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Litoria aplini sp. nov., a New Species of Treefrog (Pelodryadidae) from Papua New Guinea

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Abstract. We describe a new species in the Australopapuan pelodryadid frog genus *Litoria* from upper hill forest (940 m a.s.l.) on the northern slopes of Papua New Guinea's central cordillera. The new species is moderately small (male body length = 31.9–35.1 mm) and slender (head width/body length = 0.29–0.30), with extensive golden-yellow markings ventrally. It is most similar to *Litoria iris*, *L. majikthise*, *L. ollauro*, and *L. verae* but differs from them by a suite of morphological and colour features. The advertisement call is a series of short buzzes and clicks reminiscent of calls produced by both *L. iris* and *L. ollauro*. Phylogenetic analysis of mitochondrial *ND4* nucleotide sequences shows that the new species is closest to *L. iris* and *L. majikthise* but shows a net sequence divergence of 14–15% from both of these taxa. The new species is unusual in being found calling from forest on limestone substrate where free-standing water is rarely encountered.

Introduction

Litoria is a morphologically and ecologically diverse assemblage of pelodryadid frogs confined almost entirely to the Australopapuan region (Tyler, 1999). Although there have been attempts to divide *Litoria* into informal species groups (Tyler & Davies, 1978; King, 1981; Menzies, 2006), and into a number of genera (Duellman *et al*., 2016), relationships among many species remain poorly resolved, limiting the usefulness of proposed generic or species group concepts. One such example is *Litoria iris* and its relatives. *Litoria iris* is a small, brightly coloured, montane treefrog from mainland New Guinea, typically occurring at altitudes above c. 1500 m a.s.l. (Menzies, 2006) although there is a single record from 1000 m a.s.l. (Kraus & Allison, 2006). Adults glue their large, green eggs to vegetation hanging over small pools in a wide range of pristine and degraded habitats (Menzies, 2006). Menzies (1972) and Tyler & Davies (1978) included this species in the "*Litoria nigropunctata* Group" along with *L. nigropunctata* and *L. vocivincens*, two lowland species that differ markedly from *L. iris* in laying small pigmented eggs and in lacking bright colours ventrally (Menzies, 2006). Menzies (1993), in placing greater taxonomic emphasis on known or presumed reproductive strategies, included *L. iris* in an "*L. iris* group" along with six other species, four of them described as new: *L. chloronota*, *L. havina*, *L. majikthise* (as *L. leucova*), *L. mucro*, *L. ollauro*, and *L. pronimia*. Subsequently, Menzies (2006) expanded the "*L. iris* group" to include an additional three species, *L. leucova*, *L. multiplica,* and *L. prora*, creating a morphologically and ecologically heterogeneous assemblage defined by a single character: gluing large pale eggs on leaves above water. However, the reproductive strategies of five of the ten species in Menzies' "*L. iris* group" have not been documented as yet, and the striking morphological and ecological divergences evident among members of the group (see e.g., Menzies, 2006) suggest that it is unlikely to be monophyletic.

Keywords: New Guinea; frog; acoustics; taxonomy; phylogeny; rainforest
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Despite ongoing uncertainty about relationships among many members of the "*L. iris* group" as defined by Menzies (2006), several species within that assemblage, *L. iris*, *L. majikthise*, *L. ollauro*, share a suite of morphological, acoustic, and colour features that hint at a close relationship. These include moderately small size, enlarged tubercles along the outer margins of the limbs, bright colours in life ventrally and/or on the hidden surfaces of the thighs, and advertisement calls (where known) consisting of short chirps and buzzes. Three additional species, *L. richardsi*, *L. singadanae,* and *L. verae*, that were not included in the "*L. iris* group" by Menzies (2006) share these morphological and colour features, and two of them have similar calls; the call of *L. singadanae* has not been documented.

Discovery of a population of *Litoria* in Sandaun Province on the northern slopes of Papua New Guinea's central cordillera that exhibits characters typical of the "*L. iris* group" but differs consistently in a unique suite of morphological and acoustic features, led us to examine its molecular genetic relationships. Based on a combination of molecular genetic, morphological, and acoustic data we here describe the population from northern New Guinea as a new species.

Materials and methods

Molecular genetics

Frozen or alcohol preserved tissues were available from 25 *Litoria* from 20 locations (Appendix 1). Selection of taxa was based on the mitochondrial DNA sequence phylogenetic analysis of Rosauer *et al.* (2009) and a broader unpublished mitochondrial barcode survey of Melanesian pelodryadid frogs (Donnellan, Richards, and Mahony, unpublished). DNA was extracted using a Puregene DNA isolation kit (Gentra Systems, Minneapolis, MN, U.S.A.) following the manufacturer's protocol for DNA purification from solid tissue. A fragment of the mitochondrial *NADH dehydrogenase subunit 4* (*ND4*) gene was amplified and sequenced using the forward primers 5'-TGACTACCAAAA GCTCATGTAGAAGC-3' with the reverse primer 5'-CATT TACTTTTTACTTGGATTTGCACCA-3'. Each PCR was carried out in a volume of 25 µl with a final concentration of 1X GeneAmp PCR Gold buffer, 2–4 mM MgCl2, 200 M of each dNTP, 0.2 mM of each primer and 0.5 U of AmpliTaq Gold DNA polymerase (Applied Biosystems, Foster City, CA, U.S.A.). Amplifications consisted of an initial denaturation step of 94°C for 9 min, followed by 34 cycles of PCR with the following temperature profile: denaturation at 94°C for 45 s, annealing at 55°C for 45 s, and extension at 72°C for 1 min, with an additional final extension at 72°C for 6 min. The double-stranded amplification products were visualized on 1.5% agarose gels and purified using an UltraClean PCR clean-up DNA purification kit (Mo Bio Laboratories Inc., CA) before cycle-sequencing using the BigDye Terminator v3.1 cycle-sequencing kit (Applied Biosystems).The cycling protocol consisted of 25 cycles of denaturation at 96°C for 30 s, annealing at 50°C for 15 s, and extension at 60°C for 4 min. All samples were sequenced on an Applied Biosystems 3700 DNA sequencer. Sequences were aligned with Muscle v6.814b (Edgar, 2004) implemented in Geneious Pro v8.1.4 (Kearse *et al.*, 2012) and are deposited in GenBank (accessions numbers: MT268302–268326).

Bayes factors were used to assess all possible alternative partitioning strategies for four data subsets—1st, 2nd and 3rd codon positions and the tRNA in PartitionFinder v1.0.0 (Lanfear *et al*., 2012). The Bayes Information Criterion (BIC) was used to assess the best fit partition strategy and nucleotide substitution model for each data subset in the selected partition strategy. The data subset scheme comprised each of the codon positions as subsets with nucleotide substitution models GTR+I+G for the 1st and 2nd codon subsets and the GTR+G model for the 3rd codon position.

Sequences were analysed phylogenetically using Bayesian and maximum likelihood methods. Bayesian analysis was conducted using MrBayes v3.1.2 (Ronquist & Huelsenbeck, 2003). The analysis was run with model parameters unlinked using default priors for ten million generations with two independent runs and two chains sampling every 1000 generations. Convergence was assessed as achieved when the average standard deviation of split frequencies was <0.001 and effective sample sizes (ESS) were >3500 as determined in TRACER v1.4.1 (Rambaut & Drummond, 2007). The first 25% of sampled trees were discarded as burn-in. Partitioned maximum likelihood (ML) analysis was performed using RAxML v8.0 (Stamatakis, 2014) on the CIPRES Science Gateway (Miller *et al.*, 2010).

