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A New Species of Small Green Treefrog (Pelodryadidae: *Litoria*) from the Lakekamu Basin in Southern Papua New Guinea

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Abstract: We describe a new species of very small (male body length 22.0–22.8 mm), green treefrog in the pelodryadid genus *Litoria* Tschudi from lowland rainforest on the southern margin of Papua New Guinea's central cordillera. The new species is morphologically most similar to *Litoria leucova*, a small green treefrog known only from the north-flowing Sepik River catchment in western Papua New Guinea. It differs from that species by having longer limbs (TL/SVL 0.56–0.60 vs. 0.53–0.55), a poorly defined (vs. prominent) tympanum, in having a distinct lemon yellow mid-lateral line, and in its unique advertisement call comprising a slowly repeated series of short clicks followed by a discrete group of pulses produced rapidly but with highly variable inter-pulse intervals. Although genetic data are not available, the new species' association with a fast-flowing rocky stream suggests that its relationships may lie with other torrent-dwelling *Litoria* species.

Key words: Advertisement calls; Frog; Litoria lakekamu sp. nov.; Morphology; Taxonomy

INTRODUCTION

Pelodryadid treefrogs form a conspicuous component of frog communities associated with water bodies across the lowlands and foothills of New Guinea (Menzies, 2006). However, the island's fauna remains incompletely documented and recent studies have revealed numerous undescribed pelodryadid species (Oliver et al., 2008, 2019). Among these are a number of primarily green species including large (SVL>60 mm) canopydwelling (Richards and Oliver, 2006; Richards et al., 2006; Kraus, 2018; Oliver et al., 2019) and small (SVL<30 mm) scansorial (Menzies et al., 2008) forms. Most species within the group are tightly affiliated with water bodies where they presumably lay eggs and their tadpoles develop.

Relationships among Australopapuan pelodryadid species remain unsettled (Duellman et al., 2016; Clulow and Swan, 2018; Dubois et al., 2021) and their resolution awaits publication of a comprehensive phylogenetic analysis. Small green pelodryadids in the Melanesian region include species that reproduce in tempo-

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rary ponds and ditches in lowland savanna and forest habitats (e.g., relatives of *Litoria bicolor* (Gray, 1842); Menzies et al., 2008), species that occupy shallow seepages and slowflowing streams in forest (e.g., *Litoria wapogaensis* Richards & Iskandar, 2001), and species that occupy fast-flowing mountain streams (e.g., *Litoria bulmeri* (Tyler, 1968) and *L. leucova* (Tyler, 1968); Tyler, 1968, Johnston and Richards, 1994).

Here we describe a new species of small green treefrog in the genus Litoria that was discovered during Conservation International's 1996 Rapid Assessment Program biodiversity survey of the Lakekamu Basin in southern Papua New Guinea (Allison et al., 1998). The new species is morphologically most similar to Litoria leucova and, like that species (Johnston and Richards, 1994), it occupies clear-flowing streams. However, genetic data are not available so its relationships within the genus cannot vet be determined. Based on the failure to detect the new species during extensive surveys of similar and suitable habitats in adjacent catchments (S. Richards, personal observation), we presume that this species may be endemic to a small portion of the island of New Guinea.

MATERIALS AND METHODS

We located frogs using head torches and by tracking advertisement calls at night. We fixed voucher specimens in 10% formalin and stored them in 70% ethanol. We deposited preserved animals in the South Australian Museum, Adelaide, Australia (SAMA), and we will also repatriate one paratype to the Papua New Guinea National Museum (PNGNM). We made measurements following the methods, terminology, and abbreviations of Tyler (1968) to the nearest 0.1 mm with callipers (SVL: body length from snout to vent, TL: tibia length from heel to convex surface of flexed knee, HL: head length, from tip of snout to posterior margin of tympanum, HW: head width at widest point, normally across 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 (the tympanum of this species is poorly defined so measurements are approximate), 3FD: transverse diameter of disc of Finger 3, 3FP: transverse diameter of penultimate phalanx of Finger 3, 4TD: transverse diameter of disc of Toe 4 and 4TP: transverse diameter of penultimate phalanx of Toe 4.

