4–7 pulses at a mean pulse repetition rate of 8.7 s^{-1} (6.8–9.8 s^{-1}).

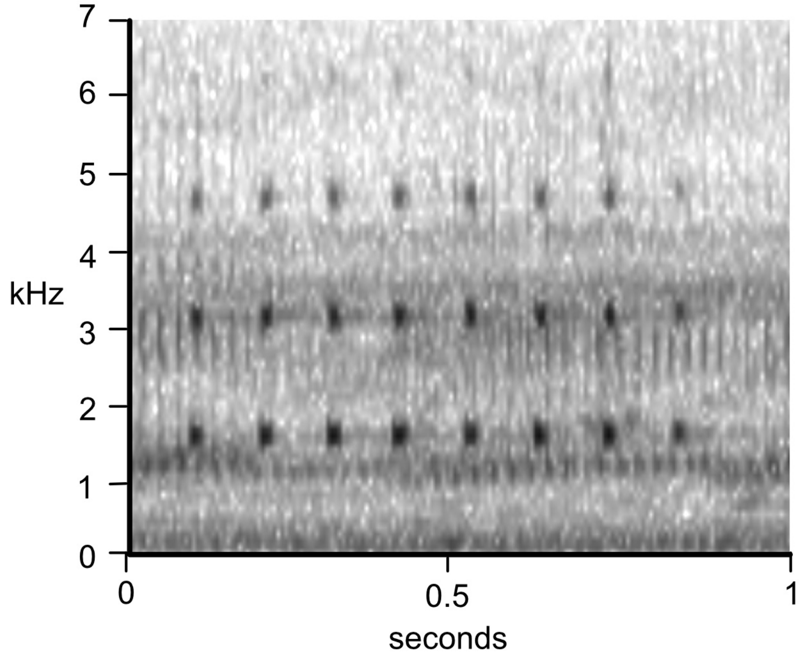

FIGURE 2. Advertisement call of *Tomopterna banhinensis* **sp. nov.** (PEM A15572) from Beira, Mozambique.

TABLE 3. Comparison of advertisement calls of the species of *Tomopterna*, giving fundamental frequency, mean and range of emphasised frequency, and mean and range of note rate.

Species	Call type	Fundamental frequency (Hz)	Mean emphasised frequency (Hz)	Mean note rate per second
T. banhinensis **sp. nov.**	series of notes	1559–1636	1581 (1559–1636)	8.7 (6.8–9.8)
T. adiastola	series of notes	1465–1729	3315 (2930–3675)	8.6 (5.2–14.5)
T. ahli	series of notes	1076–1264	2449 (2152–2694)	6.6 (2.9–8.4)
T. branchi	series of notes	913–1008	1926 (1827–2106)	2.9 (2.0–3.8)
T. cryptotis	series of notes	1268–1460	2738 (2497–2920)	8.0 (4.8–11.1)
T. delalandii	series of notes	744–1164	1859 (1488–2260)	5.4 (3.1–9.3)
T. gallmanni	knocking	980–1034	2007 (1960–2067)	7.4 (6.0–8.5)
T. krugerensis	knocking	904–1105	2009 (1808–2210)	3.3 (1.5–5.0)
T. luganga	series of notes	1050–1170	1126 (1050–1170)	5.7 (5.1–6.6)
T. marmorata	series of notes	1149–1307	2444 (2298–2614)	6.3 (5.5–7.6)
T. natalensis	series of notes	1354–1656	2987 (2708–3499)	3.2 (2.3–4.7)
T. pulchra	tapping	1034–1550	2534 (2067–3100)	9.6 (4.8–12.0)
T. tandyi	series of notes	829–1256	2190 (1658–2511)	6.8 (5.1–9.1)
T. tuberculosa	tapping	1304–1335	2963 (2608–2670)	10.5 (8.6–12.3)
T. wambensis	series of notes	1056–1476	2542 (2111–2955)	9.1 (4.8–12.1)

Morphology. Measurements and body proportions of the type series are presented in Tables 4 and 5. The new species' main differences from geographically nearby species are shown in Table 6.

TABLE 4. Measurements of the holotype and paratypes of *Tomopterna banhinensis* **sp. nov.** Holotype TM85588 in bold. See Material and methods for explanation of abbreviations. M—male; F—female.

Museum	Sex	SVL	SUL	HW	HL	HND	IOS	DAE	IND	END	SL	TYM	ED	ETD	EL	CRU	IMT	FOT
TM 85588	M	43.3	40.2	18.1	16.6	9.6	3.9	7.2	4	2.6	5.6	2.2	5.7	2	6.9	16.6	3.3	18.7
TM 85589	F	42.9	40	15.9	14.1	8.7	3.9	7.1	3.4	2.8	5.1	2.7	5.2	1.5	6.3	15.4	2.9	–
TM 85562	M	35.8	30.63	16.1	10.04	8.12	2.57	6.67	2.66	1.59	3.87	–	5.18	1.95	6.73	13.78	3.11	14.01
TM 85563	M	34.14	32.22	12.37	7.01	7.08	3.07	6.49	2.96	2.29	3.34	2.28	5.14	1.53	5.47	13.47	2.59	13.41
TM 85564	F	31.21	28.27	12.6	10.52	7.51	2.19	6.43	2.53	1.94	3.39	2.22	4.92	1.74	5.42	13.14	2.67	14.79
TM 85565	F	39.04	36.92	14.5	9.24	8.59	3.4	6.02	3.52	1.89	3.62	2.41	5.39	1.28	6.26	15.09	2.89	15.57
TM 85566	M	38.52	34.61	15.27	9.51	8.78	3.05	6.69	3.63	1.82	3.86	2.41	5.21	1.64	5.63	14.12	3.07	14.95
TM 85567	F	43.62	40	16.8	11.51	9.06	3.08	7.71	3.87	2.21	3.86	1.15	5.24	2.1	6.9	16.1	3.44	16.07
TM 85568	F	37.04	33.96	15.3	11.69	8.26	3.42	5.63	3.34	2.71	5.34	1.62	5.75	1.43	6.48	14.59	3.74	14.98

TABLE 5. Proportions of the holotype and paratypes of *Tomopterna banhinensis* **sp. nov.** Holotype TM85588 in bold. See Material and methods for explanation of abbreviations. M—male; F—female.

Museum no.	Sex	**SUL/ HW**	**HW/ HL**	**SUL/ HND**	**DAE/ IOS**	**SL/ END**	**ED/ TYM**	**TYM/ ETD**	**IMT/ TYM**	**SUL/ CRU**	**HL/ SVL**	**HW/ SVL**	**HL/ HW**	**SL/ HL**	**SL/ IND**	**END/ SL**	**ED/ HL**	**ED/ SL**	**IOS/ EL**	**IOS/ IND**	**IOS/ ED**	**TYM/ ED**	**HND/ SVL**	**CRU/ SVL**
TM 85588	M	2.22	1.09	4.19	1.85	2.15	2.59	1.10	1.50	2.42	0.38	0.42	0.92	0.34	1.40	0.46	0.34	1.02	0.57	0.98	0.68	0.39	0.22	0.38
TM 85562	M	1.90	1.60	3.77	2.60	2.43	-	-	-	2.22	0.28	0.45	0.62	0.39	1.45	0.41	0.52	1.34	0.38	0.97	0.50	-	0.23	0.38
TM 85563	M	2.60	1.76	4.55	2.11	1.46	2.25	1.49	1.14	2.39	0.21	0.36	0.57	0.48	1.13	0.69	0.73	1.54	0.56	1.04	0.60	0.44	0.21	0.39
TM 85566	M	2.27	1.61	3.94	2.19	2.12	2.16	1.47	1.27	2.45	0.25	0.40	0.62	0.41	1.06	0.47	0.55	1.35	0.54	0.84	0.59	0.46	0.23	0.37
TM 85589	F	2.52	1.13	4.60	1.82	1.82	1.93	1.80	1.07	2.60	0.33	0.37	0.89	0.36	1.50	0.55	0.37	1.02	0.62	1.15	0.75	0.52	0.20	0.36
TM 85564	F	2.24	1.20	3.76	2.94	1.75	2.22	1.28	1.20	2.15	0.34	0.40	0.83	0.32	1.34	0.57	0.47	1.45	0.40	0.87	0.45	0.45	0.24	0.42
TM 85565	F	2.55	1.57	4.30	1.77	1.92	2.24	1.88	1.20	2.45	0.24	0.37	0.64	0.39	1.03	0.52	0.58	1.49	0.54	0.97	0.63	0.45	0.22	0.39
TM 85567	F	2.38	1.46	4.42	2.50	1.75	4.56	0.55	2.99	2.48	0.26	0.39	0.69	0.34	1.00	0.57	0.46	1.36	0.45	0.80	0.59	0.22	0.21	0.37
TM 85568	F	2.22	1.31	4.11	1.65	1.97	3.55	1.13	2.31	2.33	0.32	0.41	0.76	0.46	1.60	0.51	0.49	1.08	0.53	1.02	0.59	0.28	0.22	0.39