Net average sequence divergence between lineages (dA) was calculated in Mega v5 (Tamura *et al*., 2011) as: $dA = d\text{XY} - (d\text{X} + d\text{Y})/2$, where, dXY is the average distance between groups X and Y, and dX and dY are the within-group means (Table 1).

Molecular diagnostics. Following the recommendation of Renner (2016), we visually identified diagnostic SNPs within the mitochondrial *ND4* gene in Geneious Pro v8.1.4. We selected the apomorphic SNPs that diagnosed the new species from its two closest relatives, using more distantly related members of the larger clade to assess character state polarity (Table 2).

Morphology

Measurements, terminology, and abbreviations follow Tyler (1968) and Oliver *et al.* (2019b). Measurements were made to the nearest 0.01 mm with callipers (SVL—body length from snout to vent, TL—tibia length from heel to outer surface of flexed knee, HL—head length, from tip of snout to posterior margin of tympanum, HW—head width at level of tympana) or a dissecting microscope fitted with an optical micrometer (all other measurements): EN—distance from anterior corner of eye to posterior margin of naris; IN—internarial distance, between medial margins of external nares; EYE—horizontal diameter of eye; TYM—horizontal diameter of tympanum including tympanic annulus; 3FD—transverse diameter of disc of finger III; 3FP—transverse diameter of penultimate phalanx of finger III; 4TD—transverse diameter of disc of toe IV and 4TP—transverse diameter of penultimate phalanx of toe IV. Measurements are presented as mean ± SD and range. Sex was determined by examination of vocal slits, nuptial pads, the presence of eggs and by observation of calling. Calls were recorded using a Sennheiser ME66 microphone, K6 powering module, and a Marantz PMD-660 digital recorder. Calls were analysed using Avisoft-SASLab Pro (v4.34, available from Avisoft Bioacoustics: http://www.avisoft.com/).

Type specimens are deposited in the South Australian Museum, Adelaide (SAMA), and one will be repatriated to

Table 1. Net average sequence divergence for the mitochondrial *ND4* gene between species of *Litoria*. Bold values are between pairs of sister species.

	aplini	*iris*	*maj*	*sing*	*rich*	*viv*	*mucr*	*pron*	*ver*	*nigro*	*biak*	*bic*	*olo*	*cool*	*fall*
L. aplini	—														
L. iris	0.14	—													
L. majikthise	0.15	**0.15**	—												
L. singadanae	0.21	0.22	0.23	—											
L. richardsi	0.23	0.24	0.24	**0.19**	—										
L. vivissimia	0.23	0.24	0.25	0.22	0.24	—									
L. mucro	0.21	0.23	0.22	0.24	0.25	0.19	—								
L. pronimia	0.23	0.23	0.24	0.22	0.23	0.19	**0.15**	—							
L. verae	0.22	0.25	0.22	0.22	0.24	0.22	0.22	0.23	—						
L. nigropunctata	0.23	0.24	0.23	0.22	0.23	0.22	0.24	0.24	0.23	—					
L. biakensis	0.22	0.23	0.23	0.20	0.23	0.23	0.21	0.22	0.23	**0.22**	—				
L. bicolor	0.21	0.22	0.22	0.23	0.23	0.21	0.20	0.21	0.24	0.21	0.20	—			
L. olongburensis	0.20	0.21	0.22	0.21	0.21	0.22	0.22	0.24	0.21	0.22	0.21	0.20	—		
L. cooloolensis	0.23	0.25	0.22	0.23	0.24	0.23	0.24	0.24	0.24	0.23	0.24	0.22	0.18	—	
L. fallax	0.21	0.23	0.22	0.22	0.24	0.23	0.22	0.25	0.20	0.21	0.20	0.21	0.16	**0.11**	—

the Papua New Guinea National Museum and Art Gallery, Port Moresby (PNGNM). Specimens examined are listed in Appendix 1. Other comparisons were made from the relevant literature (Menzies, 1993; Johnston & Richards, 1994; Günther, 2004; Kraus & Allison, 2004; Richards, 2005; Dennis & Cunningham, 2006).

Taxonomy

The new species described here is assigned to *Litoria sensu* Tyler & Davies (1978) based on its molecular genetic relationships pending a phylogenetic based resolution of generic boundaries within Pelodryadidae (e.g., Kraus, 2018). Our genetic, morphological, and acoustic (where available) data support its distinctiveness and indicate that the new species' relationships lie with a small group of *Litoria* characterized by their moderately small size, crenulated skin folds or pale tubercles along the outer margins of the tarsi, and brightly coloured ventral surfaces and/or limbs. These are *L. iris*, *L. majikthise*, *L. richardsi*, *L. singadanae,* and *L. verae*. One other species, *L. ollauro*, is morphologically and acoustically similar to the new species and, although molecular genetic data were not available for *L. ollauro,* it is probably closely related.

Table 2. Apomorphic nucleotide states in the mitochondrial *ND4* gene diagnosing *L. aplini* from eight most closely related species.

taxon	nucleotide position											
	7 3	9 1	2 3 4	3 1 8	3 3 9	3 5 8	3 6 3	3 8 4	5 2 2	6 0 7	6 7 4	6 7 6
L. aplini	C	C	G	A	A	A	G	C	T	A	A	G
L. iris	G	T	A	T	C	G	A	T	C	G	G	A
L. majikthise	G	T	A	C	C	G	A	T	A	G	T	A
L. richardsi	A	A	A	C	C	C	A	T	A	T	T	A
L. singadanae	A	T	A	T	T	C	T	T	A	T	T	A
L. vivissimia	A	T	A	C	T	C	T	T	G	C	T	A
L. mucro	A	A	A	T	T	C	T	T	A	C	T	A
L. pronimia	A	T	A	C	C	C	T	T	A	C	T	A
L. verae	A	T	A	C	T	C	C	T	A	C	T	A

Pelodryadidae Günther, 1858

Litoria Tschudi, 1838

Litoria aplini sp. nov.

urn:lsid:zoobank.org:pub:act:09663F46-325A-42B0-AB45-86517976962A

Figs 1–2

Holotype. SAMA R71463 (Field number SJR12829), upper Sepik River catchment, West Sepik Province, Papua New Guinea (4°38.637'S 141°40.747'E, 950 m a.s.l.), 10 xii 2009, S. Richards. **Paratypes**. (n = 3) SAMA R71464 (Field number SJR12832), SAMA R71465 (Field number SJR12833), PNGNM (Field number SJR12834), same data as for holotype except collected 11 xii 2009.

Etymology. The species epithet is an honorific for Dr Ken Aplin, in recognition of his immense contributions to New Guinean herpetology and in gratitude for his friendship and selfless collaboration with the authors over many years. Ken's tremendous intellect, boundless energy, and unfailing humour in the field are sorely missed. We recommend the common name "Aplin's Treefrog" for this beautiful species.

