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James I. Menzies

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Alytes, 2014; 30:42-68

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Gonçalo M. Rosa

Department of Biology, University of Nevada, Reno, USA
Institute of Zoology, Zoological Society of London, UK
Centre for Ecology, Evolution and Environmental Changes (CE3C), Faculdade de Ciências UL, PT

E-mail: goncalo.m.rosa@gmail.com; Skype: goncalo.m.rosa

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<http://hdl.handle.net/2440/97947>



Notes on *Nyctimystes* (Anura: Hylidae), tree frogs of New Guinea, with descriptions of four new species

James I. Menzies^{1*}

¹ University of Adelaide, North Terrace, Adelaide SA 5005, Australia

Based on six common characters, 15 species of *Nyctimystes* are segregated as the *Nyctimystes cheesmanae* group, but without implying monophyly. Four of them are herein described as new species. The diagnostic features of each new species are described and the male advertisement calls of six other species are compared. Other known populations are also described but are not allocated to any species, as the information about them is deficient. Some notes on previously described species are included.

INTRODUCTION

Two genera of hylid frogs occur in the Papuan region, *Litoria* and *Nyctimystes*. *Nyctimystes* differs from *Litoria* in possessing a vertical, as opposed to horizontal, pupil and a pattern of lines or dots on the transparent part of the lower eyelid, known as the palpebral venation. This is an important diagnostic feature as, within a species, the overall pattern of the venation does not vary. As far as known, all *Nyctimystes* species, except *N. rueppelli*, lay large, unpigmented ova from which torrent-adapted tadpoles emerge, though this character is shared by some *Litoria* species. The only comprehensive taxonomic review of *Nyctimystes* is that of Zweifel (1958) in which 14 species were described, half of them new. Zweifel did not attempt to divide the genus into natural groups but described the palpebral venation of all species, noting that it forms a network without obvious orientation (e.g. *N. kubori*), often incomplete (e.g. *N. papua*), a network with horizontal orientation (e.g. *N. narinusus*) or a series of oblique lines, sometimes forking but with few cross-connections (e.g. *N. daymani*). This last group was formalised as the “*Nyctimystes cheesmanae* group” by Menzies (1976).

In the course of a revision of the Papuan members of the hylid genus, *Hyla*, Tyler (1964a) discovered that *Hyla montana* Peters and Doria (1878) and *Hyla obsoleta* Lönnberg (1900) had vertical pupils and a palpebral venation and so transferred them to *Nyctimystes*¹ increasing the number of species to 16. This action created a senior homonym to *Nyctimystes montana* Parker (1936) for which Tyler created the new specific epithet *cheesmani*². By the time of the comprehensive account of Papuan frogs by Menzies (2006) the number of *Nyctimystes* species had increased to 21 with the description of *N. foricula* and *N. disrupta* Tyler (1963), *N. zweifeli* Tyler (1983), *N. trachydermis* and *N. tyleri* Zweifel (1983), and *N. oktediensis* Richards and Johnson (1993) but none of those newly-described species belong to the *N. cheesmanae* group and are not treated in this paper. Menzies (2006) did not use the term “*N. cheesmanae* group” but simply referred to all species with the oblique type of eyelid venation as “Group 2” adding snout shape, as expressed by a high EN/IN ratio, as a group character. In 2007, Richards described another species, *N. kuduku*, with Group 2 characteristics. Three of these “Group 2” species, *N. montanus*, *N. pulcher* and *N. kuduku*, share all but one of the characters (moderate

¹ *Nyctimystes* Stejneger (1916), derived from the Latin *mystes*, a priest, was formerly regarded as a feminine noun, but was determined by Duellman (1993) to be masculine, hence *montanus*, rather than *montana*. Why Stejneger chose this etymology is unclear.

² Tyler (1964a) chose the specific epithet in honour of the woman collector Evelyn Cheesman but, in error, made it *cheesmani* when it should have been *cheesmanae*. Menzies (1976) subsequently emended the name to the feminine form but other authors have disputed the correctness of doing this. An application to have *Nyctimystes cheesmanae* placed on the official list of names is before the International Commission on Zoological Nomenclature (Tyler & Menzies, 2013).

HB length) used to define the *N. cheesmanae* group and these three are not treated here.

However, a current problem in the description of new species has been the lack of an adequate diagnosis for *Nyctimystes cheesmanae* as several species are morphologically similar and can only be distinguished by the male advertisement calls. This problem has now been resolved with new material, including tape recordings, from a site close to the type locality and two more new species of the *N. cheesmanae* group have been described (Kraus, 2012).

The relationships of *Nyctimystes* to other hylid frogs, both in the Papuan region, and elsewhere, are contentious. Vertical pupils and a palpebral venation are to be seen in some South American hylids but neither character, individually, is to be seen in any Papuan or Australian *Litoria*. As far as is known, all *Nyctimystes* species, except *N. rueppelli*, lay comparatively large, unpigmented ova from which emerge tadpoles adapted to living in fast running water. The breeding habits of *Nyctimystes rueppelli* are currently undescribed except that the large ova are pigmented pale brown on the animal pole. The egg and tadpole characters of *Nyctimystes* suggest a close relationship to the torrent-breeding group of Papuan *Litoria* but in cranial structure Tyler and Davies (1979) found similarity to *Litoria infrafronata* and in muscular structure to *Litoria eucnemis*, neither of which have unpigmented eggs nor torrent-adapted tadpoles. Faivovich *et al.* (2005), with a sample of just three *Nyctimystes* species, confirmed a cladistic resemblance to *L. infrafronata*. More recently, Frost *et al.* (2006) have returned all *Nyctimystes* species to *Litoria* on the basis that the Australian species *N. dayi* appears to be more closely related to *Litoria nanotis* than to the New Guinean *N. pulcher*. Finally Rosauer *et al.* (2009) and Wiens *et al.* (2010) have demonstrated that nine New Guinean *Nyctimystes* species (*N. cheesmani*, *N. foricula*, *N. humeralis*, *N. kubori*, *N. narinusus*, *N. papua*, *N. pulcher*, *N. semipalmata*, *N. zweifeli*) form a sister group to *Litoria infrafronata*, together nested within *Litoria* and all *Nyctimystes* species remain in *Litoria* in the current “Amphibian species of the world” (Frost, 2013). This implies that the synapomorphies vertical pupil, palpebral venation and torrent-type tadpoles have evolved in the region at least two times. If vertical pupil and palpebral venation were independent characters, one would surely expect to see one *or* the other appearing in unrelated groups. As they do not, I, like Kraus (2012), continue to treat *Nyctimystes* as a valid genus. However, separation of the *Nyctimystes cheesmanae* group from other species does not imply monophyly of these groups as this would need to be confirmed, or refuted, by studies that have not yet been undertaken. It is merely a convenient ‘division’ in the treatment of a genus with a large number of undescribed species, and an aid to identification.

The present paper provides additional information on some species in the *Nyctimystes cheesmanae* group, describes several new species and comments on the likelihood of yet more undescribed species.

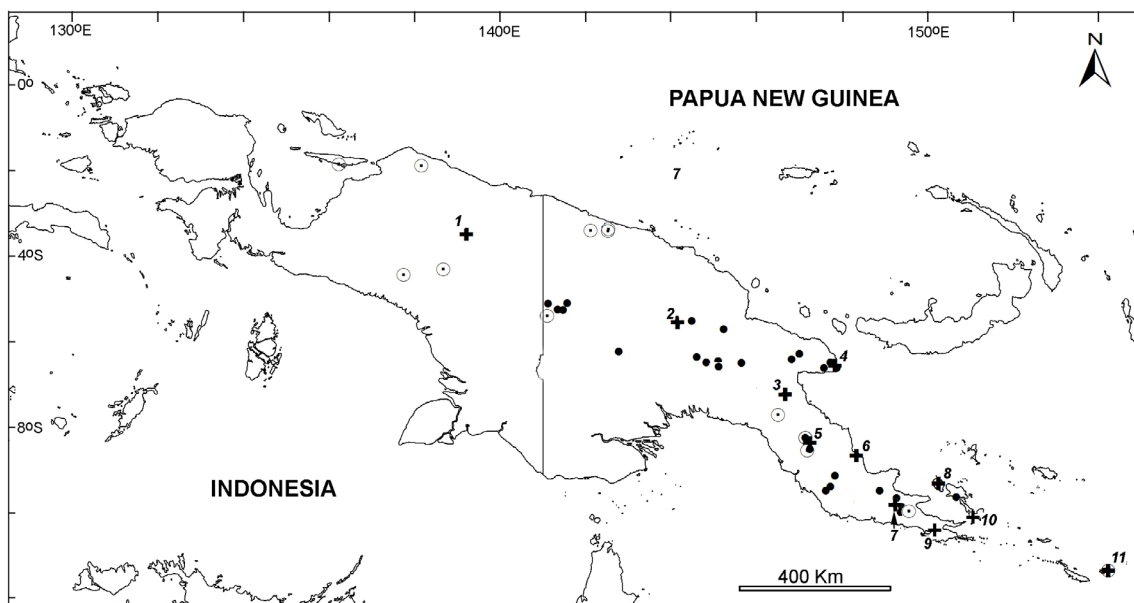


Figure 1. New Guinea showing location of members of the *Nyctimystes cheesmanae* species group. Spots refer to specimens examined, circles are museum and literature records, not examined, and crosses are type localities, west to east, as follows: 1. Idenburgh River (*N. fluviatilis*); 2. Baiyer River Sanctuary (*N. eucavatus*, *N. traunae*); 3. Bulolo (*N. calcaratus*); 4. Simbang (*N. obsoletus*); 5. Mondo (*N. cheesmanae*, *N. gularis*); 6. Kokoda (*N. semipalmatus*); 7. Mt. Dayman area (*N. daymani*, *N. latratus*, *N. persimilis*); 8. Goodenough Island (*N. avocalis*); 9. Cloudy Mts (*N. bivocalis*); 10. Normanby Island (*N. intercastellus*); 11. Sudest (Louisiade) Island (*N. perimetri*).

MATERIALS AND METHODS

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Definition

The *Nyctimystes cheesmanae* group is characterised by possession of the following characters, in addition to the generic characters of pupil shape and eyelid venation.

1. Small to moderate size, HB (adult male) 36-52 mm.
2. Palpebral venation of oblique lines with relatively few cross-connections, complete over the upper part of the lower eyelid. The lines may be thin or thick, sometimes as wide as the spaces between, and the angle of slant varies between 30° and 65° from horizontal but, within broad limits, the slope angle appears to be constant within a single population. There is some variation in pattern within a population and even between left and right eyes on the same individual and such variation may include amount of forking and cross connection and angle of slope. The angle of slope is measured against a horizontal line, as indicated by arrows in the figures.
3. Decoration on the forelimb and tarsus taking the form of pale, raised ridges, sometimes so low as to be distinguished more by colour than by elevation. The ridges may be simple or crenulated or form a row of separate, raised tubercles while, on the tarsus, they may commence at the heel with a prominent conical lappet or merely a slightly enlarged tubercle. The degree of development appears constant within a species.
4. Primarily brown dorsal colour, never wholly green. In life and after preservation often very variable with dorsum pale to dark brown with variable amounts of darker and lighter mottling; large pale ochre spots or irregular pale blotches are frequent; limbs are usually irregularly barred; ventrum immaculate white, occasionally mottled.
5. Narrowly placed nostrils, generally giving an EN/IN ratio of > 1.0, occasionally 0.9-1.0.
6. Male advertisement calls, uttered from vegetation alongside fast running streams, usually consist of long series of identical notes with the acoustic impression of a rough bark or a trill. Fundamental frequency bands lie around 2 kHz, while there may be higher prominent frequencies, above the frequency of water noise. None of the calls is well tuned, consequently they have no musical quality.

The *Nyctimystes cheesmanae* group includes the following species: *Nyctimystes avocalis* Zweifel 1958; *N. bivocalis* Kraus 2012, *N. cheesmanae* Tyler 1964a, *N. daymani* Zweifel 1958, *N. fluvialis* Zweifel 1958, *N. gularis* Parker 1936, *N. intercastellus* Kraus 2012, *N. obsoletus* Lönnberg 1900, *N. perimetri* Zweifel 1958, *N. persimilis* Zweifel 1958, *N. semipalmatus* Parker 1936 and four new species described herein. Some other *Nyctimystes* species may have a palpebral venation of oblique lines but do not display the combination of characters described above.

Material examined

These analyses are based on morphometric data from more than 400 specimens, listed in Appendix 1, derived from 20 different populations, together with acoustic information on ten of those populations. A population is here defined as a group of morphologically similar individuals from a single geographic location.

Morphological methods follow Menzies *et al.* (2009) and abbreviations used are: body length (HB) is measured from snout tip to the ‘bump’ caused by the distal end of the urostyle, which gives a slightly shorter dimension than the more common SVL, measured to the upper margin of the cloaca. However, if literature data are being cited, the original SVL measurement is quoted. TL is tibial length measured with the joints at right angles. Leg length is regarded as very long if the TL/HB ratio is > 0.62, long if between 0.59-0.62 and moderately long if 0.52-0.58. Head length (HL) is taken from the tip of the snout to the jaw articulation; head width (HW) is measured at mid-tympanic level; eye to naris distance (EN) is from the anterior margin of the eye to the mid-point of the nostril; internarial distance (IN) is between the mid-points of left and right nostrils; EY and TY are horizontal diameters of eye and tympanum; F3d and T4d are horizontal diameters of the disks on 3rd finger and 4th toe.

Statistical analyses were taken from the SPSS package, version 19 (SPSS Inc) and JMP statistics package

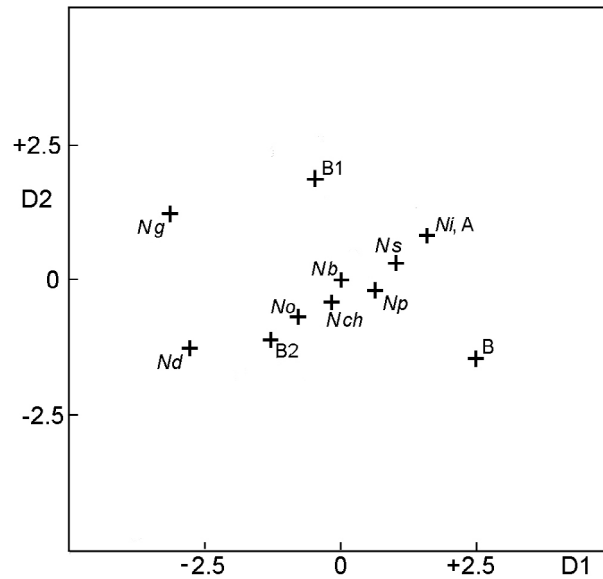


Figure 2. Multivariate analysis (discriminant analysis) of all described and undescribed species in the *Nyctimystes cheesmanae* group. Crosses are group centroids, D1, D2 are the first and second discriminant axes: Species annotated as follows: *Nd* - *N. daymani*, *Np* - *N. persimilis*, *Nch* - *N. cheesmanae*, *Ng* - *N. gularis*, *Nb* - *N. bivocalis*, *Ni* - *N. intercastellus*, *Ns* - *N. semipalmatus*; A, B, B1 and B2 are undescribed species from Agaun, Bulolo, and Baiyer River respectively. *Nyctimystes obsoletus*, *N. avocalis* and *N. fluviatilis* are excluded from this diagram due to lack of data.

(SAS Inc. Version 4.0.3). The use of “significant” in the results indicates a probability of 0.05 or better. Discriminant analyses were used to indicate morphological relationships between already-named species and populations whose identity was in doubt. Subsequently, Tukey-Kramer comparisons tests following analysis of variance looked for significant differences in the means of individual parameters. Adult male sizes (HBm) range from 36-52 mm, here 36-45 = small, 46-52 = moderate. Females were not included in the analyses as there were few, or none, in some collections.

Illustrations of the eyelid venation were drawn from excised and flattened lower eyelids, except in the case of some holotypes where the eyelids were photographed or drawn *in situ*. Arrows indicate the anterior direction.

The sex of all specimens that appeared to be adult was checked either by internal examination or by the presence of nuptial pads or vocal sac openings in the floor of the buccal cavity, if males. Few adult males displayed pigmented nuptial pads though unpigmented pads could be seen on many of them.

The extent of hand webbing in a species is somewhat variable as shown by Zweifel (1983; figure 8), and I have not used any of the numerical systems previously devised (e.g. Savage & Heyer, 1967; Myers & Duellman, 1982) in the species accounts here, rather illustrated the condition in the newly and previously described species.

