

Three new tiny species of the microhylid frog genus *Cophixalus* Boettger, 1892 from central Papua New Guinea

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Abstract.—We describe three new species of frogs in the asterophryine microhylid genus *Cophixalus* from New Guinea's central cordillera. All three are characterized by their very small size (adult body length < 18 mm), reduced first fingers, narrow ridges on the dorsum, and having terminal discs on the fingers smaller than or the same size as those on the toes. They were found on the forest floor or on low vegetation in montane rainforest, where males called at night during or after heavy rain. Each of the new species is known only from one or two locations within a small area of central Papua New Guinea, although the extent of suitable habitat in the region suggests that their distributions may be broader. This study brings to 51 the number of described *Cophixalus* species known from the New Guinea region, but numerous additional undescribed forms reside in museum collections awaiting formal description, and others undoubtedly await discovery in their natural habitats.

Keywords: Amphibia, central cordillera, Hela Province, new species, Southern Highlands Province

Microhylid frogs in the asterophryine genus *Cophixalus* are confined to the Australo-Papuan region, where they reach their greatest diversity on mainland New Guinea (Menzies 2006, Kraus & Allison 2009, Kraus 2012, Clulow & Swan 2018, Richards & Günther 2019). A particularly rich *Cophixalus* fauna occurs in the mountains of the Papuan Peninsula in south-eastern Papua New Guinea, including the Owen Stanley Mountains and on the Milne Bay islands (Kraus & Allison 2009, Kraus 2012). The Papuan Peninsula has a complex geological history (Quarles van Ufford & Cloos 2005, Toussaint et al. 2021) and the resultant mountainous terrain has promoted in situ speciation of

Cophixalus and other microhylid genera, with much of this diversity apparently endemic to that region (Kraus 2010, 2012, 2016).

The *Cophixalus* fauna of other mountainous regions of New Guinea has received less attention, but recent studies along the southern versant of the island's central cordillera documented a rich microhylid fauna, including several new *Cophixalus* species (Richards & Oliver 2010, Günther & Richards 2011, Günther et al. 2014, Richards & Günther 2019). Particularly rich microhylid assemblages containing a high proportion of undescribed species have been found in the montane forests of Hela and Southern Highlands Provinces (Günther & Richards 2016, 2017, 2018, Richards & Günther

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2019). Lying to the northwest of the Papuan Peninsula, this area forms part of the Papuan Fold Belt, a mountainous region comprising a series of steep, rugged, forest-covered ridges at the northern margin of the Australian Continental Plate (Löffler 1977). The region is also one of the wettest in New Guinea, forming part of a high rainfall belt that extends across the southern slopes of the cordillera (McAlpine et al. 1983). This combination of steep mountainous terrain, permanently wet climate and extensive forest cover has combined to generate conditions ideal for speciation of small, direct-developing frogs (e.g., Oliver et al. 2017). Here we describe three new species of *Cophixalus* based on both morphological and acoustic characters. Each is currently known only from the wet montane forests of central Papua New Guinea, and their description brings the number of named *Cophixalus* species from the New Guinea region (New Guinea and immediately adjacent islands) to 51.

Materials and Methods

Male frogs were located at night by their advertisement calls, and females were detected opportunistically during searches for males. Vouchers were euthanized in an aqueous chlorobutanol solution, fixed in 5% formalin, and transferred to 70% ethanol within two days of fixation. Measurements were taken to the nearest 0.1 mm with a digital caliper (SUL) or a binocular dissecting microscope fitted with an ocular micrometer (all other measurements) following Zweifel (1985) with some modifications (e.g., Günther 2006): SUL—snout-urostyle length: from tip of snout to posterior tip of urostyle bone; SUL is generally slightly shorter than snout-vent length (SVL) but both measurements are sufficiently similar that, where relevant, we compare our SUL measurements with published SVLs for some members of the genus; TL—tibia length: distance between

outer surface of flexed knee and tibio-tarsal articulation; TaL—tarsus length: external distance between tibio-tarsal and tarsal-metatarsal joints held at right angles; FtL—foot length: 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; HdL—hand length: 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: at widest point, typically at the level of the tympana; SL—snout length: from an imaginary line connecting centers of eyes to tip of snout; END—distance from anterior corner of orbital opening to center of naris; IND—internarial distance: between centers of nares; ED—eye diameter: from anterior to posterior corner of orbital opening; EST—distance from anterior corner of orbital opening to tip of snout; TyD—horizontal diameter of tympanum. Measurements are presented as mean \pm standard deviation and range.

With regard to descriptive terminology for the first finger, we consider a “reduced” first finger to be less than one-half the length of the second finger and lacking a terminal disc and circum-marginal groove.

Color of animals in life is described from digital photographs. Most colors were determined according to a color matching system created and administrated by the German RAL GmbH (https://en.wikipedia.org/wiki/RAL_colour_standard [last accessed 26 August 2021]). When it was not possible to find an exact match between observed colors and RAL color numbers, the most similar RAL number was chosen. Advertisement calls were recorded under natural conditions with a Sony TCM5000-EV tape recorder or a Roland R05 digital recorder, both fitted with a Sennheiser ME66 directional microphone, and analyzed with Avisoft-SAS

Lab Pro software. Terminology and acoustic analysis procedures follow Köhler et al. (2017). Photographs of the ventral surfaces of a hand and a foot of each species were produced with a Sony a7rIII-system equipped with a Canon 65 mm 2.8 MP-E lens, and images of the shoulder girdle of each species were made using X-ray computed micro-tomography to determine the presence or absence of clavicles and procoracoids.

Specimens are deposited in the collections of the South Australian Museum, Adelaide, Australia (SAMA), the Museum für Naturkunde, Berlin, Germany (ZMB), and one paratype (SJR 10580) will be repatriated to the Papua New Guinea National Museum (PNGNM). SJR denotes field number of Stephen Richards.

Compared material.—Voucher specimens, including types, of members of the genus *Cophixalus* that were studied for comparative purposes are listed in Richards et al. (1992), Günther (2003, 2006, 2010), Richards & Oliver (2007, 2010), Günther & Richards (2011), Günther et al. (2014, 2015) and Richards & Günther (2019). Additional comparative information was taken from the following original descriptions and recompiled treatises (Méhely 1901, Zweifel 1956a, b, 1962, 1979, 1980, Tyler 1963, Zweifel & Parker 1989, Menzies 2006, Kraus & Allison 2000, 2006, 2009, Kraus 2012).

The three new species are assigned to *Cophixalus* on the basis of the following combination of characters: jaws eleutherognathine; clavicles and procoracoids absent; first finger substantially reduced; third toe longer than fifth. We do not accept the recommendation of Dubois et al. (2021) to synonymize *Cophixalus* and all other asterophryine microhylid genera with *Asterophrys* Tschudi, 1838 (see Frost 2021), because this approach is a great step backwards in our attempts to solve the taxonomic issues surrounding this group of frogs.

This work has been registered in ZooBank with the registration number urn:lsid:zoobank.org:pub:1087AC4B-C4D1-439C-A5FC-C25BDABB82FE.

Cophixalus brevidigitus, new species
Figs. 1–4, Table 1

Zoobank LSID.—urn:lsid:zoobank.org:act:419B1ACF-0343-4809-95A4-5FA1ADE880FB.

Holotype.—SAMA R71751 (field number SJR 10556); adult male, collected by S. Richards, unnamed camp in Hela Province, Papua New Guinea (6.0967°S, 143.1045°E; 2060 m a.s.l.), 04 Apr 2008.

Paratypes.—ZMB 91643 (field number SJR 10552), adult male; SAMA R71750 (field number SJR 10553), adult male; PNGNM (field number SJR 10580), adult female, same details as for holotype, except SJR10580 collected on 08 Apr 2008.

Diagnosis.—A very small species of *Cophixalus* (SUL = 15.0–15.7 mm in three mature males and 17.5 mm in one mature female) distinguished from congeners by its small size and the following unique combination of characters: head short (HL/SUL 0.31–0.34); legs short (TL/SUL 0.39–0.42); third toe longer than fifth; terminal discs of toes larger than or same size as those of fingers; dorsal and dorso-lateral surfaces with conspicuous longitudinal skin ridges, ventral surfaces smooth; dorsal ground color predominantly cream-white (RAL 9001) or ochre yellow (RAL 1024), skin ridges and canthus rostralis light red orange (RAL 2008); “face mask” prominent, terra brown (RAL 8028), extending from tip of snout nearly to insertion of forelegs; advertisement calls with more than one hundred notes, the first much longer (113–147 ms) than subsequent notes (11–22 ms); repetition rate 11.7–13.6 notes/s; peak of dominant frequency at 4.6 kHz.

Description of holotype.—(Fig. 1A–D). For measurements see Table 1. Head broader than long (HL/HW 0.88); canthus

