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Another giant species of the microhylid frog genus *Cophixalus* Boettger, 1892 from the mountains of Papua New Guinea and first records of procoracoids in the genus

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Abstract

A new arboreal species of the microhylid genus *Cophixalus* Boettger, 1892 is described from montane rainforest on Papua New Guinea's central cordillera. With a male SUL exceeding 44.0 mm, the new species is among the largest members of the genus; the only other Papuan species known to reach this size is *C. riparius* Zweifel, 1962. The new species differs from *C. riparius* in a small number of mensural characters and by its distinct advertisement call, a single explosive 'bark' uttered singly or in rapid series. In contrast, calls of *C. riparius* recorded near the type locality are a series of drawn out, rasping croaks. Calls of the two species are analysed and compared. The two species also appear to have different ecologies, with the new species found only high in trees, while *C. riparius* is often encountered in vegetation on or near the forest floor. Examination of osteological features revealed the presence of cartilaginous procoracoids in both species, representing the first records of procoracoids in the speciose genus *Cophixalus*. Lack of procoracoids is traditionally considered an important diagnostic character for defining *Cophixalus* but both species also lack clavicles, a character considered diagnostic for *Cophixalus* and a key feature distinguishing the genus from the closely related *Oreophryne* Boettger, 1895. Because preliminary published genetic data indicate that they are nested within *Cophixalus*, we retain both species in that genus until a comprehensive molecular phylogeny of *Cophixalus* and related genera, particularly *Oreophryne*, is completed.

Key Words

Amphibia, bioacoustics, central cordillera, montane rainforest, morphology, New Guinea, taxonomy

Introduction

Microhylid frogs in the asterophryine genus *Cophixalus* are confined to the Australopapuan region, where they reach their greatest diversity on mainland New Guinea (Menzies 2006; Kraus and Allison 2009a, b; Kraus 2012; Hill et al. 2022). The genus exhibits substantial morphological diversity, reflecting the broad range of terrestrial (Günther 2006; Kraus and Allison 2009a; Günther and Richards 2011), scansorial (Kraus and Allison 2009a; Richards and Günther 2019) and arboreal (Zweifel 1962; Menzies 2006) habitats that the species occupy. However, the relationship between this observed morphological divergence and the species' phylogenetic relationships remains unclear (Kraus 2012). Despite this morphological diversity, the majority of *Cophixalus* species from New Guinea are tiny to small frogs; the males of many species do not exceed 20 mm in body length and few reach 30 mm (Günther 2006; Kraus and Allison 2006; Menzies 2006; Kraus and Allison 2009a, b; Kraus 2012). Exceptions include *C. caverniphilus* Kraus & Allison, 2009 with males reaching 30.2 mm, and the Sudest Island population of *C. verrucosus* (Boulenger, 1898) with males reaching 31.0 mm (Kraus and Allison 2009b; Kraus 2012).

Records of *C. cryptotympanum* Zweifel, 1956 from the mountains of western Papua New Guinea reaching up to 40 mm (presumably females but sex was not noted; Menzies 2006) are based on misidentifications (Richards and Günther 2019), and the taxonomic status of those populations requires further assessment.

The only *Cophixalus* from the island of New Guinea that is known to have a male body size exceeding 40 mm is *C. riparius*. It was described from a series of 224 specimens collected in 1959 by Hobart van Deusen at an altitude of 2,775 m a.s.l. on the east slopes of Mt Wilhelm in Chimbu Province, Papua New Guinea (Zweifel 1962). As currently understood *C. riparius* is moderately widespread at altitudes between 1,900–2,800 m a.s.l. in the mountains of central Papua New Guinea where its known distribution extends in a narrow band from Southern Highlands and Western Highlands Provinces in the west to the Schrader Mountains in Madang Province in the north and to the vicinity of Wau in Morobe Province in the southeast (Zweifel 1962; Kraus 2010; IUCN SSC Amphibian Specialist Group 2020). Recent surveys to document the altitudinal distribution of amphibians at several sites on Mt Wilhelm provided the opportunity to obtain data on the advertisement calls of *C. riparius* from the vicinity of the type locality. Calls of *C. riparius* from Mt Wilhelm differ markedly from those produced by a morphologically similar but geographically isolated population documented recently on Gigira Ridge in Hela Province approximately 260 km to the west of the type locality (Richards et al. 2021). Here we describe this western population as a species distinct from *C. riparius* and report the presence of cartilaginous procoracoids in both species. These are the first records of cartilaginous procoracoids in the genus *Cophixalus*.