Calls

Acoustic data were collected in the field, over a period of 40 years, with a variety of instruments, and analysed with the programmes winCECIL and SPEECH ANALYZER (SIL International). A call is defined as a discrete succession of sounds and calls may follow one another at irregular intervals but may not always be of the same length. Notes are the components of a call, are of similar length, and follow at regular intervals, measured in notes/s. Pulses are the separate bursts of sound within notes and cannot be subdivided. Frequency bands are the different components visible on a frequency spectrum. The lowest band is the ‘fundamental’ and the most emphasised band is the ‘dominant’. As *Nyctimystes* species invariably call from locations near fast-running mountain streams, recordings are often confused by the sound of running water.

Museum specimens

Museum specimens referred to are prefixed with AMNH for the American Museum of Natural History, New York, AMS for the Australian Museum in Sydney, BMNH for the Natural History Museum, London, BPBM for the Bernice P. Bishop Museum, Honolulu, MSNG for the Museo Civico di Storia Naturale, Genova, SAMA for the South Australian Museum, Adelaide and UPNG for the University of Papua New Guinea, Port Moresby.

Table 1. Morphometric data for the type series of four new *Nyctimystes* species. Data derived from the referred specimens are not included.

Species	Individuals	HB	TL/HB	HW/HB	EN/IN	EY/HB	TY/HB	F3/HB
<i>N. calcaratus</i>	holotype	49.3	0.57	0.35	1.15	0.121	0.050	0.048
	(males, <i>n</i> = 9)	47.4 (43-52)	0.58 (0.53-0.63)	0.36 (0.35-0.38)	1.16 (1.05-1.32)	0.121 (0.10-0.138)	0.047 (0.043-0.051)	0.053 (0.040-0.062)
	(females, <i>n</i> = 2)	58.2 (56.0-63.0)	0.58 (0.58)	0.35 (0.34-0.37)	1.18 (1.16-1.20)	0.11 (1.02-1.10)	0.051 (0.051)	0.060 (0.059-0.060)
<i>N. eucavatus</i>	holotype	38.74	0.59	0.38	1.08	0.145	0.050	0.054
	(males, <i>n</i> = 27)	39.7 (33.0-42.0)	0.59 (0.57-0.63)	0.39 (0.37-0.40)	1.15 (1.04-1.27)	0.122 (0.103-0.149)	0.051 (0.042-0.065)	0.057 (0.047-0.063)
<i>N. latratus</i>	holotype	46.66	0.53	0.34	1.00	0.12	0.051	0.058
	(males, <i>n</i> = 15)	45.5 (42.0-51.0)	0.59 (0.53-0.62)	0.36 (0.34-0.38)	1.08 (0.96-1.20)	0.115 (0.105-0.126)	0.052 (0.045-0.058)	0.060 (0.044-0.068)
	(females, <i>n</i> = 4)	59.4 (55.0-62.0)	0.58 (0.56-0.61)	0.33 (0.31-0.35)	1.04 (0.97-1.13)	0.112 (0.107-0.120)	0.051 (0.049-0.053)	0.061 (0.059-0.060)
<i>N. traunae</i>	holotype	39.8	0.62	0.37	1.00	0.129	0.060	0.052
	(males, <i>n</i> = 11)	40.4 (38.0-43.0)	0.59 (0.57-0.62)	0.37 (0.36-0.38)	1.03 (0.96-1.17)	0.126 (0.103-0.152)	0.057 (0.046-0.068)	0.054 (0.048-0.059)

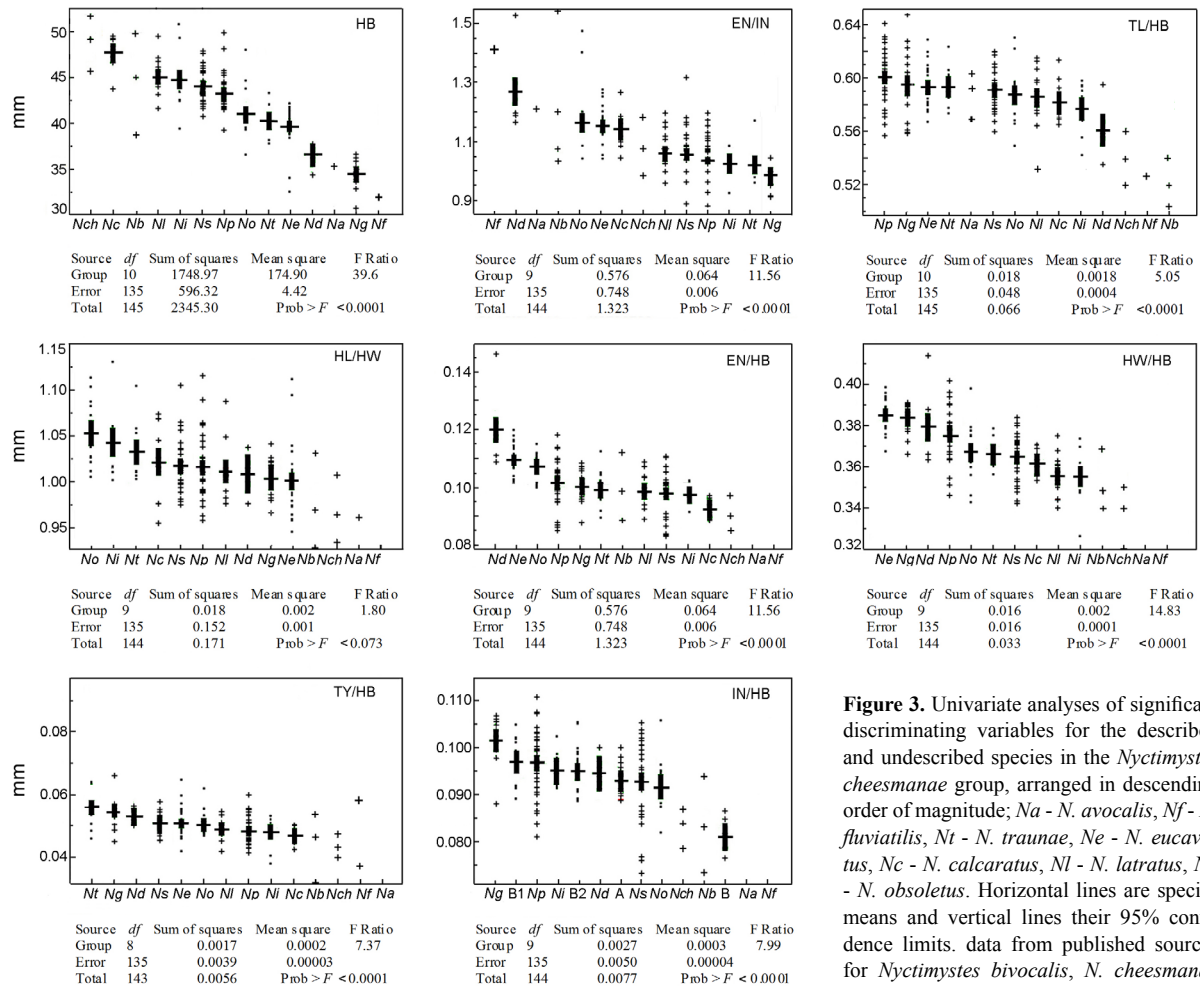


Figure 3. Univariate analyses of significant discriminating variables for the described and undescribed species in the *Nyctimystes cheesmanae* group, arranged in descending order of magnitude; *Na* - *N. avocalis*, *Nf* - *N. fluviatilis*, *Nt* - *N. traunae*, *Ne* - *N. eucavatus*, *Nc* - *N. calcaratus*, *Nl* - *N. latratus*, *No* - *N. obsoleteus*. Horizontal lines are species means and vertical lines their 95% confidence limits. data from published sources for *Nyctimystes bivocalis*, *N. cheesmanae* and *N. fluviatilis*.

All specimen localities are in Papua New Guinea unless otherwise noted and provincial abbreviations are CenP, Central Province; EHP, Eastern Highlands Province; GulP, Gulf Province.; MadP, Madang Province.; MBP, Milne Bay Province; MorP, Morobe Province; NorP, Northern Province.; SanP, Sandaun (West Sepik) Province; SimP, Simbu Province; WesP, Western (Fly River) Province; WHP, Western Highlands Province. Provincial boundaries have changed over the years and those given here are current, not always as in the original description. Fig. 1 indicates the origin of all places from where material originated and a list, with geographical coordinates, is included in Appendix 2.

RESULTS

New species

Four populations, from Baiyer River Sanctuary (type 1), Baiyer River Sanctuary (type 2), Bulolo and Agaun, for which male advertisement calls had been recorded, did not appear to match any previously described species and are herein described as new species. Fig. 2 (A, B, B1, B2) shows these four unknowns together with all previously described species. In this multivariate analysis the variables HB, HW, EN, IN and TY were used and 80% of the total variance was accounted for by functions 1 and 2. *Nyctimystes bivocalis* (*Nb*) and *N. cheesmanae* (*Nc*) and are represented only by published data and *N. avocalis* (*Na*) *N. fluviatilis* (*Nf*) are omitted from fig. 2 because insufficient data were available. All groups were deemed to be significantly different except groups A (Agaun, undescribed) and *Ni* (*N. intercastellus*) but it is clear that morphological characters alone have only limited discriminatory power between many species. Axis one is biased by body size with the smallest species, *N. daymani* (*Nd*) and *N. gularis* (*Ng*) to the left and the largest, Bulolo, undescribed, (B) to the right Axis two is strongly influenced by head width, separating *N. daymani* (*Nd*) from *N. gularis* (*Ng*) and isolating Baiyer type-1 (B1) and Bulolo (B) from the rest. Significantly discriminating characters are examined in more detail in fig. 3 and in the species accounts that follow.

No voice recordings were available for populations from Bundi, Okapa, Telefomin, Ganz River, Moro, and these were not included in the analyses but were separately compared with individual species.

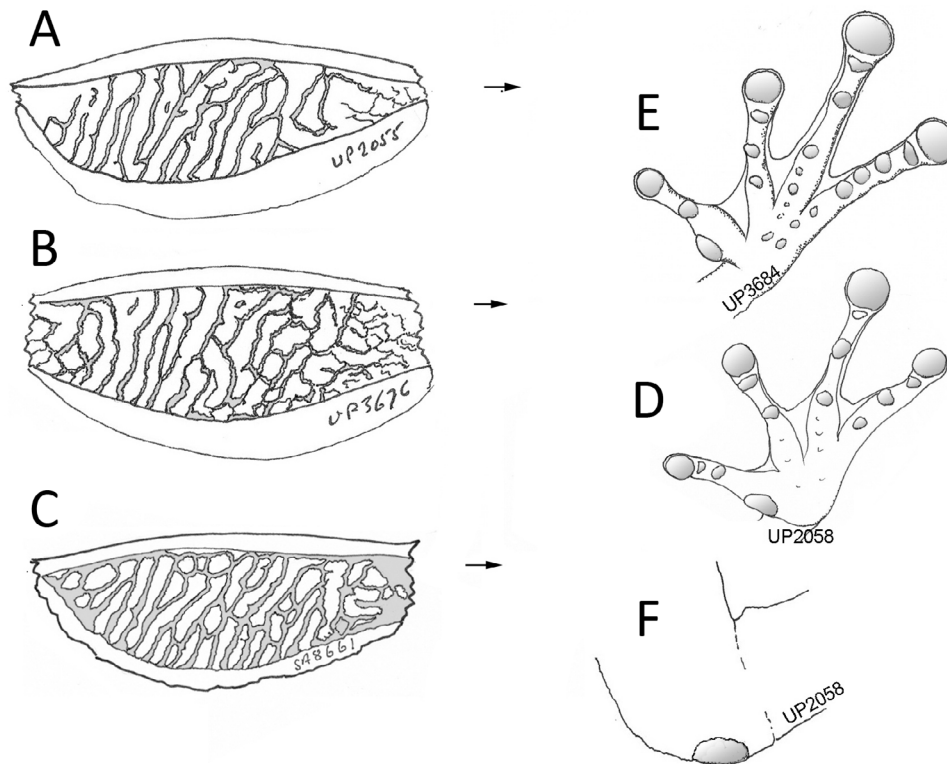


Figure 4. *Nyctimystes traunae*, new species: A-B. eyelid venation of two paratype examples; C. one referred specimen from Bundi; D-E. hands (palmar views) of a paratype and holotype; F. heel of holotype.

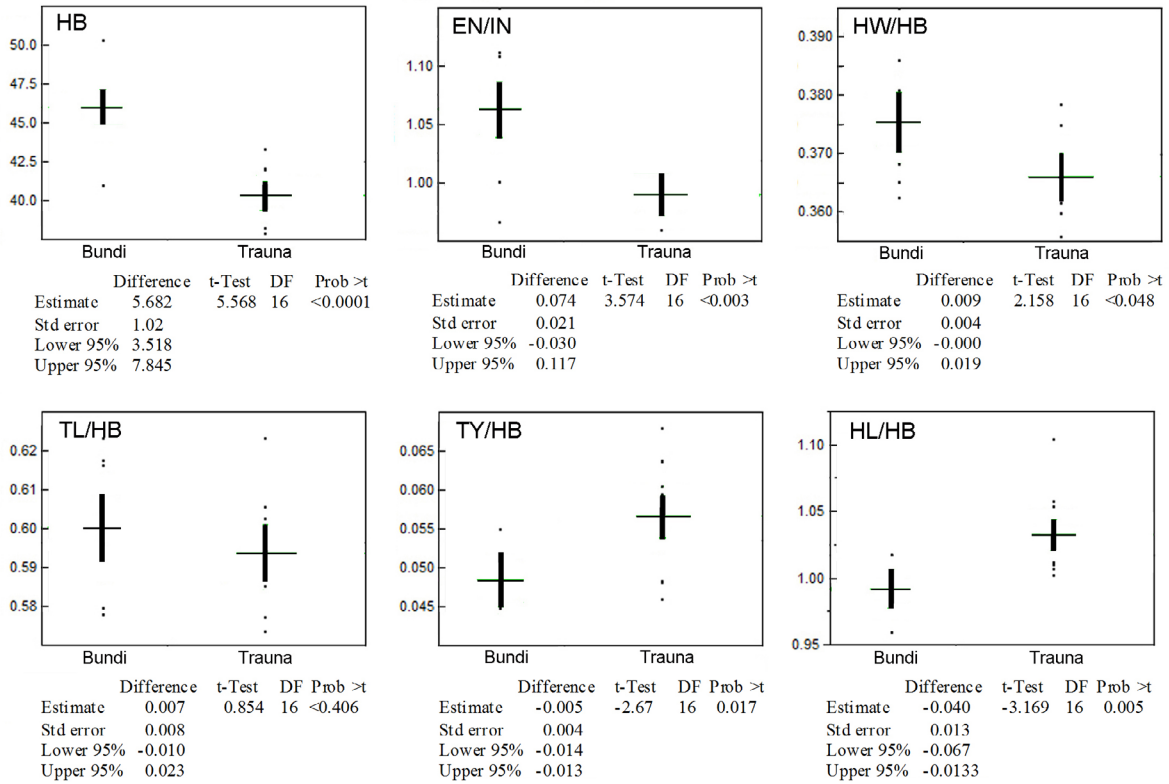


Figure 5. *Nyctimystes traunae*, new species. Comparison of material from the type locality and referred specimens from Bundi. Horizontal lines are group means, vertical lines their 95% confidence limits. All differences between means (t-Test) are significant except TL/HB.

***Nyctimystes traunae* sp. nov.**

Holotype. UPNG2058, adult male, collected by J. Menzies in reed beds on the bank of the Trauna River, Baiyer River Sanctuary, 800 m asl, WHP, between 10-15 May 1970.

Paratypes. UPNG2055-56, 2059; 2063-64; 3662, 3676, 3684, 3686, 3692, collected at the type locality; all are males.

Referred specimens. SAMAR8630, 8634, 8636, 8654, 8661, 8663-64 collected by A. Haines at Yaikoro, near Bundi, MadP, 850 m, in February 1967; all are males.

Etymology. “traunae” (feminine genitive), after the Trauna River, the holotype locality.

Diagnosis. A combination of moderate size (HBm 38-43); moderately long legs (mean TL/HB 0.59); low EN/IN ratio, mean 1.03 (0.95-1.17); small finger disks; fingers about one third webbed; large tympanum (mean TY/HB (0.057); heel tubercle only slightly enlarged; palpebral venation of wavering, forking lines with a slope angle of 60° and a call of rather short notes diagnoses this species (fig. 4, 6).