TABLE 6. Comparison of characters useful to distinguish the new species from other species of *Tomopterna* occurring in the same geographical area.

Species	*T. banhinensis* **sp. nov**	*T. adiastola*	*T. krugerensis*	*T. marmorata*	*T. natalensis*
Size	SVL 37 mm or less	SVL 37 mm or less	SVL 38–44 mm	SVL 38–44 mm	SVL 37 mm or less
Subarticular tubercles	single	single	divided	single	single
Phalanges on T4 free of webbing	>3	>3	>3	2–3	>3
Glandular ridge below tympanum	continuous	continuous	continuous	isolated glands	continuous
Tympanic membrane	distinct	hidden	hardly visible	distinct	distinct
Nostril position	closer to snout tip	midway along snout	closer to eye	closer to snout tip	closer to snout tip
Canthus rostralis	rounded	rounded	sharply angled	rounded	rounded
Tympanum	round	absent	ovoid	round	present
Vomerine teeth	absent or weak	present	present	absent or weak	absent or weak
Male gular colour	solid, dark	immaculate	solid, dark	densely mottled	solid, dark
Palmar tubercles	distinct	absent	distinct	slightly raised	absent
Ventral surface	smooth	smooth	granular near vent	smooth	smooth
Limb barring	absent	present	present	present	present
Asperities around vent	absent	absent	absent	absent	present

Body proportions are similar to those of other species: SUL/HW mean 2.3, range 1.9–2.6; HW/HL mean 1.4, range 1.1–1.8; SUL/HND mean 4.2, range 3.8–4.6; DAE/IOS mean 2.2, range 1.6–2.9; SL/END mean 1.9, range 1.5–2.4; ED/TYM mean 2.7, range 1.9–4.6; TYM/ETD mean 2.7, range 0.5–1.9; IMT/TYM mean 1.6, range 1.1–3.0; SUL/CRU mean 2.4, range 2.2–2.6. Body proportions alone may not be diagnostic for identification.

Taxonomy

Tomopterna banhinensis **sp. nov.**
Mozambique Sand Frog
urn:lsid:zoobank.org:act:71490F4F-381C-4765-AB62-82695545CFE1
Figs. 3, 4.

Holotype. A male, TM85588, field number BNP016 (Fig. 3), collected 26 November 2007 by Errol W. Pietersen in Banhine National Park, Mozambique, on the edge of a dry wetland (22.6328° S, 33.2673° E).

FIGURE 3. Holotype of *Tomopterna banhinensis* **sp. nov.** (TM85588) from Banhine National Park, Mozambique. Photo D.W. Pietersen.

Paratypes (eight specimens). A female, TM85589, from Fish Eagle Research Camp, Banhine National Park, Mozambique, collected 26 November 2007. Three males and four females, TM85562–TM85568, from the same locality, collected 7 April 2007.

Additional material (two specimens in poor condition). Adult males, PEM A15572 and PEM A15573, collected 20 December 1991 by Alan Channing, from outside Beira, Mozambique (19.7793° S, 34.8299° E).

Diagnosis. The new species is similar to all other species of sand frogs in morphology and burrowing behaviour. It has an advertisement call of a rapidly-repeated series of high-pitched notes, the most common type of vocalisation in sand frogs. We assign it to the genus *Tomopterna* based on the presence of teeth on the maxilla, the inner metatarsal tubercle strongly flanged, the outer metatarsals bound into the sole, and the presence of vomerine teeth, all characters that distinguish the genus *Tomopterna* (Poynton 1964) and the similarity of 16S rRNA sequences.

The new species has single subarticular tubercles under the toes, distinguishing it from those with divided tubercles: *T. ahli, T. branchi, T. delalandii, T. elegans, T. gallmanni, T. kachowskii, T. krugerensis, T. luganga, T. marmorata, T. monticola, T. tandyi, T. tuberculosa* and *T. wambensis*. It has more than three phalanges of the fourth toe free of web, distinguishing it from those with more webbing: *T. cryptotis, T. elegans, T. gallmanni, T. luganga, T. marmorata, T. milletihorsini, T. monticola, T. tandyi* and *T. wambensis*. There is a continuous row of glands below the tympanum, distinguishing it from *T. branchi, T. delalandii* and *T. marmorata* which have a row of isolated glands, and *T. luganga, T. milletihorsini, T. monticola*, and *T. wambensis* which have interrupted rows of glands.

This feature is variable in *T. elegans, T. gallmanni, T. kachowskii, T. pulchra* and *T. tuberculosa*. The tympanum is distinct, distinguishing it from those with a hidden tympanum: *T. adiastola, T. cryptotis, T. milletihorsoni* and *T. tandyi.* The nostrils are closer to the snout tip than to the eyes, distinguishing it from *T. adiastola, T. branchi, T. cryptotis, T. gallmanni, T. marmorata, T. pulchra* and *T. tuberculosa*. The tympanum is round, distinguishing it from those species where the tympanum is not visible or is vertically elliptical: *T. adiastola, T. delalandii, T. gallmanni, T. krugerensis, T. luganga, T. milletihorsini, T. monticola,* and *T. tandyi.* The tympanum is variable in *T. cryptotis, T. pulchra* and *T. tuberculosa*. The ventral surface is smooth, distinguishing it from the granular ventral surfaces of *T. kachowskii, T. krugerensis* and *T. tandyi*. The back is smooth or has small warts, distinguishing it from *T. gallmanni, T. pulchra* and *T. tuberculosa,* which have prominent dorsal tubercles.

The advertisement call consists of a rapidly-repeated series of high-pitched notes, distinguishing it from the knocking call of *T. krugerensis* and *T. gallmanni* and the tapping call of *T. tuberculosa* and *T. pulchra*. It can be distinguished from species with a higher emphasised frequency: *T. adiastola, T. ahli, T. branchi, T. cryptotis, T. marmorata, T. natalensis,* and *T. wambensis*. *Tomopterna luganga* has a much lower emphasised frequency. The emphasised frequency and the note rate of *T. banhinensis* **sp. nov.** may overlap with that of *T. delalandii* and *T. tandyi*, but these species do not occur with the Mozambique taxon (Table 3).

