



Re-evaluation of the status of *Bufo vertebralis grindleyi* and *Bufo jordani* (Anura: Bufonidae)

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Abstract. We use mitochondrial and nuclear gene sequences and morphology to re-evaluate the taxonomy of *Bufo vertebralis grindleyi* POYNTON, 1963, currently a junior synonym of *Poyntonophrynus fenoulheti* (HEWITT & METHUEN, 1912); and morphology and advertisement calls to re-evaluate the status of *Bufo jordani* PARKER, 1936, currently a junior synonym of *Poyntonophrynus hoeschi* (AHL, 1934). According to our results including comparisons to other congeners, we elevate both taxa to full species as *Poyntonophrynus grindleyi* (POYNTON, 1963) and *Poyntonophrynus jordani* (PARKER, 1936). Our new *P. grindleyi* record is the first record of the species for Mozambique.

Key words. Amphibia, integrative taxonomy, southern Africa.

Introduction

Small African toads, previously part of the genus *Bufo*, currently belong to four genera: *Capensibufo* GRANTON, 1980 with five species; *Vandijkophrynus* FROST, GRANT, FAIVOVICH, BAIN, HAAS, HADDAD, DE SÁ, CHANNING, WILKINSON, DONNELLAN, RAXWORTHY, CAMPBELL, BLOTTO, MOLER, DREWES, NUSSBAUM, LYNCH, GREEN & WHEELER, 2006 with six species; *Poyntonophrynus* FROST, GRANT, FAIVOVICH, BAIN, HAAS, HADDAD, DE SÁ, CHANNING, WILKINSON, DONNELLAN, RAXWORTHY, CAMPBELL, BLOTTO, MOLER, DREWES, NUSSBAUM, LYNCH, GREEN & WHEELER, 2006 with 10 species; and *Mertensophryne* TIHEN, 1960 with 15 species. Following the analysis by LIEDTKE et al. (2017), who demonstrated that *Bufo lughensis* LOVERIDGE, 1932 is not part of *Poyntonophrynus*, we recognise the species as *Mertensophryne lughensis* (LOVERIDGE, 1932).

Apart from the currently recognized dwarf toad species, various described taxa are currently listed as synonyms (FROST 2021). Within *Poyntonophrynus*, POYNTON & BROADLEY (1988) regard *Bufo jordani* PARKER, 1936, as a junior synonym of *Poyntonophrynus hoeschi* (AHL, 1934), and *Bufo vertebralis grindleyi* POYNTON, 1963 as a junior synonym of *Poyntonophrynus fenoulheti* (HEWITT & METHUEN, 1912).

In 1963 POYNTON described a new toad from the Zimbabwean side of the Chimanimani Mountains as *Bufo vertebralis grindleyi*. The type locality of NMZB 5369 was given as “floor of the Bundi Valley, Chimanimani Mountains at 1,560 m a.s.l.” (Fig. 1). In 1988 POYNTON & BROADLEY moved the taxon as a subspecies to *P. fenoulheti*. This decision was mainly based on morphological (colour pattern) variation of *P. grindleyi/fenoulheti* from various sites. As a result, in later works (e.g. DU PREEZ & CARRUTHERS 2017, CHANNING & RÖDEL 2019) the toads from the Chimani-

mani Mountains were included in the descriptions of the widespread *P. fenoulheti*.

In December 1934 Dr. KARL JORDAN collected a small toad from the farm Satansplatz, Namibia (approx. 24.8667° S, 17.55° E; JORDAN 1936). This toad was subsequently described by PARKER (1936) as *Bufo jordani* (BMNH 1947.2.20.94). It is currently referred to as a synonym of *P. hoeschi* (FROST et al. 2006). POYNTON & BROADLEY (1988) grouped these two names on the basis of their small size, absence of a tarsal fold, and having some doubled subarticular tubercles.

However, based on our own field observations, we had the impression that these four names may indeed refer to distinct species. The purpose of the present study was to use call, morphology and sequence data as an integrative approach to re-evaluate the status of the two synonymised taxa.

Material and methods

Sequences of the mitochondrial 16S rRNA and nuclear Rag-1 genes were obtained from tissues collected in the field using standard methods (CHANNING et al. 2016, LIEDTKE et al. 2016). Newly generated sequences have been deposited in GenBank (Table 1). Comparative sequences from other species of *Poyntonophrynus* were obtained from GenBank. Localities of specimens scored for morphology and/or sequences are shown in Figure 1 and summarized in Tables 1 and 2. The phylogeny was determined using the web version of IQ-TREE (NGUYEN et al. 2015, TRIFINOPOULOS et al. 2016). Support values for the phylogeny were calculated as SH-aLRT (%) and the ultrafast bootstrap (%) (MINH et al. 2013, HOANG et al. 2017). The sequences were aligned using Sequencher 5.4 (GeneCodes) and the uncorrected p-distances as percentages were determined using PAUP* (SWOFFORD 2002).

Comparative body proportions were collected from preserved museum vouchers with dial, vernier or electronic calipers (accuracy ± 0.5 mm). The following measurements were taken: SVL – snout–vent length (from the tip of the snout to the posterior margin of the vent); SUL – snout–urostyle length (from tip of the snout to the posterior margin of the urostyle); TYM – tympanum diameter (greatest horizontal width of the tympanum); EYE – eye diameter (horizontally from the anterior to posterior corner of the eye); LID – upper eyelid length (greatest length of the upper eyelid margins, measured parallel to the anterior–posterior axis); IO – inter-orbital distance (distance between eye bulges across the top of the head); ET – eye–tympanum distance (from the anterior margin of the tympanum to the posterior corner of the eye); EN – eye–nostril distance (from anterior corner of the eye to the posterior margin of the nostril); IN – internostril distance (shortest distance between the inner margins of the nostrils); HL – head length (from snout tip to behind lower jaw); SL – snout length (distance from the tip of the snout to the anterior corner of the eye); EE – distance between anterior corners of eyes; HW – head width at angle of jaw; ARM – forearm length to base of palmar tubercle, T₄ – phalanges free of web on 4th toe; HND – length of 3rd finger to include outer palmar tubercle; TIB – tibiofibula length (distance from the outer surface of the flexed knee to the heel/tibiotarsal inflection); LEG – thigh length (vent to knee); FOT – length of 4th toe to include inner metatarsal tubercle; IMT – maximum length of inner metatarsal tubercle; OMT – maximum diameter of outer metatarsal tubercle. Measurements are summarised in Table 2.

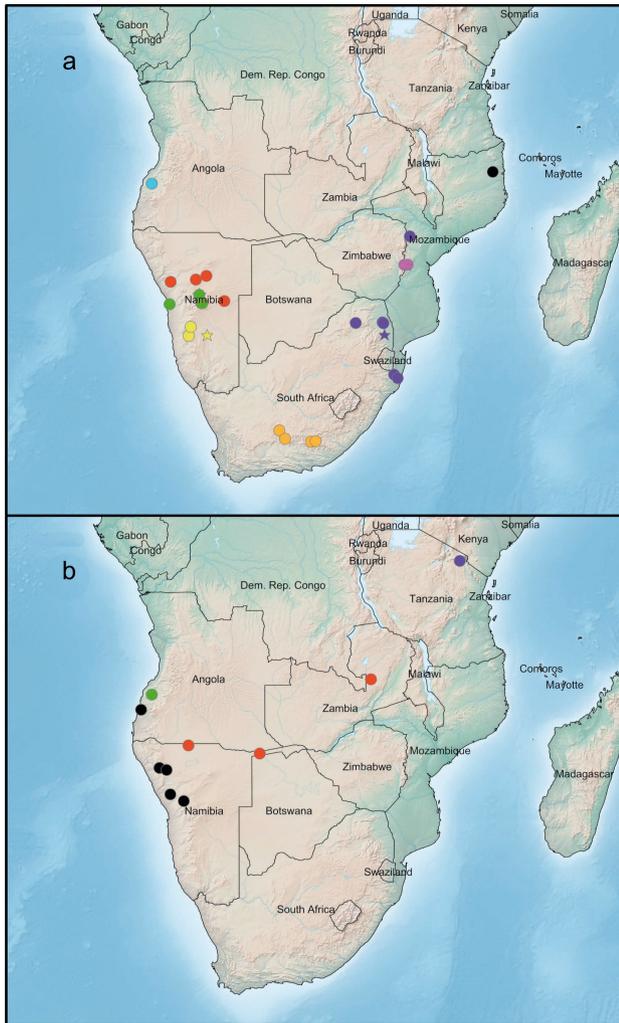


Figure 1. Localities of *Poyntonophrynus* specimens sequenced and/or scored for morphology (compare Tables 1 and 2). (a) *Poyntonophrynus beiranus* – black circle; *P. damaranus* – red circles; *P. fenoulheti* – purple circles, type – purple star; *P. grandisonae* – pale blue circle; *P. grindleyi* – violet circle, type – violet star; *P. hoeschi* – green circles, type – green star; *P. jordani* – yellow circle, type – yellow star; *P. vertebralis* – orange circles. (b) *Poyntonophrynus dombensis* – black circles; *P. kavangensis* – red circles; *P. parkeri* – purple circle; *P. pachnodes* – green circle. In a) the type locality of *P. grindleyi* and the new locality overlap.