Materials and methods

Male frogs of the new species were located at night by their advertisement calls but only one adult male and one juvenile specimen could be collected. These vouchers were anaesthetised in an aqueous chlorobutanol solution and subsequently fixed in 5% formalin. Both 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 using protocols for microhylid frogs adopted previously (e.g. Günther et al. 2014): **SUL** – snout-urostyle length from tip of snout to posterior tip of urostyle (SUL is sufficiently similar to SVL 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 held at right angles; **FTL** – length of foot, from tip of 4th toe to proximal edge of sole; **T4D** – transverse diameter of disc of 4th toe; **T1D** – transversal diameter of disc of first toe; **HDL** – length of hand, from tip of 3rd finger to proximal edge of palm; **F3D** – transverse diameter of disc of 3rd finger; **F1D**– transversal diameter of disc of first finger; **HL** – head length, from tip of snout to posterior margin of tympanum; **HW** – head width, taken in the region of the tympana; **SL** – snout length, from an imaginary line connecting the centres of the eyes to 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; **EST** – distance from anterior corner of orbital opening to tip of snout; **TyD** – horizontal diameter of tympanum. Measurements are presented as mean ± standard deviation and range.

Advertisement calls were recorded under natural conditions with a Roland R-05 digital recorder and Sennheiser ME-66 shotgun microphone and analysed with Avisoft-SAS Lab Pro software. Air temperatures were taken ~2 m above the forest floor, directly below calling males. Terminology and acoustic analysis procedures follow Köhler et al. (2017).

The colour of animals in life was described from digital photographs, and of preserved specimens from direct observations. Most colours were determined according to a colour matching system that is created and administrated by the German RAL GmbH (RAL non-profit LLC) available at https://en.wikipedia.org/wiki/RAL_colour_standard. When it was impossible to find an exact match between observed colour and a certain RAL colour number the most similar RAL number was chosen.

Due to the small sample size of the new species, osteological characters were examined by partial dissection and staining with alcian blue. Osteological features of comparative specimens in the genera *Cophixalus* and *Oreophryne* were determined using this method, or specimens were cleared and stained according to Dingerkus and Uhler (1977).

The holotype and a juvenile paratype of the new species are stored in the collection of the South Australian Museum Adelaide (SAMA). Acronyms for additional institutions mentioned herein are: AMNH (American Museum of Natural History, New York) and ZMB (Museum für Naturkunde, Berlin).

Compared material

The following specimens of *Cophixalus riparius*, the only very large *Cophixalus* species previously known from New Guinea, were examined: six paratypes from the type locality, Pengagl Creek on the east slope of Mt Wilhelm, Chimbu Province, Papua New Guinea (AMNH A.112985, A.112992, A.112995, A.113004–5, and A.113007); four additional specimens collected recently by C. Dahl from the north-eastern slopes of Mt Wilhelm within 13 km of the type locality (SAMA R71660–63);

one specimen collected by S. Richards and C. Dahl from Mt Michael near Goroka in Eastern Highlands Province (SAMA R71701); and 53 specimens collected by F. Parker from the Porol Range, 30 km SSE of Mt Wilhelm (ZMB 42575–628). Additional 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 (2003, 2006, 2010), Richards and Oliver (2007, 2010), Günther and Richards (2011) and Günther et al. (2014) and additional comparative information was taken from original descriptions and recompiled treatises (Méhely 1901; Zweifel 1956a, b, 1962, 1979; Tyler 1963; Zweifel and Parker 1989; Kraus and Allison 2006, 2009a, b; Menzies 2006; Kraus 2012; Richards and Günther 2019).

Results

The new species is assigned to the genus *Cophixalus* based on having the jaw eleutherognathine, clavicles absent, third toe longer than fifth, discs on fingers broader than on toes, and snout not elongated and lacking pad of connective tissue. The new species and *C. riparius* have cartilaginous procoracoids (see below), the lack of which has previously been considered a diagnostic character for *Cophixalus*, but genetically they are nested within *Cophixalus* (Richards et al. 2021) so we assign them to that genus pending further studies.

Cophixalus gigiraensis sp. nov.

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Mount Gigira Giant Nursery Frog

Oreophryne? sp. 5 'loud grunter' (Richards & Armstrong, 2017).
Cophixalus sp. 5 'loud grunter' (Richards & Armstrong, 2018).
Cophixalus sp. 4 'loud grunter' (Richards et al., 2021).

Type material. ***Holotype*:** SAMA R71740 (SJR 15394), adult male from Gigira Ridge, Hela Province, Papua New Guinea (5.9725°S, 142.7532°E; 2160 m a.s.l.) collected on 22 May 2017 by S. Richards and C. Dahl.

