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A new species of insular treefrog in the *Litoria thesaurensis* species group from the Nakanai Mountains, New Britain, Papua New Guinea

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Abstract

The Islands of East Melanesia have a unique and highly endemic frog fauna derived entirely from overseas colonisation events. Within East Melanesia New Britain is a notable centre of frog diversity and endemism, with at least 15 endemic species, mostly in the ceratobatrachid genus *Cornufer*. Here we describe the first endemic pelodryadid treefrog from New Britain. The new species is a member of the *Litoria thesaurensis* species group but can be distinguished from near relatives by aspects of body size, webbing extent, bone pigmentation and male advertisement call. The two known specimens of the new species were collected in Hill Forest on karst basement in the Nakanai Mountains in East New Britain. The new species provides new evidence of diversification of insular Pelodrydidae, and reinforces New Britain, and especially the predominantly karst Nakanai mountains, as a hotspot of frog diversity in East Melanesia. In light of high rates of forest loss and conversion New Britain is also a region of significant conservation concern.

Keywords

East Melanesia, forest loss, island endemism, karst endemism, overwater dispersal, Pelodryadidae, taxonomy

Introduction

The islands of East Melanesia (also sometimes in part referred to as Northern Melanesia) extend from Manus in the west through New Ireland, New Britain and the Solomon Islands in the east, and under some interpretations through to Vanuatu and Fiji (Mayr and Diamond 2002; Lucky and Sarnat 2010; Lavery et al. 2016; Oliver et al. 2016). The East Melanesian islands have never been connected with any continental landmass, and their biota is believed to be entirely derived from taxa that have arrived via overwater dispersal (Mayr and Diamond 2002; Lavery et al. 2016; Oliver et al. 2018). Accordingly, many taxa that have diversified on nearby larger landmasses such as New Guinea (herein considered to be part of West Melanesia) are absent. Nonetheless the biota of East Melanesia includes lineages with apparently diverse colonisation and diversification histories, ranging from deep relicts (Klein et al. 2016; Oliver et al. 2016, 2020; Brennan et al. 2020) to recent colonisation with subsequent evolutionary diversification (Moyle et al. 2009; Cibois et al. 2014). This combination of diverse origins

and numerous islands has led to East Melanesia being a focal area for the study of insular dispersal, diversification and community assembly, especially in birds (Mayr and Diamond 2002). These same processes of isolation and insular distributions have also rendered many East Melanesian species sensitive to environmental change, and the biodiversity of the region is increasingly threatened by a growing human population and associated agricultural expansion and forest loss (Bryan and Shearman 2015).

The frog fauna of East Melanesia shows a particularly marked differentiation from that of nearby mainland New Guinea, being dominated by a single radiation of direct-developing species in the family Ceratobatrachidae that has diversified greatly in ecology and associated body form (Menzies 2006; Brown et al. 2015; Oliver et. al. 2022). In contrast, the two frog families that dominate on nearby New Guinea are depauperate in East Melanesia (Menzies 2006). There are just two species of Microhylidae (both endemic to New Britain), while there are probably over 400 species in this radiation on New Guinea (Oliver et. al. 2022). The pelodryadid treetrogs are slightly more diverse in East Melanesia, with four species and two taxa that are considered endemic (one species and one subspecies), but this compares with over 100 taxa on nearby New Guinea.

The most diverse and widespread lineage of *Litoria* Tschudi, 1838 in East Melanesia comprises two species in the *L. thesaurensis* species group. This is a group of moderately-sized treefrogs with variable colouration and extent of finger webbing (Kraus and Allison 2004; Menzies 2006), that is defined largely on the basis of osteological features (Tyler and Davies 1978). The two East Melanesian species, *Litoria thesaurensis* (Peters, 1877) and *L. lutea* (Boulenger, 1887), occur in sympatry across most of the Solomon Islands and Bougainville, but to date only *L. thesaurensis* has been reported from New Britain and New Ireland (Tyler 1968; Menzies 2006). However on a Rapid Assessment Program (RAP) biodiversity survey organised by Conservation International to the Nakanai Mountains in East New Britain Province in 2009, the senior author established that two species in the *L. thesaurensis* species group co-occur in hill forest habitats there (Richards 2011). One of these species can be referred to the widespread *L. thesaurensis*, but the other has thus far only been recorded from one location and can be diagnosed from other populations of *L. thesaurensis* in East Melanesia by its distinctive colouration (Fig. 1), morphology and call. We herein present a scientific description of this form, which is the seventh species of frog thus far known only from the Nakanai Mountains, and the first putative endemic pelodryadid frog from New Britain.

Material and methods

The new species described herein and its putative relatives are assigned to the genus *Litoria* based on having a horizontal pupil following Kraus (2018), pending a compelling resolution of generic boundaries within Pelodryadidae.

The type material of the new species was fixed in 10% formalin and subsequently stored in 70% ethanol and lodged at the South Australian Museum. Comparative material was examined in the collections of the Natural History Museum, London (**BMNH**), The Museum of Comparative Zoology, Harvard (**MCZ**), and the South Australian Museum, Adelaide (**SAMA**). A full list of material examined is presented in Appendix 1. Additional comparative data were taken from published literature (Kraus and Allison 2004; Menzies 2006).