We determined sex by examination of vocal slits and nuptial pads, and by observation of calling. We recorded calls using a Sony Professional Walkman recorder with an Electret ECM-Z200 Condenser Microphone. We analysed calls using Avisoft-SASLab Pro v4.34 (http://www.avisoft.com/) following procedures and terminology recommended by Köhler et al. (2017). We calculated audiospectrograms with fast-Fourier transform (FFT) of 512 points, 50% overlap for long call series, and 256 points, 87.5% overlap for individual notes, using Hamming windows.

We examined comparative material at the Natural History Museum, London (BMNH), Naturalis, Leiden (RMNH), South Australian Museum, Adelaide (SAMA), Natural Sciences Resource Centre of the University of Papua New Guinea, Port Moresby (UP), Museum Zoologicum Bogoriense, Cibinong (MZB) and the Queensland Museum, Brisbane (QM). We extracted additional information for comparisons from published papers on the relevant groups (e.g., Tyler, 1968; Menzies et al., 2008). FN refers to original field collection numbers of S.J. Richards.

The new species described herein is assigned to the genus *Litoria* sensu Tyler and Davies (1978) based on having a horizontal pupil and lacking pigmentation on the nictitating membrane, pending a compelling phylogenetic based resolution of generic boundaries within Pelodryadidae. *Litoria lakekamu* sp. nov. (English name: Lakekamu pygmy treefrog)

Diagnosis

The new species is distinguished from all other Litoria by the following unique combination of characters: size very small (SVL of four males 20.0–22.8 mm, females unknown); dorsum in life predominantly green; vomerine teeth absent; tympanum indistinct; finger webbing extensive, reaching distal edge of subarticular tubercle at base of penultimate phalanx on outer edge of Finger 3 and inner edge of Finger 4; finger discs slightly larger than or same size as toe discs; webbing on toes extending nearly to base of all discs except Toe 4 where it reaches midway between subarticular tubercle at base of penultimate phalanx and disc on both sides of digit; dermal fringes on limbs and below vent absent; pigmentation on nictitating membrane restricted to scattered flecks at dorsal margin; advertisement call a series of short (0.017-0.053 s) distinctly pulsed rasping notes repeated at 2.1-6.5 s intervals, followed by a discrete group of rapidly repeated pulses with highly variable inter-pulse intervals.

Etymology

The specific name *lakekamu* is a noun in apposition referring to the type and only known locality of this species.

Holotype

SAMA R70113 (FN: Biol Survey Field Series 11623), adult male, Sapoi River adjacent to Ivimka Research Station (7.735° S, 146.496° E; 120 m asl), Lakekamu Basin, Gulf Province, Papua New Guinea, collected by Stephen Richards, David Bickford, and Geordie Torr on 3 December 1996.

Paratypes

SAMA R70114 (FN: Biol Survey Field Series 11624), R70115 (FN: USNM 209310), PNGNM (FN: Biol Survey Field Series 11625), three adult males, same data as holo-type.

Description of holotype

Adult male with vocal slits and small pale brown nuptial pads. Body slender, limbs moderately long (TL/SVL 0.56); head broad (HW/SVL 0.36), snout broadly rounded in dorsal aspect (Fig. 1A), blunt, near vertical, protruding marginally beyond lower jaw in lateral aspect; canthus rostralis broadly rounded, slightly curved; loreal region steep, slightly concave; nares round, near top of snout and closer to tip of snout than to eye, oriented anterolaterally, visible in dorsal aspect (Fig. 1A). Eves large (EYE/SVL 0.15), clearly protruding in both dorsal and lateral aspects; constricted pupil horizontal. Pigmentation on nictitating membrane restricted to scattered flecks along dorsal edge of left membrane. Tympanum (TYM/SVL<0.05), annulus poorly small defined, bordered dorsally by broad, poorly defined supratympanic fold. Vomeropalatines absent; tongue not free posteriorly, broad, heart shaped with distinct notch in posterior edge; vocal slits long, located laterally on floor of mouth, extending from behind angle of jaws to about halfway between angle of jaws and front of mouth. Nuptial excrescences very pale brown, elongate, extending 1.7 mm along proximal outer edge of first finger.