Diagnosis. *Litoria aplini* sp. nov. is diagnosed morphologically from all congeners by the combination of body size moderately small (male SVL 31.9–35.1 mm); snout relatively broad (EN/IN = 0.79–0.84) (Table 4); presence of crenulated folds on outer edge of tarsi; webbing on hands extending to slightly past penultimate tubercle on fourth finger; presence of prominent ivory conical tubercles below vent and on ventral surfaces of thighs; and in the following colour in life traits - belly golden-yellow posteriorly, hidden surfaces of limbs predominantly blue with dark brown mottling except for discrete golden-yellow patch on posteroventral surface

Table 3. Morphological and acoustic comparisons among *Litoria aplini* and similar species.

	Litoria aplini	*L. iris*	*L. majikthise*	*L. ollauro*	*L. richardsi*	*L. singadanae*	*L. verae*
SVL of males	30–35 mm	25–35 mm	30–35 mm	<34 mm	23–26 mm	27–28 mm	33–35 mm
TYM/EYE	0.45–0.49	0.36–0.53	0.35–0.47	—	0.65–0.81	0.69–0.81	0.44–0.51
Periphery of tympanic membrane	Pigmented	Pigmented	Pigmented	Pigmented	Transparent	Transparent	Pigmented
Pale post-ocular bar	Absent	Present or absent	Present; extends beyond angle of jaw to axilla	Absent	Present; narrow, complete or interrupted	Absent	Absent
Crenulated skin fold along outer margins of tarsi	Prominent	Reduced to series of low, pale tubercles	Reduced to series of low, pale tubercles	Reduced to series of low tubercles	Reduced to 2–4 large, and numerous smaller, pale tubercles	Prominent	Prominent
Dorsal colour	Head predominantly green, extent of green and brown elsewhere dorsally variable	Green and/or brown	Immaculate dark green or pale emerald green with darker green mottling	Uniform green or green with yellow spots	Grey-green with irregular black bars across dorsum and limbs	Mottled pale and darker green	Green-brown with blackish or dark green spots
Colour of posterior of venter	Golden-yellow	White	Red	Yellow	Yellow with black markings anterolaterally	Orange	Orange
Colour of posterior surfaces of thighs	Mottled blue and brown, bordered ventrally by patch of golden yellow	Blue, red, or yellow, frequently blotched with white or purple	Red	Bright sky blue, bordered below with violet	Yellow	Orange	Yellow
Advertisement calls	Normally a long note (0.026–0.062 s) followed by up to 7 short notes (0.005–0.020 s)	Series of up to 10 notes of various lengths (0.03–0.55 s); longer notes may precede or follow shorter notes	Long notes (0.29–0.36 s), and short notes (0.026–0.080 s), uttered individually	Normally a long note (0.43–0.54 s) followed by 1–2 short notes (0.04–0.3 s)	Harsh chattering notes reminiscent of an insect (SJR, unpublished data)	Call unknown	1–3 (normally two) quiet notes; first note (0.024–0.028 s) normally shorter than subsequent notes (0.057–0.090 s)

of thighs. The advertisement call is a short buzz normally followed by 1–7 clicks, the latter most commonly comprising two pulses. From a genetic perspective, apomorphic nucleotide states at 12 sites in the mitochondrial *ND4* gene reliably diagnose *L. aplini* from the eight most closely related species (Table 2).

Comparisons with other species (Table 3 and Fig. 3): *Litoria aplini* sp. nov. differs from other small (adult male SVL <40 mm), green or green and brown New Guinean *Litoria* as follows: from *L. albolabris*, *L. longicrus,* and *L. mystax* in having larger body size (male SVL = 31.9–35.1 vs <30.0 mm), having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs uniform green), and lacking pale bar below eye (vs present).

Litoria aplini sp. nov. differs from members of the *L. bicolor* group (*L. bibonius*, *L. chloristona*, *L. contrastens*, *L. eurynastes*, *L. lodesdema*, *L. viranula*) in its larger size (male SVL = < 31.6 mm in *L. bicolor* group; Menzies *et al.*, 2008), having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs predominantly green), and venter golden-yellow (vs white); from *L. bulmeri* in having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs uniform green with broad black lateral stripe), and shorter limbs (TL/SVL = 0.59–0.66 in *L. bulmeri* vs 0.56–0.57 in *L. aplini*); from *L. christianbergmanni* in its larger size (male SVL = 26.9–31.2 mm in *L. christianbergmanni*), dorsum green and brown (vs uniform green with white, yellow or pale green spots), and lacking white bar below eye (vs present in *L. christianbergmanni*); from *L. chloronota* in having larger body size (males 27–32 mm in *L. chloronota*), narrower snout (EN/IN = 0.63–0.71 in *L. chloronota* vs 0.79–0.84 in *L. aplini*), having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs mottled pale and darker green with or without yellow spots), and venter posteriorly golden-yellow (vs cream) (Menzies, 1993); and from *L. gasconi* and *L. multiplica* by its smaller size (male SVL ≥36 mm in these species), and dorsum green and brown (vs uniform green with pale spots).

Litoria aplini sp. nov. differs from members of the *L. gracilenta* group (*L. aruensis*, *L. auae*, *L. callista*, *L. elkeae*, *L. eschata*, *L. kumae,* and *L. robinsonae*) in having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs plain green with or without pale or dark spots), and pale canthal and postocular stripes absent (vs present: Menzies & Tyler, 2004; Kraus, 2013); from *L. havina* in having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs uniformly green or occasionally brown), and lacking a fleshy rostral spike in males (vs present); from *L. nigropunctata* in having prominent crenulated skin fold along outer margins of tarsi (vs absent), extensive golden-yellow on posterior of venter (vs absent in *L. nigropunctata*), grey (vs yellow) iris and extensive blue and dark brown mottling posterolaterally (vs absent); from *L. rubrops* in its larger size (male SVL = 21.4–25.2 mm in *L. rubrops*), having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs green, usually speckled with black or darker green), and iris grey with pale gold inner rim (vs iris red in *L. rubrops*); and from *L. wapogaensis* in having prominent crenulated skin fold along outer margins of tarsi (vs absent), dorsum green and brown (vs uniform green with or without pale spots), and hidden surfaces of thighs and groin golden-yellow (vs dark brown in *L. wapogaensis*).

