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Three new scansorial species of microhylid frogs (Anura: *Cophixalus*, *Oreophryne*) from Papua New Guinea

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Abstract. Three new scansorial species of the speciose microhylid genera *Cophixalus* Boettger, 1892 and *Oreophryne* Boettger, 1895 are described from rainforest habitats on the southern slopes of Papua New Guinea's central cordillera. The two *Cophixalus* are small- (adult SUL 20.4–23.2) and moderate-sized (adult male SUL 26.1 mm) species with expanded finger discs that are marginally to substantially larger than the toe discs. The *Oreophryne* is a large-sized species reaching 38 mm SUL that has finger discs substantially larger than the toe discs. The advertisement calls of each species are described and illustrated. The descriptions of these three species confirm the status of *Cophixalus* and *Oreophryne* as the most species rich microhylid frog genera in the New Guinea region. The number of *Cophixalus* species recognised from New Guinea and immediately adjacent islands now stands at 48, and of *Oreophryne* at 61, and numerous additional species in both genera await formal description. The high-rainfall belt that extends along the southern flanks of New Guinea's central cordillera has a rich known frog fauna, and the ongoing discovery and description of previously unknown forms in this region underscores the need to better document and ultimately to preserve this rich but poorly known fauna.

Key words. Amphibia, Anura, Melanesia, systematics, taxonomy, bioacoustics, morphology, central cordillera.

Introduction

Cophixalus and *Oreophryne* are the most speciose genera of microhylid frogs in the New Guinean region, containing, respectively, 46 and 60 named species on New Guinea and adjacent islands (Kraus 2012, 2016, 2017a, b, Frost 2018). Numerous additional undescribed species in both genera are known (Kraus 2012, 2017a, b). The genus *Cophixalus* has a broad distribution in the Australopapuan region, from the islands immediately west of mainland New Guinea to the rainforests of northern Queensland, Australia (Hoskin 2012, Günther et al. 2015, Anstis 2017). The genus reaches its greatest diversity on New Guinea and adjacent islands, where it exhibits substantial morphological diversity, including short-legged terrestrial forms with reduced digits (Günther 2006, Kraus & Allison 2009a), and scansorial species with long limbs and substantially expanded digital discs (Kraus & Allison 2009b). Several recent molecular studies of Papuan Asterophryinae that have included *Cophixalus* (Köhler & Günther 2008, Rittmeyer et al. 2012, Peloso et al. 2016) concluded that the genus is non-monophyletic, but Rivera et al. (2017) reported that *Cophixalus* forms a sister clade to the remaining Asterophryine genera and is monophyletic pending only inclusion of a single species of *Copiula* Méhely, 1901.

The 72 known species of *Oreophryne* (AmphibiaWeb 2019) are distributed from the Philippines in the northwest through New Guinea to the islands of Milne Bay Province and New Britain in the east (Menzies 2006). Like *Cophixalus*, *Oreophryne* exhibits substantial morphological diversity, including short-legged terrestrial species with reduced discs that occupy alpine habitats above the tree line (Zweifel et al. 2005) but most are arboreal species with long limbs and greatly enlarged digital discs (Menzies 2006). Morphologically, *Cophixalus* and *Oreophryne* can usually be distinguished by the presence of toe webbing in the latter (vs. absent in the former) but there are several exceptions to this rule and confirmation of generic status can be difficult without confirming the presence of procoracoids and clavicles in *Oreophryne* (vs. lacking in *Cophixalus*). Species of the two genera routinely occur in sympatry.

Herpetological surveys in south-central Papua New Guinea over many years by the senior author have accumulated material containing a large number of undescribed microhylid frogs, including several species of *Cophixalus* and *Oreophryne* (Richards 2002). Here we describe two new *Cophixalus* species and an *Oreophryne* species that was previously misidentified as *Cophixalus* by Richards (2002) due to its morphological similarity to several

Cophixalus species. All three species are currently known only from the extensively forested high-rainfall belt that extends across the southern slopes of New Guinea's central cordillera (McAlpine et al. 1983).

Material and methods

Most male frogs were located at night by their advertisement calls; others were detected on low foliage along forest trails using a headlamp. Voucher animals were anaesthetised in an aqueous chlorobutanol solution and subsequently fixed in 10% formalin. Liver samples were taken from some specimens before fixation and stored in 95% ethanol to enable later DNA sequencing. All specimens were transferred to 70% ethanol within two days of fixation. The following measurements were taken with a digital calliper (> 10 mm) or with a binocular dissecting microscope fitted with an ocular micrometer (< 10 mm) to the nearest 0.1 mm from preserved specimens only: SUL – snout–urostyle length, from tip of snout to posterior tip of urostyle; SUL is generally slightly shorter than snout–vent length (SVL). As the measurement error is higher in the latter, we prefer to use the former. Both measurements are sufficiently similar (unpublished data) that, where relevant, we compare our SUL measurements with SVLs presented for members of the genus in some papers; TL – tibia length: external distance between knee and tibio–tarsal articulation; TaL – length of tarsus: external distance between tibio–tarsal and tarsal–metatarsal joints when held at right angles; T4L – length of 4th toe, from tip of 4th toe to proximal edge of sole; T4D – transverse diameter of disc of 4th toe; T1D – transverse diameter of disc of first toe; F3L – length of 3rd finger, from tip of 3rd finger to proximal edge of palm; F3D – transverse diameter of disc of 3rd finger; F1D – transverse diameter of disc of first finger; HL – head length, from tip of snout to posterior margin of tympanum; HW – head width, taken across the tympana; SL – snout length, from an imaginary line connecting the centres of the eyes to the tip of the snout; END – distance from anterior corner of orbital opening to centre of naris; IND – internarial distance between centres of nares; ED – eye diameter, from anterior to posterior corner of orbital opening; TyD – horizontal diameter of tympanum. Measurements are presented as mean ± standard deviation, range.

Advertisement calls were recorded under natural conditions with a Marantz PMD-661 or Edirol R09 digital recorder and a Sennheiser ME66 Microphone with K6 power module; calls were analysed with Avisoft-SAS Lab Pro software. Terminology and acoustic analysis procedures follow Köhler et al. (2017) except where indicated otherwise.

Assignment of frogs to the genus *Cophixalus* was based on the following combination of characters: presence of an eleutherognathine jaw, absence of clavicles and procoracoids, and *M. depressor mandibulae* arising mostly from the dorsal musculature; assignment to *Oreophryne* was on the basis of presence of an eleutherognathine jaw and presence of procoracoids and clavicles (Parker 1934). Specimens are stored in the collections of the South Australian Museum, Adelaide, Australia (SAMA), and the Museum für Naturkunde, Berlin, Germany (ZMB) and bear registration numbers of these institutions. Several types will also be deposited in the PNG National Museum (PNGNM). SJR refers to the original field collection tag of Stephen Richards.

All statistical calculations were done with the program Statgraphics Centurion Version 15.2.14 (Statpoint Technologies, Inc., Warrenton, Virginia, USA). All p-values are calculated by the non-parametric Mann-Whitney (Wilcoxon) Test for comparison of medians. Voucher specimens, including types, of the genus *Cophixalus* that were studied for comparative purposes are listed in the papers by Richards et al. (1992), Günther (2003a, 2006, 2010), Richards & Oliver (2007, 2010), Günther & Richards (2011), Günther et al. (2014, 2015), and of *Oreophryne* in the papers by Richards & Iskandar (2000), Günther et al. (2001, 2009, 2012, 2014), Günther (2003b, c, 2015), Zweifel et al. (2005), Günther et al. (2009) and Günther & Richards (2011, 2016). Additional comparative information was taken from other original descriptions and recompiled treatises (Méhely 1901, Parker 1934, Zweifel 1956a, b, 1962, 1979, 1980, Tyler 1963, Zweifel & Parker 1989, Menzies 2006, Kraus & Allison 2006, 2009a, b, Kraus 2012, 2013, 2016, 2017a, b).

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are 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: 7FB6E574-5E66-4C53-9605-AA580CEE496B. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: www.salamandra-journal.com, Zenodo.org.

Cophixalus cateae sp. n.

(Figs 1–4)

ZooBank LSID: urn:lsid:zoobank.org:act: 1117F530-B7F2-4EC4-90BA-D2C9B02B8054

Holotype: SAMA R71378 (SJR 15389), adult male from Iagifu Ridge, Agogo Range near Moro, Southern Highlands Province, Papua New Guinea (6.4409° S, 143.2256° E; 1,400 m a.s.l.) collected on 18 May 2017 by S. J. Richards.

Diagnosis: A species of *Cophixalus* characterized by the unique combination of: (1) moderate size (SUL 26.1 mm

in one adult male); (2) body slender; (3) legs long (TL/SUL 0.55); (4) third toe clearly longer than fifth; (5) toe and finger discs distinct and all with circum-marginal grooves; (6) discs of fingers considerably larger than those of toes (T4D/F3D 0.64); (7) dorsum with some tubercles, ventral surfaces smooth; (8) dorsal surfaces heavily spotted, ventral surfaces light with indistinct mottling; (9) dark framed W-figure in scapular region and eye-spot in lumbar region; (10) advertisement call composed of multiple peeping notes and having a total duration of more than 10 s; mean note length 268 ms, mean inter-note length 112 ms, repetition rate 2.7 notes/s, dominant frequency at 2.6 kHz.

Cophixalus cateae sp. n. is readily distinguished from congeners of a similar size (mean SVL ~24–30 mm) and with peeping/whistling voices by the following features: *Cophixalus balbus* Günther, 2003 has fairly uniform tan dorsal colouration (vs. mottled green-yellow and black); shorter head length (HL/SUL 0.28–0.33 vs. 0.36); higher ratio END/IND (0.93–1.09 vs. 0.92); smaller eyes (ED/SUL 0.099–0.109 vs. 0.142); and shorter advertisement call notes (28–50 ms vs. 179–638 ms) produced in much longer sequences (> 1 min vs. <25 s) than *C. cateae*. *Cophixalus biroi* (Méhely, 1901) lacks scapular ridges and a W-shaped scapular figure (vs. present in *C. cateae*); is reddish on ventral surfaces of legs (vs. yellowish in *C. cateae*); with slower repetition rate of advertisement call notes (< 1 note/s vs. 2.7 notes/s in *C. cateae*). *Cophixalus caverniphilus* Kraus & Allison, 2009 has similar colouration (see Fig. 1b in Kraus & Allison [2009]) and body ratios, and *C. cateae* would key to *caverniphilus* using the dichotomous key provided by Kraus (2012). However calls of *C. caverniphilus* are 1.45–2.18 s duration (vs. 13.6 s and 18.5 s) with 5–9 notes (vs. >30 notes), and note repetition rate of 5.65–7.57 notes/s (vs. 2.7 notes/s in two calls from *C. cateae*). *Cophixalus clapporum* Kraus, 2012 has equal sized finger discs and toe discs or slightly wider toe discs than fingers discs (vs. clearly wider finger discs in *C. cateae*); call notes of *C. clapporum* with pronounced harmonic structure, repetition rate 1.82–2.15 notes/s, dominant frequency 2.3 kHz (vs. lacking harmonic structure, repetition rate 2.7 notes/s, dominant frequency 2.7 kHz in two calls from *C. cateae*). *Cophixalus cupricarenus* Kraus & Allison, 2009 differs from *C. cateae* by dorsal colour of head (copper in *C. cupricarenus* vs. yellowish in *C. cateae*); equal sized finger and toe discs (vs. clearly wider discs of fingers than those of toes in *C. cateae*); well-developed subarticular tubercles (vs. poorly developed in *C. cateae*); and calls with note repetition rate of about 5 notes/s (vs. 2.7 notes/s in *C. cateae*). *Cophixalus cryptotympanum* Zweifel, 1956 differs from *C. cateae* by indistinct (vs. distinct) tympana, small size (males to 25 mm vs. 26.1 mm), rugose skin (vs. substantially smooth) and a pale stripe through tympanum (vs. absent) (see Discussion below). *Cophixalus kaindiensis* Zweifel, 1979 has shorter legs (TL/SVL 0.41–0.47 vs. 0.55), lower ratios END/IND (0.70–0.80 vs. 0.92) and END/SVL (0.070–0.083 vs. 0.092); and call notes of about 100 ms, with repetition rate 1.8–2.1 notes/s (vs. mean length 268 ms, repetition rate 2.7 notes/s). *Cophixalus monosyllabus* Günther, 2010 is smaller (males ≤ 24.3 mm vs. 26.1 mm SUL) with smaller discs on finger one and toe one (F1D/SUL 0.017–0.031 vs. 0.054 and T1D/SUL 0.022–0.031 vs. 0.038) and monosyllabic calls (vs. polysyllabic calls in *C. cateae*). *Cophixalus nubicola* Zweifel, 1962 has shorter hind legs (TL/SUL of holotype 0.42 [original ratio of 0.35 provided by Zweifel (1962), based on a different measurement technique, is 21% smaller – extrapolation of this difference to the type series assuming difference is uniformly applicable provides a range of 0.42–0.46] vs. 0.57 in *C. cateae*) and lower END/IND ratio (0.63–0.74 vs. 0.92). In *C. parkeri* Loveridge, 1948, third toe is slightly longer than fifth or of same length (vs. distinctly longer third toe than fifth toe in *C. cateae*); calls are clearly pulsed (vs. unpulsed) with double or triple notes (vs. more than 30 notes in *C. cateae*).