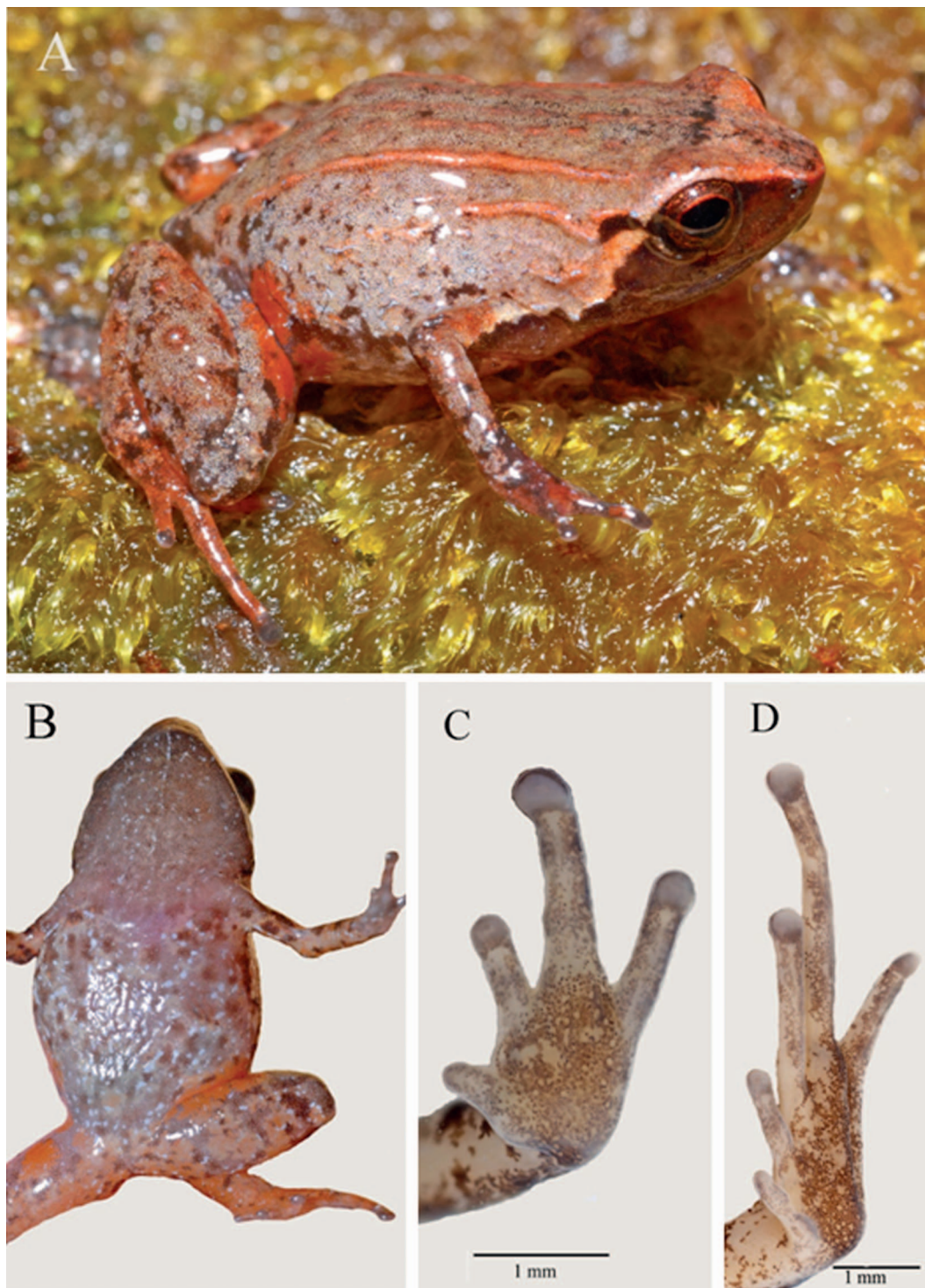


Fig. 1. Holotype (SAMA R71751) of *Cophixalus brevidigitus*. A, dorsolateral view in life; B, ventral view in life; C, palmar view of left hand of preserved specimen; D, plantar view of left foot of preserved specimen.

Table 1.—Body measurements and body ratios of the type series of *Cophixalus brevidigitus*. SAMA R71751 is the male holotype; ZMB 91643 and SAMA R71750 are male paratypes and PNGNM (SJR 10580) is a female paratype. For explanation of abbreviations see “Materials and Methods.”

Reg.-No.	ZMB 91643	SAMA R71750	SAMA R71751	PNGNM (SJR 10580)	$\bar{X} \pm SD$
SUL	15.0	15.2	15.7	17.5	
TL	6.3	6.0	6.1	7.4	
TaL	4.4	4.1	4.3	5.0	
FTL	6.6	6.0	6.2	7.9	
T4D	0.6	0.5	0.5	0.6	
T1D	0.3	0.25	0.26	0.3	
HDL	3.2	2.8	3.4	4.2	
F3D	0.45	0.40	0.50	0.60	
F1D	0.25	0.20	0.25	0.25	
HL	5.1	4.8	5.1	5.5	
HW	6.3	5.9	5.8	6.5	
END	1.1	1.1	1.0	1.2	
IND	1.8	1.9	1.7	2.1	
SL	2.7	2.6	2.3	2.8	
EST	1.9	2.1	1.8	2.0	
ED	2.1	2.0	2.1	2.4	
TyD	0.7	0.7	0.8	1.0	
TL/SUL	0.42	0.39	0.39	0.42	0.41 ± 0.017
TaL/SUL	0.29	0.27	0.27	0.29	0.28 ± 0.019
FTL/SUL	0.44	0.39	0.39	0.45	0.42 ± 0.032
T4D/SUL	0.040	0.033	0.032	0.034	0.035 ± 0.004
T1D/SUL	0.020	0.016	0.017	0.023	0.019 ± 0.003
HDL/SUL	0.21	0.18	0.22	0.24	0.21 ± 0.025
F3D/SUL	0.030	0.026	0.032	0.034	0.031 ± 0.003
F1D/SUL	0.017	0.013	0.016	0.014	0.015 ± 0.002
T4D/F3D	1.33	1.25	1.00	1.00	1.15 ± 0.170
T1D/F1D	1.20	1.25	1.04	1.20	1.17 ± 0.091
HL/SUL	0.34	0.32	0.32	0.31	0.32 ± 0.013
HW/SUL	0.42	0.39	0.37	0.37	0.39 ± 0.024
HL/HW	0.81	0.81	0.88	0.85	0.84 ± 0.034
END/SUL	0.073	0.072	0.064	0.069	0.070 ± 0.004
IND/SUL	0.120	0.125	0.108	0.120	0.118 ± 0.007
END/IND	0.61	0.58	0.59	0.57	0.59 ± 0.017
ED/SUL	0.140	0.132	0.134	0.137	0.136 ± 0.004
TyD/SUL	0.047	0.046	0.051	0.057	0.050 ± 0.005
TyD/ED	0.33	0.35	0.38	0.42	0.37 ± 0.039
SL/SUL	0.180	0.171	0.146	0.160	0.164 ± 0.015
EST/SUL	0.127	0.138	0.115	0.114	0.124 ± 0.011

rostralis well defined, reaching dorsal tip of snout; loreal region steeply oblique, slightly concave; snout moderately protruding in profile, roundish in dorsal view; nostrils close to canthus rostralis and near tip of snout (Fig. 1A); eye diameter about twice length of eye-naris distance (ED/END 2.1); tympanum relatively small (TyD/ED 0.38), poorly demarcated; supratympanic fold continues as lateral skin ridge almost to middle of flank; internarial

distance significantly greater than eye-naris distance (END/IND 0.59); tongue large, free laterally and posteriorly, posterior margin rounded; prepharyngeal ridge weakly developed with about eight denticles; vocal slits on both sides of tongue. Legs relatively short (TL/SUL 0.39); webbing between fingers and toes absent; discs on fingers 3 and 4 clearly wider than penultimate phalanx, disc on finger 2 scarcely wider than penultimate phalanx,

all three with circum-marginal grooves; finger 1 strongly reduced, reaching to base of finger two, tip not expanded, with shallow ridge on outer edges; relative lengths of fingers $3 > 4 > 2 > 1$ (Fig. 1C); toes 3 and 4 with clearly expanded discs, toes 2 and 5 with scarcely expanded discs, all with circum-marginal grooves, toe 1 reduced, without expanded disc, tip with small skin ridge on outer edges; disc of toe 4 same size as disc of finger 3 (T4D/F3D 1.00); relative length of toes $4 > 3 > 5 > 2 > 1$; subarticular tubercles on fingers and toes as well as metacarpal and metatarsal tubercles not or only scarcely developed (Fig. 1D). Well-developed dorsolateral skin ridge from behind eye to lumbar region; one less well-developed mid-dorsal and two paravertebral skin ridges degenerate into rows of tubercles posteriorly. Shanks with few scattered tubercles dorsally; abdomen slightly wrinkled, all other ventral surfaces smooth. Skin ridges and tubercles are visible in life and in preservative.

Color in life: Iris sepia brown (RAL 8014) with sunny yellow (RAL 1037) and yellow orange (RAL 2000) dots and dashes and orange inner margin. Dorsal ground color predominantly cream-white (RAL 9001), skin ridges and canthus rostralis red orange (RAL 2008), lateral surfaces of head terra brown (RAL 8028), forming dark "face mask" (Fig. 1A), these terra-brown areas extending ventrally to insertion of upper arm and, less intensively, onto lower flanks; a semilunar nut-brown supratympanic spot present; throat and chest beige grey (RAL 7006) with numerous small light ivory (RAL 1015) dots and few larger white dots; abdomen ground color light ivory with mixture of white, loam brown (RAL 8003) and stone grey (RAL 7030) flecks. Inner surfaces of forelegs light yellow with dark-brown spots; inguinal region grey-white (RAL 9002) with numerous cement-grey (RAL 7023) dots and few large yellow-orange (RAL 2000) patches. Anterior and poste-

rior surfaces of thighs and shanks, inner surfaces of tarsi and part of dorsal surfaces of toes and fingers orange of variable intensity. Orange in groin and on inner surfaces of knee more intense than other orange markings.

Color in preservative: Dorsal ground color ivory-white (RAL 1015) with extensive brown-beige (RAL 1011) peppering and some diffuse clusters of darker dots mainly on dorsal surfaces of limbs. Skin ridges uniformly signal grey (RAL 7004). Ventrally throat and chest nearly uniform brown beige, abdomen and extremities light sulphur yellow (RAL 1016) with reticulum of dense brown-beige pigmentation and scattered terra-brown (RAL 8028) spots.

Morphological variation.—Variation in measurements and body ratios of the type series is minimal (Table 1), and narrow dorsal ridges are a consistent feature among the type series. Length and shape of first finger ranges from that moderately well-developed in the holotype (Fig. 1C) to a very short stub in ZMB 91643. Intensity and extent of orange areas and flecks is somewhat variable, but they are always present. Dorsal surfaces of ZMB 91643 are olive grey rather than ivory white.

Distribution, habitats, and habits.—*Cophixalus brevidigitus* is known with certainty only from a single locality at an altitude of 2060 m a.s.l. in the mountains of Hela Province, Papua New Guinea (Fig. 9). The habitat at the type locality is extremely wet, mossy, mid-montane rain-forest with an open understory (Fig. 2). Males called from the surfaces of, or from hidden positions within, leaf litter on the forest floor at night during and after rain. Calls similar to those of *C. brevidigitus* were heard at an altitude of 1400 m a.s.l. in lower-montane forest about 20 km to the southeast of the type locality, but collection of voucher material is required to confirm the taxonomic status of that population.