Fingers with relative lengths 3>4>2>1, webbing extending beyond distal edge of subarticular tubercle at base of penultimate phalanx on Finger 4 (distal subarticular tubercle), and to about distal subarticular tubercle on outer edge of Finger 3 before continuing as broad flange to base of disc. Distal subarticular tubercles low, that on Finger 3 partially bifid; remainder unilobed. Small narrow inner, and broad but low outer, metacarpal tubercles present (Fig. 1B). Toes with relative lengths 4>5=3>2>1, webbing extending nearly to base of discs on Toe 3 and Toe 5, and to midway between distal subarticular tubercle and disc on both sides of Toe 4. Subarticular tubercles low, poorly defined. Inner metatarsal tubercle small, elongate, poorly defined; outer metatarsal tubercle

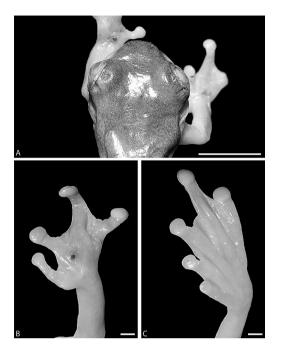


FIG. 1. Holotype of *Litoria lakekamu* sp. nov. (SAMA R70113) in preservative. A: dorsal view of head (scale bar=5 mm), B: palmar view of right hand, C: plantar view of right foot (scale bars =1 mm).

not detectable (Fig 1B). Tips of fingers and toes expanded into terminal discs, those of fingers slightly broader than those of toes (4TD/3FD 0.92), all with distinct marginal grooves. A small puncture wound present in centre of each hand.

Skin with orange-peel texture dorsally and laterally, including head; dorsal surfaces of limbs with numerous low tubercles; ventral surfaces granular. Limbs without dermal ornamentation, heels without tubercles or dermal spikes, surfaces around vent without raised tubercles.

Colour of holotype in preservative

Dorsal surfaces of body uniform grey with scattered darker grey flecks; lemon-yellow lateral line in life has faded to white, ventral surfaces to off-white. Green spots on limbs in life (see below) are no longer evident while dense brown peppering has become more intense across all surfaces of limbs.

Colour of the new species in life

All specimens near-uniform green dorsally, white laterally and ventrally, with narrow but distinct lemon-yellow lateral stripe. The following extra details on colour in life are based on images of SAMA R70114 and PNGNM (FN 11625) taken in life shortly after capture (Fig. 2). Green dorsum of PNGNM (FN 11625) overlain with scattered small but distinct brown flecks, these less evident in SAMA R70114. Narrow lemon-yellow lateral line extends posteriorly from tip of snout along upper lip, below eye and tympanum continuing mid-laterally to groin, separating green of dorsum from white ventrolateral and ventral surfaces (Fig. 2). Limbs, including hidden surfaces of thighs, translucent with dense purplish-brown peppering, overlain on upper surfaces by lime green spots, these mostly restricted to surfaces of low tubercles. Green colour on arms restricted predominantly to areas below elbow; fingers, toes, and webbing translucent with scattered tiny purplish-brown spots. Iris creamy-white with scattered short veins of brown pigment, most dense in narrow rim around edge of pupil.

Variation

The type series is extremely uniform morphologically (Table 1). Body size of adult males 20.0–22.8 mm, females unknown. Dorsal colour consistently near uniform green in life, all specimens with lemon-yellow midlateral line. In preservative all specimens grey with fine darker grey flecks, variation restricted to degree of concentration of flecks into small blotches (small blotches most evident in PNGNM (FN 11625). Tongue nearly round in SAMA R70115 (vs. heart-shaped in holotype), nuptial pads of R70114–70115 present but barely detectable.