***Paratype*:** SAMA R71700 (FN SJR15396), juvenile, same details as holotype except collected on 23 May 2017.

Referred specimens. SAMA R71748 (FN SJR[J-CUNQ]5097), Summit ridge of Mt Sisa, Hela Province, Papua New Guinea (6.1343°S, 142.7536°E; 2450 m a.s.l.) collected on 29 October 1999 by S. Richards; SAMA R71749 (FN SJR8645), Summit of Mount Elimbari, Chimbu Province, Papua New Guinea (6.1899°S, 145.1486°E; 2566 m a.s.l.) collected on 01 December 2004 by S. Richards and C. Dahl.

Diagnosis. With a snout-urostyle length of 44.4 mm in an adult male the new species is among the largest species of the genus; in New Guinea only *Cophixalus riparius* reaches a similar size. It is distinguished from *C. riparius* and all other congeners by the following unique combination of characters: body robust, head short (HL/SUL 0.31); legs moderately short (TL/SUL 0.42), third toe longer than fifth; fingers and toes with greatly expanded triangular terminal discs, all with circum-marginal grooves; discs of fingers much larger than those of toes (T4D/F3D 0.76); dorsal surfaces including rear of tarsus with scattered low tubercles, ventral surfaces smooth; most of dorsal surfaces brown-olive (RAL 8008) with irregular beige (most similar to RAL 1001) flecking; ventral surfaces whitish overlain with moderately dense reddish-brown pigmentation; advertisement call a loud explosive 'bark' produced singly or in groups of up to eight, each containing 13–19 pulses lasting 60–80 ms, dominant frequency 1.5 kHz.

Description of the holotype (Fig. 1a–d). An adult male with vocal slits, calling when collected. For measurements see Table 1. Head slightly broader than long (HL/HW 0.89), canthus rostralis rounded; loreal region steep, slightly concave; snout protruding in profile, slightly pointed in dorsal view; nostrils directed dorsolaterally, closer to tip of snout than to eyes; horizontal eye diameter much greater than eye-naris distance (ED/END 1.48); tympanum relatively small (TyD/ED 0.37), not well-demarcated; supratympanic skin fold narrow but well defined in life and preservative; internarial distance greater than distance between eye and naris (END/IND 0.83); tongue large, pear-shaped, posterior margin rounded and free; two prepharyngeal ridges, anterior ridge with 10 tiny lobes, posterior one with 14 denticles; vocal slits moderately long, located on both sides of tongue. Legs relatively short (TL/SUL 0.42); webbing between fingers and toes absent; discs of fingers triangular, wider than triangular discs of toes (T4D/F3D 0.76); all finger and toe discs with circum-marginal grooves; relative length of fingers 3>4>2>1 (Fig. 1c). Third toe slightly longer than fifth; relative length of toes 4>3>5>2>1 (Fig. 1d); most subarticular, metatarsal and metacarpal tubercles indicated by light colour but structurally only scarcely developed. In life dorsal surfaces and posterior of tarsus with scattered low tubercles; all ventral surfaces smooth.

Dorsal surfaces in life predominantly clay-brown (RAL 8003) (Fig. 1a), paler on flanks than mid-dorsum; mid-dorsum, upper flanks and incomplete lumbar spots with several irregular beige flecks; upper arms including elbows, and tarsi including tibio-tarsal joints, also with beige flecking; ventral surfaces whitish with more (on extremities) or less (on abdomen, chest and throat) dense reddish-brown pigmentation (Fig. 1b); rear of thighs monochromatic pale brown (RAL 8025). Iris whitish with sparse network of dark brown reticulations.

In preservative dorsal and lateral surfaces darker brown, beige flecks less obvious prior to staining with alcian blue. After staining, dorsal surfaces uniformly slate gray (RAL 7015) with pale brown (RAL 8025) areas detectable through the gray; dorsal surfaces of hands beige brown (RAL 8024); throat pale brown with soft blue tinge; chest and abdomen with pronounced blue tinge; ventral surfaces of extremities predominantly pale brown.

Figure 1. Holotype of *Cophixalus gigiraensis* sp. nov. in life **a.** Dorsolateral view; **b.** Ventral view; **c.** Palmar view of right hand; **d.** Plantar view of right foot.

