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A new species of torrent-breeding treefrog (Pelodryadidae: *Litoria*) from the mountains of Papua, Indonesia, with new records and observations of *Litoria dorsivena* (Tyler, 1968)

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Abstract

The mountains of New Guinea are home to species-rich but poorly understood communities of stream or torrent-breeding pelodryadid treefrogs. Here we describe a new species of moderately sized torrent-breeding *Litoria* from the mountains of Papua Province, Indonesia. The new species is most similar to *Litoria dorsivena* but differs from that species in aspects of body size, skin texture and especially the shape of the snout. Based on recent collections, we also present new data on the distribution and colour in life of *L. dorsivena*. Both species show marked sexual size dimorphism when compared to most other pelodryadid treefrogs, and the colour pattern of the new species may also vary between males and females. The torrent-breeding treefrogs of New Guinea remain poorly known and, given declines of ecologically similar pelodryadids in Australia, should be a priority group for taxonomic research and population monitoring.

Keywords

Cryptic extinction risk, New Guinea, sexual size dimorphism, taxonomy

Introduction

The mountains of New Guinea are home to a diverse and highly endemic frog biota (Menzies 2006; Oliver et al. 2022). One prominent component of these upland biotas consists of approximately 20 species of torrent-breeding treefrogs in the family Pelodryadidae that most workers in Melanesia currently ascribe to the genus *Litoria* (Menzies 2006; Richards et al. 2021). Torrent-breeding *Litoria* are present in most mountain areas in New Guinea, and can form communities of as many as four or five sympatric species (Richards et al. 2000). Their moderate diversity and habitat specialisations make these mountain-associated *Litoria* a potentially important group to

complement the growing literature around how the uplift of New Guinea's Central Cordillera has generated and shaped regional biodiversity (Oliver et al. 2017; Tallowin et al. 2018; Slavenko et al. 2021; Toussaint et al. 2021; Pujolar et al. 2022). The frog pathogen *Batrachochytrium dendrobatidis* has also devastated communities of ecologically similar *Litoria* species from nearby upland areas of Australia, suggesting it is also important to resolve the diversity of New Guinea torrent-breeding *Litoria* in order to create a baseline for monitoring these potentially vulnerable species. Fortunately, this pathogen appears to have not yet colonised New Guinea (Bower et al. 2017).

There has been a steady accumulation of new species of torrent-breeding *Litoria* documented from New Guinea over the last two decades. This includes descriptions of species from both Papua New Guinea in the east (Richards and Oliver 2006a), and especially Indonesia in the west (Richards 2001; Günther and Richards 2005; Richards and Iskandar 2006). Richards et al. (2000) documented a community of four torrent-breeding *Litoria* species in the headwaters of the Wapoga River in montane forest at around 2000 m a.s.l. in Papua Province, Indonesia, of which three were considered undescribed. *Litoria fuscula* was subsequently described from these collections (Oliver and Richards 2007) and two other species were left unnamed pending further comparisons. Subsequent fieldwork and morphological examinations have confirmed the distinctiveness of one of the remaining two species, and we present a formal description of it herein. This new species is morphologically most similar to *L. dorsivena* so we also present new data on the colouration, morphology and distribution of the latter.

Material and methods

Following recent papers on the taxonomy of Australopapuan treefrogs (e.g., Kraus 2018; Oliver et al. 2019), the species described herein are assigned to *Litoria* sensu Tyler and Davies (1978) pending a comprehensively sampled and phylogenetically informed resolution of generic boundaries within Pelodryadidae. Our morphological data support the distinctiveness of the new species and indicate that its relationships lie with other *Litoria* from New Guinea that are characterised by their torrent-breeding ecology.

Frogs were located using head torches and by tracking advertisement calls. Voucher specimens were fixed in 10% formalin, stored in 70% ethanol and lodged in the Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB), and at the South Australian Museum, Adelaide, Australia (SAMA). Measurements, terminology, and abbreviations largely follow Tyler (1968) and Richards and Oliver (2006b). Measurements made to the nearest 0.1 mm with callipers were: 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. Measurement made with a dissecting microscope fitted with an ocular micrometer were: 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 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. Sex was determined by examination of vocal slits, nuptial pads, the presence of eggs and by observation of calling.

Calls were recorded using a Sony Professional Walkman recorder with an Electret ECM-Z200 Condenser Microphone. We analysed calls using Avisoft-SASLab Pro (v4.34, available from Avisoft Bioacoustics: 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, using Hamming windows.

Comparative material (Appendix 1) was examined at the American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Museum of Comparative Zoology, Harvard (MCZ); South Australian Museum, Australia (SAMA); Museum für Naturkunde Berlin (ZMB); the Natural Sciences Resource Centre of the University of Papua New Guinea, Port Moresby (UPNG); Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB); Museo Civico di Storia Naturale, Genoa (MSNG); and the Queensland Museum, Brisbane (QM). Additional information for comparisons was taken from Tyler (1968) and Günther and Richards (2005). SJR and JCU refer to original field collection numbers of S.J. Richards.

Systematics

Litoria hastula sp. nov.

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Figs 1–3, 7

Litoria sp. 10 in Richards et al. (2000)

Holotype. MZB Amph.32873 (SJR[JCUNQ]4141), adult male, ~2090 m altitude, unnamed mountain range, Derewo River Basin, Papua Province, Indonesia, (3.4416°S, 136.4738°E), collected by Stephen Richards and Djoko Iskandar, 4th April 1998.

Paratypes (n = 4). SAMA R72334–5 (SJR[JCUNQ]4142, 4144), MZB Amph.32874 (SJR[JCUNQ]4152) all adult males, MZB Amph.32872 (SJR[JCUNQ4140]) adult female, same locality and collectors as holotype, between 4–5 April 1998.