Table 1. Body measurements and body ratios of the male holotype of *Cophixalus cateae* sp. n. All measurements in mm; for explanation of abbreviations see "Material and methods".

Reg.No	SAMA R71378	Reg.No	SAMA R71378
SUL	26.1	TL/SUL	0.55
TL	14.4	TaL/SUL	0.34
TaL	9.0	T4L/SUL	0.54
T4L	14.0	T4D/SUL	0.054
T4D	1.4	F3L/SUL	0.33
T1D	1.0	F3D/SUL	0.084
F3L	8.7	T4D/F3D	0.64
F3D	2.2	T1D/F1D	0.71
F1D	1.4	HL/SUL	0.36
HL	9.4	HW/SUL	0.39
HW	10.3	HL/HW	0.91
END	2.4	END/SUL	0.092
IND	2.6	IND/SUL	0.100
SL	5.2	END/IND	0.92
ED	3.7	ED/SUL	0.142
TyD	1.1	TyD/SUL	0.042
		TyD/ED	0.30
		SL/SUL	0.199

Description of the holotype: A male of 26.1 mm SUL; measurements are presented in Table 1. Head somewhat broader than long (HL/HW 0.91), canthus rostralis straight and distinct; loreal region concave; snout protruding in profile and slightly tapered in dorsal view; nostrils directed laterally; horizontal eye diameter clearly greater than eye–naris distance; tympanic annulus indistinct, tympanum about one third of eye diameter (TyD/ED 0.30), supratympanic fold weakly expressed; internarial distance slightly greater than distance between eye and naris (END/IND 0.92); tongue oval and posterior margin rounded, more than half free posteriorly, first prepharyngeal fold trilobate and second strongly serrated with 10 denticles. Fairly long vocal slits on both sides of tongue at level of corner of mouth. In life, some tubercles on all dorsal surfaces, and a weakly

developed skin fold from eye to scapular region (forming lateral margin of "scapular W"); all ventral surfaces smooth. In preservative, most dorsal surfaces smooth, lateral surfaces of body rugose; all ventral surfaces smooth except a transverse skin fold on throat as part of subgular vocal sac. Legs long (TL/SUL 0.55), no webbing between fingers or toes; discs of fingers much wider than discs of toes (T4D/F3D 0.64), first finger and first toe moderately long and with clearly pronounced disc; disc of first finger about two thirds as wide as disc of third finger; relative length of fingers 3>4>2>1. Third toe clearly longer than the fifth, disc of fifth toe slightly smaller than disc of first toe, all finger and toe discs with terminal grooves; relative length of toes 4>3>5>2>1; subarticular, metatarsal and metacarpal tubercles not or only scarcely developed.

Colour pattern: In life, dorsal surfaces of body and extremities yellowish with irregular dark-grey mottling. Flanks whitish with only a few indistinct grey spots. Conspicuous is a yellowish "W" bordered by dark-grey longitudinal and cross stripes on the anterior back, a dark-grey dorsolateral stripe and a yellowish zig-zag stripe extending between lumbar ocelli (Fig. 1A). Overall impression of ventral surfaces is whitish blue-grey (strong magnification of these areas shows many small dark grey dots arranged in irregular groups), throat lighter and chest darker than remaining areas. Skin with yellowish hue on anterior throat, on ventral upper arms, in inguinal region and on ventral thighs. Most ventral surfaces with white dots (Fig. 1B). Dorsal and ventral part of iris silvery with blackish venation, anterior and posterior region orange-red with blackish venation.

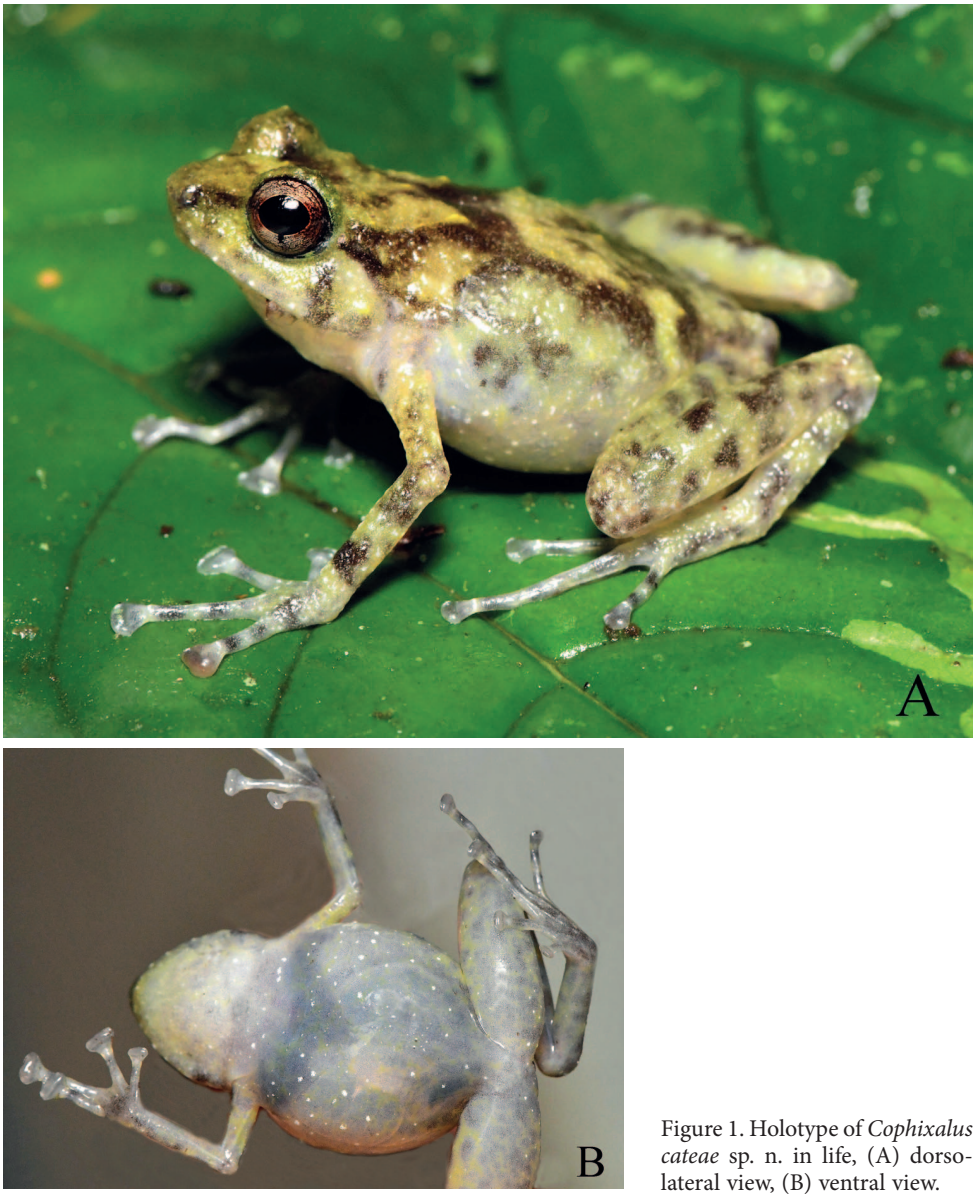

Figure 1. Holotype of *Cophixalus cateae* sp. n. in life, (A) dorsolateral view, (B) ventral view.

In preservative, dorsal colouration a mixture of off-white and grey-brown areas. Surfaces that are mostly or completely off-white are dorsal snout, interior of W-figure on anterior dorsum, middle-dorsum, lumbar ocelli, posterior dorsum, inferior flanks and tympana. A broad interocular band, irregular dorsolateral band from eye to lumbar ocellus, triangular spot posterior to W-figure, and most of posterior dorsum are grey brown. Dorsal extremities are off-white mottled with grey-brown, coloured and uncoloured areas are of about same size. Overall impression of ventral surfaces is off-white; a closer inspection indicates countless fine dark dots that form reticula and/or flecks. White dots disappeared.

Vocalization: We analysed one complete call from the holotype. One additional call that was of insufficient quality for comprehensive analysis lasted 13.6 s. The analysed call is composed of 49 peeping (whistling) notes with a total duration of 18.5 s (Fig. 2). Notes start with a burst of maximum amplitude that quickly decreases to minimum amplitude then gradually rises from minimum to the second highest level and drops thereafter quickly to zero (Fig. 3A); pulses are absent (Fig. 3B). With a length of 551 ms first note is about twice as long as all remaining ones. These range from 179 ms to 400 ms, mean note length 268 ± 66.4 ms. Mean duration of inter-note intervals is 112.2 ± 11.9 ms, range 72–152 ms (last interval longest), n=48, repetition rate 2.7 notes/s; dominant frequency is at 2.6 kHz (Fig. 4).

Distribution and ecology: *Cophixalus cateae* is known from the type locality on Iagifu Ridge at the eastern edge of the Agogo Range in Southern Highlands Province, Papua New Guinea, and from approximately 22 km to the

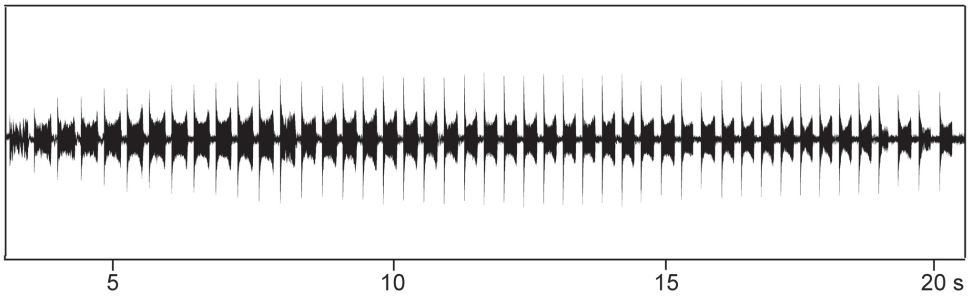

Figure 2. Oscillogram of a nearly complete advertisement call from *Cophixalus cateae* sp. n. First three notes were cut off because of poor quality. Sampling rate at 96 kHz and 16 Bit.