Description of the paratype (Fig. 2a–c). A juvenile (SUL 15.4 mm) of undetermined sex. For measurements see Table 1. General body and head shape, and presence of low tubercles on dorsum and tarsi similar to holotype but colour pattern in life strikingly different. Head and nape in dorsolalateral and dorsal views with large light ivory (RAL 1015) blotch (Fig. 2a, b). This blotch continues anteriorly to nostrils where it is interrupted at tip of snout by triangular brown-grey (RAL 7013) spot; and posteriorly to urostyle. Light ivory area framed dorsolaterally by two irregularly shaped gray-brown (RAL 8019) stripes extending from behind eyes to well-defined lumbar spots. Additional light ivory areas on dorsal surfaces of upper arms, around tibio-tarsal articulations, on dorsal surfaces of tarsi and on upper flanks. Snout partially beige-red (RAL 3012) dorsally and laterally. Dorsal surfaces of thighs and shanks, lower flanks, anterior forearm and subocular region olive grey (RAL 7002). Throat, chest, abdomen and lower surface of thighs rather uniform olive grey with few irregular whitish spots (Fig. 2c). Iris pebble grey (RAL 7032) with

Figure 2. a–c. Juvenile paratype of *Cophixalus gigiraensis* sp. nov. in life.

dark brown reticulations (Fig. 2a). Several morphological ratios of the juvenile paratype deviate substantially from those of the adult paratype (Table 1). Further material is required to determine whether these differences represent ontogenetic change.

Vocalisation. The advertisement call of *Cophixalus gigiraensis* is a short, harsh barking note uttered singly or in series containing 2–8 notes (Fig. 3a–c). Eight calls (two single calls and three sets of couplets) of the holotype were of sufficient quality for analysis. Intervals between these note=call series were 28–37 s but many other frogs were heard calling at longer intervals of up to several minutes (S. Richards, personal observations). The number of pulses and length of calls is difficult to assess exactly, due to an echo possibly associated with their calling position inside small holes in tree trunks, but these eight notes=calls contain 8–17 pulses (mean 14.6±3.2), some incompletely divided, lasting approximately 68–106 ms (mean 78.5±12.4 ms). Intervals between calls produced in couplets are 812–910 ms (n = 3); dominant frequency is at 1.5 kHz and there is a weak fundamental frequency band at 0.6 kHz (Fig. 3b, c). An unvouchered specimen uttered three call series in a row consisting of 5, 8 and 7 calls. These calls were much shorter than those produced by the holotype (50–77 ms, mean 64.7±6.4 ms, n=20) and intercall intervals were also shorter (240–349 ms, mean 266.9±29.0 ms, n=17) than in the calls from the holotype.

Distribution. *Cophixalus gigiraensis* is known with certainty only from Gigira (Hides) Ridge at the northern edge of the Kikori River basin in Hela Province, Papua New Guinea (Fig. 4). It may also occur on nearby Mount Sisa (Richards and Armstrong 2018; this location falls within the yellow square indicating the type locality in Fig. 4), and on Mount Elimbari about 270 km east of the type locality (Richards et al. 2021) but resolution of the status of those populations will require collection of additional material. If the Mount Elimbari population is confirmed to belong to *C. gigiraensis* then this will represent a large range extension and demonstrate that this species occurs in close proximity to its close relative *C. riparius*. *Cophixalus gigiraensis* was not found at lower altitudes elsewhere in the Kikori River basin, despite intensive surveys on the Agogo Range at altitudes between 1,000 and 1,700 m a.s.l. over many years.

Table 1. Body measurements and body ratios of the male holotype (SAMA R71740) and a juvenile paratype (SAMA R71700) of *Cophixalus gigiraensis* sp. nov. All measurements in mm; for explanation of abbreviations see Material and methods section.

Reg.No	SAMA R 71740	SAMA R 71700
SUL	44.4	15.4
TL	18.5	7.6
TaL	12.5	4.5
T4L	19.6	3.9
T4D	2.5	0.8
T1D	2.2	0.6
F3L	15.0	3.1
F3D	3.3	0.9
F1D	2.5	0.6
HL	13.7	5.8
HW	15.4	5.7
END	3.3	1.6
IND	4.0	1.8
SL	6.5	3.4
ED	4.9	2.5
EST	5.2	2.2
TyD	1.8	0.9
TL/SUL	0.42	0.49
TaL/SUL	0.28	0.29
T4L/SUL	0.44	0.25
T4D/SUL	0.056	0.052
F3L/SUL	0.34	0.20
F3D/SUL	0.074	0.058
T4D/F3D	0.76	0.89
T1D/F1D	0.88	1.00
HL/SUL	0.31	0.38
HW/SUL	0.35	0.37
HL/HW	0.89	1.02
END/SUL	0.074	0.104
IND/SUL	0.090	0.117
END/IND	0.83	0.89
ED/SUL	0.110	0.162
EST/SUL	0.117	0.143
TyD/SUL	0.041	0.058
TyD/ED	0.37	0.36
SL/SUL	0.146	0.221