Description of holotype. A male (Fig. 3) SVL 43.3 mm; the body is robust; head short (HL/SVL 0.38, HW/SVL 0.42), not wider than trunk, not longer than wide (HL/HW 0.92); snout short (SL/HL 0.34), rounded in dorsal view, truncated in profile, slightly projecting beyond lower jaw, narrow (SL/IND 1.4); canthus rostralis rounded; loreal region slightly concave; nostrils situated on slight projections, about in the middle of the snout (END/SL 0.46); eyes directed anterolaterally, slightly protruding, relatively small (ED/HL 0.34); eye diameter subequal to snout length (ED/SL 1.02); interorbital distance is less than upper eyelid length (IOS/EL 0.57), and nearly equal to internarial distance (IOS/IND 0.98); internarial distance greater than half eye diameter (IOS/ED 0.68); vomerine teeth inconspicuous; tympanum visible, smaller than eye diameter (TYM/ED 0.39); a continuous row of glands below tympanum; upper jaw without dentition; choanae small, round, vomerine teeth represented by a roughened protrusion; tongue notched posteriorly, 6.3 mm at widest part; median lingual processes present; vocal sac single, darkly pigmented anteriorly; dorsal surfaces of head, trunk and limbs smooth with rounded or elongated warts; ventral surface of limbs, gular and abdomen smooth. Arms slender; hand moderately large (HND/SVL 0.22); tips of fingers not enlarged into discs; relative length of fingers: IV < II < I <III; subarticular tubercles single and distinct, basal tubercles double with one on fingers I, II and IV, and two on finger III; fingers without webbing; thenar tubercle distinct; metacarpals with supernumerary tubercles; pale nuptial pads present on upper surface of fingers I and II.

Hind limbs stout, tarsal tubercle present as a small raised area; crus short (CRU/SVL 0.38); heels not reaching each other when knees are flexed and thighs are held at right angle to body; foot longer than crus (CRU/FOT 0.89); relative length of toes: I<II<V<III<IV; toes without expanded discs; subarticular tubercles single: one on toe I and II, two on toe III, three on toe IV and two on toe V; pedal webbing formula **I**1–2 **II**1–2.5 **III** 1–3 **IV**3.9–1**V**; thin margin of webbing extending to tips; inner metatarsal tubercle prominent and shovel-shaped, continuing as a tarsal ridge, larger than eye diameter (IMT/ED 0.58); outer metatarsal tubercle present as a small white bump.

Colour in life. The dorsal pattern of the holotype consists of olive-green patches with brown warts with thin black margins on a pale grey background (Fig. 3). A thin pale vertebral stripe is present. There is no pale transverse bar between the eyes, but a darker marking which tapers to the rear. The iris is pale golden with dark veins. Small tubercles are scattered over the back and sides. The flanks have irregular dark and white marbling, with a weakly defined pale band extending diagonally from behind the eye to the lower posterior flanks. The upper surfaces of the limbs are grey, with green or darker brown blotches, but indistinct transverse bars. The venter is white with a black throat.

Colour in preservative. The pattern is clearly visible as a darker brown on a paler brown background, after 15 years in 70% ethanol.

Paratype variation. The measurements of the holotype and paratypes are shown in Table 4. The body proportions of the holotype and paratypes are given in Table 5. Body proportions of males and females overlap in our sample size.

The dorsal pattern is variable, but always with darker blotches on a pale background. One of the specimens from Beira (PEM A15572) shows brown patches on a pale grey background, with brown warts (Fig. 4). It has a distinct pale bar between the eyes, and dark cross bars on the limbs. In one specimen the background colour has a greenish tinge. In life this specimen was light metallic green, later developing pale blue sides as the green dorsal sheen faded. The glandular fold running from below the eye to the angle of the jaw may be white to partially brown. Two of the paratypes had very faded blotches with white warts.

FIGURE 4. *Tomopterna banhinensis* **sp. nov.** (PEM A15572) from Beira, Mozambique. Photo A. Channing.

Distribution. This species is presently only known from Banhine National Park, northern Gaza Province and Beira, Sofala Province, Mozambique (Fig. 5). Photographs of sand frogs from Gorongoza National Park show frogs that look very similar to the new species, but await genetic confirmation.

Tomopterna banhinensis **sp. nov.** is currently only known from two widely separated localities. It is likely to be more widespread than these current records suggest, occurring widely across the Mozambique plain, possibly including extreme south-eastern Zimbabwe (specifically Gonarezhou National Park), to which the sandveld and drainage systems of Banhine National Park are linked.

Habitat. This new species' ecology is unknown, but is probably similar to that of congeners. The habitat is low-lying sandveld on the edge of an extensive wetland. It is savanna woodland, with miombo vegetation. This is a widespread habitat, suggesting that the new species should also be widespread. The habitat at the type locality consists of open sandveld on deep sandy soils overlying calcrete at a depth of ca. 7 m (Stalmans & Wishart, 2005), with annual rainfall averaging about 410 mm (Stalmans, 2003) (Fig. 6). The specimens collected near Beira were also found on deep sandy soils in open savanna, near the northern margin of the Mozambique plain.

Etymology. The new species is named for the Banhine National Park. The specific epithet is an adjective.

