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Notes on tree frogs, *Nyctimystes* species (Anura: Hylidae) of New Guinea; the *Nyctimystes papua* species group

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The definition of the *Nyctimystes papua* Species Group, as created by Zweifel (1983), is further elaborated and the differences between *N. papua* and *N. disruptus*, including morphology and geography, are discussed. The possibility that *Nyctimystes disruptus*, as currently recognised, includes more than one species, with either green or brown eyes, is also investigated. The diagnostics of *Nyctimystes oktediensis* are reviewed leading to the conclusion that it is not distinct from *N. disruptus*.

INTRODUCTION

Two genera of tree frogs (Hylidae) occur in the Papuan Region, *Litoria* and *Nyctimystes*. *Nyctimystes* species are distinguished from *Litoria* by a vertical (as opposed to horizontal) pupil and a pattern of lines on the clear part of the lower eyelid. The monophyly of *Nyctimystes* is currently in doubt and recent authors (Frost *et al*., 2006; Rosauer *et al*., 2009; Wiens *et al*., 2010), on molecular grounds, have placed the species of *Nyctimystes* within *Litoria* as a sister group to *Litoria infrafrenata*. However, not all authors have accepted this significant reclassification (Kraus, 2012, 2013; Menzies, 2014a, 2014b) and have retained *Nyctimystes* as a valid genus.

If the somewhat aberrant *Nyctimystes rueppelli* from Halmahera is excluded, *Nyctimystes* species are restricted to the island of New Guinea and the d'Entrecasteaux and Louisiade islands to the south-east. Some species have been placed into groups sharing similar morphology such as the *Nyctimystes cheesmanae* species group (Menzies, 1976), the *Nyctimystes papua* species group (Zweifel, 1983) and the *Nyctimystes narinosus* species group (Menzies, 2014b), but the monophyly of *Nyctimystes* has not been conclusively demonstrated.

The *Nyctimystes papua* group of species is distinguished from other *Nyctimystes* species by having an eyelid reticulum that leaves the posterior portion of the eyelid clear (Zweifel, 1958, figure 19a; Menzies, 2006, figure 17e) or with a vestigial venation. Prior to 1963, all *Nyctimystes* with an incomplete palpebral venation had been identified as *N. papua*, giving it a very wide distribution through the central and south-eastern mountains of New Guinea (e.g. Zweifel, 1958, figure 13). Tyler (1963) then described *Nyctimystes disruptus* from the Schrader Mountains of central Papua New Guinea and distinguished it from *N. papua* by "more extensive webbing between the fingers and a palpebral venation which, although disrupted, is far more pronounced than in that species". His illustration (Tyler, 1963 figure 1) shows an eyelid pattern of short, oblique, broken lines more or less absent from the posterior quarter of the eyelid. There is no mention of eye colour in the original description nor has any author referred to comparative body size in *N. papua* and *N. disruptus*. By 1983, it had been realised that frogs previously identified as *N. papua* from the central highlands of Papua New Guinea were, in fact, *N. disruptus* and that "the only specimens that can be referred with confidence [to *N. papua*] were those of the syntype series" (Zweifel, 1983). In that paper, Zweifel designated a lectotype for *N. papua*, formally recognised a '*Nyctimystes papua* species group' and described two new species of that group, *N. trachydermis* and *N. tyleri*. The only other

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relevant discovery has been the description of the new species, *Nyctimystes oktediensis* (Richards & Johnson, 1993) distinguished from *N. disrupta* by, inter alia, iris colour.

The precise type locality for *Nyctimystes papua* is not known. The collector, A.S. Anthony, collecting for Lord Rothschild, had "his final camp on Mt. Victoria and Mt. Knutsford" between April and June 1896 (Wichmann, 1912). Mt. Knutsford is about 16 km north of Mt. Victoria. Mt. Victoria is the highest point in the Owen Stanley Mountain Range which forms the backbone of the south-eastern peninsula of New Guinea. To my knowledge, no one has attempted to trace Anthony's route and no new material has been collected in the immediate region. However, frogs that agree well with the lectotype of *N. papua* have been collected in several locations in the Owen Stanley Mountains, including Mt. Albert Edward, about 50 km to the north of Mt. Victoria, Woitape 70 km further west and the vicinity of Mt. Dayman, 200 km to the south-east (listed in the species account). It is now possible to give a more information on *Nyctimystes papua* and its allies and their distribution.

MATERIALS AND METHODS

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Standard measurements were taken as follows: body length, male or female (HBm, HBf) is taken from the tip of the snout to the 'bump' caused by the distal end of the urostyle. This gives a slightly shorter measurement than the more common snout-vent length (SVL) and consequently, a slightly longer tibial/body length ratio. If SVL measurements are taken from the literature for comparative purposes, they are converted to HB by a factor of 0.952 which I derived by comparing both measurements in a batch of *Nyctimystes disruptus* from a single locality. Tibial