Habitat and habits. *Cophixalus gigiraensis* is an arboreal species that calls at night from ~15–30 m high in *Nothofagus* trees in mid-montane rainforest on karst terrain (Fig. 5). It is not possible to safely climb these large

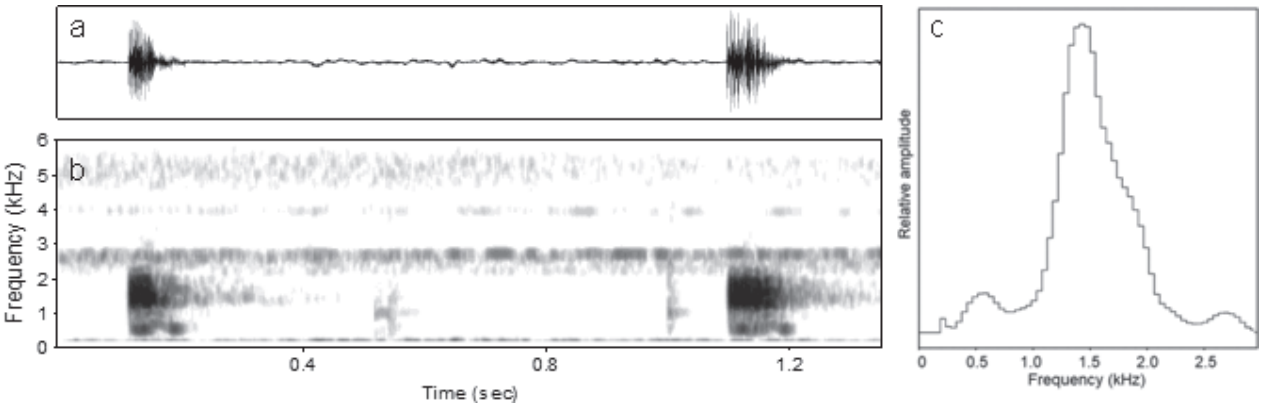

Figure 3. Oscillogram (**a**), spectrogram (**b**) and relative amplitude (**c**) of an advertisement call series from the holotype of *Cophixalus gigiraensis* sp. nov. consisting of two calls. Basic noise was deleted up to 0.3 kHz. Sampling rate conversion from 24 kHz to 12 kHz; spectrogram parameters: FFT length 256, Frame size 75%, Window FlatTop, Bandwidth 313 Hz, resolution 63 Hz, Overlap 87.5%.

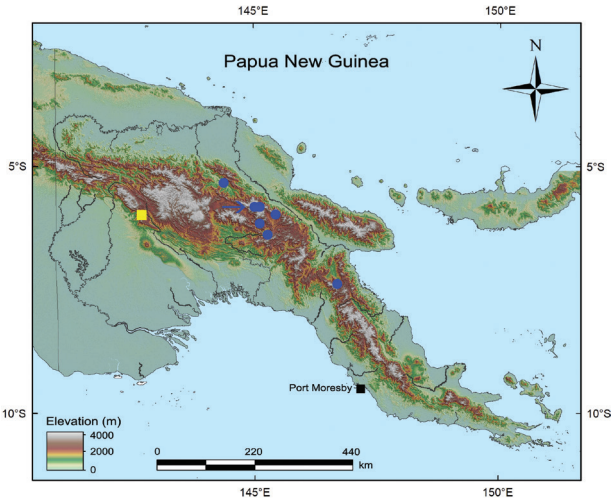

Figure 4. Distribution of *Cophixalus gigiraensis* sp. nov. (yellow square) and *C. riparius* (blue circles). The arrow indicates the type locality of *C. riparius*.

trees so, although the species appears to be moderately abundant because numerous specimens were heard calling in the vicinity of the type locality in 2005 and again between 2015 and 2019, only one adult male and one juvenile have been captured. The adult male was calling from a height of about six metres at the entrance to a small hole in the vertical trunk of a large *Nothofagus* tree, while the juvenile was on low foliage in the forest understorey at night. The new species occurs in sympatry with six other microhylid frog species: *Choerophryne brevicrus* (Günther & Richards, 2012), two undescribed *Choerophryne* species, *Hylophorbus richardsi* Günther, 2001, *Oreophryne anamiatoi* Kraus & Allison, 2009 and *O. notata* Zweifel, 2003, the limnodynastid *Platyplectrum aganoposis* (Zweifel, 1972) and the pelodryadids *Litoria iris* (Tyler, 1962) and *L. vivissimmia* Oliver, Richards & Donnellan, 2019.