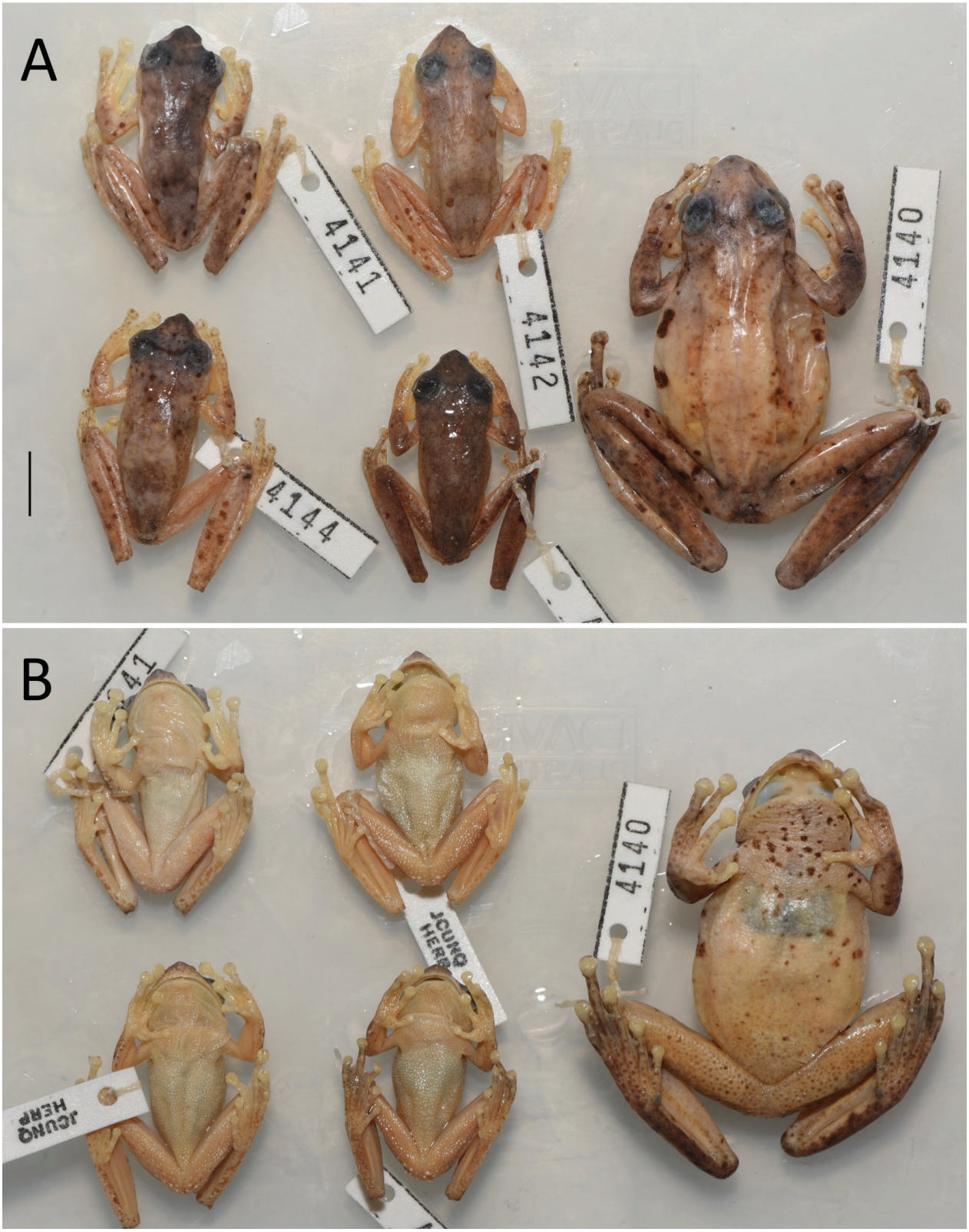

Figure 1. Type series of *Litoria hastula* **sp. nov.** showing distinctly acuminate snout tip and marked sexual size dimorphism: **A** dorsal view and **B** ventral view. Smaller males from top left to bottom right are: MZB Amph.32873 (holotype); SAMA R72334, SAMA R72335, MZB Amph.32874. Much larger female on far right is MZB Amph.32872. Tags on the specimens are field numbers. Scale bar = 10 mm.

Diagnosis. A species of *Litoria* that can be distinguished from all congeners by the following unique combination of characters: moderate size and strong sexual size dimorphism (4 adult males 30.4–31.8 mm SVL, one adult female 48.9 mm SVL); snout moderately long (EN/IN 0.69–0.80), with sharply acuminate tip and with concave dorsal surface; canthus rostralis nearly straight, sharply defined; limbs moderately long (TL/SVL 0.55–0.60); fin-

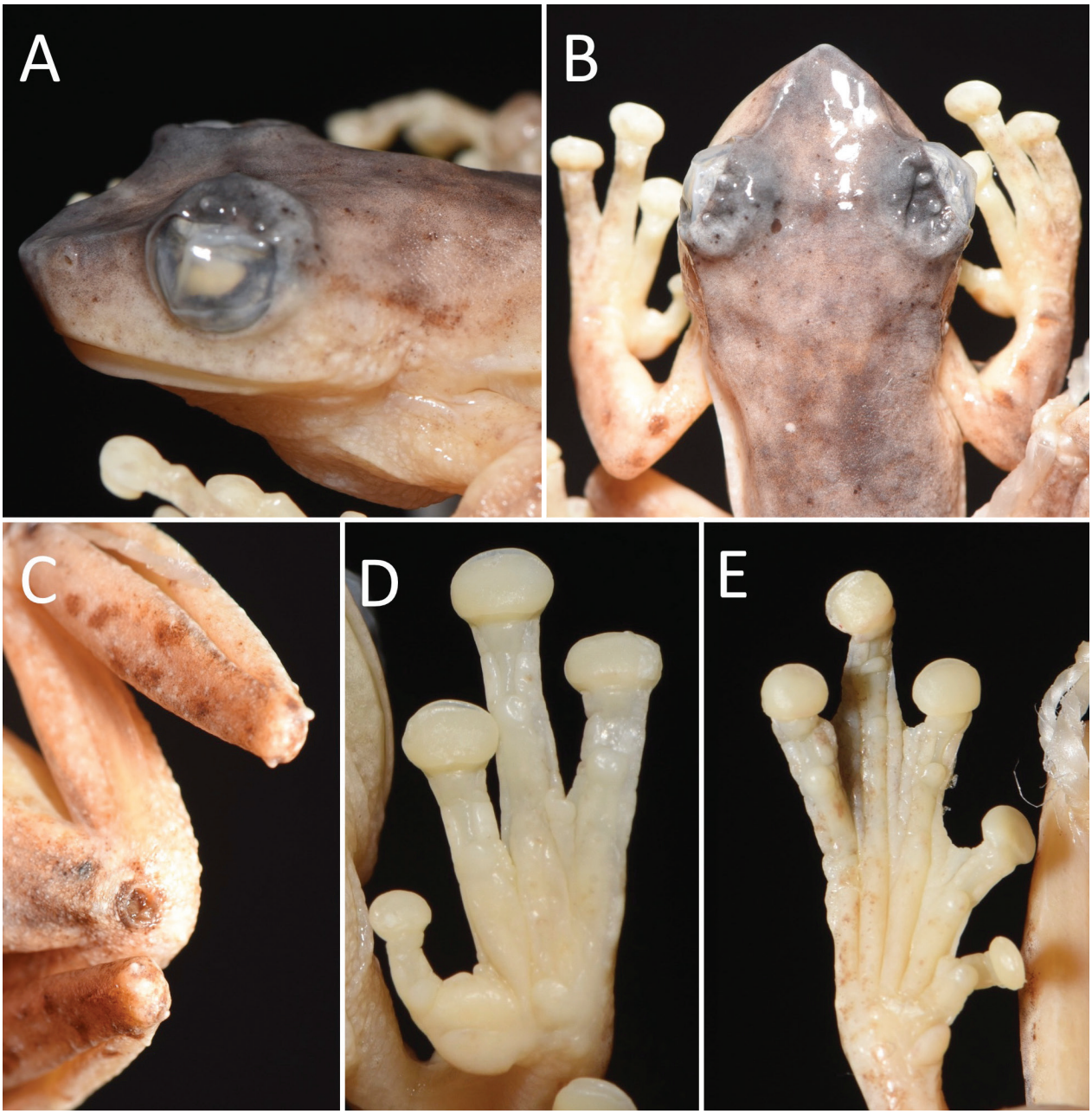

Figure 2. Details of holotype of *Litoria hastula* **sp. nov.** MZB Amph.32873: **A** lateral view of head; **B** dorsal view of head; **C** heels with conical tubercles, **D** ventral view of hand, and E) ventral view of foot.

ger webbing moderate, not extending beyond third phalanx between Finger 3 and Finger 4; toe webbing extensive, extending to penultimate phalanx between all digits except Toe 1 and Toe 2; dorsal skin relatively smooth with scattered small tubercles; heel with 2–3 distinct conical tubercles; vomeropalatines prominent; vocal slits present in males; dorsal colouration predominately light to mid-brown with scattered darker-brown spots and or blotches; venter largely buff with little to no pattern; and advertisement calls produced in series of 5–7 calls, each comprising a single short note that is unpulsed or slightly pulsatile but may become longer, with discrete pulses, in terminal calls of the series.