Measurements (to the nearest 0.1 mm) were taken with dial calipers and a stereomicroscope fitted with an ocular micrometer. Morphological measurements largely follow Richards et al. (2006). They are: SVL (snout-vent length), TL (tibia length), HW (head width at tympana), HL (head length from tip of snout to posterior edge of tympanum), EYE (horizontal eye diameter), TYM (horizontal tympanum diameter), IN (inter-narial distance, distance between dorsomedial edges of nares), EN (distance between anterior edge of eye and posterior edge of naris), 3FD (horizontal diameter of 3rd finger disc) and 3FP (narrowest horizontal width of penultimate phalanx of the same digit), 4TD (horizontal diameter of 4th toe disc) and 4TP (narrowest horizontal width of penultimate phalanx of the same digit).

Advertisement calls were recorded with a Marantz PMD-661 Solid-state Recorder and Sennheiser ME66 microphone at distances of 0.5–2 m. Ambient temperatures were noted during recordings. Calls were analysed using Avisoft-SASLab Pro (v4.34, available from Avisoft Bioacoustics: http://www.avisoft.com/) following procedures and terminology recommended by Kohler et al. (2017). We calculated audiospectrograms with fast-Fourier transform (FFT) of 1024 points, 96.87% overlap, using Hamming windows.

Systematics

Litoria insularis sp. nov.

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Holotype. SAMA R64781 (FN SJR10776), adult male with nuptial pads, Vouvou Camp, Nakanai Mountains, East New Britain Province, Papua New Guinea (5.4456°S, 151.4640°E, 850 m a.s.l.), collected by S. Richards on 16th April 2009.

Paratype. SAMA R66896 (FN SJR10738), adult male with nuptial pads, same collector and locality details as holotype, collected on 12th April 2009.

Diagnosis. A species of *Litoria* that can be distinguished from all other taxa by the following unique combination of characters: moderately small size (male SVL 38.7–

Figure 1. *Litoria insularis* **sp. nov.** holotype SAMA R64781 from the Nakanai Mountains, East New Britain, Papua New Guinea in life. Images A and B show temporal variation in dorsal colouration, but consistent pattern of mottling and dark-brown flecks. Photographs S.J. Richards.

41.7 mm); finger webbing moderate, not extending beyond base of second phalanx on any fingers; toe webbing moderate, extending to base of second phalanx on both sides of toe 4; finger discs moderately expanded (3FD/SVL 0.059–0.062); toe discs moderately expanded (4TD/SVL 0.052–0.058); bones of limbs green in life; lower forelimbs and hindlimbs with low crenulated dermal ridges along lateral edges; male throat and neck smooth or ridged, but lacking numerous obvious round bumps in life; venter plain off-white in life; dorsal colouration mottled pale grey or brown with scattered very small dark-brown flecks; head lacking dark lateral band or mask; iris reddish-brown with prominent sky blue outer rim; and call very long (> 13 s), consisting of more than 90 notes repeated at a rate of 6.7 notes/s.

Figure 2. Details of holotype of *Litoria insularis* **sp. nov.** SAMA R64781. **A** Ventral view of fingers and webbing; **B** ventral view of toes and webbing (scale bars = 5 mm); **C** ventral colouration; **D** hidden colouration of thighs. All photographs by S.J. Richards.

Description of holotype. Habitus moderately robust (Fig. 1A–B), limbs moderately long (TL/SVL 0.53); snout narrowly rounded in dorsal aspect, distinctly sloping in lateral aspect. Canthus poorly defined, broadly rounded, slightly curved in dorsal view; loreal region sloping, slightly concave; nostrils near tip of snout, oriented laterally. Eyes large (EYE/SVL 0.127). Tongue broadly oval with distinct posterior notch; vocal slits short, extending anteriorly from level of angle of jaw. Vomero-palatine ridges located midway between internal nares, prominently raised, about 0.6 mm apart, each with 3–4 distinct teeth. Tympanum moderately large (TYM/SVL 0.070), annulus distinct except for postero-dorsal edge obscured by thick, curved, postocular fold extending from posterior edge of eye to above axillary junction. Skin finely but distinctly granular dorsally; abdomen coarsely granular; throat and chest coarsely ridged.

Fingers moderately long, relative lengths 3>4>2>1, terminal discs moderately wide (3FD/SVL 0.062), with circum-marginal grooves (Fig. 2A); webbing reaches to ultimate subarticular tubercle on inner side of Finger 4 and outer side of Finger 2, to base of third phalanx on inner side of Finger 3, to halfway along third phalanx on outer side of Finger 3, restricted to thin basal strip between Fingers 1 and 2. Subarticular tubercles prominent, circular, undivided. Inner plantar tubercle prominent, ovoid. Nuptial pads low, brown, granular, extending 3.5 mm along base of Finger 1. Prominent tubercles along posterior-ventral edge of forelimbs form crenulated ridge extending from base of Finger 4 to elbow.