Etymology. The specific epithet *gigiraensis* refers to the type locality of this species, Gigira Ridge, otherwise known as Hides Ridge. Gigira is the local Huli Community's name for this mountain.

Comparison with other species. Only one other species of *Cophixalus* on New Guinea, *C. riparius* (Fig. 6), reaches the size of *C. gigiraensis*. *Cophixalus riparius* was described by Zweifel in 1962 on the basis of a large series (224 specimens including the holotype) from the east slope of Mt Wilhelm in Western Highlands Province.

The holotype of *C. gigiraensis* differs biometrically from five randomly selected adult males and five adult females from the Porol *riparius*-series in having a longer head (HL/SUL 0.31 vs. 0.26–0.30), a higher HL/HW ratio (0.89 vs. 0.72–0.88), and a broader disc on the first toe (T1D/SUL 0.050 vs. 0.040–0.049; T1D/F1D 0.88 vs. 0.63–0.77). Males from the Porol Range are somewhat smaller than females (14 adult males measured 37.8–41.1 mm SUL and 10 adult females 41.2–47.1 mm SUL). Sexual size dimorphism is common among many anuran species but has rarely been recorded for species in the genus *Cophixalus*. This also suggests that *C. gigiraensis* may be slightly larger than *C. riparius*, but additional material of the new species is required to confirm this.

The advertisement calls of *C. riparius* and the new species are different (compare Figs 3, 7). A series of four calls produced by a *C. riparius* (SAMA R71660) near the type locality on Mt Wilhelm are long, guttural croaks lasting 751–1031 ms (mean 927 ms) and contain 34–35 pulses. Calls in the series are separated by intervals of 4.5–5.4 s. A conspicuous feature of these calls is that pulse rate is much faster at the beginning of the call than at the end (Fig. 7a, b). Dominant frequency is at 1.55 kHz (Fig. 7c). A second call series produced by a *C. riparius* (SAMA R71701) on Mt Michael, about 70 km SSW of the type locality, is of poorer quality but in all pertinent respects agrees with calls produced by the near-topotypic animal. It also contains four long, rasping calls, and pulse rate declines markedly during each call. In contrast, the short, barking calls of *C. gigiraensis* last just 50–106 ms, contain 8–17 pulses, and pulse rate does not change during the call; call intervals within series last 0.24–0.90 s.

There also appear to be some ecological differences between the two species. The large series of *C. riparius* collected at the type locality by Hobart Van Deusen

Figure 5. Emergent *Nothofagus* trees in montane forest on Gigira Ridge. Male *Cophixalus gigiraensis* called from the upper canopy of these large emergent trees making collection difficult.

Figure 6. A male *Cophixalus riparius* (SAMA R71661) from near the type locality of this species on Mt Wilhelm, Papua New Guinea. The dorsal colour pattern of this species is highly variable.

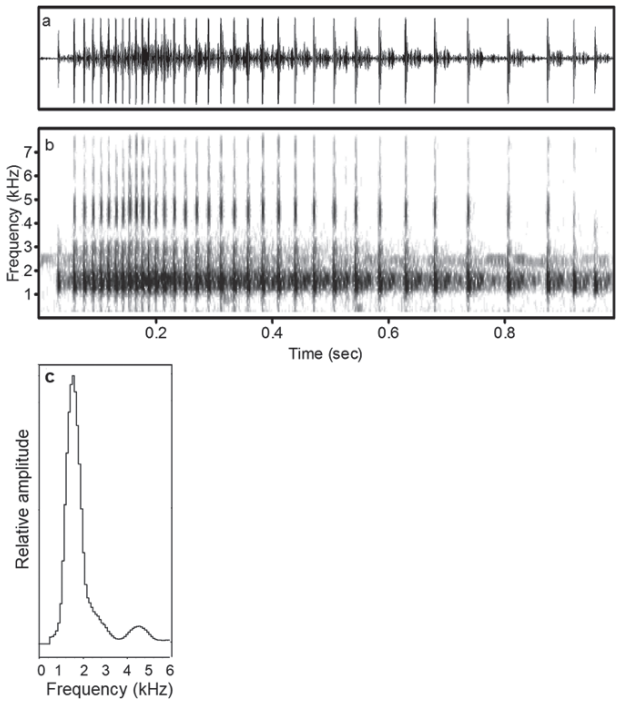

Figure 7. Oscillogram (**a**), spectrogram (**b**) and relative amplitude (**c**) of an advertisement call of *Cophixalus riparius* from Mt Wilhelm consisting of 35 pulses. Basic noise was deleted up to 0.3 kHz. Sampling rate conversion from 24 kHz to 16 kHz; spectrogram parameters: FFT length 256, Frame size 75%, Window FlatTop, Bandwidth 313 Hz, resolution 63 Hz, Overlap 87.5%.

