RAFFLES BULLETIN OF ZOOLOGY **72**: 268–279
Date of publication: 19 August 2024
DOI: 10.26107/RBZ-2024-0022
http://zoobank.org/urn:lsid:zoobank.org:pub:6DA644DF-04B1-4697-BBD8-ACB51B9CCE92

A new species of torrent-breeding treefrog (Pelodryadidae, *Nyctimystes* Stejneger) from the mountains of New Guinea with comments on the distribution of the genus

Stephen J. **Richards**

Abstract. The mountains of New Guinea support a diverse assemblage of torrent-breeding pelodryadid frogs in the genera *Litoria* Tschudi, 1838 and *Nyctimystes* Stejneger, 1916. *Nyctimystes* occurs between the Arfak Mountains of Indonesian New Guinea in the west and the Milne Bay Islands off southeastern Papua New Guinea in the east. The genus reaches its greatest diversity in southeastern Papua New Guinea, and only six of 33 currently recognised species occur in Indonesia. Here I describe a new species of *Nyctimystes* from lower-montane forest in central Papua New Guinea. In its moderate body size, predominantly brown colouration, and advertisement call comprising a long series of harsh notes, *Nyctimystes hanwara*, new species, shows similarities to members of the *N. cheesmani* Tyler, 1964 species group. However, it can be distinguished from all of them by the form of the palpebral venation and by lacking irregular barring on the thighs. Males produce a biphasic call reminiscent of *N. bivocalis* Kraus, 2012 but calls of the two species differ in several features. The new species is known from a single location at an altitude of 1,390 m a.s.l on the southern slope of the Karius Range in Hela Province. Its discovery highlights the importance of Papua New Guinea's mountainous interior as the centre of diversity for this speciose clade of pelodryadid frogs. The paucity of *Nyctimystes* records from eastern Indonesia appears to reflect a genuine pattern of lower diversity on the western half of the island than in Papua New Guinea rather than a disparity in collection effort, although this discrepancy is undoubtedly compounded by the comparably lower survey effort on the Indonesian side of the border.

Keywords. central cordillera, Indonesia, Melanesia, montane forest, torrential streams, taxonomy

INTRODUCTION

The complex orogeny of New Guinea's mainland has promoted diversification in a wide range of animal taxa (Toussaint et al., 2014, 2021; Oliver et al., 2017; Tallowin et al., 2018; Kennedy et al., 2022). Significant among these geological processes is the uplift of the island's central cordillera between 12–3 MYA (Quarles van Ufford & Cloos 2005) that produced the steep mountainous terrain of the island's interior. This steep terrain presents challenges for species breeding in lotic environments because streams are typically fast flowing and subject to rapid increases in velocity following heavy rain. Two groups of pelodryadid treefrogs (*Nyctimystes* and a monophyletic clade of torrent-breeding *Litoria*), are known or presumed to all have aquatic larvae with a suite of morphological features that allow them to persist in fast-flowing mountain streams (with one exception: *L. amnicola* Richards, Krey, Tjaturadi & Donnellan, 2021 (Richards et al., 2021)). These features include large, pale eggs, and tadpoles with reduced tail fins and large, ventrally oriented suctorial mouths (Menzies, 2006). *Nyctimystes* is a moderately diverse, monophyletic lineage containing 33 recognised species (Oliver et al., 2022; IUCN, 2023) that are endemic to New Guinea and a few offshore islands previously connected to New Guinea. While torrent-breeding *Litoria* are broadly distributed across New Guinea and occur on islands to the east and west of the mainland (Kraus & Allison, 2004; Menzies, 2006; Richards et al., 2021), *Nyctimystes* does not occur on the Indonesian islands to the west of New Guinea, and the genus is also poorly represented on the western (Indonesian) half of the main island (Menzies, 2006). *Nyctimystes* diversity is particularly high on the Papuan Peninsula in eastern Papua New Guinea (Kraus, 2012a) and, although additional species may be detected in the less intensively sampled mountains of western New Guinea, it is likely that the genus is a predominantly eastern lineage.

Here I describe a new species of *Nyctimystes* from the Karius Range in central Papua New Guinea that is most similar to *N. bivocalis* Kraus, 2012, from which it differs in aspects of colour, form of the palpebral venation, extent of finger webbing, and in its unique advertisement call. I also comment on the striking disparity in species richness reported for the genus in western (Indonesia) and eastern (Papua New Guinea) New Guinea.

Accepted by: Chan Kin Onn

Herpetology Department, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia: Email: steve.richards@samuseum.sa.gov.au

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

MATERIAL AND METHODS

The new species described herein is assigned to the genus *Nyctimystes* as traditionally recognised (Zweifel, 1958; Kraus, 2012a, b; Menzies, 2014 a–c) based on having a vertical pupil, unpigmented ova, and a well-developed palpebral reticulum on the nictitating membrane (Richards, 2007; Kraus, 2012a). As noted by Kraus (2013), the test of *Nyctimystes* monophyly by Frost et al. (2006) that resulted in synonymisation of *Nyctimystes* into *Litoria* was invalid due to problematic taxonomic sampling and those conclusions are not accepted here.

Type material of the new species was fixed in 10% formalin and subsequently stored in 70% ethanol and lodged at the South Australian Museum, Adelaide (SAMA) and the Papua New Guinea National Museum (PNGNM). Comparative material was examined in the collections of the American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Hawaii (BPBM); Museum of Comparative Zoology, Harvard (MCZ); Museo Civico di Storia Naturale, Genoa (MSNG); South Australian Museum, Adelaide (SAMA); Queensland Museum, Brisbane (QM); and the Natural Sciences Resource Collection, University of Papua New Guinea, Port Moresby (UPNG). A full list of material examined is presented in Appendix 1. Additional comparative data were taken from published literature (Kraus, 2012a, b; Menzies 2014a–c).

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) from heel to outer surface of flexed knee, 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, between proximal edges of nares), EN (distance between anterior edge of eye and posterior edge of naris), 3FD (horizontal diameter of 3rd finger disc), 3FP (narrowest horizontal width of penultimate phalanx), 4TD (horizontal diameter of 4th toe disc) and 4TP (narrowest horizontal width of penultimate phalanx). Terminology for description and comparisons of eyelid venation follow Kraus (2012a, b) and Menzies (2014a–c).

Advertisement calls were recorded with a Marantz PMD-661 Solid-state Recorder and Sennheiser ME66 microphone at distances of 0.5–>2 m. Ambient temperature, taken with a Pocket Temp Digital Probe thermometer, was 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 Köhler et al. (2017). The audiospectrogram was calculated with fast-Fourier transform (FFT) of 256 points, 50% overlap, using Hamming windows. Sex was determined by presence of nuptial pads and vocal slits in males, and of eggs in a female.

SYSTEMATICS

Nyctimystes hanwara, new species

(Figs 1–2, 4, 6)

Holotype. SAMA R72452 (FN SJR10255). Adult male with nuptial pads, Baia River headwaters, Karius Range, Hela Province, Papua New Guinea (5.9910°S, 142.6767°E, 1,390 m a.s.l.), collected by S. Richards on 7 February 2008.

Paratypes (n=6). PNGNM (FN SJR10258), SAMA R72453–72454 (FN SJR10256–10257), R72456 (FN SJR10285), and SAMA R72451 (FN SJR10231), males with vocal slits, all with same collection details as holotype but R72451 collected on 6 February 2008 and R72456 collected on 9 February 2009; SAMA R72455 (FN SJR10259), adult female, same collection details as holotype.