Distribution and natural history

Litoria lakekamu is to date known only from the Lakekamu Basin on the southern fringe of Papua New Guinea's central cordillera (Fig. 3).



FIG. 2. Images in life of: (A) *Litoria lakekamu* sp. nov. paratype SAMA R70114, (B) *Litoria lakekamu* sp. nov. paratype PNGNM (FN: 11625), (C) *Litoria leucova* SAMA R71844 from the Sepik River catchment, northern Papua New Guinea, (D) *Litoria lodesdema* SAMA R64772 from New Britain Island, Papua New Guinea. Photographs by S. Richards.

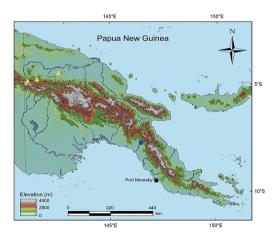


FIG. 3. Distribution of *Litoria lakekamu* sp. nov. (blue square), and its most similar congener *L. leucova* (yellow triangles).

The type series was collected from vegetation adjacent to or overhanging the Sapoi River which at the type locality is a large, clear,



FIG. 4. Torrential stream habitat of *Litoria lakekamu* sp. nov. on the Sapoi River near Ivimka Camp, Lakekamu Basin, Gulf Province, Papua New Guinea. Males were calling from vegetation along the stream bank. Photograph by S. Richards.

rocky stream (Fig. 4) flowing through primary lowland forest. Other individuals were heard calling from about 10–15 m high in the lower canopy over the same stream.

specificity are t	SAMA R70113	SAMA R70114	SAMA R70115	PNGNM (FN 11625)	Mean	SD	Range
SVL	22.5	22.8	22.0	22.8	22.43	0.40	22.0-22.8
TL	12.6	13.5	13.3	13.4	13.13	0.47	12.6-13.5
HL	7.2	7.6	7.5	7.6	7.43	0.21	7.2–7.6
HW	8.0	8.0	7.7	8.2	7.90	0.17	7.7-8.0
EYE	3.3	3.2	3.0	3.2	3.17	0.15	3.0-3.3
ТҮМ	0.8	1.0	1.0	1.0	0.93	0.12	1.0-1.0
EN	1.7	2.0	2.0	2.	1.90	0.17	1.7-2.0
IN	2.3	2.5	2.5	2.6	2.43	0.12	2.3-2.5
3FD	1.3	1.3	1.3	1.3	1.30	0.00	1.3-1.3
3FP	0.9	0.9	0.9	0.9	0.90	0.00	0.9-0.9
4TD	1.2	1.2	1.1	1.3	1.17	0.06	1.1-1.2
4TP	0.9	0.9	0.9	0.9	0.90	0.00	0.9-0.9
TL/SVL	0.56	0.59	0.60	0.59	0.59	0.02	0.56-0.60
EN/IN	0.74	0.80	0.80	0.77	0.77	0.03	0.74-0.80
EYE/SVL	0.15	0.14	0.14	0.14	0.14	0.01	0.14-0.15
HL/SVL	0.32	0.33	0.34	0.33	0.33	0.01	0.32-0.34
HW/SVL	0.36	0.35	0.35	0.36	0.35	0.00	0.35-0.36
HW/HL	1.11	1.05	1.03	1.08	1.06	0.04	1.03-1.11
4TD/3FP	0.92	0.92	0.85	1	0.92	0.06	0.85-1.00
4TD/4TP	1.33	1.33	1.22	1.44	1.30	0.06	1.22-1.33
3FD/3FP	1.44	1.44	1.44	1.44	1.44	0.00	1.44-1.44

TABLE 1. Measurements and proportions of *Litoria lakekamu* sp. nov. SAMA R70113 is the holotype. All specimens are adult males.