Table 1. Available *Poyntonophrynus* sequences and respective vouchers; given are locality, co-ordinates, GenBank accession numbers, and sources.

Species	GenBank identification	Voucher	Locality	Latitude	Longitude	16S	Rag-1	Source
<i>P. beiranus</i>	<i>P. beiranus</i>	HF 30	Taratibu, Mozambique	-12.8179	39.6989	KY555650/ KY177012		LIEDTKE et al. 2017; BARRATT et al. 2018 (same specimen!)
<i>P. damaranus</i>		NMNW-R 11186	Farm Marne, Namibia	-22.4184	18.854	ON510304		This study
<i>P. damaranus</i>	<i>P. kavangensis</i>	BP 001	Ondobe, Namibia	-17.52	16.0611	KY555648		LIEDTKE et al. 2017
<i>P. dombensis</i>	<i>P. damaranus</i>		Brandberg, Namibia	-21.0221	14.6830	AF220905		CUNNINGHAM & CHERRY 2004
<i>P. dombensis</i>	<i>P. damaranus</i>		Brandberg, Namibia	-21.0221	14.6830	AF220906		CUNNINGHAM & CHERRY 2004
<i>P. dombensis</i>	<i>P. dombensis</i>		Warmquelle, Namibia	-19.1821	13.8143	AF220907		CUNNINGHAM & CHERRY 2004
<i>P. fenoulheti</i>	<i>P. fenoulheti</i>	AACRG 1599	Phalaborwa, South Africa	-23.9424	31.1409	KF665081	KF666357	LIEDTKE et al. 2016
<i>P. fenoulheti</i>	<i>P. fenoulheti</i>	AACRG 1598	Phalaborwa, South Africa	-23.9424	31.1409	KF665265	KF666249	LIEDTKE et al. 2016
<i>P. fenoulheti</i>	<i>P. fenoulheti</i>		Mkuze, South Africa	-27.6178	32.0340	AF220908		CUNNINGHAM & CHERRY 2004
<i>P. grandisonae</i>	<i>P. grandisonae</i>	AMB 10337	Base of Serra da Neve, Angola	-13.7107	13.2219	MH469716		CERÍACO et al. 2018
<i>P. grindleyi</i>		ZMB 90082	Chimanimani Mts, Mozambique	-19.7637	33.0881	ON510296	ON623708	This study
<i>P. hoeschi</i>		FB 341	Avis Dam, Windhoek, Namibia	-22.5726	17.1333	ON510295		This study
<i>P. hoeschi</i>		NMNW-R 11197	Avis Dam, Windhoek, Namibia	-22.5726	17.1333	ON510300	ON623709	This study
<i>P. pachnodes</i>	<i>P. pachnodes</i>	UF 184184	Serra da Neve, Angola	-13.7107	13.2219	MH469718		CERÍACO et al. 2018
<i>P. vertebralis</i>		PEM A11497	Commando Drift NR, 9 km west of dam wall	-32.1093	25.9444	PEM A11497		W. CONRADIE, unpublished
<i>Vandijkophrynus gariepensis</i>	<i>Vandijkophrynus gariepensis</i>	XRP 3	Klein Antjies Fontein, South Africa			KF665465		LIEDTKE et al. 2016

The following ratios were calculated: HW/FOT – relative foot length; SUL/HW – relative head width; SUL/SL – relative snout length; HW/EYE – relative eye size; ET/EYE – relative distance between eye and tympanum; SUL/TIB – relative tibiafibula length; TIB/FOT – relative foot to tibia length; HW/HND – relative hand length; SL/EYE – snout length relative to eye width; FOT/SUL – length of foot relative to body length; EN/TYM – relative size of tympanum.

The colour pattern was compared based on our own observations, literature descriptions and published photographs. Because *Poyntonophrynus* toads are morphologically very similar, we limited the inclusion of colour descriptions/photos to those sources that: i) are included in first descriptions (type material); ii) showed diagnostic features (although morphological diagnosis is difficult, some taxa can be recognized by certain features); iii) show genotyped animals; and/or iv) could be assigned to a specific taxon based on the range (see Fig. 1).

Most advertisement calls were obtained in the field using a Marantz PMD660 digital recorder with a directional microphone. Older recordings using a Sony cassette recorder were also included. Analysis of the calls, consisting of chirps or longer buzzes, was carried out using Raven Pro

1.6.3 (K. Lisa Yang Center for Conservation Bioacoustics 2022). Call parameters were determined following KÖHLER et al. (2017) using a call-centered approach. The following call parameters were noted: dominant harmonic midpoint, other emphasised harmonics, pulses per note, pulse rate, and note rate.

Museum acronyms follow SABAJ (2022). PEM – Port Elizabeth Museum (Bayworld), Gqeberha; SAIAB – South African Institute for Aquatic Biodiversity, Makhanda; NMNW – Museum of Namibia, Windhoek; NMZB – National Museums of Zimbabwe, Bulawayo; ZMB – Museum für Naturkunde Berlin – Leibniz Institute for Evolution and Biodiversity Science.

Results

Sequences were available from eight of the currently recognised *Poyntonophrynus* species plus one of the two synonyms discussed here. Only *P. parkeri* (LOVERIDGE, 1932) and *P. kavangensis* (POYNTON & BROADLEY, 1988) were not sequenced. Unfortunately, our material of *P. jordani* failed to produce comparative sequences. Uncorrected p-dis-

Table 2. *Poyntonophrynus* voucher specimens examined for morphology. See Material and methods for definitions.