Table 4. Measurements (mm) and ratios of the type series of *Litoria aplini* sp. nov. R71463 is the holotype. All specimens are adult males.

trait	R71463	R71464	R71465	SJR12834	mean	SD
SVL	32.30	31.90	35.09	33.85	33.29	1.468
TL	18.08	17.80	20.15	19.08	18.78	1.067
HL	11.36	11.00	11.15	11.18	11.17	0.148
HW	9.85	9.81	10.16	9.90	9.93	0.158
EYE	4.20	4.20	4.30	4.10	4.20	0.080
EAR	1.90	1.90	2.10	1.90	1.95	0.100
EN	3.00	3.10	3.20	3.00	3.08	0.096
IN	3.80	3.70	3.90	3.80	3.80	0.082
3FD	1.60	1.50	1.70	1.50	1.58	0.096
3FP	1.10	1.10	1.30	1.00	1.13	0.126
4TD	1.50	1.40	1.50	1.30	1.43	0.096
4TP	1.10	1.00	1.10	0.90	1.03	0.096
HL/SVL	0.35	0.34	0.32	0.33	0.34	0.101
HW/SVL	0.30	0.31	0.29	0.29	0.30	0.107
HL/HW	1.15	1.12	1.10	1.13	1.13	0.937
EYE/SVL	0.13	0.13	0.12	0.12	0.12	0.065
EAR/EYE	0.48	0.49	0.50	0.48	0.48	0.853
EAR/SVL	0.06	0.06	0.06	0.06	0.06	0.056
TL/SVL	0.56	0.56	0.57	0.56	0.56	0.727
EN/IN	0.79	0.84	0.82	0.79	0.81	1.173
IN/SVL	0.12	0.12	0.11	0.11	0.11	0.056
EN/SVL	0.09	0.10	0.09	0.09	0.09	0.065
4TD/4TP	1.36	1.40	1.36	1.44	1.39	1.000
3FD/3FP	1.45	1.36	1.31	1.50	1.40	0.761

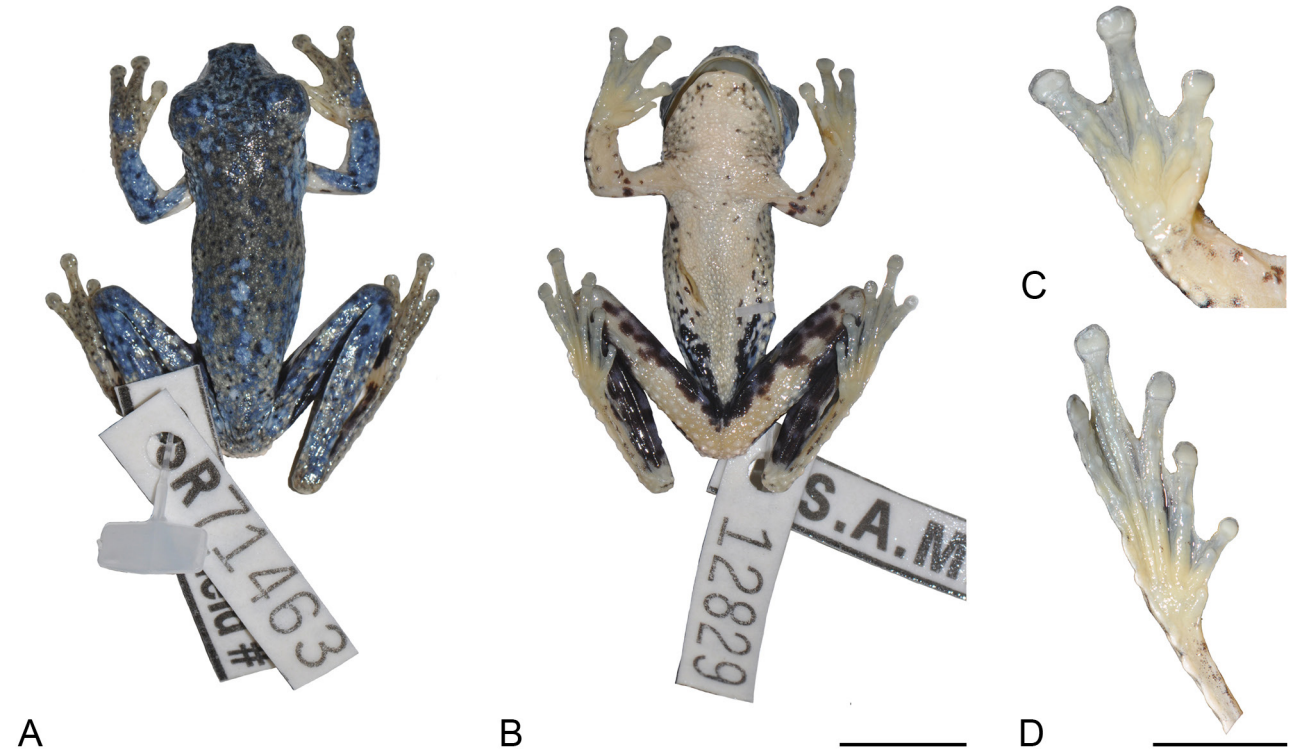

Figure 1. Views of *Litoria aplini* holotype (SAMA R71463) in preservative. (*A*) dorsal; (*B*) ventral (scale bar = 10 mm); (*C*) palmar; and (*D*) plantar surfaces (scale bar = 5 mm).

In its moderate size (male SVL 30–35 mm), green and brown dorsal colour, extensively webbed fingers, and colourful ventrum and limbs in life, *Litoria aplini* most closely resembles the following six species: *L. iris*, *L. majikthise*, *L. ollauro*, *L. richardsi*, *L. singadanae*, and *L. verae*. It differs from all of these except *L. singadanae* and *L. verae* in having a prominent crenulated skin fold along outer margins of tarsi (vs a series of isolated pale tubercles along margins of tarsi). *Litoria aplini* can be further distinguished from *L. iris* by having posterior of belly and plantar surfaces golden-yellow (vs belly white and plantar surfaces without yellow), axilla without violet patch (vs present), posterior surfaces of thighs mottled blue and brown bordered ventrally by golden-yellow patch (vs posterior of thighs blue, red, or yellow, frequently blotched with white or purple); from *L. majikthise* by having posterior surfaces of thighs mottled blue and brown bordered ventrally by golden-yellow patch (vs uniform red), and by lacking a pearl-white post-ocular bar (vs present); from *L. ollauro* in having dorsum variably green and brown (vs uniform green or green with yellow spots), posterolateral surfaces of venter, ventral surfaces of tibiae, and hidden surfaces of thighs with extensive blue and dark-brown mottling (vs posterolateral surfaces of venter and hidden surfaces of thighs sky-blue without brown mottling, and ventral surfaces of thighs and tibiae uniform yellow); from *L. richardsi* in its larger size (males 31–35 mm vs < 27 mm SVL); dorsum without irregular black lines, and throat and finger and toe webbing without extensive black markings (vs present), and periphery of tympanic membrane not transparent (vs transparent); from *L. singadanae* in its larger size (males 31–35 mm vs <30 mm SVL); in having posterolateral surfaces of belly and posterior surfaces of thighs with blue and brown mottling (vs posterior of venter and hidden surfaces of legs uniform orange), tympanum much smaller (TYM/EYE = 0.45–0.49 vs 0.69–0.81), and pigmented (vs tympanic membrane transparent); and from *L. verae* in having posterolateral surfaces of belly and posterior surfaces of thighs with blue and brown mottling (vs posterior of venter and hidden surfaces of legs uniform yellow), feet dorsally with extensive areas of yellow (vs yellow absent) and dorsum without small brown spots aligned transversely (vs present). A summary of the major characters useful for distinguishing among these seven most similar species is presented in Table 3.

Molecular genetic comparisons. The final alignment for the mitochondrial *ND4* gene comprised 694 bp. In a phylogram of relationships among mitochondrial *ND4* sequences, the two sequences from *L. aplini* were the well supported sister group to a clade comprising *L. iris* and *L. majikthise* (Fig. 4). The net uncorrected sequence divergence (*d*A) for *ND4* between *L. aplini* and the two species in its sister clade was 0.14 for *L. iris* and 0.15 for *L. majikthise* (Table 1). *d*A between sister species pairs ranged from 0.11 to 0.22 (Table 1).