Advertisement call

We recorded two complete call series produced by SAMA R70115 at a height of 3 m above the stream, and one series produced by an unvouchered animal at least 10 m high in a tree adjacent to the stream, all at an air temperature of 25.5°C. Litoria lakekamu produces two call types. Call type 1 is a single short, distinctly pulsed note repeated slowly in long series. This call type is here referred to as a short call. Call type 2 is longer than short calls and comprises a sequence of pulses produced at highly variable inter-pulse intervals resulting in the acoustic impression of a 'spluttering' sound. These calls do not contain clearly defined notes and are here referred to as long calls. Long calls always followed a series of short calls and, although sample size is small, additional calls with a similar structure were heard at the type locality. Detailed analysis is

restricted to the call series produced by SAMA R70115 due to the poor quality of the unvouchered call.

The three recorded call series consisted of seven, eight and 11 short calls produced at intervals of 2.1-6.5 s (0.28-0.48 calls/s, n=3) (Fig. 5). Each series of short calls was followed by a single long call. Total lengths of the three call series (including long calls) were 21.5, 29.4, and 45.2 s. Short calls (=notes) in the series analysed in more detail were 0.017-0.053 s long (mean=0.033, SD=0.010, n=18), and contained 4-8 pulses (mean=5.7, SD=1.3, n=18) produced at a rate of 100-312 pulses/s (mean=164.2, SD=47.01, n=18). The two long calls of sufficient quality for detailed analysis were much longer than short calls, lasting 1.6 and 1.7 s. They contained 34 and 32 pulses, respectively, uttered at a rate of 18.8 and 21.3 pulses/s. However, pulse interval in the two

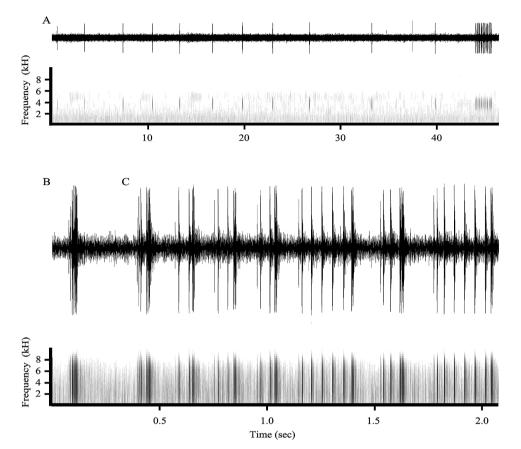


FIG. 5. Waveform (top) and spectrogram (bottom) of: (A) an entire call series containing 12 calls produced by *Litoria lakekamu* sp. nov. (SAMA R70115), (B) detail of the last short call illustrated in (A), and (C) detail of the terminal long call from that series. The interval between the last short call illustrated in (B) and the terminal call (C) has been reduced to aid comparison.

long calls was extremely variable, ranging from 0.0003 to 0.17 s resulting in the acoustic impression of a rapid series of spluttering clicks. Dominant frequency of short calls was 3560–3860 kHz (mean=3714.4, SD=85.76, n=18), and that of the two long calls fell within this range (3759.5 and 3595 kHz). Fig. 5A illustrates a full call series and Fig. 5B–C illustrates the final short call and the following long call in that series, produced by SAMA R70115.