Fig. 2. Forest interior at the type locality of *Cophixalus brevidigitus*.

Vocalization.—We analyzed one advertisement call from ZMB 91643 and two calls from a specimen that eluded capture, all recorded at air temperatures between 15.8–16°C. Calls were uttered at intervals of several minutes, and the three calls lasted 10.9 s with 122 notes, 12.0 s with 141 notes, and 21.6 s with 295 notes. The first note in each call is much longer than those that follow (Fig. 3A), and notes have a distinct harmonic structure (Fig. 3B). The call sounds to the ear like ‘weep-di-di-di-di-di.....’. Mean length of first note 127 ± 18 ms, range 113–147 ms, $n = 3$; mean length of 115 randomly selected short notes 15 ± 2.8 ms, range 11–22 ms; length of first inter-note interval same as or slightly longer than following ones, mean of 112 randomly selected internote-intervals 59 ± 4 ms, range 47–68 ms; mean note repetition rate 12.2 ± 0.96 notes/s, range 11.2–13.7 notes/s, $n = 3$; range of peak dominant frequencies 4.4–4.70 kHz.

The initial note starts with a moderately low amplitude that increases slowly until it plateaus about one-half of the way through the note before terminating sharply at the end (Fig. 3A). In contrast, short notes exhibit a rapid rise in amplitude to about halfway through the note followed by an equally rapid decline (Fig. 3A). Fundamental frequency is at 2.35 kHz, with upper harmonics at 4.70 (dominant; Fig. 4), 7.05 and 9.40 kHz (Fig. 3B).

Etymology.—*Brevis* is a Latin adjective meaning “short”; *digitus* is a singular masculine Latin substantive and means “finger” or “toe”. The specific epithet “*brevidigitus*” is a compound masculine substantive in apposition and refers to the very short first finger of the new species.

Comparison with other species.—*Cophixalus brevidigitus* differs from all congeners, except *C. desticans* Kraus & Allison, 2009, by its combination of small body size (SUL less than 20 mm), narrow dorsal skin ridges, dark brown face mask, significantly

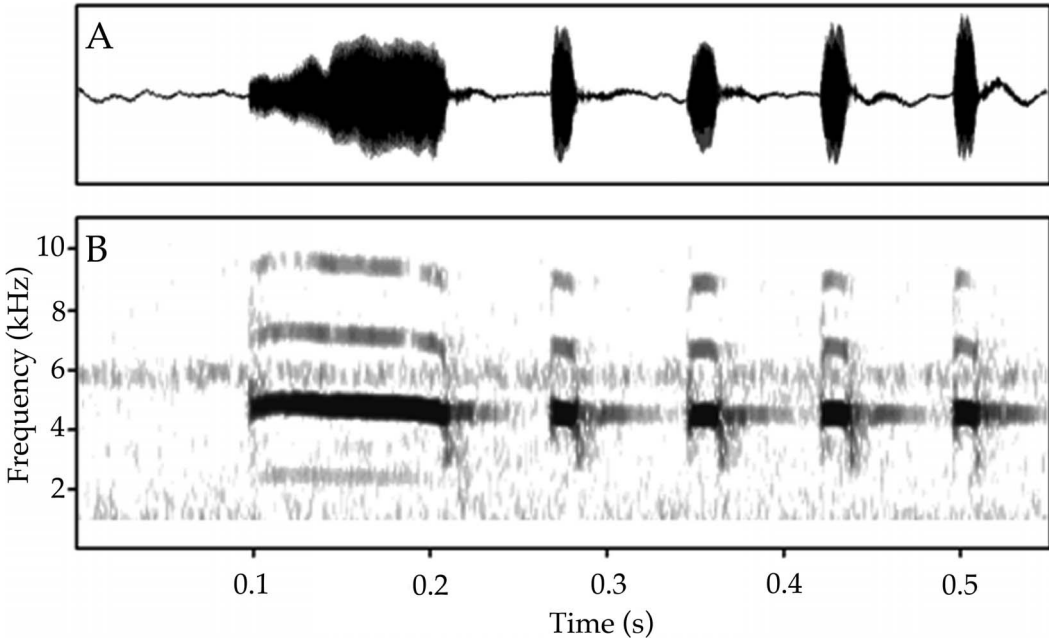


Fig. 3. A, waveform of the first five notes of an advertisement call containing 122 notes from an unvouchered male of *Cophixalus brevidigitus*; B, spectrogram of this call. Spectrogram parameters: FFT length 256; Frame size 75%; Window FlatTop; Bandwidth 313 Hz, Resolution 63 Hz; Overlap 87.5%. Sampling rate conversion from 96 kHz to 22 kHz; sample units 32. Basic noise was deleted up to 1.0 kHz.

reduced first finger, and toe discs larger or same size as finger discs. *Cophixalus desticans* can be distinguished from *C. brevidigitus* by the following combination of characters: longer hind legs (TL/SVL 0.48–0.58 vs. TL/SUL 0.39–0.42), a larger disc on fourth toe (T4D/SVL 0.048–0.068 vs. T4D/SUL 0.032–0.040), one or more dark chevrons on the dorsum, and calls containing 5–25 notes with a mean repeti-

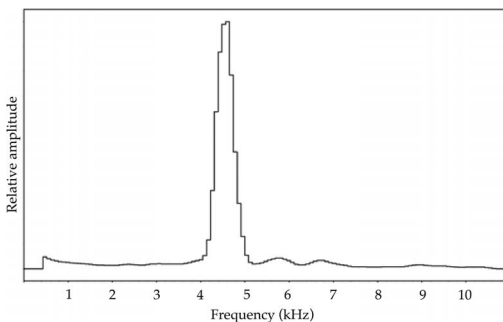


Fig. 4. Amplitude spectrum of the call section shown in Fig. 3.

tion of 0.4 notes/s (vs. > 120 notes at 12.7 notes/s).

Several morphologically similar species lacking dorsal skin ridges can be further distinguished from *Cophixalus brevidigitus* as follows: *C. ateles* (Boulenger, 1898) [including syn. *Cophixalus sisypus* Kraus & Allison, 2006] has longer hind legs (TL/SVL 0.43–0.52 vs. TL/SUL 0.39–0.42), a greater eye to naris distance (END/SVL 0.079–0.096 vs. END/SUL 0.064–0.073), larger discs on third finger and fourth toe (F3D/SVL 0.039–0.063 and T4D/SVL 0.044–0.060 vs. 0.026–0.034 and 0.032–0.040), and produces 5–10 peeping notes with a repetition rate of 1.35–2.26 notes/s (vs. more than 120 notes with a repetition rate of 11.7–13.6 notes/s); *C. bewaniensis* Kraus & Allison, 2000 has longer hind legs (TL/SVL 0.53–0.59 vs. TL/SUL 0.39–0.42), a greater distance between eye and naris (END/SVL 0.080–0.090 vs. END/SUL 0.064–0.073), and a conspicuous dark

brown lateral blotch above and behind each upper arm (absent in *C. brevidigitus*); *C. humicola* Günther, 2006 has longer hind legs (TL/SUL 0.48–0.51 vs. 0.39–0.42), a larger disc on fourth toe (T4D/SUL 0.041–0.068 vs. 0.032–0.040), a greater END/IND ratio (0.83–0.89 vs. 0.57–0.61), a dark-brown blackish area above and behind insertion of upper arm (vs. lacking); and shorter advertisement calls (< 2 s vs. > 12 s), consisting of pulsed (vs. unpulsed) notes; *C. interruptus* Kraus & Allison, 2009 has longer hind legs (TL/SVL 0.55–0.59 vs. TL/SUL 0.39–0.42), a greater eye to naris distance (END/SVL (0.075–0.083 vs. END/SUL 0.064–0.073), and calls containing 24 notes with a repetition rate of about two notes/s (vs. > 120 notes at 12.7 notes/s); *C. iovaorum* Kraus & Allison, 2009 has a lower F3D/T4D ratio (0.52–0.65 vs. 0.75–1.00), and calls containing 21–68 notes (vs. > 120 notes) with a repetition rate of 2.7–3.8 notes/s (vs. 11.7–13.6 notes/s; *C. pulchellus* Kraus & Allison, 2000 has a small terminal disc with circum-marginal groove on the first finger (vs. lacking), and conspicuous large black blotches on the dorsum (vs. black blotches absent); *C. shellyi* Zweifel, 1956 has much longer hind legs (TL/SVL 0.49–0.52 vs. TL/SUL 0.39–0.42), much wider discs on fingers 2–4 (compare drawing of palmar view of right hand of holotype of *C. shellyi* [Zweifel 1980, Fig. 9] and Fig. 1C this paper); *C. sphagnicola* Zweifel & Allison, 1982 is larger (SVL to 21 mm vs. SUL to 17.5 mm) and lacks expanded discs on all fingers and toes (vs. distinct terminal discs present on fingers 2–4 and toes 2–5); *C. tomaiodactylus* Kraus & Allison, 2009 lacks conspicuous orange blotches in inguinal region and on hind legs (vs. present), and a call comprising 2–13 notes (vs. > 120 notes) produced at a rate of 2.3–6.1 notes/s (vs. 11.7–13.6 notes/s); *C. tridactylus* Günther, 2006 has a wider disc on fourth toe (T4D/SUL 0.043–0.067 vs. 0.032–0.040), a higher END/IND ratio (0.83–1.00 vs. 0.57–0.61), anterior flanks

heavily spotted (vs. unspotted), and advertisement calls with a duration of 0.86–1.46 s (vs. more than 12 s).

Cophixalus pusillus, new species

Figs. 5–7, Table 2

Zoobank LSID.—urn:lsid:zoobank.org:act:58B12332-EA9A-44D8-915D-B849246E348B.

Holotype.—SAMA R71752 (field number SJR 8583); adult male, calling when collected, unnamed mountain range, Hela Province, Papua New Guinea (6.2469°S, 143.1253°E; 1760 m a.s.l.), coll. S. Richards, C. Dahl, and J. Hiaso, 19 Nov 2004.