Species	Voucher	Locality	Gen-der	SUL	TYM	EYE	LID	IO	ET	EN	IN	HL	SL	EE	HW	ARMHND	TIB	LEG	FOT	IMT	OMT		
<i>P. damaranus</i>	SAIAB 194515	Okakarara, Namibia	?	35.5	1.8	3.2	4.1	-	0.6	3.2	2.2	10.0	4.2	6.9	13.0	7.5	8.7	11.8	9.6	12.2	1.2	1.5	
<i>P. damaranus</i>	NMNW-R 11198	Okonjima, Namibia	F	24.4	-	2.7	3.2	2.5	-	2.2	1.7	7.9	3.4	4.7	8.5	5.0	5.5	7.8	9.3	8.1	1.0	0.7	
<i>P. damaranus</i>	NMNW-R 11200	Okonjima, Namibia	M	36.7	1.7	3.5	4.4	3.6	0.8	3.1	2.6	9.9	4.7	6.5	12.2	6.9	8.4	12.3	13.8	12.9	1.8	1.1	
<i>P. damaranus</i>	NMNW-R 11199	Okonjima, Namibia	M	33.0	1.3	3.4	4.1	3.0	0.8	3.1	2.2	9.2	4.1	5.9	11.0	6.6	7.2	11.5	12.2	11.8	1.4	0.9	
<i>P. damaranus</i>	NMNW-R 25804	Okakarara, Namibia	M	37.8	1.2	3.7	4.0	-	1.3	2.9	2.5	10.3	4.5	6.1	12.3	7.1	7.3	10.9	11.8	12.4	1.5	1.2	
<i>P. dombensis</i>	NMNW-R 26330	Hobatere Lodge, Namibia	F	35.1	1.7	3.2	4.1	3.8	0.7	2.8	2.8	9.1	4.7	6.5	12.7	7.4	8.1	13.6	14.1	13.8	1.6	1.1	
<i>P. dombensis</i>	NMNW-R 26276	Wasserfallfäche, Brandberg, Namibia	?	30.4	1.2	3.1	3.9	3.3	0.8	2.5	2.5	8.7	4.1	5.9	11.1	6.8	7.3	11.9	12.3	11.9	1.6	1.2	
<i>P. dombensis</i>	NMNW-R 26331-1	Wilderness Lodge, Erongo, Namibia	?	15.2	-	2.0	2.2	2.2	-	1.5	1.4	5.1	2.5	3.2	6.0	3.3	3.5	5.2	5.7	5.3	0.1	0.4	
<i>P. dombensis</i>	NMNW-R 26331-2	Wilderness Lodge, Erongo, Namibia	?	15.5	-	2.0	2.4	2.2	-	1.6	1.7	5.5	2.5	3.0	6.3	3.6	3.7	5.4	5.5	6.0	1.0	0.7	
<i>P. fenoulheti</i>	PEM A12264	5.2 km W of Percy Fyfe-Mokopane Junction, South Africa	M	31.4	1.5	3.4	3.4	3.8	0.5	3.0	1.9	10.0	4.8	5.1	10.8	7.4	6.6	13.2	13.0	12.0	1.3	1.1	
<i>P. fenoulheti</i>	PEM A12253	Cleveland Nature Reserve (SE of Phalaborwa), South Africa	M	28.0	1.7	3.2	3.6	3.4	0.5	2.8	1.9	9.2	3.9	4.8	9.5	6.6	6.1	10.4	10.9	11.3	1.2	1.1	
<i>P. fenoulheti</i>	PEM A07509	Phinda Private Game Reserve, South Africa	M	32.9	1.3	2.7	3.9	3.6	0.6	2.6	2.1	9.9	4.1	5.1	10.8	6.8	6.8	11.7	11.9	9.3	1.4	1.2	
<i>P. fenoulheti</i>	PEM A05530	near Ndumo, South Africa	F	28.5	1.3	3.2	3.6	3.0	0.6	2.8	2.4	8.4	4.0	5.2	9.2	5.9	6.9	10.6	11.0	10.5	0.8	1.0	
<i>P. fenoulheti</i>	PEM A07879	15 km South of Gurue towards Catandica, Mozambique	F	28.6	1.2	3.2	3.7	3.3	0.7	2.7	2.2	9.8	3.7	5.5	9.8	6.1	6.5	9.8	11.3	9.8	1.2	1.0	
<i>P. fenoulheti</i>	PEM A07876	15 km South of Gurue towards Catandica, Mozambique	M	22.3	1.3	2.9	3.4	2.6	0.3	2.7	2.1	8.6	3.7	4.4	9.6	5.6	5.3	9.6	9.7	8.8	1.1	0.6	
<i>P. fenoulheti</i>	PEM A07881	15 km South of Gurue towards Catandica, Mozambique	F	26.9	1.2	2.8	3.9	2.9	0.5	3.2	2.0	8.6	4.1	4.5	9.5	5.6	5.4	8.3	10.5	8.7	0.7	0.7	
<i>P. fenoulheti</i>	PEM A05529	near Ndumo, South Africa	M	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	29.8	5.8	10.7	10.4	10.9	1.1	0.7
<i>P. grindleyi</i>	ZMB 90082	Chimanimani Mts., Mozambique	M	22.1	1.5	2.1	2.7	3.7	1.2	2.5	1.5	8.7	3.1	3.6	9.2	6.0	5.6	9.4	9.6	9.1	1.0	0.8	
<i>P. hoeschi</i>	NMNW-R 26166	Okahandja, Namibia	?	16.5	-	2.1	2.6	2.3	-	1.4	1.8	6.1	2.7	3.4	7.0	3.7	4.0	6.5	6.6	6.0	0.7	0.6	
<i>P. hoeschi</i>	NMNW-R 25707	Windhoek, Namibia	?	28.6	-	3.2	3.9	3.8	-	2.7	2.2	8.2	4.5	5.8	11.6	6.4	6.0	10.7	12.4	11.9	1.5	1.1	
<i>P. hoeschi</i>	NMNW-R 11197	Windhoek, Namibia	M	28.8	-	3.5	3.5	3.2	-	2.2	2.1	8.8	3.8	5.6	11.3	6.7	7.2	11.3	12.1	12.2	1.7	0.9	
<i>P. hoeschi</i>	NMNW-R 11189	Windhoek, Namibia	M	30.6	-	2.7	3.4	3.3	-	2.9	2.2	8.6	3.8	5.8	10.6	6.6	6.0	11.1	11.8	11.6	1.1	0.7	
<i>P. jordani</i>	PEM A15079	Naukluft, Namibia	M	28.5	-	3.1	3.6	2.9	-	2.6	2.2	8.2	4.2	5.5	10.8	6.3	7.0	10.5	11.4	11.3	1.2	1.2	
<i>P. jordani</i>	PEM A15080	Naukluft, Namibia	F	29.8	-	2.8	3.7	2.9	-	2.8	2.2	8.4	4.2	5.5	10.7	6.0	6.7	11.1	11.5	11.6	1.2	0.9	

Re-evaluation of the status of *Bufo vertebralis grindleyi* and *Bufo jordani*

Table 1 continued

Species	Voucher	Locality	Gen-der	SUL	TYM	EYE	LID	IO	ET	EN	IN	HL	SL	EE	HW	ARMHND	TIB	LEG	FOT	IMT	OMT	
<i>P. jordani</i>	PEM A15081	Naukluft, Namibia	M	28.8	-	3.1	3.4	2.9	-	2.5	2.3	8.2	3.9	2.3	10.1	6.5	6.6	11.3	12.7	11.2	1.4	1.2
<i>P. kavangensis</i>	NMNW-R 25622	Popa Falls, Namibia	M	31.9	1.1	3.6	4.0	4.2	0.8	2.7	2.1	9.1	4.3	5.6	10.3	6.3	6.7	10.7	11.4	10.9	1.1	0.8
<i>P. kavangensis</i>	AC33368	Chikufwe, Zambia	F	21.2	0.8	2.0	2.7	1.1	0.5	1.9	1.2	5.7	2.7	4.0	7.5	5.0	4.6	7.1	8.6	7.2	0.6	0.5
<i>P. kavangensis</i>	AC3341	Chikufwe, Zambia	F	18.3	0.7	1.8	2.6	0.8	0.3	1.6	1.0	5.1	2.6	3.2	6.4	4.4	4.2	6.2	6.1	6.0	0.5	0.6
<i>P. damaranus</i>	NMNW-R 25784	Omatako Canal, Namibia	M	34.6	1.6	3.6	4.2	4.2	0.9	3.5	2.2	11.8	4.8	7.0	14.1	6.8	8.1	11.7	12.5	13.1	1.6	1.1
<i>P. parkeri</i>	SAIAB 88523	Kilimanjaro International Airport, Tanzania	F	28.0	1.8	2.9	4.1	-	-	2.9	2.1	8.7	4.7	6.6	11.1	6.3	7.4	10.8	11.5	10.9	1.3	1.3
<i>P. vertebralis</i>	PEM A15082	Victoria West, South Africa	F	27.5	1.5	3.1	3.7	2.9	0.7	2.2	2.2	8.0	3.5	5.7	9.0	5.3	6.0	9.9	9.7	10.2	1.3	1.0
<i>P. vertebralis</i>	PEM A15085	Victoria West, South Africa	F	32.8	1.7	3.1	3.6	2.8	0.8	2.9	2.6	9.3	4.1	6.4	11.3	5.9	7.5	11.5	11.0	13.2	1.4	1.3
<i>P. vertebralis</i>	PEM A15083	Victoria West, South Africa	F	30.0	1.7	3.3	3.6	3.0	0.8	2.3	2.5	8.3	4.1	5.9	10.2	6.0	6.8	10.3	10.6	11.7	1.4	1.4
<i>P. vertebralis</i>	PEM A15090	Victoria West, South Africa	M	26.4	1.6	2.9	3.6	2.4	0.5	2.4	2.3	7.7	3.3	5.5	9.2	5.7	5.9	10.1	9.6	10.9	1.2	1.0
<i>P. vertebralis</i>	PEM A15094	Victoria West, South Africa	M	24.6	1.4	2.9	3.5	2.3	0.6	2.2	2.3	7.6	3.6	5.2	8.6	4.8	5.3	8.6	8.3	9.1	1.3	1.1
<i>P. vertebralis</i>	PEM A15084	Victoria West, South Africa	M	26.7	1.5	2.9	3.6	2.2	0.6	2.4	2.2	7.7	3.8	5.6	9.4	5.7	5.9	9.8	9.9	10.2	1.3	0.8

Table 3. Uncorrected p-distances for 16S rRNA (top) and Rag-1 (below, bold) between species of *Poyntonophrynus*. FEN – *P. fenoulheti*, DOM – *P. dombensis*, DAM – *P. damaranus*, HOE – *P. hoeschi*, JOR – *P. jordani*, BEI – *P. beiranus*, GRI – *P. grindleyi*, GRA – *P. grandisonae*, VER – *P. vertebralis*, PAC – *P. pachnodes*.

	FEN	DOM	DAM	HOE	BEI	GRI	GRA	VER
FEN	0.2–0.9 –							
DOM	7.2–7.9	0–1.8 –						
DAM	8.1–9.6 1.8–2.5	7.0–8.3	0–0.5 0–0.5					
HOE	4.3–5.6 0.2	5.9–7.6	5.2–8.2 2.1–2.7	0.5–				
BEI	8.0–8.2 1.7	7.4–8.6	9.8–10.0 2.5–3.6	7.6–8.0 1.9	0.0–			
GRI	3.4–3.8 0.8	6.8–7.0	7.5–8.5 2.1–3.2	3.4–4.1 0.8	8.0 2.2	–		
GRA	9.5–10.0 3.1	11.1	10.3–11.4 4.4–5.0	9.1–10.2 2.9	12.1–12.2 4.0	8.9 2.8	–	
VER	7.0–7.2 3.1–3.6	8.8–9.5	9.0–11.4 4.2–5.1	6.1–7.3 2.8–3.3	9.3–9.4 3.8–4.3	5.6 2.8–3.3	8.6 1.4–1.9	–
PAC	6.6–6.8 1.0	8.9–9.1	10.0–10.3 2.5–3.4	6.1–6.4 0.8	9.22.3	7.3 1.4	9.4 3.3	7.3 0.5

tances for 16S rRNA between all species of *Poyntonophrynus* varied from 3.4–12.2%. 16S rRNA sequences of a specimen, here recognised as *P. grindleyi*, differed by 3.4–8.9% from other species. The Rag-1 sequence of the *P. grindleyi* specimen differed by 0.8–3.3% from other species (Table 3).