Description of holotype. An adult male with right-lateral incision in abdomen. Vomero-palatines with two patches of small, poorly-defined teeth between internal nares. Vocal slits lateral, very long, extending from well behind angle of jaws to approximately 1/3 distance between angle of jaws and front of mouth. Tongue oval with distinct posterior notch. Head moderately wide (HW/SVL = 0.30), slightly less than length (HL/SV = 0.35, HL/HW = 1.15); loreal region steep, slightly concave; canthus rostralis rounded, distinctly curved; nostrils closer to tip of snout than to eyes; internarial distance greater than distance from external naris

Figure 2. Type series of *Litoria aplini* in life: (*A*) SAMA R71463; (*B*) SAMA R71465; (*C*) SAMA R71464; (*D*) SJR12834 (PNGNM); (*E*) SAMA R71463, in ventral view; and (*F*) SAMA R71463, ventral surfaces of hind limb.

to eye (EN/IN = 0.79, IN/SVL = 0.12, EN/SVL = 0.09); snout truncate when viewed from above, with slightly angular tip; steeply sloping when viewed from side; eyes large (EYE/SVL = 0.13), prominent, protruding in dorsal and ventral views; tympanum prominent, raised above surrounding skin; tympanic ring distinct but top margin covered by thick supratympanic skin fold, horizontal diameter slightly less than half width of eye (TYM/EYE = 0.45).

Skin of dorsal and lateral surfaces including limbs, finely granular; ventral surfaces including limbs coarsely granular; patches of large ivory tubercles on ventral surface of thighs and around vent—largest around vent; a series of low tubercles along outer margin of tibiae and crenulated white skin fold on outer margin of F4 from proximal edge of disc extending along forearm to elbow, and prominent on outer margin of T5 from proximal edge of disc along tarsus to heel (Fig. 2F), patch of low ivory tubercles on heel.

Fingers moderately short with distinct lateral fringes, extensively webbed, webbing reaching slightly past penultimate tubercle on F4, to slightly below penultimate tubercle on outside of F3, and to level of penultimate tubercle on outside of F2; webbing between F1 and F2 greatly reduced; finger relative lengths 3 > 4 > 2 > 1; tips of all fingers expanded into discs bearing circum-marginal grooves; disc on F3 approximately 1.4 times width of penultimate phalanx; palmar surfaces with numerous prominent tubercles (Fig. 1), subarticular tubercles at base of penultimate phalanx on F3–4 bilobed; first finger with elongate, brown nuptial

Figure 3. Closely related species that could be confused with *Litoria aplini*: (*A*) *Litoria iris* (SAMA R71615), adult male in life (Hindenburg Range, Western Province); (*B*) *Litoria iris* showing bright colours on hidden surfaces of the hind legs (unvouchered animal, Hela Province); (*C*) *Litoria majikthise* (SAMA R65042), in life, Muller Range, Western Province); (*D, E*) *Litoria majikthise* (SAMA R65042), showing colour ventrally and on hidden surfaces of hind limbs; and (*F*) *Litoria ollauro*, Milne Bay Province, photo courtesy of Fred Kraus.

pad with narrow "handle" proximally, broadening distally at approximately mid-length (1.7 mm long, 0.9 mm at widest point and 0.5 mm at narrowest point). Toes nearly fully webbed, web reaching to base of disc on T5, and on outside of T2 and T3, to base of penultimate phalanx on both sides of T4, and slightly beyond penultimate tubercle on T1 (Fig. 1); relative lengths 4 > 5 = 3 > 2 > 1; tips of all toes expanded into discs with circum-marginal grooves; disc of T4 approximately 1.4 times wider than penultimate phalanx; subarticular tubercles at base of penultimate phalanx on T2–5 partially or completely bilobed; inner metatarsal tubercle elongate, bean shaped; outer absent. Hind legs moderately long (TL/SV = 0.56), with patch of small but prominent tubercles at heel.

Colour in life: body and limbs rufous brown dorsally and laterally, with small flecks of dark brown and large patches of green mottling posterolaterally and on arms, and pale green blotches on dorsum and limbs, most prominent being five blotches aligned anteroposteriorly on posterior half of mid-dorsum (Fig. 2A). Head predominantly pale green, mottled with flecks of dark green, green colouration extending laterally across tympanum to dorsal edge of axilla and on to forearms, blotch of green on dorsal surface of hand isolated from green on forearm. Iris pale grey with