Paratypes.—ZMB 91644 (field number SJR 8582), SAMA R71753 (field number SJR8847), adult males, same details as for holotype, except SAMA R71753, coll. 13 Nov 2004.

Diagnosis.—A very small species of *Cophixalus* (SUL of three adult males 12.1–12.8 mm). Body squat; legs of medium length (TL/SUL 0.45–0.48); third toe longer than fifth; first finger strongly reduced; first toe vestigial, fused externally with second toe along almost its entire length; discs of toes clearly larger than those of fingers; skin with long irregular paravertebral ridge, short irregular scapular ridge, and conspicuous tubercles on shank and tarsus; advertisement calls with 32–59 notes, the first longer (105–112 ms) than those following (7–15 ms); note repetition rate 23.0–24.2 notes/s; dominant frequency 5.8 kHz.

Description of holotype.—(Fig. 5A–D). For measurements see Table 2. Head broader than long (HL/HW 0.90), canthus rostralis extending to dorsal tip of snout; loreal region oblique, slightly concave; snout moderately protruding in profile, roundish in dorsal view; nostrils close to canthus rostralis, near tip of snout; eye diameter nearly twice as long as eye-naris distance (ED/END 1.8); tympanum relatively small (TyD/ED 0.33), poorly demarcated; supratympanic fold continues as

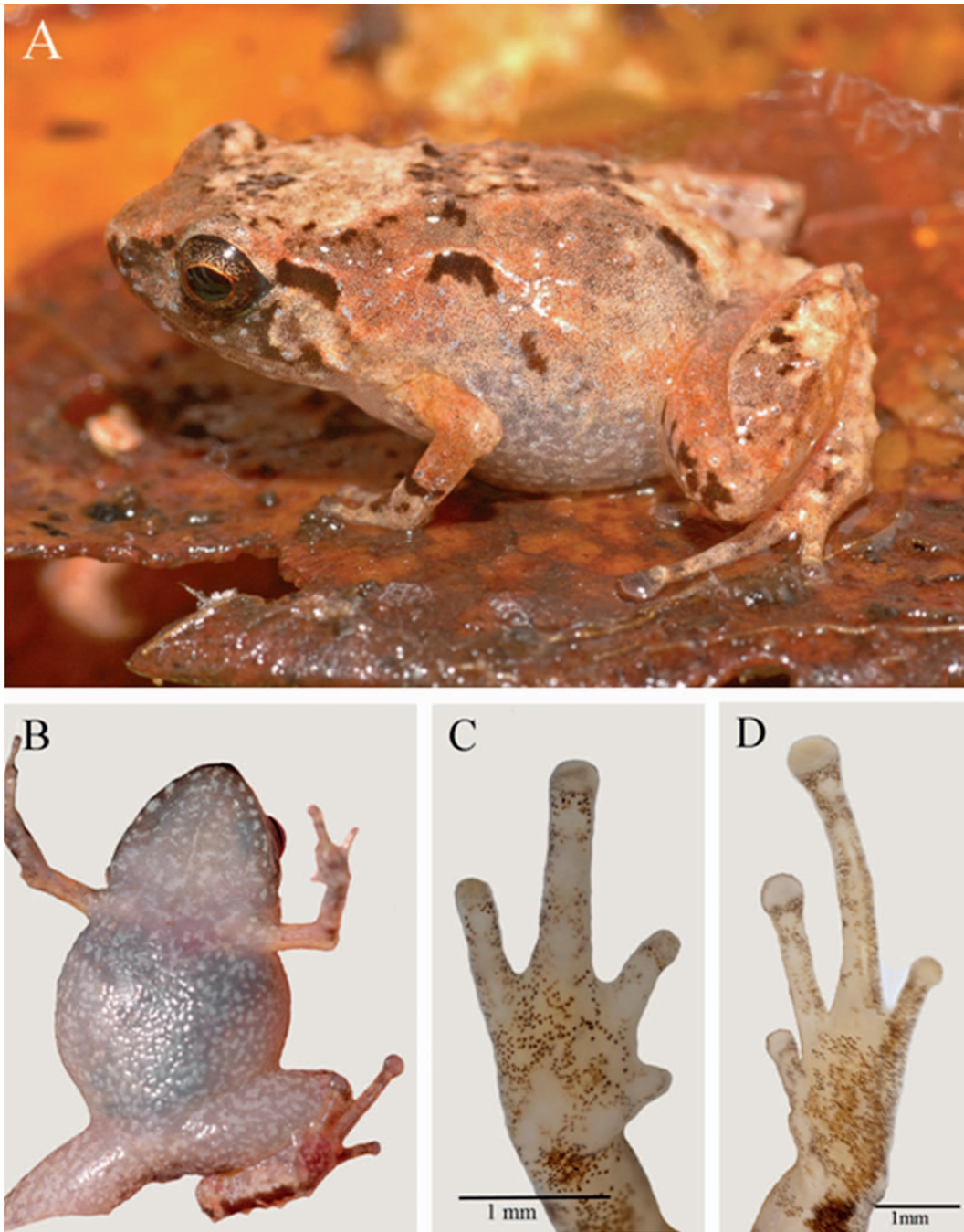


Fig. 5. Holotype (SAMA R71752) of *Cophixalus pusillus*. A, dorsolateral view in life; B, ventral view in life; C, palmar view of right hand of preserved specimen; D, plantar view of left foot of preserved specimen.

Table 2.—Body measurements and body ratios of the type series of *Cophixalus pusillus*. SAMA R71752 is the male holotype; ZMB 91644 and SAMA R71753 are male paratypes. For explanation of abbreviations see “Materials and Methods.”

Reg.-No.	ZMB 91644	SAMA R71752	SAMA R71753	$\bar{X} \pm SD$
SUL	12.8	12.5	12.1	
TL	5.7	5.6	5.8	
TaL	3.7	3.4	3.8	
FTL	5.1	5.3	5.5	
T4D	0.5	0.6	0.5	
T1D	0.2			
HDL	2.4	2.5	2.5	
F3D	0.35	0.30	0.30	
F1D	0.20	0.20	0.15	
HL	4.0	4.3	4.1	
HW	5.1	4.8	4.8	
END	1.0	1.0	0.9	
IND	1.6	1.5	1.4	
SL	2.1	2.1	1.9	
EST	1.4	1.4	1.3	
ED	1.7	1.8	1.8	
TyD	0.7	0.6	0.7	
TL/SUL	0.45	0.45	0.48	0.46 ± 0.017
TaL/SUL	0.29	0.27	0.31	0.29 ± 0.020
FTL/SUL	0.40	0.42	0.45	0.42 ± 0.025
T4D/SUL	0.039	0.048	0.041	0.043 ± 0.005
T1D/SUL	0.016			
HDL/SUL	0.19	0.20	0.21	0.20 ± 0.010
F3D/SUL	0.027	0.024	0.025	0.025 ± 0.002
F1D/SUL	0.016	0.016	0.012	0.015 ± 0.002
T4D/F3D	1.43	2.00	1.67	1.70 ± 0.286
T1D/F1D	1.00			
HL/SUL	0.31	0.34	0.34	0.33 ± 0.017
HW/SUL	0.40	0.38	0.40	0.39 ± 0.012
HL/HW	0.78	0.90	0.85	0.84 ± 0.060
END/SUL	0.078	0.080	0.074	0.077 ± 0.003
IND/SUL	0.125	0.120	0.116	0.120 ± 0.005
END/IND	0.63	0.67	0.64	0.65 ± 0.021
ED/SUL	0.133	0.144	0.149	0.142 ± 0.008
TyD/SUL	0.055	0.048	0.058	0.054 ± 0.005
TyD/ED	0.41	0.33	0.39	0.38 ± 0.042
SL/SUL	0.164	0.168	0.157	0.163 ± 0.006
EST/SUL	0.109	0.112	0.107	0.109 ± 0.003

lateral skin ridge almost to middle of flanks; internarial distance significantly greater than distance between eye and naris (END/IND 0.67); tongue large, free laterally and posteriorly, posterior margin rounded; prepharyngeal ridge weakly developed, with four teeth; vocal slits on both sides of tongue. Legs of medium-length (TL/SUL 0.45); fingers and toes without webbing; finger 1 strongly reduced, without terminal disc or circum-

marginal groove; terminal disc of finger 2 not wider than penultimate phalanx, finger 3 and 4 with discs slightly wider than penultimate phalanges, all with circum-marginal grooves; relative lengths of fingers 3 > 4 > 2 > 1; toes 3, 4, and 5 with clearly expanded terminal discs, toe 2 with disc scarcely broader than penultimate phalanx, all with circum-marginal grooves; toe 1 vestigial, fused to second toe along almost entire length; circum-marginal

grooves on most fingers and toes continue onto lateral edges of digits; relative length of toes $4 > 3 > 5 > 2 > 1$; disc of fourth toe twice as wide as disc of third finger; subarticular tubercles on fingers and toes, as well as metacarpal and metatarsal tubercles, not or only scarcely developed. Skin on dorsum with two irregular paravertebral ridges extending from behind eye to lumbar region, one irregular middorsal skin ridge and another irregular skin ridge from behind eye along upper flank to middle of flank. Some conspicuous tubercles on dorsal shank and outer edge of tarsus; abdomen slightly wrinkled, all other ventral surfaces smooth. Skin ridges and tubercles remain visible in preservative.

Color in life: Iris sepia-brown (RAL 8014) with narrow golden reticulations and orange inner margin. Dominant color of dorsal surfaces beige-red (RAL 3012) over pale gray ground color, with conspicuous brown spots below eye, posterior to eye (supratympanic), on upper anterior flank, in lumbar region, on anterior forearm, in knee region (Fig. 5A), on posterior tarsus and as triangular patch below vent. Large ivory-white (RAL 1015) patches on nape, in sacral region and on dorsal shank, and smaller patch in tympanic region. Ventral surfaces concrete grey (RAL 7023) with numerous irregular papyrus-white (RAL 9018) spots (Fig. 5B), most conspicuous in row along edge of lower jaws.

Color in preservative: Dorsal ground color ivory-white overlain by numerous tiny brown dots. Light ivory patch on nape and in sacral region no longer visible. Dorsal and lateral dark spots changed from grey-brown to sepia-brown. Ground color of ventral surfaces ivory-white with variably dense network of tiny brown spots. Papyrus-white spots on lower jaws still visible.