Diagnosis. Assigned to *Nyctimystes* on the basis of having a vertical pupil, prominent palpebral reticulum, and large unpigmented eggs (Kraus, 2013). The new species can be distinguished from all congeners by the following unique combination of characters: size moderate (male SVL 38.5–43.5 mm, sole female 52.9 mm); finger webbing reduced, not extending beyond distal subarticular tubercle on Fingers 3 and 4; toe webbing extensive, extending beyond distal subarticular tubercle on both sides of Toe 4; finger and toe discs prominently expanded (3FD/SVL 0.055–0.064; 4TD/SVL 0.052–0.061), those on Finger 3 same size or slightly larger than those on Toe 4 (3FD/4TD 1.00-1.15); palpebral venation forming thick gold (in life) reticulate pattern without obvious vertical or horizontal orientation; lateral edges of forearm and hindlimb with row of low but distinct tubercles, 1–4 small tubercles on each heel; dorsal colouration in life mottled pale russet and dark brown, or brown with yellow and darker-brown to black spots; and call comprising 1–3, but most commonly two, rapidly repeated notes produced at intervals of approximately 1–10 seconds for long periods.

Description of holotype. An adult male with vocal slits and nuptial pads. Measurements are presented in Table 1. Habitus slender (Fig. 1A), head moderately wide (HW/SVL 0.32), slightly narrower than long (HL/SVL 0.34; HW/HL 0.93). Snout broadly rounded in dorsal view, except at tip where distinct swelling forms short protuberance in dorsal view (Fig 2A), narrowly rounded and distinctly protruding in lateral view (Fig. 1A); canthus rostralis sharp, nearly straight, loreal region sloping, distinctly concave, nostrils closer to tip of snout than to eyes, oriented laterally; internarial distance greater than distance from external naris to eye (EN/IN 0.94). Eyes moderately large (EYE/SVL 0.12), barely protruding in dorsal view (Fig. 2A). Tongue broadly oval, nearly round, with shallow posterior notch. Paired vocal slits laterally in floor of mouth extend anteriorly from point approximately level with angle of jaw to half-way to tip of snout. Vomeropalatines with two patches of 4–5 low, poorly defined teeth, each elevation approximately 1.5 mm across the longest axis, angled posteromedially from about midway between choanae where they are separated by 2.0 mm, to about 0.8 mm behind posterior edge of choanae where

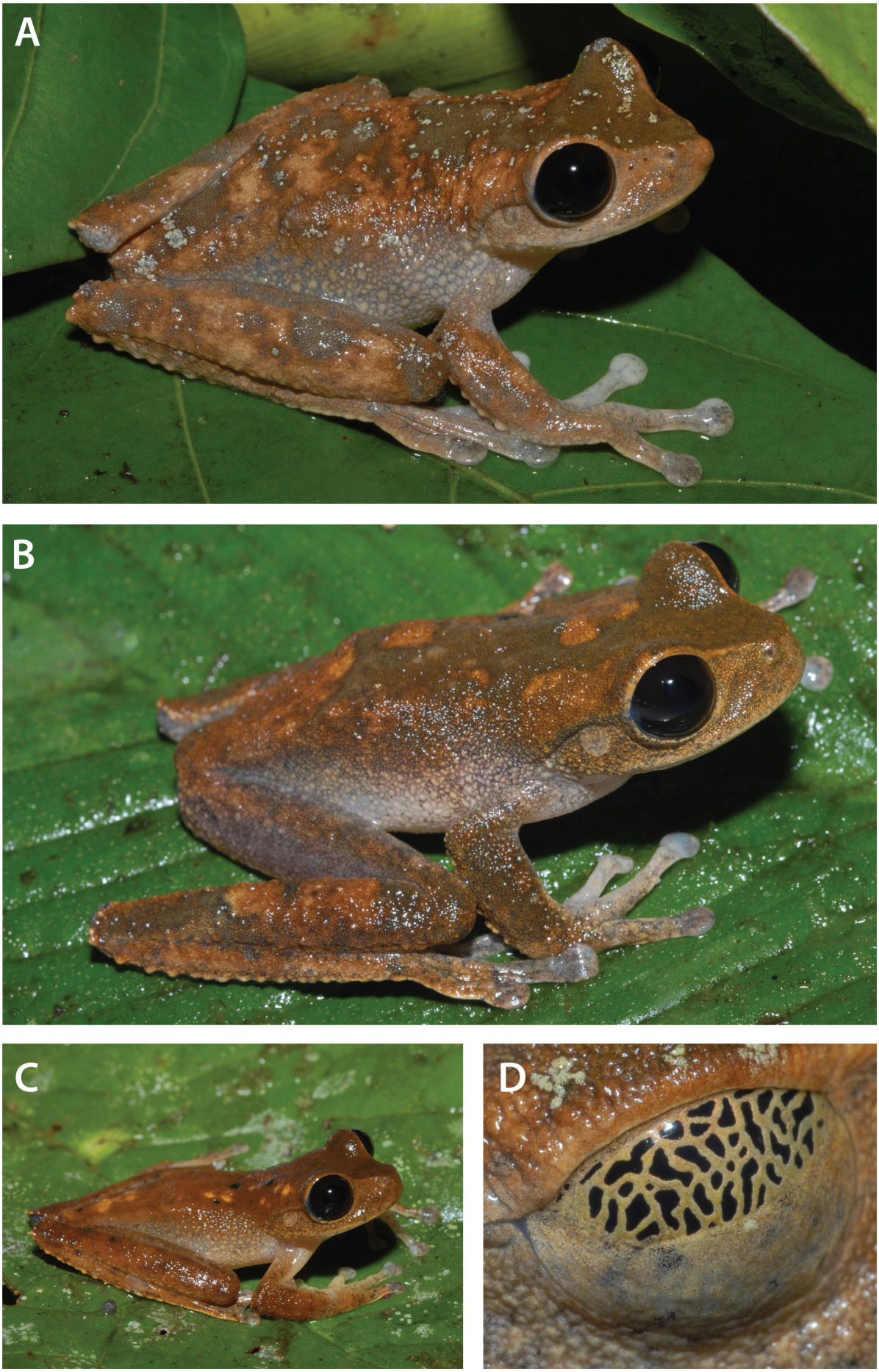

Fig. 1. *Nyctimystes hanwara*, new species, in life. A, holotype SAMA R72452, B, paratype SAMA R72453, C, paratype SAMA R72451, D, palpebral reticulum of holotype. Photographs: Stephen Richards.

Table 1. Measurements and ratios of the type series of *Nyctimystes hanwara*, new species.

Reg. No.	**R72452**	**R72451**	**R72456**	**PNGNM**	**R72453**	**R72454**	**R72455**			
	Holotype	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Males only**		
Sex	male	male	male	male	male	male	female	Mean	SD	Range
SVL	43.4	36.4	38.5	43.5	41.5	41.3	52.9	40.7	2.815	36.4–43.5
TL	24.8	21.9	20.3	24.7	24.1	24.4	29.0	23.4	1.835	20.3–24.8
HW	13.9	12.3	13.9	14.9	14.4	14.1	18.3	13.9	0.882	12.2–14.9
HL	14.9	12.9	13.7	15.2	14.9	14.5	17.9	14.3	0.888	12.9–15.2
EYE	5.1	4.8	5.0	5.8	5.5	5.2	6.0	5.2	0.361	4.8–5.8
EAR	2.0	2.0	1.9	2.0	2.0	2.0	2.2	2.0	0.040	1.9–2.0
EN	3.1	2.9	2.9	3.5	3.2	3.5	4.2	3.2	0.271	2.9–3.5
IN	3.3	2.8	3.1	3.6	3.4	3.1	4.5	3.2	0.279	2.8–3.6
FD1	1.7	1.4	1.2	1.5	1.5	1.5	2.2	1.5	0.163	1.2–1.7
FP1	1.1	0.9	0.8	1.0	1.1	1.1	1.6	1.0	0.126	0.8–1.1
FD3	2.7	2.3	2.2	2.8	2.3	2.6	3.8	2.5	0.248	2.2–2.8
FP3	1.5	1.1	1.1	1.5	1.3	1.3	1.7	1.3	0.179	1.1–1.5
TD1	1.5	1.4	1.4	1.7	1.5	1.7	2.4	1.5	0.137	1.4–1.7
TP1	1.0	0.9	1.0	1.2	1.1	1.2	1.7	1.1	0.121	0.9–1.2
TD4	2.5	2.0	2.0	2.6	2.3	2.5	3.5	2.3	0.264	2.0–2.6
TP4	1.6	1.3	1.4	1.7	1.5	1.9	2.4	1.6	0.216	1.3–1.9
TL/SVL	0.57	0.60	0.53	0.57	0.58	0.59	0.55	0.57	0.025	0.52–0.60
EN/IN	0.94	1.04	0.94	0.97	0.94	1.13	0.93	0.99	0.077	0.94–1.13
HW/SVL	0.32	0.34	0.36	0.34	0.35	0.34	0.35	0.34	0.014	0.32–0.36
HW/HL	0.93	0.95	1.02	0.98	0.97	0.98	1.02	0.97	0.029	0.93–1.02
HL/SVL	0.34	0.35	0.35	0.35	0.36	0.35	0.34	0.35	0.006	0.34–0.36
EYE/SVL	0.12	0.13	0.13	0.13	0.13	0.13	0.11	0.13	0.006	0.12–0.13
EAR/SVL	0.046	0.055	0.049	0.046	0.048	0.048	0.042	0.048	0.003	0.046–0.055
4TD/SVL	0.058	0.055	0.052	0.060	0.055	0.061	0.066	0.057	0.003	0.052–0.061
4TD/4TP	1.56	1.54	1.43	1.53	1.53	1.32	1.46	1.48	0.095	1.32–1.56
3FD/SVL	0.062	0.063	0.057	0.064	0.055	0.063	0.072	0.061	0.004	0.055–0.064
3FD/3FP	1.80	2.09	2.00	1.87	1.77	2.00	2.24	1.92	0.128	1.77–2.09
3FD/4TD	1.08	1.15	1.10	1.08	1.00	1.04	1.09	1.07	0.051	1.00–1.15