The phylogeny (Fig. 2) revealed *P. dombensis* (BARBOZA DU BOCAGE, 1895) and *P. damaranus* (MERTENS, 1954) to be sister species. These have a significant p-distance of 7.0–8.3% for the 16S rRNA sequences (Table 3). *Poyntonophrynus beiranus* (LOVERIDGE, 1932) is the sister spe-

cies to (*P. dombensis* + *P. damaranus*), with *P. hoeschi* being sister to those three species. The second clade showed that the widespread *P. fenoulheti* is sister to the range restricted *P. grindleyi*. *Poyntonophrynus pachnodes* CERÍACO, MARQUES, BANDEIRA, AGARWAL, STANLEY, BAUER, HEINICKE & BLACKBURN, 2018 is sister to the two clades mentioned already, and *P. grandisonae* (POYNTON & HAACKE, 1993) was revealed the most basal related species in this

phylogeny [*Poyntonophrynus vertebralis* (SMITH, 1848) apparently is not part of this genus].

Rag-1 sequences were available for only two specimens of *P. fenoulheti*, and one specimen each of *P. grandisonae*, *P. beiranus*, *P. grindleyi* and *P. pachnodes*. In this very small sample we found no shared haplotypes, and thus no evidence of hybridization.

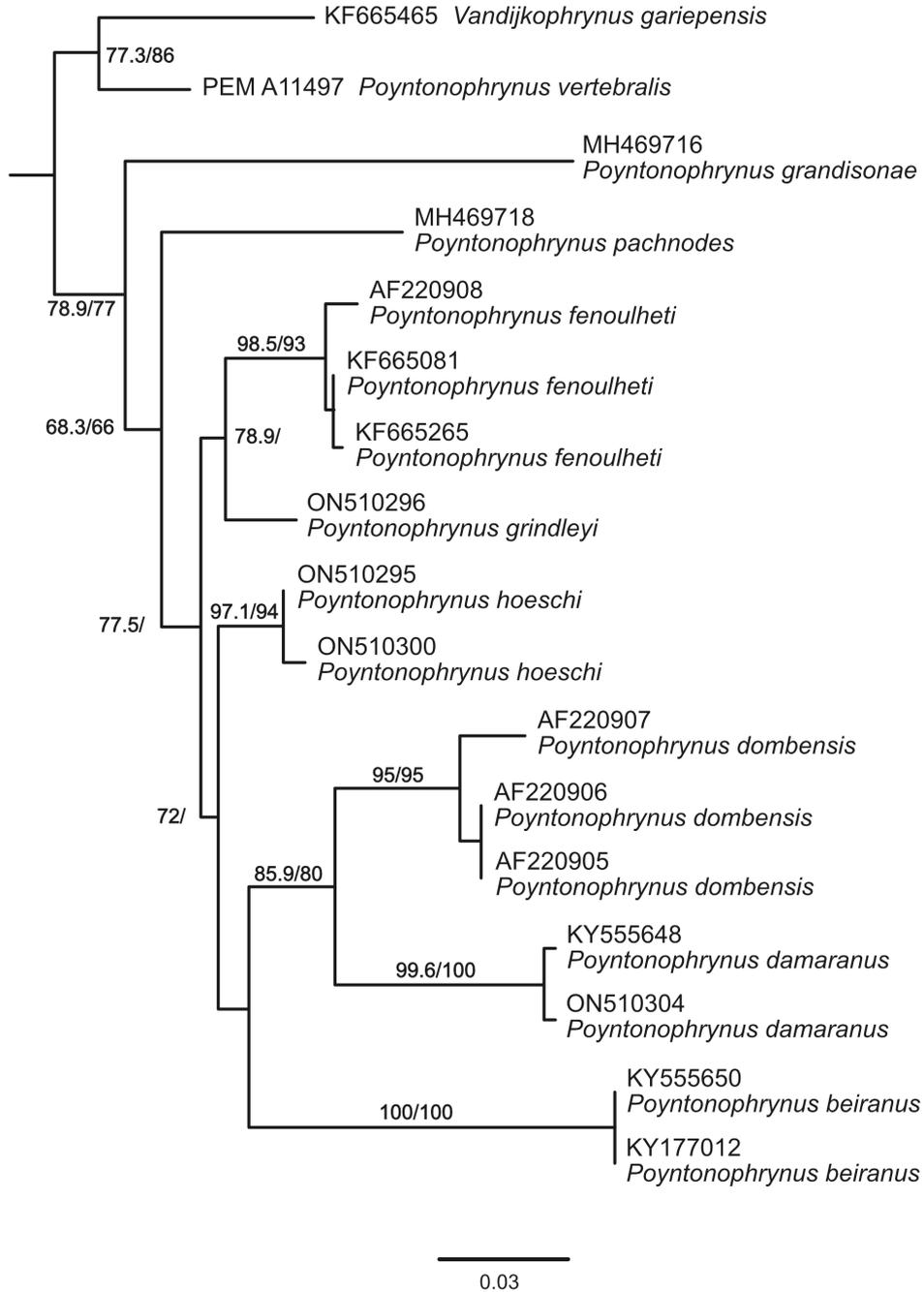


Figure 2. Maximum likelihood phylogeny of *Poyntonophrynus*, based on 16S sequences, showing GenBank accession numbers, and species identification. Support values for the phylogeny were calculated as SH-aLRT (%) and the ultrafast bootstrap (%), shown as SH-aLRT/UF bootstrap.

Table 4. Summary parameters of advertisement calls of seven species of *Poyntonophrynus*.

Species	Locality	Description	Mean dominant harmonic	Note rate	Pulse rate	n
<i>P. damaranus</i>	Namibia: Okonjima	Buzz	2536 Hz (2498–2670 Hz)	0.5–1.0 s ⁻¹	27.1–31.0 s ⁻¹	9
<i>P. dombensis</i>	Namibia: Ongongo	Brief chirp	2349 Hz (1981–2670 Hz)	1.0–2.1 s ⁻¹	71.4 s ⁻¹	7
<i>P. fenoulheti</i>	South Africa: Shirombe, Kruger National Park	Short buzz	3083 Hz (3015–3186 Hz)	1.3–1.4 s ⁻¹	102.0–111.7 s ⁻¹	5
<i>P. hoeschi</i>	Namibia: Windhoek	Brief chirp (0.15–0.16 s)	2178 Hz (2067–2326 Hz)	1.8–2.6 s ⁻¹	108.0–119.8 s ⁻¹	7
<i>P. jordani</i>	Namibia: Naukluft	Long buzz (3.1–9.0 s)	1998 Hz (1981–2153 Hz)		52.1–89.8 s ⁻¹	5
<i>P. kavangensis</i>	Namibia: Popa Falls, Okati, Kranzfontein	Brief chirp	3070 Hz (2497–3359 Hz)	1.0–1.8 s ⁻¹	52.2–68.4 s ⁻¹	16
<i>P. parkeri</i>	Tanzania: Usangu	Chirp	4237 Hz (4134–4393 Hz)	0.8 s ⁻¹	51.3–109.6 s ⁻¹	5
<i>P. vertebralis</i>	South Africa: Beaufort West, Jamestown, Loxton	Rapid chirps	2515 Hz (2412–2670 Hz)	10.0–10.7 s ⁻¹	55.2–79.4 s ⁻¹	18

The morphology of the species in this genus was remarkably similar, with minimal sexual dimorphism apparent. This ‘compact’ morphology (FROST 2022) was shown in our data by the overlap of many body proportions. However, in our sample, *P. grindleyi* could be distinguished from *P. fenoulheti* by a relatively smaller eye (HW/EYE 4.4 vs. 2.9–4.1), larger hand (HND/EE 1.6 vs. 1.2–1.3), and a relatively larger eye to tympanum distance (ET/EYE 0.6 vs. 0.1–0.2). All other proportions overlapped. Colour pattern differences are explained below.

All body proportions overlapped between *P. hoeschi* and specimens here referred to *P. jordani*. While *P. hoeschi* has flattened parotids that are sometimes barely visible, they are represented by a cluster of glands in *P. jordani*. Both species have similar colour patterns.

Calls were available for seven *Poyntonophrynus* species, plus *P. jordani*. All calls consisted of series of pulses, varying from brief chirps to longer buzzes. The calls varied by note rate, pulse rate, and dominant harmonic. A summary of available advertisement calls is presented in Table 4.