Morphological variation.—Measurements and body ratios of the type series are similar (Table 2). Coloration of both paratypes is similar to the holotype, except

that in life ZMB 91644 lacked the ivory-white patches on nape, in sacral region and on dorsal shank.

Distribution, habitats, and habits.—*Cophixalus pusillus* is known only from a single location at an altitude of 1760 m a.s.l. in the mountains of Hela Province, Papua New Guinea (Fig. 9). The type locality is an unnamed ridge immediately to the north of the Agogo Range, where frogs were calling from the surfaces of leaf litter on the forest floor or from up to 50 cm high on low vegetation during rain at night in extremely wet lower-montane rainforest on a karst substrate.

Vocalization.—Three calls from the holotype (SAMA R71752) and six calls from one paratype (ZMB 91644) were recorded at an air temperature of 18°C. Calls of both specimens are similar, and they are pooled in the following analyses. Calls last 1.3–2.4 s ($\bar{X} = 1.95 \pm 0.37$), consist of 31–58 notes ($\bar{X} = 46.2 \pm 9.0$) and are uttered at intervals of several minutes. In all calls, the first note is much longer than those following (Fig. 6A, B), with mean length of first notes 107.4 ± 2.1 ms, range 105–112 ms, $n = 9$, and mean length of subsequent notes 11.5 ± 2.2 ms, range 7–15 ms, $n = 180$ (90 from each vocalizing male). Mean length of internote intervals is 28.1 ± 2.9 ms, range 20–38 ms, $n = 180$, but length of the first inter-note interval is slightly longer than following ones and length of intervals in the first third of the call are somewhat shorter than in the last third. Mean note repetition rate is 23.7 ± 0.34 notes/s, range 23.0–24.2 notes/s, $n = 9$. There is a peak of weakly expressed fundamental frequency at 2.9 kHz and a peak of strongly expressed dominant frequency at 5.8 kHz (Fig. 7). The first note starts with a moderately low amplitude that increases slowly until it plateaus about one-third of the way through the note before terminating sharply at the end (Fig. 6A). In contrast, short notes exhibit a rapid rise in amplitude to about halfway

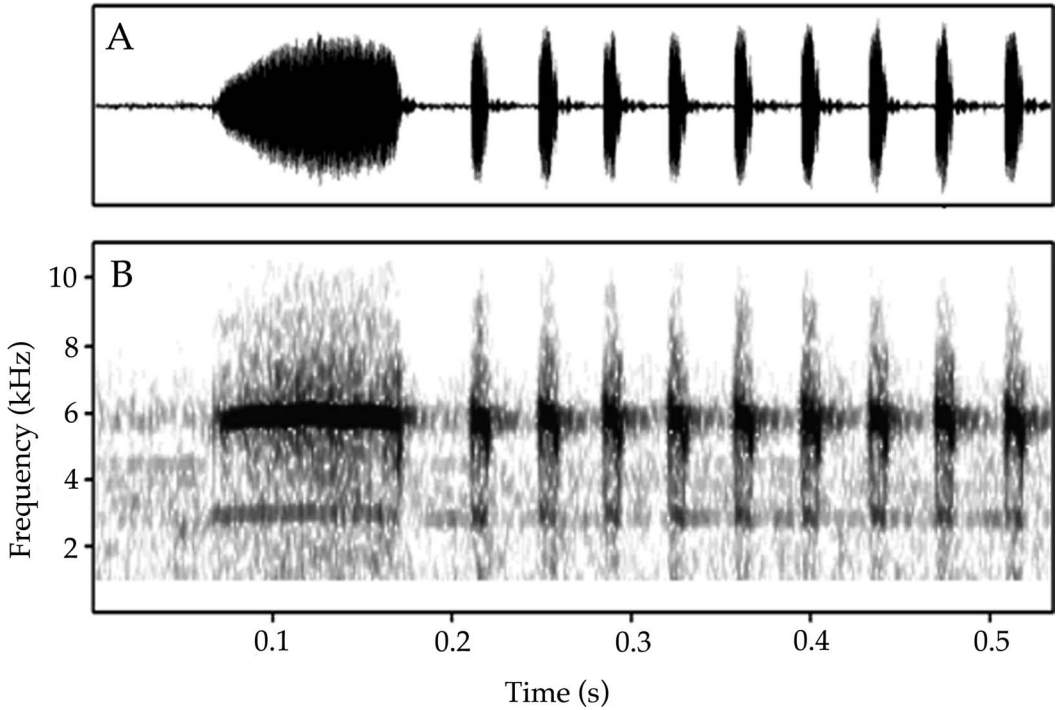


Fig. 6. A, waveform of the initial note followed by nine short notes of an advertisement call containing 46 notes from the holotype of *Cophixalus pusillus*; B, spectrogram of this call. Spectrogram parameters: FFT length 256; Frame size 75%; Window FlatTop; Bandwidth 313 Hz, Resolution 63 Hz; Overlap 87.5%. Sampling rate conversion from 96 kHz to 22 kHz; sample units 32. Basic noise was deleted up to 1.0 kHz.

through the note followed by an equally rapid decline (Fig. 6A).

Etymology.—The specific epithet *pusillus* is a nominative Latin masculine adjective meaning “tiny” and refers to the very small body size of this new species.

Comparison with other species.—*Cophixalus pusillus* is distinguished from all

congeners, except *C. brevidigitus* and *C. desticans*, by its combination of very small body size (male SUL less than 13 mm), partial face mask, dorsum with narrow ridges, toe webbing absent, first finger significantly reduced, first toe vestigial, and toe discs larger or same size as finger discs. *Cophixalus brevidigitus* is larger than *Cophixalus pusillus* (males 15.0–15.7 mm vs. 12.1–12.8 mm SUL) with shorter hind legs (TL/SUL 0.39–0.42 vs. 0.45–0.48), a lower T4D/F3D ratio (1.00–1.33 vs. 1.43–2.00), a shorter eye-naris distance (END/SUL 0.064–0.073 vs. 0.074–0.080), a lower END/IND ratio (0.57–0.61 vs. 0.63–0.67), a longer snout (EST/SUL 0.114–0.138 vs. 0.107–0.112), longer advertisement calls (> 12 s vs. < 3 s), and a lower note repetition rate (11.7–13.6 notes/s vs. 23.0–24.2 notes/s). *Cophixalus desticans* has an irregular dark lateral band (vs. absent),

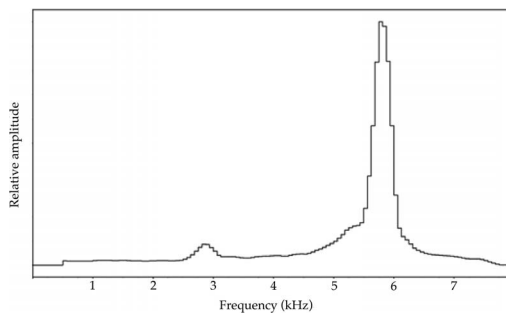


Fig. 7. Amplitude spectrum of the call section shown in Fig. 6.

longer hind legs (TL/SVL 0.48–0.58 vs. TL/SUL 0.45–0.48), a larger disc on fourth toe (T4D/SVL 0.048–0.068 vs. T4D/SUL 0.039–0.048), and calls containing 5–25 notes with a mean repetition rate of 0.4 notes/s (vs. 32–59 notes with a mean repetition rate of 23.7 notes/s).

Several morphologically similar species lacking dorsal skin ridges can be further distinguished from *Cophixalus pusillus* as follows: *C. amabilis* is slightly larger (SVL of four males 13.6–14.3 mm vs. 12.1–12.8 mm SUL in three males), has smaller internarial distance (IND/SVL 0.087–0.101 vs. IND/SUL 0.116–0.125), and calls are single notes (vs. calls with > 30 notes); *C. ateles* has a larger terminal disc on third finger (F3D/SVL 0.039–0.063 vs. F3D/SUL 0.024–0.027), and a call with 5–10 peeping notes with a repetition rate of 1.35–2.26 notes/s (vs. > 30 notes with a repetition rate of 23.0–24.2 notes/s); *C. humicola* has longer hind legs (TL/SUL 0.48–0.51 vs. 0.45–0.48), a greater END/IND ratio (0.83–0.89 vs. 0.63–0.67), a dark brown to blackish patch above and behind insertion of upper arm (vs. absent); and first note of advertisement call pulsed, lasting 62–87 ms (vs. first note unpulsed, lasting 105–112 ms); *C. iovaorum* is slightly larger (SVL of 29 males 13.2–16.0 mm vs. SUL 12.1–12.8 mm in three males); and has calls with a note repetition rate of 2.7–3.8 notes/s (vs. 23.0–24.2 notes/s); *C. kethuk* has a shorter internarial distance (IND/SVL 0.087–1.03 vs. IND/SUL 0.116–0.125), a higher END/IND ratio (0.75–0.92 vs. 0.63–0.67), a dark hourglass marking on dorsolateral surfaces (vs. absent), and calls with 12–13 (vs. 32–59) notes per call with a note repetition rate of 7.9–8.8 notes/s (vs. 23.0–24.2 notes/s); *C. pulchellus* has a small terminal disc with circum-marginal groove on first finger (vs. both disc and groove lacking), and dorsum with conspicuous large black blotches (vs. dark blotches absent); *C. tomaiodactylus* has dorsal color dark brown with scattered darker-brown flecks (vs. beige-red with

only a few dark-brown spots), and calls containing 2–13 notes with a repetition rate of 2.3–6.1 notes/s, and initial note not longer than the following ones (vs. calls with 30–58 notes, repetition rate 23.0–24.2 notes/s and initial note much longer than following ones); *C. tridactylus* is slightly larger (SUL 14.3–16.2 mm in 17 males vs. 12.1–12.8 mm in three males), has a higher END/IND ratio (0.83–1.00 vs. 0.63–0.67), anterior flanks heavily spotted (vs. unspotted), and initial notes of advertisement calls pulsed with duration of 150–240 ms (vs. unpulsed and lasting 105–112 ms).

Cophixalus melanogenys, new species

Figs. 8–12, Table 3

Zoobank LSID.—urn:lsid:zoobank.org:act:4772D50B-DCB1-494F-ACB8-80FFD7866047.