Toes moderately short, relative lengths 4>5>3>2>1, terminal discs moderately wide (4TD/SVL 0.058) with circum-marginal grooves (Fig. 2B); webbing reaches penultimate phalanx on Toes 1–3 and 5, and to base of third phalanx on both sides of Toe 4. Inner metatarsal tubercle and subarticular tubercles prominent, not divided (Fig. 2B). Tubercles along outer edge of lower limbs form weak crenulations. Skin on postero-ventral surface of thighs coarsely granular.

In life at night dorsal and upper-lateral surfaces of torso varying shades of mottled light to medium brown (Fig. 1B), but during photography colour quickly changed to varying shades of mottled light grey overlain with extensive fine brown stippling (Fig. 1A); scattered small dark-brown flecks present across torso. Head with same variable base colouration as torso but lacking dark-brown flecks and having denser dark-brown stippling on snout, around canthus rostralis and on anterior surface of orbit-

Figure 3. Details of species in the *Litoria thesaurensis* Group in life. **A** *Litoria insularis* **sp. nov.** paratype SAMA R66896 in life; **B** *Litoria thesaurensis* SAMA R64668 from New Britain showing yellow lateral pigmentation; **C** ventral view of *L. thesaurensis* from New Britain, with round tubercles on the throat faintly visible; **D** *L. thesaurensis* from Bougainville showing dark brown weakly striped pattern; **E** *Litoria thesaurensis* from Bougainville showing plain green dorsum; **F** *Litoria lutea* from Bougainville showing light green dorsum colouration with off-white flecks. All photographs by S.J. Richards.

als. Exposed surfaces of limbs and digits same colouration as torso but with more obvious and intricate mottling, denser brown stippling and lacking dark-brown flecks. Lateral and ventral surfaces of torso, throat and limbs unpatterned, largely off-white with small areas of near translucent skin, especially on thighs and upper arms (Fig. 2C–D). Iris patterned with dense light-brown stippling and a prominent light-blue outer ring.

In preservative dorsal and upper lateral surfaces of head and torso mottled with varying shades of light brown and light grey, anterior portion of head distinctly greyer than remainder of dorsal surfaces, scattered small dark-brown flecks on dorsal surfaces of torso clearly apparent, with smaller number of small white flecks. Exposed surfaces of limbs show similar base colouration to dorsum, but also have areas of off-white mottling and lack dark-brown flecks. Vent bordered dorsally by dark brown blotch and then irregular white band. Dorsal surfaces of digits buff with varying amounts of fine brown stippling, stippling especially dense on outer digits, but tending to very sparse on inner digits. Ventral surfaces buff, largely unpatterned, except for small areas of dense stippling close to lower jaw, and along extremities of forelimbs and hindlimbs.

Summary meristic data for holotype (all measurement in mm). SVL 41.7; TL 22.1; HW 15.3; HL 14.8; EYE 5.3; TYM 2.9; IN 3.3; EN 4.2; 3FD 2.6; 3FP 1.4; 4TD 2.4; 4TP 1.8.