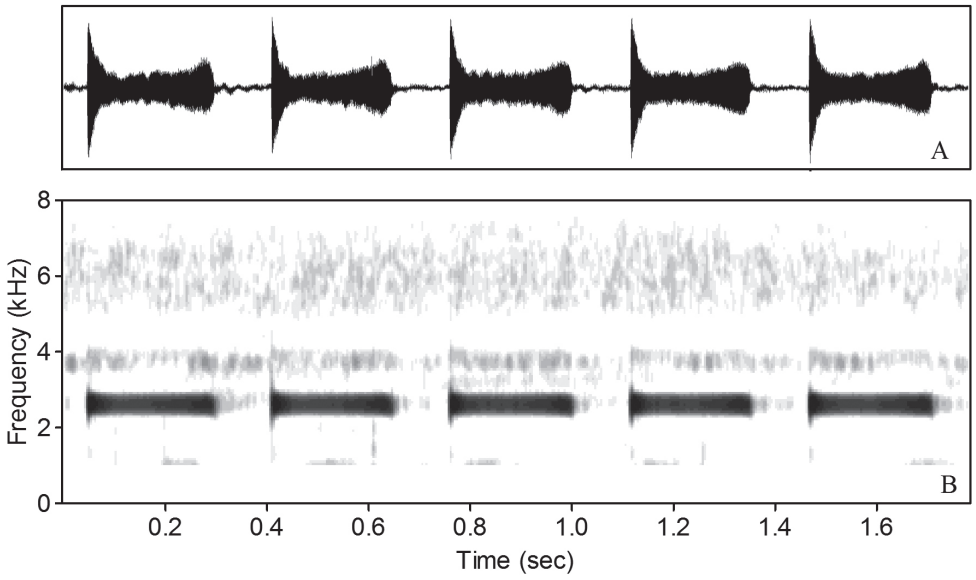

Figure 3. Oscillogram (A) and spectrogram (B) of five notes from an advertisement call of *Cophixalus cateae* sp. n. Sampling rate conversion from 96 kHz to 16 kHz; spectrogram parameters: FFT length 512, Window FlatTop, Bandwidth 157 Hz, resolution 31 Hz, Overlap 93.75%.

north-west in the Moran area of the Agogo Range, where calls of this species were also heard (Fig. 15). The habitat at both of these localities is extremely wet, mossy lower-montane rainforest on limestone karst substrates at altitudes between 1,400 and 1,800 m a.s.l. (Fig. 5). The holotype was calling from a small shrub emerging from a large limestone block that jutted approximately 2 m above the forest floor.

Etymology: The specific epithet is a genitive honorific for the senior author's older daughter, Cate Richards, in gratitude for her understanding and patient acceptance of his long periods of absence in the field.

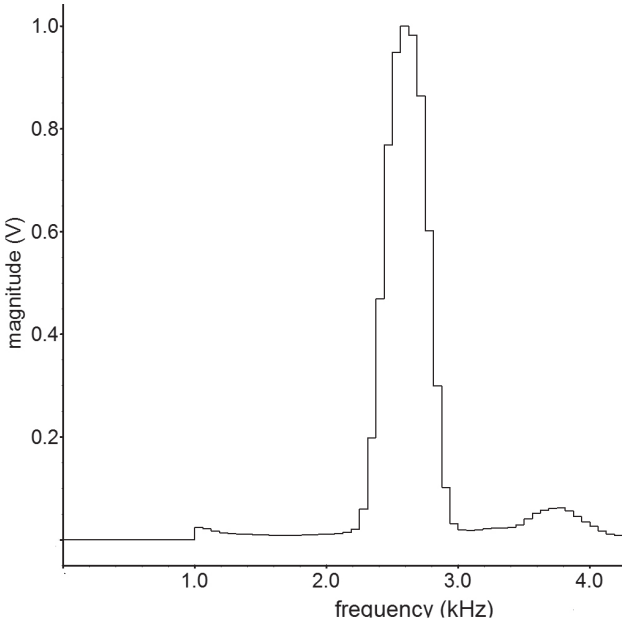

Figure 4. Amplitude spectrum of an advertisement call from *Cophixalus cateae* sp. n. Same parameters as in Fig. 3. Basic noise was deleted up to 1 kHz.

Figure 5. Forest interior at the type locality of *Cophixalus cateae* sp. n. The limestone block that is visible in the left foreground of the image is typical of the karst habitat where this species occurs.

***Cophixalus hannahae* sp. n.**
(Figs 6–10)

ZooBank LSID: urn:lsid:zoobank.org:act: A5F659E5-8A23-4F55-BDF1-92AB27C967E6

Holotype: SAMA R71379 (SJR 10314), adult male from Baia River Valley, Western Province, Papua New Guinea (6.0205° S, 142.5473° E; 330 m a.s.l.) collected on 11 February 2008 by S. J. Richards.

Paratypes: SAMA R71380 (SJR 10330), PNGNM (FN SJR 10331), ZMB 88566 and 88567 (FN SJR 10354, 10355), same data as holotype except PNGNM (SJR 10331) is female, all collected 12–13 February 2008; SAMA R71381 (SJR 14153), adult male from approximately 13 km east of Ludesa Mission, Southern Highlands Province, Papua New Guinea (6.4483° S, 142.5956° E; 400 m a.s.l.) collected on 5 August 2014 by S. J. Richards.

Diagnosis: A species of *Cophixalus* characterized by the unique combination of : (1) small size (SUL 20.4–21.8 mm in five adult males and 23.2 mm in one adult female); (2) body slender, legs medium length (TL/SUL 0.48–0.50); (3) third toe considerably longer than fifth; (4) toe and finger discs distinct and all with circum-marginal grooves, discs of fingers marginally wider than or equal to those of toes (T4D/F3D 0.87–1.00); (5) dorsal and ventral surfaces smooth; (6) dorsal surfaces fairly uniform yellowish- to reddish-brown or grey with reddish-brown flecking in life, dorsal snout marked by a conspicuous light triangular spot bordered by a dark fleck posteriorly; (7) ventral surfaces of hind limbs in life dark orange, venter grey with whitish flecks and throat orange with brown flecks, in preservative ventral surfaces pale yellowish with a few small brown spots on throat and chest; (8) advertisement call consists of a single short, peeping note (duration 46–75 ms) uttered singly or in groups of 2–10 for between 1 and 2 minutes; call repetition rate within call groups is 5–6 calls/s.

Cophixalus hannahae sp. n. is here compared with congeners of a similar size (~20–25 mm mean SUL) and with peeping/whistling voices. The new species has many similarities in body proportions, colouration and advertisement calls to *C. balbus* but that species differs from *C. hannahae* in absolute body size (SUL of 15 *C. balbus* males 23.9–30.8 mm vs. five *C. hannahae* males 20.4–21.8 mm) and having conspicuous dark-purple colour on anterior and posterior surfaces of thighs (vs. dark orange in *C. hannahae*). It differs further in having shorter legs (TL/SUL 0.46–0.48 vs. 0.48–0.50, p=0.013, TaL/SUL 0.28–0.30 vs. 0.31–0.33, p=0.0064); substantially larger finger discs than toe discs (vs. marginally larger or same size: T4D/F3D 0.67–0.79 vs. 0.87–1.00); calls of *C. balbus* often contain more than 20 calls=notes in call groups (vs. no more than 10 calls [mean 3.93 calls per group] in *C. hannahae*). Other differences include: shorter mean note duration (35.7±5.1 ms vs. 54.5±4.2 ms in *C. hannahae*) and shorter internote duration (95±12 ms vs. 132±36.8 ms in *C. hannahae*).

Cophixalus biroi differs from *C. hannahae* in the following characters: larger size (males to 27 mm SVL, females to 33 mm vs. 21.8 and 23.2 mm respectively in *C. hannahae*); note-repetition rate of less than 1 note/s (vs. 5–6 calls=notes/s in *C. hannahae*). *Cophixalus clapporum* is larger than *C. hannahae* (males 23.2–27.5 mm SVL) and can be further distinguished by the following features: lower END/IND ratio (0.72–0.96 vs. 0.95–0.105 in *C. hannahae*); longer note length (195–343 ms vs. 46–75 ms in *C. hannahae*); and slower repetition rate (1.82–2.15 notes/s vs. 5–6 notes/s in *C. hannahae*). *Cophixalus cupricarenus* differs from *C. hannahae* by larger body size (SVL 23.4–28.7 mm);

Figure 6. Holotype of *Cophixalus hannahae* sp. n., (A) dorsolateral view in life, (B) ventral view in preservative.

Figure 7. A light morph of *Cophixalus hannahae* sp. n. (SAMA R71380).

Table 2. Body measurements and body ratios of the type series of *Cophixalus hannahae* sp. n. SAMA R 71379 is the male holotype; PNGNM (SJR 10331) is an adult female, all others are adult males. All measurements in mm; for explanation of abbreviations see "Material and methods".

Reg.No	SAMA R71379	SAMA R71380	PNGNM (SJR 10311)	ZMB 88566	ZMB 88567	SAMA R71381	Mean±SD
SUL	21.2	21.0	23.2	21.8	20.6	20.4	
TL	10.2	10.6	11.7	10.7	10.3	10.3	
TaL	6.5	6.9	7.2	6.9	6.4	6.4	
T4L	10.2	10.2	11.5	10.4	10.1	10.1	
T4D	1.2	1.2	1.3	1.3	1.2	1.0	
T1D	0.7	0.7	0.8	0.7	0.7	0.5	
F3L	5.6	5.8	6.5	6.0	5.4	5.7	
F3D	1.2	1.3	1.5	1.4	1.3	1.1	
F1D	0.6	0.6	0.8	0.7	0.6	0.4	
HL	7.0	6.9	7.5	6.7	7.0	6.8	
HW	8.4	8.3	8.8	8.5	8.4	8.3	
END	2.3	2.1	2.4	2.0	2.2	2.0	
IND	2.3	2.0	2.5	2.1	2.2	2.1	
SL	3.5	3.5	4.0	3.6	3.7	3.5	
ED	2.5	2.3	2.6	2.7	2.3	2.5	
TyD	1.2	1.0	1.0	1.0	0.8	0.9	
TL/SUL	0.48	0.50	0.50	0.49	0.50	0.50	0.50±0.008
TaL/SUL	0.31	0.33	0.31	0.32	0.31	0.31	0.32±0.008
T4L/SUL	0.48	0.49	0.50	0.48	0.49	0.50	0.49±0.009
T4D/SUL	0.057	0.057	0.056	0.060	0.058	0.049	0.056±0.004
F3L/SUL	0.26	0.28	0.28	0.28	0.26	0.28	0.27±0.010
F3D/SUL	0.057	0.062	0.065	0.064	0.063	0.054	0.061±0.004
T4D/F3D	1.00	0.92	0.87	0.93	0.92	0.91	0.93±0.040
T1D/F1D	1.17	1.17	1.00	1.00	1.17	1.25	1.13±0.103
HL/SUL	0.33	0.33	0.32	0.31	0.34	0.33	0.33±0.010
HW/SUL	0.40	0.40	0.38	0.39	0.41	0.41	0.40±0.012
HL/HW	0.83	0.83	0.85	0.79	0.83	0.82	0.83±0.020
END/SUL	0.108	0.100	0.103	0.092	0.107	0.098	0.101±0.006
IND/SUL	0.108	0.095	0.108	0.096	0.107	0.103	0.103±0.006
END/IND	1.00	1.05	0.96	0.95	1.00	0.95	0.99±0.039
ED/SUL	0.118	0.110	0.112	0.124	0.112	0.123	0.117±0.006
TyD/SUL	0.057	0.048	0.043	0.046	0.039	0.044	0.046±0.006
TyD/ED	0.48	0.43	0.38	0.37	0.35	0.36	0.40±0.050
SL/SUL	0.165	0.167	0.172	0.165	0.180	0.172	0.170±0.006