Holotype.—SAMA R71754 (field number SJR 15386); adult male, calling when collected, summit of Iagifu Ridge, Southern Highlands Province, Papua New Guinea (6.4414°S, 143.2254°E; 1370 m a.s.l.), coll. S. Richards, 15 May 2017.

Paratype.—ZMB 91645 (SJR 15387), adult female, same details as holotype.

Referred specimens.—SAMA R71755 (field number SJR 8585), PNGNM (SJR 8586), unnamed locality in Hela Province (6.2726°S, 143.1329°E; 1450 m a.s.l.). These two specimens are similar in overall morphology to *C. melanogenys* but are not included in the type series due to some differences in biometric and acoustic features. We tentatively refer them to *C. melanogenys* pending DNA studies to confirm their relationships.

Diagnosis.—A small species of *Cophixalus* (SUL 14.3 mm in one male and 16.6 mm in one female). Body slender, hind legs relatively long (TL/SUL 0.49–0.50); third toe longer than fifth; first finger strongly reduced, without expanded terminal disc; first toe reduced, with marginally expanded disc; discs of toes larger than those of fingers; head with dark “face mask” and

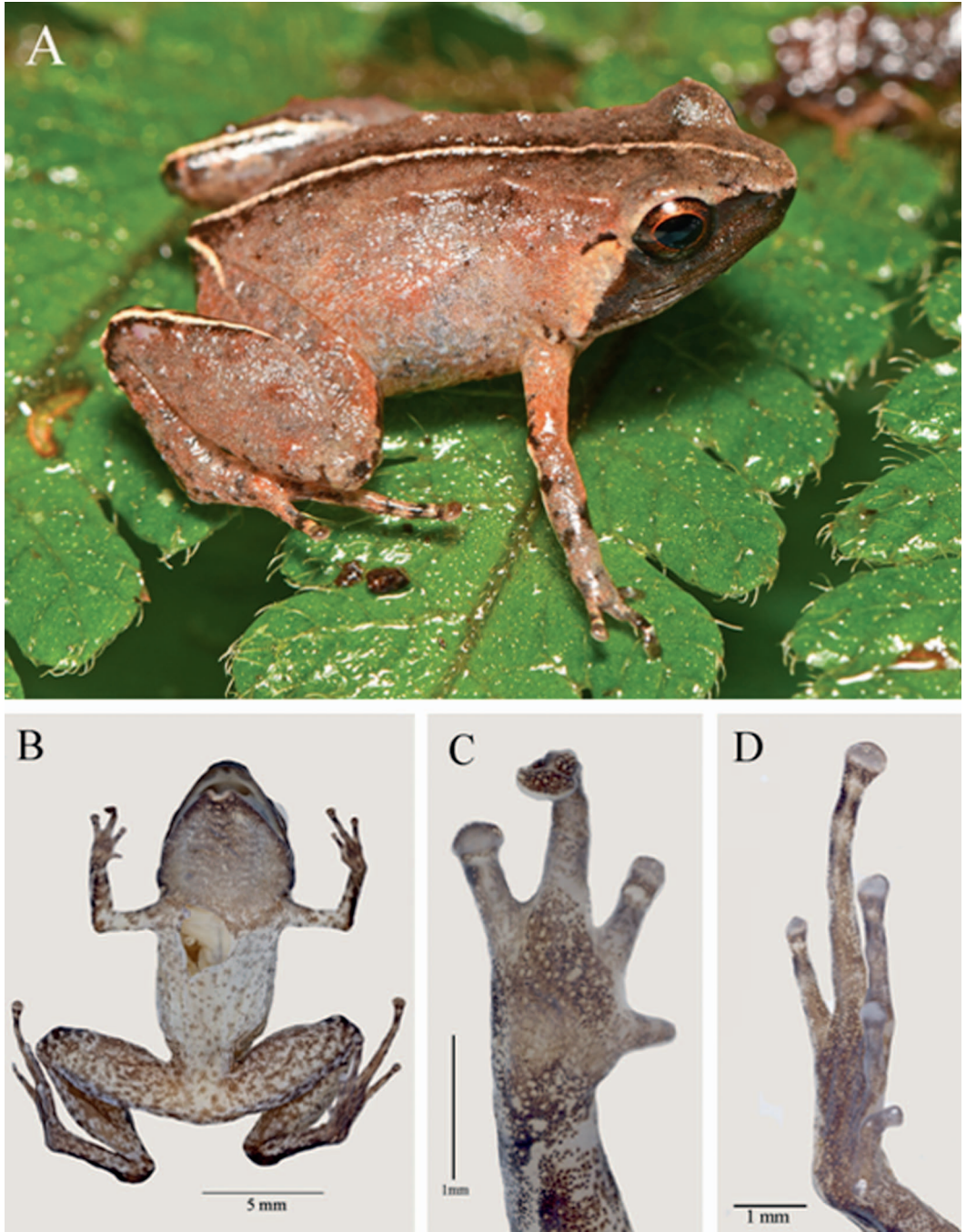


Fig. 8. Holotype (SAMA R71754) of *Cophixalus melanogenys*. A, dorsolateral view in life; B, ventral view of preserved specimen; C, palmar view of right hand of preserved specimen; D, plantar view of right foot of preserved specimen.

Table 3.—Body measurements and body ratios of the type series of *Cophixalus melanogenys* SAMA R71754 is the male holotype; ZMB 91645 is the female paratype. For explanation of abbreviations see “Materials and Methods.”

Reg.-No.	SAMAR71754	ZMB 91645	Reg.-No.	SAMAR71754	ZMB 91645	\bar{x}
SUL	14.3	16.6	TL/SUL	0.50	0.49	0.50
TL	7.2	8.1	TaL/SUL	0.31	0.29	0.30
TaL	4.5	4.8	FTL/SUL	0.46	0.45	0.46
FTL	6.6	7.5	T4D/SUL	0.042	0.045	0.044
T4D	0.60	0.75	T1D/SUL	0.017	0.024	0.21
T1D	0.25	0.40	HDL/SUL	0.18	0.20	0.19
HDL	2.6	3.3	F3D/SUL	0.031	0.036	0.34
F3D	0.45	0.60	F1D/SUL	0.010	0.012	0.011
F1D	0.15	0.20	T4D/F3D	1.33	1.25	1.29
HL	5.0	5.5	T1D/F1D	1.67	2.00	1.84
HW	5.7	6.0	HL/SUL	0.35	0.33	0.34
END	1.4	1.6	HW/SUL	0.40	0.36	0.38
IND	1.7	1.9	HL/HW	0.88	0.92	0.90
SL	2.5	2.9	END/SUL	0.098	0.096	0.097
EST	1.7	2.3	IND/SUL	0.119	0.114	0.117
ED	1.8	2.2	END/IND	0.82	0.84	0.83
TyD	0.6	1.2	ED/SUL	0.126	0.133	0.130
			TyD/SUL	0.042	0.072	0.057
			TyD/ED	0.33	0.54	0.44
			SL/SUL	0.175	0.175	0.175
			EST/SUL	0.119	0.139	0.129

narrow, arched grey-brown supratympanic spot; advertisement call a long (107–139 ms) harmonic note occasionally followed by up to 10 shorter notes, uttered at intervals of ~ 30 s, with peak dominant frequency at 6.0 kHz.

Description of the holotype.—(Fig. 8A–D). For measurements see Table 3. Head slightly broader than long (HL/HW 0.88), canthus rostralis well defined, extending to dorsal tip of snout; loreal region oblique, slightly concave; snout roundish in dorsal view, moderately protruding in profile; nostrils close to canthus rostralis, near tip of snout; eye medium size (ED/SUL 0.126); tympanum moderately small (TyD/ED 0.33), supratympanic fold poorly demarcated; internarial distance greater than distance between eye and naris (END/IND 0.82); tongue large, free laterally and posteriorly, posterior margin without notch; prepharyngeal ridge weakly developed with about 10 “teeth”; vocal slits present on both sides of tongue. Hind legs relatively long (TL/SUL 0.50); fingers

and toes without webbing; discs on fingers 3 and 4 clearly wider than penultimate phalanx, disc on finger 2 scarcely wider than penultimate phalanx (Fig. 8C), all three discs with circum-marginal grooves; finger 1 strongly reduced, tip tapered; relative length of fingers $3 > 4 > 2 > 1$; toes 2–5 with expanded discs, all with circum-marginal grooves, toe 1 reduced in size, with scarcely expanded tip (Fig. 8D) lacking circum-marginal groove; disc of toe 4 wider than disc of finger 3 (T4D/F3D 1.33); relative length of toes $4 > 3 > 5 > 2 > 1$; subarticular tubercles on fingers and toes as well as metatarsal and metacarpal tubercles not or only scarcely developed. Skin on dorsum with irregular paravertebral ridge extending from behind eye to lumbar region, and few tubercles on hind legs; all other dorsal, lateral, and ventral surfaces smooth. Skin ridges and tubercles remain detectable in preservative.