Description of the holotype. Adult male with vocal slits and pale-brown nuptial pads. Body moderately slender, limbs long (TL/SVL 0.60), head moderately wide (HW/SVL 0.34), slightly longer than wide (HL/SVL 0.34, HL/HW = 1.04). Vomerine teeth in two small but prominent clumps, each approximately 0.5 mm in diameter. Tongue large, broadly oval; lateral margins with distinct indentations, posterior margin with deep notch; vocal slits laterally in floor of mouth, extending from near angle of jaws to about one third distance to front of jaw. Snout protruding distinctly beyond lower jaw, tip sharply acuminate in both dorsal and lateral views, only slightly less so in lateral view, dorsal surface of snout distinctly concave (Figs 1, 2A). Canthus rostralis nearly straight, sharply defined (Fig. 2B); loreal region steeply sloping, slightly concave in dorsal view; nostrils slightly closer to tip of snout than to eyes; internarial distance greater than distance from external naris to eye (EN/IN 0.73, IN/SVL 0.12, EN/SVL

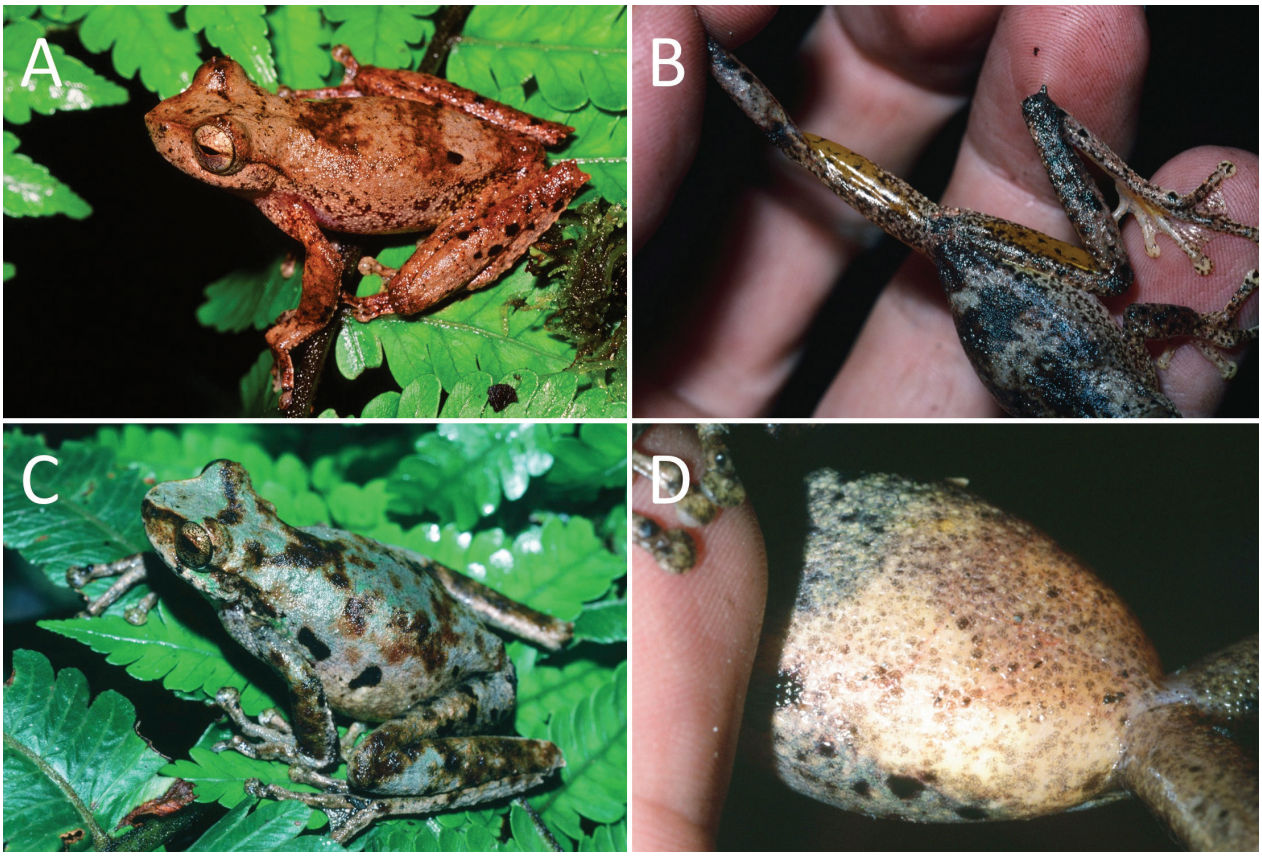

Figure 3. Colouration of *Litoria hastula* **sp. nov.** in life: **A** lateral view of adult male paratype SAMA R72334; **B** hidden coloration in thighs of male paratype SAMA R72335; **C** lateral view of adult female paratype MZB Amph.32872; **D** ventral view of adult female paratype MZB Amph.32872. All photographs by S.J. Richards.

0.086). Eyes large (EYE/SVL 0.13), prominent, protruding in dorsal and ventral views; pupil horizontal, pigmentation on nictitating membrane restricted to narrow band along dorsal edge. Tympanum small (TYM/SVL 0.04), less than half diameter of eye (TYM/EYE = 0.35), annulus poorly defined, particularly on right side, dorsal ~1/3 obscured by moderately thick, slightly curved supratympanic ridge.

Skin of dorsum and dorsal surfaces of limbs smooth except for scattered low, indistinct tubercles (Fig. 1); skin on throat and chest loose, folded and with patches of low granules; abdomen coarsely granular; patch of low, pale buff tubercles extends posteriorly from behind and below eye, under lower edge of tympanum to axilla. Ventral surfaces of forelimbs smooth with scattered tubercles; ventral surfaces of thighs coarsely granular proximally, becoming less so distally, with patch of large pale buff tubercles below vent; tarsus and tibia smooth ventrally. Low, pale buff tubercles form indistinct ridge along outer edge of forearm; heels both with one enlarged, conical and two smaller but distinct tubercles (Fig. 2C); eyelids with two prominent and several smaller conical tubercles dorsally.

Fingers moderately long with prominently expanded terminal discs (3FD/3FP 1.85; 3FD/SVL 0.08) with distinct circum-marginal grooves (Fig. 2D); relative lengths of fingers 3>4>2>1, subarticular tubercles unilobed. Webbing moderate, reaching halfway to subarticular tubercle at base of penultimate phalanx on inside of Finger 4; to tubercle at base of ultipenultimate phalanx before continuing as narrow flange to subarticular tubercle at base of penultimate phalanx on outside of Finger 3; in a narrow basal flange between fingers 2 and 3; and absent between fingers 1 and 2. Hand with indistinct round (0.6 mm diameter), unpigmented outer, and oval (1.5 mm long) inner metacarpal tubercles. Narrow pale-brown nuptial pad on first finger low, granular, extending 2.5 mm along outer edge of Finger 1, wider proximally than distally, distal ~25% angled at nearly right angles across base of thumb. Toes with expanded terminal discs with terminal grooves (Fig. 2E), disc on Toe 4 slightly narrower than on Finger 3 (3FD/4TD 1.14). Webbing between toes reaches to proximal edge of subarticular tubercle at base of penultimate phalanges on both sides of Toe 4, nearly to base of disc on all other toes except Toe 1 where it reaches only to subarticular tubercle at base of penultimate phalanx; relative lengths of toes 4>5>3>2>1. Inner metatarsal tubercle oval, small (1.3 mm long) but prominent; outer metatarsal tubercle absent (Fig. 2E).