Fig. 2. Details of holotype of *Nyctimystes hanwara*, new species. SAMA R72452. A, dorsal view of head, B, ventral view of fingers and webbing, C, ventral view of toes and webbing. Scale bars: A = 5 mm, B–C = 2.5 mm.

they are just 0.3 mm apart. Tympanum small (EAR/SVL 0.046), less than half width of eye (EAR/EYE 0.39), annulus narrow but clearly defined, except dorsal edge obscured by strong, nearly straight supratympanic fold extending from posterior edge of eye to above arm insertion; posterior edge of annulus of right tympanum less clearly defined than that of left tympanum.

Skin finely shagreened dorsally without prominent tubercles, finely but more distinctly granular around tympana; skin above arm insertion and posterior to supratympanic fold strongly tuberculate; ventral surfaces, including of thighs, coarsely granular except throat striated; ventral surfaces of tibiae and feet smooth; tubercles below vent prominent; posteroventral edge of forearm with single row of small but distinct tubercles transitioning to low, slightly serrated dermal ridge along outer edge of fourth finger; posteroventral edge of tarsus with low, serrated dermal ridge, transitioning to straight-edged ridge along outer edge of fifth toe; each heel with 2–4 small tubercles.

Fingers moderately long, relative lengths 3>4>2>1, terminal discs prominently expanded (3FD/SVL 0.062; 3FD/3FP 1.80), with circum-marginal grooves (Fig. 2B). Fingers slightly more than one-quarter webbed, web reaching to base of distal subarticular tubercle on inner side of Finger 4 and just short of base of distal subarticular tubercle on outside of Finger 3, to base of proximal subarticular tubercle on inside of Finger 3 and outside of Finger 2, restricted to basal fringe between Fingers 1 and 2 (Fig. 2B). Subarticular tubercles prominent, distal tubercles on Fingers 1, 3 and 4 partially lobed, remainder unilobed, circular. Inner plantar tubercle prominent, ovoid; outer plantar tubercle low but distinct, nearly circular (Fig. 2B). Nuptial pads low, brown, finely granular, extending 3.0 mm distally from base of Finger 1.

Hind limbs long (TL/SVL 0.57), toes moderately short, relative lengths 4>5>3>2>1 on left foot, Toes 3 and 5 subequal on right foot, terminal discs prominently expanded (4TD/SVL 0.058; 4TD/4TP 1.56) with circum-marginal grooves (Fig. 2C); toes extensively webbed, web reaching to base of disc on Toes 1–3 and inside of Toe 5, and to midway between distal subarticular tubercle and disc on both sides of Toe 4 (Fig. 2C). Subarticular tubercles prominent, not divided or at most with shallow indentation in midline; inner metatarsal tubercle small, narrow; outer metatarsal tubercle poorly defined, barely detectable.

In life, dorsal surfaces mottled pale russet and darker brown, dark-brown areas concentrated on top of head and in scapular region, these overlain by fine grey stippling; some patches on mid dorsum orange brown, those on dorsal surfaces of limbs grey brown (Fig. 1A); mottled dorsal surfaces overlain with scattered fine, grey, lichenose pigment patterns; lateral surfaces of head orange grey, paler than adjacent dorsum, these paler areas of head sharply delineated from darker dorsal surfaces along canthus rostralis (Fig. 1A); remaining lateral surfaces grey, overlain with small creamy blotches; tubercles along outer edges of forearms and tarsi, large tubercles below vent, and dermal folds along edges of hands and feet all cream. Ventral surfaces white, hidden surfaces of thighs grey. Palpebral venation gold (Fig. 1D).

In preservative, ground colour of dorsum pale ivory brown with grey and dark-brown patches (Fig. 2A), grey elements within dark brown patches more prominent than in life; lichenose spots grey; dorsal surfaces of fingers and toes ivory with grey patches; ventral surfaces white.

Variation. Snout-vent length of adult males with well-developed nuptial pads and vocal slits ranges from 38.5–43.5 mm (Table 1). The smallest specimen (SAMA R72451; 36.4 mm SVL) is a male with short vocal slits but without nuptial pads and is possibly just maturing; the largest specimen (SAMA R72455; 52.9 mm SVL) is the only adult female in the series. None of the paratypes has the short protuberance at the tip of the snout exhibited by the holotype (Fig 1A vs. 1B–C). Leg length is rather variable, with TL/SVL ranging from 0.53–0.60, but otherwise morphometric variation among the type series is limited (Table 1). Palpebral venation of all specimens was gold in life and formed a thick reticulum without obvious vertical or horizontal orientation. All specimens have at least one, and as many as four, small but distinct tubercles on each heel. All specimens were predominantly brown dorsally in life but the extent of darker and lighter mottling, and presence of grey lichenose pigment patches and yellow or dark-brown to black spots was highly variable (Fig. 1A–C). SAMA R72453 was more

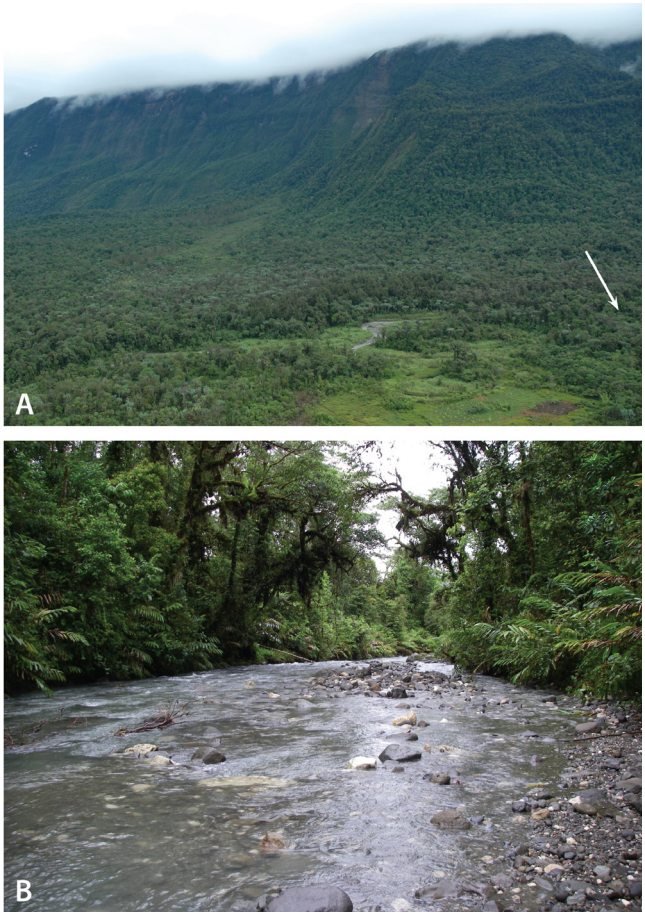

Fig. 3. Habitat of *Nyctimystes hanwara*, new species. A, Aerial view of the type locality showing upper Baia River in middle foreground and main spine of Karius Range in background. The type series was collected near the point of the arrow; B, stream habitat at the type locality. Males were calling from low riparian vegetation, and from high in trees, along this section of the stream. Photographs: Stephen Richards.