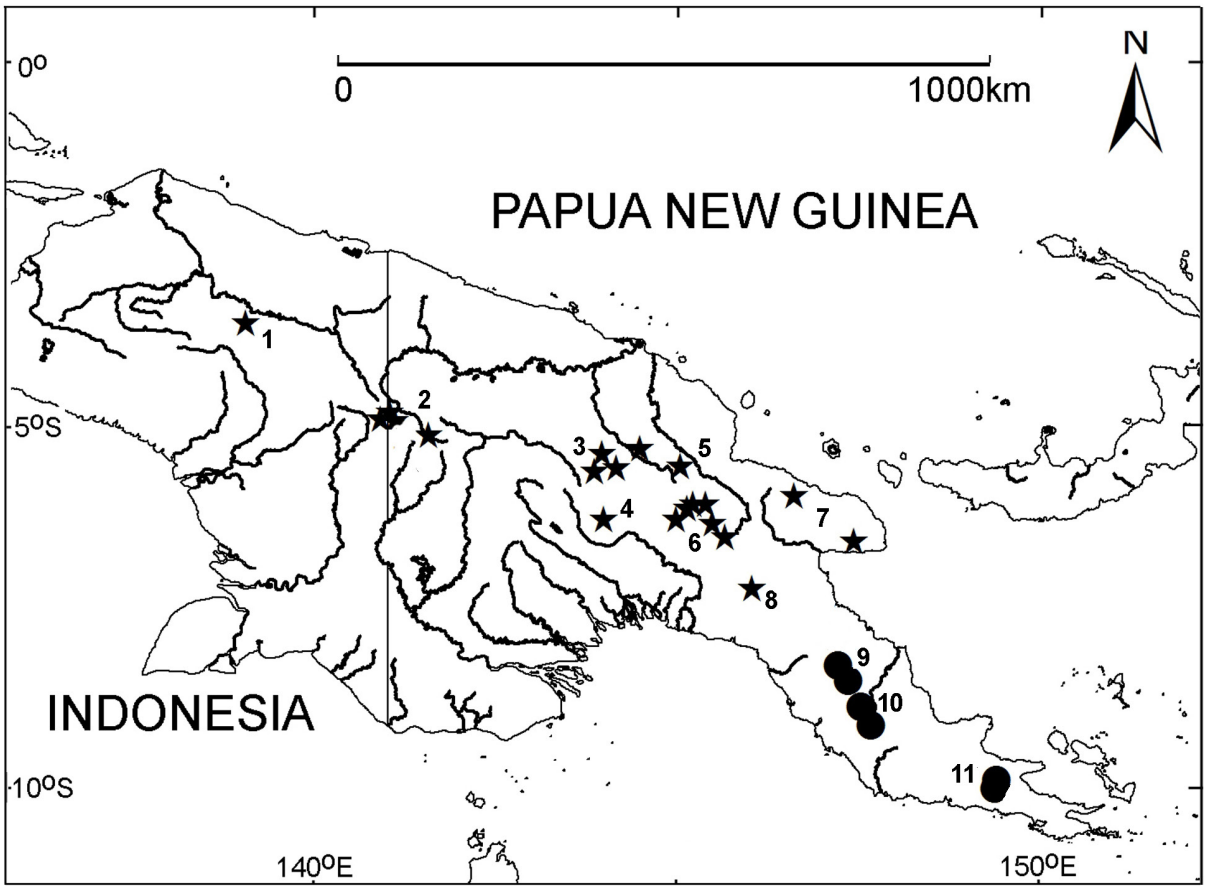

Figure 1. Distribution of *Nyctimystes papua* (spots), *N. disruptus* (stars) and *N. oktediensis* (cross). Not all known localities for *N. disruptus* are shown. 1 Mistkamp, Idenburgh River; 2 Star Mountains localities; 3 Western Highlands localities; 4 Southern Highlands localities; 5 Schrader Mountains; 6 Eastern Highlands and Simbu localities; 7 Huon Mountains localities; 8 Kratke Mts. (Wonenara); 9 Mt. Albert Edward and Woitape; 10 Mt. Victoria, Efogi and Myola; 11 Mt. Dayman (Agaun and Bonenau).

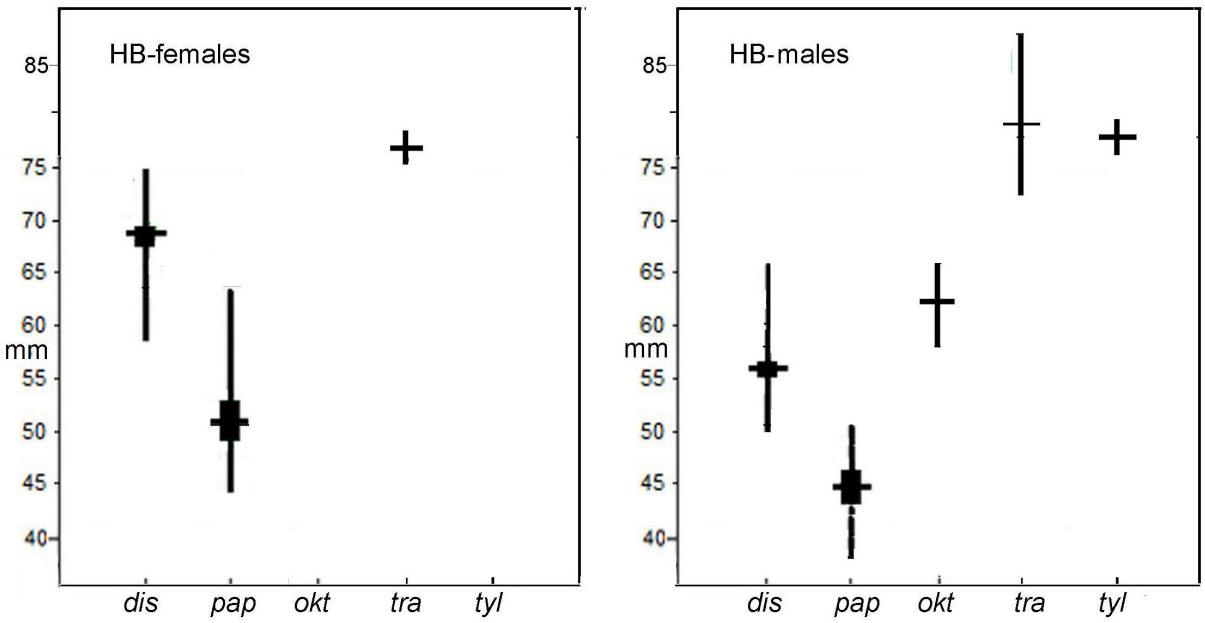

Figure 2. Comparative sizes of members of the *Nyctimystes papua* species group: *N. disruptus* (dis), *N. papua* (pap), *N. oktediensis* (okt), *N. trachydermis* (tra) and *N. tyleri* (tyl). Some data for *N. oktediensis*, *N. trachydermis* and *N. tyleri* were taken from the literature. Horizontal lines are the means and thick vertical lines their standard deviations which are not calculated for *Nyctimystes trachydermis* and *N. tyleri* due to very small sample size. Probabilities for the difference between means are (females) $p < 0.0001$; (males) $p < 0.0001$.

length (TL) is the external measurement with the joints held at right angles. Head length is taken from the tip of the snout to the angle of the jaws and head width (HW) is measured at mid-tympanic level. Eye-naris distance (EN) is from anterior rim of the orbit to mid-point of the nostril and inter-narial distance is between mid-points of the nostrils. Eye diameter (EY) and tympanic diameter (TY) are horizontal measurements. F3d and T4d are horizontal widths of the 3rd finger and 4th toe disks.

The statistical analyses used were taken from the JMP statistics package (SAS Inc. Version 4.0.3) for t-Tests and the SPSS package, version 20 (IBM SPSS Corporation, 2014) for multivariate analyses. The use of "significant" in the results indicates a probability of 0.05 or better. Details of the analyses are placed in appendix one.

Museum specimens referred to have the following abbreviations: AMNH for the American Museum of Natural History, New York, AMS for the Australian Museum Sydney, BMNH for the Natural History Museum, London, MZB for the Indonesian Zoology Museum, Cibinong, QMJ for the Queensland Museum, Brisbane, NML for Naturalis, Leiden, SAMA for the South Australian Museum, Adelaide and UPNG for the University of Papua New Guinea, Port Moresby.

All specimen localities are in Papua New Guinea or the Indonesian Province of Papua and provincial abbreviations are as follows: CenP, Central Province; EHP, Eastern Highlands Province; EngP, Enga Province; MadP, Madang Province.; MBP, Milne Bay Province; MorP, Morobe Province; NorP, Northern Province.; PapP, Papua (Indonesia); 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 localities of all places from where material originated and a list, with geographical coordinates, is included in Appendix 2.

RESULTS

The *Nyctimystes papua* species group

As diagnosed by Zweifel (1983) this group of species is distinguished by a "palpebral venation sparse or at least much reduced compared with other *Nyctimystes*, males lacking vocal sac; snout relatively high, short and rounded; EN/IN ratio 1.20 or less; outer fingers one half or less webbed; size moderate to large (males 50 to 80 mm SV)." To this, I can add the coloration, which, on the dorsum, consists of a blotchy mottle of dark on a lighter background which is brown or often with a purplish or greenish tinge. Although males in this group appear to

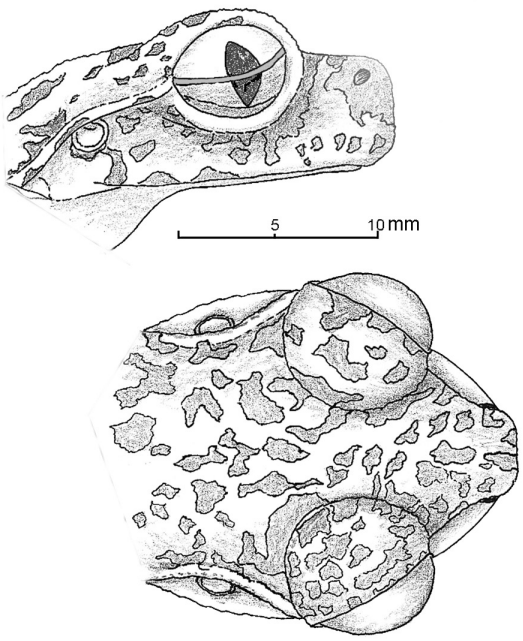

Figure 3. *Nyctimystes papua* lateral and dorsal views of the head of specimen UPNG 4065 from Woitape. Scale line = 10 mm.