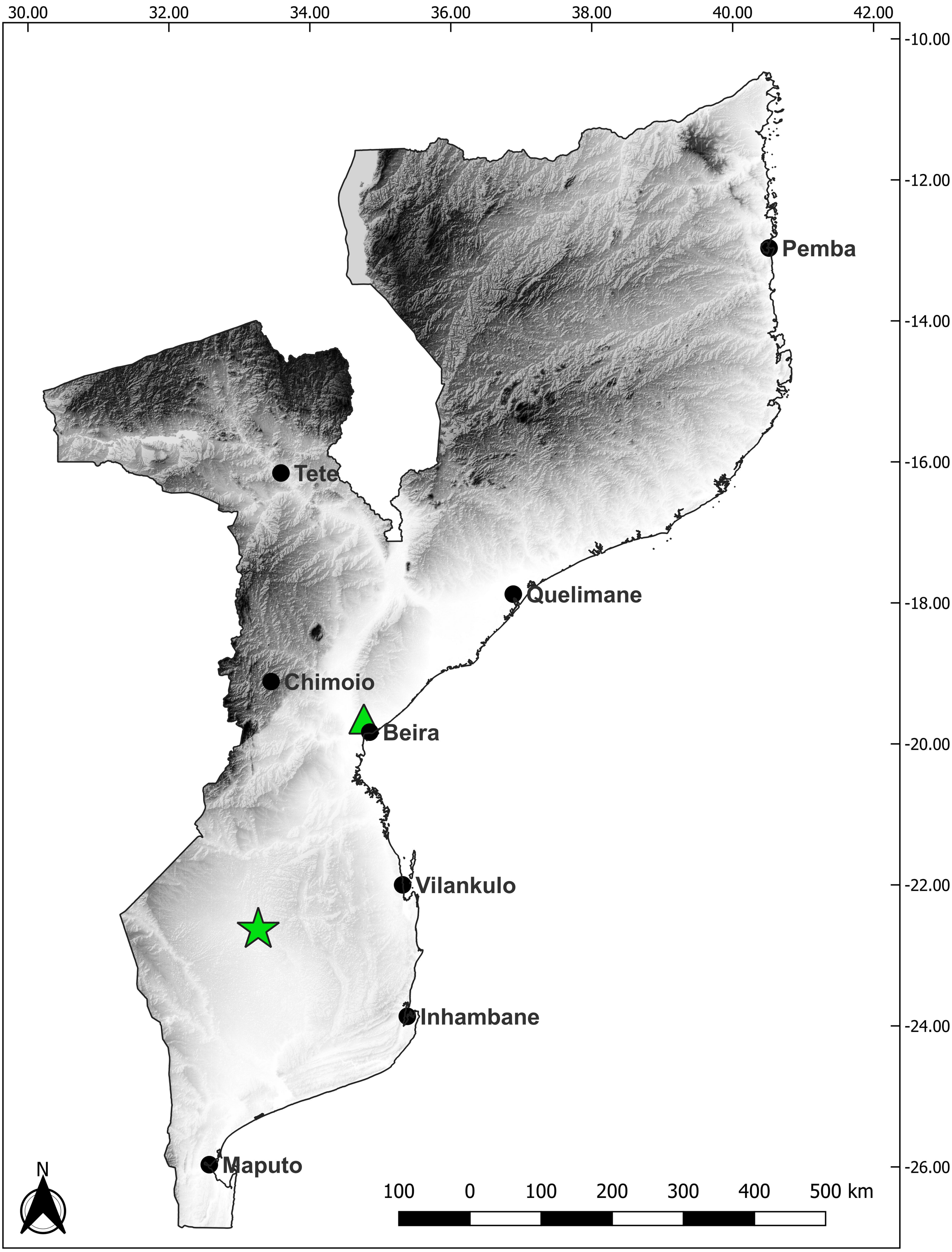

FIGURE 5. Elevation map of Mozambique, showing the localities where *Tomopterna banhinensis* **sp. nov.** specimens have been collected. Lighter colours indicate lower elevations, while darker colours indicate higher elevations. Star = type locality, triangle = additional locality.

FIGURE 6. Habitat at the type locality of *Tomopterna banhinensis* **sp. nov.** The pan was dry at the time the photo was taken. Photo D.W. Pietersen.

Discussion

Other species known to occur in the area include *Tomopterna adiastola* Channing & Du Preez; *T. krugerensis* Passmore & Carruthers; *T. marmorata* (Peters), and *T. natalensis* (Smith) (Pietersen *et al*. 2013; Channing & Rödel 2019; Channing & Du Preez 2020);

Xenopus muelleri (Peters); *Sclerophrys pusilla* (Mertens); *S. garmani* (Meek); *S. gutturalis* (Power); *Schismaderma carens* (Smith); *Hemisus marmoratus* (Peters); *Breviceps adspersus* Peters; *B. mossambicus* Peters; *Phlyctimantis maculatus* Duméril; *Kassina senegalensis* (Duméril & Bibron); *Afrixalus fornasini* (Bianconi); *A. crotalus* Pickersgill; *A. aureus* Pickersgill; *H. marmoratus* Rapp; *H. pusillus* (Cope); *H. tuberilinguis* Smith; *H. argus* Peters; *Chiromantis xerampelina* Peters; *Leptopelis mossambicus* Poynton; *L. broadleyi* Poynton; *Arthroleptis stenodactylus* Pfeffer; *Phrynobatrachus natalensis* (Smith); *P. acridoides* (Cope); *P. mababiensis* FitzSimons; *Hildebrandtia ornata* (Peters); *Ptychadena oxyrhynchus* (Smith); *P. nilotica* (Seetzen); *P. mossambica* (Peters); *Pyxicephalus angusticeps* Parry; and *P. edulis* Peters. These are all common species occurring on the southern Mozambique coastal plain.

The discovery of many cryptic sand frog species using DNA sequencing, suggests that there are more frog species waiting to be found. Sand frogs often occur sympatrically, but the high diversity of *Tomopterna*, up to five species, on the coastal plain is remarkable.

Since the summary of northern Mozambican amphibians by Poynton (1966), many new discoveries have been made for northern Mozambique (Branch 2004; Portik *et al.* 2013; Farooq *et al.* 2015a, b; Jones *et al.* 2017; Weinell *et al.* 2017; Conradie *et al.* 2016, 2018a,b; Farooq *et al.* 2022; Bittencourt-Silva *et al.* 2020; Ohler & Frétey 2014), while the amphibians of southern Mozambique remain poorly studied (Poynton & Broadley 1991), with only a few recent studies (Jacobsen *et al.* 2010; Pietersen *et al.* 2013, 2014). The amphibian fauna of Mozambique reflects the distribution of dry forest amphibians in Tanzania (Ohler & Frétey 2014). Despite the recent advances, the amphibians of Mozambique remain under-studied.

Comprehensive sampling and sequencing are required across the continent to confirm or correct our present understanding of species taxonomic and geographic boundaries. The addition of nuclear genes to the *Tomopterna* phylogeny should improve the support and confirm the relationships.

Acknowledgements

Adriaan Jordaan is thanked for his assistance with gaining access to the specimens in the Ditsong National Museum of Natural History. The Mozambican authorities are thanked for permit 0004/2007. Werner Conradie contributed significantly to the overall paper.

References

Bittencourt-Silva, G.B. (2019) A herpetological survey of western Zambia. *Amphibian & Reptile Conservation*, 13 (e181), 1–28.

Bittencourt-Silva, G.B., Bayliss, J. & Conradie, W. (2020) First herpetological surveys of Mount Lico and Mount Socone, Mozambique. *Amphibian & Reptile Conservation*, 14 (2) [General Section], e247, 198–217.

Blackburn, D.C., Nielsen, S.V., Barej, M.F., Doumbia, J., Hirschfeld, M., Kouamé, N.G., Lawson, D., Loader, S., Ofori-Boateng, C., Stanley, E.L. & Rödel, M.-O. (2020) Evolution of the African slippery frogs (Anura: *Conraua*), including the world's largest living frog. *Zoologica Scripta*, 49, 684–696.
https://doi.org/10.1111/zsc.12447

Bogart, J.P., Dawood, A., Becker, F.S. & Channing, A. (2022) Chromosomes in the African frog genus *Tomopterna* (Pyxicephalidae) and probing the origin of tetraploid *Tomopterna tandyi*. *Genome*, 65, 585–604.
https://doi.org/10.1139/gen-2022-0053

Bossuyt, F., Brown, R.M., Hillis, D.M., Cannatella, D.C. & Milinkovitch, M.C. (2006) Phylogeny and Biogeography of a cosmopolitan frog radiation: Late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. *Systematic Biology*, 55, 579–594.
https://doi.org/10.1080/10635150600812551

Braae, A. (2007) *Genetic structuring in the clicking stream frog (Strongylopus grayii); evidence of a cryptic species?* B.Sc Honours Thesis, University of Cape Town, Cape Town. [unknown pagination]

Branch, W.R. (2004) *Herpetological Survey of The Niassa Game Reserve: Report prepared for Sociedade para a Gestão e Desenvolvimento da Reserva do Niassa*. Bayworld, Port Elizabeth. [unknown pagination]

Buruwate, T.C. & Lloyd-Jones, D.J. (2024) Amphibian and Reptile Diversity of Niassa Special Reserve, Northern Mozambique. *Journal of East African Natural History*, 113 (1), 1–18.
https://doi.org/10.2982/028.113.0101

Ceríaco, L.M.P., de Sá, S.d.A.C., Bandeira, S., Valério, H., Stanley, E.L., Kuhn, A.L., Marques, M.P., Vindum, J.V., Blackburn, D.C. & Bauer, A.M. (2016) Herpetological Survey of Iona National Park and Namibe Regional Natural Park, with a Synoptic List of the Amphibians and Reptiles of Namibe Province, Southwestern Angola. *Proceedings of the California Academy of Sciences*, Series 4, 63, 15–61.

Channing, A. & Becker, F. (2019) Correction to the type locality of *Tomopterna ahli* (Deckert, 1938) (Anura: Pyxicephalidae), with the designation of a neotype. *Zootaxa*, 4688 (4), 549–560.
https://doi.org/10.11646/zootaxa.4688.4.6

Channing, A., Dehling, J.M., Lötters, S. & Ernst, R. (2016) Species boundaries and taxonomy of the African river frogs (Amphibia: Pyxicephalidae: *Amietia*). *Zootaxa*, 4155 (1), 1–76.
https://doi.org/10.11646/zootaxa.4155.1.1

Channing, A. & Du Preez, L.H. (2020) Taxonomic status of the cryptic sand frog, *Tomopterna cryptotis* (Anura, Pyxicephalidae). *Alytes*, 37, 1–21.