Further fieldwork in the Eastern Highlands of Zimbabwe and the corresponding mountains in Mozambique is required to collect calls of *P. grindleyi*.

Taxonomy

Poyntonophrynus grindleyi (POYNTON, 1963)

Bufo vertebralis grindleyi POYNTON, 1963 (Holotype: NMZB 5369)

Bufo fenoulheti grindleyi–POYNTON & BROADLEY, 1988

Bufo fenoulheti grindleyi–LAMBIRIS, 1989

Poyntonophrynus fenoulheti (part)–FROST, GRANT, BAIN, HAAS, HADDAD, DE SA, CHANNING, WILKINSON, DONNELLAN, RAXWORTHY, CAMPBELL, BLOTTO, MOLER, DREWES, NUSSBAUM, LYNCH, GREEN & WHEELER, 2006

New record. An adult male, ZMB 90082 (field number GNP_2019_130; GenBank ON510296 [16S rRNA], ON623708 [Rag-1]; Fig. 3), collected in montane grassland, at 1669 m (base of Mount Binga, 2436 m; Fig. 4), 33.0881° S,

19.7637° E, Chimanimani Mountains, Mozambique, 11 December 2019, leg. M.–O. RÖDEL.

The type locality of *P. fenoulheti* (HEWITT & METHUEN, 1912) is Woodbush Forest Reserve in northern South Africa. The 16S rRNA sequences of *P. fenoulheti* KF665081 and KF665265 (LIEDTKE et al. 2016) were derived from specimens AACRG 1598 and 1599 collected at Phalaborwa, 100 km east of the type locality. The 16S rRNA sequence of the Mount Binga specimen has an uncorrected p-distance of 3.8% from the Phalaborwa specimens. This value is comparable to inter-specific differences in other African frog genera, e.g. *Hyperolius* 1.3–6.4% (CHANNING et al. 2013a, BELL 2016); *Arthroleptella* 1.4–8.8% (TURNER & CHANNING 2008); *Cacosternum* 1.1–6.8% (CHANNING et al. 2013b); *Amietia* 1.3–10.0% (CHANNING et al. 2016); *Tomopterna* 1.0–9.5% (WILSON & CHANNING 2019); *Sclerophrys* 4.4–11.5% (BAREJ et al. 2011); *Capensibufo* 2.4–4.6% (CHANNING et al. 2017) and *Schismaderma* 3.3% (BAPTISTA et al. 2021).

Nuclear Rag-1 sequences were derived from the same two *P. fenoulheti* specimens from Phalaborwa as the 16S rRNA sequences (LIEDTKE et al. 2016). *Poyntonophrynus grindleyi* differed by 0.8–1.0% from these.

Description of the new voucher (measurements in mm). Small (SVL 27.7; SUL 22.1), elegant, long but robust adult male, with moderately robust limbs (Fig. 3); head rounded in dorsal and ventral view, slightly wider (9.2) than long (8.7); snout pointed to truncated in lateral view, slightly projecting beyond lower jaw; eyes projecting laterally just beyond eyelids and not beyond margins of head in dorsal view; eyes slightly projecting above dorsal margin of head in lateral view; interorbital distance (3.7) greater than eye diameter (2.1); pupil large and ellipsoidal; loreal region concave; naris small, round, directed laterally; canthus rostral sharp; eye–narial distance (2.5) equals eye diameter; eye diameter twice distance naris to rostral tip (1.1); interorbital distance more than twice internarial distance (1.5); tympanum visible, round with narrow margin, tympanum diameter (1.5) much smaller than eye diameter;

narrow, flat, almost parallel parotid glands extending from level with tympanum to behind level of forearm insertion, covered by small conical warts with spines, separated from posterior part of eyelid by large gap; a narrow supratympanic fold, slightly bent from behind posterior corner of the eye to behind tympanum.

Skin of venter and ventral surfaces of limbs granular; skin of gular region fine granular; dorsal skin rough, skin of limbs, dorsal and dorsolateral surface of head and body with scattered large warts; back and flanks with large, mostly blackish warts with single brownish and large conical spines, spines absent from middorsal area; flatter warts often composed by several small warts with less conspicuous, shorter spines.

Limbs and digits well-developed; femur length (9.6), only marginally longer than crus length (9.4); both short-

er than foot including longest toe (14.0); relative length of fingers: $I = II < IV < III$; finger tips with rounded tips, not expanded; fingers with rounded, prominent double subarticular tubercles; palm of hand with very prominent, longish oval, light brown palmar tubercle and flatter, large, brown oval thenar tubercle, seven small roundish accessory tubercles; no webbing between manual digits; dorsal and lateral surfaces of thumb and thenar tubercle with larger brownish nuptial coating; relative length of toes: $I < II < V < III < IV$; toe tips rounded, not expanded; toes with prominent and rounded double subarticular tubercles; double subdigital tubercles; very basal vestiges of webbing between toes I–IV; prominent, longish-oval, inner metatarsal tubercle, almost equals length of toe I; outer metatarsal tubercle prominent, oval shaped about two-thirds of inner metatarsal tubercle; tarsal fold absent.

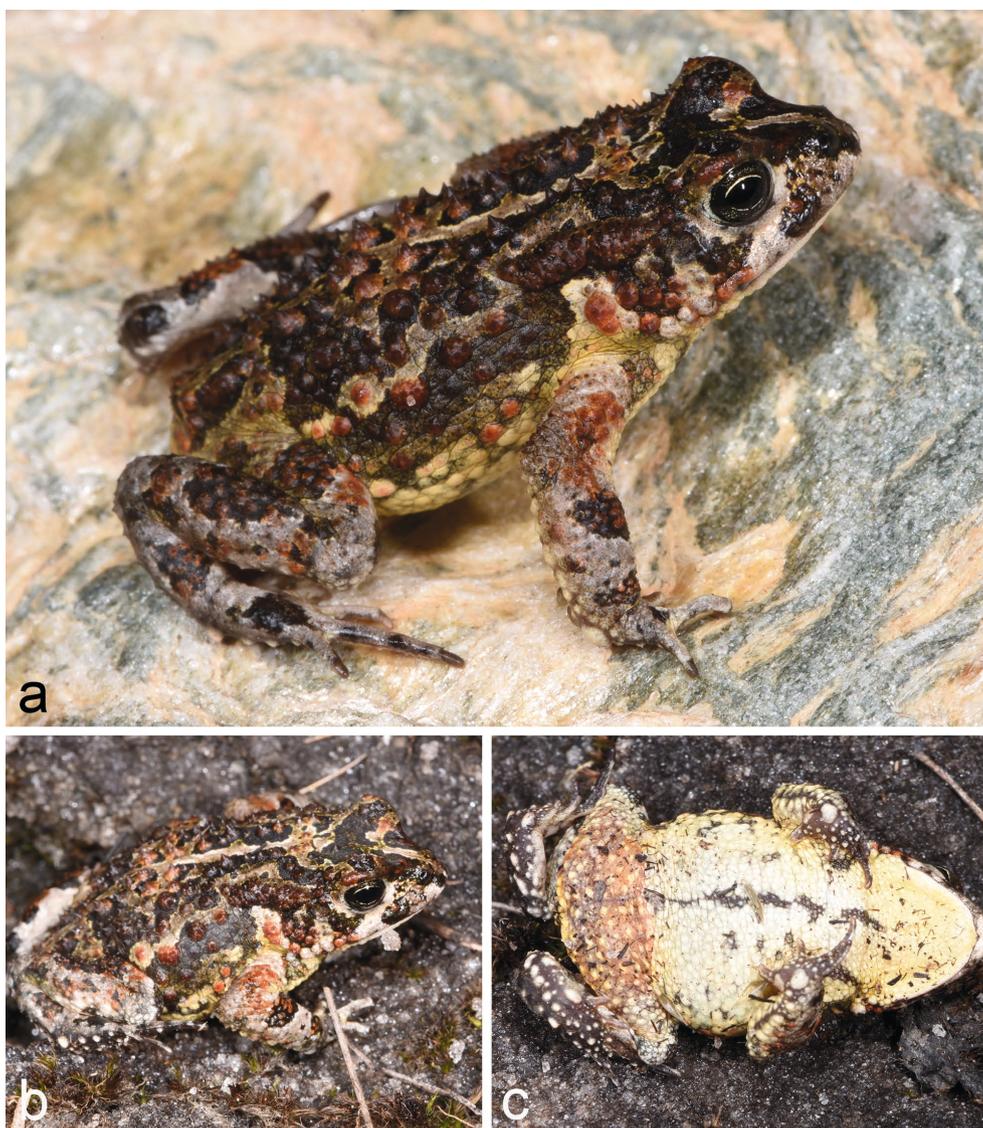


Figure 3. Life coloration and skin texture of *Poyntonophrynus grindleyi* male (ZMB 90082) from the Chimanimani Mountains, Mozambique.