Comparisons

Litoria lakekamu sp. nov. is compared here with small (male SVL 20-30 mm), predominantly green New Guinean Litoria that are known or presumed to breed in lentic water bodies as follows: It differs from *L. albolabris* (Wandolleck, 1911) and *L. mystax* (Van Kampen, 1906), both from the northern lowlands of New Guinea, in having longer limbs (TL/SVL 0.56–0.59 vs. 0.50–0.55 in *L. albolabris* and 0.54 in *L. mystax*; Tyler, 1968), and in lacking (vs. having) a prominent, short white bar below the eye; from New Guinean members of the *L. bicolor* (Gray, 1842) group (*L. bibonius* Kraus & Allison, 2004, *L. chloristona* Menzies, Richards & Tyler, 2008, *L. contrastens* (Tyler, 1968), *L. eurynastes* Menzies, Richards & Tyler, 2008, *L. lodesdema* Menzies, Richards & Tyler, 2008, and *L. vira-* nula Menzies, Richards & Tyler, 2008) (Tyler 1968; Kraus and Allison, 2004; Menzies et al. 2008), in having a moderately robust (vs. slender) body (Fig. 2D), with snout not projecting and near-vertical in lateral view (vs. projecting, distinctly rounded in lateral view) (Kraus and Allison, 2004; Menzies et al., 2008), and having (vs. lacking) a distinct lemon yellow mid-lateral line in life (Fig. 2D); from L. christianbergmanni Günther, 2008 in its smaller size (male SVL 20.0-22.8 mm vs. 26.9-31.2 mm in L. christianbergmanni), and white bar below eye lacking (vs. present in L. christianbergmanni) (Günther, 2008); from L. chloronota (Boulenger, 1911) by its smaller body size (males 27-32 mm in L. chloronota), and broader snout (EN/IN 0.74-0.80 vs. 0.63-0.71 in L. chloronota; Menzies, 1993); from members of the L. gracilenta (Peters, 1869) group (L. aruensis (Horst, 1883), L. auae Menzies & Tyler, 2004, L. callista Kraus, 2013, L. elkeae Günther & Richards, 2000, L. eschata Kraus & Allison, 2009, L. kumae Menzies & Tyler, 2004, and L. robinsonae Oliver, Stuart-Fox and Richards, 2008) in its smaller size (male SVL<23 mm vs. >25 mm) and lacking pale canthal and postocular stripes (vs. present: Menzies and Tyler, 2004; Oliver et al., 2008; Kraus and Allison, 2009; Kraus, 2013); from L. havina Menzies, 1993 in lacking (vs. having) a fleshy rostral spike in males; from L. rubrops Kraus & Allison, 2004 in having dorsum without (vs. with) black or darker green speckling, and iris predominantly creamy white (vs. iris red in L. rubrops; Kraus and Allison, 2004); from L. nigropunctata (Meyer, 1875), L. iris (Tyler, 1962), L. majikthise Johnston & Richards, 1994, and L. ollauro Menzies, 1993, in its smaller size (male SVL<23 mm vs. >25 mm) and further from these species in having posterior surfaces of thighs translucent with purplish-grey spotting (vs. posterior of thighs blue, red, or yellow, sometimes blotched with white or purple) (Menzies, 1993); from L. richardsi Dennis & 2006 and L. singadanae Cunningham, Richards, 2005 in having a pigmented (vs. transparent) tympanic membrane (Dennis and

Cunningham, 2006; Richards, 2005); and from *L. verae* Günther, 2004 in lacking (vs. having) crenulated skin folds along outer margins of tarsi (Günther, 2004).

Among small, green, stream-dwelling Litoria the new species differs from L. bulmeri (Tyler, 1968) by its smaller size (males 20.0-22.8 mm vs. 29-34 mm SVL), and black lateral stripe absent (vs. present); from L. longicrus (Boulenger, 1911) in having dorsum slightly granular (vs. smooth), and in lacking (vs. having) a distinct white bar beneath the tympanum (Tyler, 1968), and from L. wapogaensis Richards & Iskandar, 2001 in its smaller size (males 20.0-22.8 mm vs. 30.5-33 mm SVL), lacking (vs. having) vomerine teeth and having (vs. lacking) a distinct lemon yellow midlateral line (Tyler, 1968; Richards and Iskandar, 2001). The new species is morphologically most similar to L. leucova (Tyler, 1968), a small (males 21.7-24 mm SVL; S. Richards, personal observation) green treefrog known from the northern slopes of New Guinea's central cordillera and from the Hunstein Mountains (Tyler, 1968; Johnston and Richards, 1994; Kraus and Allison, 2006; S. Richards, personal observation). It differs from that species by having longer limbs (TL/SVL 0.56–0.60 vs. 0.53–0.55; Johnston and Richards, 1994), a poorly defined (vs. prominent) tympanum, in having (vs. lacking) a distinct lemon yellow mid-lateral line (Figs. 2A-C), and in its unique advertisement call (Fig. 5). Litoria lakekamu and L. leucova both produce short and long calls but the short call of L. lakekamu is a distinctly pulsed note containing 4–8 pulses (vs. a single pulse in *L. leucova*) and two long calls of L. lakekamu contained 32 and 34 pulses and lasted 1.6-1.7 s (vs. 10 pulses in L. leucova and lasting 0.09 s); Johnston and Richards, 1994; S. Richards, personal observation).