Channing, A. Moyer, D.C. & Dawood, A. (2004) A new sand frog from Tanzania (Anura: Ranidae: *Tomopterna*). *African Journal of Herpetology*, 53, 21–28.
https://doi.org/10.1080/21564574.2004.9635495

Channing, A., Schmitz, A., Zancolli, G., Conradie, W. & Rödel, M.-O. (2022) Phylogeny and taxonomy of the African frog genus *Strongylopus* (Anura: Pyxicephaliidae). *Revue suisse de Zoologie*, 129, 243–281.
https://doi.org/10.35929/RSZ.0074

Channing, A. & Rödel, M.-O. (2019) *Field Guide to the Frogs and other Amphibians of Africa*. Struik Nature, Cape Town, 408 pp.

Conradie, W., Bittencourt-Silva, G.B., Engelbrecht, H.M., Loader, S.P., Menegon, M., Nanvonamuquitxo, C., Scott, M. & Tolley K.A. (2016) Exploration into the hidden world of Mozambique's sky island forests: new discoveries of reptiles and amphibians. *Zoosystematics and Evolution*, 92 (2), 163–180.
https://doi.org/10.3897/zse.92.9948

Conradie, W., Bittencourt-Silva, G.B., Farooq, H.M., Loader, S.P., Menegon, M. & Tolley, K.A. (2018a) New species of Mongrel Frogs (Pyxicephalidae: *Nothophryne*) for northern Mozambique inselbergs. *African Journal of Herpetology*, 67, 61–85.
https://doi.org/10.1080/21564574.2017.1376714

Conradie, W., Verburgt, L., Portik, D.M., Ohler, A., Bwong, B.A. & Lawson. L.P. (2018b) A new reed frog (Hyperoliidae: *Hyperolius*) from coastal northeastern Mozambique. *Zootaxa*, 4379 (2), 177–198.
https://doi.org/10.11646/zootaxa.4379.2.2

Dawood, A. & Channing, A. (2002) Description of a new cryptic species of African sand frog, *Tomopterna damarensis* (Anura: Ranidae), from Namibia. *African Journal of Herpetology*, 51, 129–134.
https://doi.org/10.1080/21564574.2002.9635468

Dawood, A., Channing, A. & Bogart, J.P. (2002) A molecular phylogeny of the frog genus *Tomopterna* in southern Africa: examining species boundaries with mitochondrial 12S rRNA sequence data. *Molecular Phylogenetics and Evolution*, 22, 407–413.
https://doi.org/10.1006/mpev.2001.1060

Dawood, A. & Uqubay, S.M. (2004) A molecular phylogeny of the sand frog genus *Tomopterna* (Amphibia: Anura: Ranidae) based on mitochondrial 12S and 16S rRNA sequences. *African Zoology*, 39, 145–151.

Dawood, A. & Stam, E.M. (2006) The taxonomic status of the monotypic frog genus *Anhydrophryne* Hewitt from South Africa: a molecular perspective. *South African Journal of Science*, 102 (5), 249–253.

De Sá, R.O., Streicher, J.W., Sekonyela, R., Forlani, M.C., Loader, S.P., Greenbaum, E., Richards, S. & Haddad, C.F.B. (2012) Molecular phylogeny of microhylid frogs (Anura: Microhylidae) with emphasis on relationships among New World genera. *BMC Evolutionary Biology*, 12, 241.
https://doi.org/10.1186/1471-2148-12-241

Du Preez, L.H., Netherlands, E.C., Rödel, M.-O. & Channing, A. (2024) A new bullfrog from southern Africa (Pyxicephalidae, *Pyxicephalus* Tschudi, 1838). *African Journal of Herpetology*, 73, 61–89.
https://doi.org/10.1080/21564574.2023.2296654

Farooq, H.O. & Conradie, W. (2015a) A second record of *Scolecomorphus kirkii* Boulenger, 1883 (Gymnophiona: Scolecomorphidae) for Mozambique. *Herpetology Notes*, 8, 59–62.

Farooq, H., Liedtke, H.C., Bittencourt-Silva, G., Conradie, W & Loader, S.P. (2015b) The distribution of *Mertensophryne anotis* with a new record in northern Mozambique. *Herpetology Notes*, 8, 305–307.

Farooq, H., Nanvonamuquitxo, C., Nassongole, B., Conradie, W., Bills, R., Soares, A. & Antonelli, A. (2022) Shedding light on a biodiversity dark spot: survey of amphibians and reptiles of Pemba Region in northern Mozambique. *Herpetological Conservation and Biology*, 17, 423–432.

Frost, D.R. (2024) *Amphibian Species of the World: an Online Reference. Version 6.2*. American Museum of Natural History, New York, New York. Electronic Database. Available from: https://amphibiansoftheworld.amnh.org/index.php (accessed 18 December 2024)
https://doi.org/10.5531/db.vz.0001

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., De Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.O., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P. Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
https://doi.org/10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2

Guindon, S., Dufayard, J.-F., Lefort, V., Anismova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, 59, 307–321.
https://doi.org/10.1093/sysbio/syq010

Haas, A., Mitgutsch, C., Hertwig, S., Dawood, A. & Channing, A. (2006) The tadpole of *Tomopterna luganga* Channing, Moyer & Dawood, 2004 (Anura: Ranidae). *Salamandra*, 42, 1–12.

Heinicke, M.P., Ceríaco, L.M.P., Moore, I.M., Bauer, A.M. & Blackburn, D.C. (2017) *Tomopterna damarensis* (Anura: Pyxicephalidae) is broadly distributed in Namibia and Angola. *Salamandra*, 53, 461–465.

Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2017) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518–522.
https://doi.org/10.1093/molbev/msx281

Jacobsen, N.H.G., Pietersen, E.W. & Pietersen, D.W. (2010) A preliminary herpetological survey of the Vilanculos Coastal Wildlife Sanctuary on the San Sebastian Peninsula, Vilankulo, Mozambique. *Herpetology Notes*, 3, 181–193.

Jones, S.E., Clause, J.K., Geeraert, L., Jamie, G.A., Sumbane, E., van Berkel, T. & Jocque, W. (2017) *The Njesi Plateau expedition: a biological assessment of Mt Chitagal, Mt Sanga and the Njesi Plateau in Niassa Province, Mozambique: BES Report 6.3*. Biodiversity Inventory for Conservation, Glabbeek. [unknwon pagination]

K. Lisa Yang Center for Conservation Bioacoustics (2022) *Raven Pro: Interactive Sound Analysis Software. Version 1.6.5*. The