Coloration. Life coloration is described with reference to Figures 3a–c. The colourful toad exhibits black bands on pale brownish ground colour. Two parallel, narrow black bands start at the snout tip, bordering a narrow median lighter brown stripe with almost yellow edges. On the right side of the head this band fuses with a broad inter-orbital band. On the left side the median light band turns towards the anterior part of the eyelid where it fuses with a reddish-brown spot. Upper lip with dark bars, lower lip uniform white. Four irregular shaped black lines extend from behind the eyes to the posterior part of the body, edging a light vertebral line and irregular shaped, narrow,

pale brown dorsal lines. The light vertebral line branches anteriorly to the upper eyelids, forming a light Y-shape. Anterior to the eyes an almost white line extends to the upper lip below the eyes. Another light line turns from below the tympanum to the upper arm insertion where it extends to a large white spot surrounding a reddish large wart. Other large black, dark brown or reddish warts are scattered across the dorsal surfaces. Below the black dorso-lateral band, the flanks gradually turn into beige colour, granular ‘cells’ edged black. The upper surfaces of extremities are grey with reddish warts and black spots and bands. The throat and belly are creamy white, the throat

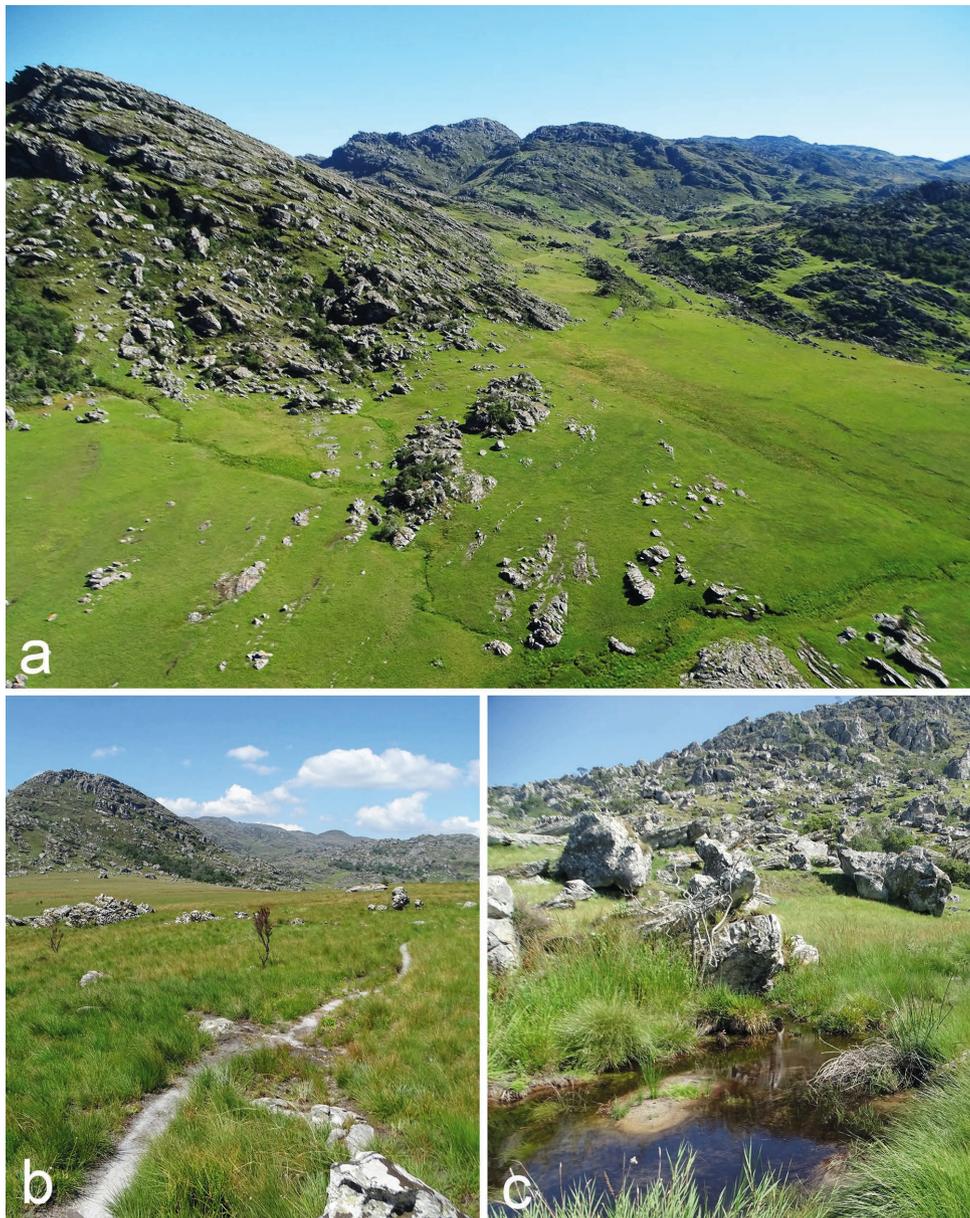


Figure 4. Montane grassland (about 1700 m) habitat of *Poyntonophrynus grindleyi* in the Mozambican part of the Chimanimani Mountains. (a) Aerial view of the region; (b) site where ZMB 90082 was collected; (c) potential nearby breeding site of *Poyntonophrynus grindleyi*, swampy parts of a small creek in montane grassland.

with a yellow tinge. An interrupted narrow median line of black blotches extends from the posterior edge of the throat to the hind legs. Lower part of hind legs reddish with cream warts. Lower surfaces of feet and hands, black with white tubercles. Colour in preservative as in life but faded.

Comparison to published description. This description is very much in line with the description provided by POYNTON & BROADLEY (1988). In particular our toad has much less conspicuous parotid glands compared to *P. fenoulheti* where these are more bulging, and kidney shaped, the posterior end turning down towards the forearm (DU PREEZ & CARRUTHERS 2017). Typical *P. fenoulheti* also seem to exhibit different dorsal pattern, plain white venters, less conspicuous warty spines, and larger body size (up to 43 mm; DU PREEZ & CARRUTHERS 2017). According to POYNTON & BROADLEY (1988) the females of *P. f. grindleyi* reach 33 mm SVL. These authors mention some differences to our voucher, i.e. concerning the parotid glands, which they describe to 'tend to break into separate spinose patches in specimens from lower altitudes', or 'become very flattened in toads from higher altitudes'. They mention that in particular males from lower altitudes are very spiny, males from higher altitudes tend to have smaller spines and females generally possess less rough skin. The abdominal and pectoral region may be darkly marbled. These authors also list a few additional colour and skin texture variations from toads of various sites, differences which were also confirmed and illustrated by LAMBIRIS (1989), e.g. mentioning the absence of a light occipital patch in *P. grindleyi* (present in *P. fenoulheti*), as well as more contrasting dorsal pattern and dark markings on the venter (less conspicuous and plain in *P. fenoulheti*, respectively). POYNTON & BROADLEY (1988) conclude that if the subspecific status has to be rejected [as suggested by TANDY & KEITH (1972), generally rejecting subspecies as a valid biological category]; the toads should be better treated as a full species instead of being sunk as a synonym of *P. fenoulheti*. This assumption seems to be supported by our morphological and genetic data, as well as on the habitat preferences of *P. grindleyi* (see below). We thus formally elevate *P. grindleyi* to species level.

Natural history. The small toad was encountered at the beginning of the rainy season, moving during daytime through the montane, short grass savanna on sandy soil (Fig. 4b). After capture the male uttered soft release calls. Unfortunately, we had no device at hand to record these calls. The syntopic herpetofauna comprised *Arthroleptis troglodytes* POYNTON, 1963, *Amietia delalandii* (DUMÉRIE & BIBRON, 1841), *Pyxicephalus* sp., *Strongylopus fasciatus* (SMITH, 1849), and *Bitis atropos* (LINNAEUS, 1758). Potential breeding sites might be shallow streams and swampy areas in the near vicinity (Fig. 4c). POYNTON & BROADLEY (1988) mention 'shallow pools on gently sloping grass-covered rock faces' as breeding sites near the summit of the Chimanimani Mountains. According to these authors the

toad occurs in the western Chimanimani Mountains of Zimbabwe from 1560 m to the summit. Our record thus is from the lower part of the species range. It is the first country record for Mozambique. In Figure 1a the type locality and the new locality overlap as both are close to the border between Mozambique and Zimbabwe, which cannot be shown at this scale.

Advertisement call. The call is unknown.

Molecular. The 16S rRNA sequence differed by 3.4–8.9% from all other *Poyntonophrynus* species for which sequences were available. The Rag-1 sequences differed by 0.8–4.2% from other *Poyntonophrynus* species with available sequences (Table 3).