Colouration in preservative. Dorsal base colouration mottled varying shades of light brown, patterned with scattered darker-brown maculations across snout, back and limbs, with larger indistinct darker-brown blotches on hindblimbs and posterior portion of torso (Fig. 1A). Dark colouration of eyeball visible through dorsal skin of orbital. Ventral surfaces buff, largely unpatterned except

Table 1. Summary of measurement data for the type series of *Litoria hastula* **sp. nov.**

	MZB	MZB	SAMA	SAMA	MZB
	Amph.32873	Amph.32874	R72334	R72335	Amph.32872
	holotype	paratype	paratype	paratype	paratype
Sex	m	m	m	m	f
SVL	31.3	30.4	31.4	31.8	48.9
TL	18.7	16.6	17.8	19	29.2
HW	10.5	10	10.2	10.9	15
HL	10.9	10.6	11.1	11.2	14.8
EYE	4	4	3.8	4	5
TYM	1.4	1.3	1.2	1.5	2
EN	2.7	2.4	2.5	2.8	3.5
IN	3.7	3.4	3.5	3.5	5.1
4TD	2.1	1.6	1.8	1.7	2.5
4TP	1.3	1.1	1.2	1.1	1.9
3FD	2.4	1.8	1.9	2	2.9
3FP	1.3	1	1.2	1.2	1.8
TL/SVL	0.6	0.55	0.57	0.6	0.6
HW/SVL	0.34	0.33	0.32	0.34	0.31
HL/SVL	0.35	0.35	0.35	0.35	0.3
HL/HW	1.04	1.06	1.09	1.03	0.99
EN/IN	0.73	0.71	0.71	0.8	0.69
EYE/SVL	0.13	0.13	0.12	0.13	0.1
TYM/SVL	0.04	0.04	0.04	0.05	0.04
TYM/EYE	0.35	0.33	0.32	0.38	0.4
4TD/SVL	0.07	0.05	0.06	0.05	0.05
3FD/SVL	0.08	0.06	0.06	0.06	0.06
4TD/4TP	1.62	1.45	1.5	1.55	1.32
3FD/3FP	1.85	1.8	1.58	1.67	1.61
3FD/4TD	1.14	1.13	1.06	1.18	1.16

for dense light-brown maculations on outer edges of lower forelimbs and lower hindlimbs (Fig. 1B).

Variation in the type series. Measurements and proportions of males in the type series show relatively limited variation (Table 1), and all have similar extents of webbing on the hands and feet and conspicuous conical tubercles above the eyes and on the heel. Dorsal base colouration varies from light to medium brown, and the amount and extent of darker-brown maculations and blotching varies from a few blotches on the hindlimbs, to darker patches forming broad bands across the torso and forelimbs (Fig. 1A). Base colouration of venter is always buff, generally without pigmentation (Fig. 1B). When compared against the holotype, paratype SAMA R72335 has tubercles below vent larger and more elongate, lateral margins of tongue less emarginate, and vomerine teeth that are somewhat less conspicuous. Paratype SAMA R72334 has lateral margins of tongue that are smooth and a narrower and straighter supratympanic fold. Paratype MZB Amph.32874 is noticeably darker brown on the dorsum, and the pale tubercles along outer edge of forearm are more conspicuous.

The single female paratype, MZB Amph.32872, is considerably longer than the males, more robust in body form and has a less acute snout tip (Fig. 1A) but does not show obvious differences in ratios or proportions from the males (Table 1). Compared to males, the ventral surfaces of the female paratype show more extensive dark-brown blotches and maculations across the limbs, torso and throat (Fig. 1B).

Colouration in life. The following description of colour in life is based on images of three different paratypes (Fig. 3). Dorsal and lateral surfaces of male paratype SAMA R72334 light brown, with variable amounts of medium-brown mottling and small dark-brown spots (Fig. 3A). Female paratype with dorsal pattern comprising extensive areas of dark-green pigmentation across head, torso and limbs (Fig. 3C) and ventral colouration buff with numerous dark-brown maculations that in some areas coalesce to form indistinct spots (Fig. 3D). Hidden surfaces of thighs of SAMA R72335 dark orange with extensive dark-brown spots and flecks (Fig. 3B). Iris predominately light brown, with extensive thin darker-brown reticulations.

Vocalisation. We analysed two call series produced by SAMA R72335 at an air temperature of 16.4° C. Calls were recorded against a background of loud rushing water. The first series contained seven calls and lasted six seconds, and the second series, separated from the first by 23 seconds, lasted 3.4 seconds and contained five calls (Fig. 4). Inter-call intervals for both series were relative-

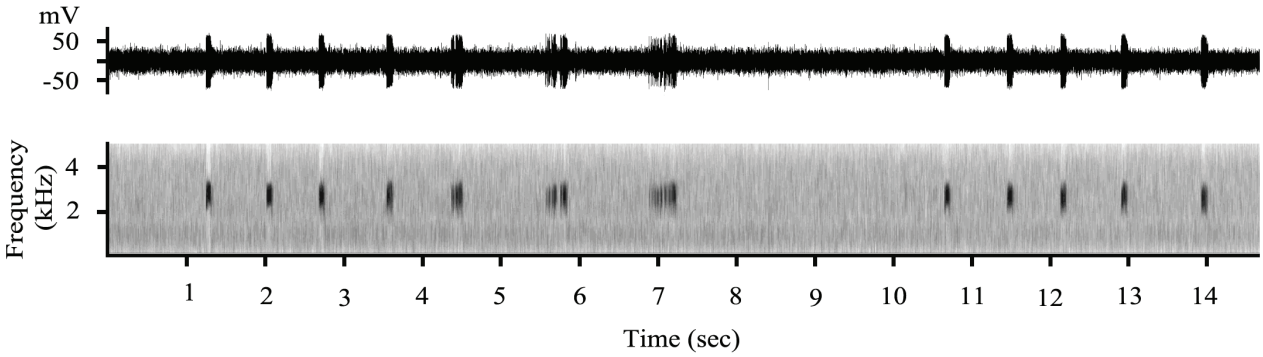

Figure 4. Two complete advertisement call series produced by paratype of *Litoria hastula* **sp. nov.** SAMA R72334, top = waveform, bottom = spectrogram. Time between the two call series has been shortened to allow comparisons.