uniformly brown dorsally than the holotype, with scattered large, discrete orange-brown patches, lateral surfaces more white than grey, and side of face grey rather than orange grey (Fig. 1B). SAMA R72451 was uniform pale brown with yellow and dark-brown to black spots dorsally, the latter also extending onto dorsal surfaces of limbs (Fig. 1C). Very dark-brown to black spotting on the dorsum is most conspicuous on SAMA R72452 and is also present, to a lesser extent, on the female SAMA R72455. The pale, lichenose pigment patches are most conspicuous on the holotype and on PNGNM (SJR 10285); they are absent or barely detectable on the remaining specimens. Distinct barring is absent from hidden surfaces of the thighs of all specimens. All of these colour-pattern differences remain visible in preservative.

Advertisement call. I recorded calls produced by several males along a turbulent, fast-flowing stretch of the upper Baia River (Fig. 3A–B) in heavy rain at an air temperature of 19°C. Three consecutive calls produced by the holotype (R72452) are described below; it was not possible to confidently associate calls from more distant individuals with voucher specimens, and they are of insufficient quality for detailed analysis due to the loud background noise of the flooding stream and heavy rainfall. However, I provide general comments on their structure to support the call description where relevant. The call of *Nyctimystes hanwara*, new species is a pair of rapidly repeated, distinctly pulsed notes (Fig. 4) produced in series lasting at least several minutes; recording conditions precluded more extended observations. The three consecutive calls produced by the holotype were 8.4 and 10.8 seconds apart but some unvouchered males were producing calls as frequently as every 1–2 seconds. Calls produced by the holotype are 0.36–0.40 s long, the first note is longer (0.17–0.23 vs. 0.08–0.10 s) and softer than the second note and notes within calls are separated by intervals of 0.07–0.08 s. All notes are distinctly pulsed, producing a rasping sound, but first notes are more finely pulsed than second notes in a couplet (Fig. 4). Furthermore, amplitude increases gradually before decreasing rapidly at the end of the first note, producing a 'buzz' sound, while amplitude increases and decreases rapidly at the start and end of second notes producing a more explosive 'chick' sound. It was not possible to count all pulses in any of the first notes due to their fine structure and background noise, but pulse rates calculated from the best 0.07 s segments extracted from two first notes were nearly three times as fast (357 and 385 vs. 112–128 pulses/s) as those from three second notes. Dominant frequency of the three calls is 2750–2850 Hz, and there is no consistent difference in dominant frequency between first and second notes.

Of 55 additional calls recorded from a distance of more than 5 m in heavy rain, 44 (80%) were produced in couplets like the holotype, nine (16%) appeared to comprise a single note, and two (4%) were triple notes. However, first notes were always softer than second notes and it is possible that some apparent single-note calls were couplets in which the first note was not detected. Additional variation in these calls involves the relative length and pulse structure of the first note, which in a small number of couplets appears to be of equivalent length (vs. longer) to the second note and to have a similar, more coarsely pulsed structure. Unfortunately, the quality of recordings precluded more detailed analysis of this variation.

Comparisons with other species. *Nyctimystes hanwara*, new species, differs from all congeners for which the call is known, except *N. bivocalis*, by having an advertisement call comprising two rapidly repeated notes (vs. calls not biphasic). It further differs from *N. avocalis* Zweifel, 1958, *N. disruptus* Tyler, 1963a, *N. oktediensis* Richards & Johnston, 1993, *N. papua* (Boulenger, 1897), *N. trachydermis* Zweifel, 1983, and *N. tyleri* Zweifel, 1983 in having (vs. lacking) vocal slits in males; from *N. cryptochrysos* Kraus, 2012, *N. foricula* Tyler, 1963a, *N. granti* (Boulenger, 1914), *N. gularis* Parker, 1936, *N. humeralis* (Boulenger, 1912), *N. kubori* Zweifel, 1958, *N. kuduki* Richards, 2007, *N. montanus* (Peters & Doria, 1878), *N. narinosus* Zweifel, 1958, *N. persimilis* Zweifel, 1958, and *N. zweifeli* Tyler, 1967 in having (vs. lacking) at least one distinct tubercle on the heel; from *N. calcaratus* Menzies, 2014 and *N. cheesmani* Tyler, 1964 in its smaller size (male SVL 38.5–43.5 vs. 43.0–52.0 mm in *calcaratus*

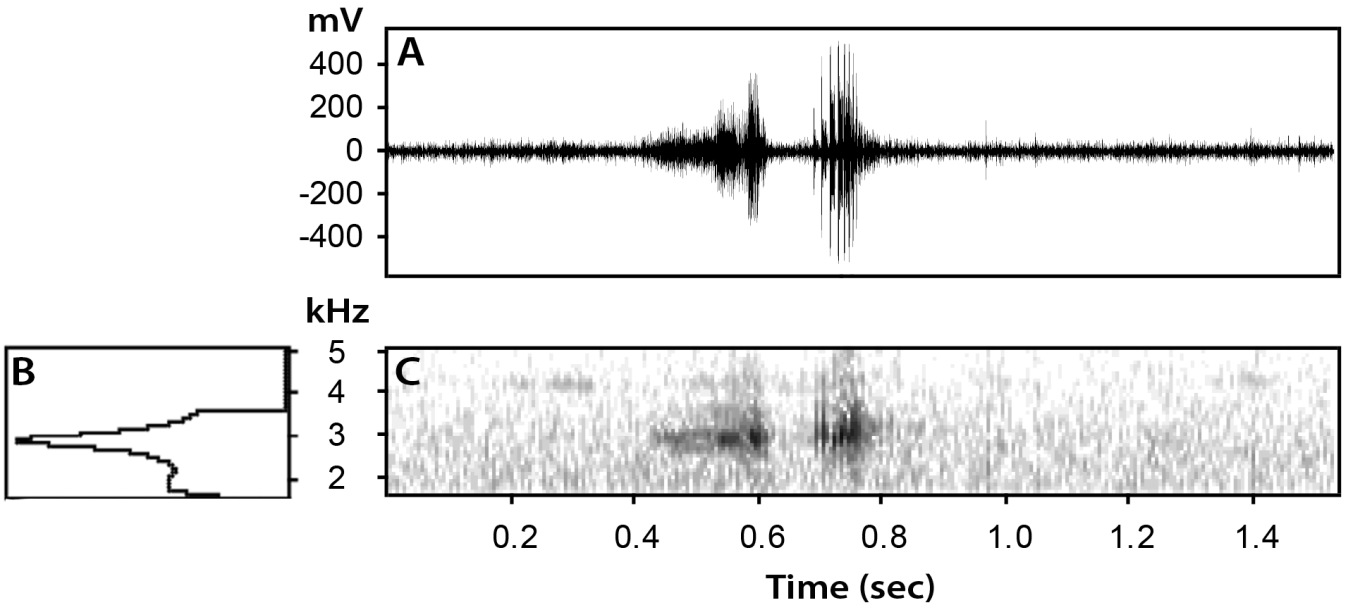

Fig. 4. A, waveform, B, amplitude spectrum, and C, spectrogram of a single biphasic call produced by the holotype of *Nyctimystes hanwara*, new species (SAMA R72452) at an air temperature of 19°C.