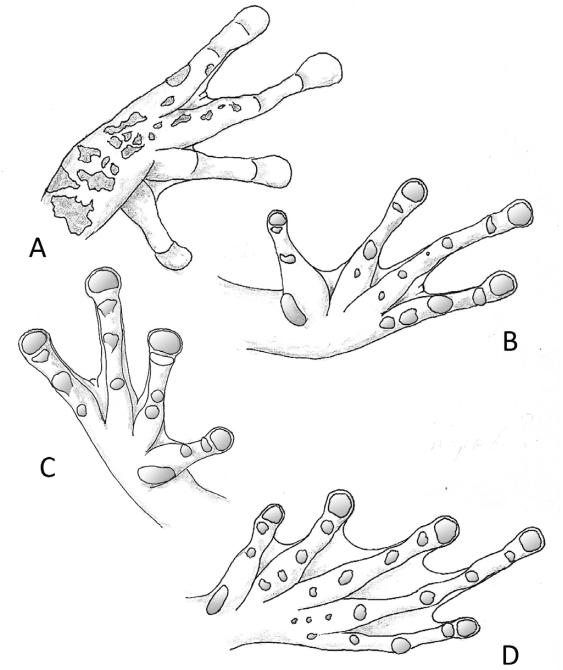

Figure 4. *Nyctimystes papua*: **A, B.** hand, dorsal and palmar views, UPNG 4065; **C.** hand, palmar view UPNG 4083; **D.** foot, plantar view, UPNG 4083.

have no vocal sacs this does not necessarily mean that they have no voice as one specimen, in captivity, made a clucking sound, rather like a chicken

Zweifel did not suggest monophyly for the *Nyctimystes papua* species group as there was no evidence to show that the shared characters were attributable to common ancestry. The current content of this group is five species, *N. papua* (Boulenger, 1897), *N. disruptus* Tyler, 1963, *N. trachydermis* Zweifel, 1983, *N. tyleri* Zweifel, 1983, *N. oktediensis* Richards & Johnston, 1993 and the distribution of *Nyctimystes disruptus* and *N. papua* in New Guinea is shown in fig. 1. *Nyctimystes trachydermis* and *N. tyleri* are much larger than the other species (fig. 2) and are not included in subsequent statistical analyses.

Nyctimystes papua (Boulenger)

Nyctimantis papua, Boulenger 1897, 12.

Nyctimystes papua, Stejneger 1916, 85.

Hyla papua Noble, 1931, 513.

Litoria papua, Frost *et al*., 2006, 362.

Lectotype. BMNH 1896.10.31.50 collected by A.S. Anthony on Mt. Victoria, Central Province of Papua New Guinea, between April and June 1896, designated as lectotype by Zweifel (1983). The exact altitude is unknown but as Anthony spent several weeks in the area it is likely that he established camps at different altitudes between the main peak of Mt. Victoria and Mt. Knutsford. Birds collected on this trip were "mostly taken at elevations of from 5000 to 7000 feet (=1500-2100 m)." (Rothschild and Hartert 1896).

The original description did not specify a holotype and merely noted "several specimens." Of the four remaining in the Natural History Museum one (BMNH 1896.10.31.51), recognised by both Tyler (1963) and Zweifel (1983) as different, has been reallocated to *Nyctimystes ocreptus* (Menzies, 2014b). A fifth specimen, not examined, is now in the Museum of Comparative Zoology at Harvard (MCZ 12838).

Material examined. The lectotype, BMNH 1896.10.31.50, and paralectotypes 1896.10.52-53, Mt. Victoria, CenP, 1500-2150 m; UPNG 2876-2879, Avios, Mt. Albert Edward, CenP, 2600 m; UPNG 4049, 4062-4069, 4081-4083 and AMR 23449-23451, Woitape, CenP, 1570 m; UPNG 4735-4736, Agaun, MBP, 1385 m; UPNG 5037, Bonenau, MBP, 1550 m; UPNG 5505-5506, 8853, Efogi, CenP, 1250 m.

Diagnosis. The original description listed, inter alia, a short snout with strong canthus rostralis and concave

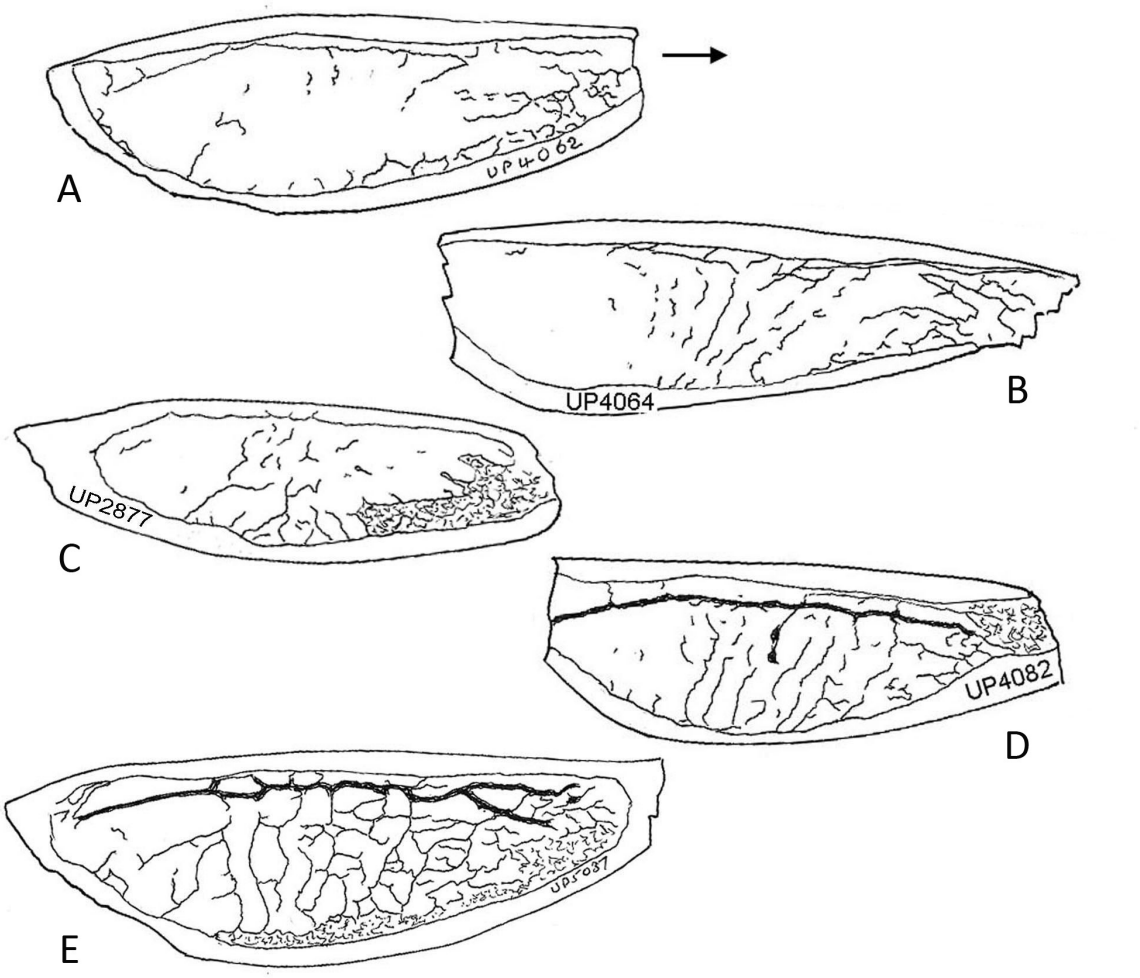

Figure 5. *Nyctimystes papua*, eyelid venation: **A.** UPNG 4062, Woitape; **B.** UPNG 4064, Woitape; **C.** UPNG 2877, Mt. Albert-Edward; **D.** UPNG 4082, Woitape; **E.** UPNG 5037, Bonenau. Arrow denotes anterior direction.