Description of the holotype. An adult male with sublingual vocal sac opening by lateral slits on the floor of the buccal cavity; snout obtusely angled from above, rounded and slightly projecting in profile; canthus rostralis slightly concave, sharp; lores oblique, slightly concave; low EN/IN ratio (EN/IN 1.00; EN/HB 0.15; IN/HB 0.15); eyes large (EY/HB 0.13); iris dark brown; palpebral venation of narrow wavering oblique lines, frequently forking, with a slope angle of 60° (as in fig. 4.A, B, C); tympanum well

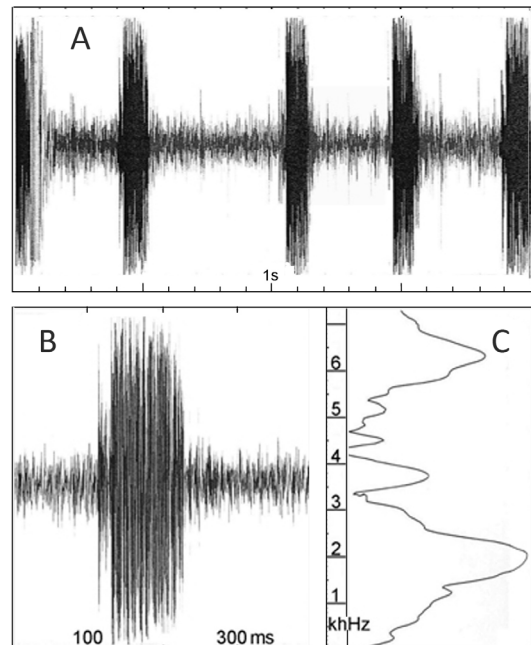


Figure 6. *Nyctimystes traunae*, new species. Call recorded at the type locality, specimen UPNG3675, air temperature 19.5 °C: **A.** five notes from a long series; **B.** single note; **C.** frequency spectrum.

Table 2. Call data for eleven members of the *Nyctimystes cheesmanae* species group.

ID	<i>Nyctimystes</i> species	Locality	Temperature (°C)	Note length (ms) mean (range)	Note rate (notes/s) mean (range)	Mean pulses/note	Notes analysed
UP4712	<i>bivocalis</i>	Agaun	21	53 (52-54)	1.28	7	32
Kraus 2012	<i>bivocalis</i>	Cloudy Mts	22-24	80 (80-106)			96
UP5406*	<i>calcaratus</i>	Bulolo	24	325 (250-400)	0.5	unclear	20
AMNH80933	<i>calcaratus</i>	Busu	22.8	72 (60-89)	3.19 (3.00-3.33)	9	21
AMNH130671	<i>calcaratus</i>	Wau	24.2	70 (57-83)	2.26 (2.15-2.43)	8	19
Kraus 2012	<i>cheesmanae</i>	Fane	20	326 (289-365)	0.82 (0.74-0.97)	20	11
UP4711	<i>daymani</i>	Agaun	20.0	45 (28-56)	2.93 (2.9-2.95)	7	27
UP3665	<i>eucavatus</i>	Baiyer R.S.	20.5	160 (55-255)	1.01 (0.65-1.38)	11	10
UP3677	<i>eucavatus</i>	Baiyer R.S.	21.5	132 (69-240)	2.05 (0.94-3.45)	10	25
UP5414	<i>intercastellus</i>	Goodenough Is	20.2	204 (165-229)	0.77 (0.58-0.83)	6	14
UP5413	<i>intercastellus</i>	Goodenough Is	20.7	281 (233-309)	0.72 (0.62-0.81)	7	14
Kraus 2012	<i>intercastellus</i>	Normanby Is	25-26	236 (189-320)		5	55
UP4696	<i>latratus</i>	Agaun	23.5	432 (396-464)	0.58 (0.54-0.64)	20	10
UP4715	<i>persimilis</i>	Agaun	18	85 (70-90)	0.72 (0.67-0.74)	14	5
UP5238	<i>semipalmatus</i>	Aieme Ck	25.5	99 (76-119)	2.17 (1.58-2.62)	11	20
UP1409	<i>semipalmatus</i>	Garaina		96 (72-119)	2.36 (1.89-3.00)	unclear	11
UP1410	<i>semipalmatus</i>	Garaina		97 (61-123)	2.90 (2.44-3.10)	8	9
UP2957	<i>traunae</i>	Trauna. R.	23	82 (64-117)	2.61 (2.53-2.72)	10	21
UP3675	<i>traunae</i>	Trauna. R.	19.5	98 (96-118)	1.91 (1.34-2.07)	12	17
UP3676	<i>traunae</i>	Trauna. R.	19.5	106 (85-107)	2.00 (1.88-2.2)	8	15
ns (Johnstone)	<i>traunae</i>	Ok Ma		108 (93-130)	1.14	9	7
ns (Zweifel)	<i>traunae</i>	Baiyer R.S.	20	128 (113-142)		11	23
AMNH80917	sp. inc.	Garaina	21.9	154 (139-172)	0.73 (0.56-0.84)	12	15
ns	sp. inc.	Agaun	19	172 (142-206)	0.13 (0.13-1.24)	14	7
ns	sp. inc.	Bonenau	18	160 (118-188)	1.11 (0.82-2.62)	15	6
ns	sp. inc.	Agaun	20	198 (163-222)	1.23 (1.48-1.81)	16	14

* data suspect due to poor quality recording.

defined (TY/HB 0.060); skin fold covering the upper margin terminates above the axilla; fingers with moderate disks, with moderate webbing (as in fig. 4.D, E), a fringe of separate, shallow tubercles along the outer surface of the forearm; legs long (TL/HB 0.62); toes fully webbed except on the fourth where half the penultimate phalanx is free of web; very shallow tubercles fringe the tarsus, commencing with a slightly enlarged tubercle on the heel (as in fig. 4.F); skin minutely granular dorsally, more coarsely granular on the ventral side; numerous tiny white tubercles in the cloacal area;

Colouration. In life (Trauna River), dorsum light brown, irregularly mottled in the mid-dorsal region, some more boldly than others, one specimen with scattered cream-coloured light spots; anterior and posterior thigh surfaces plain grey-brown; ventrum immaculate, whitish; iris dark brown. This species was illustrated in Menzies (2006, plate 97) as *Nyctimystes* cf. *cheesmanae*. The series from Bundi, in spirit, are, with one exception, fairly uniform dark brown, with vague mottle and barring on the hind limbs; one has a three white spots. An exception is SAMAR8663, a lighter grey-brown with more distinct mottle and barring. The ventrum is off-white faintly speckled pale brown, darker below the limbs.

Variation. The extent of dimensions and proportions is shown in tab. 1 and individual parameters are compared in fig. 3 (group *Nt*). Small frogs, HBm mean 40.4 (38-43); legs moderate to long, mean TL/HB 0.59 (0.57-0.62); EN/IN ratio low, mean 1.03 (0.96-1.17); head width unremarkable, mean HW/HB 0.37 (0.36-0.38); tympanum rather larger than average, mean TY/HB 0.057 (0.046-0.068). The palpebral venation varies in that, in some specimens, an irregular network occupies almost half of the eyelid (fig. 4.B). The hand webbing varies to the extent shown in fig. 4.D, E. Fig. 5 compares the type series with the referred specimens from Bundi, approximately 120

km east of Baiyer River. The two populations differ in body size (mean HBm 46 cf. 40) and show significant differences in mean head width, mean inter-narial distance and mean tympanic diameter (with considerable overlap), but not in leg length. In form of the palpebral venation they are similar (fig. 4.A, B, C). Both sample sizes are small ($n = 7$ and 11) and the apparent differences may not be real. None of the males displays pigmented nuptial pads.

Vocalization. Call recorded at the type locality, is a long series of short to medium length, loud, rough notes; mean note length 95 ms (64-118); mean repetition rate 2.24 notes/s; dominant frequency around 2 kHz with a prominent band around 6 kHz. There are 8-12 pulses per note, emitted at a steady rate (fig. 6, table 2). Acoustic impression “chak...chak...chak”. The call, recorded at Baiyer River Sanctuary and illustrated in Zweifel (1980, figure 6.B), is not *N. cheesmanae* but *N. traunae*.

Comparison with other species. Comparison is restricted to other members of the *cheesmanae* group and excludes *N. avocalis* which has no vocal sac and *N. perimitri*, only known from remote Louisiade Islands. *Nyctimystes traunae* is morphologically quite similar to several others in this species group. It is significantly larger than either *N. avocalis*, *N. gularis* or *N. daymani* and significantly smaller than all other species except *N. eucavatus* and *N. obsoletus* (fig. 3, sp. *Nt*). The TL/HB ratio is unremarkable. The EN/IN ratio is significantly lower than the sympatric *N. eucavatus* but similar to that of several other species (fig. 3, spp. *Nt*, *Ne*). Tympanic size is larger, on average, than all other *N. cheesmanae* group species but the difficulty of accurately measuring this organ makes the character less useful. It has a significantly narrower head than *N. eucavatus* but is best distinguished from that sympatric species by the lower EN/IN ratio, less extensive hand webbing and form of the palpebral reticulum. The call notes are of medium length, with evenly spaced pulses and are slightly shorter than those of the sympatric *N. eucavatus* where the pulses are not evenly spaced but in acceleration (cf. fig. 6, 9) giving a different acoustic impression. The specimens from Bundi are not included in the paratype series as no call data are available for them.

Ecology. These frogs were calling from 2-3 m above ground in tall *Saccharum* reed beds alongside the Trauna River, a tributary of the Baiyer River. Although broadly sympatric with *N. eucavatus*, they tended to be in the more open parts of the river while that species appeared to congregate by the smaller, forested streams. No females were collected and the tadpoles are unknown.

Distribution. The only known localities, Baiyer River Sanctuary and Bundi, span 120 km through the central mountains of eastern New Guinea. The only other member of the *Nyctimystes cheesmanae* group that is known to occur in this area is *N. eucavatus*.

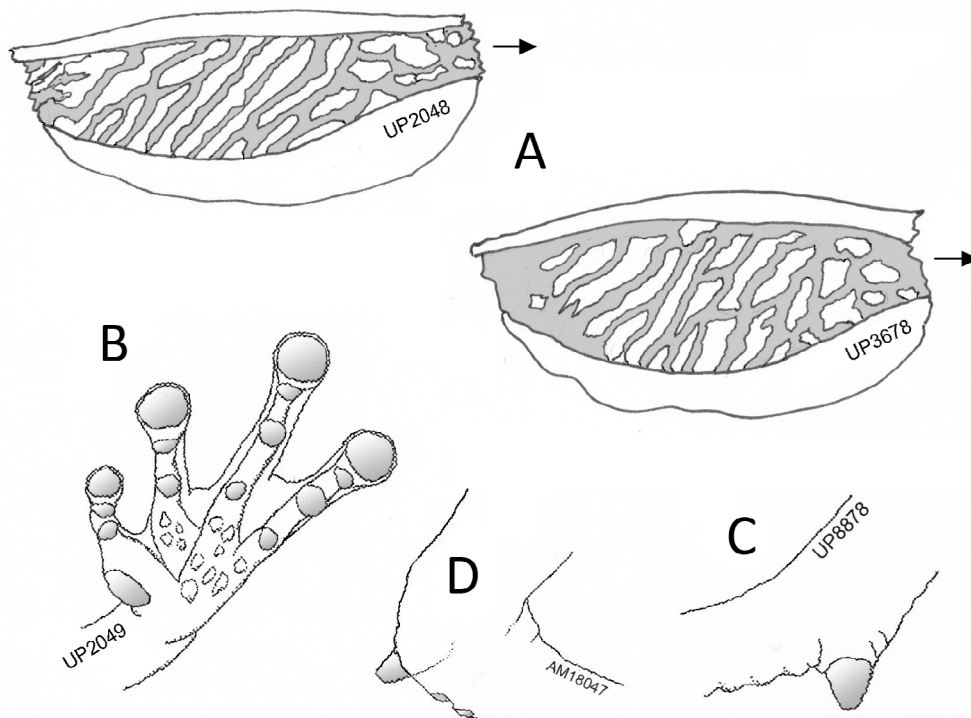


Figure 7. *Nyctimystes eucavatus*, new species: A. eyelid venation of two paratypes; B-C. hand (palmar view) and heel of paratypes; D. heel of referred specimen from Ganz River.

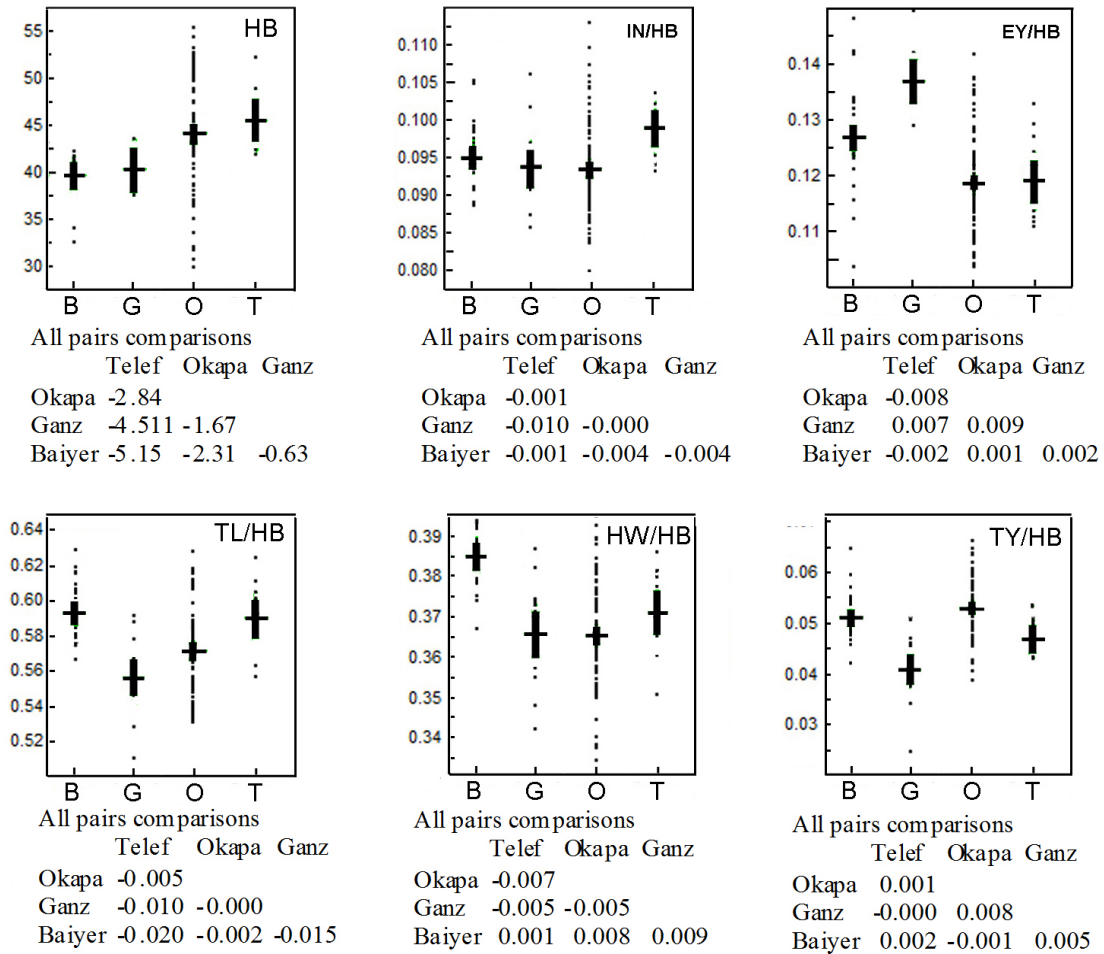


Figure 8. *Nyctimystes eucavatus*, new species. Univariate comparison (Tukey-Kramer, all pairs) of variables from type locality (B), with referred specimens from other areas, G-Ganz River, O-Okapa, T-Telefomin. Only positive comparisons are significantly different.

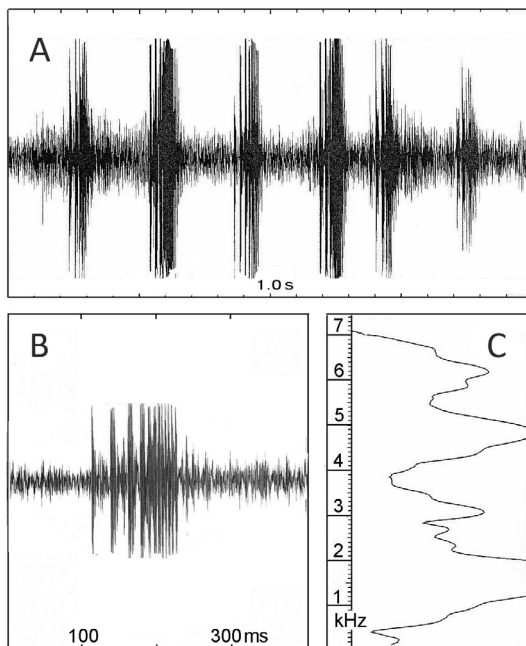


Figure 9. *Nyctimystes eucavatus*, new species. Call of paaratype UPNG3677 recorded at the type locality, air temperature 21.5 °C: A. six notes terminating a long series; B. single note; C. frequency spectrum.