and 47.6–56.5 mm in *cheesmani*), palpebral venation of thick lines forming dense reticulum (vs. thinner, obliquely oriented lines with few cross connections); from *N. daymani* Zweifel, 1958 in its shorter snout (EN/IN *0.94–1.13 vs.* 1.17–1.39; Kraus, 2012a), and palpebral venation of thick lines forming dense reticulum (vs. thin, obliquely oriented lines with few cross connections; from *N. eucavatus* Menzies, 2014 in having palpebral venation of thick lines forming dense reticulum without obvious orientation (vs. thick gold palpebral venation oriented obliquely with few cross connections), and less extensively webbed fingers (webbing not extending beyond base of distal subarticular tubercle on Finger 4 (vs. webbing extending beyond distal subarticular tubercle); from *N. intercastellus* Kraus, 2012 in having palpebral venation of thick lines forming dense reticulum without obvious orientation (vs. venation predominantly vertical but with many horizontal cross connections; from *N. latratus* Menzies, 2014 and *N. traunae* Menzies, 2014 in having palpebral venation of thick lines forming dense reticulum (vs. thinner, obliquely oriented lines with few cross connections). It further differs from *N. latratus* in its smaller size (male SVL 38.5–43.5 vs. 42.0–51.0 mm); from *N. myolae* Menzies, 2014 in its smaller size (male SVL 38.5–43.5 vs. 46.0–51.0 mm) and white venter (vs. "pinkish-white, speckled grey all over"; Menzies, 2014); from *N. ocreptus* Menzies, 2014 by its higher EN/IN values (0.94–1.13 vs. 0.73–0.84), near-smooth (vs. warty) dorsum and uniformly grey (vs. with distinct yellow spots) hidden surfaces of thighs; from *N. obsoletus* Lönnberg, 2019, in having a distinct tympanum (vs. not visible); from *N. pulcher* Wandolleck, 1911 in its smaller size (male SVL 38.5–43.5 vs. males to 65 mm) and small tubercle (vs. large, triangular lappet) on heel; from *N. fluviatilis* Zweifel, 1958 in lacking bright orange on rear of thighs (vs. present); from *N. perimetri* Zweifel, 1958, in its smaller size (male SVL 38.5–43.5 vs. males to 61 mm), shorter snout (EN/IN 0.94–1.13 vs. 1.23–1.56; Kraus, 2012a) and lacking yellow on hidden surfaces of the thighs; from *N. semipalmatus* Parker, 1936 in having rear of thighs grey (vs. uniform bright orange), lacking tiny black spots across the dorsum (F. Kraus, pers. comm.), and less finger webbing (not extending beyond base of distal subarticular tubercle on Finger 4 vs. extending to or beyond distal subarticular tubercle; Kraus, 2012a).

The only other species of *Nyctimystes* known to have a biphasic advertisement call is *N. bivocalis*, and that species is also morphologically similar to *N. hanwara*, new species. However, the new species differs from *N. bivocalis*, a species restricted to the easternmost portion of Papua New Guinea's southeast peninsula (Fig. 5) in its less extensive hand webbing (web reaching no further than base of distal subarticular tubercle on fourth finger vs. extending to middle of or beyond distal subarticular tubercle), and in having palpebral venation of thick lines forming a dense reticulum without obvious orientation (vs. thinner lines with vertical to oblique orientation and few cross connections; Fig. 6).Furthermore, although both species produce biphasic calls in long series there are differences between their calls. Those of *N. hanwara*, new species are shorter (0.36–0.40 s vs. 0.44–0.52 s), pulsed (vs. unpulsed), have a higher dominant frequency (2750–2850 vs. 1560–1720 Hz) and appear to be produced at a much slower rate (~0.1–0.5 vs. 1.05-1.44 calls/s) than those of *N. bivocalis* (Kraus, 2012a).

Distribution and natural history. *Nyctimystes hanwara*, new species, is known only from the type locality at an altitude of 1,390 m a.s.l. at the base of the Karius Range in Hela Province, central mainland Papua New Guinea (Fig. 5). Adult males called from foliage 2–3 meters above the ground, or from high in trees, in lower montane forest along a narrow (~5 m wide; centre-background of Fig. 3B) section of a fast-flowing rocky stream that is part of a complex of streams and swamps forming the headwaters of the Baia River. The female contains large yellow eggs; five eggs

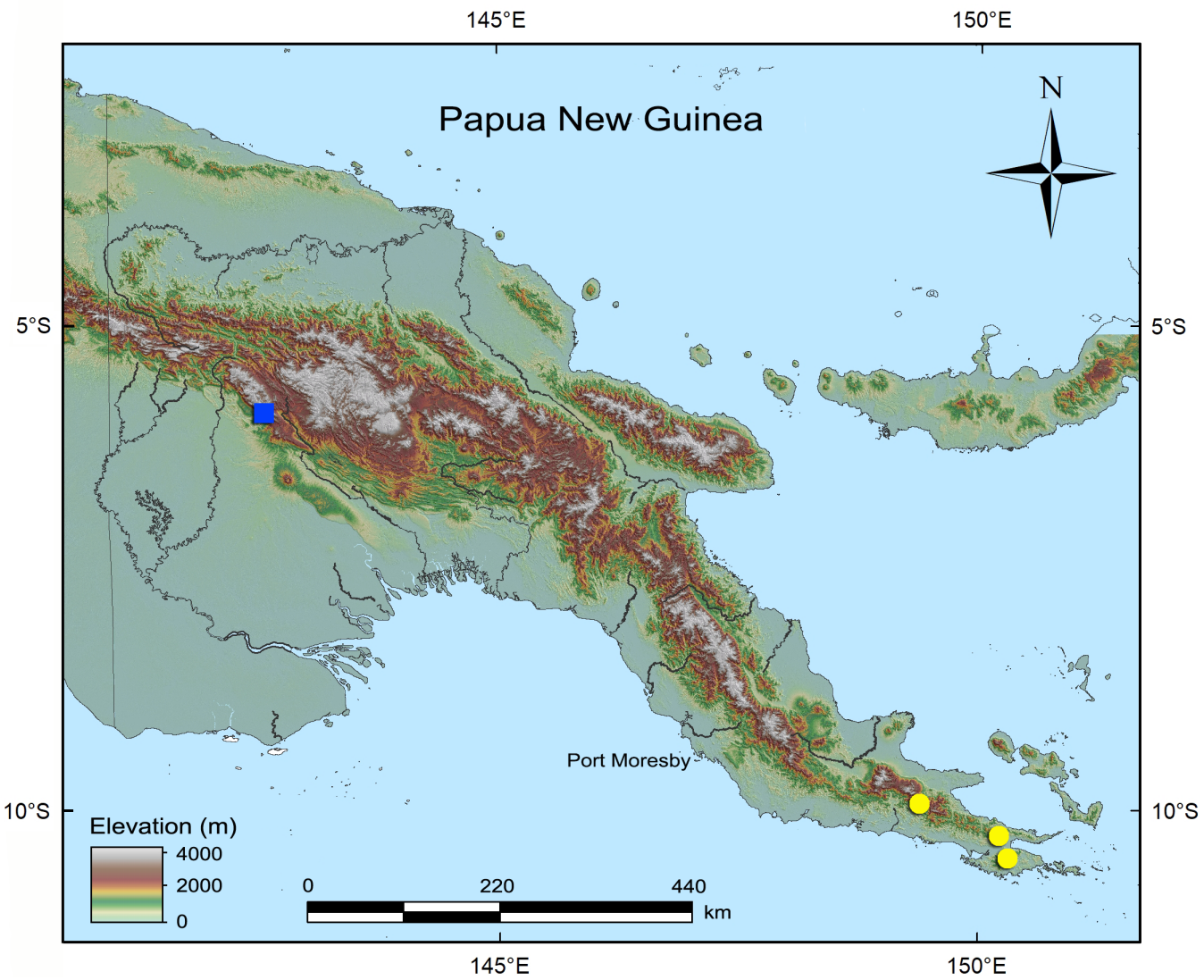

Fig. 5. Map of Papua New Guinea showing the type locality of *Nyctimystes hanwara*, new species (blue square) and the known distribution of the most similar species, *N. bivocalis* (yellow circles).

measured in situ were 1.9–2.2 mm in diameter (mean = 2.1, SD = 0.11). No animals were seen or heard where the stream broadened (to > 10 m wide) downstream.