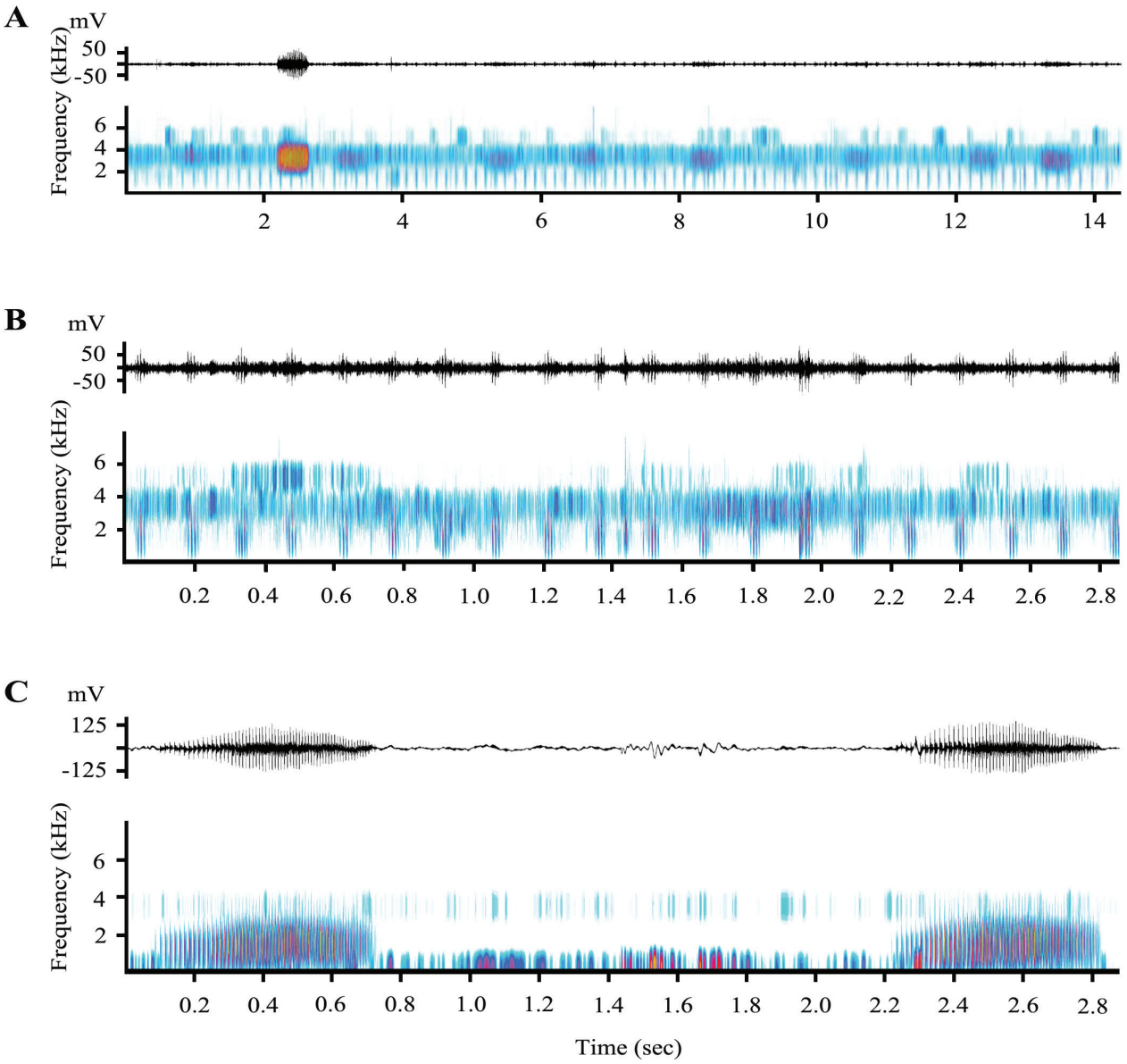

Figure 4. Waveform (top) and spectrogram (bottom) of (**A**) an entire call of *Litoria insularis* **sp. nov.**; **B** a three second section from the middle of this call illustrating the distinctly pulsed nature of the notes; **C** two consecutive calls of *L. thesaurensis* recorded in sympatry with the new species, showing strikingly different call structure. The strong signal at ~2.2 s on A) is a call of the New Britain endemic microhylid frog *Oreophryne brachypus*.

Variation. The sole paratype (SAMA R66896) is an adult male (Fig. 3A) with the following measurements: SVL 38.8; TL 21.9; HW 13.4; HL 12.4; EYE 5.2; TYM 2.5; IN 2.9; EN 3.8; 3FD 2.3; 3FP 1.2; 4TD 2.0; 4TP 1.3. It is similar in colour and pattern to the holotype, with the following differences, base colouration in both life and preservative lighter grey with less obvious mottling, dark-brown flecks much more numerous and extending onto limbs, and dorsum with two small off-white blotches.

Advertisement call. We recorded a single complete call produced by the holotype at an air temperature of 22.0°C. It was recorded from approximately 2 m distance and the call of this species is very quiet so detailed analysis of some features was not possible due to reduced resolution and high background noise. The call is a long (13.9 s) series of 94 short, distinctly pulsed notes repeated rapidly (6.7 notes/s) at relatively uniform inter-note intervals of 0.106–0.144 s (mean = 0.120, SD = 0.012, n = 25). Twenty-five notes measured in detail are 0.027–0.050 s long (mean = 0.034, SD = 0.005) and contain 3–5 pulses (3 pulses = 4 notes, 4 pulses = 17 notes, 5 pulses = 4 notes). Energy in the call is distributed broadly between ~0.5 and 3 kHz and dominant frequency is between 1260 and 2156 Hz in five randomly selected notes. The call produced by the holotype is illustrated and compared with two calls of a sympatric *L. thesaurensis* in Fig. 4.

Comparisons with other species. *Litoria insularis* **sp. nov.** was found in sympatry with *L. thesaurensis* and is most likely to be confused with that species, but differs in having wider finger discs (3FD/SVL 0.059–0.062 versus 0.037–0.052) and toe discs (4TD/SVL 0.052–0.058 versus 0.038–0.047); dorsum with scattered small dark-