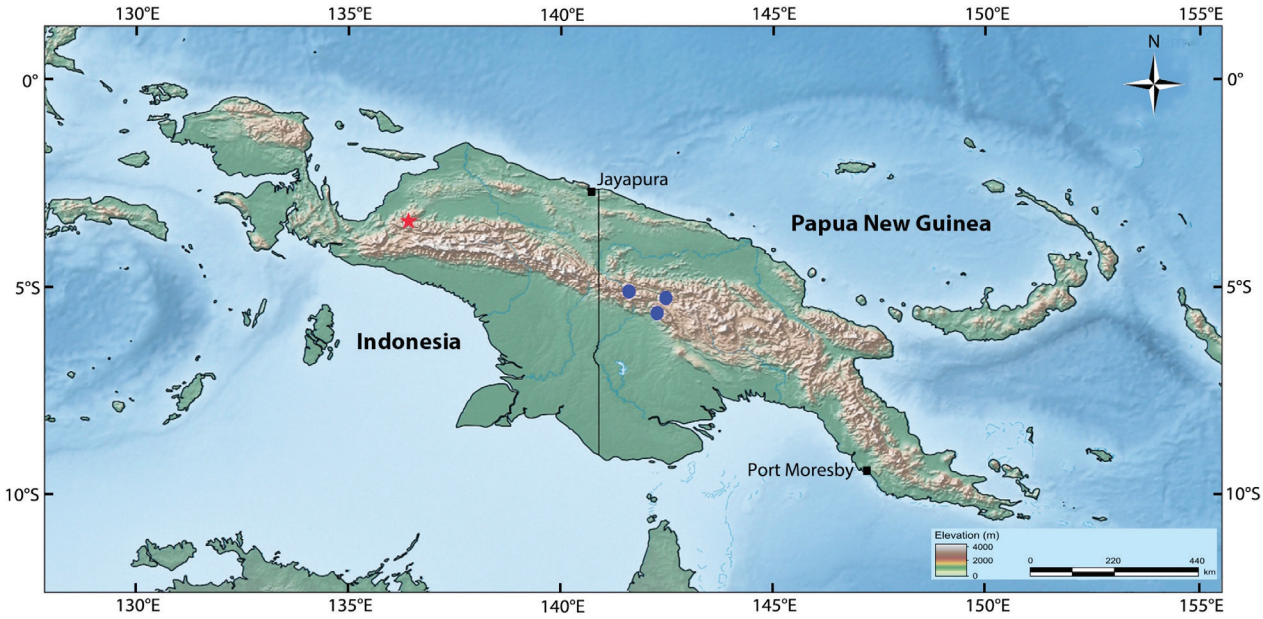

Figure 5. Known distribution of *Litoria hastula* **sp. nov.** in Indonesia (red star) and *L. dorsivena* in western Papua New Guinea (blue circles).

ly uniform (0.58–1.03 s, mean 0.78, SD 0.16, n = 10). Dominant frequency was 2530–2730 Hz (mean 2650, SD 67.4, n = 12). Length of individual calls in Series 1 increased substantially from 0.06 s in the first call to 0.35 s in the last call, and calls 5–7 in this series were characterized by increasingly pulsatile structure and subdivision into groups of variably well-defined pulses (Fig. 4). In contrast, call length in Series 2 increased only slightly during the series, from 0.071 s in Call 1 to 0.091 s in Call 5. Excluding calls 5–7 in Series 1, call length for all calls combined was 0.06–0.09 s (mean 0.07, SD 0.01, n = 9).

Etymology. Latin, "little spear', combining spear "*hasta*" with the diminutive suffix "*-ula*" in reference to the elongate and sharply pointed snout of the species.

Distribution and ecological notes. *Litoria hastula* **sp. nov.** is known only from the type locality in the mountains of Papua Province, Indonesia (Fig. 5). The habitat at this locality consisted of very mossy wet mid-montane rainforest at about 2000 m a.s.l (Fig. 6A). The type series was collected on vegetation along a fast-flowing stream in very rugged and steep terrain (Fig. 6B) where males called from leaves at night. The single female paratype is gravid and contains numerous large (2.4–2.6 mm) yellow eggs. Nine species of frog were collected at the type locality, including three other species of torrent-breeding pelodryadid treefrogs (*Litoria angiana*, *L. fuscula* and *L.* cf. *pratti*), four species of microhylid frogs in the genus *Oreophryne* and the limnodynastid frog *Lechriodus platyceps* (Richards et. al. 2000).

Suggested IUCN status. *Litoria hastula* **sp. nov.** is currently only known from a single locality. However, large areas of suitable habitat at similar elevations remain in nearby areas. This species also occurs at elevations around which *Batrachochytrium dendrobatidis* has devastated communities of ecologically similar *Litoria* in Australia, and is predicted to be very sensitive to this frog pathogen. Given the species' poorly known distribution and that threats are poorly understood, we recommend that this species be considered as Data Deficient at this stage.

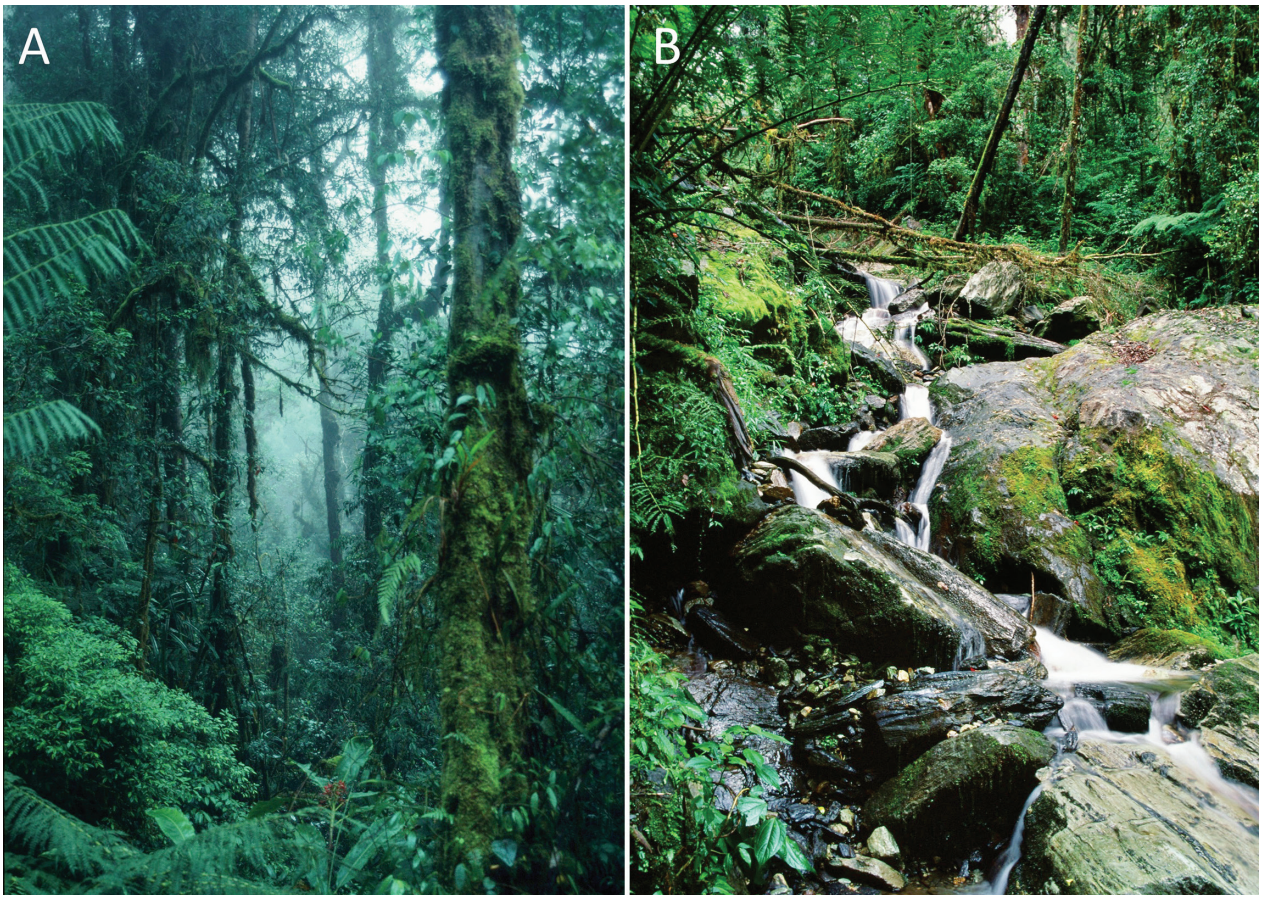

Figure 6. Details of habitat at the type locality for *Litoria hastula* **sp. nov.**: **A** dense and very mossy mid-montane forest, and **B** small fast-flowing rocky stream. The type series was collected from low vegetation along this stream at night. All photographs by S.J. Richards.