Other torrent-breeding treefrogs found along the same stream were *Litoria angiana* (Boulenger, 1915), *L. arfakiana* (Peters & Doria, 1878), *L. micromembrana* (Tyler, 1963b), and *L. modica* (Tyler, 1968). A torrent-breeding *Papurana* Dubois, 1992 species was also encountered along streams at the type locality.

Suggested IUCN Conservation Status. *Nyctimystes hanwara,* new species, is known only from a single location and, although the region is topographically rugged (Fig. 3A) and human population density is low, potential threats to this species are unknown. Until data are available to better assess this species' distribution, habitat requirements and any threats, its conservation status should be considered Data Deficient.

Etymology. The name *hanwara* is Melanesian pidgin for stream and refers to this species' occurrence along forest streams.

DISCUSSION

The relationships of *N. hanwara*, new species, to other *Nyctimystes* are uncertain. Kraus (2012a) recognised an informal *Nyctimystes cheesmani* "complex" comprising four species of moderate-sized, predominantly brown *Nyctimystes*; *N. bivocalis*, *N. cheesmani*, *N. daymani*, and *N. intercastellus*, having in common a palpebral reticulum of predominantly oblique lines and usually with an irregular 'tiger-striped or blotched' pattern on the rear of the thighs. Menzies (2014) expanded the group to include a further 11 species: *Nyctimystes avocalis*, *N. calcaratus*, *N. latratus*, *N. traunae*, *N. eucavatus*, *N. fluviatilis*, *N. gularis*, *N. obsoletus*, *N. perimetri*, *N. persimilis*, and *N. semipalmatus* based on six morphological and acoustic criteria including three of those proposed by Kraus (2012a): small to medium size (adult males 36–52 mm SVL), predominantly brown colouration and palpebral reticulum of predominantly oblique lines. The other three criteria were pale, raised ridges on the forearm and tarsus, narrowly placed nostrils (EN/IN generally >1) and advertisement calls normally comprising long series of identical notes (Menzies, 2014). In its moderately small

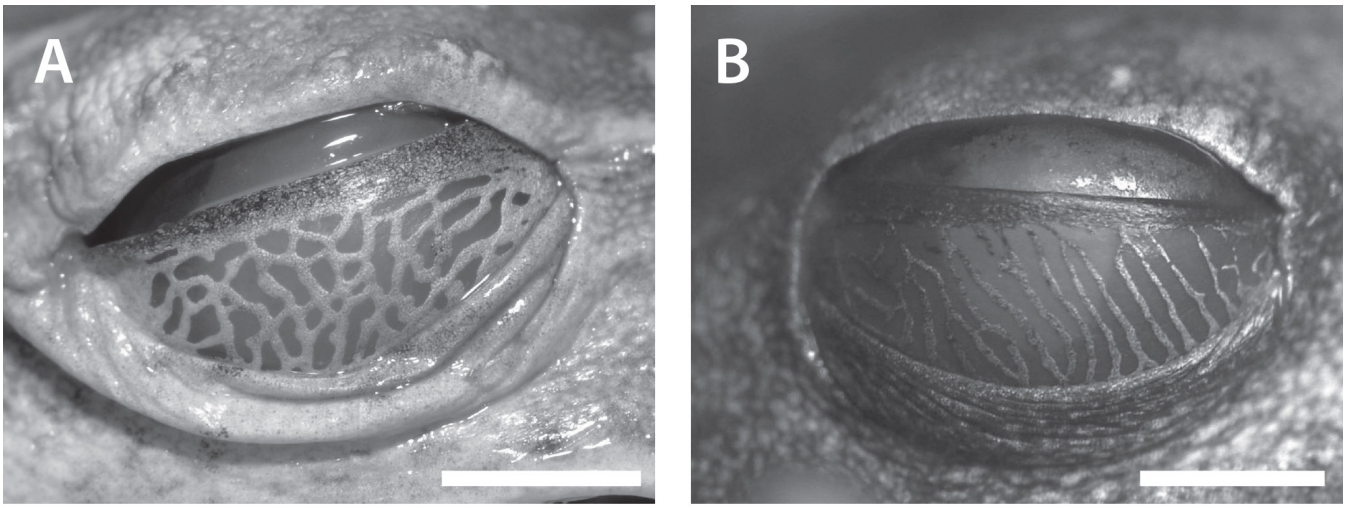

Fig. 6. Palpebral venation of A, *Nyctimystes hanwara*, new species (holotype, SAMA R72452) and B, *N. bivocalis* (BPBM 15201) illustrating thinner, more obliquely oriented reticulum in the latter species. Scale bars = 2 mm.

size and predominantly brown colouration, *N. hanwara*, new species resembles several members of the *N. cheesmani* group ("complex" of Kraus (2012a)). Furthermore, its advertisement call is biphasic, a character shared in the genus only with *N. bivocalis*, a species referred to the *N. cheesmani* group by both Kraus (2012a) and Menzies (2014a). However, the new species differs from *N. bivocalis* and all other members of the *N. cheesmani* group by having a dense palpebral reticulum of thick gold lines with numerous horizontal cross-connections and without an obviously oblique orientation. Unfortunately, molecular data for many *Nyctimystes* species are currently not available and I refrain from assigning the new species to the *N. cheesmani* group pending availability of genetic data to test relationships among members of that group and more broadly within *Nyctimystes*.

Recognition of this new species brings the number of described *Nyctimystes* to 34 and reinforces the importance of Papua New Guinea's central cordillera as a centre of diversity for this clade (Kraus, 2013) of torrent-breeding frogs. Nearly one third of this diversity has been described in the past 12 years (Kraus, 2012a, b; Menzies, 2014a–c) and at least 10 additional species await description (Oliver et al., 2022).

Until recently, *Nyctimystes* was considered to occur widely in the Australopapuan region between the Moluccan islands in the west and the Milne Bay islands and Australia in the east and southeast (Menzies, 2006). However, with recognition that both "*Nyctimystes rueppelli*" (Boettger, 1895) from Halmahera and "*N. dayi*" (Günther, 1897) from Australia belong in *Litoria* (Kraus, 2013; Menzies & Riyanto, 2015) the known distribution of the genus is now restricted to the New Guinea mainland and some high adjacent islands in Papua New Guinea's D'Entrecasteaux and Louisiade archipelagos that were formerly connected to the mainland. Diversity within the genus is not uniform across New Guinea, with species richness highest in the eastern mountains of Papua New Guinea's Papuan Peninsula (Kraus, 2012a) and lowest in western (Indonesian) New Guinea. For example, of the 34 species of *Nyctimystes* now recognised, 31 occur in Papua New Guinea (the eastern half of New Guinea) while only six are known from the western (Indonesian) half of the island (Menzies, 2014; IUCN, 2024; this study). Three species of *Nyctimystes* reported from Indonesia on AmphibiaWeb (2024): *N. foricula*, *N. kubori*, and *N. narinosus*, are unlikely to occur there (IUCN, 2024), and while the number of species known from the mountains of Papua New Guinea has increased steadily in recent decades (Richards, 2007; Kraus 2012a, b; Menzies, 2014a–c; this study) no members of the genus have been discovered and described from Indonesian New Guinea for more than 65 years (Zweifel, 1958) despite intensive surveys of several mountainous regions there (e.g., Wapoga River headwaters (Richards et al., 2000), Snow Mountains (Richards et al., 2015), and Foya Mountains (Richards & Tjaturadi, unpublished data)). Although it is possible that the lower documented diversity of the genus in eastern Indonesia simply reflects lower herpetofaunal sampling effort there, it is notable that no *Nyctimystes* species are represented among the 11 candidate species of Pelodryadidae known from Indonesian New Guinea in 2022, whereas the genus represented 21% (10 of 47) of candidate pelodryadid species reported from Papua New Guinea (Oliver et al., 2022). It is likely that improved survey effort will increase the known diversity of *Nyctimystes* in western New Guinea somewhat, but it is also clear that the genus is a predominantly eastern New Guinea lineage (Kraus, 2012a). This centre of diversity matches with a number of other faunal groups, including some microhylid frogs (Kraus, 2016), skinks (Slavenko et al., 2021) and geckos (Kraus, 2019) pointing to the potential origin of *Nyctimystes* in the formerly disjunct East Papuan Composite Terrane (currently the southeastern Peninsula) and/or nearby regions.