Color in life: Iris dark-brown (RAL 8022) with dense network of orange dots and reticulations and narrow orange rim;

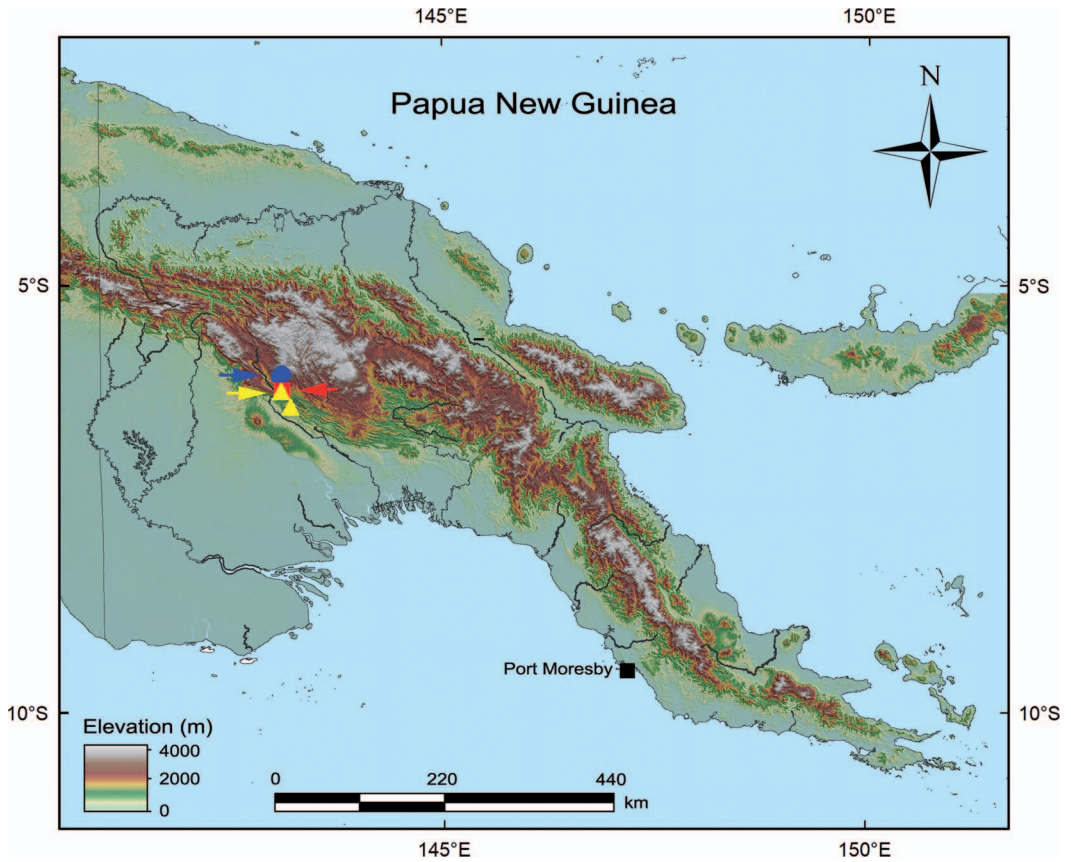


Fig. 9. Map showing the known distributions of *Cophixalus brevidigitus* (blue circle), *C. pusillus* (red square), and *C. melanogenys* (yellow triangles). Arrows indicate the type localities.

dorsal surfaces nearly uniform tan with reddish hue; a narrow pearl-white (RAL 1013) vertebral line from tip of snout to urostyle, continuing onto rear of thighs, shanks and tarsi. From mid-head posteriorly to urostyle and on limbs vertebral line bordered on both sides by narrow darker band formed by dense aggregations of dark-brown to blackish pigmentation (Fig. 8A); lateral surfaces of head from tip of snout to anterior insertion of foreleg and including lower tympanum grey-brown (RAL 8019), forming distinct “face mask”; a small, semilunar dark-brown supratympanic spot and dark-brown spots on forearms, fingers, toes, outer edge of knees and tarsi.

Color in preservative: Ground color of dorsal surfaces light ivory with dense network of quartz grey (RAL 7039) dots and reticulations. Vertebral line paler than in life, spots and blotches forming dark band adjacent to pale line darker than in life; dorsal surfaces of head slightly darker than dorsal surfaces posteriorly. Ground color of ventral surfaces light ivory; throat and chest with very dense network of fine brown dots and reticulations (Fig. 8B); abdomen paler than remainder of venter with only few irregular aggregations of brown dots; ventral surfaces of thighs with dense aggregations of brown dots.

Morphological variation.—The female paratype is larger than the male holotype, but body ratios of both specimens are very



Fig. 10. Lower montane rainforest at the type locality of *Cophixalus melanogenys*. Males called from low foliage up to about 50 cm above the forest floor.

similar (Table 3). Overall coloration is also similar, except that the paratype lacks a light mid-dorsal line that continues onto the hind limbs.

Distribution, habitats, and habits.—*Cophixalus melanogenys* is known from the type locality at an altitude of 1370 m a.s.l. in the mountains of Southern Highlands Province, Papua New Guinea (Fig. 9), and we tentatively assign two specimens from approximately 21 km to the northwest of the type locality at 1450 m a.s.l. in Hela Province (Fig. 9) to this species. The habitat at both localities is wet, mossy, lower-montane rainforest on karst substrates (Fig. 10). All three males were calling from about 25–30 cm above the forest floor, on low foliage (two specimens) and a limestone rock (one specimen) in steady rain. The female was perched on low foliage near a calling male.

Vocalization.—Three calls from the holotype (SAMA R71754) were recorded

at an air temperature of 16.5°C. Hundreds of other calls heard at the type locality were indistinguishable from these calls to the human ear. Each call is a single, high-pitched squeak uttered at intervals of more than 20 s. Mean length of three calls is 129 ± 18.8 ms, range 107–140 ms. Structure of these calls (Fig. 11A, B) appears to be unique among advertisement calls of Australo-Papuan frogs. They are divided into four or five “segments”, with each segment exhibiting a different structure, course, and number of harmonic bands. The first segment comprises eight short harmonics with decreasing frequencies, the second segment is longer and contains nine harmonics with weak frequency modulation, the third (longest) segment of the call contains five unmodulated harmonics, the fourth segment contains seven scarcely modulated harmonics, and the fifth segment seems to have a pulsatile character (Fig. 11A). The second, and dominant (at

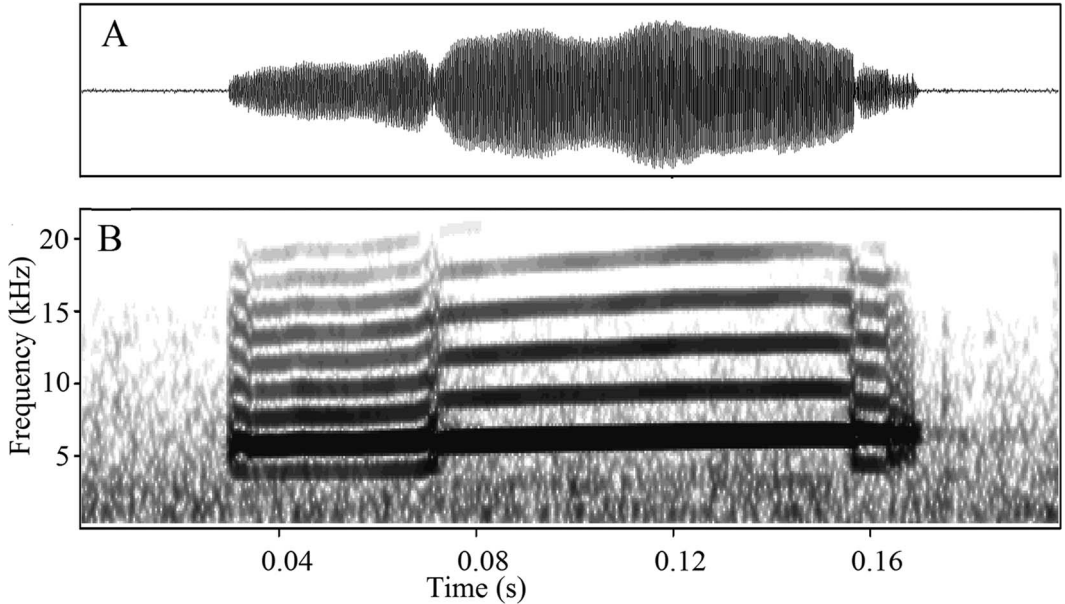


Fig. 11. A, waveform of an advertisement call from the holotype of *Cophixalus melanogenys*; B, spectrogram of this call. Spectrogram parameters: FFT length 256; Frame size 75%; Window FlatTop; Bandwidth 864 Hz, Resolution 172 Hz; Overlap 93.75%. Sampling rate conversion from 96 kHz to 40 kHz; sample units 16.

6.2 kHz; Fig. 12) harmonic is the only one that continues throughout the five segments (Fig. 11B).

The two referred specimens (SAMA R71755 and PNGNM SJR 8586) from Hela Province produced calls that differ in the structure of the first note, which was also normally followed by up to 10 slowly repeated shorter notes (Fig. 13). Genetic data will be required to confirm the

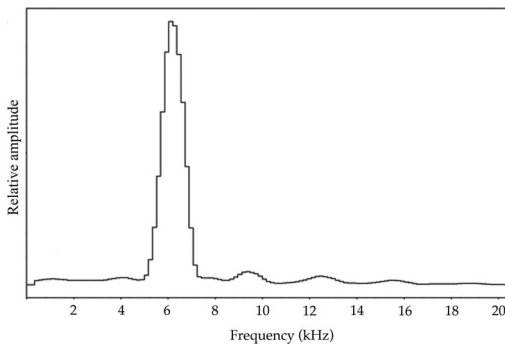


Fig. 12. Amplitude spectrum of the call shown in Fig. 11.

taxonomic status of these animals. At the type locality, we occasionally heard calls with several short notes, but vouchers were not obtained so conclusions about the status of the frogs making these calls must await collection of additional data.

Etymology.—The specific epithet *melanogenys* is a single-ending Latinized Greek compound substantive in apposition combining *melanus*, meaning “black”, and *genys* (from *gena*), meaning “cheek”.