Cornell Lab of Ornithology, Ithaca, New York. Available from: https://ravensoundsoftware.com/ (accessed 23 December 2024)
Kosuch, J., Vences, M., Dubois, A., Ohler, A. & Böhme, W. (2001) Out of Asia: Mitochondrial DNA evidence for an oriental origin of tiger frogs, genus *Hoplobatrachus*. *Molecular Phylogenetics and Evolution*, 21, 398–407.
https://doi.org/10.1006/mpev.2001.1034
Lehtinen, R.M., Richards, C.M. & Nussbaum, R.A. (2004) Origin of a complex reproductive trait: phytotelm breeding in mantelline frogs. *In*: Lehtinen, R.M. (Ed.), *Ecology and Evolution of Phytotelm-Breeding Anurans*. Museum of Zoology, University of Michigan, Ann Arbor, Michigan, pp. 45–54.
Lobón-Rovira, J., Vaz Pinto, P.S., Becker, F., Tolley, K.A., Measey, J., Bennet, B., Boon, B., de Sá, S. & Conradie, W. (2022) An updated herpetofaunal species inventory of Iona National Park in southwestern Angola. *Check List*, 18 (2), 289–321.
https://doi.org/10.15560/18.2.289
Minh, B.Q., Nguyen, M.A.T. & Von Haeseler, A. (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30, 1188–1195.
https://doi.org/10.1093/molbev/mst024
Nguyen, L.-T., Schmidt, H.A., Von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.
https://doi.org/10.1093/molbev/msu300
Ohler, A. & Frétey, T. (2014) Going back to Rovuma: The frog fauna of a coastal dry forest, and a checklist of the amphibians of Mozambique. *Journal of East African Natural History*, 103, 73–124.
https://doi.org/10.2982/028.103.0203
Pietersen, D.W., Pietersen, E.W. & Haacke, W.D. (2013) First herpetological appraisal of the Parque Nacional de Banhine, Gaza Province, southern Mozambique. *Annals of the Ditsong National Museum of Natural History*, 3, 153–163.
Pietersen, D.W. (2014) New distribution records of herpetofauna in Mozambique south of the Zambezi River, including additional records from Parque Nacional de Banhine. *Annals of the Ditsong National Museum of Natural History*, 4, 174–180.
Portik, D.M., Mulungu, E.A., Sequeira, D. & McEntee, J.P. (2013) Herpetological surveys of the Serra Jeci and Namuli massifs, Mozambique, and an annotated checklist of the southern Afromontane archipelago. *Herpetological Review*, 44, 394–406.
Poynton, J.C. (1964) The Amphibia of Southern Africa: a faunal study. *Annals of the Natal Museum*, 17, 1–334.
Poynton, J.C. (1966) Amphibia of northern Mozambique. *Memórias do Instituto de Investigação Cientifica de Moçambique. Série A Ciências Biológicas*, 8, 13–34.
Poynton, J.C. & Broadley, D.G. (1991/0. Amphibia Zambesiaca 5. Zoogeography. *Annals of the Natal Museum*, 32, 221−277.
Rambaut, A. (2018) FigTree - Tree Figure Drawing Tool. Version 1.4.4. Available from: http://tree.bio.ed.ac.uk/ (accessed 12 January 2019)
Reeder, J.E. (2019) *Amphibians of Northern KwaZulu-Natal: A Phylogenetic Study*. M.Sc. Dissertation, North-West University, Potchefstroom. [unknown pagination]
Rödel, M.-O. & Hallermann, J. (2006) Rediscovery and identity of *Phrynobatrachus monticola* Fischer, 1884. *African Journal of Herpetology*, 55, 69–74.
https://doi.org/10.1080/21564574.2006.9635540
Stalmans, M. (2003) *Plant communities and landscapes of the Parque Nacional de Banhine Mozambique*. African Wildlife Foundation, Johannesburg. [unknown pagination]
Stalmans, M. & Wishart, M. (2005) Plant communities, wetlands and landscapes of the Parque Nacional de Banhine, Moçambique. *Koedoe*, 48 (2), 43–58.
https://doi.org/10.4102/koedoe.v48i2.99
Stecher, G., Tamura, K. & Kumar, S. (2020) Molecular Evolutionary Genetics Analysis (MEGA) for macOS. *Molecular Biology & Evolution*, 37, 1237–1239.
https://doi.org/10.1093/molbev/msz312
Tamura, K., Stecher, G. & Kumar, S. (2021) MEGA 11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution*, 38, 3022–3027.
https://doi.org/10.1093/molbev/msab120
Tolley, K.A., Telford, N.S., Makhubo, B.G., Power, R.J. & Alexander, G.J. (2022) Filling the gap: Noteworthy herpetological discoveries in North West Province, South Africa. *Zoosystematics and Evolution*, 99, 101–116.
https://doi.org/10.3897/zse.99.90181
Turner, A.A., De Villiers, A.L., Dawood, A. & Channing, A. (2004) A new species of *Arthroleptella* Hewitt, 1926 (Anura: Ranidae) from the Groot Winterhoek Mountains of the Western Cape Province, South Africa. *African Journal of Herpetology*, 53, 1–12.
https://doi.org/10.1080/21564574.2004.9635493
Trifinopoulos, J., Nguyen, L.-T., Von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W1, W232–W235.
https://doi.org/10.1093/nar/gkw256
Van der Meijden, A., Vences, M., Hoegg, S. & Meyer, A. (2005) A previously unrecognized radiation of ranid frogs in Southern Africa revealed by nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 37, 674–685.
https://doi.org/10.1016/j.ympev.2005.05.001

Van der Meijden, A. Crottini, A., Tarrant, J., Turner, A. & Vences, M. (2011) Multi-locus phylogeny and evolution of reproductive modes in the Pyxicephalidae, an African endemic clade of frogs. *African Journal of Herpetology*, 60, 1–12. https://doi.org/10.1080/21564574.2010.523904

Van Dijk, D.E. (1966) Systematic and field keys to the families, genera and described species of southern Africam anural tadpoles. *Annals of the Natal Museum*, 18, 231–286.

Vences, M., Glaw, F., Kosuch, J., Das, I. & Veith, M. (2000) Polyphyly of *Tomopterna* (Amphibia: Ranidae) based on sequences of the mitochondrial 16S and 12S rRNA genes, and ecological biogeography of Malagasy relict amphibian groups. *In*: Lourenco, W.R. & Goodman, S.M. (Eds.), *Diversity and endemism in Madagascar*. Memoires de la Société de Biogéographie, Paris, pp. 229–242.

Wasonga, D.V. & Channing, A. (2013) Identification of sand frogs (Anura: Pyxicephalidae: *Tomopterna*) from Kenya with the description of two new species. *Zootaxa*, 3734 (2), 221–240. https://doi.org/10.11646/zootaxa.3734.2.7

Weinell, J.L., Portik, D.M. & Bauer, A.M. (2017) Noteworthy records of amphibians and reptiles from Mozambique. *African Herp News*, 65, 3–10.

Willems, F. & Channing, A. (2023) The status of *Tomopterna pulchra* Boulenger, 1896 (Anura: Pyxicephalidae). *Zootaxa*, 5374 (3), 361–389. https://doi.org/10.11646/zootaxa.5374.3.3

Wilson, L. & Channing, A. (2019) A new sand frog from Namaqualand, South Africa (Pyxicephalidae: *Tomopterna*). *Zootaxa*, 4609 (2), 225–246. https://doi.org/10.11646/zootaxa.4609.2.2

Zhang, P., Liang, D., Mao, R.L., Hillis, D.M., Wake, D.B. & Cannatella, D.C. (2013) Efficient sequencing of anuran mtDNAs and a mitogenomic exploration of the phylogeny and evolution of frogs. *Molecular Biology and Evolution*, 30 (8), 1899–1915. https://doi.org/10.1093/molbev/mst091

Zimkus, B.M. & Larson, J.G. (2011) Examination of the molecular relationships of sand frogs (Anura: Pyxicephalidae: *Tomopterna*) and resurrection of two species from the Horn of Africa. *Zootaxa*, 2933 (1), 27–45. https://doi.org/10.11646/zootaxa.2933.1.2

Supplementary Table S1. List of *Tomopterna* sequences used in the phylogenetic analyses, with species names, GenBank accession numbers, locality details and original source of published sequences. NR—Nature Reserve, NP—National Park, NA—not available.