(> 200 specimens "amid grass, low shrubs, or boulders") and by Fred Parker in the Porol Range suggests that not only was the species abundant at those locations but that they were commonly encountered on or near the forest floor. In contrast, *C. gigiraensis* appears to be restricted to the mid and upper canopy of *Nothofagus* trees (Fig. 5). The only animal encountered near the ground during 1.5 months of survey effort in the vicinity of the type locality, spread over several years (2015–2019), was the juvenile paratype. It was perched on a leaf approximately 2 m above the ground in the forest understorey. The adult holotype was the lowest-calling individual heard during numerous surveys, being only ~6 m above the forest floor. It was collected by binding several long saplings together to dislodge it from its arboreal calling perch.

Procoracoids in the genus *Cophixalus*

According to Parker (1934), Zweifel and Parker (1989), Burton and Zweifel (1995), Kraus and Allison (2000, 2009a), Kraus (2012) and Richards and Günther (2019) one of the key features defining the genus *Cophixalus* is the lack of procoracoids. During investigation of the ventral elements of the pectoral girdle to determine generic allocation of the new species, we discovered that the holotype of *C. gigiraensis* and several randomly chosen specimens of *C. riparius* from the Porol Range all have cartilaginous procoracoids. Their structure is similar to that of *Oreophryne* species wherein the procoracoids do not reach the scapulae. Lateral processes of procoracoids in a preserved and partly dissected specimen of *C. riparius* stained with alcian blue (ZMB 42612, Fig. 8a) and in two cleared and double stained specimens (ZMB 42593 and ZMB 42625) of this species are longer (reaching roughly to middle of the coracoid bone) and narrower than in the holotype of C. *gigiraensis*, and the shape of the proximal part is flat in *C. riparius* from the Porol Range but high (triangular) in *C. gigiraensis* (compare Fig. 8a, b). Based on the existing preparations it is not possible to determine whether the procoracoids are connected directly with the sternum or whether an omosternum is a component of the structure of proximal parts of the procoracoids.

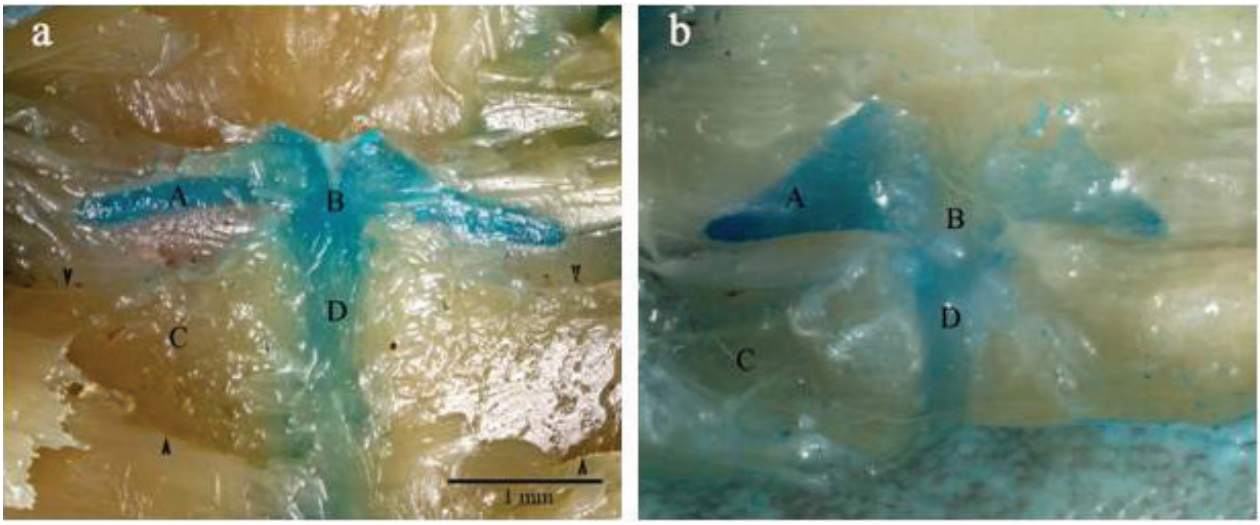

Figure 8. (**a**) Ventral view of procoracoids of *Cophixalus riparius* (ZMB 42612) from the Porol Range and (**b**) ventral view of procoracoids of *Cophixalus gigiraensis* sp. nov. (SAMA R71740). (A) lateral process of the right procoracoid, (B) omosternum (?), (C) coracoid, (D) sternum, arrows in Fig. 8a mark anterior and posterior edges of coracoids.