Comparison with other species. The combination of predominantly brown dorsal colouration, canthus rostralis sharply defined and straight, snout tip pointed in dorsal view, moderate webbing on fingers, and moderate size (adult male SVL 30–35 mm) readily distinguishes *Litoria hastula* **sp. nov.** from all other non-torrent-breeding *Litoria* in New Guinea. It differs from all species we currently ascribe to the genus *Nyctimystes* (most of which are also torrent-breeders) in these same characters, in having a horizontal (versus vertical) pupil, and in lacking palpebral venation.

In comparison to other torrent-breeding *Litoria* from New Guinea, *Litoria hastula* **sp. nov.** is smaller than *L. angiana*, *L. arfakiana*, *L. becki*, *L. macki*, *L. oenicolen*, *L. spartacus*, *L. spinifera* and *L. wollastoni* (max male SVL < 35mm versus >35mm); and further differs from *L. arfakiana*, *L. becki*, *L. macki*, *L. oenicolen*, *L. spinifera* and *L. wollastoni* in having moderately extensive webbing between fingers 2 to 4 (versus absent, or at most a thin basal strip between fingers 3 and 4); from *L. angiana* in having a snout that is sharply pointed in dorsal and lateral profile (versus slightly pointed in dorsal profile only); from *L. macki*, *L. spartacus* and *L. spinifera* in having a predominately brown dorsum (versus mottled green and brown) and in lacking prominent tubercles along the legs and much of the body (versus spiniform and/or conical tubercles prominent and widespread on body and/or limbs).

Litoria hastula **sp. nov.** is larger than *L. amnicola*, *L. brongersmai*, *L. megalops*, *L. napaea*, *L. rara* and *L. rivicola* (male SVL >30 mm versus <25 mm); and further differs from *L. amnicola*, *L. brongersmai* and *L. napaea* in having prominent vomerine teeth (versus indistinct and detectable only as slight bumps) and prominent heel tubercles (versus absent); from *L. megalops* in having webbing on the hand (versus absent), canthus rostralis relatively straight in dorsal profile (versus curved), and in its smaller eye (EYE/SVL 0.13 versus 0.14–0.17); from *L. rivicola* by it smooth dorsal skin (versus strongly tuberculate); and from *L. rara* by its sharply pointed snout in dorsal and lateral views (versus rounded). *Litoria hastula* **sp. nov.** is slightly larger than *L. scabra* (male SVL 30.4–31.8 versus 23.6–27.2.1, female SVL 48.9 versus 27.2–30.6 mm), and further differs in having a relatively smooth dorsum (versus covered in distinct tubercles), relatively straight canthus rostralis (versus curved) and pointed snout tip in dorsal and lateral views (versus rounded and truncate).

Litoria hastula **sp. nov.** differs from five similar-sized (max male SVL between 30–40 mm) torrent-breeding taxa (*L. bulmeri*, *L. fuscula*, *L. micromembrana*, *L. modica* and *L. pratti*) in having moderately extensive finger webbing that extends to the third phalanx on fingers 2, 3 and 4 (versus at most basal webbing between fingers 3 and 4) and in having a sharply pointed snout and rela-

Figure 7. Comparison of head profile of a male paratype of *Litoria dorsivena* SAMA R7907 (left) and holotype of *Litoria hastula* MZB Amph.32873 (right). Note much more sharply pointed tip of snout on *Litoria hastula* **sp. nov.**

tively straight canthus rostralis (versus typically rounded snout and curved canthus rostralis). It further differs from the sympatric *L. fuscula* in having prominent vomerine teeth (versus indistinct and detectable only as slight bumps), dorsum light brown with dark-brown spots and blotches (versus dark brown with no obvious pattern), and in having small conical tubercles on the heel (versus no tubercles).

Litoria hastula **sp. nov.** is most similar to *Litoria dorsivena*, a species known from about 700 km to the east in the Telefomin and upper Strickland River areas of Papua New Guinea (Fig. 5) but differs from that taxon in its slightly larger size (male SVL 30.4–31.8 versus 27.2–29.1, female SVL 48.9 versus 41.0–48 mm); proportionately longer snout (EN/IN ratio 0.71–0.80 versus 0.57–0.65); more angular canthus rostralis and more sharply pointed snout (Fig. 7); dorsal surface of snout concave (versus not obviously concave); dorsum with only sparse tubercles (versus tubercles scattered across the dorsum); and in having at least two moderately prominent conical tubercules on the heel (Fig. 2C) (versus one).

Notes on the distribution, ecology and colour in life of *Litoria dorsivena*. Material of *Litoria dorsivena* collected from localities in the Muller Range (5.657°S, 142.305°E,~1600 m a.s.l.) and Upper Strickland River region (5.288°S, 142.494°E, ~1100 m a.s.l.) (Richards and Dahl 2011) (Fig. 5) extends the range of this species approximately 80 km east of the type locality at Telefomin. The specimen from the Muller Range (SAMA R65133) is a subadult female. In contrast the collections from the Upper Strickland region comprise four adult males, allowing us to present new information on the colouration and variation in adult males of this species. In life (Fig. 8A–C) and preservative (Fig. 8D) these frogs are predominately light brown on the dorsum, with dark-brown spotting and blotching of greatly varying extent. The canthus rostralis is highlighted by either a sharp boundary between dark-brown lateral colouration on the snout and paler-brown dorsal colouration (Fig. 8A) or by a thin yellowish-brown canthal stripe (Fig. 8B). The venter and hidden surfaces of limbs have a buff base colouration, overlain with light orange on the posterior portion of torso and most of the hindlimbs and groin, and sparse to dense patches of light-brown maculations (Fig. 8C). Iris is predominately silvery grey, with light-brown vermiculations and dark-brown blotching across the ventral half.

Summary measurements of the new adult male *Litoria dorsivena* specimens are presented in Table 2 along with newly obtained measurements of the female holotype (SAMA R7901) and five male paratypes (SAMA R7907–7911). Measurements of the newly documented specimens agree closely with those taken from the type series and confirm that males of this species are consistently smaller than males of *L. hastula* **sp. nov.** (see above and