IUCN Status.

Litoria lakekamu is known from a single location in primary lowland forest in southern Papua New Guinea. Although extensive areas of apparently suitable habitat remain in the region, this species was not detected during numerous fauna surveys in the Kikori and Purari basins to the west between 2001 and 2017 (S. Richards, personal observations). Until this species' distribution, habitat requirements and potential threats have been better documented we recommend that it be listed as Data Deficient.

DISCUSSION

The Lakekamu basin incorporates a large expanse of primary foothill and alluvial forest on the southern fringe of Papua New Guinea's central cordillera. The basin was the focus of intensive efforts during the 1990s to establish a protected area for both conservation and research (Allison et al., 1998). As part of these efforts, a survey conducted in 1996 to identify the region's biodiversity documented numerous undescribed species of flora and fauna and a number of these are still known only from the basin including the frogs Callulops eremnosphax Kraus & Allison, 2009, Litoria robinsonae, and the damselfly Nososticta acuminata Michalski, Richards & Theischinger, 2012 (Oliver et al., 2008; Kraus and Allison, 2009; Michalski et al., 2012).

Litoria lakekamu is the third new frog species to be described based on the collections of the 1996 Lakekamu basin survey. Its distribution remains poorly known, and intensive surveys in apparently suitable habitats to the west of Lakekamu in the catchments of the adjacent Purari and more distant Kikori rivers have failed to detect it or the other two frog species described recently from Lakekamu (Richards, 2002; S. Richards, personal observations). Nor have these species been reported from the more intensively surveyed lowland forests to the east near Port Moresby (Menzies, 2006). In addition, during the 1996 Lakekamu survey, we only detected these frogs from one small area of a single stream. Together these observations suggest that the forests of the Lakekamu basin may support a small assemblage of locally endemic frogs and that further species from the world's largest tropical island await

discovery and description.

Litoria lakekamu is amongst the smallest pelodryadid frogs currently known from New Guinea (Menzies, 2006). In its very small size and predominantly green dorsal coloration, it closely resembles Litoria leucova, a streambreeding frog from northern New Guinea (Johnston and Richards, 1994; Kraus and Allison, 2006), and members of the lenticbreeding Litoria bicolor group (Menzies et al., 2008). The species' ecology suggests that it is more likely to be related to the clade of torrentdwelling frogs including L. leucova (Richards et al., 2021), but this requires confirmation. This torrent-dwelling group is particularly diverse in the mountains of New Guinea but also contains a number of lowland forms. All of the specimens reported here were encountered along, and others were heard calling from the canopy above, a torrential, clear-flowing stream in primary forest. Collection of genetic material, and of additional information about species' reproductive behaviour. this is required to elucidate its relationships, habitat requirements, and ecology.

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Appendix

Specimens examined for morphological comparisons.

Litoria albolabris (Wandolleck, 1911). Papua New Guinea: Sandaun Province, Aitape, SAMA R4947 (syntype).

Litoria auae Menzies & Tyler, 2004. Papua New Guinea: Gulf Province, Purari River, near McDowell Is, UP2490 (holotype), SAMA R57262–63 (paratypes).

Litoria bulmeri (Tyler, 1968). Papua New Guinea: Madang Province, Upper Aunjung Valley, Schrader Mtns, SAMA R5625 (holo-type).

Litoria chloristona Menzies, Richards & Tyler, 2008. Papua New Guinea: National Capital District, Waigani, SAMA R9122a; Central Province, Brown River, SAMA R13251a–c; Gulf Province, Kopi, SAMA R63502–9 (all paratypes).

Litoria chloronota (Boulenger, 1911). Indonesia: West Papua Province, Arfak Mountains, BM1947.2.31.20 (syntype), UP8380–8.