It is possible that Zweifel (1962) did not detect these small and fragile elements in *C. riparius* because most specimens examined internally were done so via dissection, and only the absence of a clavicle was confirmed in two cleared and stained specimens (Zweifel 1962). It is also possible that the Porol Range material does not represent *C. riparius*, but the large series from that location examined by us is indistinguishable from topotypic *C. riparius*. We do not speculate further on this discrepancy other than to note that further investigations of these structures in topotypic *C. riparius* are required. Studies of additional material are also required to determine whether the observed differences in the shape of the procoracoids between three *C. riparius* from the Porol Range and one *C. gigiraensis* are species specific.

Discussion

The presence or absence of both procoracoids and clavicles has traditionally been a key morphological feature used to identify and classify Australopapuan microhylid frogs (Parker 1934). However, there appear to have been multiple independent losses of procoracoids and clavicles among lineages of Australopapuan frogs (e.g., Burton 1990), and recent studies have indicated that *Oreophryne* (defined by traditional morphological characters) comprises two unrelated clades (Hill et al. 2022) so that the loss of procoracoids and clavicles has occurred at least twice in this group. Indeed, increased use of molecular phylogenetic techniques in combination with the rapidly increasing number of Australopapuan microhylid species available for study (Oliver et al. 2022) have demonstrated that many of the morphological traits traditionally used to classify this fauna at the genus level may be phylogenetically uninformative due to convergence (Hill et al. 2022). *Cophixalus riparius* was not included in recent molecular phylogenetic studies of New Guinean microhylid frogs (Köhler and Günther 2008; Peloso et al. 2016; Rivera et al. 2017; Hill et al. 2022) but a preliminary study of the relationships among more than 100 microhylid species using genome-scale DNA sequencing placed both *C. riparius* and *C. gigiraensis* (as *Cophixalus* cf. *riparius*) within *Cophixalus*, not *Oreophryne* (Richards et al. 2021). Further studies are required to determine whether the presence of procoracoids and clavicles is more widespread among the rapidly increasing known diversity of Australopapuan *Cophixalus*. Interestingly, the two species closest to *riparius* and *gigiraensis* in the molecular tree presented by Richards et al. (2021), *Cophixalus nubicola* Zweifel, 1962 and *C. kaindiensis* Zweifel, 1979 are both reported to lack these elements (Zweifel 1962, 1979).

Cophixalus gigiraensis and *C. riparius* are the largest *Cophixalus* in New Guinea, with male SVL of both species exceeding 40 mm. They are morphologically similar but acoustically distinct, and phylogenetic analyses of SNP data support their distinctiveness (Richards et al. 2021; *C. gigiraensis* presented as *Cophixalus* cf. *riparius*). The two species also appear to be ecologically divergent, with *C. gigiraensis* normally calling from more than 15 m, and commonly up to 30 m, above the forest floor in large *Nothofagus* trees on karst terrain (Fig. 5; Richards & Dahl, unpublished observations). In contrast, although Kraus and Allison (2000) reported *C. riparius* from epiphytes up to 20 m above the ground, large numbers of *C. riparius* have also been encountered on or near the ground (grass, low shrubs and boulders; Zweifel 1962), in habitats quite unlike those encountered at the type locality of *C. gigiraensis*. Chomiki (2020) also reported *C. riparius* inhabiting the epiphytic ant-plant *Hydnophytum myrtifolium* in the highlands of Papua New Guinea, but erroneously implied that this species was breeding in the accumulated rainwater within the ant plants. Like other Australopapuan microhylid frogs *C. riparius* and *C. gigiraensis* almost certainly have direct development, in which embryos develop directly into small juveniles, bypassing the tadpole stage (Anstis et al. 2011). It is not known whether *C. gigiraensis* also occupies the ant plants that occur at the type locality.

The description of *Cophixalus gigiraensis* from the limestone terrain of Gigira Ridge adds to the growing number of frog species known predominantly or entirely from karst habitats along the southern fringe of New Guinea's Central Cordillera (Richards and Oliver 2010; Richards and Günther 2019; Richards et al. in press). However, additional information on the distribution of *C. gigiraensis* is required before it can be determined whether this species is confined to karst habitats or is more broadly distributed at suitable altitudes across this mountainous region.

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