Comparison with other species.—*Cophixalus melanogenys* is distinguished from all congeners, except *C. brevidigitus* and *C. desticans*, by its combination of small body size (SUL less than 20 mm), dark face mask, narrow dorsal ridges, toe webbing absent, first finger significantly reduced, and toe discs wider than or same size as finger discs. *Cophixalus brevidigitus* has shorter hind legs (TL/SUL 0.39–0.42 vs. 0.49–0.50), a smaller disc on toe 4 (T4D/SUL 0.032–0.040 vs. 0.042–0.045), a shorter eye-naris distance (END/SUL 0.064–

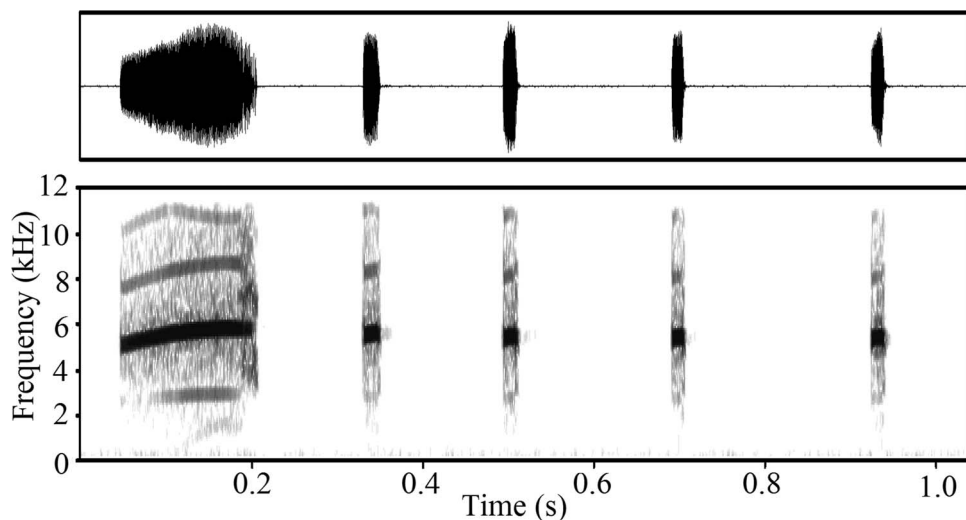


Fig. 13. Above, waveform of an advertisement call consisting of five notes from SAMA R71755, tentatively referred to *Cophixalus melanogenys*; Below, spectrogram of this call. Spectrogram parameters: FFT length 256; Frame size 75%; Window FlatTop; Bandwidth 470 Hz, Resolution 94 Hz; Overlap 87.5%. Sampling rate conversion from 96 kHz to 24 kHz; sample units 32.

0.073 vs. 0.096–0.098), and advertisement calls consisting of more than 100 notes (vs. normally one). *Cophixalus desticans* has a wider disc on toe 4 (T4D/SVL 0.048–0.068 vs. 0.042–0.045), a lower ratio F3D/T4D (0.58–0.71 vs. 0.75–0.80) and calls containing 5–25 notes (vs. normally one) each lasting more than 300 ms (vs. less than 150 ms).

Several morphologically similar species lacking dorsal skin ridges can be further distinguished from *Cophixalus melanogenys* as follows: *C. amabilis* has shorter hind legs (TL/SVL 0.42–0.48 vs. TL/SUL 0.49–0.50), a smaller internarial distance (IND/SVL 0.087–0.101 vs. IND/SUL 0.114–0.119), face and body laterally black with pale blue spots (vs. uniformly black), and produces calls comprising single pulsed notes (= calls) lasting 0.97–1.31 s (vs. single unpulsed notes of < 150 ms); *C. ateles* [including syn. *C. sisypus*] has a larger terminal disc on finger 3 (F3D/SVL 0.039–0.063 vs. 0.031–0.036) and produces calls containing 5–10 uniformly peeping notes with a repetition rate of 1.35–2.26 notes/s (vs. single notes with intervals of more

than 20 s; *C. bewaniensis* has longer hind legs (TL/SVL 0.53–0.59 vs. TL/SUL 0.49–0.50), and a large dark-brown lateral blotch above and behind each upper arm (vs. absent); *C. humicola* has a higher ratio T4D/F3D (1.40–2.25 vs. 1.25–1.33), a large black-brown fleck on anterior flanks (vs. absent) and produces calls with first note pulsed, lasting 62–87 ms (vs. first note unpulsed, lasting >100 ms); *C. interruptus* has longer hind legs (TL/SVL 0.55–0.59 vs. TL/SUL 0.49–0.50); shorter eye-naris distance (END/SVL 0.075–0.083 vs. END/SUL 0.096–0.098), lower END/IND ratio (0.68–0.78 vs. 0.82–0.84), and advertisement calls consisting of long series of peeping notes (vs. one squeaky note possibly followed by a few short notes); *C. iovaorum* has shorter hind legs (TL/SVL 0.41–0.49 vs. TL/SUL 0.49–0.50), a shorter eye-naris distance (END/SVL 0.062–0.077 vs. END/SUL 0.096–0.098) and advertisement calls are long series of raspy chirps with first note shorter than following ones (vs. normally one squeaky note); *C. kethuk* has shorter hind legs (TL/SVL 0.42–0.47 vs. TL/SUL 0.49–0.50), a short-

er eye-naris distance (END/SVL 0.073–0.087 vs. END/SUL 0.096–0.098), a shorter internarial distance (IND/SVL 0.087–1.03 vs. IND/SUL 0.114–0.119), and a dark hourglass marking on dorsolateral surface, (vs. lacking); *C. pulchellus* has a small terminal disc with circum-marginal groove on first finger, (vs. both structures absent), and dorsal color pattern dominated by large black blotches (vs. absent); *C. shellyi* has a lower END/IND ratio (according to Zweifel [1980] 23 specimens of *C. shellyi* from the Highland region had a mean END/IND ratio of 0.61, range 0.52–0.68 vs. 0.82–0.84 in *C. melanogenys*), a poorly defined tympanum (vs. clearly visible) and advertisement calls comprising a series of high pitched peeps lasting 10–20 s at a repetition rate of about 6/s (vs. normally one note uttered at > 20 s intervals); *C. tomaiodactylus* has a shorter eye-naris distance (END/SUL 0.060–0.083 vs. 0.096–0.098), a lower END/IND ratio (0.59–0.73 vs. 0.82–0.84), and its call consists of 2–13 notes with repetition rate of 2.3–6.1 notes/s, with initial note shorter than the following ones (vs. normally one repeated at > 20 s intervals); *C. tridactylus* has the first finger reduced to a vestigial nub, a higher T4D/F3D ratio (1.40–2.25 vs. 1.25–1.33), head laterally with only some dark brown flecks (vs. completely dark brown “face mask”), flanks spotted anteriorly (vs. unspotted) and initial note of advertisement call without harmonics and starting with low pulse followed by 10–20 fast and much louder pulses (vs. initial note unpulsed and with several harmonics).

Discussion

A large proportion of *Cophixalus* species discovered and described from New Guinea in the past two decades are tiny small frogs that do not exceed 20 mm in body length (Günther 2006, Kraus & Allison 2006, 2009, Menzies 2006, Kraus

2012). This fits a broader pattern of emerging diversity of tiny microhylid frogs in New Guinea (e.g., *Paedophryne*: Kraus 2010, 2011, Rittmeyer et al. 2012 and *Choerophryne*: Richards & Burton 2003, Oliver et al. 2017) and Madagascar (e.g., *Stumpffia*: Rakotoarison et al. 2017). Among the tiny New Guinean *Cophixalus* are terrestrial species that occupy leaf litter on the forest floor and others that spend at least part of their lives above the ground in low vegetation. Of the three species described herein, two (*C. brevidigitus* and *C. pusillus*) appear to be predominantly, if not entirely, terrestrial, whereas the third (*C. melanogenys*) is at least partially scansorial. Perhaps surprisingly, *C. melanogenys* shares with the two terrestrial species a reduced first finger lacking a terminal disc and finger discs smaller than the toe discs. These traits are generally associated with a terrestrial lifestyle, although some small scansorial *Cophixalus* (e.g., *C. ateles*, and *C. tomaiodactylus*) also exhibit them (Kraus 2012), suggesting that small size may be a stronger correlate of digit reduction than lifestyle per se in these species. The tiny *Cophixalus pusillus* also exhibits a significant reduction in the size of the first toe, which is fused along almost its entire length with the second toe, a feature seen also in the miniature asterophryine microhylid *Choerophryne allisoni* (Richards & Burton 2003). Most members of the miniature microhylid genus *Paedophryne* also have the first toe reduced to a rudimentary “nub” (Kraus 2010, 2011).

The relationships of the species described here to other small *Cophixalus* species from New Guinea remain unclear. Kraus (2012) noted that *C. shellyi*, *C. pipilans*, *C. iovaorum*, *C. desticans*, and *C. bewaniensis* share a number of characteristics, including a reduced first finger, a black “face mask” and a terrestrial lifestyle, whereas *C. ateles*, *C. variabilis*, *C. timidus*, and *C. tomaiodactylus* have a reduced first finger but lack a black “face mask” and have a scansorial lifestyle. He

concluded that reduced finger size may have evolved independently in these two groups, and possibly in a third group containing *C. humicola* and *C. tridactylus*. These latter species are terrestrial forms without “face masks” and represent the most extreme example of first-finger reduction among *Cophixalus* species, in which the first digit is reduced to a rudimentary “nub” (Günther 2006).

Of the three species described here, only *C. brevidigitus* fits into one of these “groups” discussed by Kraus (2012). It shares with *C. shellyi*, *C. pipilans*, *C. iovaorum*, *C. desticans*, and *C. bewaniensis* a reduced first finger, a prominent dark brown (though not black) “face mask” and a terrestrial lifestyle. However, although *C. pusillus* has a reduced first finger and a terrestrial lifestyle, it has a barely defined “face mask”; and *C. melanogenys* has a reduced first finger and a strongly defined dark “face mask” but it has a scansorial lifestyle. Phylogenetic studies of this speciose genus suggest that scansoriality has arisen independently four times (Rivera et al. 2017), but many of the species discussed here were not included in that analysis. Broader genetic sampling, particularly of miniaturized forms, will be required to better understand relationships among the constituent species and the evolution of their ecomorphological traits.

The discovery of three new tiny species of *Cophixalus* in the central mountains of Papua New Guinea is not surprising. The region’s steep mountainous landscape has long prevented access to remote regions and, when accessed, the collection of tiny, difficult-to-detect frogs has rarely been a high priority. However, recent surveys on the wet, forested southern slopes of Papua New Guinea’s central cordillera revealed an exceptionally diverse frog fauna and documented numerous new species (e.g., Richards & Oliver 2010, Oliver et al. 2012, Richards & Günther 2019). Given the small size and terrestrial or scansorial lifestyles of the frogs described here, they

are likely to have limited dispersal abilities, and it is possible that they have limited distributions. If so, it is likely that other, as-yet undetected, narrow-range endemics occur in the region. Conversely, the presence of extensive suitable habitat in this rugged and remote area suggests potential for these newly described species to be more widely distributed. Although further efforts are required to document the distributions of these poorly known species, their descriptions confirm the significance of the southern slopes of the central mountains as a regional hotspot of frog diversity.

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