by having dark dorsolateral and dorsal stripes on green or yellow-brown ground colour (vs. absent in *C. hannahae*); a copper-colored head; and constant inter-note intervals (vs. variable inter-note intervals). *Cophixalus kaindiensis* differs from the new species by its variably dark-brown spotted/mottled dorsal surfaces (vs. uniform or reddish mottled), larger body size (males to 28 mm SVL vs. 23 mm in *C. hannahae*); shorter legs (TL/SVL 0.41–0.47 vs. 0.48–0.50 in *C. hannahae*); broader snout (END/IND 0.70–0.80 vs. 095–0.105 in *C. hannahae*); call notes lasting about 100 ms (vs. ~50 ms in *C. hannahae*), with repetition rate of 1.9–2.1 notes/s (vs. 5–6 notes/s in *C. hannahae*). *Cophixalus monosyllabus* has a dark "face mask" and blackish or dark brown W-mark in scapular region, both absent in *C. hannahae*; broader snout (END/IND 0.84–0.96 vs. 0.95–1.05 in *C. hannahae*); long, single-note calls of 173–224 ms (vs. calls in groups of 1–10 each with 46–75 ms duration in *C. hannahae*). *Cophixalus nubicola* is larger than *C. hannahae* (SVL to 30 mm vs. 23.2 mm) with shorter shanks (TL/SUL 0.42–0.46 vs. 0.48–0.50 in *C. hannahae*) and lower END/IND ratio (0.63–0.74 vs. 0.95–1.05). *Cophixalus pipilans* Zweifel, 1980 has a dark "face mask" (vs. absent in *C. hannahae*); longer legs (TL/SVL 0.52–0.62 vs. 0.48–0.50 in *C. hannahae*); first finger small without a broadened disc (vs. moderately developed and with a broadened disc in *C. hannahae*); repetition rate of about 1.5 notes/s (vs. 5–6

calls/s in *C. hannahae*). *Cophixalus salawatiensis* Günther et al., 2015 has a dark "face mask", whitish canthal stripe and dark supratympanic stripe (all absent in *C. hannahae*). It further differs in the following features: broader snout (END/IND 0.78–0.94 vs. 0.95–1.05 in *C. hannahae*); advertisement call notes with faster repetition rate (13.5–15.6 notes/s vs. 5–6 calls/s in *C. hannahae*). *Cophixalus tenuidactylus* Günther & Richards, 2012 differs from the new species in having finger and toe tips not expanded into discs (vs. expanded discs in *C. hannahae*). *Cophixalus tetzlaffi* Günther, 2003 has a black "face mask" and dorsolateral glandular ridges embedded in blackish longitudinal stripes (vs. both absent in *C. hannahae*); advertisement calls of *C. tetzlaffi* are 2–4 peeping notes, with note length of 347–518 ms (vs. single-note calls of 46–75 ms duration in *C. hannahae*).

Description of the holotype (Figs 6A–B): A male of 21.2 mm SUL. Its measurements are presented in Table 2. Head broader than long (HL/HW 0.83), canthus rostralis distinct; loreal region slightly oblique; snout protruding in profile and rounded in dorsal view; nostrils directed laterally; eye diameter about the same as eye–naris distance (ED/END 1.08); entire tympanic annulus visible, tympanum nearly half of eye diameter (TyD/ED 0.48), supratympanic fold from eye to insertion of foreleg present but

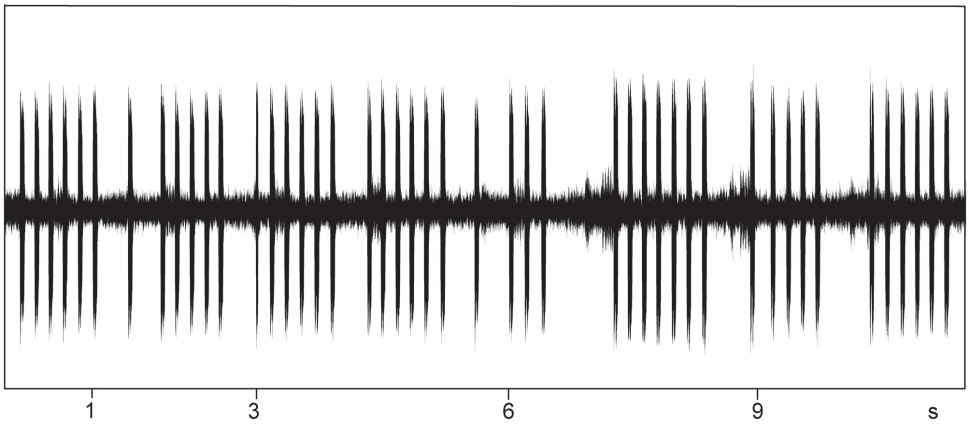

Figure 8. Oscillogram of eight call groups and two single calls in chronological sequence from *Cophixalus hannahae* sp. n. Sampling rate at 96 kHz and 16 Bit.

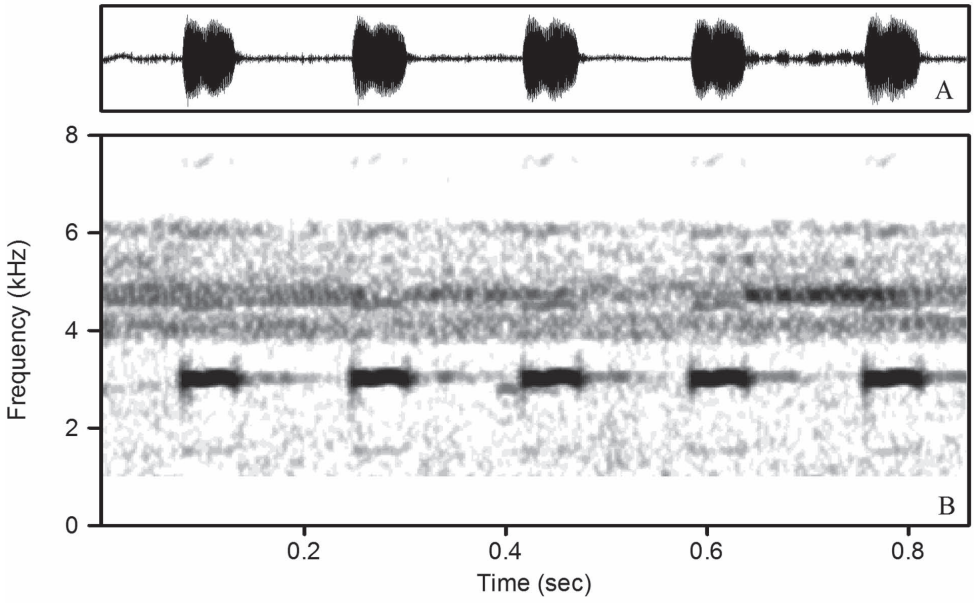

Figure 9. Oscillogram (A) and spectrogam (B) of a call=note group consisting of five elements from *Cophixalus hannahae* sp. n. Sampling rate conversion from 96 kHz to 16 kHz; spectrogram parameters: FFT length 512, Window FlatTop, Bandwidth 157 Hz, resolution 31 Hz, Overlap 93.75%.

weakly pronounced; internarial distance the same as distance between eye and naris (END/IND 1.00); tongue wide and long, posterior margin weakly indented; prepharyngeal ridge with 11 denticles. In life, dorsal surfaces smooth with only a few indistinct tubercles, all ventral surfaces smooth; in preservative, all dorsal and ventral surfaces smooth. Vocal slits on both sides of tongue at level of corner of the mouth. Legs of medium length (TL/SUL 0.48), no webbing between fingers or toes; discs of fingers same width as those of toes (T4D/F3D 1.00), first finger and first toe moderately long, with clearly pronounced discs; disc of first finger considerably smaller than disc of fourth finger; relative lengths of fingers 3>4>2>1. Third toe clearly longer than fifth, disc of fifth toe about same width as disc of first toe, all finger and toe discs with terminal grooves; relative lengths of toes 4>3>5>2>1; palmar, plantar and subarticular tubercles not or scarcely expressed.

Colour pattern: In life, dorsal surfaces red-brown with some grey tones, which dominate on flanks and shanks. Red-brown dorsum becoming darker on posterior of head, this darker region sharply delineated anteriorly by lighter region that extends to sides of head; tympanum does not differ in colour from its surrounding. Superior and inferior parts of iris golden with dark-brown venation, anterior and posterior parts wine-red; some whitish spots on lower flanks; no lumbar ocellus. In preservative, throat, chest, belly, thighs, shanks and upper arms uniform pale yellowish; palms, soles, forearm and tarsus with dark grey-brown patches and spots. All dorsal surfaces off-white with small dark-brown dots, these less dense on snout, sides of head and body, upper arms, and anterior and posterior extremities, most dense on thighs, shanks, forearms and mid-dorsum, where they constitute continuous dark-brown flecks.

Variation: Mensural variation in the type series is minimal (Table 2). Colouration of dorsal surfaces in life varies from light yellow with a greenish hue (Fig. 7) to red-brown (Fig. 6A), ventral surfaces show different tones of yellowish. Dorsal surfaces in preservative vary from light grey-brownish (SAMA R71380) to dark red-brown (ZMB 88567), conspicuous in all specimens is a lighter snout top that is sharply delineated from darker colours posteriorly, light finger tips, a light tympanic region and light anterior and posterior thighs. Four specimens exhibit a dark-brown hourglass mark between head and scapular region; in two specimens this mark is only faintly indicated. Ventral surfaces are straw yellow without spots (Fig. 6B) or with only a few distinct middle-brown to dark-brown spots on throat and chest.

Vocalization: We analysed calls of SAMA R71380 and SAMA R71381. Calls from both are very similar, so they are combined in the following analyses. Advertisement calls of *Cophixalus hannahae* are not neatly described by the terminology provided by Köhler et al. (2017). The call is a single short, peeping note that is uttered singly or in groups, with calls produced at irregular intervals for more than one minute before a long silence. Because calls produced during this period are 'clumped' into call groups of varying duration separated by distinctly irregular intervals, they do not meet the criteria for a call 'series' as defined by Köhler et al. (2017). However for the purposes of this description we define the single, unpulsed notes with internote intervals longer than note lengths produced by *C. hannahae* as 'calls' (and they are compared with individual notes from congeners in species comparisons), the distinctly clumped groups of calls as 'call groups', and the combined call groups as a 'call series'. Advertisement call series are extremely long, with a duration of more than one minute (four series lasted 72–88 s). Within these series, calls are produced singly or they are produced in 2–10 calls per group (Fig. 8), mean 4.1 ± 2.4 calls/group, n=135. There is a tendency for call groups at the beginning of a series to comprise fewer calls at longer inter-call intervals than groups in the second half of a series. Intervals between call groups within series are 0.22–1.26 s, mean 0.56 ± 0.25 s, n=86. Intervals between calls (=notes) within call groups are 89–250 ms, mean 132 ± 36.8 ms, n=168. Amplitude of calls rises rapidly at the beginning and decreases rapidly at the end of a call, with a deep indentation after about one third of the call duration (Fig. 9A). Calls are tonal, unpulsed, and with very weak frequency modulation over the duration of the call (Fig. 9B). Mean duration of calls is 54.5±4.2 ms, range 46–75 ms, n=150. Repetition rate in call groups is 5–6 calls/s. Dominant frequency is at 3.0 kHz (Fig. 10).