Nyctimystes eucavatus sp. nov.

Holotype. UPNG3665, male, collected by J. Menzies in vegetation alongside a forest stream in Baiyer River Sanctuary (WHP), 800 m asl, between 10-15 May 1970.

Paratypes. UPNG2040-48, males, collected with the holotype; UPNG3663, 3677, 3679, 3680-82, 3691, 8875-80, males, SAMR11797-98, males, collected in the same place, between 11-16 September 1972.

Referred specimens. SAMAR5210a-Ax; (48 male, 32 female) collected near Okapa, (EHP) 1780 m, by J.Y. Hancock on 6 Nov 1963; SAMAR5425a-d, f-k (males) SAMR5425e (female) collected near Telefomin, (SanP) 1310 m, by B. Craig in November 1963, AMS R14701, -24, -25, 17998, 18000-01, 18013, 18022, 18047, 18078 (10 males); Manjim, Ganz River, (WHP), about 1500 m, collected in 1962. Photographs of AMNH80948, Baiyer River Sanctuary and AMNH130853, Ubaigubi, were examined.

Etymology. The specific epithet *eucavatus*, 'well caged', is compounded from the Greek prefix *eu-*, well, and Latin *cavea*, a cage, and refers to the thick bars forming the eyelid venation.

Diagnosis. a combination of moderate size; moder-

ate to very long legs; broad head; moderate to high EN/IN ratio; fingers one third to one half webbed (fig. 7.B); prominent, small, pointed heel tubercle (fig. 7.C, D); palpebral venation of thick, gold lines with a slope angle of 40-60° (fig. 7.A, B) and a call consisting of medium length notes with 7-25 pulses in acceleration (fig. 9) is diagnostic.

Description of the holotype. an adult male, is a moderate size member of the *Nyctimystes cheesmanae* group, HB 38.7; snout blunt above and square in profile, not protruding; canthus rostralis concave, sharp; lores slightly oblique, flat; legs long (TL/HB 0.59); nostrils narrowly placed (EN/IN 1.08, EN/HB 0.11, IN/HB 0.10); eyes large (EY/HB 0.15); tympanum small but distinct (TY/HB 0.05); prominent supra-tympanic skin fold covering upper tympanic margin, terminating above the axilla; fingers with extensive web and moderate disks (as in fig. 7.B); toes webbed to the base of penultimate phalanx on toe 4; a conspicuous, shallow white crenulated fold fringing forearm; conspicuous raised, crenulated, white fold fringing tarsus, commencing with a prominent conical tubercle on the heel (as in fig. 7.C, D); skin minutely granular above, more coarsely granular below; small white tubercles around the cloaca; no pigmented nuptial pad but a raised smooth white area on first digit where a pad would be expected; sublingual vocal sac opening by lateral slits on the floor of the buccal cavity; eyelid venation of oblique, thick gold lines with a slope angle of 60°, few cross connections but tending towards a reticulum at the anterior end (as in fig. 7.A). Dorsum now pale tan, unmarked except for faint barring on thighs; ventrum immaculate white.

Colouration. In life (Baiyer River) very variable; dorsum mottled fawn to dark chocolate brown frequently with vague irregular, orange-buff, lichen-like patches and small dark spots and squiggles; irregular dark cross bars on hind limbs; anterior and posterior surfaces of thighs plain brown; ventrum immaculate white but greyish on throat and limbs; iris light brown, tending towards golden. Referred specimens from Ganz River (in spirit) have a light to mid-brown dorsum, almost plain or with dark vermiculations or irregular pale blotches; ventrum off-white, immaculate. A photograph of a frog from Ubaigubi (AMNH130853) shows a very pale tan frog with dark cross bars across the back and on hind limbs. The lores and flanks are almost white.

Variation. range in dimensions and proportions is shown in tab. 1 and compared with other species in fig. 2, 3; mean HBm 39.7 (32.0-42.0); legs long, mean TL/HB 0.59 (0.57-0.63); mean EN/IN 1.15 (1.04-1.27); head broad, mean HW/HB 0.39 (0.37-0.40).

Fig. 8 compares the type series with the referred specimens from Telefomin, Ganz River and Okapa. The Telefomin and Okapa frogs are significantly larger (mean HBm, 42.1 and 44.9 cf. 39.7) than those from the type locality; those from Ganz River are similar. There are also significant differences in mean TL/HB, HW/HB, EY/

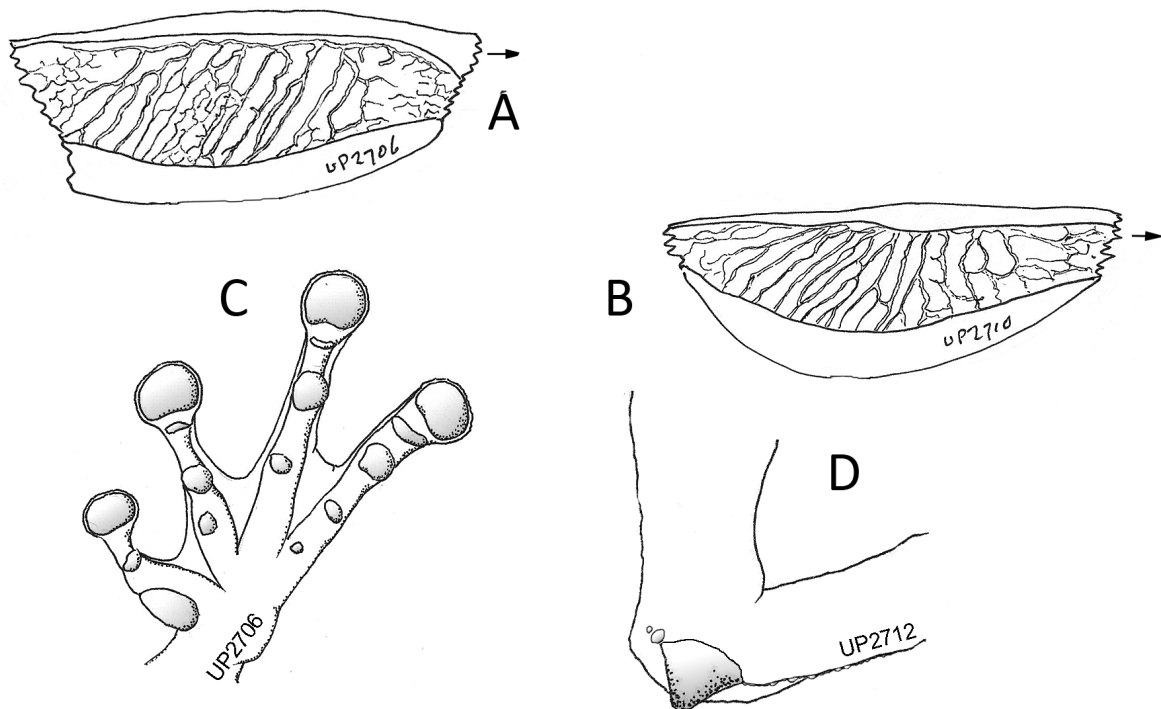


Figure 10. *Nyctimystes calcaratus*, new species: A-B. eyelid venation, holotype and paratype; C. hand (palmar view), holotype; D. heel, paratype.

HB and TY/HB ratios between some, but not all, groups but, in most cases, the range in proportions of the Okapa sample ($n = 48$) completely encompasses all the others. All are referred to this species on account of the unmistakable thick gold lines of the reticulum and the small, pointed heel tubercle. The mean length of adult females in the large sample from Okapa ($n = 32$) is 50.9 mm (range 42-55), approximately 30% larger than males but they were not significantly different from the males in any other variable. None of the males in the Baiyer, Okapa or Telefomin samples has a strongly pigmented nuptial pad but some of those from Ganz River have a faint brown pad. The eyelid venation varies in that some specimens have more cross connections between the oblique lines and the anterior part may be more or less reticulate. (fig. 7.A).

Vocalization. Recorded at the type locality and at Ok Ma, was a long series of quiet notes, mean note length 124 ms (71-239), repetition rate 1-3 notes/s; dominant frequency about 1.7 kHz with prominent frequency bands at 4.9 and 6.2 kHz (fig. 9). There are 7-25 pulses per note with the first three or four widely spaced and the remainder close together; acoustic impression, “raak...raak...”.

Comparison with other species. *Nyctimystes eucavatus* differs from sympatric new species *N. traunae* in call, eyelid pattern, heel tubercle, wider head and more extensive hand webbing, as discussed in the account of that species. In possession of a prominent heel tubercle, this species resembles *N. calcaratus* new species, *N. cheesmanae* and *N. daymani* but these do not have the heavy gold reticulum on the eyelid. *Nyctimystes cheesmanae* and *N. calcaratus* are larger, *N. daymani* is smaller.

Ecology. Notes on this species together with *Nyctimystes traunae* are given in the account of that species.

Distribution. Known localities span 460 km from Ok Ma and Telefomin to Okapa along the central mountain ranges of eastern New Guinea with altitudes ranging from 800-1800 m asl.

Nyctimystes calcaratus sp. nov.

Holotype. UPNG2706, male, collected by J. Menzies on vegetation over a mountain forest stream near Bulolo (MorP), 1230 m, between 17-22 December 1970.

Paratypes. UPNG2702 (female) UPNG2703-05, 09-12, -14 (males) collected with the holotype; UPNG3561, -63 (males); UPNG3585 (female), collected at the Mt. Suckling base camp (NorP) approximately 12 km west of Biniguni, 300 m.

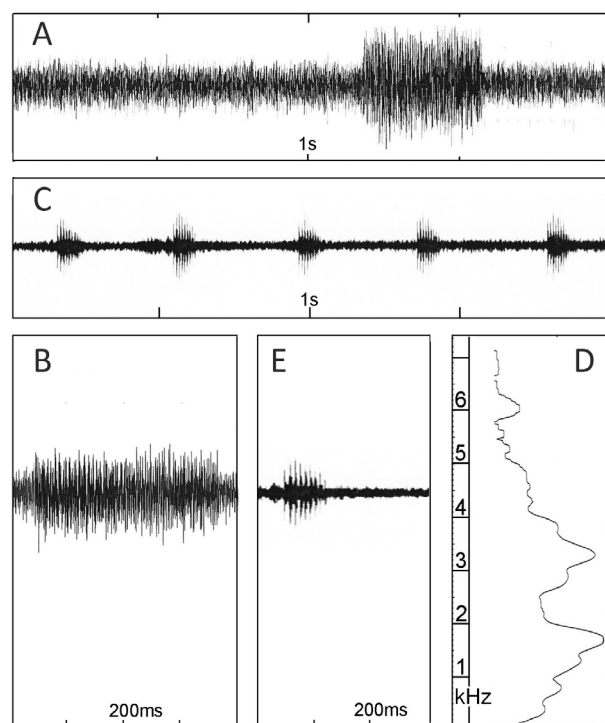


Figure 11. *Nyctimystes calcaratus*, new species. Call of specimen UPNG5406, air temperature 24 °C recorded at Bulolo: **A.** single note from a long series; **B.** single note, expanded scale; **C.** frequency spectrum; **D.** five notes from a long series, specimen AMNH13061 recorded at Wau by R.G. Zweifel, air temperature 24.2 °C; **E.** single note from (D).

Referred specimens. AMNH 80933, Busu logging area, 200 m MorP; AMNH130671 Wau, 800 m MorP; Boana, MorP. Photographs of the AMNH specimens, in life, were examined and their advertisement calls were analysed.

Etymology. The specific epithet *calcaratus*, ‘spurred’, from the Latin *calcar*, a spur, and refers to the small, but conspicuous, heel tubercle.

Diagnosis. A moderate (HBm mean 47.4) species of the *Nyctimystes cheesmanae* group with moderate legs; unremarkable EN/IN ratio (1.16); but low EN/HB and IN/HB ratios (sp. *Nc* in fig. 3); one third to one half webbed hands (fig. 10.C); small, but prominent, white tipped, conical heel tubercles (fig. 10.D); palpebral venation of thin oblique lines with a slope angle of 60-70°, tending to form a network at the anterior and posterior ends (fig. 10.A, B); iris pale gold with darker flecks.

Description of the holotype. An adult male with sublingual vocal sac opening by slits on the buccal floor but no pigmented nuptial pads; a larger member of the *N. cheesmanae* group (HB 49.3); snout square from above and in profile, scarcely projecting; canthus rostralis slightly concave, sharp; lores oblique, concave; internarial space narrow (EN/IN 1.15); eyes large (EY/HB 0.12); iris gold; tympanum small, well defined (TY/HB 0.05); strong skin fold

covering upper tympanic margin and fading above axilla; fingers with moderate web (fig. 10.C) and moderate disks (2nd right partly amputated); no pigmented nuptial pads; low, crenulated, white ridge fringing forearm; legs moderately long (TL/HB 0.57); toes fully webbed leaving only part of the penultimate phalanx on toe 4 free of web; low, crenulated, white fold fringing tarsus commences on heel with a small, conical, white-tipped tubercle as in fig. 10.D; small white tubercles above the cloaca; skin minutely granular above, more coarsely so ventrally; skin loose and wrinkled on throat; sublingual vocal sac opening by lateral slits on the floor of the buccal cavity; eyelid venation of thin oblique lines with a slope angle of 60-70°, but forming a reticulum at the anterior and posterior ends (fig. 10.A).

Colouration. In life (Bulolo and Mai-u River) dorsum from tan to mid brown with irregular darker and lighter marks which may form irregular bands across the dorsum and limbs; occasionally light yellowish or whitish lichen-like patches and spots; iris gold; ventrum greyish, faintly speckled on throat. Plate 9a, titled *Nyctimystes* sp. (*cheesmanae* group), in Menzies (1976) and plate 98 in Menzies (2006), titled *Nyctimystes daymani*, are both *N. calcaratus*. A photograph of the referred AMNH130671, in life, shows a frog with a mid-brown dorsum and darker bars across the back and limbs. AMNH80933 is altogether darker with the cross bars hardly showing. The iris appears pale in all these photographs.

Variation. Range in dimensions and proportions is shown in tab. 1 and compared with other species in fig. 3 (sp. *Nc*). HBm mean 47.4 (43.0 to 52.0); legs moderate to very long, mean TL/HB 0.58 (0.53-0.63); internarial space narrow to very narrow (EN/IN 1.05-1.32); eyelid pattern of thin oblique lines often interrupted at one or both ends and in the centre by a fine, obscure reticulum (fig. 10.A, B). The single female paratype is 14% greater than the mean male size (HBf 55.6).

Vocalization. The call (fig. 11, tab. 2) of paratype UPNG2704, consisted of trains of rather long notes (250-400 ms) at a slow rate of 0.61 notes/s. The pulse structure is unclear, perhaps due to the rain falling during the recording. The dominant frequency lies around 1.5 kHz with prominent bands around 3.2 and 5.9. The acoustic impression was of a repeated squeal. Other species uttering calls with long notes are *N. cheesmanae*, *N. intercastellus* and *N. latratus* but their acoustic impressions were quite different. The notes in the calls made by the referred specimens recorded at Busu and Wau were shorter and uttered at a much faster rate (fig. 11.B, D, tab. 2) and may be more typical. The call of the specimens from the Mai-u River was noted in the field to be “a continuously repeated short trill” but attempts to record this were not successful.