lores, tympanum distinct, fingers webbed at the base, disks larger than the tympanum, but made no mention of the eyelid venation. In the revision of 1958, Zweifel noted *Nyctimystes papua* to be "A moderate sized species with much reduced and indistinct palpebral venation, scantily webbed fingers and no vocal sac or vocal sac openings in the male." The original description included "Male with an external subgular vocal sac." (Boulenger, 1897). This contradiction has not been investigated other than to confirm that there are no openings from the floor of the buccal cavity into a vocal sac. "Moderate size", with the addition of more material shows that the maximum male HB is 51 mm and HBf is 63 mm (fig. 2). *Nyctimystes papua* is the smallest member of the *N. papua* species group.

Morphology. Characteristic features of the external morphology are listed in the diagnosis above and fig. 3 illustrates the head of a typical *Nyctimystes papua*. Zweifel (1983) describes the hand web as 'scant' while Parker (1936, figure 2) illustrates a hand with the web not reaching the penultimate tubercle on digit 4. Two specimens from Woitape (fig. 4.A-C) show slightly more webbing so, collectively, the hand web can be described as basal to one third. None of the males from Woitape shows a pigmented nuptial pad but there is an unpigmented, swollen area on the first digit. As these specimens were taken from an (apparently) breeding population, lack of pigmented pads is surprising. Commenting on a large sample from Mondo, about 16 km from Woitape, Parker (1936) notes a "small, round nuptial pad on the first finger of the males but does not say if the pad was pigmented.

The syntype series is now so faded that the palpebral venation is hardly visible but it appears to have been very sparse, perhaps just a few broken lines and dots. In the specimens from Woitape the venation varies from very sparse (fig. 5.A) to extending over the anterior two thirds of the eyelid (fig. 5.D) but, in all cases, the lines are thin and broken. In the two specimens from above Agaun, on the slopes of Mt. Dayman, the venation is just a few vague lines on the lower edge and anterior end of the eyelid. Contrarily, the female from Bonenau, a short distance from Agaun (fig. 5.E) shows a more or less complete venation, but distinctly sparse on the posterior third of the eyelid and the lines are, again, very thin. In summary the venation is usually sparse all over and always reduced on the

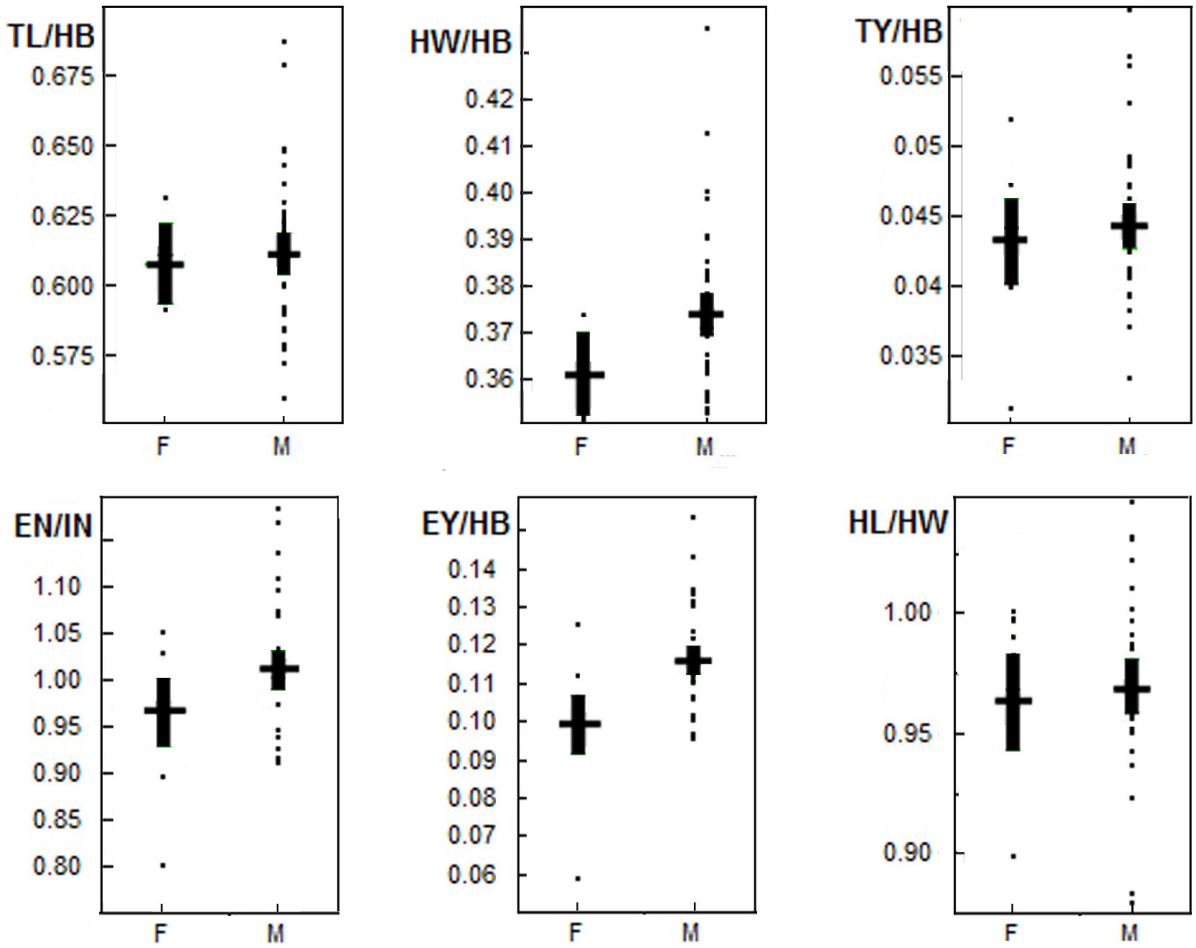

Figure 6. *Nyctimystes disruptus* comparison of male and female proportions. Horizontal lines are the means and thick vertical lines their standard deviations. Probabilities for the differences between means are TL/HB $p > 0.7646$; HW/HB $p > 0.0700$; TY/HB $p > 0.6515$; EN/IN $p > 0.1542$; EY/HB $p > 0.0085$; HL/HW $p > 0.6954$.

posterior part of the eyelid.