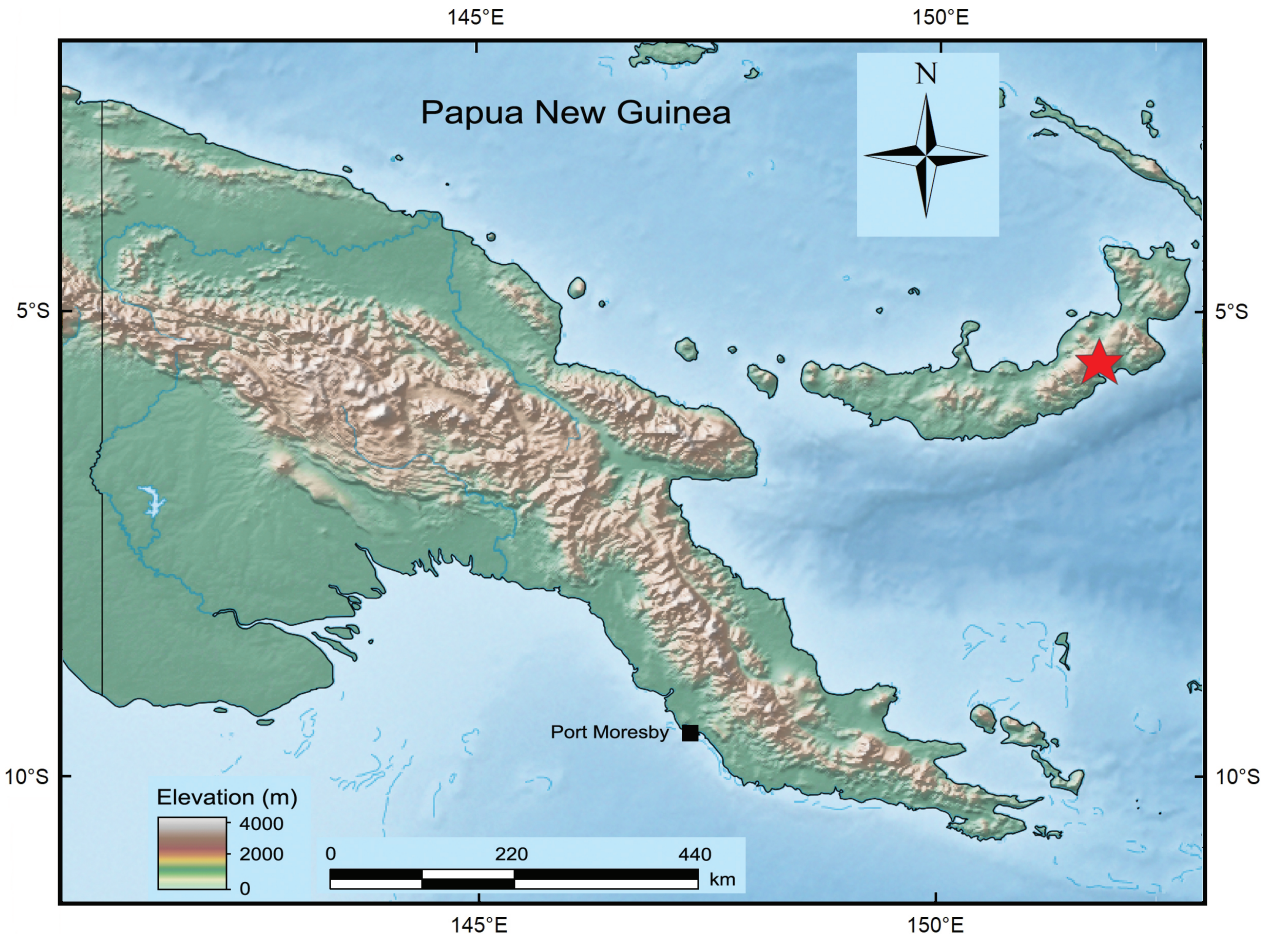

Figure 5. Map of Papua New Guinea with type locality for *Litoria insularis* **sp. nov.** on New Britain indicated by a red star.

brown flecks (versus base colouration and pattern highly variable, but usually not with small scattered dark-brown flecks) (Fig. 3B–D); skin on male throat smooth (Fig. 2C) (versus with prominent unpigmented bumps (Fig. 3E)); and in having an extremely distinct call comprising a series of 90 rapidly repeated short (~0.03 s), distinctly pulsed notes produced at a rate of 6.7 notes/s (versus a single drawn out note lasting ~0.6 s (Fig. 4; Kraus and Allison 2004).

It has been suggested that *Litoria thesaurensis* as currently construed may be a complex of several species (Kraus and Allison 2004). The characters listed above serve to distinguish the new species from all populations referred to *L. thesaurensis* from East Melanesia, including near-topotypic material from Bougainville in the biogeographic (versus political) Solomon Islands. Comparisons of photographs of *L. insularis* **sp. nov.** with *L. thesaurensis* from East Melanesia further suggest that the new species differs in having plain off-white ventral and hidden surfaces of the limbs (versus typically with large areas of yellow) and in having a distinctive rim of sky-blue pigmentation on the outer edge of the iris (versus brown to bright red iris with no obvious pale blue rim). However, given the propensity for frogs in the *Litoria thesaurensis* species group to undergo rapid shifts in colouration and for iris colouration to be obscured by the degree of pupil dilation, we note these potential differences here, but do not include them as diagnostic features at this stage.