ACKNOWLEDGEMENTS

The late Jim Robins, and Georgia Kaipu, of the PNG National Research Institute approved the author's research visa and the late Barnabas Wilmott (PNG Department of Environment and Conservation, now Conservation and Environment

Protection Authority) approved the permit (number DEC 080220) under which the specimens were exported. Field work was supported by ExxonMobil PNG Ltd (EMPNG). Rose Singadan and Paulus Kei (University of PNG) provided support in Port Moresby and Mark Hutchinson, Ralph Foster, Carolyn Kovach and Domenic Capone provided support and access to material at the South Australian Museum. Other curators and collection managers who provided access to material in their care were Barry Clarke (BMNH); Molly Hagemann (BPBM); José Rosado (MCZ); Linda Ford and Darrel Frost (AMNH); Rose Singadan and Paulus Kei (UPNG); Giuliano Doria (MSNG) and Paul Oliver (QM). Fred Kraus and Paul Oliver provided extremely useful comments that greatly improved the manuscript and Fred Kraus generously provided information about *N. bivocalis* and permission to examine material that he had collected. I am particularly grateful to Molly Hagemann and Nicholas Walvoord from BPBM who provided images of *N. bivocalis* for comparison with the new species and to Lisa Capon who kindly produced the figures.

LITERATURE CITED

AmphibiaWeb (2024) https://amphibiaweb.org. University of California, Berkeley, USA. (Accessed 4 August 2024).

Boettger O (1895) Liste der Reptilien und Batrachier der Insel Halmaheira nach den Sammlungen Prof. Dr. W. Kükenthal's. Zoologischer Anzeiger, 18: 129–138.

Boulenger GA (1897) Descriptions of new lizards and frogs from Mount Victoria, Owen Stanley Range, New Guinea, collected by Mr. A. S. Anthony. Annals and Magazine of Natural History, Series 6, 19: 6–13.

Boulenger GA (1912) On some treefrogs allied to *Hyla caerulea*, with remarks on noteworthy secondary sexual characters in the family Hylidae. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere, 15: 211–218.

Boulenger GA (1914) An annotated list of the batrachians and reptiles collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. Transactions of the Zoological Society of London, 20: 247–275.

Boulenger GA (1915) Description of a new tree-frog of the genus *Hyla* discovered by Mr. A.E. Pratt in the Arfak Mountains, Dutch New Guinea. Annals and Magazine of Natural History, Series 8, 16: 402–404.

Dubois A (1992) Notes sur la classification des Ranidae (Amphibiens anoures). Bulletin Mensuel de la Société Linnéenne de Lyon, 61: 305–352.

Frost DR, Grant T, Faivovich J, Bain R, Haas A, Haddad CFB, de Sa RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy C, Campbell JA, Blotto BL, Moler P, Drewes R, Nussbaum RA, Lynch JD, Green D & Wheeler W (2006) The amphibian tree of life. Bulletin of the American Museum of Natural History, 297: 1–370.

Günther ACLG (1897) Descriptions of new species of lizards and of a tree-frog from north-eastern Queensland. Novitates Zoologicae, 4: 403–406.

IUCN (2024) The IUCN Red List of Threatened Species. Version 2024-1. https://www.iucnredlist.org. (Accessed 4 August, 2024).

Kennedy JD, Marki PZ, Reeve AH, Blom MPK, Prawiradilaga DM, Haryoko T, Koane B, Kamminga P, Irestedt M & Jønsson KA (2022) Diversification and community assembly of the world's largest tropical island. Global Ecology and Biogeography, 31: 1078–1089.

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.

Kraus F (2012a) Identity of *Nyctimystes cheesmani* (Anura: Hylidae), with description of two new related species. Zootaxa, 3493: 1–26.

Kraus F (2012b) A new species of *Nyctimystes* (Anura: Hylidae) from Papua New Guinea. Herpetologica, 68: 541–550.

Kraus F (2013) Morphological data show that *Hyla dayi* Gunther, 1897 (Amphibia: Anura: Hylidae) should never have been assigned to *Nyctimystes*. Memoirs of the Queensland Museum, 56: 581–587.

Kraus F (2016) Ten new species of *Oreophryne* (Anura, Microhylidae) from Papua New Guinea. Zootaxa, 4195: 1–68.

Kraus F (2019) New species of *Lepidodactylus* (Squamata: Gekkonidae) from New Guinea and adjacent islands. Zootaxa, 4651: 305–329.

Kraus F & Allison A (2004) New records for reptiles and amphibians from Milne Bay Province, Papua New Guinea. Herpetological Review, 35: 413–418.

Lönnberg E (1900) Reptiles and batrachians collected in German New Guinea by the late Dr. Erik Nyman. Annals and Magazine of Natural History, Series 7, 6: 574–582.

Menzies JI (2006) The frogs of New Guinea and the Solomon Islands. Pensoft Publishers, Sofia, 346 pp.

Menzies JI (2014a) Notes on *Nyctimystes* (Anura: Hylidae), tree frogs of New Guinea, with descriptions of four new species. Alytes, 30: 42–68.

Menzies JI (2014b) Notes on tree frogs, *Nyctimystes* species (Anura: Hylidae) of New Guinea; the *Nyctimystes papua* species group. Alytes, 31: 59–76.

Menzies JI (2014c) Notes on *Nyctimystes* (Anura: Hylidae), of New Guinea: the *Nyctimystes narinosus* species group with descriptions of two new species. Transactions of the Royal Society of South Australia, 138: 135–143.

Menzies JI & Riyanto A (2015) On the generic status of "*Nyctimystes rueppelli*" (Anura: Hylidae), a tree frog of Halmahera Island, Indonesia. Alytes, 32: 17–22.

Oliver PM, Bower DS, McDonald PJ, Kraus F, Luedtke J, Neam K, Hobin L, 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.

Oliver PM, Iannella A, Richards SJ & Lee MSY (2017) Mountain colonisation, miniaturisation and ecological evolution in a radiation of direct-developing New Guinea Frogs (*Choerophryne*, Microhylidae). PeerJ 5: e3077.

Parker HW (1936) A collection of reptiles and amphibians from the mountains of British New Guinea. Annals and Magazine of Natural History, Series 10, 17: 66–93.

Peters WCH & Doria G (1878) Catalogo dei rettili e dei batraci raccolti da O. Beccari, L.M. D'Albertis e A.A. Bruijn nella sotto-regione Austro-Malese. Annali del Museo Civico di Storia Naturale di Genova, 13: 323–450.

Quarles van Ufford AQ & Cloos M. (2005) Cenozoic tectonics of New Guinea. American Association of Petroleum Geologists, 89: 119–140.

Richards SJ (2007) A new species of *Nyctimystes* (Anura, Hylidae) from Papua New Guinea and comments on poorly-known members of the genus. Phyllomedusa – Journal of Herpetology, 6: 105–118.

Richards SJ, Iskandar DT & Allison A (2000) Amphibians and reptiles of the Wapoga River area, Irian Jaya, Indonesia. In: Mack A & Alonso L (eds.) A biological assessment of the Wapoga River area of northwestern Irian Jaya, Indonesia.