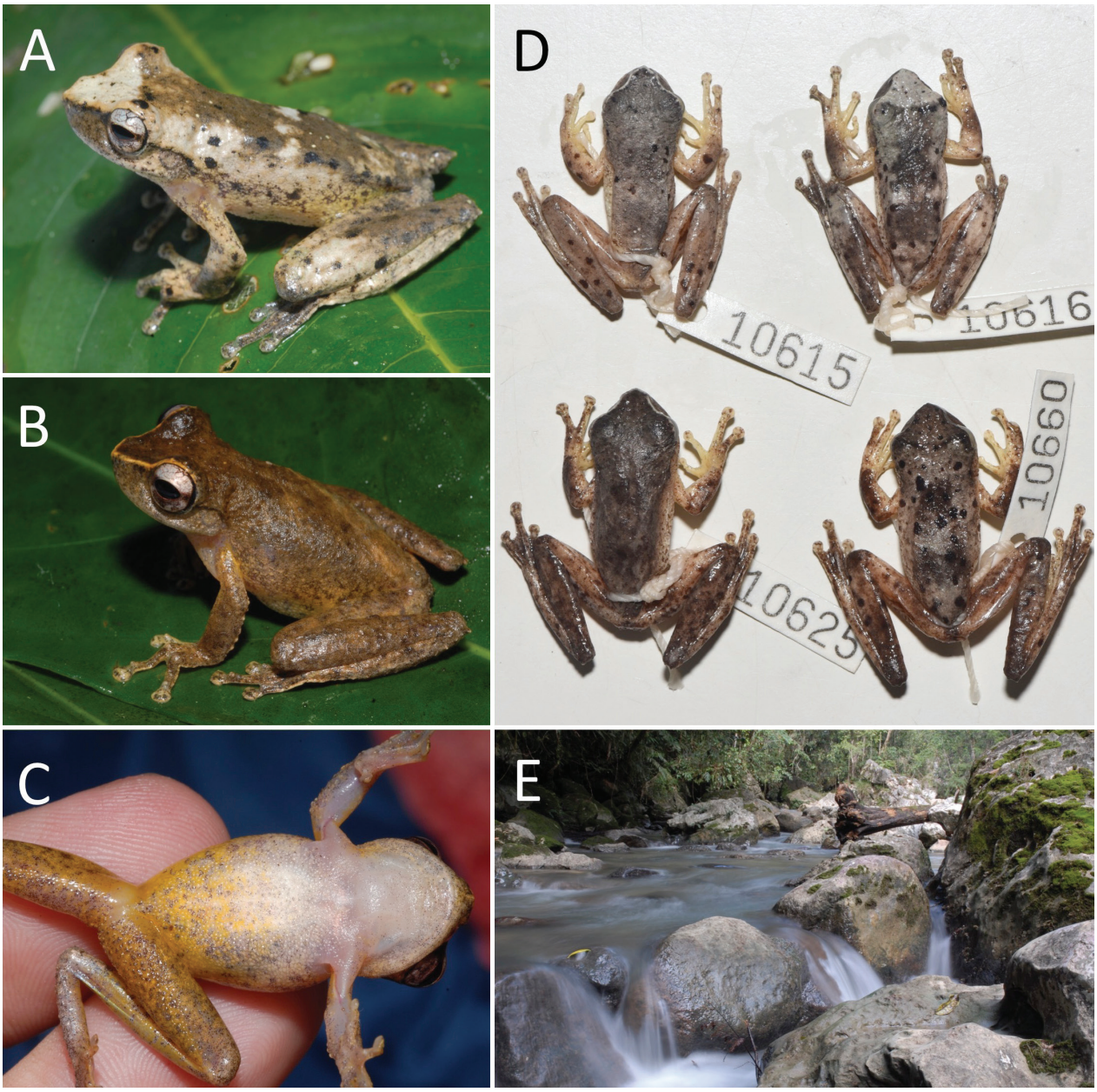

Figure 8. Colour variation and habitats details for male *Litoria dorsivena* from Tualapa in the upper Strickland River basin, Hela Province, Papua New Guinea: **A** SAMA R72320; **B** SAMA R72321; **C** SAMA R72321 ventral surfaces; **D** preserved samples (SAMA R72321–4) illustrating variation in dorsal pattern; and **E** swift-flowing stream habitat in the upper Strickland River region. All photographs by S.J. Richards.

Table 2). The specimen from the Muller Range (SAMA R65133) is a subadult female with an SVL of 32.9 mm).

The new specimens from Tualapa in the upper Strickland River basin were collected from trees along a large torrential stream with a rocky substrate flowing through relatively undisturbed lower montane forest at an altitude of 1,100 m a.s.l. (Fig. 8E). Although we did not observe reproduction in the field, examination of two adult females in the type series of *L. dorsivena* revealed that they contain large yellow eggs typical of torrent-breeding *Litoria* in New Guinea. SAMA R7904 (SVL 45mm) had eggs approximately 2 mm in diameter and SAMA R7903 (SVL 46 mm) had eggs between 1.4–1.6 mm in diameter.

Menzies and Zweifel (1976) reported specimens of *L. dorsivena* in the paralectotype series of *L. arfakiana*, which was collected from the Arfak Mountains and stored in the Museo Civico di Storia Naturale (MSNG). One of us (SJR) has examined this material. None of these specimens from far western New Guinea identified as *L. dorsivena* overlap the size range of either the type series of *L. dorsivena*, additional material confirmed by us to be *L. dorsivena* or *L. hastula*; and the snouts of the MSNG material identified by Menzies and Zweifel are much more bluntly rounded than those of both *L. dorsivena* and *L. hastula* **sp. nov.** On this basis we consider that neither species is represented in this series, and the specific status of this far western material is unresolved.

Table 2. Summary of measurement data for adult *Litoria dorsivena*, including male specimens from the type series (SAMA R7901, R7907–11), recently collected males from the upper Strickland River region (SAMA R72319–22) and the female holotype (SAMA R7901)**.**

	R7901	R7907	R7908	R7909	R7910	R7911	R72319	R72320	R72321	R72322
	holotype	paratype	paratype	paratype	paratype	paratype				
Sex	F	M	M	M	M	M	M	M	M	M
SVL	44.8	27	27.2	27.3	28	28	27.3	27.2	29.1	28
TL	27.7	16.4	17.2	16.1	17	17.2	16.7	16.8	16.9	17.6
HW	14.2	10.5	10	9.1	9.8	10.1	9.3	9.6	10.5	9.8
HL	14.6	10.2	10.2	9.4	10.2	10.2	9.8	9.9	11	10.4
EYE	4.8	3.8	3.6	3.1	3.5	3.6	3.5	3.2	3.9	3.5
TYM	1.8	1.5	1.5	1.1	1.5	1.6	1.4	1.4	1.2	1.4
EN	3.2	2.1	2.2	2	2	2.1	2.1	2.1	2.4	2.3
IN	5	3.7	3.6	3.1	3.2	3.3	3.3	3.3	3.7	3.6
4TD	2.4	1.5	1.4	1.3	1.4	1.4	1.3	1.3	1.6	1.5
4TP	1.7	1	0.9	1	1	1	0.9	0.9	1	1.1
3FD	2.8	1.9	1.7	1.6	1.6	1.5	1.4	1.5	1.7	1.7
3FP	1.4	1	0.9	0.9	1	1	0.9	0.8	1	1
TL/SVL	0.62	0.61	0.63	0.59	0.61	0.61	0.61	0.62	0.58	0.63
HW/SVL	0.32	0.39	0.37	0.33	0.35	0.36	0.34	0.35	0.36	0.35
HL/SVL	0.33	0.38	0.38	0.34	0.36	0.36	0.36	0.37	0.38	0.36
HL/HW	1.03	0.97	1.02	1.03	1.04	1.01	1.05	1.03	1.05	1.06
EN/IN	0.64	0.57	0.61	0.65	0.63	0.64	0.64	0.64	0.65	0.64
EYE/SVL	0.11	0.14	0.13	0.11	0.13	0.13	0.13	0.12	0.13	0.13
TYM/SVL	0.04	0.06	0.06	0.04	0.05	0.06	0.05	0.05	0.04	0.05
TYM/EYE	0.38	0.39	0.42	0.35	0.43	0.44	0.4	0.44	0.31	0.4
4TD/SVL	0.05	0.06	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
3FD/SVL	0.06	0.07	0.06	0.06	0.06	0.05	0.05	0.06	0.06	0.06
4TD/4TP	1.41	1.5	1.56	1.3	1.4	1.4	1.44	1.44	1.6	1.36
3FD/3FP	2	1.9	1.89	1.72	1.6	1.5	1.56	1.88	1.7	1.7
3FD/4TD	1.17	1.27	1.21	1.19	1.14	1.07	1.08	1.15	1.06	1.13

Discussion

Richards et al. (2000) documented communities of up to five species of stream-breeding pelodryadid treefrogs co-occuring at multiple sites in the Wapoga River area. At its type locality *L. hastula* **sp. nov.** co-occurs with three other species of *Litoria*. Two of these species can be ascribed to named taxa (*L. angiana* and *L. fuscula*). The identity of the final species is unclear; it is most similar to *L. pratti* and is presumably related to that species, but in the absence of fresh material of *L. pratti* from at or near the type locality it is difficult to make comparisons. As is typical for New Guinean frog communities, elevational turnover was also particularly marked in surveys of the Wapoga River area (Richards et al. 2000). None of the species recorded at the type locality for *L. hastula* **sp. nov.** were recorded at lower-elevation sites ~1000 m. a.s.l. At least two of the species recorded at the type locality for *L. hastula* **sp. nov.** have also not, as far as we aware, been recorded from any other site. This apparent faunal differentiation juxtaposed against wide gaps in sampling highlights our poor understanding of the distributions of frogs in New Guinea, and especially the western half of the Central Cordillera.