The new species differs from other species in the *L. thesaurensis* species group as follows; from *L. flavescens* Kraus & Allison, 2004 by its smaller size (male SVL 38.7–41.7 mm versus 44.5–45.6), by having green limb bones (versus white), and by having a light grey and/or brown dorsum (versus yellow); from *L. lutea* by its smaller maximum size (adult male maximum 42 mm versus 62 mm), and dorsum with scattered small dark-brown flecks (versus dark brown flecks absent (Fig. 5F)); and from *L. impura* (Peters & Doria, 1878) by having green limb bones (versus white), in having only moderate webbing on the fingers, by having a chin without dark pigmentation in breeding males (versus chin and throat black), and by lacking a prominent dark-brown canthal stripe (versus present). The call of *Litoria insularis* is the most divergent among currently recognised members of the group (the call of *L. lutea* has not been described). In contrast to the multi-note call of the new species, *Litoria flavescens*, *L. impura* and *L. thesaurensis* all produce single-note calls containing > 50 pulses. Vocalising males can therefore be readily distinguished from these taxa.

Only two other species of *Litoria* occur in East Melanesia. *Litoria insularis* **sp. nov.** can be readily distinguished from these as follows: from *L. infrafrenata* (Günther, 1867) by its much smaller size (male SVL 41.2 mm versus up to at least 135 mm), mottled brown or grey dorsal colouration (versus typically plain green or brown), and by lacking a prominent white labial strip (versus present);

Figure 6. Habitat at type locality of *Litoria insularis* **sp. nov.** in the Nakanai Mountains, East New Britain Province, Papua New Guinea. **A** Aerial view of upper hill forest on rugged karst; **B** forest profile; **C** slow-flowing stream along which the type series was collected.

and from *L. lododesma* Menzies, Richards & Tyler, 2008 by its much larger size (max male SVL 41.2 mm versus 23.8 mm), dorsum brown or grey with scattered brown flecks (versus typically green without pattern), and the absence of white lateral stripe on the head (versus usually present).

Distribution and natural history. Known only from the type locality in the Nakanai Mountains in the eastern portion of the island of New Britain (Fig. 5). The species was not heard or recorded at nearby sites at higher (~1500 m. a.s.l.) or lower elevations (~200 m a.s.l.) during the same expedition (Richards 2011). As far as we are aware it has also not been recorded on other surveys elsewhere in New Britain, suggesting it may be endemic to moderate elevations in the Nakanai mountains.

The type series was collected in relatively undisturbed Hill Forest (Fig. 6A, B) at around 890 m a.s.l. in an area of complex and heavily dissected karst. When collected the holotype was calling sporadically from an elevated position on vegetation approximately 1 metre above the ground along a small slowly flowing stream (Fig 6C). The paratype was collected from low vegetation along the same stream. *Litoria insularis* occurs in sympatry with *L. thesaurensis* and *L. lododesma*, both of which were much more abundant at the type locality. Other species encountered at the type locality were the microhylid *Oreophryne brachypus* (Werner, 1898), the ranid *Papurana novaebritanniae* (Loveridge, 1948) and a diverse community of at least nine species of Ceratobatrachidae (Richards 2011).

Suggested IUCN Conservation Status. *Litoria insularis* is known only from a single locality despite moderately intense survey effort elsewhere in New Britain, suggesting that it may have a localised distribution. The type locality is immediately adjacent to a road that has been constructed into the interior of the island from Pomio on the coast and this will undoubtedly improve access to, and increase pressure on, the surrounding forest. Rainforests across New Britain are also under threat from rapid

expansion of Oil Palm plantations so, given the combination of very limited knowledge about the new species' distribution, ecology and habitat requirements, and potential threats, we recommend that it be listed as Data Deficient under the IUCN Redlist Criteria.

Etymology. The name insularis alludes to both the new species' likely endemic status on the island of New Britain, and the potential that it is further restricted to the Nakanai Mountains, which are themselves a 'sky island'.

Discussion

Litoria insularis **sp. nov.** is currently known only from a single site in upper Hill Forest, and we consider that it is probably endemic to New Britain, and potentially to the Nakanai Mountains. Although numerous endemic ceratobatrachid frogs have been described from New Britain, *Litoria insularis* **sp. nov.** provides the first evidence of a pelodryadid treefrog endemic to this island. This new species brings the number of endemic frogs on New Britain to 16 species, the highest number of any island in East Melanesia (Bougainville [including adjacent Buka]) is closest with seven endemic species) (Menzies 2006; Richards 2020). Remarkably, eight of the New Britain endemics are known only from the Nakanai Mountains, and most have been described only recently (Kraus and Allison 2007; Brown and Richards 2008; Brown et al. 2013; Travers et al. 2018). These data emphasise that the rugged and moderately high Nakanai Mountains are a notable centre for insular frog diversity, and likely also for other taxa such as mammals (Aplin and Opiang 2011). Further surveys are needed to better understand the distribution and conservation needs of the endemic fauna of the region, and in particular to understand the extent to which endemic species may be limited by substrate (karst) and/or elevation.