Colouration of the syntypes (Boulenger 1897) is "Grey, olive or reddish brown above, uniform or marbled with darker or with large insuliform spots; a light line may run along the canthus rostralis and superciliary edge",

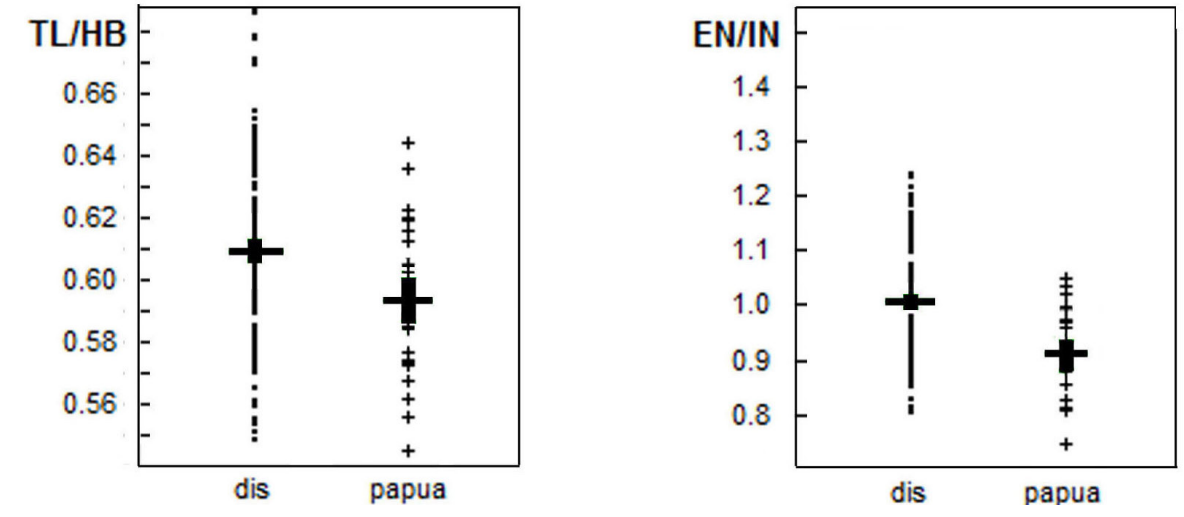

Figure 7. Comparison of TL/HB and EN/IN ratios in *Nyctimystes disruptus* and *N. papua*. Horizontal bars are the means and thick vertical bars their 95% confidence limits. Probabilities for the difference between means are 0.006 (TL/HB) and 0.0001 (EN/IN).

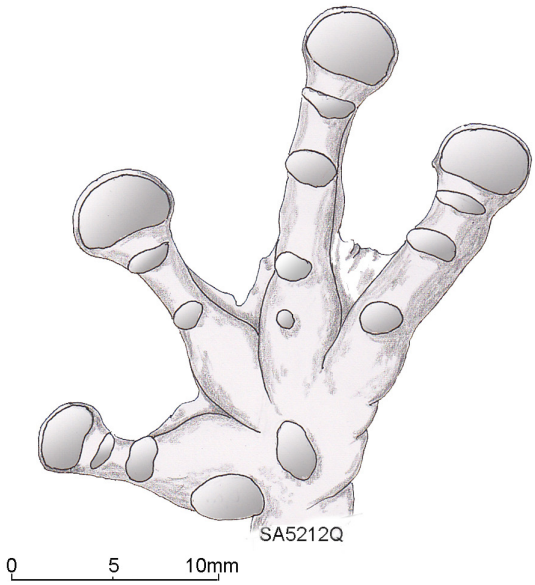

Figure 8. *Nyctimystes disruptus*, SAMR 5212Q, palmar view of left hand.

and Parker's 1936 description of the large series from Mondo is similar. In general, this description would apply to all the material here studied. The colour fades on the flanks but the mottling may persist; ventrum is usually plain white or grey. In specimens from Avios on Mt. Albert Edward the dorsum is brownish without distinct marks, paler on the flanks; on the anterior sides of the thighs and lips are bright yellowish spots and the canthus rostralis and supraciliary margin are outlined in the same bright colour; ventrum dark with white blotches. After many years in spirit the colours duller but otherwise unchanged. The Agaun and Bonenau specimens have the dorsum yellowish brown mottled all over with irregular inter-linking blackish patches which form irregular bars across the limbs; the flanks paler but still with bold blackish markings; the concealed surfaces of the thighs black with white mottle. One specimen is illustrated in life, in Menzies 2006, plate 95. Some Woitape specimens have the dorsum tan with irregular purple-red-brown mottle, vaguely barred on the limbs, others have the dorsum dark slate-coloured with darker mottle, ventrum always white but with darker mottle on throat of females. One specimen from the Kokoda area displays a rather uniform tan coloration with a greenish wash over the dorsum while another has dark green and brown blotches on the hind limbs (fig. 10. A-B).

Distribution. The south-eastern peninsula of New Guinea, from 1200-2600 m, the known limits being Mount Albert-Edward in the west to Mt. Dayman in the south-east (fig. 1). The single male specimen (BMNH 1980.650) from Lake Trist, about 100 km north-west of Mt. Albert Edward, may represent this species but is 2 mm longer than maximum HB and has a higher EN/IN ratio. Identification is not confirmed.

Nyctimystes disruptus[1] Tyler

Nyctimystes disrupta Tyler, 1963, 118

Litoria disrupta Frost *et al*., 2006, 362.

Holotype. AMR 15923 Kaironk Valley, Schrader Mts, MadP, about 1850 m, collected by R.N.H Bulmer in February 1960.

Material examined. 181 specimens from localities in the central highlands of New Guinea as follows: AMR 124127 Nokopo, MadP; NML 12103-04, 47925 Ok Minam PapP; SAMR 5601a-n Goroka, EHP; SAMR 6155a Rintibe, EHP; SAMR 9373a-c, Lafoyufa, EHP; SAMR 9374 Andandara, EHP; SAMR 8281, 9388a, 8671, 8672 Bundi, MadP; SAMR 9123a-b Dumun, EHP; SAMR 9388a-b Kaironk, MadP; SAMR 5212a-bm, 5066a-h Okapa, EHP; SAMR 9337a-c Menyamya, MorP; SAMR 9367 Ialibu, SHP; SAMR6845-47 Tulum, SHP; SAMR 6824 Tumia, SHP; SAMR 5424a-k, 54117a-b Telefomin, SanP; SAMR 6515a-c, 6455a-b Busilmin, SanP; SAMR 6508a-c Moiyokabip, WesP; SAMR 4928, 9290 Wapenamunda, EngP; SAMR 6156 Igindi, WHP, SAMR 5551a-c Watabung, EHP; SAMR 5616 Baiyer River, WHP; SAMR 5716a-c Koko (not located); SAMR 8655, 8659 New Bonome (not located); SAMR 7156a-c no data. UPNG 3210, 3211, 3461 Chuave, SimP; UP1226-28 Wonenara, EHP; UP9223, 9239 Mt. Gulno, MadP; UPNG 3509-10, 5151 Kompiam, WHP; UPNG 3258, 3259, 3261, 3262, 3264-3269 Kaironk, MadP.

The sample of *Nyctimystes disruptus* from Okapa (n = 40 females, 33 males) was large enough to test for differences between males and females and showed that females were approximately 20% longer than males but revealed no significant differences in the ratios TL/HB, HL/HW, and EN/IN (fig. 6). There was a significant difference (p = 0.02) in eye size, males had larger eyes than females and males appeared to have wider heads but the difference was not significant (p = 0.07). Males and females were therefore combined in analyses using all variables except HB.

[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 *disruptus*, rather than *disrupta*.