Poyntonophrynus jordani (PARKER, 1936)

Bufo jordani PARKER, 1936 (Holotype: BMNH 1947.2.20.94)

Bufo vertebralis jordani–POYNTON, 1964

Bufo jordani–MERTENS, 1971

Bufo hoeschi–POYNTON & BROADLEY, 1988 (by implication)

Poyntonophrynus hoeschi–FROST, GRANT, BAIN, HAAS, HADDAD, DE SÁ, CHANNING, WILKINSON, DONNELLAN, RAXWORTHY, CAMPBELL, BLOTTO, MOLER, DREWES, NUSSBAUM, LYNCH, GREEN & WHEELER, 2006

New records. Two adult males (PEM A15079, A15080; field numbers AC 2655, AC 2656) and one adult female (PEM A15081; field number AC 2657), were collected along a small temporary stream near the campsite at Naukluft in what is now the Namib-Naukluft National Park (24.2632° S, 16.2381° E), 1465 m, Naukluft Mountains, Namibia (Fig. 5) on 23 January 2006 by A. CHANNING. The specimen is similar to photos of the holotype (BMNH 1947.2.209.94) collected from Satansplatz, ~145 km to the southeast. The type locality of *P. hoeschi* (AHL, 1934) is Okahandja in Namibia, ~255 km to the northeast of the new records.

Description of the new voucher PEM A15080 (measurements in mm). Small, (SVL 30.8; SUL 29.8), flattened, moderately robust, adult male with moderately well-developed limbs (Fig. 5); head triangular in dorsal view with truncated snout, slightly wider (10.7) than long (8.4); snout bluntly rounded in lateral view, projecting beyond lower jaw; eyes projecting laterally just beyond eyelids and not beyond margins of head in dorsal view; eyes slightly projecting above dorsal margin of head in lateral view; internarial distance (2.2) less than eye diameter (2.8); pupil large and ellipsoidal; loreal region concave; naris small, round, directed laterally; canthus rostral rounded; eye–narial distance (2.6) less than eye diameter (2.8); eye diameter less than snout length; distance between anterior corners of eyes (5.5) more than twice internarial distance (2.2); tympanum not visible; parotid glands indistinct, a slightly raised area behind the eye covered with red conical warts with black-tipped spines; a curved supratympanic fold is present.

Skin of venter and ventral surfaces of limbs granular; skin of gular region finely granular; dorsal skin rough, skin of limbs, dorsal and dorsolateral surface of head and body with scattered large warts; large, mostly reddish warts with single brownish and large conical spines. A thin vertebral groove present.

Limbs and digits well-developed; femur length (11.5), as long as tibia (11.5); both nearly equal to foot including longest toe (11.6); relative length of fingers: I < II < IV < III;

finger tips with rounded tips, not expanded; fingers with rounded, prominent single subarticular tubercles, except first finger which has double subarticular tubercles; palm of hand with very prominent, round, pale palmar tubercle and flatter, elongated pale oval thenar tubercle with nuptial pad developed on the posterior surface, dark round nuptial pad on dorsal surface of first finger; seven small roundish accessory tubercles; no webbing between manual digits; dorsal and lateral surfaces of thumb and thenar tuber-

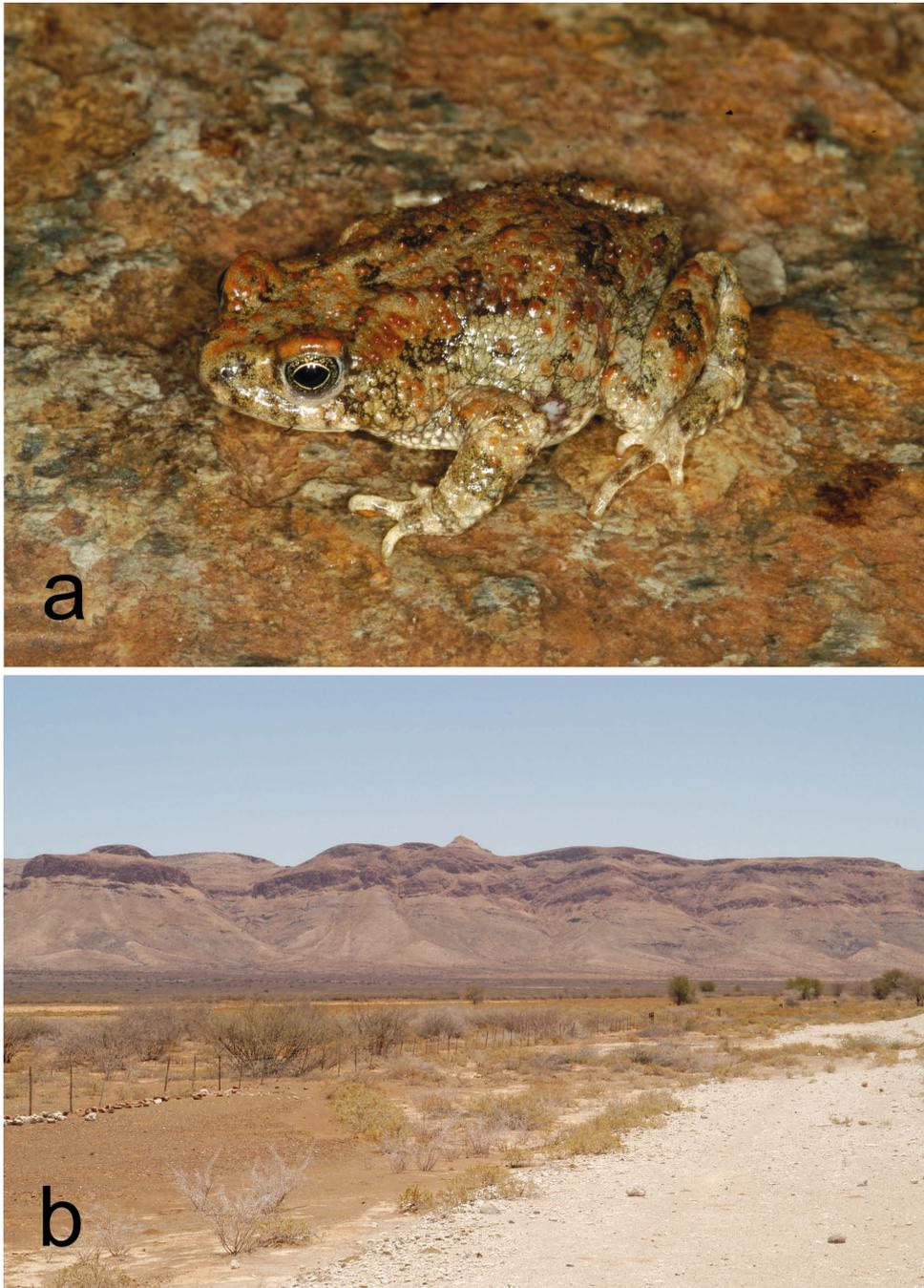


Figure 5. (a) *Poyntonophrynus jordani* in life (PEM A15080), recorded from Naukluft, Namibia; (b) Naukluft Mountains.

cle with larger brownish nuptial coating; relative length of toes: $I < II < V < III < IV$; toe tips rounded, not expanded; toes with prominent and rounded double subarticular tubercles; single subdigital tubercles; basal vestiges of webbing between toes I–IV; prominent, oval inner metatarsal tubercle, almost equals length of toe I; outer metatarsal tubercle prominent, round, about two-thirds of inner metatarsal tubercle; tarsal fold absent.

Coloration. Life coloration can be seen in Figure 5a. The colourful toad has black and red blotches on a grey background, which are similar to the background colours of the local rocks.

Eyelids reddish-brown, with the same colour on the dorsal warts, many with black-tipped spines. Many irregular black blotches on a grey background. Sides with less black and red blotches than dorsum. Upper lip with dark bars, lower lip uniform white. An almost white band extends to the upper lip below the eye. Other large black, dark brown or reddish warts are scattered across the dorsal surfaces. The throat and belly are creamy white. Lower surfaces of feet and hands white. Colour in preservative as in life but faded to grey.



Figure 6. (a) *Poyntonophrynus jordani* eggs are attached to rocks and vegetation in shallow water; (b) the temporary stream at Naukluft Namibia.

Comparison to published description. The specimens from Naukluft agree with the description of the type by the absence of bony ridges on the head, snout longer than eye, canthus rostralis rounded, vertical loreal region, tympanum absent, interorbital space flat and broader than the upper eyelid. The fingers are similarly proportioned relative to each other, the presence of two large flat metacarpal tubercles, and reduced webbing. The type description refers to “toes nearly one-third webbed” (PARKER 1936), but examination of the type shows it to have similar webbing to the Naukluft specimen. The Naukluft specimens agree further by possessing double subarticular tubercles, no tarsal fold, and the tibia being nearly one third of body length. They also agree with the presence of small conical warts on the back each tipped with a blunt spine, and nuptial asperities on the inner two fingers.