The new species also serves to emphasise the important role that island colonisation and diversification has played in the evolution of the *Litoria thesaurensis* species group. While not species rich, this radiation now includes two species that are only known from islands that have never had connections with the much more species-rich frog fauna of nearby New Guinea (the other being *L. lutea* from Bougainville and the Solomon Islands). Acoustic evidence further suggests that the diversity of insular endemic taxa in this clade remains underestimated (Kraus and Allison 2004). This species group also show evidence of ecological diversification along a number of interesting axes – *L. insularis* is potentially restricted to moderately high-elevation karst habitats (this paper), *Litoria lutea* is a specialist tree-hole breeder (Zug and Fisher 2018), and many populations of *Litoria thesaurensis* show marked ontogenetic colour shifts (Pikacha et al. 2008). Thorough molecular and morphological analyses of the whole *Litoria thesaurensis* species group are now needed to better understand the diversity, evolution and biogeographic history of this small but interesting radiation of treefrogs.

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References

Aplin K, Opiang M (2011) The mammal fauna of the Nakanai Mountains, East New Britain Province, Papua New Guinea. In: Richards S J, Gamui BG (Eds), Rapid Biological Assessments of the Nakanai Mountains and upper Strickland Basin: surveying the biodiversity of Papua New Guinea's submime karst environments. Conservation International, Arlington, pp. 85–103.

Brennan IG, Lemmon, AR, Lemmon, EM, Portik DM, Weijola V, Welton L, Donnellan SC, Keogh JS (2020) Phylogenomics of monitor lizards and the role of competition in dictating body size disparity. Systematic Biology 70: 120–132. https://doi.org/10.1093/sysbio/syaa046

Brown RM, Richards SJ (2008) Two new frogs of the genus *Platymantis* (Anura: Ceratobatrachidae) from the Isabel Island group, Solomon Islands. Zootaxa 68: 47–68. https://doi.org/10.11646/zootaxa.1888.1.3

Brown RM, Richards SJ, Broadhead TS (2013) A new shrub frog in the genus *Platymantis* (Ceratobatrachidae) from the Nakanai Mountains of eastern New Britain Island, Bismarck Archipelago. Zootaxa 3710: 31–45. https://doi.org/10.11646/zootaxa.3710.1.2

Brown RM, Siler CD, Richards SJ, Diesmos AC, Cannatella, DC (2015) Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae). Zoological Journal of the Linnean Society 173: 130–168. https://doi.org/10.1111/zoj.12232

Bryan JE, Shearman PL (Eds) (2015) The state of the forests of Papua New Guinea 2014: Measuring change over the period 2002–2014. University of Papua New Guinea, Port Moresby.

Cibois A, Thibault JC, Bonillo C, Filardi CE, Watling D, Pasquet E (2014) Phylogeny and biogeography of the fruit doves (Aves: Columbidae). Molecular Phylogenetics and Evolution 70: 442–453. https://doi.org/10.1016/j.ympev.2013.08.019

Klein ER, Harris RB, Fisher RN, Reeder TW (2016) Biogeographical history and coalescent species delimitation of Pacific island skinks

(Squamata: Scincidae: *Emoia cyanura* species group). Journal of Biogeography 43: 1917–1929. https://doi.org/10.1111/jbi.12772

Köhler J, Jansen M, Rodríguez A, Kok PJR, Toledo LF, Emmrich M, Glaw F, Haddad CFB, Rödel M-O, Vences M (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods and recommendations for best practice. Zootaxa 4251: 1–124. https://doi.org/10.11646/zootaxa.4251.1.1

Kraus F (2018) Taxonomy of *Litoria graminea* (Anura: Hylidae), with descriptions of two closely related new species. Zootaxa 4457: 264–284. https://doi.org/10.11646/zootaxa.4457.2.3

Kraus F, Allison A (2004) Two New Treefrogs from Normanby Island, Papua New Guinea. Journal of Herpetology 38: 197–207. https://doi.org/10.1670/100-03A

Kraus F, Allison A (2007) Two new species of *Platymantis* (Anura: Ranidae) from New Britain. Zootaxa 32: 13–32. https://doi.org/10.11646/zootaxa.1485.1.2

Lavery TH, Olds AD, Seddon JM, Leung LKP (2016) The mammals of northern Melanesia: Speciation, ecology, and biogeography. Mammal Review 46: 60–76. https://doi.org/10.1111/mam.12057

Lucky A, Sarnat EM (2010) Biogeography and diversification of the Pacific ant genus *Lordomyrma* Emery. Journal of Biogeography 37: 624–634. https://doi.org/10.1111/j.1365-2699.2009.02242.x

Mayr E, Diamond JM (2002) The Birds of Northern Melanesia: Speciation, Dispersal, Biogeography. Oxford University Press, Oxford.

Menzies J (2006) The frogs of New Guinea and the Solomon Islands. Pensoft Publishers, Sofia.