Distribution and ecology: *Cophixalus hannahae* is known only from the southern versant of New Guinea's central cordillera in Western and Southern Highlands provinces in

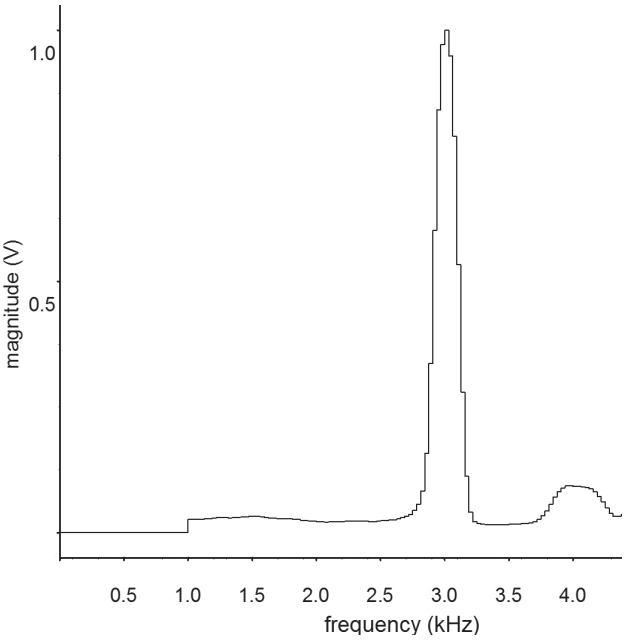

Figure 10. Amplitude spectrum of an advertisement call group from *Cophixalus hannahae* sp. n. Same parameters as in Fig. 9. Basic noise was deleted up to 1 kHz.

Papua New Guinea (Fig. 15). Males called from low foliage in wet, foothill rainforest (Fig. 14) at night after rain. Other individuals were perched on low foliage at night; none was encountered during the day.

Etymology: The specific epithet is a genitive honorific for the senior author's younger daughter, Hannah Richards, in gratitude for her understanding and patient acceptance of his long periods of absence in the field.

Oreophryne nicolasi sp. n.
(Figs 11–13)

ZooBank LSID: urn:lsid:zoobank.org:act: 99A45E4E-2D1A-4E73-89BB-A992DE76D7B1

Holotype: SAMA R71382 (SJR 10356), adult male, Baia River Valley, Western Province, Papua New Guinea (6.0205° S, 142.5473° E; 330 m a.s.l.) collected on 13 February 2008 by S. J. Richards.

Paratypes: SAMA R71383 (SJR 10360), PNGNM (SJR 10361, 10370), same data as holotype except all collected on 14 February 2018 and SAMA R71383 is female; ZMB 88568 (SJR 10398; female), SAMA R71384 (SJR 10432; subadult female, SAMA R71385; male), ZMB 88569 (SJR10461; female), upper Strickland River catchment, Western Province, Papua New Guinea (5.9018° S, 142.4360° E; 950 m a.s.l.) collected on 18–21 February 2008 by S. J. Richards; SAMA R71386 (SJR 10495; male), upper Strickland River catchment, Western Province, Papua New Guinea (5.8078° S, 142.3083° E; 215 m a.s.l.) collected on 28 March 2008 by S. J. Richards.

Diagnosis: A species of *Oreophryne* characterised by the following unique combination of: (1) snout–urostyle length 24.8–29.3 mm in five adult males and 33.7–37.6 mm in three adult females; (2) procoracoids and clavicles present, procoracoids with ligamentous connection to the scapulae; (3) body slender, legs medium length (TL/SUL 0.49–0.53), third toe clearly longer than fifth; (4) toe and finger discs distinct and all with circum-marginal grooves, discs of fingers considerably larger than those of toes (T4D/F3D 0.71–0.82); (5) no webbing between toes; (6) dorsum with some tubercles, ventral surfaces smooth; (7) dorsal surfaces light yellow to medium-brown with distinct blackish spots and a W-mark in the scapular region, ventral surfaces whitish, heavily mottled by distinct and indistinct brown flecks; (8) advertisement calls consist of 1–5 rasping notes with a duration of 1–2 seconds, a mean note length of about 300 ms, mean internote length about 160 ms, mean repetition rate 2.5 notes/s, dominant frequency at 2.75 kHz.

Oreophryne nicolasi can be distinguished from most congeners in the New Guinea region in its combination of having a ligamentous connection between the procoracoid and the scapula, and having the third toe in most specimens clearly longer than the fifth. Only two species – *O. atrigularis* Günther, Richards & Iskandar, 2001 and *O. wapoga* Günther, Richards & Iskandar, 2001 – share these characters, and they also share with the new species a lack of webbing between the toes. However both of these species – which are known only from western New Guinea – are much smaller than *O. nicolasi* (SUL of both species < 27 mm vs. up to 38 mm), exhibit a dark loreal mask (absent in *nicolasi*), and their calls are long series of notes lasting up to 30 seconds (vs. 1–5 rasping notes with a duration of 1–2 seconds). Several other *Oreophryne* species with a ligamentous connection between the procoracoid and the scapula have the 3rd and 5th toes of sub-equal length. These are compared here: *Oreophryne albopunctata* (Van Kampen, 1909), *O. banshee* Kraus, 2016, *O. biroi* (Méhely, 1897), *O. brunnea* Kraus, 2017, *O. equus* Kraus, 2016, *O. furu* Günther et al., 2009, *O. hypsiops* Zweifel, Menzies & Price, 2003, *O. insulana* Zweifel, 1956, *O. kapisa* Günther, 2003, and *O. meliades* Kraus, 2016 are smaller than *O. nicolasi* (SUL <30 mm vs. up to 38 mm), and all have webbing between the toes (vs. webbing absent). All these smaller species can also be distinguished from *O. nicolasi* by their advertisement calls. The call of *O. nicolasi* is a series of 1–5 rasping notes with a duration of 1–2 seconds. In contrast the call of *Oreophryne albopunctata* is a 'series of 20–23 loud, finely pulsed buzzes lasting about 2.5–3 seconds'(Richards et al. 2015); *O. banshee*, *O. equus*, *O. hypsiops*, and *O. insulana* produce 'peeping' calls; *O. biroi*, *O. brunnea*, *O. furu* and *O. kapisa* produce 'rattle' calls; and *O. meliades* produces a series of 41–61 clicks. *Oreophryne ampelos* Kraus, 2011, *O. unicolor* Günther, 2003 and *O. pseudunicolor* Günther & Richards, 2016 are similar in size to *O. nicolasi* (SUL to ~30–36 mm vs. to 38 mm) but all three species have conspicuous webbing between the toes (vs. absent), lack dark-edged tubercles on the dorsum (vs. present), and *O. unicolor* and *O. pseudunicolor* further differ from *nicolasi* in having calls consisting of a series of melodious peeps (vs. 1–5 rasping notes). The call of *O. ampelos* is not known (Kraus 2011).

Description of the holotype (Figs. 11A–B): A male of 26.1 mm SUL. Full measurements are presented in Table 3. Head slightly broader than long (HL/HW 0.94), canthus rostralis straight and distinct; loreal region weakly concave; snout protruding in profile and truncate in dorsal view; nostrils directed laterally; eye diameter clearly greater than eye–naris distance (ED/END 1.38); tympanic annulus partly covered by skin folds, tympanum about one third of eye diameter (TyD/ED 0.30), supratympanic fold extends from eye to region posterior to tympanum; internarial distance same as distance between eye and naris (END/IND 1.00); tongue very long, posterior margin indistinctly rounded; first prepharyngeal fold scarcely visible, second strongly serrated. Vocal slits on both sides of tongue at level of corner of mouth. Legs of medium length (TL/SUL 0.51), no webbing between fingers or toes; discs of fingers clearly wider than discs of toes (T4D/F3D 0.73), first finger and first toe moderately long and with clearly pronounced discs; disc of first finger about two thirds as wide as disc of third finger; relative length of fingers 3>4>2>1. Third toe

Table 3. Body measurements and body ratios of the type series of *Oreophryne nicolasi* sp. n. SAMA R 71382 is the male holotype; PNGNM (SJR 10361, 10370), SAMA R71385 and SAMA R71386 are adult males, SAMA R71383, ZMB 88568 and ZMB 88569 are adult females and SAMA R71384 is a subadult female. All measurements in mm; for explanation of abbreviations see "Material and methods".

Reg.No.	SAMA R71382	SAMA R71383	PNGNM (SJR10361)	PNGNM (SJR10370)	ZMB 88568	SAMA R71384	SAMA R71385	ZMB 88569	SAMA R71386	Mean±SD
SUL	27.5	36.6	26.1	25.4	33.7	27.9	29.3	37.6	24.8	
TL	13.9	17.8	13.9	13.4	17.0	14.4	14.5	19.1	12.7	
TaL	8.8	10.5	8.3	8.4	9.9	9.1	8.6	10.8	7.6	
T4L	12.8	17.0	13.6	13.0	16.1	13.8	13.7	19.8	12.8	
T4D	1.6	2.2	1.5	1.5	2.0	1.6	1.7	2.5	1.4	
T1D	1.3	1.7	1.2	1.2	1.6	1.5	1.2	2.0	1.2	
F3L	8.4	11.6	8.0	8.1	10.7	8.5	9.4	12.2	8.0	
F3D	2.2	3.0	2.0	1.9	2.8	2.1	2.1	3.2	1.8	
F1D	1.5	2.1	1.3	1.2	2.0	1.4	1.4	2.3	1.1	
HL	9.8	11.5	9.0	9.1	11.1	9.6	10.7	12.4	8.8	
HW	10.4	13.0	9.4	9.5	12.2	10.0	11.5	13.9	8.9	
END	2.6	3.3	2.5	2.6	3.0	2.6	2.7	3.2	2.5	
IND	2.6	3.4	2.5	2.5	3.3	2.7	2.8	3.4	2.5	
SL	4.7	5.5	4.8	4.7	5.1	4.9	5.1	6.5	4.5	
ED	3.6	4.4	3.4	3.3	4.1	3.6	4.1	4.5	3.2	
TyD	1.2	1.6	1.4	1.4	1.6	1.4	1.5	2.0	1.2	
TL/SUL	0.51	0.49	0.53	0.53	0.50	0.52	0.49	0.51	0.51	0.51±0.015
TaL/SUL	0.32	0.29	0.32	0.33	0.29	0.33	0.29	0.29	0.31	0.31±0.018
T4L/SUL	0.47	0.46	0.52	0.51	0.48	0.49	0.47	0.53	0.52	0.49±0.026
T4D/SUL	0.058	0.060	0.057	0.059	0.059	0.057	0.058	0.066	0.056	0.059±0.003
F3L/SUL	0.31	0.32	0.31	0.32	0.32	0.30	0.32	0.32	0.32	0.32±0.007
F3D/SUL	0.080	0.082	0.077	0.075	0.083	0.075	0.072	0.085	0.079	0.078±0.005
T4D/F3D	0.73	0.73	0.75	0.79	0.71	0.76	0.81	0.78	0.82	0.76±0.038
T1D/F1D	0.87	0.81	0.92	1.00	0.80	1.07	0.86	0.87	1.09	0.92±0.108
HL/SUL	0.36	0.31	0.34	0.36	0.33	0.34	0.37	0.33	0.35	0.34±0.019
HW/SUL	0.38	0.36	0.36	0.37	0.36	0.36	0.39	0.37	0.36	0.37±0.011
HL/HW	0.94	0.88	0.96	0.96	0.91	0.96	0.93	0.89	0.99	0.94±0.036
END/SUL	0.095	0.090	0.096	0.102	0.089	0.093	0.092	0.085	0.100	0.094±0.005
IND/SUL	0.095	0.093	0.096	0.098	0.098	0.097	0.096	0.090	0.100	0.097±0.005
END/IND	1.00	0.97	1.00	1.04	0.91	0.96	0.96	0.94	0.93	0.97±0.040
ED/SUL	0.131	0.120	0.130	0.130	0.122	0.129	0.140	0.120	0.129	0.127±0.009
TyD/SUL	0.044	0.044	0.054	0.055	0.047	0.050	0.051	0.053	0.048	0.050±0.004
TyD/ED	0.33	0.40	0.41	0.42	0.39	0.39	0.37	0.44	0.38	0.39±0.032
SL/SUL	0.171	0.150	0.184	0.185	0.151	0.176	0.174	0.173	0.181	0.171±0.013