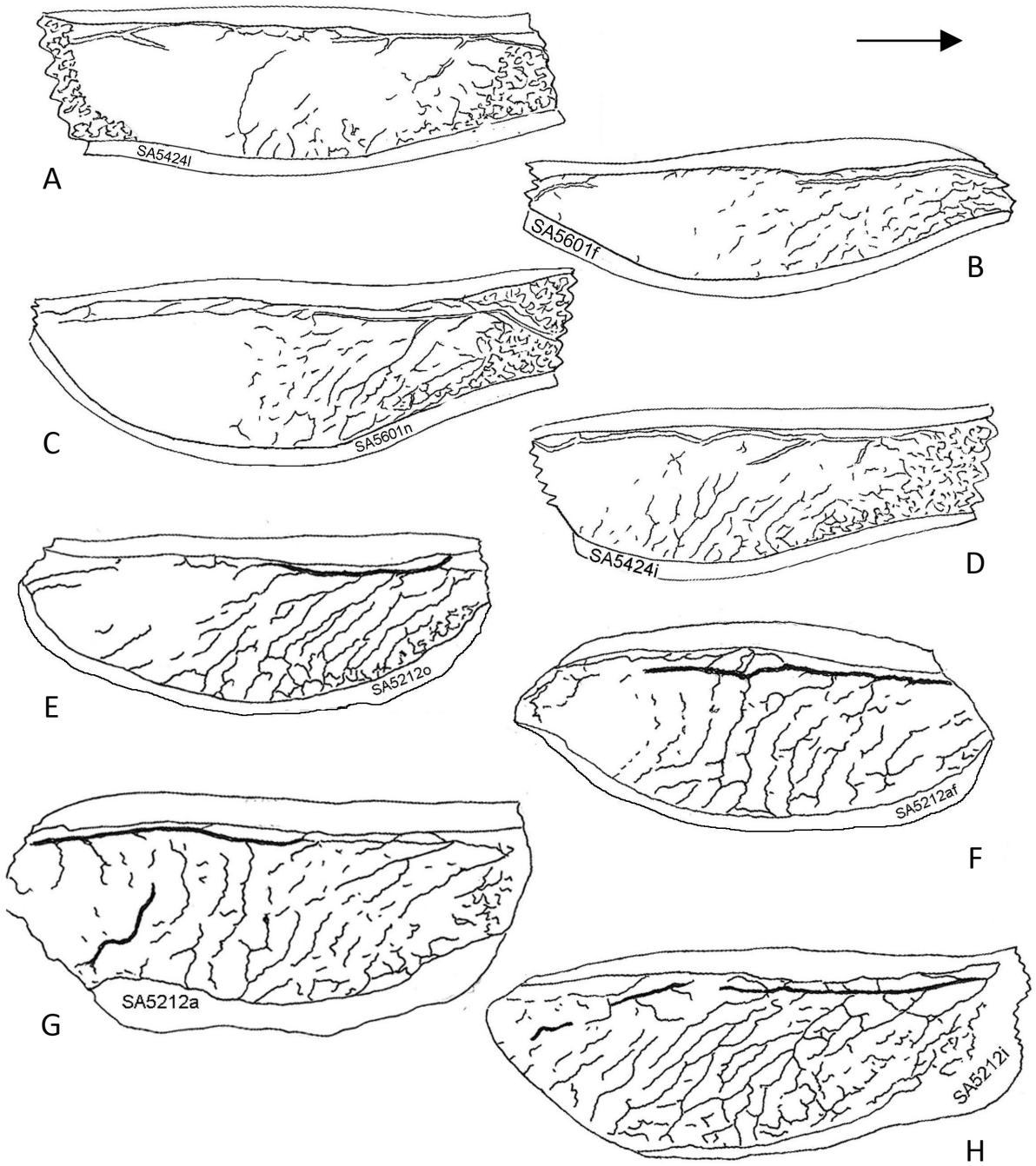

Figure 9. *Nyctimystes disruptus* variation in eyelid venation. **A.** SAMR5424l Telefolmin; **B.** SAMR5601f, Goroka; **C.** SAMR5601n, Goroka; **D.** SAMR5424i, Telefolmin; **E.** SAMR5212o, Okapa; **F.** SAMR5212af, Okapa; **G.** SAMR5212a, Okapa; **H.** SAMR5212i, Okapa. Arrow indicates anterior direction.

Diagnosis. Tyler (1963), in the diagnosis, described *Nyctimystes disruptus* "a species with close affinity to *Nyctimystes papua*" but distinguished from that species by "more extensive webbing between the fingers and a palpebral venation which, although disrupted, is far more pronounced than in that species". His illustration (Tyler, 1963, figure 1) shows an eyelid pattern of short, oblique, broken lines more or less absent from the posterior quarter. He further distinguished it from *N. papua* by difference in EN/IN ratio (no overlap) and partial overlap in TL/SVL ratios. With the larger samples now available, I find significant differences in the mean ratios but the overlap is so great that the characters have little utility in distinguishing between the species (fig. 7). There is no mention of eye colour in the original description and size is not discussed although the female holotype, at 70 mm, indicates a larger species than *Nyctimystes papua* where the largest female in the current sample measured 63 mm HB.

Zweifel (1983), establishing a '*Nyctimystes papua* Species Group', further diagnosed *N. disruptus* by