Species	GenBank	Locality	Country	Source
T. adiastola	AF215506	Bredell	South Africa	Vences *et al*. 2000
T. adiastola	AY255090	Bubye	Zimbabwe	Dawood & Uqubay 2004
T. adiastola	AY255099	Bloemfontein	South Africa	Dawood & Uqubay 2004
T. adiastola	MK335431	Khorab	Namibia	Wilson & Channing 2019
T. adiastola	MN057690	Cleveland	South Africa	Channing & Du Preez 2020
T. adiastola	MN057692	Okavango	Botswana	Channing & Du Preez 2020
T. adiastola	OP508717	SA Lombard NR	South Africa	Tolley *et al*. 2022
T. adiastola	OP508718	Bloemhof Dam	South Africa	Tolley *et al*. 2022
T. ahli	AF215419	Khorixas	Namibia	Vences *et al.* 2000
T. ahli	AY255091	Khorixas	Namibia	Dawood & Uqubay 2004
T. ahli	DQ019610	Khorixas	Namibia	Van der Meijden *et al*. 2005
T. ahli	KU662310	Pediva Hot Springs	Angola	Ceríaco *et al*. 2016
T. ahli	KX869908	Epupa Falls	Namibia	Heinicke *et al*. 2017
T. ahli	KX869909	Farm Omandumba	Namibia	Heinicke *et al*. 2017
T. ahli	MK335418	Naukluft	Namibia	Wilson & Channing 2019
T. ahli	MK335419	Farm Oas	Namibia	Wilson & Channing 2019
T. ahli	MK335420	Weavers Rock	Namibia	Wilson & Channing 2019
T. ahli	MN104599	Windhoek	Namibia	Channing & Becker 2019
T. ahli	MN104600	Windhoek	Namibia	Channing & Becker 2019
T. ahli	MN104601	Windhoek	Namibia	Channing & Becker 2019
T. ahli	MN104602	Okonjima	Namibia	Channing & Becker 2019
T. ahli	MN104603	Iona NP	Angola	Channing & Becker 2019
T. ahli	MN104604	Iona NP	Angola	Channing & Becker 2019
T. ahli	ON006589	Iona NP	Angola	Lobon-Rovira *et al*. 2022
T. ahli	ON006590	Iona NP	Angola	Lobon-Rovira *et al*. 2022
T. ahli	ON693440	Naukluft	Namibia	Bogart *et al*. 2022
T. ahli	ON693446	Daan Viljoen NR	Namibia	Bogart *et al*. 2022
T. ahli	ON693447	Daan Viljoen NR	Namibia	Bogart *et al*. 2022
T. ahli	ON693448	Daan Viljoen NR	Namibia	Bogart *et al*. 2022
T. ahli	ON693451	Daan Viljoen NR	Namibia	Bogart *et al*. 2022
T. banhinensis **sp. nov.**	AY255092	Beira	Mozambique	Dawood & Uqubay 2004
T. banhinensis **sp. nov**.	AY255093	Beira	Mozambique	Dawood & Uqubay 2004
T. branchi	MG450789	Buffels River	South Africa	Wilson & Channing 2019
T. branchi	MG450790	Buffels River	South Africa	Wilson & Channing 2019
T. branchi	MG450791	Buffels River	South Africa	Wilson & Channing 2019
T. branchi	MG450791	Buffels River	South Africa	Wilson & Channing 2019
T. branchi	MG450792	Buffels River	South Africa	Wilson & Channing 2019
T. branchi	MK289551	Buffels River	South Africa	Wilson & Channing 2019
T. branchi	ON693452	Leliefontein	South Africa	Bogart *et al*. 2022
T. cryptotis	AY255095	Shankara	Namibia	Dawood & Uqubay 2004
T. cryptotis	MK335429	Ondjiva	Angola	Wilson & Channing 2019
T. cryptotis	MK335430	Mbambi	Namibia	Wilson & Channing 2019
T. cryptotis	MK464282	Sioma Ngwezi	Zambia	Bittencourt-Silva 2019

T. cryptotis	MK464283	Sioma Ngwezi	Zambia	Bittencourt-Silva 2019
T. cryptotis	MK464284	Sioma Ngwezi	Zambia	Bittencourt-Silva 2019
T. cryptotis	MK464285	Sioma Ngwezi	Zambia	Bittencourt-Silva 2019
T. cryptotis	MK464286	Sioma Ngwezi	Zambia	Bittencourt-Silva 2019
T. cryptotis	MN057687	Calais	Angola	Channing & Du Preez 2020
T. cryptotis	MN057688	Maun, Exit 5	Botswana	Channing & Du Preez 2020
T. cryptotis	MN057689	Thamalakane	Botswana	Channing & Du Preez 2020
T. cryptotis	MN057691	Moremi	Botswana	Channing & Du Preez 2020
T. cryptotis	ON693444	Farm Marne	Namibia	Bogart *et al*. 2022
T. delalandii	AY255085	Stellenbosch	South Africa	Dawood & Uqubay 2004
T. delalandii	AY255086	Stellenbosch	South Africa	Dawood & Uqubay 2004
T. delalandii	AY454372	Stellenbosch	South Africa	Lehtinen *et al*. 2004
T. delalandii	DQ283403	Stellenbosch	South Africa	Frost *et al*. 2006
T. delalandii	EF136565	Anysberg	South Africa	Braae 2007
T. delalandii	HQ014421	NA	South Africa	Van der Meijden *et al*. 2011
T. delalandii	MG450762	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450763	Gqeberha	South Africa	Wilson & Channing 2019
T. delalandii	MG450764	Gqeberha	South Africa	Wilson & Channing 2019
T. delalandii	MG450765	St Francis Bay	South Africa	Wilson & Channing 2019
T. delalandii	MG450766	St Francis Bay	South Africa	Wilson & Channing 2019
T. delalandii	MG450767	Gqeberha	South Africa	Wilson & Channing 2019
T. delalandii	MG450768	Seal Point	South Africa	Wilson & Channing 2019
T. delalandii	MG450769	Seal Point	South Africa	Wilson & Channing 2019
T. delalandii	MG450770	Seal Point	South Africa	Wilson & Channing 2019
T. delalandii	MG450771	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450772	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450773	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450774	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450775	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450776	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450777	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450778	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450779	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450780	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450781	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450782	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450783	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450784	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450785	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450786	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MG450787	Port Alfred	South Africa	Wilson & Channing 2019
T. delalandii	MK289561	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	MK289562	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	MK289563	Noordhoek	South Africa	Wilson & Channing 2019
T. delalandii	MK289564	Noordhoek	South Africa	Wilson & Channing 2019
T. delalandii	MK289565	Noordhoek	South Africa	Wilson & Channing 2019