Moyle RG, Filardi CE, Smith CE, Diamond J (2009) Explosive Pleistocene diversification and hemispheric expansion of a "great speciator." Proceedings of the National Academy of Sciences of the United States of America 106: 1863–1868. https://doi.org/10.1073/pnas.0809861105

Oliver PM, Clegg JR, Fisher RN, Richards SJ, Taylor PN, Jocque MMT (2016) A new biogeographically disjunct giant gecko (*Gehyra*: Gekkonidae: Reptilia) from the East Melanesian Islands. Zootaxa 4208: 61–76. https://doi.org/10.11646/zootaxa.4208.1.3

Oliver PM, Heiniger H, Hugall AF, Jospeh L, Mitchell KJ (2020) Oligocene divergence of frogmouth birds (Podargidae) across Wallace's line. Biology Letters 16: 20200040. https://doi.org/10.1098/rsbl.2020.0040

Oliver PM, Travers SL, Richmond JQ, Pikacha P, Fisher RN (2018) At the end of the line: Independent overwater colonizations of the Solomon Islands by a hyperdiverse trans-Wallacean lizard lineage (*Cyrtodactylus*: Gekkota: Squamata). Zoological Journal of the Linnean Society 182: 681–694. https://doi.org/10.1093/zoolinnean/zlx047

Oliver PM, Bower D, Mcdonald PJ, Kraus F, Luedtke J, Neam K, Hobin K, Chauvenet ALM, Allison A, Arida E, Clulow S, Günther R, Nagombi E, Tjaturadi B, Travers SL, Richards SJ (2022) Melanesia holds the world's most diverse and intact insular amphibian fauna. Communications Biology 5: 1182. https://doi.org/10.1038/s42003-022-04105-1

Pikacha P, Morrison C, Richards SJ (2008) Frogs of the Solomon Islands. Quality Print Limited, Fiji.

Richards SJ (2020) Herpetofauna of the Aiope River Basin, Kunua District, Bougainville Island. Pp 1–34. Unpublished report to the Critical Ecosystems Partnership Fund and the University of Queensland.

Richards SJ (2011) The Herpetofauna of the Nakanai Mountains, East New Britain Province, Papua New Guinea. In: Richards SJ, Gamui BG (Eds), Rapid Biological Assessments of the Nakanai Mountains and upper Strickland Basin: surveying the biodiversity of Papua New Guinea's sublime karst environments. Conservation International, Arlington, pp. 75–80.

Richards SJ, Oliver P, Dahl C, Tjaturadi B (2006) A new species of large green treefrog (Anura: Hylidae: *Litoria*) from northern New Guinea. Zootaxa 1208: 57–68. https://doi.org/10.11646/zootaxa.4903.1.7

Travers SL, Richards SJ, Broadhead TS, Brown RM (2018) A new miniature Melanesian Forest Frog (Ceratobatrachidae: *Cornufer*) from New Britain Island, constituting the first record of the subgenus *Batrachylodes* from outside of the Solomon Archipelago. Zootaxa 4370: 23–44. https://doi.org/10.11646/zootaxa.4370.1.2

Tyler M, Davies M (1978) Species-groups within the Australopapuan hylid frog *Litoria* Tschudi. Australian Journal of Zoology, Supplementary Series 26: 1–47.

Tyler MJ (1968) Papuan hylid frogs of the genus *Hyla*. Zoologische Verhandelingen 96: 1–203.

Zug GR, Fisher RN (2018) Amphibians of the Pacific: natural history and conservation. In: Heatwole H, Rowley J (Eds), Status of conservation and decline of amphibians. CSIRO Publishing, Clayton South, pp. 201–212.

Appendix 1

Material examined

Litoria lutea (n = 11): BMNH 1947.2.23.50–52, Faro Island, Solomon Islands, syntypes; SAMA R04269D — Bougainville, Papua New Guinea; SAMA R05155A–D,F — Kunua, Bougainville, Papua New Guinea; SAMA R08777 — Matsiogu, Papua New Guinea; SAMAR56929, Posarae, Solomon Islands.

Litoria thesaurensis (n = 40): BMNH 1947.2.23,47, Treasury Islands, Solomon Islands, holotype of *Hyla macrops*; SAMA R56893 — Kolopakisa, Isabel, Solomon Islands; MCZ 11652, 'Milne Bay, Papua New Guinea, holotype of *Nyctimystes milneana*; SAMA R56959–60 — Rob Roy, Solomon Islands; SAMA R04222 — Kunua, Bougainville, Papua New Guinea; SAMA R04226–9 — Buin, Bougainville, Papua New Guinea; SAMA R04230–5, SAMA R04923A–B, D, SAMA R05156 — Kunua, Bougainville Island, Papua New Guinea; SAMA R08059 — Turiboiru, Papua New Guinea; SAMA R08258 — Ramagon River, Papua New Guinea; SAMA R08779_B; SAMA R08780 — Matsiogu, Papua New Guinea; SAMAR60628 - Yapsiei Village, Papua New Guinea; SAMA R60635 — Mainbu-ef stream, Yapsiei Village, Papua New Guinea; SAMA R60642 — Tongar River, Wamangu, Papua New Guinea; SAMA R64668–70 — Lamas Camp, Papua New Guinea; SAMA R64780, SAMA R64782–6, SAMA R64786–8, SAMA R64790, SAMA R64792 — Vouvou Camp, Papua New Guinea.