Comparison with other species. This species is unremarkable in most mean dimensions, other than larger than average size and low EN and IN/HB ratios. Other *Nyctimystes* of the *N. cheesmanae* group with distinct pointed heel tubercles are *N. cheesmanae*, *N. daymani*, *N. eucavatus* and *N. obsoletus* and they are compared in the account of *N. eucavatus*. *Nyctimystes calcaratus* is, on average, larger than all *Nyctimystes cheesmanae* group

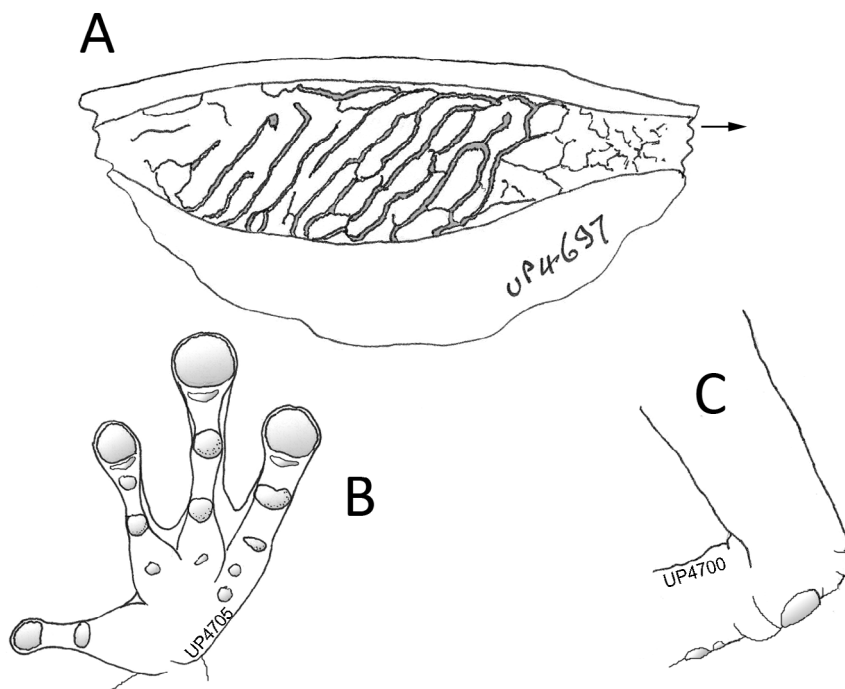


Figure 12. *Nyctimystes latratus*, new species: **A.** eyelid venation; **B.** hand (palmar view); **C.** heel, paratypes.

species except *N. cheesmanae* itself (sp. *Nch* in fig. 3). It is unremarkable in leg length and head size but has narrowly placed nostrils (mean EN/IN 1.14, mean IN/HB 0.081). *Nyctimystes daymani* has a call consisting of very short notes (mean note length 49 ms with 7-9 pulses per note). *N. eucavatus* is smaller, has a distinctive eyelid pattern of broad bars. Male *N. pulcher* less than 52 mm in length could be confused with spurred members of the *N. cheesmanae* group but that species has longer legs (mean TL/HB 0.63, high EN/IN ratio (1.13) and a much longer heel lappet.

Ecology. The type series was collected by a forest stream together with *Nyctimystes foricula*.

Distribution. Known, for certain, only from the type locality, Bulolo, and Mt. Suckling 400 km to the south-east. The referred specimens are from Wau, approximately 20 km higher up the Bulolo River valley than the type locality, and Busu, approximately 90 km to the north of Bulolo, but within the Bulolo-Watut-Markham River system.

Nyctimystes latratus sp. nov.

Holotype. UPNG4696, adult male collected by J. Menzies, beside a rush-bordered stream near Agaun village, MBP, between June 15-22, 1974; 1077 m.

Paratypes. UPNG4697-4701, 4703 (adult males), UPNG4704 (adult female), UPNG4705-10 (adult males) collected with the holotype; UPNG5033, 5035 (male, female), same locality, collected between November 1-9, 1974; UP5037, UPNG7137 (adult females) collected near Bonenau village, MBP, 1300 m, 15 July 1984; UPNG3562 collected at the Mt. Suckling base camp (NorP) approximately 12 km west of Biniguni, 300 m.

Etymology. From “*latro*” the Latin verb ‘to bark’.

Diagnosis. A combination of moderate to large size; moderately long legs; narrow head; low EN/IN ratio; lack of pointed heel tubercle and male call with very long notes is diagnostic.

Description of the holotype. A larger than average male of the *N. cheesmanae* group with slits on the buccal floor opening to a sublingual vocal sac but without pigmented nuptial pads; snout rounded, slightly projecting, obtusely pointed from above; lores oblique, concave; canthus rostralis concave, sharp; nostrils moderately placed (EN/IN 1.00); eyes large (EY/HB 0.12), iris gold, speckled black; palpebral reticulum of narrow gold lines with a slope angle of 50° as in fig. 12.A with few cross connections; at the extreme anterior end lines becoming reticulate; tympanum distinct; sharp skin fold covering upper tympanic margin, fading above axilla.

Fingers with moderate webbing as in fig. 12.B; forearm fringed with row of small white tubercles; toes well webbed leaving only the disk and penultimate phalanx free; legs moderately long (TL/HB 0.53), tarsus fringed with row of obscure, shallow, white tubercles commencing with a slightly enlarged, rounded tubercle on the heel as in fig. 12.C; dorsum smooth, ventral skin more granular.

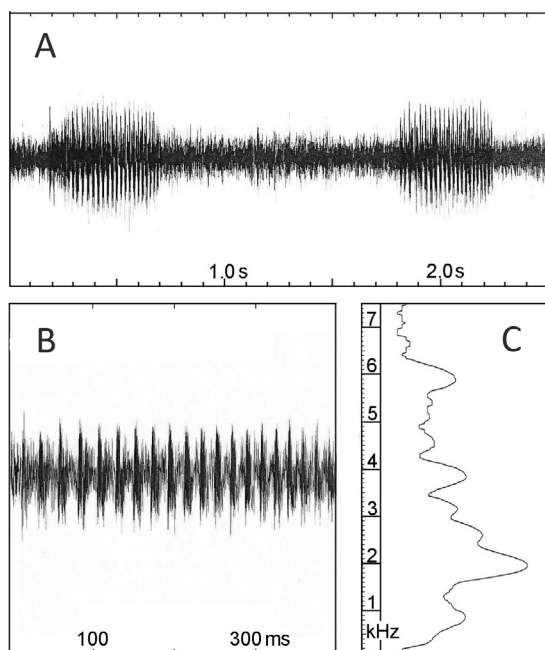


Figure 13. *Nyctimystes latratus*, new species. Call of holotype (UPNG4696) air temperature 23.5 °C: **A.** two notes from a long series; **B.** single note; **C.** frequency spectrum.

Colouration. The dorsum is highly variable. Two specimens are more or less uniform pale brown with only the vaguest mottle, most are medium brown with more or less distinct mottle, one is mostly tan with irregular dark brown patches, some have irregular pale spots, one has large white blotches on the head; hind limbs of all are irregularly barred with lighter and darker bands. In all, the ventrum is off white with faint darker mottle, especially on the throat; the anterior and posterior surfaces of the thighs are not markedly different.

After preservation, dorsum pale brown vaguely mottled with darker and lighter brown tending to form obscure cross bars; tarsus irregularly barred lighter and darker brown; anterior and posterior surfaces of thighs slightly reddish but not markedly distinct; ventrum creamy white, faintly mottled pale brown on throat. In life, the dorsal colour was more intense.

Variation. Range in dimensions and proportions is shown in tab. 1 and compared with other species in fig. 3 (sp. *Nl*); all are of moderate size, mean HBm 45.0 (42.0-50.0) and mean HBf 58.4 (55.0-62.0); leg length unremarkable, mean TL/HB 0.58 (0.53-0.62); head rather

narrow, mean HW/HB 0.33 (0.32-0.35), mean HL/HW 1.02 (0.98-1.09); nostrils widely placed, mean EN/IN 1.04 (0.97-1.33); eyes large mean EY/HB 0.12 (0.11-0.13); tympanum moderate, mean TY/HBm 0.052 (0.045-0.058) and mean TY/HBf 0.051 (0.049-0.053). The eyelid reticulum is similar in all specimens except that in some the bars are replaced by a network at the anterior end.

Vocalization. Call (fig. 13, tab. 2) of the holotype (the only specimen recorded) is a series of long (250-460 ms) notes uttered at a relatively slow rate (mean note repetition rate 0.58 notes/s) with prominent frequency bands at 2, 3.9 and 5.9 kHz. There are about 20 pulses per note. Acoustic impression is of a rough, repeated bark. A similar call was heard, but not recorded, near the Mai-u River, 35 km north west of Agaun

Comparison with other species. Apart from the larger than average size and rather narrow head, this species has no outstanding characters other than its call and is not easily distinguished from other, similarly sized species. Initially, it was thought to be *Nyctimystes cheesmanae* but comparison with the new description of that species (Kraus, 2012) shows some differences though the difference in method of measuring (e.g SVL or HB) might affect, but not eliminate, the differences; i.e. *N. cheesmanae* is larger with a mean SVL of 49.5 mm; has shorter legs (TL/HB 0.54 cf. 0.58) and shorter head (HW/HB 0.32 cf. 0.36). The call notes of *N. latratus* are much longer, mean note length 432 cf. 326 ms but these two species utter longer notes than any other species so far recorded. The heel tubercle of *N. cheesmanae* is pointed (Kraus, 2012, figure 1a, b) while that of *N. latratus* is rounded. In the Agaun area, *N. latratus* is morphologically most similar to *N. persimilis*, as sympatric *N. daymani* is much smaller and has a more distinct, pointed, tubercle on the heel. *Nyctimystes persimilis* has a darker, speckled ventrum and a more rugose dorsum, these are probably the best distinguishing features. Other *Nyctimystes* species occurring in the southeastern peninsula of New Guinea include *N. avocalis*, *N. daymani* and *N. gularis* which are significantly smaller than *N. latratus* (fig. 3) with adult male HB < 40 mm. *Nyctimystes latratus* has longer legs than *N. cheesmanae*, *N. bivocalis* or *N. intercastellus* and a narrower head than all except *N. cheesmanae*, *N. bivocalis* and *N. intercastellus*; *N. semipalmatus* appears to be uniformly pale brown, not displaying the variety of dorsal colouration seen in *Nyctimystes latratus*. *Nyctimystes cheesmanae*, *N. daymani* and *N. calcaratus* all have small but prominent heel spurs. None of the other species whose voices have been recorded utter such long notes as *N. latratus*.

Ecology. The type series were all collected by small streams in the Agaun Valley or on the surrounding hillsides, altitudes between 1000-1200 m. The Agaun valley is largely deforested, such forest as remains is restricted to stream sides. Eggs and tadpoles are unknown.

Distribution. Agaun and Bonenau (MBP) on the east side of Mt. Dayman and Mai-u River (NorP) 35 km northwest; altitudes from about 500 to 1200 m.

Notes on described species of the *Nyctimystes cheesmanae* group

Nyctimystes bivocalis Kraus, 2012

Nyctimystes bivocalis Kraus, 2012, 7.

Holotype. BPBM15201 collected in the Cloudy Mountains (MBP) 8 April 2002 by F. Kraus.

Material examined. UPNG4712, east slope of Mt. Dayman, above Agaun.

Diagnosis. This specimen was originally thought to be *Nyctimystes daymani* on account of the small size (HBm 37.9) and high EN/IN ratio (1.27) but the recorded call (fig. 14), with notes uttered in pairs, clearly allies it with *Nyctimystes bivocalis*. No other *Nyctimystes* species yet recorded utters calls with notes in pairs. The mean length of a note pair, including the interval, is 236 ms (481), mean length of first note 49 (88), the second note 53 (92), figures in parenthesis taken from the original description (Kraus, 2012). Morphologically, this specimen fits, in all variables, within the range given in the original description, except that the HB length is just below the minimum (cf. sp. *Nb* in fig. 3). The eyelid venation is of thin oblique lines with few cross connections and there is a small conical heel tubercle (fig. 15.B, C).

Colouration. In colour, the specimen was not noted to be different from the *N. daymani* collected at the same place except that the inner three toes were not orange in colour.

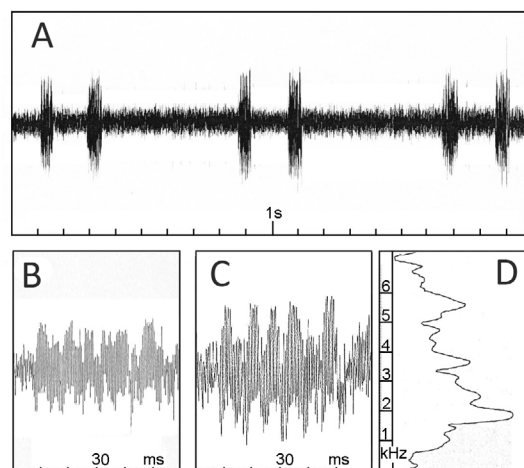


Figure 14. *Nyctimystes bivocalis* (UPNG4712) recorded near Agaun, air temperature 21 °C: **A.** three double notes from a long series; **B-C.** first and second notes of a pair; **D.** frequency spectrum.

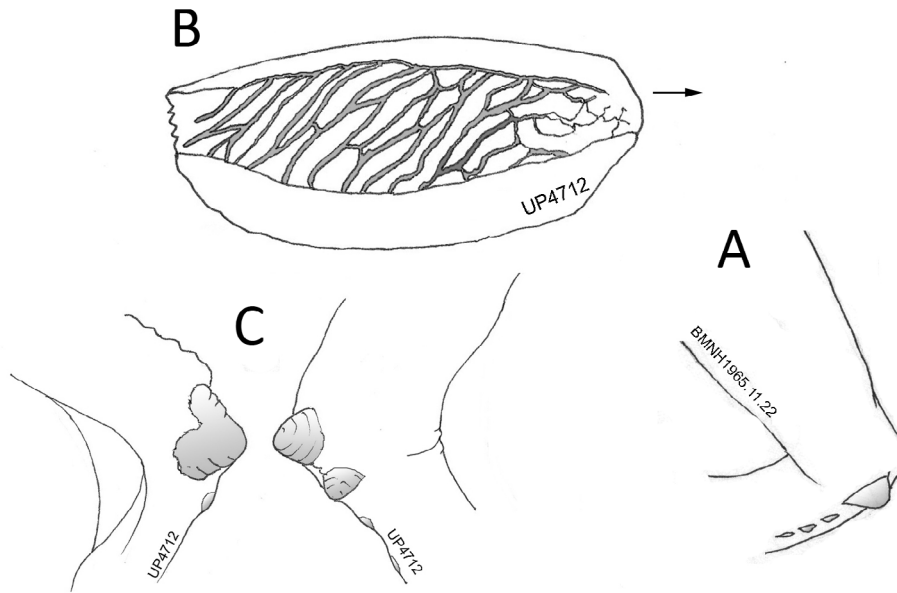


Figure 15. *Nyctimystes daymani*: A. heel of paratype from Mt. Dayman; B-C. *Nyctimystes bivocalis* eyelid venation and left and right heels of a specimen collected near Agaun.

Distribution. Known from the Cloudy Mountains 120 km north-west to Agaun, in the eastern Owen Stanley Mountains.

Nyctimystes daymani Zweifel, 1958

Nyctimystes daymani Zweifel, 1958, 8.

Holotype. AMNH57070 collected “on the north slope of Mt. Dayman (MBP) at an elevation of 700 m on July 22, 1953 by G.M. Tate”. 25 paratypes from the type locality.

Material examined. Two paratypes (BMNH 1965.1122-23) and 2 adult males (UPNG4711, 4713) collected above Agaun Mission, 1300 m, on the east side of Mt. Dayman and 30 km from the type locality.

Diagnosis. This species is distinguished by small size, maximum HBm 42 mm; relatively short legs, mean TL/SV 0.56 (0.54-0.60), high EN/IN ratio (mean 1.27, 1.17-1.53) and a distinct small, pointed tubercle on the heel (sp. *Nd* in fig. 3). The palpebral venation consists of thin, wavering oblique lines with some cross-connections and the call consists of very short notes in rapid series (fig. 16).

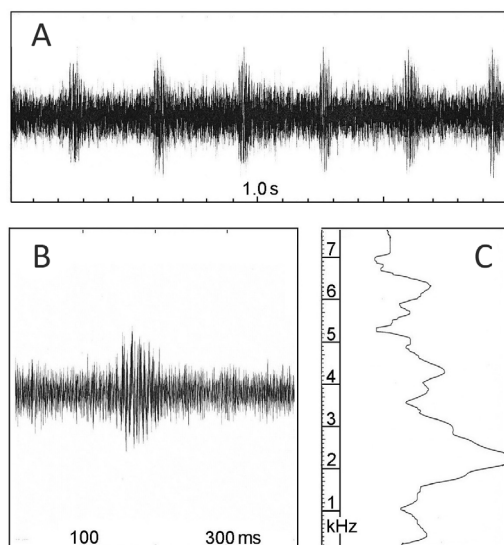


Figure 16. *Nyctimystes daymani* (UPNG4711) recorded near Agaun, air temperature 20 °C: A. six notes from a long series; B. single note from (A); C. frequency spectrum.

Comment. The difference from other species with pointed heel tubercles has been discussed in the accounts of *N. eucavatus* and *N. calcaratus*. In its small size, *N. daymani* can be compared with *N. avocalis* (which lacks vocal sacs) and with *N. gularis*, both of which have longer legs and a lower EN/IN ratio; *N. gularis* has a low eyelid venation slope angle with more cross connections and does not have a pointed heel tubercle. The current small sample of *N. daymani* ($n = 2$) differs from the original description in several ways, the maximum HBm is only 38 (cf. 42), mean leg length (TL/HB) is 0.56 (cf. 0.51), but not measured in the same way), mean EN/IN ratio is 1.27 (cf. 1.30). Figures in parenthesis are from the original description and in view of the small size of the present sample, differences may not be significant.