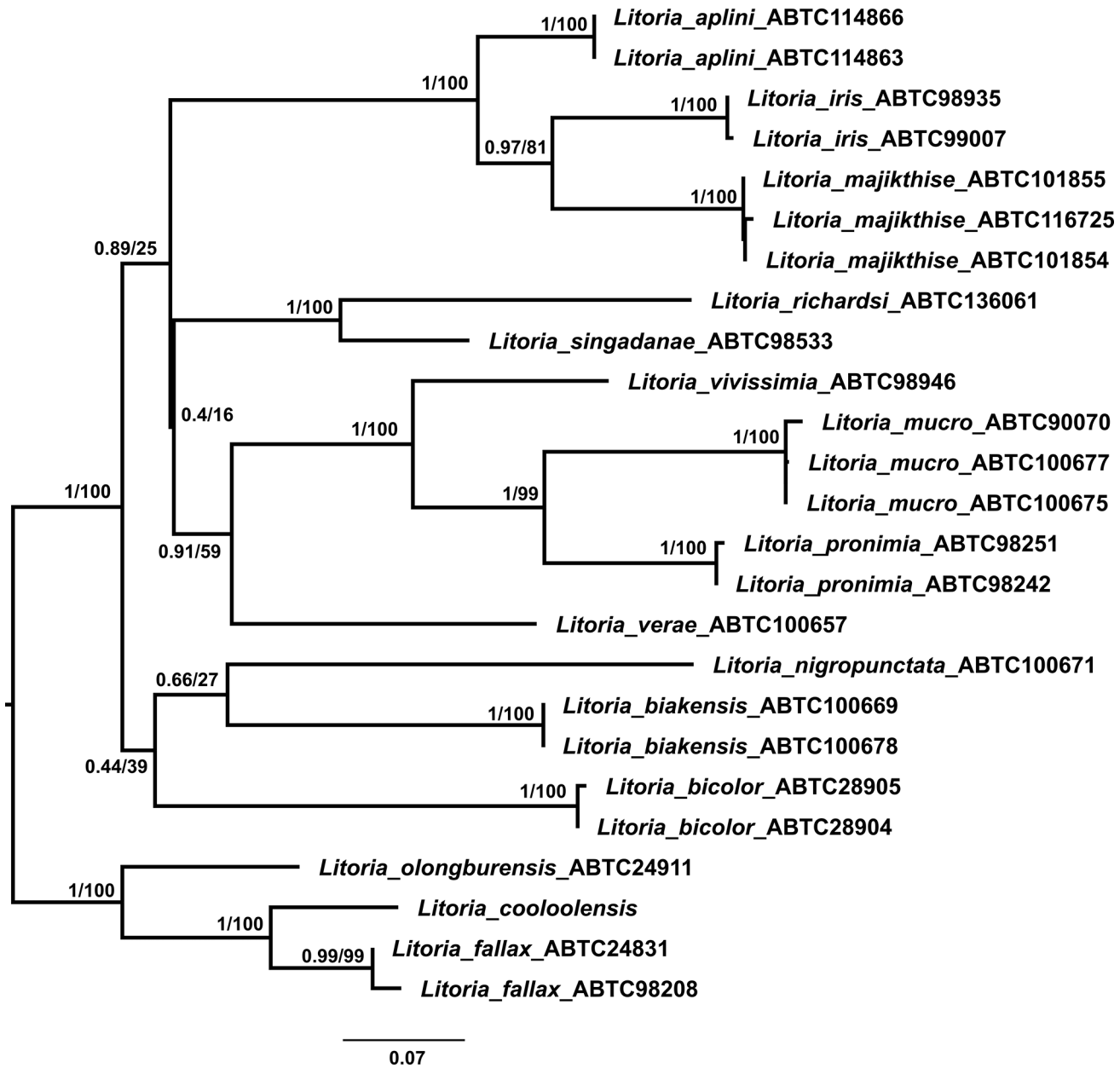

Figure 4. Maximum likelihood (ML) phylogram of relationships between mitochondrial *ND4* nucleotide sequences of *Litoria*. Numbers at nodes are: left—Bayesian posterior probabilities, right—ML bootstrap proportions.

moderately dense dark-brown reticulations and pale gold inner rim without reticulations. Intensity and shade of dorsal green and brown colouration in life varied from beige to rufous brown depending on time of day, being darker (rufous brown, as shown in Fig. 2A) at night.

Ventrally white anteriorly with patches of grey laterally on throat, and small flecks and short reticulations of dark brown concentrated in a broad band around ventral edge of lower jaw; posterior half of venter and patch around axilla that extends on to base of arm golden-yellow; laterally dark-brown flecks extend from axilla to groin, these small and scattered anteriorly, becoming large interconnected blotches near groin. Anterior surfaces of thighs and tibiae pale blue, extensively mottled with deep brown; blue colouration extends anteriorly onto ventrolateral surfaces of belly but barely intrudes onto ventral golden-yellow patch. Posterior surfaces of thighs extensively mottled with blue and brown, bordered ventrally by broad band of golden yellow that narrows towards heel and incorporates patch of prominent tubercles of same colour. Ventral surfaces of tibiae pale iridescent blue with large dark-brown blotches; of tarsus suffused with golden-yellow, with peppering of fine dark-brown specks (Fig. 2E); plantar surfaces golden-yellow, except disc of T3, distal half of T4, and entirety of T5; these areas with, at most, light peppering of fine, dark-brown specks. Outer margins of limbs with pale crenulated skin folds, vent surrounded by patch of prominent pale tubercles, heel with cluster of small, ivory tubercles (Fig. 2F).

Colour in preservative: green markings have become shades of blue, large green dorsal blotches palest; background beige-brown has become mottled grey; dark-brown patches and flecks remain dark brown, but blue on limbs is darker and without iridescence; ivory of crenulated skin folds, and prominent tubercles around vent, have become more

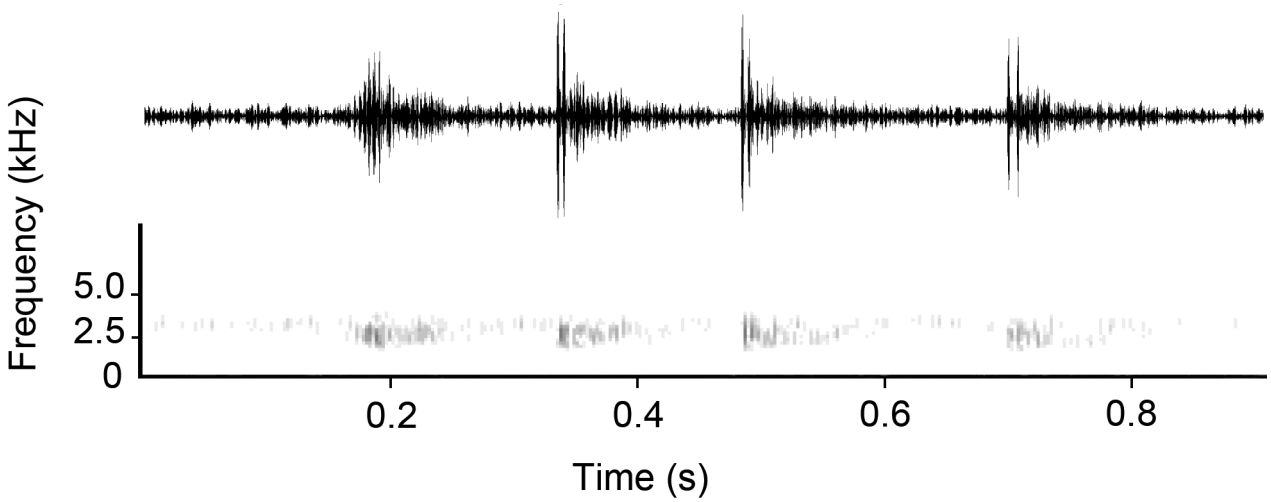

Figure 5. Advertisement call of the holotype of *Litoria aplini* (SAMA R71463), showing (*top*) wave form and (*bottom*) audiospectrogram of a four-note call recorded at 23.7°C.

cream. Ventral surfaces predominantly cream, golden-yellow patches have disappeared except for slight suffusion on plantar surfaces and posterior of thighs.

Variation. The three paratypes are adult males; morphometric variation in the type series is limited (Table 4). The extent of green markings on the dorsum is variable (Fig. 2). All of the types have predominantly green heads and limbs, but in SAMA R71465 (Fig. 2B) brown on dorsum extends further anteriorly than in the other types, reaching to mid-way between eyes, and there are more extensive patches of mottled green, with more numerous pale green blotches dorsally; SAMA R71464 (Fig. 2C) is predominantly brown dorsally, with green restricted to dorsal surfaces of arms and legs, a large patch of mottled green posterolaterally, small, scattered patches of mottled green on dorsum and small green spot on each hand. SJR12834 (PNGNM) (Fig. 2D) is more uniformly green than the other specimens, lacking pale green spots and mottling. In life the three paratypes shared with the holotype a large golden-yellow patch posteriorly on the venter that was bordered by dark brown blotches; a large golden-yellow patch on the posteroventral surfaces of the thighs; and blue with dark brown blotches on the other hidden surfaces of the limbs. However, there is variation in the size, distribution, and connectivity of the brown blotches that border the ventral golden-yellow patch. In SAMA R71465 and SJR12834 (PNGNM) these are similar to the holotype, being interconnected to form a single large, irregular blotch, though the size of the blotch is variable; in SAMA R71464 the dark markings in the groin are not interconnected, instead forming a cluster of smaller, discrete blotches. Brown spotting on the anterior half of the venter is barely detectable in the holotype and two of the paratypes, but extensive in SAMA R71465.