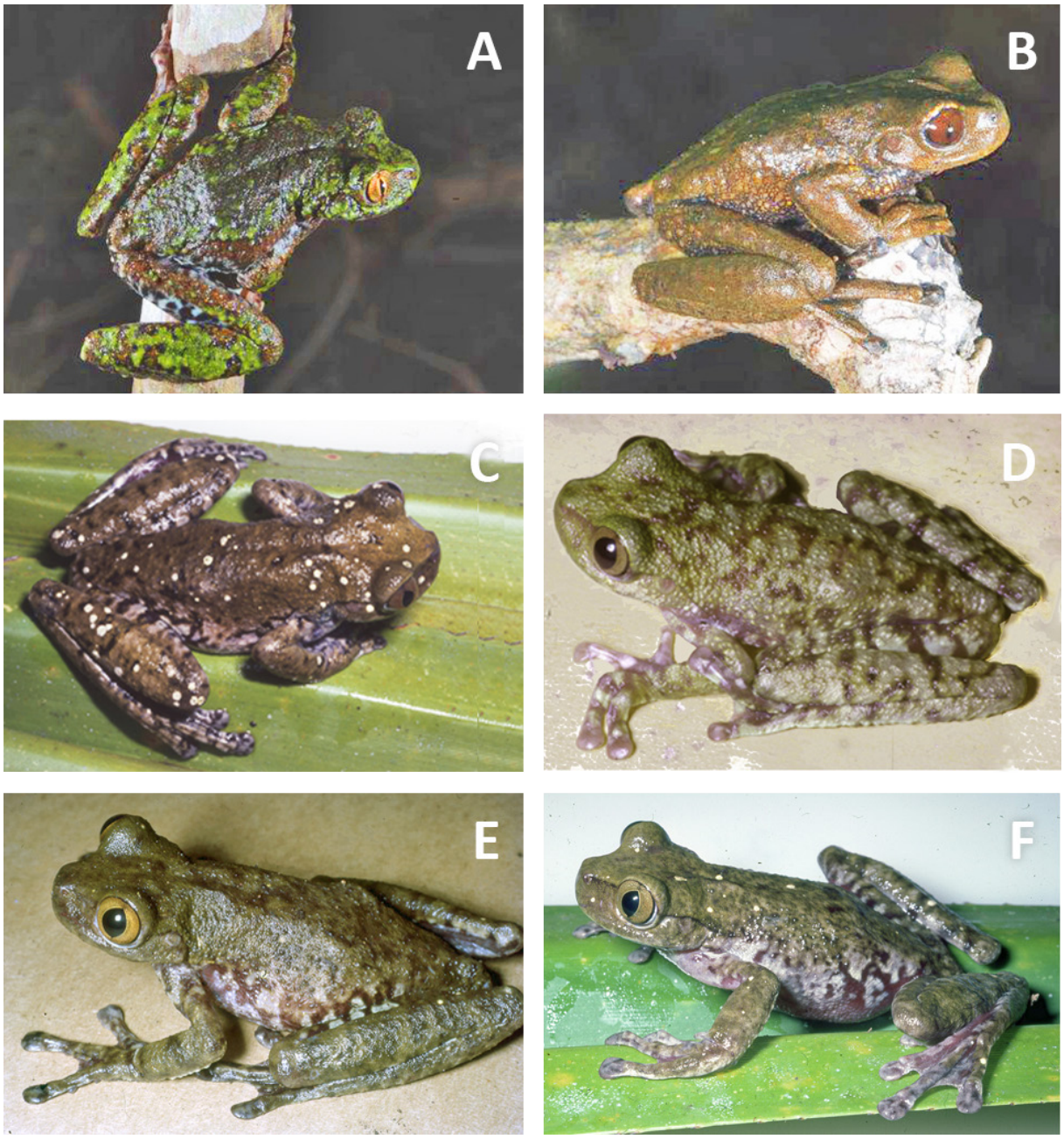

Figure 10. Colour varieties of *Nyctimystes papua* from Kokoda (**A**, **B**) and *Nyctimystes disruptus* (**C-F**) from the eastern highlands of Papua New Guinea; **C.** Ubaigubi; **D.** Watabung; **E.** Purosa; **F.** Ubai Gubi. Photos by Allen Allison (A, B) and Fred Parker (C-F).

"moderately large size" (male SVL < 74 mm, female SVL < 80), outer fingers "about one-half webbed", tympanum visible and "iris green in life". The iris colour was not mentioned in Tyler's original description but a green colour was noted in some other specimens that Zweifel had seen. These included specimens from the Western Highlands Province, "iris green with a greyish tint", from the Eastern Highlands Province, "iris greenish tan" and one from the Huon Peninsula "iris green" (Zweifel 1983).

Woodruff (1972) noted that a single specimen that he had collected in the Simbai Valley (close to the Kaironk type locality) was intermediate in three diagnostic characters (palpebral venation, finger webbing and EN/IN ratio) between *N. disruptus* and *N. papua* and therefore "*N. disrupta* must be regarded as a species of doubtful validity." He did not mention body size.

Tyler's third diagnostic feature concerns the amount of webbing between the fingers. Finger webbing in *N. papua* has been illustrated by Parker (1936, figure 2), Zweifel (1983, figure 1) and here in fig. 4. Zweifel showed hand webbing, in *N. disruptus*, to be somewhat variable. I have examined a large number of specimens and the

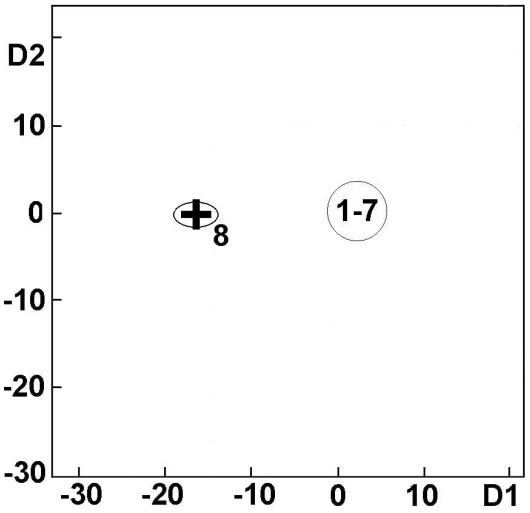

Figure 11. Multivariate analysis of eight geographical groups of *Nyctimystes disruptus* and *N. papua*. + centroid of group 8 and ellipse its 95% confidence limits; centroids of groups 1-7 are contained in the circle and are too close to show separately. 1 Eastern Highlands, 2 Schrader Mts., 3 Huon Mts., 4 Okapa, 5 Southern Highlands, 6 Star Mts., 7 Western Highlands, 8 Owen Stanley Mts (see fig. 1). D1 and D2 are the first and second discriminant axes.

maximum finger webbing that I have seen is illustrated in fig. 8, slightly less than the maximum illustrated by Zweifel (1983, figure 8) and not greatly different from that seen in my, admittedly small, sample of *N. papua*.

Tyler's diagnostic statement about palpebral venation is true in general but there is far more variation in both species than suggested and this feature does not distinguish *N. disruptus* from *N. papua*. Fig. 9 displays the condition in eight examples of *Nyctimystes disruptus* covering 470 km through the central highlands of Papua New Guinea. The venation ranges from very sparse (fig. 9.A) to half the eyelid (fig. 9.E-F) to a complete cover (fig. 9.H) but, as with *Nyctimystes papua*, the lines on the posterior part of the eyelid, when present, are distinctly more broken than those anterior. Specimen NML 12103 is interesting in that the patterns on left and right are different. On the left is a dense network of thin lines and dashes with horizontal lines towards the upper margin and the posterior third clear, on the right, oblique lines fill the anterior half leaving the rest clear.

In colouration, *Nyctimystes disruptus* is highly variable. I described one specimen in life from the Schrader Mountains as "lead colour, obscurely mottled with purple blotches, flanks paler but with purple blotches, barred purplish on the thighs, reddish purple below but mottled with grey on throat". Another specimen (Menzies, 2006, plate 93) was similar but more greenish, yet another was spotted with white. Photographs (fig. 10), in life, of four specimens from various eastern highlands localities differ in ground colour from pale to very dark but all display the often inter-linked dark blotches tending to form bars across the limbs. Brongersma and Venema (1962) describe a specimen from the Ok Minam in the Star Mountains thus "(*Nyctimystes papua*) was brown with large white-edged black blotches on the after part of its back…". Iris colour was not mentioned.

Nyctimystes disruptus is a very common frog in the central highlands of Papua New Guinea and I have collected many of them, but never one with a green iris. A specimen collected at the type locality was described in my field notebook as having "iris dark grey-brown" and one with a brown iris from the same locality is illustrated in colour in Menzies (2006, figure 93). A specimen from the Kratke Mts (Menzies, 2006, figure 92) clearly shows a brown iris. Photographs (fig. 10) taken by Fred Parker include eight different examples of *N. disruptus* from the Eastern Highlands, all show unequivocally, brown, greyish-brown or golden irises. After preservation the iris may appear dark or mid brown but the colour is usually milky and obscure. It is possible that two similar species, with green or brown irises, may exist syntopically but, unfortunately, the majority of museum specimens bear no information on iris colour in life and there is nothing else to separate them. Iris colour obviously needs more study and, presently, cannot be used as a diagnostic feature for *N. disruptus*.

Distribution. *Nyctimystes disruptus*, as presently understood, is common throughout the central highlands of Papua New Guinea from Wonenara in the east to the international border at 141°E and also in the Huon Peninsula Mountains, approximately 1500-2000 m asl. The distribution map (fig. 1) shows a gap of approximately 120 km between the Star Mountains and 144°E. This is probably due to lack of surveys in that region but may also be due to the predominance of karst formations with scarcity of surface water, so unsuitable for water-breeding frogs. Richards and Dahl (2011) did not collect this species in the Muller Range, "not surprising given the scarcity of surface water."