Litoria hastula **sp. nov.**, *L. dorsivena* and *L. pratti* exhibit pronounced sexual size dimorphism (SSD); indeed in the original description of *L. dorsivena* the author noted some initial doubts as to whether males and females represented the same species (Tyler 1968). Based on the small available samples (Tyler 1968; this paper) the sexual dimorphism index (SDI) [(female max body size/male max body size) –1] (following Han and Fu 2013)) for these three taxa is as follows: *Litoria hastula* **sp. nov.** –0.54; *L. dorsivena* –0.66; and *L. pratti* –0.55). These are amongst the highest SSD values reported for pelodryadid treefrogs (Han and Fu 2013). In Australia, the rainforest treefrog *L. serrata* does, however, show similar marked size differentiation (SDI 0.57, based on maximum SVL values presented in Anstis (2013)). In *L. serrata*, the two sexes also differ in their ecologies, with females moving into the forest canopy when not breeding, while males remain by streams for longer periods (S. Richards, unpublished observations). We speculate that marked sexual size dimorphism in these three species of New Guinean torrent-breeding *Litoria* may likewise be indicative of

ecological differences between sexes. While sample sizes are very small, apparent differences in dorsal colour between male (brown) and female (brown and green) *L. hastula* **sp. nov.** (Fig. 3) may represent further evidence that sexes use differing microhabitats.

The description of *L. hastula* **sp. nov.** brings the number of torrent-breeding *Litoria* in New Guinea to 21 species. Preliminary genetic data indicate that these taxa represent a monophyletic radiation (Richards et al. 2021), that are all as far as we know characterised by tadpoles adapted to swift-flowing streams (Günther and Richards 2005; Menzies 2006). Species in the group show a great diversity in body size, form and ornamentation, degree of sexual-size dimorphism and potentially also the extent to which they are tied to stream environments throughout their lives (Günther and Richards 2005). We are aware of at least 15 other candidate species in this guild, and we emphasise that large areas of New Guinea remain undersurveyed, especially in Indonesia (Oliver et al. 2022). Given precipitous declines in high-elevation torrent-breeding *Litoria* in nearby Australia (Bower et al. 2017), cryptic extinction risk (i.e., where knowledge gaps and predictors of vulnerability overlap: McDonald et al. 2022) is an important issue for this clade. In this context, documenting and understanding the diversity of this fascinating radiation is a high research priority for Melanesian frogs (Oliver et al. 2022).

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Appendix 1

Comparative material examined for this study. Institutional codes are explained in methods. PNG = Papua New Guinea.

Litoria amnicola: MZB Amph.12116 (holotype), MZB Amph.12099–12104, MZB Amph.12106, MZB Amph.12113–12115, 12117, MZB Amph.12099 (paratypes), Weybya Camp, Salawati Island, Raja Ampat Archipelago, West Papua Province, Indonesia.

Litoria arfakiana: MSNG 29723A, Hatam, Arfak Mountains, Papua Province, Indonesia (lectotype).

Litoria brongersmai: MCZ 15203 (holotype) Snow Mountains, Papua, Indonesia; MZB Amph.11824–27, SAMA R61630–32 Wapoga River Headwaters, northern Papua province, Indonesia.

Litoria bulmeri: SAMA R5625 (holotype) Upper Aunjung Valley, Schrader Mtns, Madang Province, PNG.

Litoria dorsivena: SAMA R7902–R7911 (type series) Telefomin area, Sanduan Province, PNG; SAMA R65133 Muller Range, Western Province, Papua New Guinea; SAMA R72319–22, Upper Strickland River Region, Hela Province, Papua New Guinea.

Litoria fuscula: MZB Amph.11822 (holotype), SAMA R60724 (paratype) unnamed mountain range, Derewo River Basin, Papua Province, Indonesia.

Litoria macki: MZB Amph.3870 (holotype), MZB Amph.3871–2, QM J75810, SAMA R55363 (all paratypes, Wapoga Alpha Mineral Exploration Camp, Papua, Indonesia; SAMA R55364 Lagori Landing site 21, Papua, Indonesia.

Litoria micromembrana: SAMA R4150 (holotype) Mount Podamp, PNG; SAMA R61629, SAMA R61637–40, UPNG 10031 Finimterre, Hindenberg Range, Western Province, PNG; SAMA R61599–01, UPNG 10029, UPNG 10032, SAMA R61602 Abalgamut, SAMA R61603 Kikiapa, both localities on the Huon Peninsula, PNG.

Litoria modica: SAMA R8108 (paratype) Oruge, PNG; SAMA R61616–19, UPNG 10030, Mount Akrik, Star Mountains, Western Province, PNG; SAMA R61609–12, UPNG 10035–36, Mount Binnie Summit, Western Province, PNG; SAMA R61604–07, UPNG 10033, Mount Sisa, Southern Highlands Province, PNG; SAMA R61608, UPNG 10030, Mount Stolle, Sanduan Province, PNG.

Litoria napaea: AMNH 49575 (paratype) Idenburg River, Snow Mountains, Papua Province, Indonesia; SAMA R61620–28, MZB Amph.11833–42 Wapoga LS21, Papua Province, Indonesia.

Litoria oenicolen: AMNH 87922 (holotype) Baiyer River, Western Highlands Province, PNG.

Litoria pratti: BMNH 1947.2.23.54 (female), 1947.2.23.55, 1947.2.23.56 Wendessi, Papua Province, Indonesia; BMNH 1947.2.23.57, BMNH 1947.2.23.58 (both cotypes) Arfak Mountains, Papua Province, Indonesia.

Litoria rivicola: ZMB 60327, ZMB 60328 (paratypes) 30 km SE of Nabire, Papua Province, Indonesia.

Litoria scabra: MZB Amph.11335(holotype), MZB Amph.11336–40, SAMA R60706–60709, ZMB 67357-67359 (paratypes) headwaters of the Wapoga River, Papua Province, Indonesia.

Litoria spartacus: SAMA R60290 (holotype), UP8864–5, SAMA R60291–6 Moro Camp, at base of Iagifu Ridge, Southern Highlands Province, PNG; SAMA R61238 Benaria River, Southern Highlands Province, PNG.

Litoria spinifera: SAMA R6295–6301 (paratypes) Oruge, Western Highlands Province, PNG; SAMA R9167, Camp 1, Pio River, PNG; SAMA R9108A–D, Elmagale, Southern Highlands Province, PNG; SAMA R55357–62, UPNG 9963–4 Crater Mountain Wildlife Management area, 55–75 km S of Kundiawa, Eastern Highlands Province, PNG.

Litoria wollastoni: BM 1947.2.23.59 (holotype) Octakwa River, Papua Province, Indonesia.