clearly longer than fifth, disc of fifth toe about same width as disc of first toe, all finger and toe discs with terminal grooves; relative length of toes 4>3>5>2>1; inner metatarsal tubercle and distal-most subarticular tubercle on fourth toe flat but distinct, other metatarsal, subarticular and metacarpal tubercles not or only scarcely developed. All dorsal surfaces and especially flanks covered by tubercles and wrinkles; in life some tubercles on all dorsal surfaces, especially conspicuous are a dorsolateral row of large tubercles that continue on upper eye lid and a paravertebral tubercle row with tubercles clearly smaller than those in dorsolateral row. All ventral surfaces smooth. In preservative, all dorsal surfaces with some small tubercles, body sides corrugated, ventral surfaces smooth.

Colour pattern: In life, overall colouration of dorsal surfaces grey-yellow dorsally, with most tubercles encircled by blackish spots, and those spots also arranged in a W-figure from eye to scapular region; tympanum lighter than all other dorsal surfaces and bordered by two dark brown flecks. Iris dark orange with blackish venation; there is neither a dark nor a light interocular band, dorsal snout is not lighter than other dorsal areas and there is no lumbar ocellus. All ventral surfaces off-white with a network of small brown dots.

In preservative, ground colouration of all dorsal surfaces light brown with dark-brown and blackish spots forming an interocular asymmetric T-figure with the base of the T pointing backwards, a W-figure between eyes and scapular region and four rows of spots on middle and posterior back; flanks whitish and mottled with dark-brown spots. Ventral surfaces off-white and mottled with a network of brown flecks; density and intensity of these brown flecks is highest on throat and hind legs.

Variation: Mensural variation for the type series is shown in Table 3. Most paratypes have a mucronate snout tip in dorsal view, in contrast to the holotype with a truncate snout tip. In life, ground colour of dorsal surfaces varies from light greenish-yellow to grey-brown, interspersed with numerous brown dots and larger blackish spots of different shapes and sizes, but mostly roundish. Main difference between specimens in life and in preservative is the overall dorsal colour: light yellowish, greenish, greyish or

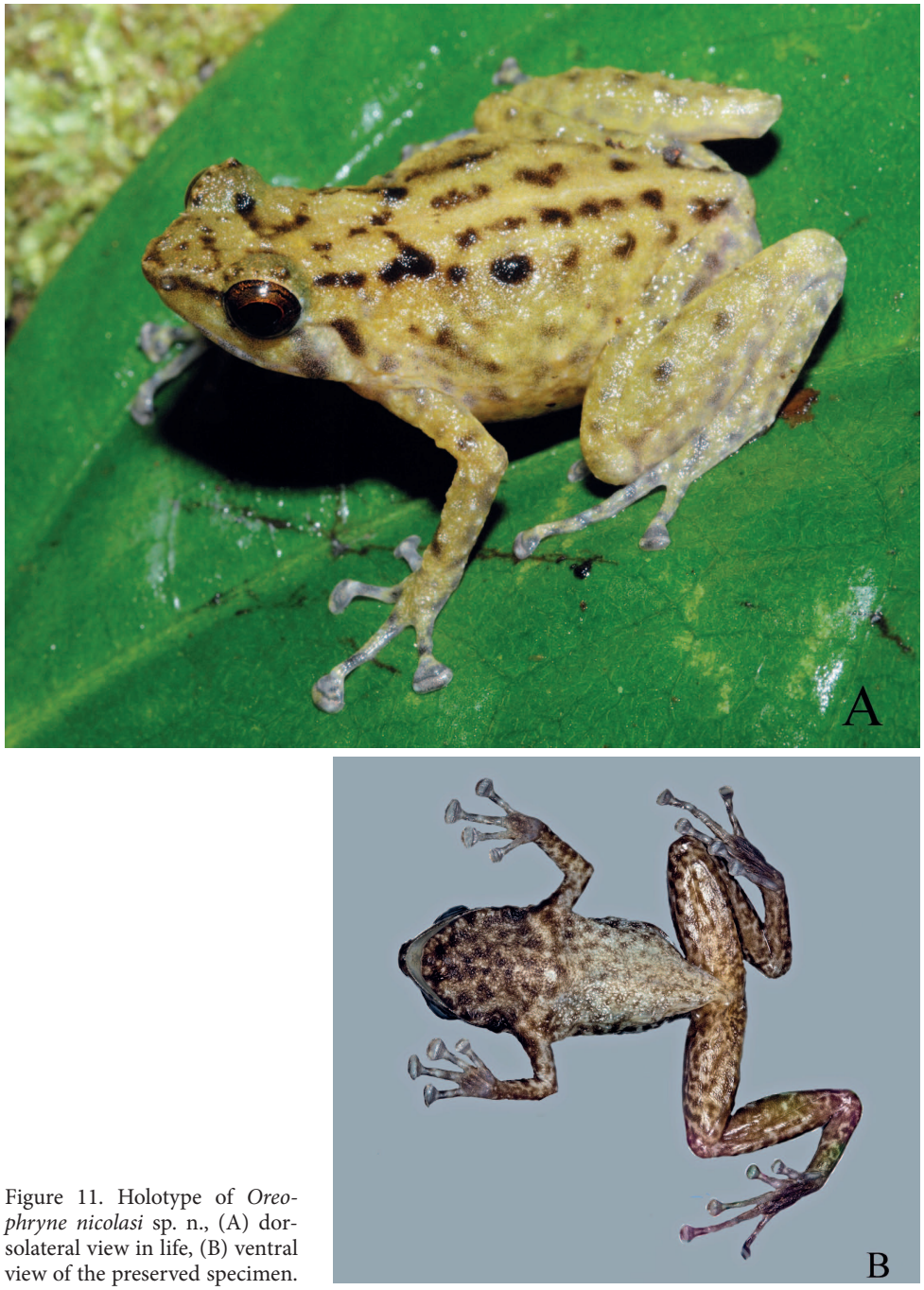

Figure 11. Holotype of *Oreophryne nicolasi* sp. n., (A) dorsolateral view in life, (B) ventral view of the preserved specimen.

brownish in life but middle brown to dark reddish brown in preservative; only two specimens exhibit light dorsal surfaces in preservative. Five specimens show a complete W-mark in the scapular region, four have an incomplete W-mark. All types exhibit some longitudinal rows of roundish flecks and/or stripes of blackish or dark-brown colour on dorsum and in some cases also on upper flanks. Most of those flecks have a tubercle in their centre, only a few tubercles are not surrounded by dark brown or blackish pigmentation. Ground colour of ventral surfaces is off-white and covered by a network of brown flecks in all specimens, and the distribution of these flecks in all paratypes is similar to the pattern exhibited in the holotype (Fig. 11B).

Vocalization: We analysed three calls from SAMA R71385 and seven calls of an unvouchered male from the same locality. Calls are extremely similar so they were combined for analysis. Advertisement calls of *Oreophryne nicolasi* are finely pulsed (Figs. 12A and 13) and have a distinctly unmelodious rasping sound. Calls contain 1–5 notes and have a duration of 0.41–1.89 s (mean 1.04±0.67 s). Mean note length is 293 ± 79.9 ms, range 161–452 ms, n=27. Mean internote interval length is 158 ± 16 ms, range 137–197 ms, n=17. Mean note-repetition rate in polysyllabic calls is 2.5 ± 0.15, range 2.3–2.7 notes/s. The first pulse of each note has a maximum amplitude, and amplitudes of the following pulses decrease slowly until termination of the note or may be reduced and then increase again during the course of the note (Fig. 12A). There are slight frequency modulations in the course of most notes (Fig. 12B). Pulse repetition rate in notes is about 300 pulses/s. Calls followed one another in intervals of 1.8–5.6 s. Dominant frequency is at 2.75 kHz (Fig. 14); five harmonics are visible (Fig. 12B). Calls are produced in call groups, with several calls produced over a period of up to about 1–2 minutes, separated by long periods of silence (~5–10 minutes).

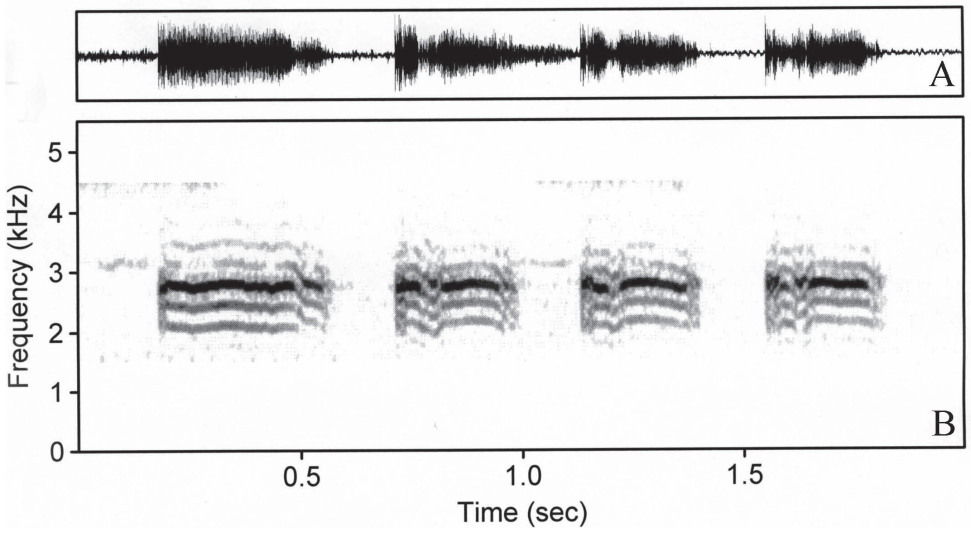

Figure 12. Oscillogram (A) and spectrogram (B) of an advertisement call, consisting of four notes, from *Oreophryne nicolasi* sp. n. Sampling rate conversion from 96 kHz to 12 kHz; spectrogram parameters: FFT length 512, Window FlatTop, Bandwidth 108 Hz, resolution 22 Hz, Overlap 93.75%.