Colouration. In life, dorsum light brown with an orange tinge, a few white spots and darker mottling; limbs barred; anterior and posterior surfaces of thighs more or less as dorsum but more orange in colour; inner three toes bright orange; ventrum immaculate white.

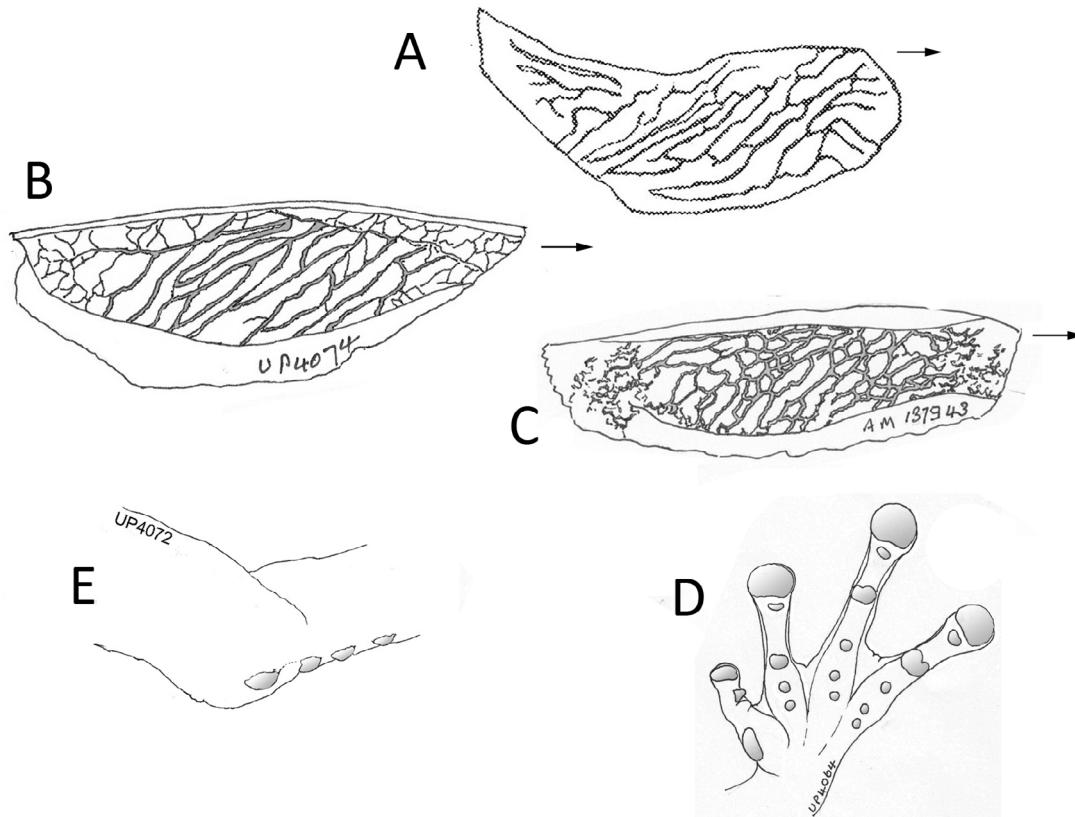


Figure 17. *Nyctimystes gularis*: **A.** eyelid venation of the holotype, drawn from a photograph; **B.** eyelid venation, specimen from Waitape; **C.** eyelid venation, specimen from Agaun area; **D-E.** hand (palmar view) and heel, specimens from Waitape.

Vocalization. Recorded at Agaun (fig. 16, tab. 2) is a rapid series of very short, rough notes, mean note length, 46 ms, mean rate 1.28 notes/s. Acoustic impression is “chak..chak..chak...”. The dominant frequency is about 2 kHz with other prominent frequencies at 4.2 and 6.2 kHz. The call illustrated in Menzies (2006, figure 67, p. 287) from Baiyer River is not *N. daymani* but the new species *N. eucavatus* described above.

Distribution. Known only from localities on the lower slopes of Mt. Dayman, MBP, but Zweifel (1958) ‘tentatively’ assigned a specimen (AMNH60376) from Mafulu, approximately 280 km west of Mt. Dayman.

***Nyctimystes gularis* Parker, 1936**

Nyctimystes gularis Parker, 1936, 78.

Holotype. “A male, number BMNH1947.2.24.29... from Mondo, Papua”, 1540 m, “collected in January 1934 by Miss Evelyn Cheesman”. One male paratype, BMNH1947.2.24.30.

Material examined. The holotype and UPNG4072-4080, 8850-53, Waitape, CenP, 1500 m; AMR137942 -43, -66, -93 -94, Agaun area, MBP.

Diagnosis. The outstanding features of this species are the small size (sp. *Ng* in fig. 3), very low slope angle (30-40°) of the oblique eyelid venation, which may have numerous cross-connections (fig. 17.A, B, C), and large eyes, uniform dark olive brown dorsal coloration and plain dark colour of the concealed surface of the thighs. There is a slightly enlarged, rounded heel tubercle (fig. 17.E). Parker (1936) distinguished this species from *N. cheesmanae*, collected at the same site, and *N. semipalmatus*, from Kokoda, by having fingers only one quarter webbed and compared it with *N. papua*, which only has a sparse reticulate venation in the anterior part of the eyelid, elsewhere blank.

Comment. Zweifel’s 1958 description and illustration of the eyelid (“venation is distinct and forms a reticulum without obvious orientation of the lines”) was not based on the holotype but on a specimen from Mt. Tafa and he also notes specimens from Mt. Dayman with “palpebral venation similar in form”. However, recent examination of the holotype (fig. 17.A) and paratype (not figured) show an oblique venation with a low slope angle and relatively few cross connections. When Tyler (1962) re-examined the holotype he also found that Zweifel’s description of the eyelid venation did not match it and suggested “that [Zweifel’s] specimens must be distinct from

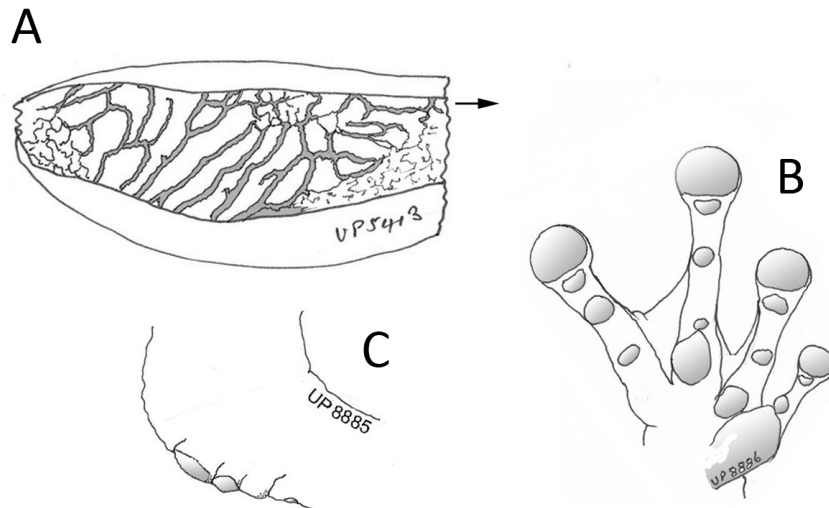


Figure 18. *Nyctimystes intercastellus*: A. eyelid venation; B. hand (palmar view); C. heel of specimens from Goodenough Island.

gularis". The frogs from Waitape (fig. 17.B) show a similar oblique venation to that of the holotype but those from the Agaun area have many cross connections (fig. 17.C). Pending contrary information, it must be assumed that the eyelid venation of *Nyctimystes gularis* shows some variation in the amount of cross-connection but this is merely variation within a single species.

Mean measurements for the Waitape sample with holotype data in parenthesis are: HBm 34.2 (36.9); HBf 47.4; TL/HB 0.60 (0.57); EY/HB 0.15 (0.15); EN/IN 0.99 (1.08). In its small size it can be compared only with *N. daymani* and *N. avocalis* but the legs are longer than in *daymani* and the EN/IN ratio much lower (sp. *Ng* in fig. 3). *Nyctimystes avocalis* is small but has no vocal sacs and is only known from Goodenough Island. *N. fluviatilis* is only known from northern coastal ranges far away from the south-eastern peninsula.

Zweifel (1958) notes a female specimen from Mt. Tafa with an SVL of 56 mm and two females from Mt. Dayman at 42 and 43 mm. Adult females from Waitape range from 45 to 52 mm. The large size of the Mt. Tafa specimen suggests that it may have been misidentified.

Colouration. *Nyctimystes gularis* appears to be rather plainly coloured, lacking the variation seen in other species, and the dark thighs are distinctive. One specimen has a vague dark 'hour-glass' mark on the dorsum.

Vocalization. The call has not been recorded.

Distribution. Mondo and Waitape (CenP), 23 km distant, extending south-east to the Agaun (MBP) area. These localities span approximately 300 km in the Owen Stanley Mountains.

Nyctimystes intercastellus Kraus, 2012

Nyctimystes intercastellus Kraus, 2012, 14.

Holotype. BPBM17938 collected by F. Kraus on Normanby Island (MBP), January 2003.

Material examined. UPNG5413-15; 8883-87 collected on Goodenough Island at 900 m asl.

Diagnosis. *Nyctimystes intercastellus* was diagnosed, *inter alia*, by an extensive hand web "extending as far as the top of the penultimate tubercle on fourth finger" (Kraus, 2012). The Goodenough Island frogs range from 39-51 mm HBm and all have vocal sacs. Morphologically, they fit comfortably within the

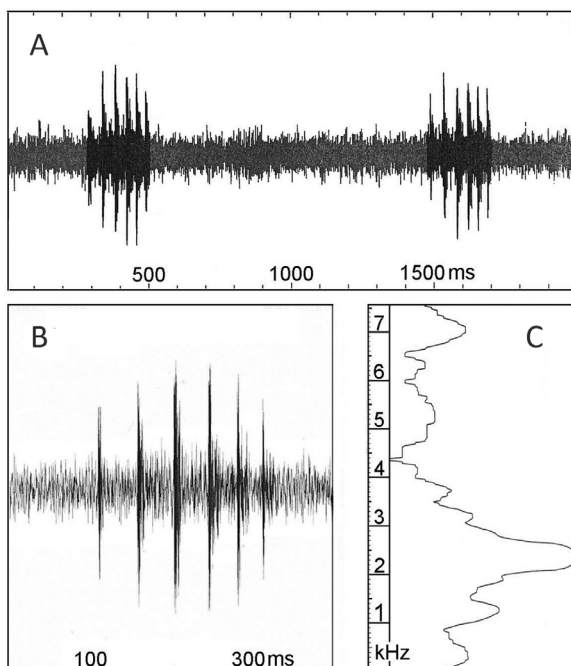


Figure 19. *Nyctimystes intercastellus* (UPNG5414) recorded on Goodenough Island, air temperature 20.7 °C: A. two notes from a long series; B. single note; C. frequency spectrum.

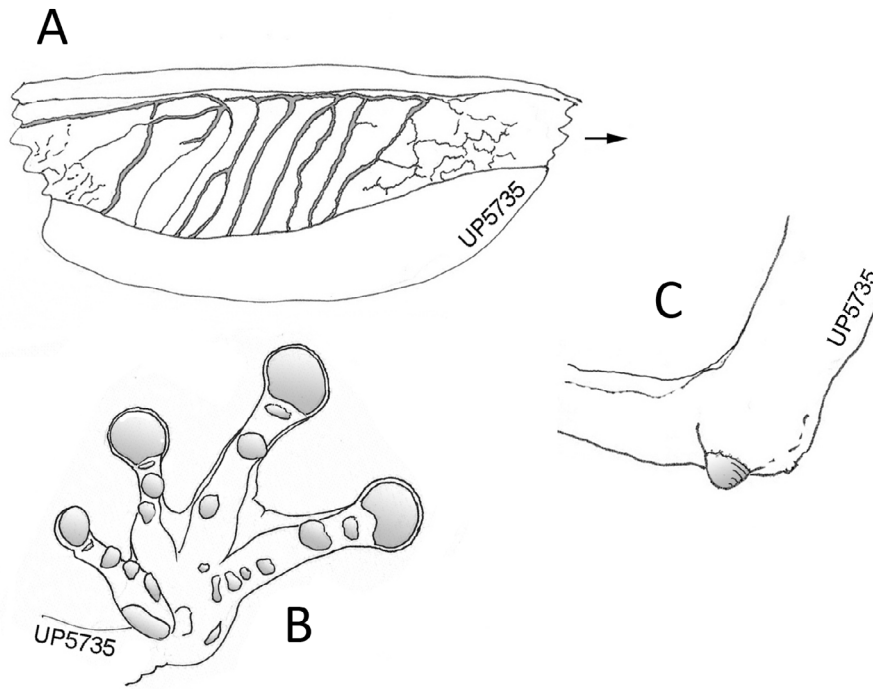


Figure 20. *Nyctimystes obsoletus*, specimen from Finschhafen: **A.** eyelid venation; **B.** hand (palmar view); **C.** heel.

description of *Nyctimystes intercastellus* except that, in no specimen, is the web as extensive as described (fig. 18.B). The legs are longer, TL/HB mean 0.58 cf. 0.53. Two specimens (UPNG5413, 5414) were recorded at the same site on Goodenough Island (fig. 19, tab. 2). The calls appear to differ from calls recorded on Normanby Island (Kraus, 2012, figure 3c) in that a note contains six to seven distinct pulses rather than being ‘slightly pulsed’. Before describing the Goodenough frogs as distinct species, one needs more information on inter-island variation.

Another *Nyctimystes* species known from Goodenough Island is *N. avocalis*, which lacks vocal sacs. Zweifel (1958) records *N. cheesmanae* from that island but that record needs confirmation.

***Nyctimystes obsoletus* (Lönnberg, 1900)**

Hyla obsoleta Lönnberg, 1900, 580.

Nyctimystes obsoleta Tyler, 1964b, 92.

Holotype. University of Uppsala, Sweden, uncatalogued, from Simbang, MorP, near sea level; adult male, collected in 1899 by Dr. E. Nyman.

Material examined. SAMAR4250a-f, 4252a-c, Finschhafen, MorP; UPNG5734-35, Go River, MorP.; UPNG2978, Sattelberg, MorP.

Diagnosis. Tyler (1964b) gave a detailed description of the holotype, including the following data, with means from the Finschhafen population in parentheses. Small size, SVL 35 (41), very long legs, TL/SVL 0.64 (0.59); moderate EN/IN ratio, 1.10 (1.19); obscure tympanum; outer fingers half webbed; small, conical heel tubercle.

Comment. Before Tyler (1964b) re-examined the holotype, this species remained in *Litoria* and so was omitted from Zweifel’s (1958) revision. The species has been known only from the holotype and, although diagnosed by its long limbs and hidden tympanum, the range in variation of these characters was unknown. The holotype was collected at the coastal locality, Simbang, though the collector, Erik Nyman, also spent time at Sattelberg, a short distance inland. Simbang is close to the one-time German New Guinea capital, Finschhafen. I assign the population from Finschhafen, one specimen from Sattelberg and two other specimens from the Huon Peninsula to this species on account of medium-small size and long legs but apart from the supposed hidden tympanum, there is little to distinguish this species from several others in the mid-size range (sp. *No* in fig. 3). The eyelid pattern of thin, oblique lines with gaps anterior and posterior (fig. 20.A) is somewhat similar to Tyler’s illustration of the holotype eyelid in that the lines are thin and disappear at anterior and posterior ends but are not vertical. The tympana of the preserved Finschhafen specimens are quite visible but the specimens are somewhat desiccated and so made the tympana more visible than they would have been in life. Tyler (1964b) wrote (of the holotype)

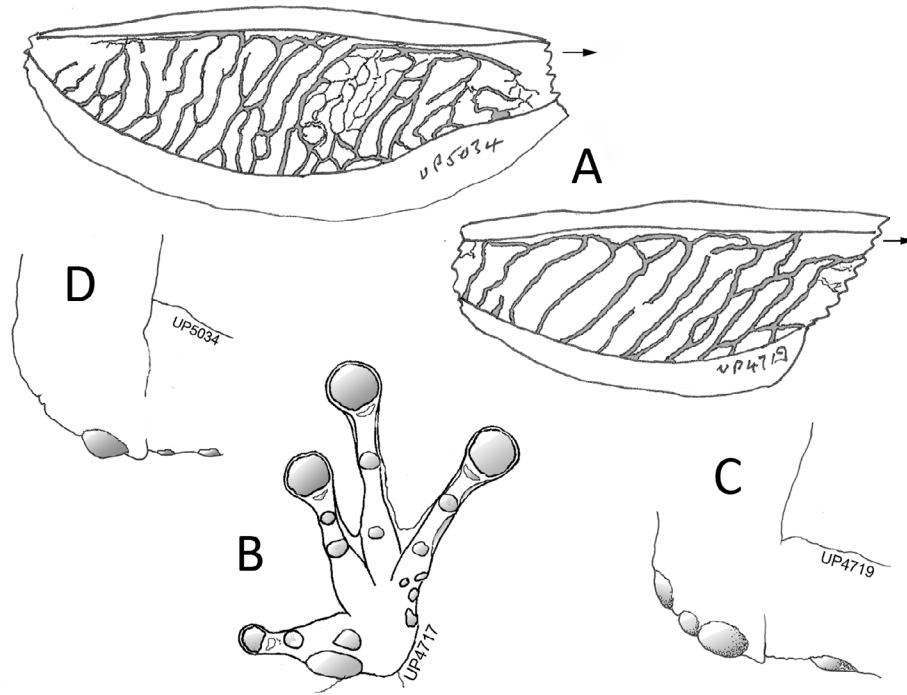


Figure 21. *Nyctimystes persimilis*, specimens from Agaun: **A.** eyelid venations; **B.** hand (palmar view); **C-D.** heels.