T. delalandii	MK289552	Riet River	South Africa	Wilson & Channing 2019
T. delalandii	MK289553	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	MK289554	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	MK289555	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	MK289556	Rondevlei	South Africa	Wilson & Channing 2019
T. delalandii	MK289557	Bellville	South Africa	Wilson & Channing 2019
T. delalandii	MK289558	Bellville	South Africa	Wilson & Channing 2019
T. delalandii	MK289559	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	MK289560	Stellenbosch	South Africa	Wilson & Channing 2019
T. delalandii	ON693441	Wolverfontein	South Africa	Bogart *et al*. 2022
T. elegans	HQ700692	Buq	Somalia	Zimkus & Larson 2011
T. elegans	JX564898	Buq	Somalia	Zhang *et al*. 2013
T. gallmanni	JX088641	Mogwooni	Kenya	Wasonga & Channing 2013
T. gallmanni	JX088642	Lewa Conservancy	Kenya	Wasonga & Channing 2013
T. gallmanni	JX088643	Laikipia	Kenya	Wasonga & Channing 2013
T. gallmanni	JX088644	Baawa	Kenya	Wasonga & Channing 2013
T. gallmanni	JX088645	Baragoi	Kenya	Wasonga & Channing 2013
T. kachowskii	HQ700687	Addis Ababa	Ethiopia	Zimkus & Larson 2011
T. kachowskii	HQ700688	Addis Ababa	Ethiopia	Zimkus & Larson 2011
T. kachowskii	HQ700689	Addis Ababa	Ethiopia	Zimkus & Larson 2011
T. kachowskii	HQ700690	Borama	Ethiopia	Zimkus & Larson 2011
T. kachowskii	HQ700691	Borama	Ethiopia	Zimkus & Larson 2011
T. kachowskii	MG700264	Day village	Djibouti	Gotte *et al*. Unpublished
T. kachowskii	MG700265	Day village	Djibouti	Gotte *et al*. Unpublished
T. kachowskii	MG700266	Day village	Djibouti	Gotte *et al*. Unpublished
T. kachowskii	MG700267	Day village	Djibouti	Gotte *et al*. Unpublished
T. kachowskii	MG700268	Day village	Djibouti	Gotte *et al*. Unpublished
T. kachowskii	MN954763	Harenna	Ethiopia	Zinenko *et al*. Unpublished
T. krugerensis	AY255098	Tembe Elephant Park	South Africa	Dawood & Uqubay 2004
T. krugerensis	AY255094	Tembe Elephant Park	South Africa	Dawood & Uqubay 2004
T. krugerensis	MH115787	Selesele Pan	South Africa	Reeder 2019
T. krugerensis	MH115788	KwaZulu-Natal	South Africa	Reeder 2019
T. krugerensis	MH115789	Sodwana	South Africa	Reeder 2019
T. krugerensis	MH115790	Ndumu NR	South Africa	Reeder 2019
T. krugerensis	MH115791	Tembe Elephant Park	South Africa	Reeder 2019
T. krugerensis	MH115792	Ndumu NR	South Africa	Reeder 2019
T. krugerensis	MH115793	Ndumu NR	South Africa	Reeder 2019
T. krugerensis	ON693442	Farm Marne	Namibia	Bogart *et al*. 2022
T. krugerensis	OP508720	Molopo NR	South Africa	Tolley *et al*. 2022
T. luganga	AY547275	Kigwembimbe	Tanzania	Channing *et al*. 2004
T. luganga	AY547276	Dodoma	Tanzania	Bogart *et al*. 2022
T. luganga	AY751302	Iringa	Tanzania	Haas *et al*. 2006
T. luganga	DQ017056	Iringa	Tanzania	Haas *et al*. 2006
T. luganga	HQ700695	Iringa	Tanzania	Zimkus & Larson 2011
T. marmorata	AF371233	Polokwane	South Africa	Dawood *et al*. 2002
T. marmorata	AY255084	Zambesi Nkuku	Zambia	Dawood & Uqubay 2004

T. marmorata	MK464287	Livingstone	Zambia	Bittencourt-Silva 2019
T. milletihorsini	AY014383	Ayoun el-Atrouss	Mauritania	Kosuch *et al*. 2001
T. milletihorsini	AY255101	Ayoun el-Atrouss	Mauritania	Dawood & Uqubay 2004
T. natalensis	AF215508	Itala Park	South Africa	Vences 2000
T. natalensis	AF215509	Port St Johns	South Africa	Vences 2000
T. natalensis	AY205286	Mafefe Road	South Africa	Turner *et al*. 2004
T. natalensis	AY255088	Mafefe Road	South Africa	Dawood & Uqubay 2004
T. natalensis	AY255089	Andries Vosloo NR	South Africa	Dawood & Uqubay 2004
T. natalensis	AY547277	Kyalami	South Africa	Channing *et al*. 2004
T. natalensis	DQ347300	NA	Africa	Bossuyt *et al*. 2006
T. pulchra	KC179967	Tatanda	Tanzania	De Sá *et al*. 2012
T. pulchra	MK335427	Mutinondo	Zambia	Wilson & Channing 2019
T. pulchra	MK335428	Mutinondo	Zambia	Wilson & Channing 2019
T. pulchra	ON693453	Muso Hills	Zambia	Bogart *et al*. 2022
T. pulchra	ON693454	Muso Hills	Zambia	Bogart *et al*. 2022
T. tandyi	AF215507	Mt Meru	Tanzania	Vences *et al*. 2000
T. tandyi	AF371234	Grootfontein	Namibia	Dawood *et al*. 2002
T. tandyi	AF436071	Adelaide	South Africa	Dawood *et al*. 2002
T. tandyi	AF436072	Blouberg	South Africa	Dawood *et al*. 2002
T. tandyi	AF436073	Hardap	Namibia	Dawood *et al*. 2002
T. tandyi	AY838891	Blouberg	South Africa	Dawood & Stam 2006
T. tandyi	MK335421	Okonjima	Namibia	Wilson & Channing 2019
T. tandyi	MK335422	Komani	South Africa	Wilson & Channing 2019
T. tandyi	ON693443	Farm Marne	Namibia	Bogart *et al*. 2022
T. tandyi	ON693445	Witvlei	Namibia	Bogart *et al*. 2022
T. tandyi	ON693449	Koes	Namibia	Bogart *et al*. 2022
T. tandyi	ON693450	Waterberg	Namibia	Bogart *et al*. 2022
T. tandyi	OP508719	Tamasikwa	South Africa	Tolley *et al*. 2022
T. tuberculosa	AY255087	Ongongo	Namibia	Dawood & Uqubay 2004
T. tuberculosa	AY255100	Ongongo	Namibia	Dawood & Uqubay 2004
T. tuberculosa	MK036490	Malanje	Angola	Hayes *et al*. unpublished
T. tuberculosa	MK036492	Malanje	Angola	Hayes *et al*. unpublished
T. tuberculosa	MK036493	Malanje	Angola	Hayes *et al*. unpublished
T. tuberculosa	MK036494	Malanje	Angola	Hayes *et al*. unpublished
T. tuberculosa	MK036496	Malanje	Angola	Hayes *et al*. unpublished
T. tuberculosa	MK335423	Estação Zootécnica da Humpata	Angola	Wilson & Channing 2019
T. tuberculosa	MK335425	Estação Zootécnica da Humpata	Angola	Wilson & Channing 2019
T. tuberculosa	MK355424	Humpata	Angola	Wilson & Channing 2019
T. tuberculosa	MT669432	Malanje	Angola	Blackburn *et al*. 2020
T. tuberculosa	ON006591	Iona NP	Angola	Lobon-Rovira *et al*. 2022
T. tuberculosa	"WC- 3840"	10 km SW Cuito	Angola	Unpublished
T. tuberculosa	"WC- 5234"	Malova village	Angola	Unpublished
T. wambensis	AY547278	Arusha	Tanzania	Channing *et al*. 2004
T. wambensis	HQ700693	Iringa	Tanzania	Zimkus & Larson 2011
T. wambensis	HQ700694	Iringa	Tanzania	Zimkus & Larson 2011

T. wambensis	JX088646	Ikave Sec. school	Kenya	Wasonga & Channing 2013
T. wambensis	JX088647	Mpala Research	Kenya	Wasonga & Channing 2013
T. wambensis	JX088649	Mpala Research	Kenya	Wasonga & Channing 2013
T. wambensis	JX088650	Allia Bay	Kenya	Wasonga & Channing 2013
T. wambensis	JX088651	Sordor Pan	Kenya	Wasonga & Channing 2013
T. wambensis	JX088652	Kitobo Forest	Kenya	Wasonga & Channing 2013
T. wambensis	JX088653	Illeret	Kenya	Wasonga & Channing 2013
T. wambensis	JX088654	Kasa Well	Kenya	Wasonga & Channing 2013
T. wambensis	JX088655	Lugga Daudi	Kenya	Wasonga & Channing 2013
T. wambensis	JX088656	Bura Hasuma	Kenya	Wasonga & Channing 2013
T. wambensis	JX088684	Mpala Research	Kenya	Wasonga & Channing 2013
T. wambensis	MK335426	Usangu	Tanzania	Wilson & Channing 2019