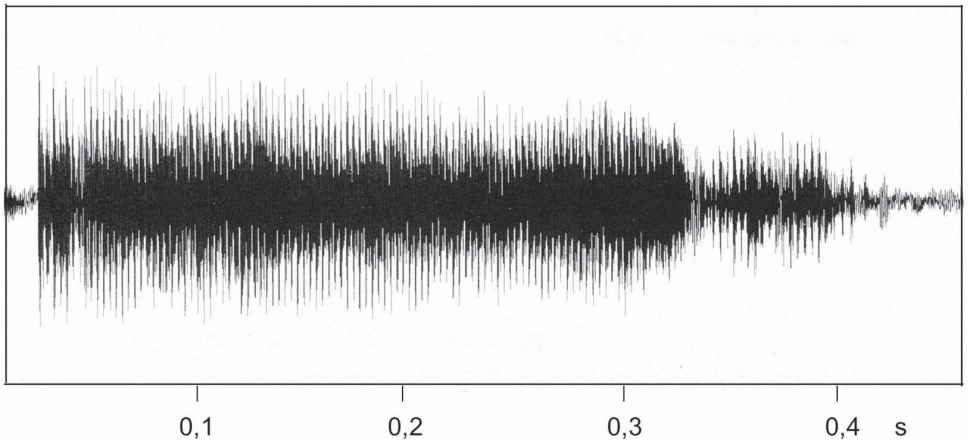

Figure 13. Enlarged oscillogram of the first note of the call in Fig. 12.

Distribution and ecology: *Oreophryne nicolasi* is known from a narrow band along the southern fringe of New Guinea's central cordillera that extends to the lowlands of the Kikori River basin, in Gulf, Western and Southern Highlands Provinces in Papua New Guinea at altitudes between near sea level at Kopi to almost 1,000 m a.s.l. (Fig. 16). Males call from foliage between ~0.5 and 2.0 m above the ground in wet, foothill rainforest (Fig. 15) at night after rain. Other individuals were perched on low foliage at night; none was encountered during the day.

Etymology: The specific epithet is a genitive honorific for the senior author's son, Nicolas Richards, in gratitude for his understanding and patient acceptance of the author's long periods of absence in the field.

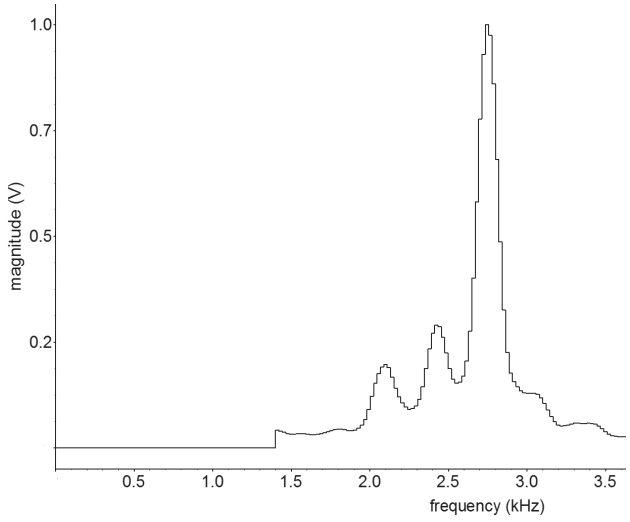

Figure 14. Amplitude spectrum of an advertisement call from *Oreophryne nicolasi* sp. n. Same parameters as in Fig. 12. Basic noise was deleted up to 1.4 kHz.

Figure 15. Habitat of *Cophixalus hannahae* and *Oreophryne nicolasi* at the type locality. Note the rugged terrain and steep limestone cliffs where these species were encountered.

Discussion

Important recent contributions to knowledge about New Guinean *Cophixalus* were provided by Kraus & Allison (2009a) and Kraus (2012), which together described 14 new species of this speciose genus. The two species described in this paper bring the total number of named *Cophixalus* species in the New Guinean region to 48 (Frost 2018), and numerous species in museum collections await formal description. Furthermore, there is no doubt that additional species await discovery in poorly explored regions of New Guinea (Kraus 2012).

To assist identification of species within the diverse New Guinean assemblage of *Cophixalus*, Kraus (2012) constructed a key to named species from the region. This key uses a combination of morphological and acoustic characters to distinguish among species and will become more useful as additional information about a number of poorly known species accumulates during field surveys. One species for which additional information – particularly on advertisement call structure – is required is *Cophixalus cryptotympanum*, a species described from Mt Dayman in south-eastern Papua New Guinea (Zweifel 1956b). That species was subsequently redefined by Zweifel (1962) to include populations elsewhere in the central cordillera with a much larger body size, and this interpretation was accepted by Menzies (2006) who reported *C. cryptotympanum* from nearly the entire length of the central cordillera in Papua New Guinea but noted "Further study may show that more than one species is included in this name as frogs from the central highlands are distinctly larger than those of the type series from Mt Dayman (HB < 30 mm.)" (vs. to 40 mm in animals from more westerly populations; Menzies 2006). This is relevant to our study because in the absence of genetic and acoustic data from the type locality, the broader interpretation of species boundaries in *C. cryptotympanum* by Menzies (2006) reduces the number of characters useful for distinguishing that species from several congeners, including *C. cateae* described here. These include the inference that the 'clarity' of the tympanic membrane may be subject to state of preservation, and that a W-shaped hour-glass mark may be present on some specimens (Menzies 2006).

Kraus & Allison (2009b) suggested that *C. cryptotympanum* is a species complex, with the named form known only from the type locality on Mt Dayman. Unfortunately, in the original description Zweifel (1956b) did not provide detailed body measurements for males and females from the type locality nor a description of variation in colour patterns. We have briefly examined six paratypes of *C. cryptotympanum* (AMNH 56740, 56743, 56747, 56827–8, 56843) and provide some comments which may prove useful, in conjunction with the key provided by Kraus, for distinguishing *C. cryptotympanum* from the new species described here, and from additional new *Cophixalus* species described in future. Four of the six paratypes examined are males, with SVLs of 19.4–25.0 mm. At least three of these (the three largest) have vocal slits, a feature

reported to be absent in this species in the original description (Zweifel 1956b). The remaining two are females containing mature eggs, and these are 28.1 and 28.6 mm SVL. None of the specimens exhibits a distinct W-shaped scapular fold but there are indistinct, narrow dark dorsolateral bands that merge mid-dorsally behind the head on some specimens. Dorsally the skin is distinctly 'rugose', with numerous small tubercles and folds (not 'smooth' as stated by Kraus & Allison, 2009b). The pale narrow line that runs from the eye through the tympanum is distinct.

Based on these observations (presented here to supplement the characters noted in Kraus's [2012] species comparisons and key), *C. cryptotympanum* is a moderately small species (SVL to 25 mm in males, and to ~29 mm in females) with a distinctly rugose dorsum, and a pale narrow line that runs from the eye through the tympanum. These characters distinguish *C. cryptotympanum* from *C. cateae*, described here, and will aid with comparisons of other new *Cophixalus* species described in future. Populations from the central mountains referred to *C. cryptotympanum* by

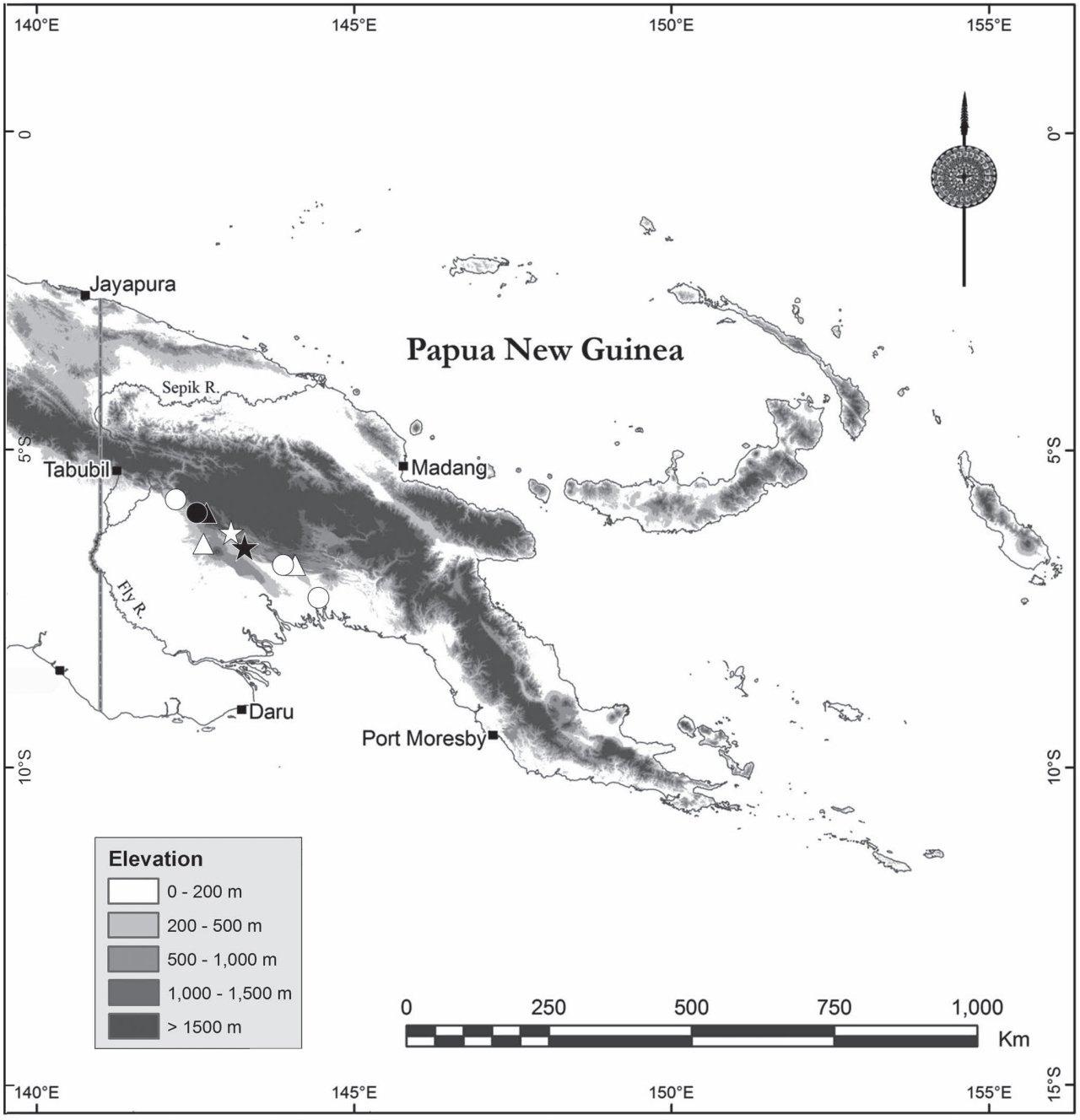

Figure 16. Map showing the distributions of three new microhylid species in New Guinea: star = *Cophixalus cateae* sp. n.; triangle = *C. hannahae* sp. n.; circle = *Oreophryne nicolasi* sp. n. Black symbols indicate the type localities for each species.

Menzies (2006) require further study to determine their taxonomic status.