“Tympanum completely hidden, its site indicated by a slight depression, which is oval, and about one quarter the diameter of the eye...”.

In its size *N. obsoletus*, as defined here, is smaller than average for the *cheesmanae* group but larger than *N. avocalis*, *N. daymani* and *N. gularis*. From the former it differs in possession of vocal sacs and from the latter, by longer legs and lower EN/IN ratio, means 0.59 and 1.17 (*N. obsoletus*) and 0.56 and 1.30 (*N. daymani*).

There is “a small conical dermal appendage on the heel” (fig. 20.C), similar to that of several other species. In every Finschhafen specimen the tympanum was distinct enough to be measured and the average size found to be 0.4 x eye diameter.

Vocalization. The call is unknown.

Distribution. several sites on the eastern end of the Huon Peninsula at moderate to low altitudes. Maximum distance between these localities is 25 km.

***Nyctimystes persimilis* Zweifel, 1958**

Nyctimystes persimilis Zweifel, 1958, 34.

Holotype. adult male “AMNH56838, collected on the north slope of Mt. Dayman at an elevation of 1370 m, on July 2, 1953 by G.M. Tate”. One paratype (AMNH56838) from same area.

Material examined. UPNG4715-4734; 4737-4739; 4819-4820; 5034; 5036, east slope Mt. Dayman, above Agaun, MBP, 1400 m, all male; AMR137937, -44, -51, Muminun, MBP; AMR137982, -86, -90, Param, MBP, all males.

Diagnosis. A combination of rugose dorsal skin and coloured ventrum will distinguish this species. In the original description, Zweifel notes “There is no heel tubercle.” but in all the specimens that I have examined

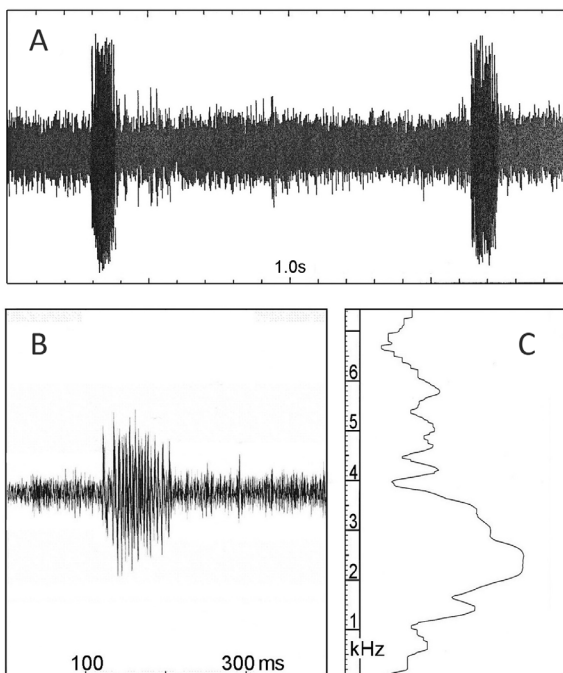


Figure 22. *Nyctimystes persimilis* (UPNG4715), call recorded above Agaun, air temperature 18 °C: **A.** two notes from a long series; **B.** single note); **C.** frequency spectrum.

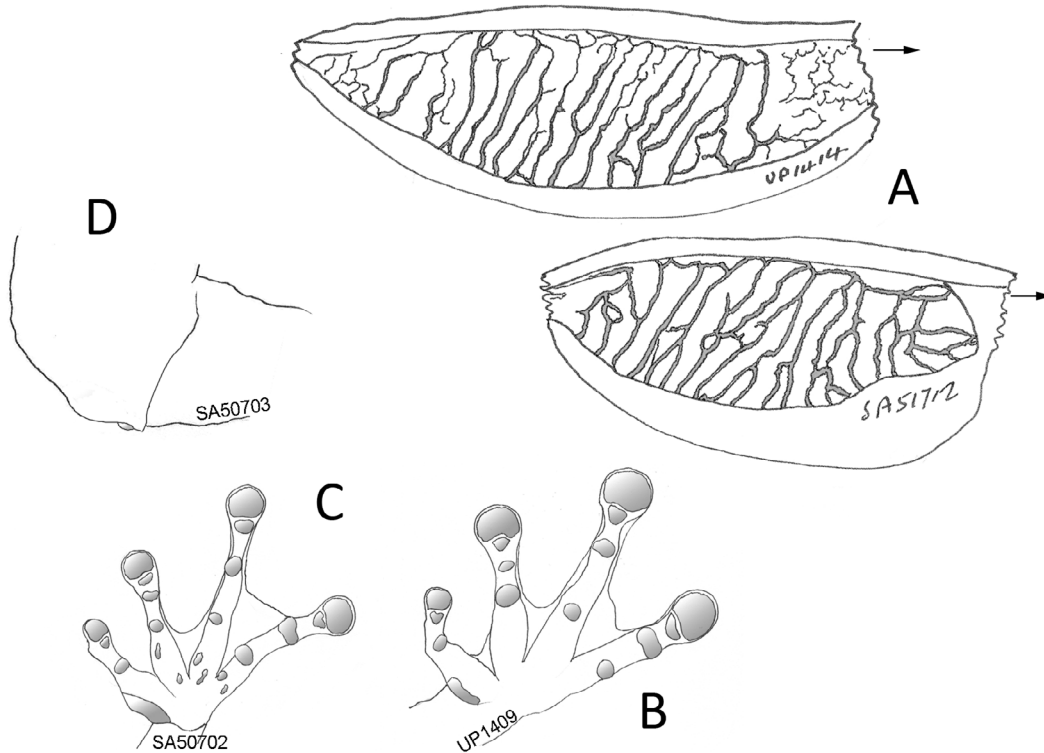


Figure 23. *Nyctimystes semipalmatus* specimens from Garaina: **A.** eyelid venation; **B-C.** hands (palmar views); **D.** heel.

the heel is as illustrated in fig.21.C, D.

These are small to moderate size frogs (HBm 37-50) with long to very long legs, mean TL/SV 0.60 (0.56-0.64), low EN/IN ratio, mean 1.04 (0.90-1.2); hand with moderate webbing (fig. 21.B) and a slightly enlarged, rounded heel tubercle; (fig. 21.C, D). The eyes are larger than those of other species, mean EY/HBm 0.12 (0.11-0.13); eyelid venation consists of narrow oblique lines with a slope angle of 60° (fig. 21.A). In some specimens some lines may be interrupted or replaced by a network.

Colouration. In life, dorsum highly variable but usually a light golden brown with green or brown blotches or plain or greyish olive with bold dark spots or altogether darker brown; the flanks dark, speckled white; limbs with irregular dark transverse bands; anterior and posterior surfaces of thighs bluish-grey or blackish; ventrum ‘liverish’, speckled grey, off-white with vague darker mottling after preservation, especially on throat; inner three toes uncoloured, not orange as in sympatric *N. daymani*.

Comment. Material examined comes morphologically close to the original description but legs are longer (mean TL/HB 0.60 vs 0.56, but note difference in measuring technique, and mean HBm is larger (maximum 50 vs. 40). There is a slightly enlarged heel tubercle. As the type series consists of just two specimens, these differences can probably be ignored. A morphometric comparison with other species from the same area is included in the account of *N. latratus*.

Vocalization. Specimen UPNG4715 recorded at 18 °C emitted short notes in fairly rapid series, mean note length 85 ms (70-90), 14 pulses per note; frequency band structure unclear but prominent bands at approximately 2.2 and 5.8 kHz (fig. 22, tab. 2); acoustic impression a rough “chak, chak, chak...”.

Distribution. Only known from the slopes of Mts. Dayman and Simpson in the Owen Stanley Mountains (Kraus & Allison, 2004), 1300-1700 m.

***Nyctimystes semipalmatus* Parker, 1936**

Nyctimystes semipalmata Parker, 1936, 83.

Holotype. “A female no. BMNH1935.3.9.198 in the British Museum, from Kokoda”, NorP, about 370 m. There are no paratypes but Parker referred one of the co-types of *N. papua* (BMNH1996.10.31.54) from Mt. Victoria to *N. semipalmatus*.

Material examined. The holotype and cotype; SAMAR50702-30, 51703-06-18; UPNG1409-24, near

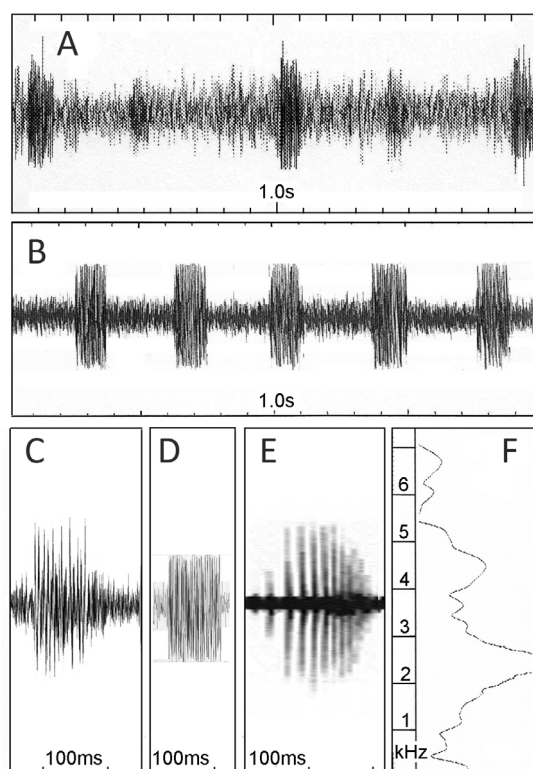


Figure 24. *Nyctimystes semipalmatus*, calls of (A) UPNG1409 recorded at Garaina, air temperature not recorded, 3 notes from a long series with a second frog (UPNG1410) in the background; B. UPNG5238 recorded by Aieme Creek, five notes from a long series, air temperature 25.5 °C; C. single note from (A); D. single note from (B); E. single note from a series recorded at Garaina by R.G. Zweifel, air temperature 21.9 °C; F. frequency spectrum from (B).

Garaina, MorP, about 1200 m; UPNG5238-39, 5326, Aieme Creek, CenP, 450 m.

Comment. Because the species was described from a single female individual and diagnosed by its half-webbed hands, male dimensions and the extent of variation are unknown and these notes are based on the series from Garaina, about 120 km to the south-east of the type locality (species *Ns* in fig. 2, 3).

Description. *Nyctimystes semipalmatus* appears to be a moderate size species (mean HBm 44) with long legs, mean TL/SVL 0.59 (0.56-0.62) and a low EN/IN ratio, mean 1.06 (0.90-1.20). “Fingers about half-webbed”. The illustration (figure 5 in Parker, 1936) shows a hand with the web not quite reaching up to the penultimate subarticular tubercle on the 3rd finger. None of the 21 Garaina specimens has such as extensive web (fig. 23.B, C) though the webbing is certainly more extensive than in most other species. The two females in the collection show a similar condition to the males. In some specimens there is a very small conical tubercle on the heel (fig. 23.D) but hardly the “triangular heel lappet” of Parker (1936). Most specimens have no heel tubercle at all and the row on the forearm and tarsus is so low as to be almost undetectable. The colouration of the holotype is compared to that of the Garaina specimens later.

The holotype is a female, SVL 59 mm (HB 57.4 when remeasured in 1964) and, based on comparison with other species, the male HB would be 40-45 mm thus of moderate size. Parker (1936) distinguished this new species by hands that were half webbed, but the second specimen that he referred to “has fingers with “slightly less webbing”. The frog on which Zweifel’s 1958 description of *N. semipalmatus* is based is not *N. semipalmatus* but *N. pulcher* and Menzies’ (2006) description of *N. semipalmatus* is also confused with *N. pulcher*. Apart from the more extensive hand webbing,

this species is morphologically indistinguishable from several other species so that the rather plain dorsal colouration, and lack of prominent tubercles on forearm and tarsus of the Garaina specimens seem to be the only reliable distinguishing features. *Nyctimystes semipalmatus* and *N. cheesmanae* are said to occur sympatrically at Kokoda and Garaina (Zweifel, 1980) but can only be distinguished by differences in calls and colouration. However, the call (specimen AMNH80917) recorded by Zweifel at Garaina and said to be *N. cheesmanae* has notes of only half the length and pulse number as those of *N. cheesmanae* recorded by Kraus (2012) at Fane so is unlikely to be of that species. My specimens from Aieme Creek are referred to *N. semipalmatus* on the basis of similarity in call to those from Garaina.

Colouration. The dorsum of the holotype, after nearly 75 years in spirit, is pale fawn (pinkish-grey in the original description) covered all over with tiny black spots, denser on the head; femora with broken reddish-tan transverse bars. The series from Garaina and the specimens from Aieme Creek are now uniformly pale fawn to dark brown, with only the faintest indication of mottling on the dorsum and transverse bars on the legs; one has a faint hour-glass pattern; thighs are dark slate-brown, not much different in colour from the dorsum; iris appears dark. In life, they were noted to be “very dull frogs”, dorsally grey, ochre or any shade of brown, some irregularly mottled; others plain; ventrum greyish white with faint marks on throat, more pronounced in the darker individuals.

Vocalization. Call of a specimen (UPNG1409) recorded at Garaina (fig. 24.A.C; tab. 2), consisted of a long series of shortish, rough notes, mean note length 78 ms (64-118), uttered at a mean rate of 2.36 notes/s. Prominent frequencies show at 2.2, 4.0, 5.5 and 6.3 mHz. A second specimen (UPNG1410) recorded at Garaina uttered slightly longer notes (mean 135 ms) at a rate of 2.42 notes/s (tab. 2). The call recorded at Aieme Creek (fig 24.B, D) had a mean note length of 108 ms uttered at a mean rate of 2.72 notes/s; there are 8-11 pulses/note uttered at a steady rate. A specimen (AMNH80917) recorded at Garaina, by R.G. Zweifel, uttered calls with a mean note length of 154 ms (fig. 24.E) but the notes are in acceleration. Acoustic impression of all is of a rough, rapid

barking. Notes in the calls of *N. latratus* (fig. 13), *N. calcaratus* and *N. cheesmanae*. are much longer, those of *N. daymani* and *N. persimilis* are shorter.

Ecology. A specimen laid, in captivity, 400 pale, cream coloured eggs, each 2.6 mm in diameter.

Distribution. Currently, only known from Kokoda (the type locality) and Garaina, MorP, about 120 km to the south-east, on the north flank of the Owen Stanley Mountains, and Aieme Creek, (CenP), a tributary of the Musgrave River, on the opposite side of those mountains.