Advertisement call. The advertisement call of *L. aplini* is a finely pulsed note (a "buzz") normally followed by one or more shorter clicking notes ("clicks") (Fig. 5). Twenty-two calls of the holotype recorded at an air temperature of 23.7°C were produced at a rate of 1.26 calls/s, lasted 0.16–1.21 s (mean = 0.34, SD = 0.24, n = 20), and had a dominant frequency of 2150–3336 hz (mean = 2550, SD = 360, n = 18; however in most calls dominant frequency was between 2300 and 2400 hz). Most calls (20 of 22; 91%) comprised a single buzz note lasting 0.026–0.062 s (mean = 0.046, SD = 0.010), followed by one (13 of 22; 60%) or up to seven, sharp multi-pulsed clicking notes lasting 0.005–0.020 s (mean = 0.014, SD = 0.004, n = 29). Note rate for multi-note calls was 3.98–6.99 notes/s (mean = 5.40, SD = 0.81, n = 17). Pulses in buzz notes were produced too rapidly to count in all but one call, in which 15 pulses were produced at a rate of 272 pulses/s. Clicks consisted predominantly of two, but occasionally 1 or 4, discrete pulses each lasting c. 0.005 s. Pulse rate in click notes was much slower than in buzz notes, at around 166 pulses/s. The distribution of energy in the two types of notes also differed, with amplitude in buzzes increasing gradually from the start of the call, and reaching maximum intensity near the end of the call before rapidly declining (Fig. 5); in contrast amplitude in the clicks was at or near maximum from the start of the call and then distributed uniformly until the end (Fig. 5). Although only one recorded buzz was not followed by one or more clicks, and only one recorded call was represented solely by a click, a number of additional calls comprising buzz and click calls produced in isolation were heard at the type locality.

Distribution and habitat. *Litoria aplini* is known from one location on the northern slopes of Papua New Guinea's central cordillera (Fig. 6), where it was collected from primary hill forest (Fig. 7A) at an altitude of 940 m a.s.l. The substrate at the type locality is limestone, and free-standing water was limited. The type series was collected from trees adjacent to a narrow, mostly dry gully where males called from perches up to five metres high over small (< 1 m^2), isolated pools of water in the base of the gully (Fig. 7B). However, no eggs or larvae were observed so the breeding strategy of this species remains unknown.

It is not known whether this species is endemic to forest on karst substrates, but there is increasing evidence for a suite of karst associated herpetofauna on the southern slopes of Papua New Guinea's central cordillera (Oliver *et al*., 2019a) so it is possible that a similar assemblage occurs in the much more poorly surveyed northern karst habitats.

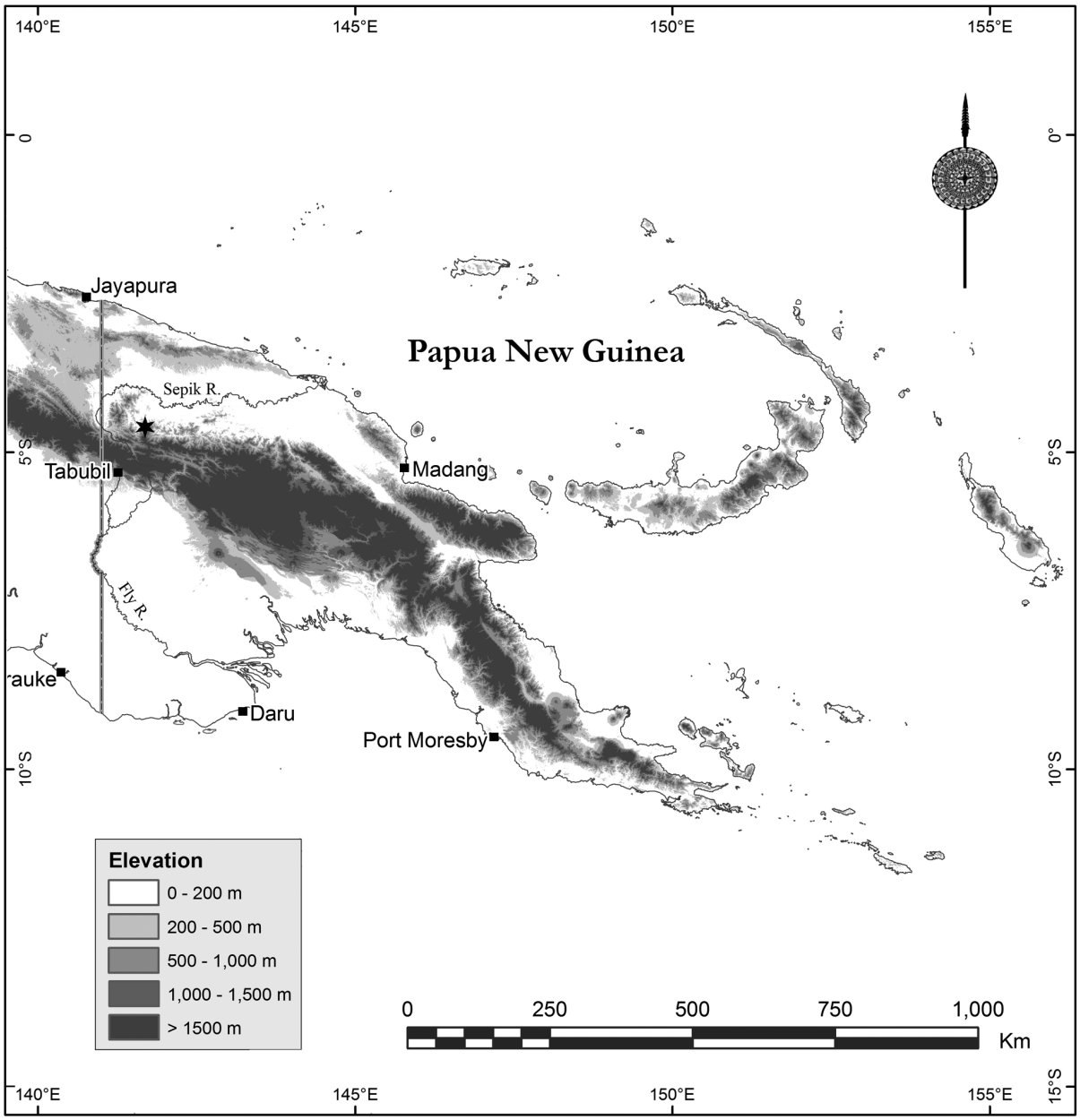

Figure 6. Map of Papua New Guinea showing the type locality of *Litoria aplini*.