Natural history and distribution. Males call around the edge of temporary pools. Eggs are deposited in shallow water, attached to vegetation and rocks (Fig. 6a). The distribution is not well understood, with records in the arid south of Namibia in the pro-Namib. The species appears to be associated with rocky areas, specifically sandstone and shale formations in south-western Namibia, with the coloration being very similar to the native rock formations.

Advertisement call. The calls of the described male and others were recorded at Naukluft on 23 January 2006, after dark. Comparative calls of *P. hoeschi* were recorded in Windhoek. The call of *P. jordani* is a long buzz (mean 7.2 s, 3.1–9.3 s), with a mean pulse rate of 72.1 s⁻¹ (52.1–89.8 s⁻¹) and a mean dominant harmonic of 1998 Hz (1809–2153 Hz). The call of *P. hoeschi* is a series of brief notes consisting of chirps. Mean note duration is 0.15 s (0.15–0.16 s), with a mean note rate of 2.1 s⁻¹ (1.8–2.6 s⁻¹) and a dominant harmonic of 2170 Hz (2067–2326 Hz) (Fig. 7).

Discussion

African dwarf toads in the genus *Poyntonophrynus* show little morphological variation between species. Apart from *P. grandisonae*, which has a very large tympanum (POYNTON & HAACKE 1993), the other species are remarkably similar. The tympanum may not be visible (even if present) in some specimens of *P. damaranus*, *P. dombensis*, *P. hoeschi*, *P. jordani*, *P. vertebralis*, and *P. beiranus*. The tympanum is absent in *P. pachnodes*, a feature that is shared with *Mertensoophryne*. CERÍACO et al. (2018) provide a summary of morphological features in the genus. Here we re-investigated the taxonomic status of two described but currently synonymised taxa and concluded that both deserve to be treated as valid species. Our phylogeny also confirmed that *P. vertebralis* groups outside the genus *Poyntonophrynus*, as already shown by LIEDTKE et al. (2017), but the necessary taxonomic re-arrangement is beyond the scope of this paper.

Poyntonophrynus grindleyi can be distinguished from *P. fenoulheti* by mitochondrial 16S rRNA sequences, nuclear Rag-1 sequences, and small differences in morphology and colour pattern (see Results), supporting POYNTON & BROADLEY (1988) who suggested that the taxon might deserve species status. The phylogeny showed that *P. fenoulheti* is the sister species to *P. grindleyi*. We interpret the p-distance of 3.4–3.8% as a strong evidence that they are distinct species. Similar p-differences have been demonstrated for other bufonids (LIEDTKE et al. 2016, 2017; CHANNING et al. 2017; BAPTISTA et al. 2021). Early evidence for hybridization in toads, i.e. between *Sclerophrys capensis* and *S. gutturalis* (GUTTMAN 1967), was based on polymorphic blood proteins. Crossing experiments showed that large sized toads in the genus *Sclerophrys* produced highly viable but generally sterile hybrids (Blair 1972). Unfortunately, toads now in the genus *Poyntonophrynus* were not examined by these authors, and our sample size was too small to meaningfully test for haplotype sharing. The advertisement call of *P. fenoulheti* is a series of short buzzes, but the call of *P. grindleyi* has yet to be recorded. However, *P. grindleyi* is only known from moister grasslands and rock surfaces at higher elevations (> 1560 m, POYNTON & BROADLEY 1988) within the Chimanimani Mountains (LAMBIRIS 1989), while *P. fenoulheti* is widespread from northeastern Namibia, eastern Botswana, Zimbabwe, northeastern South Africa and southern Mozambique (CHANNING & RÖDEL 2019), where it occurs from grassland to woodland, mostly in rocky habitats at lower altitudes (POYNTON 1964, POYNTON & BROADLEY 1988, LAMBIRIS 1989). Apart from mor-

phology (i.e. smaller body size, less conspicuous parotids, more spinose warts, patterned venter) and genetics, the apparent differences in altitudinal distribution and habitat preferences of the different genetic lines, is a further strong argument to accept *P. grindleyi* and *P. fenoulheti* as two valid, biologically different toad species.

Poyntonophrynus jordani can be distinguished from *P. hoeschi* by advertisement call (a long buzz versus a series of chirps), and 3–3.5 phalanges of web free on the fourth toe, while *P. hoeschi* has four phalanges free of web. The parotids of *P. hoeschi* tend to be flattened and concealed, while those of *P. jordani* consist of a cluster of glands. In all other body proportions the two species are indistinguishable. A pale occipital patch is present in *P. hoeschi* but absent in *P. jordani*. Similarity in morphology may have resulted in previous misidentifications. PARKER (1936) noted that the tympanum and eustachian tubes were absent in the type of *P. jordani*, but this was shown to be in error by Alice Grandison (POYNTON & BROADLEY 1988). Based on the consistent morphological, coloration and call differences stated above we formally elevate *P. jordani* to species level. The collection of fresh genetic material is needed to further test the status of this species.

There appears to be a biogeographical split between *P. hoeschi* and *P. jordani*, although increased surveys in the intervening regions may reveal habitat overlap. Thus far, *P. jordani* appears to inhabit sandstone or shale formations in the arid to hyper-arid south and southwest of Namibia. By contrast, *P. hoeschi* may be restricted to the Khomas Group schists and adjacent Damara Group granites

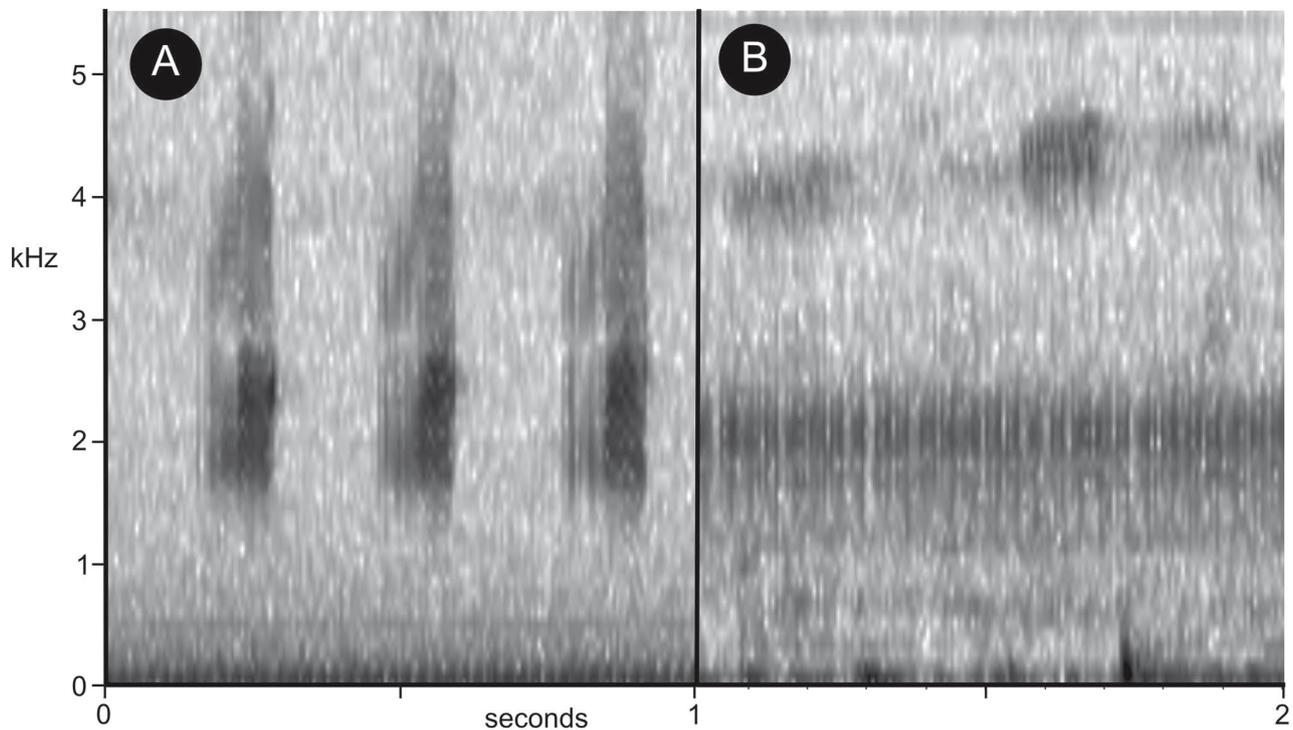


Figure 7. Advertisement calls of (A) *Poyntonophrynus hoeschi* (Windhoek) and (B) *P. jordani* (Naukluft).

of the central plateau and central western escarpment (see MENDELSON et al. 2002). The known range of *P. jordani* is also considerably more arid than the Khomas Highlands, although not more arid than the western populations of *P. hoeschi* (MENDELSON et al. 2002).

Considering the remarkable morphological similarity across, and past taxonomic confusions within *Poyntonophrynus*, a comprehensive molecular biogeographic study across the range of the genus is required to understand both taxonomic and geographic boundaries.

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