Other, possibly undescribed, species

1. A *Nyctimystes* species was recorded several times in the Agaun area but, though seen, specimens were not captured (tab. 2 and fig. 25). Call notes were of intermediate length, mean 160-198 ms, with 14 pulses per note. A similar call was recorded at Efogi (not figured), and associated with a voucher specimen but could not be associated with any described species. These calls do not match that of any other species so far recorded. A call recorded at Garaina by Zweifel (fig. 24.E) has a similar note length (154 ms) but the 11 pulses are in acceleration. This call (AMNH80917) was said to be *N. cheesmanae* but has notes of only half the length and pulse number as those of *cheesmanae* recorded by Kraus (2012) at Fane so is unlikely to be of that species.
2. Samples of moderate sized ‘*N. cheesmanae* group’ frogs from Karimui and Bomai, on the south flowing tributaries of the Purari River (SAMAR 6302a-d; 8373; 8920a-d; 9365; 9369-9371; 9377; 9378a-ax; UPNG8916-17; 8923-24; 8927; 8930-32; 8958-61; 8963-69) display no particular distinguishing features and are without heel tubercles. No call data are available and they cannot be morphologically distinguished from other species in the moderate body-size cluster. It is not possible to assign a name to this population.
3. I have photographs of two specimens collected at Garaina which I cannot identify. AMNH80917, in life, shows a rather dull brown frog with vague darker cross bands on dorsum and legs. There is a tiny heel tubercle made conspicuous by its white colour. The iris is gold with dark veins and the hand appears to have a rather extensive web. Another specimen is a much brighter animal with irregular fawn patches and large white spots all over the dorsum. The heel tubercle is more prominent and the hands appear to have less webbing. The iris colour is unclear. Neither of these specimens match the series from Garaina listed under *Nyctimystes semipalmatus* above. Zweifel (1980) notes the occurrence of two species at Garaina “which are readily distinguished by differences in calls and pigmentation (webbing bright orange in *semi-palmata*, gray in *cheesmani*)”. I am not convinced that AMNH80917 represents *N. semipalmatus* as the tarsal tubercles are too prominent and the call (fig. 24.E), with its notes in acceleration, does not match the calls in fig. 24.A, B. Nor can this call be that of *N. cheesmanae* as it does not match the description of that species in Kraus (2012). It seems possible that there are three species broadly sympatric at Garaina.

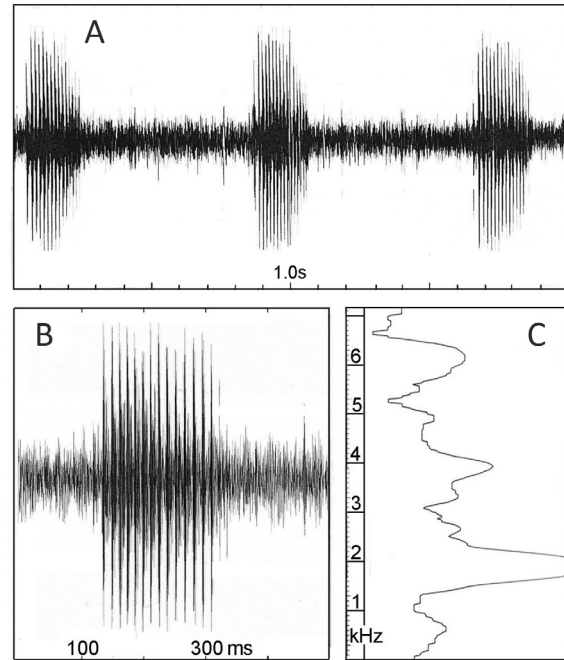


Figure 25. *Nyctimystes* species recorded near Agaun, no voucher specimen, air temperature 20 °C: A. three notes from a long series; B. single note; C. frequency spectrum.

Distribution and ecology

Nyctimystes species of the *N. cheesmanae* group as defined here, are widespread throughout New Guinea, from the Idenburg River and Foya Mountains in the west (*Nyctimystes fluviatilis*) to the Louisiade Islands in the south-east (*Nyctimystes perimitri*). *Nyctimystes* species appear to be more abundant east of the international border at 141° (fig. 1) and there are very few specimens from west New Guinea in museum collections. *Nyctimystes fluviatilis* (Idenburgh River) is the only type locality in west New Guinea. David Price lived on Yapen Island for

many years and made extensive collections of frogs there but tells me that he never collected a single *Nyctimystes*. Rainer Günther has made extensive collections in Indonesian New Guinea but failed to collect any *Nyctimystes*. The lack of specimens from west of the border may be a bias of collecting rather than a natural phenomenon but, until proved otherwise, remains a puzzle as the various species are often common in Papua New Guinea where several species may be broadly sympatric.

Nyctimystes appears to have a centre of endemism with nine species in the south-eastern peninsular, extending from the Bulolo Valley to Milne Bay and three others in the d'Entrecasteaux and Louisiade Islands, with as many as five species being broadly sympatric on the mainland, together with other *Nyctimystes* species of different groups. This, again, may be an artefact of intensive collecting but parts of the central highlands of Papua New Guinea have been equally well collected but only two of the *N. cheesmanae* group (*N. eucavatus*, and *N. traunae*) have their type localities there.

These *Nyctimystes* species are all inhabitants of hill or lower montane forest, between altitudes near sea level and 2000 m. It is the nature of the environment with forest on steep slopes and fast running streams that appears to be important, rather than altitude *per se*. Those ten species whose male advertisement calls have been recorded show similarity, with long trains of notes that are not well-tuned and usually have a rough “barking” quality. The length of a call is highly variable and some males may call for several minutes without a break. All notes recorded have a similar frequency spectrum with a dominant band near 2 kHz and higher frequency bands at 5-7 kHz, above the noise of running water. The principal differences between species appear to be in note length, number of pulses per note (or else notes appear unpulsed) and pulse repetition rate (tab. 2) and these differences may be the primary pre-mating isolating mechanism where morphologically similar species share a breeding site. In the eastern Owen Stanley Mountains, four broadly sympatric *Nyctimystes* species occur (*N. daymani*, *N. bivocalis*, *N. persimilis*, and *N. latratus*). Apart from body size, they are similar in general appearance but the notes in their calls are of quite different length, mean note lengths being 46, 85, 198 and 411 ms respectively. Possibly, note length can be adjusted to accentuate the differences but there is no experimental support for this. Note repetition rate is variable within species; it may be influenced by ambient temperature but more strongly by interaction with other nearby males.

All species, where females are known, produce relatively large unpigmented ova giving rise to tadpoles of the torrent-adapted type illustrated in Menzies (2006), fig. 7, but the tadpoles of no species have been positively identified. As several *Nyctimystes* and *Litoria* species may share a breeding habitat and all may produce similar tadpoles, it may be impossible to identify tadpoles without molecular analysis or else rearing them to adulthood.

ACKNOWLEDGEMENTS

Thanks are due to all those museum curators who have facilitated examination of specimens in their care, or sent them on loan; to Richard Zweifel for comments on the original manuscript and for sound spectrograms and photographs of various species; to Stephen Richards for his photographs of the eyelids of *Nyctimystes gularis*; to Harry Hines for specimens that he collected; to Greg Johnstone for sound recordings made at Ok Ma; to Fred Kraus for unpublished data on *Nyctimystes fluviatililis* and to the Universities of Papua New Guinea and Adelaide for supporting this research. Numerous local field assistants made this work possible.

LITERATURE CITED

- Duellman, W.E. (1993). *Additions and corrections to amphibian species of the world by Darrel R. Frost*, Special publication no. 21. University of Kansas Museum of Natural History, Lawrence, Kansas.
- Faivovich, J., Haddad, C.F.B, Garcia, P.C.A, Frost, D.R., Campbell, J.A., Wheeler, W.C. (2005). Systematic review of the frog family Hylidae, with special reference to Hyalinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History*, 2904: 1-240.
- Frost, D.R. (2013). *Amphibian species of the World: an online reference*. Version 5.6. American Museum of Natural History, New York. Available from <http://research.amnh.org/herpetology/amphibia/index.html> (accessed August 2013).
- Frost, D.R., Grant, T., Faivovich, J. (2006). The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297: 1-370
- Kraus, F. (2012). Identity of *Nyctimystes cheesmani* (Anura: Hylidae), with description of two new related species. *Zootaxa*, 3493: 1-26.

- 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*, (7), 6: 574-582.
- Menzies, J.I. (1976). *Handbook of common New Guinea frogs*. Wau Ecology Institute, Wau.
- Menzies, J.I. (2006). *Frogs of New Guinea and the Solomon Islands*. Pensoft, Sofia.
- Menzies, J.I., Richards, S.J., Tyler, M.J. (2009). Systematics of the Australo-Papuan tree frogs known as *Litoria bicolor* (Anura: Hylidae) in the Papuan region. *Australian Journal of Zoology*, 56: 257-280.
- Myers, C.W., Duellman, W.E. (1982). A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. *American Museum Novitates*, 2752: 1-32.
- Parker, H.W. (1936). A collection of reptiles and amphibians from the mountains of British New Guinea. *Annals and Magazine of Natural History*, (10), 17: 66-93.
- Peters, W., Doria, G. (1878). Catalogo dei rettili e dei batraci raccolto E. Beccari, L.M. d'Albertis e A.A. Bruijn nella sotto-regione Austro-Malese. *Annali dei Museo Civico di Storia Naturale, Genova*, 13: 325-450.
- Richards, S.J. (2007). A new species of *Nyctimystes* (Anura: Hylidae) from Papua New Guinea and comments on poorly known members of the genus. *Phyllomedusa*, 6: 105-118.
- Richards, S.J., Johnston, G.R. (1993). A new species of *Nyctimystes* (Anura: Hylidae) from the Star Mountains, Papua New Guinea. *Memoirs of the Queensland Museum*, 33: 73-76.
- Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C., Cook, L.G. (2009). Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, 18: 4061-4072.
- Savage, J.M., Heyer, W.R. (1967). Digital webbing formulae for anurans: a refinement. *Herpetological Review*, 28: 131-131.
- Stejneger, L. (1916). New generic name for a tree-toad from New Guinea. *Proceedings of the Biological Society of Washington*, 29: 85-85.
- Tyler, M.J. (1962). Notes on the Papuan hylid frog *Nyctimystes gularis* Parker. *Copeia*, 1962(2): 435-436.
- Tyler, M.J. (1963). An account of collections of frogs from central New Guinea. *Records of the Australian Museum*, 26: 113-130.
- Tyler, M.J. (1964a). An investigation of the systematic position and synonymy of *Hyla montanus* Peters and Doria (Anura, Hylidae). *Zoologische Abhandlungen aus dem staatliches Museum fur Tierkunde in Dresden*, 27: 265-270.
- Tyler, M.J. (1964b). Taxonomic studies of some hylid frogs of Australia and New Guinea. *Proceedings of the Zoological Society of London*, 145: 91-106.
- Tyler, M.J. (1983). A new species of the hylid genus *Nyctimystes* from the highlands of New Guinea. *Transactions of the Royal Society of South Australia*, 91: 191-195.
- Tyler, M.J., Davies, M. (1979). Redefinition and evolutionary origin of the Australopapuan hylid frog genus *Nyctimystes* Stejneger. *Australian Journal of Zoology*, 27: 755-772.
- Tyler, M.J., Menzies, J.I. (2013). Case 3613. An application to have *Nyctimystes cheesmani* Tyler (1964) set aside in favour of *Nyctimystes cheesmanae* Tyler 1964. *Bulletin of Zoological Nomenclature*, 70: 30-32.
- Wiens, J.J., Kuczyński, C., Xia, H., Moen, D. (2010). An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution*, 55: 871-882.
- Zweifel, R.G. (1958). Results of the Archbold Expeditions No. 78: Frogs of the Papuan hylid genus *Nyctimystes*. *American Museum Novitates*, 1896: 1-51.
- Zweifel, R.G. (1980). Results of the Archbold Expeditions No. 103: Frogs and lizards from the Huon Peninsula, Papua New Guinea. *Bulletin of the American Museum of Natural History*, 165: 387-434.
- Zweifel, R.G. (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 1

Nyctimystes specimens examined.

N. bivocalis Kraus: UPNG4712 (Agaun).

N. calcaratus new species: UPNG2706 (holotype), 2702, 2703-05, 2709-12, 2714 (Bulolo); UPNG3561, -63, -85 (Mt. Suckling base camp nr. Biniguni).

N. cheesmanae Tyler: BMNH1947.2.24.31(holotype) (Mondo), BMNH1947.2.24.42-44 (paratypes) (Kokoda).

N. daymani Zweifel: AMNH57070 (holotype); BMNH1965.1122-23 (paratypes), (Mt. Dayman); UPNG 4711, -13 (Agaun).

N. eucavatus new species: UPNG3665 (holotype), 2040-41, 2043, 2045-49, 3663, 3677-79, 3683, 8875-80; (Baiyer River Sanctuary); SAMAR5210a-eee (Okapa), 5425a-k (Telefomin), 11797-98, AMSR14701, 14724-25, 17998, 18000-01, 18013, 18022, 18047, 18078 (Ganz River).

N. gularis Parker: BMNH 1935.3.9.173 (holotype); 1935.3.9.174-175 (paratypes) Mondo; UPNG 4072-80, 8850-53 (Woitape).

N. intercastellus Kraus: UPNG4883, 5413-15.8884-87 (Goodenough Island).

N. kuduki Richards: SAMA R62753 (holotype), SAMA R62750-52, 62754; UPNG 10047-48 (Moro).

N. latratus new species: UPNG4696 (holotype); UPNG4697-4701, 4703-10; UPNG5033, -35 (near Agaun); UPNG7137 (Bonenu); UPNG3562 . (Mt. Suckling base camp nr. Biniguni).

N. montanus Peters and Doria: MCSN 29720 (holotype) (Hatam, Arfak Mts);

N. obsoletus Lönnberg: SAMAR4250a-f; R4252a-c (Finschhafen); UPNG5734-35 (Go River); UPNG2978 (Sattelberg).

N. persimilis Zweifel: UPNG4715-34, 4737-39, 4819-20, 5034, 5036 (Agaun); AMR137937, -49-50, -52-54 (Agaun).

N. pulcher Wandolleck: SAMAR66921-25 (Haia), SAMAR39774-75 (Magidobo); SAMR39776-84, (Bobole and Namosado), SAMAR8646 (Bundi), SAMAR9293-95 (Mt. Nibo), SAMAR11149 (Migalsimbip); SAMAR11471 (Imegabip).

N. semipalmatus Parker: BMNH1947.2.24.45 (holotype) BMNH1947.2.24.46 (paratype) (Kokoda); SAMAR50702-30, 51703-18 (nr. Garaina); UPNG 1409-24 (nr. Garaina); UPNG 5238-39, 5326 (Aieme Creek).

N. traunae new species: UPNG 2058 (holotype), 2055-56, 2058-59, 2063-64, 3662, 3676, 3684, 3686, 3692; SAMAR8630, 8634, 8636, 8654, 8661, 8663-64 (Bundi).

Unnamed populations: SAMAR8373, 8920a-d, 9365 (Bomai and Karimui); SAMAR50831-39 (Bobole and Namosado); 67278-85 (Haia); SAMR39785 (Fau).

APPENDIX 2**Table 3.** Coordinates (decimal degrees) of places mentioned in the text.

Site	Coordinates	Site	Coordinates
Agaun	10.00°S, 149.37°E	Mafulu	8.26°S, 147.14°E
Aieme Creek	9.50°S, 147.62°E	Mai-u River, nr. Biniguni	9.50°S, 148.88°E
Baiyer River Sanctuary	5.57°S, 144.15°E	Manjim, Ganz R.	5.47°S, 144.50°E
Bobole	6.25°S, 142.78°E	Mondo	approx. 3 km E Fane Mission
Bomai	6.38°S, 144.60°E	Moro	6.35, 143.23°E
Bonenau	9.88°S, 149.40°E	Mount Dayman	9.83°S, 149.27°E
Bulolo	7.25°S, 146.67°E	Mount Simpson	10.02°S, 149.60°E
Bundi	5.73°S, 145.23°E	Musgrave R.	9.4°S, 147.73°E
Busu	6.30°S, 147.00°E	Namosado	(see Bobole)
Efogi	9.15°S, 147.83°E	Ok Ma	approx. 16 km SSE Tabubil
Fane Mission	8.38°S, 147.25°E	Okapa	6.52°S, 145.65°E
Fau	6.23°S, 142.70°E	Paup	3.23°S, 142.58°E
Finalbin,	approx. 6.5 km NNE Tabubil	Rossel Island	11.37°S, 154.22°E
Finschhafen	6.63°S, 147.87°E	Sattelberg	6.50°S, 147.73°E
Garaina	9.65°S, 150.67°E	Simbang	(see Finschhafen)
Goodenough Island	9.33°S, 150.25°E	Sudest Island	11.58°S, 153.47°E
Go River	6.63°S, 147.58°E	Tabubil	5.28°S, 141.22°E
Goroka	6.08°S, 145.42°E	Telefomin	5.12°S, 141.57°E
Guwasa	6.47°S, 145.10°E	Ubai Gubi	approx. 60 km SW Goroka
Haia	6.70°S, 144.98°E	Wau	7.37°S, 146.75°E
Karimui	6.50°S, 144.82°E	Woitape	8.55°S, 147.25°E
Kavorabip	5.13°S, 142.12°E	Yapen Island (Serui)	1.87°S, 136.28°E
Kokoda	8.88°S, 147.75°E		