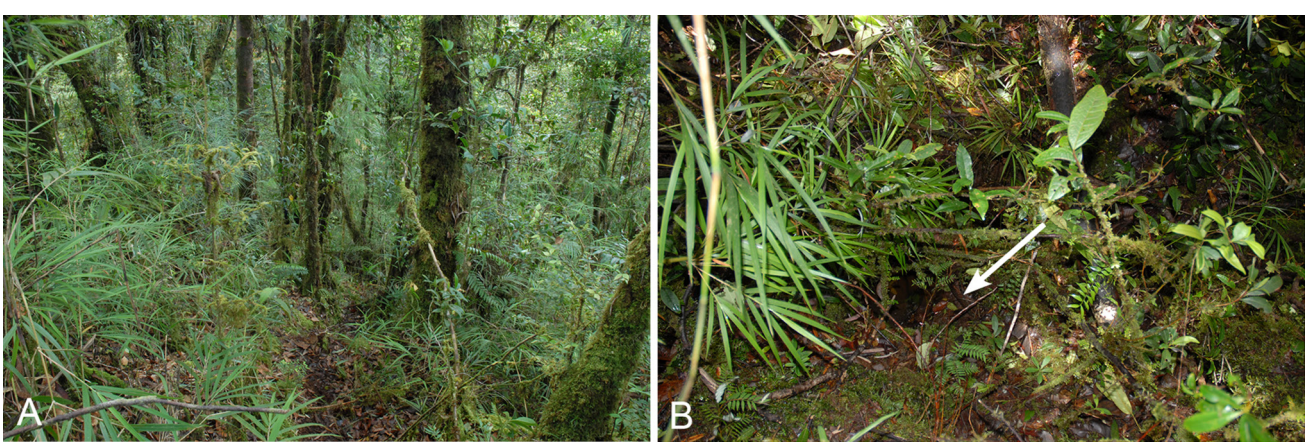

Figure 7. Habitat of *Litoria aplini*: (*A*) forest interior at the type locality; and (*B*) males were calling from trees over small pools (arrow) in the bed of a steep, narrow limestone gully.

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Appendix 1. Specimens examined: ABTC—The Australian Biological Tissue Collection, South Australian Museum; M—morphological analysis; G—genetic analysis. Voucher origin (number of specimens in parentheses): BM—Natural History Museum, London; MJM—Michael J. Mahony field collection; MZB—Museum Zoologicum Bogoriense, Cibinong; QM—Queensland Museum, Brisbane; RMNH—Naturalis, Leiden; UP—University of Papua New Guinea Natural Sciences collection; SJR—Stephen J. Richards field collection; ZMB—Zoological Museum, Berlin.

species	ABTC	voucher	locality	state/prov	country	comments
L. albolabris		SAMA R4947 M	Aitape	Sandaun	PNG	syntype
L. aplini	ABTC114863	SAMA R71463 G	Frieda River	East Sepik	PNG	holotype
L. aplini	ABTC114866	SAMA R71464 G	Frieda River	East Sepik	PNG	paratype
L. auae		UP2490 M	Purari River	Gulf	PNG	holotype
L. auae		SAMA R57262–3 M	Purari River	Gulf	PNG	paratypes
L. biakensis	ABTC100669	ZMB 67737 G	Biak Is.	Papua	Indonesia	paratype
L. biakensis	ABTC100678	ZMB 68418 G	Biak Is.	Papua	Indonesia	paratype
L. bicolor	ABTC28905	not found G	Black Point	NT	Australia	
L. bicolor	ABTC28904	not found G	Black Point	NT	Australia	
L. chloronota		BM1947.2.31.20 M	Arfak Mtns	West Papua	Indonesia	syntype
L. chloronota		UP8380–8 M	Arfak Mtns	West Papua	Indonesia	
L. contrastens		SAMA R5845 M	Barabuna	Eastern Highlands	PNG	holotype
L. contrastens		SAMA R5847 (5) M	Noreikova	Western Highlands	PNG	paratypes
L. cooloolensis	—	—	no locality	Qld	Australia	
L. elkeae		MZB Amph.3866–9, MZB Amph.3866–7, QM J70490–2 M	Siewa	Papua	Indonesia	paratypes
L. fallax	ABTC24831	MJM M008 G	Commissioners Ck	NSW	Australia	
L. fallax	ABTC98208	QM J72429 G	Littabella NP	Qld	Australia	
L. havina		UP 7281 M	Ok Kam	Western	PNG	holotype
L. havina	—	SAMA R69345–49 M	Ok Tedi headwaters	Western	PNG	
L. iris		BM 1961.1226 M	Bamna	Chimbu	PNG	holotype
L. iris		SAMA R5423, 5874 M	Telefomin	Sandaun	PNG	
L. iris	ABTC98935	SAMA R71598 G,M	Gigira Ridge	Hela	PNG	
L. iris	ABTC99007	SAMA R71599 G,M	Lake Tawa, Porgera	Enga	PNG	
L. kumae		UP3108 M	Tari	Southern Highlands	PNG	holotype
L. kumae		SAMA R52760–61 M	Tari	Southern Highlands	PNG	paratypes
L. leucova		SAMA R44091–2 M	Mt Stolle	Sandaun	PNG	
L. longicrus		BM 1947.2.22.60–61 M	Wendessi	Papua	Indonesia	syntypes
L. majikthise	ABTC116725	SAMA R65042 G,M	Muller Range	Western	PNG	
L. majikthise	ABTC101854	SAMA R71600 G,M	Upper Strickland	Western	PNG	
L. majikthise	ABTC101855	SAMA R71601 G,M	Upper Strickland	Western	PNG	
L. majikthise		SAMA R44093 M	Tabubil	Western	PNG	holotype
L. majikthise		SAMA R44094–44101, UP 6734, 7305–9, 8501–8, 8602–3 M	Tabubil	Western	PNG	paratypes
L. majikthise		SAMA R65042-45 M	Muller Range	Western	PNG	
L. mucro		UP 2741–3, UP 2745–56 M	Rauit	East Sepik	PNG	paratypes
L. mucro	ABTC90070	SJR6187 G	Marina Valen	Papua	Indonesia	
L. mucro	ABTC100675	ZMB 70497 G	Mt Waira, Yapen Is.	Papua	Indonesia	
L. mucro	ABTC100677	ZMB 70498 G	Mt Amoman, Yapen Is.	Papua	Indonesia	
L. mystax		RMNH 4632 M	Moaif	Papua	Indonesia	holotype
L. nigropunctata	ABTC100671	ZMB 63977 G	Mt Waira, Yapen Is.	Papua	Indonesia	
L. nigropunctata		SAMA R61799 M	Nr Konti, Yapen Is.	Papua	Indonesia	
L. ollauro		UP 4644 M	Agaun	Milne Bay	PNG	holotype
L. olongburensis	ABTC24911	MJM 39700 G	20 km N Byron Bay	NSW	Australia	
L. pronimia	ABTC98242	SAMA R71131 G,M	Moran	SHP	PNG	
L. pronimia	ABTC98251	SAMA R71133 G,M	Gobe	SHP	PNG	
L. richardsi	ABTC136061	SAMA R71604 G, M	Upper Fly River	Western	PNG	
L. richardsi		SAMA R71602–3, 71605 M	Upper Fly River	Western	PNG	
L. richardsi		SAMA R60283 M	Ok Tedi headwaters	Western	PNG	holotype
L. richardsi		MZB Amph.11823 M	Mamberamo Basin	Papua	Indonesia	paratype
L. singadanae	ABTC98533	SAMA R60172 G,M	Surim	Morobe	PNG	holotype
L. singadanae		SAMA R60171, UP 9968 M	Surim	Morobe	PNG	paratypes
L. umarensis		ZMB 62350 M	Umar Bay	West Papua	Indonesia	paratype
L. verae	ABTC100657	ZMB 62384 G	Wondiwoi Mountains	West Papua	Indonesia	
L. vivissimia	ABTC98946	SAMA R71127 G,M	Gigira	Hela	PNG	holotype