RAP Bulletin of Biological Assessment 14. Conservation International, Washington, DC, pp. 54–57, 113–120.

Richards SJ & Johnston GR (1993) A new species of *Nyctimystes* (Anura: Hylidae) from the Star Mountains, Papua New Guinea. Memoirs of the Queensland Museum, 33: 73–76.

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.

Richards SJ, Tjaturadi B, Krey K & Donnellan SC (2021) A new stream-dwelling frog of the genus *Litoria* Tschudi, 1838 (Anura: Pelodryadidae) from Salawati Island, Indonesia. In: Telnov D, Barclay MVL & Pauwels OSG (eds.) Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea. Vol. IV. The Entomological Society of Latvia, Riga, pp. 19–33.

Richards SJ, Tjaturadi B, Mumpuni & Puradyatmika P (2015) Field guide to frogs of the Mimika region – Papua, Indonesia. PT Freeport Indonesia, Jakarta, 66 pp.

Slavenko A, Tamar K, Tallowin OJS, Kraus F, Allison A, Carranza S, & Meiri S (2021) Revision of the montane New Guinean skink genus *Lobulia* (Squamata: Scincidae), with the description of four new genera and nine new species. Zoological Journal of the Linnean Society, 195(1): 220–278.

Stejneger L (1916) New generic name for a tree-toad from New Guinea. Proceedings of the Biological Society of Washington, 29: 86.

Tallowin OJS, Tamar K, Meiri S, Allison A, Kraus F, Richards SJ & Oliver PM (2018) Early insularity and subsequent mountain uplift were complementary drivers of diversification in a Melanesian lizard radiation (Gekkonidae: *Cyrtodactylus*). Molecular Phylogenetics and Evolution, 125: 29–39.

Toussaint EFA, Hall R, Monaghan MT, Sagata K, Ibalim S, Shaverdo HV, Vogler AP, Pons J & Balke M (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. Nature Communications, 5: 4001.

Toussaint EFA, White LT, Shaverdo H, Lam A, Surbakti S, Panjaitan R, Sumoked B, von Rintelen T, Sagata K & Balke M (2021) New Guinean orogenic dynamics and biota evolution revealed using a custom geospatial analysis pipeline. BMC Ecology and Evolution 21: 1–28.

Tschudi JJ von (1838) Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Neuchâtel: Petitpierre.

Tyler MJ (1963a) An account of collections of frogs from Central New Guinea. Records of the Australian Museum, 26: 113–130.

Tyler MJ (1963b) A taxonomic study of amphibians and reptiles of the Central Highlands of New Guinea, with notes on their ecology and biology. 2. Anura: Ranidae and Hylidae. Transactions of the Royal Society of South Australia, 86: 105–130.

Tyler MJ (1964) An investigation of the systematic position and synonymy of *Hyla montana* Peters and Doria (Anura, Hylidae). Zoologische Abhandlungen. Staatliches Museum für Tierkunde in Dresden, 27: 265–270.

Tyler MJ (1967) A new species of frog of the hylid genus *Nyctimystes* from the highlands of New Guinea. Transactions of the Royal Society of South Australia, 91: 191–195.

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

Wandolleck B (1911) Die Amphibien und Reptilien der papuanischen Ausbeute Dr. Schlaginhaufens. Abhandlungen und Berichte des Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden, 13: 1–15.

Zweifel RG (1958) Results of the Archbold Expeditions. No. 78. Frogs of the Papuan hylid genus *Nyctimystes*. American Museum Novitates, 1896: 1–51.

Zweifel RG (1983) Two new hylid frogs from Papua New Guinea and a discussion of the *Nyctimystes papua* species group. American Museum Novitates, 2759: 1–21.

Appendix I – Specimens Examined
Abbreviations: AMNH = American Museum of Natural History, New York; BM = Natural History Museum, London; MSNG = Museo Civico di Storia Naturale, Genoa; SAMA = South Australian Museum, Adelaide; QM = Queensland Museum, Brisbane. UPNG = Natural Sciences Resource Collection, University of Papua New Guinea, Port Moresby.

Litoria rueppelli – BM 1947.2.23.11–14; Halmahera Island, Indonesia, paratypes
Nyctimystes avocalis – AMNH 56486; East slope of Goodenough Island, Milne Bay Province, PNG, 900 m a.s.l, paratype.
Nyctimystes cheesmani – BM 1947.2.24.42–44; Kokoda, Central Province, PNG, ~ 370 m a.s.l., paratypes.
Nyctimystes disruptus – AMS R15923; Kaironk Valley, Schrader Mountains, PNG, ~2,000 m a.s.l., holotype. (digital images examined).
Nyctimystes daymani – AMNH 57081, 57229; North slope of Mt Dayman, Milne Bay Province, 700 m a.s.l., paratypes.
Nyctimystes eucavatus – SAMA R4525a–d, f–k; near Telefomin, Sandaun Province, PNG, 1310 m a.s.l.
Nyctimystes fluviatilis – AMNH 49567; Bernhard Camp, Idenburg River, Papua Province, Indonesia, ~ 50 m a.s.l., holotype; Uncatalogued series (SJR & B. Tjaturadi collectors), Kwerba, Mamberamo Basin, Papua Province, Indonesia, ~ 50–100 m a.s.l.
Nyctimystes granti – BMNH 1947.2.24.47; Oktakwa River, Mimika, Papua Province, Indonesia, ~ 915 m a.s.l., holotype.
Nyctimystes gularis – 1947.2.24.29; Mondo, Central Province, PNG, ~1500 m a.s.l., holotype; 1947.2.24.30 same data, paratype.
Nyctimystes humeralis – BM 1947.2.23.48; 'Madew', PNG, ~ 600–900 m a.s.l., holotype.
Nyctimystes kubori – SAMA R69654–57; Abalgamut, Huon Peninsula, PNG, 1850 m a.s.l.
Nyctimystes kuduki – SAMAR62753, holotype, UPNG10047–48, SAMA R62750–52, paratypes; Iagifu Ridge, Moro, Southern Highlands Province, Papua New Guinea.
Nyctimystes montanus – MSNG 29720; Hatam, Arfak Mtns, Papua Province, Indonesia, 1800 m a.s.l., holotype.
Nyctimystes narinosus – AMNH 56269, 65859 (plus 3 additional paratypes); Mt Hagen, Western Highlands Province, PNG, ~ 2500 m a.s.l., paratypes; SAMA R5579a–t, Schrader Mountains, Papua New Guinea.
Nyctimystes oktediensis – QM J56896; Mt Akrik, Star Mountains, Western Province, PNG, 1625 m a.s.l., holotype; QM J56897-8, SAMA R40771 paratypes, same data as holotype; UPNG 5137–9, Kamfon, Star Mountains, Western Province, PNG, 2200 m a.s.l., paratypes.
Nyctimystes papua – BM 96.10.31.50; Mt Victoria, PNG, lectotype; MCZ 12838; same data as lectotype, paralectotype.
Nyctimystes perimetri – AMNH 60080; West slope of Mt Riu, Sudest (= Tagula) Island, Milne Bay Province, PNG, 250–300 m a.s.l., paratype.
Nyctimystes persimilis – AMNH 56783, 89787, north slope of Mt Dayman, Milne Bay Province, PNG, 1370 m a.s.l.
Nyctimystes semipalmatus – BM. 1947.2.24.46; Mt Victoria, PNG, ~ 400 m a.s.l.
Nyctimystes trachydermis – AMNH 81038–42; Gapaia Creek, Morobe Province, PNG, 1280 m a.s.l., paratypes.
Nyctimystes traunae – SAMA R8630, 8634, 8636, 8654, 8661, 8663–64, Yaikoro, Madang Province, PNG.
Nyctimystes tyleri – AMNH 82878; Gapaia Creek, Morobe Province, PNG, 1280 m a.s.l., holotype.
Nyctimystes zweifeli – SAMA R5426; Telefomin, Sandaun Province, PNG, holotype; SAMA R8812-19, same data as holotype, 1400–1680 m a.s.l., paratypes.