The description of *Oreophryne nicolasi* brings to 61 the number of species in this genus known from the New Guinea region. The morphology of the new species is unusual; in its general body and snout shape, in having a third toe that is longer than the fifth, extremely long digits with exceptionally large discs (for an *Oreophryne*) on the hands and feet and no trace of webbing between the toes it more closely resembles several *Cophixalus* species (including *C. cateae*, *C. caverniphilus* and *C. cryptotympanum*) than most congeners. Although some of these characters are not entirely unknown in *Oreophryne* (Günther et al. 2001, Kraus 2013), in combination they are unique in the genus and this species was originally identified as an undescribed *Cophixalus* by Richards (2002) on the basis of this suite of characters. We acknowledge that the presence of procoracoids and clavicles (or the *Cophixalus*-like structure of the hands and feet) in *O. nicolasi* may represent morphological homoplasy (or indeed plesiomorphy), but in the absence of molecular evidence to independently assess its relationships we currently retain the existing morphology-based classification for this species.

The three species described herein are to date known only from the extremely wet rainforests that cover most of the high-rainfall belt extending along the southern flanks of New Guinea's central cordillera (McAlpine et al. 1983). This region has a rich known frog fauna (Hyndman & Menzies 1990, Richards 2002), knowledge of which has increased rapidly in recent years, and the ongoing discovery and description of previously unknown forms (Günther & Richards 2016, 2017, 2018) underscores the need to better document and ultimately to preserve this rich but poorly known fauna.

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References

AmphibiaWeb (2019): Berkeley, California: AmphibiaWeb: Information on amphibian biology and conservation. – Available at http://amphibiaweb.org/, accessed 9 January 2019.

Frost, D. R. (2018): Amphibian Species of the World: an Online Reference. Version 6.0 (accessed 01 September 2018). – Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Günther, R. (2003a): First record of the microhylid frog genus *Cophixalus* from western Papua, Indonesia, with descriptions of two new species (Anura: Microhylidae). – Herpetozoa, **16**: 3–21.

Günther, R. (2003b): Three new species of the genus *Oreophryne* from western Papua, Indonesia. – Spixiana, **26**: 175–191.

Günther, R. (2003c): Further new species of the genus *Oreophryne* (Amphibia, Anura, Microhylidae) from western New Guinea. – Zoologische Abhandlungen (Dresden), **53**: 65–85.

Günther, R. (2006): Two new tiny *Cophixalus* species with reduced thumbs from the west of New Guinea (Anura: Microhylidae). – Herpetozoa, **19**: 59–75.

Günther, R. (2010): Another new *Cophixalus* species (Amphibia: Anura: Microhylidae) from western New Guinea. – Bonn Zoological Bulletin, **57**: 231–240.

Günther, R. (2015): Two new *Oreophryne* species from the Fakfak Mountains, West Papua Province of Indonesia (Anura, Microhylidae). – Vertebrate Zoology, **65**: 357–370.

Günther, R. & S. J. Richards (2011): Five new microhylid frog species from Enga Province, Papua New Guinea, and remarks on *Albericus alpestris* (Anura, Microhylidae). – Vertebrate Zoology, **61**: 343–372.

Günther, R. & S. J. Richards (2016): Description of two new species of the microhylid frog genus *Oreophryne* (Amphibia: Anura: Microhylidae) from southern Papua New Guinea. – Vertebrate Zoology, **66**: 157–168.

Günther, R. & S. J. Richards (2017): Three new species of the microhylid frog genus *Choerophryne* (Amphibia, Anura, Microhylidae) from Papua New Guinea. – Zoosystematics and Evolution, **93**: 265–279.

Günther, R. & S. J. Richards (2018): A new species of the microhylid frog genus *Choerophryne* from Papua New Guinea. – Alytes, **36**: 159–169.

Günther, R., S. J. Richards, D. Bickford, & G. R. Johnston (2012): A new egg-guarding species of *Oreophryne* (Amphibia, Anura, Microhylidae) from southern Papua New Guinea. – Zoosystematics and Evolution, **88**: 225–232.

Günther, R., S. J. Richards & C. Dahl (2014): Nine new species of microhylid frogs from the Muller Range in western Papua New Guinea (Anura, Microhylidae). – Vertebrate Zoology, **64**: 59–94.

Günther, R., S. J. Richards & D. Iskandar (2001): Two new species of the genus *Oreophryne* from Irian Jaya, Indonesia (Amphibia, Anura, Microhylidae). – Spixiana, **24**: 257–274.

Günther, R., S. Richards, B. Tjaturadi & D. Iskandar (2009): A new species of the microhylid frog genus *Oreophryne* from the Mamberano Basin of northern Papua Province, Indonesian New Guinea. – Vertebrate Zoology, **59**: 147–155.

Günther, R., S. J. Richards, B. Tjaturadi & K. Krey (2015): Two new species of the genus *Cophixalus* from the Raja Ampat Islands west of New Guinea (Amphibia, Anura, Microhylidae). – Zoosystematics and Evolution, **91**: 199–213.

Hoskin, C. (2012): Two new frog species (Microhylidae: *Cophixalus*) from the Australian Wet Tropics region, and redescription of *Cophixalus ornatus*. – Zootaxa, **3271**: 1–16.

Hyndman, D. & J. I. Menzies (1990): Rain Forests of the Ok Tedi headwaters, New Guinea: an ecological analysis. – Journal of Biogeography, **17**: 241–273.

Köhler, F. & R. Günther (2008): The radiation of microhylid frogs (Amphibia: Anura) on New Guinea: A mitochondrial phylogeny reveals parallel evolution of morphological and life history traits and disproves the current morphology-based classification. – Molecular Phylogenetics and Evolution, **47**: 353–365.

Köhler, J., M. Jansen, A. Rodríguez, P. J. R. Kok, L. F. Toledo, M. Emmrich, F. Glaw, C. F. B. Haddad, M-O. Rödel & M. Vences (2017): The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. – Zootaxa, **4251**: 1–124.

Kraus, F. (2011): New frogs (Anura: Microhylidae) from the mountains of western Papua New Guinea. – Records of the Australian Museum, **63**: 53–60.

Kraus, F. (2012): Papuan frogs of the genus *Cophixalus* (Anura: Microhylidae): new synonyms, new species, and a dichotomous key. – Zootaxa, **3559**: 1–36.

Kraus, F. (2013): Three new species of *Oreophryne* (Anura, Microhylidae) from Papua New Guinea. – Zookeys, **333**: 93–121.

Kraus, F. (2016): Ten new species of *Oreophryne* (Anura: Microhylidae) from Papua New Guinea. – Zootaxa, **4195**: 1–68.

Kraus, F. (2017a): A new insular species of *Oreophryne* (Anura, Microhylidae) from Papua New Guinea. – Journal of Herpetology, **51**: 552–558.

Kraus, F. (2017b): A new species of *Oreophryne* (Anura, Microhylidae) from the mountains of southeastern Papua New Guinea. – Current Herpetology, **36**: 105–115.

Kraus, F. & A. Allison (2006): Three new species of *Cophixalus* (Anura: Microhylidae) from southeastern New Guinea. – Herpetologica, **62**: 202–220.

Kraus, F. & A. Allison (2009a): New species of *Cophixalus* (Anura: Microhylidae) from Papua New Guinea. – Zootaxa, **2128**: 1–38.

Kraus, F. & A. Allison, (2009b): New microhylid frogs from the Muller Range, Papua New Guinea. – ZooKeys, **26**: 53–76.

Méhely, L.v. (1901): Beiträge zur Kenntniss der Engystomatiden von Neu-Guinea. – Természetrajzi Füzetek, **24**: 169–271.

McAlpine, J. R., G. Keig & R. Falls (1983): Climate of Papua New Guinea. – Australian National University Press, Canberra.

Menzies, J. I. (2006): The frogs of New Guinea and the Solomon Islands. – Pensoft, Sofia-Moscow.

Parker, H. W. (1934): A Monograph of the Frogs of the Family Microhylidae. – British Museum (Natural History), London, U.K.

Peloso, P. L. V., D. R. Frost, S. J. Richards, M. T. Rodrigues, S. C. Donnellan, M. Matsui, C. J. Raxworthy, S. D. Biju, E. M. Lemmon, A. R. Lemmon & W. C. Wheeler (2016): The impact of anchored phylogenomics and taxon sampling on phylogenetic inference in narrow-mouthed frogs (Anura, Microhylidae). – Cladistics, **32**: 113–140.

Richards, S. J. (2002): Rokrok: An illustrated guide to frogs of the Kikori Integrated Conservation and Development Project area (Moro, Gobe and Kopi), Papua New Guinea. – WWF-South Pacific, Port Moresby.

Richards, S. J. & D. Iskandar (2000): A new minute *Oreophryne* (Anura: Microhylidae) from the mountains of Irian Jaya, Indonesia. – The Raffles Bulletin of Zoology, **48**: 257–262.

Richards, S. J., G. R. Johnston & T. C. Burton (1992): A new species of microhylid frog (genus *Cophixalus*) from the Star Mountains, central New Guinea. – Science in New Guinea, **18**: 141–145.

Richards, S. J. & P. M. Oliver (2007): A new species of *Cophixalus* (Anura: Microhylidae) from Misima Island, Papua New Guinea. – Pacific Science, **61**: 279–287.

Richards, S. J. & P. M. Oliver (2010): A new scansorial species of *Cophixalus* (Anura: Microhylidae) from the Kikori River Basin, Papua New Guinea. – Journal of Herpetology, **44**: 555–562.

Richards, S. J., B. Tjaturadi, Mumpuni & P. Puradyatmika (2015): Field guide to frogs of the Mimika region – Papua, Indonesia. – PT Freeport Indonesia, Jakarta.

Rittmeyer, E. N., A. Allison, M. C. Grundler, D. K. Thompson & C. C. Austin (2012): Ecological guild evolution and the discovery of the world's smallest vertebrate. – PLoS ONE, **7**: e29797.

Rivera, J. A., F. Kraus, A. Allison & M. A. Butler (2017): Molecular phylogenetics and dating of the problematic New Guinea microhylid frogs (Amphibia: Anura) reveals elevated speciation rates and need for taxonomic reclassification. – Molecular Phylogenetics and Evolution, **112**: 1–11.

Tyler, M. J. (1963): A taxonomic study of amphibians and reptiles of the central highlands of New Guinea, with notes on their ecology and biology. 1. Anura: Microhylidae. – Transactions of the Royal Society of South Australia, **86**: 11–29.

Zweifel, R. G. (1956a): Results of the Archbold Expeditions. No. 72, Microhylid frogs from New Guinea with descriptions of new species. – American Museum Novitates, **1766**: 1–49.

Zweifel, R. G. (1956b): Notes on Microhylid Frogs, genus *Cophixalus*, from New Guinea. – American Museum Novitates, **1785**: 1–8.

Zweifel, R. G. (1962): Results of the Archbold Expeditions. No. 83, Frogs of the Microhylid Genus *Cophixalus* from the Mountains of New Guinea. – American Museum Novitates, **2087**: 1–26.

Zweifel, R. G. (1979): A new cryptic species of microhylid frog (genus *Cophixalus*) from Papua New Guinea, with notes on related forms. – American Museum Novitates, **2678**: 1–14.

Zweifel, R. G. (1980): Results of the Archbold Expeditions. No. 103. Frogs and lizards from the Huon Peninsula, Papua New Guinea. – Bulletin of the American Museum of Natural History, **165**: 390–434.

Zweifel, R. G. & F. Parker (1989): New species of microhylid frogs from the Owen Stanley Mountains of Papua New Guinea and resurrection of the genus *Aphantophryne*. – American Museum Novitates, **2954**: 1–20.

Zweifel, R. G., H. G. Cogger & S. J. Richards (2005): Systematics of microhylid frogs, genus *Oreophryne*, living at high elevations in New Guinea. – American Museum Novitates, **3495**: 1–25.