Litoria contrastens (Tyler, 1968). Papua New Guinea: Eastern Highlands Province, Barabuna, SAMA R5845 (holotype), SAMA R6450 (paratype); Western Highlands Province, Noreikova, SAMA R5847 (five specimens).

Litoria elkeae Günther & Richards, 2000. Indonesia: Papua Province, Siewa River, MZB Amph.3866–9, QMJ70490–2 (all paratypes).

Litoria eurynastes Menzies, Richards & Tyler, 2008. Indonesia: Papua Province, Siewa River, MZB Amph.14651–5; Papua New Guinea: Manus Province, Lorengau, SAMA R63497–501 (all paratypes).

Litoria havina Menzies, 1993. Papua New Guinea: Western Province, Ok Kam, UP7281 (holotype); Western Province, Ok Ma, UP 8406–7 (paratypes); Western Province, Ok Kam, SAMA R38596–7; Southern Highlands Province, Agogo Range, SAMA R60173–7.

Litoria kumae Menzies & Tyler, 2004. Papua New Guinea: Southern Highlands Province, Tari, UP3108 (holotype), SAMA R52760–61 (paratypes).

Litoria leucova (Tyler, 1968). Papua New Guinea: Sandaun Province, Mt Stolle, SAMA R44091–2, UP8604–6, upper Sepik River basin, SAMA R71844.

Litoria lodesdema Menzies, Richards & Tyler, 2008. Papua New Guinea: East New Britain Province, Kerevat, SAMAR7046–47, R7049, R7055–56, R7058–59, R8439a, b., Vouvou SAMA R64772.

Litoria longicrus (Boulenger, 1911). Indonesia: Papua Province, Wendessi, BM 1947.2.22.60–61 (syntypes).

Litoria majikthise Johnston & Richards, 1994. Papua New Guinea: Western Province, Tabubil, SAMA R44093 (holotype), UP6734, 7305–9, 8501–8, 8602–3, SAMA R44094–44101 (all paratypes).

Litoria modica (Tyler, 1968). Papua New Guinea: Eastern Highlands Province, Oruge, MCZ 52856 (holotype), MCZ 52857–52861, SAMA R8108 (paratypes).

Litoria mucro Menzies, 1993. Papua New Guinea: East Sepik Province, Near Rauit Village, UP2741–3, 2745–56 (paratypes).

Litoria mystax (van Kampen, 1906). Indonesia: Papua Province, Moaif, RMNH 4632 (holotype).

Litoria nigropunctata (Meyer, 1875). Indonesia: Papua Province, Yapen Island, Mount Waira, ZMB 63977, Yapen Island near Kontiunae, SAMA R61799.

Litoria richardsi Dennis & Cunningham,

2006. Papua New Guinea: Western Province, Tabubil, SAMA R60283 (holotype); Upper Fly River, SAMA R71602–5; Indonesia: Papua Province, Tiri River, Mamberamo Drainage, MZB Amph.11823 (paratype).

Litoria robinsonae Oliver, Stuart-Fox & Richards, 2008. Papua New Guinea: Gulf Province, Ivimka, Lakekamu Basin, SAMA R55527 (holotype), R55528–9 (paratypes).

Litoria singadanae Richards, 2005. Papua New Guinea: Morobe Province, Ridge above Surim Camp, eastern Finisterre Mountains, SAMA R60172 (holotype), UP 9968, SAMA R60171 (paratypes).

Litoria verae Günther, 2004. Indonesia: Border of Papua and West Papua Provinces, Wondiwoi Mountains, ZMB 62384.

Litoria viranula Menzies, Richards & Tyler, 2008. Papua New Guinea: Western Province, Bensbach River, SAMA R63487 (holotype), Wegamu, SAMA R63486–92 (paratypes); Indonesia: Papua Province, Merauke, SAMA R13666a–c, R13667a–d.

Litoria wapogaensis Richards & Iskandar, 2001. Indonesia: Papua Province, Wapoga River, MZB Amph.3873 (holotype), MZB Amph.3874–76, SAMA R54595–98 (paratypes).