Confirmed records from western New Guinea include three specimens in the Naturalis Museum, Leiden (NML 12103-104, 47925, labelled *N. papua*), from the Ok Minam in the Star Mountains. Ok Minam is quite close to the international border. There are also two specimens in the American Museum of Natural History (AMNH 49671, 49674) from Mistkamp, a site at 1800 m in the valley of the Idenburg River. Zweifel made comment on these, allocating them to the *Nyctimystes papua* species group and so implying that they had an incomplete palpebral venation though he did not specifically say so. Zweifel did not include these within *N. disruptus* because of their "unusually low EN distance" (EN/IN 0.85). This value is within the range of my very large series of *N. disruptus*, though close to the lower limit, and I would not exclude them from *N. disruptus* on that character alone. There is also an example (MZB 15010) from the Jayawijaya Mountains, not examined, in the Indonesian Museum that is labelled *Nyctimystes papua* but, with a high EN/IN ratio, the identification is suspect. It seems likely that

the distribution of *Nyctimystes disruptus* extends right through the central mountains of New Guinea and the mountains of the Huon Peninsula. There are no records for any of the other north coast mountain ranges.

There are no known areas of sympatry for *N. disruptus* and *N. papua*, *N. trachydermis* or *N. tyleri*. The closest approach would be Wonenara (*N. disruptus*) and Mt. Albert-Edward (*N. papua*), about 200 km distant.

Nyctimystes oktediensis Richards & Johnston

Nyctimystes oktediensis Richards & Johnston, 1993, 73.

Litoria oktediensis Frost *et al*., 2006, 362.

Holotype. QMJ 56896 collected by S.J. Richards and G.R. Johnston on Mt. Akrik, Star Mountains, WesP, in 1991, altitude 1625 m.

Material examined. paratype SAMR 4077 (locality as holotype).

Diagnosis: *Nyctimystes oktediensis* was distinguished from *N. papua* by (inter alia) much larger size and more extensive palpebral venation; from *N. trachydermis* by smaller size, smooth skin and a tympanum that is visible, not concealed; from *N. tyleri* by smaller size and by brown, not yellow iris and from *N. disruptus* by similar body size but brown, not green, iris and more extensive palpebral venation.

Comment. The question of iris colour has already been discussed and ruled out as a diagnostic feature for *N. disruptus*, therefore one distinction from that species disappears. Other diagnostic features are the "more extensive webbing between the fingers and palpebral venation of very fine disrupted lines" in *N. disruptus*. The holotype eyelid (Richards & Johnston, 1993, figure 1) shows a pattern of thin, forking lines more or less covering the entire eyelid, though rather sparser posteriorly. Comparison of that illustration with fig. 9 here shows some eyelids with more veins. Zweifel (1983, figure 8) has pointed the considerable variation in finger webbing so that character is also unreliable in distinguishing *N. disruptus* from *N. oktediensis*. The excellent photo of the *Nyctimysstes oktediensis* holotype, in life, (Richards & Johnston, 1993, figure 3) shows a coloration typical of the *Nyctimystes papua* group and similar to what I have described for *N. disruptus*, above.

My conclusion is that the species *Nyctimystes oktediensis* is of doubtful validity and it is here regarded as a junior synonym of *N. disruptus*.

Distribution. *Nyctimystes oktediensis* is only known from two localities in the Star Mountains, 1625-2200 m where *N. disruptus* has also been collected.

Nyctimy trachydermis Zweifel

Nyctimystes trachydermis Zweifel, 1983, 12.

Litoria trachydermis Frost, 2006, 362.

Holotype. AMNH 82866 collected by R.G. Zweifel by Gapaia Creek, nr. Garaina, MorP, 1280 m, on 1 September 1969.

Diagnosis. "tympanum completely concealed; palpebral reticulum relatively sparse; large size-males to 88 mm SVL; maximum size of females unknown; dorsal skin roughened; iris brown in life; males without a vocal sac." (Zweifel 1983).

Material examined. SAMR 24079 from the type locality.

Nyctimystes trachydermis is larger than all other species in this group and, in fact, larger than all other *Nyctimystes* species except *granti*, *humeralis*, *pulcher* and *zweifeli*, which all have vocal sacs and complete palpebral reticula. *Nyctimystes trachydermis* is not known to overlap in distribution with *N. disruptus* but the rough, rather than warty, dorsal skin and larger size would distinguish it. In the single specimen that I examined, the tympanum is quite distinct but there may have been some shrinkage after years in alcohol. Measurements given in Menzies (2006) are incorrect, the species is 'large' not 'moderate' and the illustration (plate 96) is not *N. trachydermis* but the recently described species *N. ocreptus* (Menzies, 2014b).

Distribution. Several localities in the south-eastern peninsula of New Guinea from Mt. Kaindi to Garaina (type locality) east to Mt. Simpson (Kraus and Allison 2004), 1280-2480 m. It is known to be sympatric with *Nyctimystes tyleri* and all localities are within the geographic range of *Nyctimystes papua*.

Nyctimystes tyleri Zweifel

Nyctimystes tyleri Zweifel 1983, 16.

Litoria tyleri Frost *et al*., 2006, 362.

***Holotype*.** AMNH 82878, collected by R.G. Zweifel by Gapaia Creek, nr. Garaina, (MorP) 1280 m, on 1 September 1969. The holotype is the only known specimen.

***Material examined*.** none

***Diagnosis*.** (Zweifel, 1983) "large size, absence of a vocal sac, weak palpebral pigmentation and golden iris."

Large size (SVL 77.6 mm) rules out confusion with *N. papua* and the yellow iris with *N. disruptus* and *N. trachydermis*, as well as the warty, rather than rugose dorsal skin. The question of iris colour in *N. disruptus* has already been discussed.

***Distribution*.** *Nyctimystes tyleri* is only known from the holotype, and the type locality, near Garaina, is about 180 km distant from any locality for *N. disruptus*. It is sympatric with *N. trachydermis*. Several species of the *Nyctimystes cheesmanae* group (Menzies, 2014a) are known from the Garaina area and it is conceivable that *N. papua* could occur in the mountains above Garaina.

DISCUSSION

In 1983, Zweifel wrote "There remains however, a substantial residue of specimens that do not fit comfortably into any of the taxa that I now recognize but yet are not sufficiently well characterized to be described… As preserved specimens most of these unassigned frogs cannot readily be distinguished from *Nyctimystes disrupta*.". These included some from the Southern Highlands Province with a brown iris and others from the Wau area and as far east as Mt. Dayman, also with brown irises. He suggested that as many as four species were represented. If one disregards the problem of iris colour, and accepts that there is some variation in the extent of hand webbing and palpebral venation, there is no problem in calling all these frogs, including *N. oktediensis*, variants of *Nyctimystes disruptus*, excepting those from the south-east, from Wau to Mt. Dayman, which, by body size alone, can be allied with *N. papua*. If there is, as Zweifel has suggested, more than one species currently included in *N. disruptus*, I have not found any means to separate them. A multi variate (discriminant) analysis dividing specimens into geographical groups selected HL, HW, and IN as the only variables with sufficient power to discriminate between them but the percentage of a priori classifications deemed to be correct was very low, between 7 and 52% except 100% for the south-eastern group. Fig. 11 shows all the geographic groups (1-7) from the central highlands forming a tight cluster, distinct from the south-eastern group (8). In this analysis, the first two axes accounted for 99.9% of the between-groups variance and in axis 1 most weight was carried by head width (HW). A second analysis leaving out the south-eastern group selected tibial length (TL) as the only discriminating variable and the level of 'correct' a priori classifications was only 20%. It would be unwise to consider any of these geographical groups, other than the south-eastern group, as more than geographical variants of *Nyctimystes disruptus*.

An alternative way to reveal the presence of sympatric cryptic species is to check for normality in the distribution of different variables. Only in group 6, Star Mountains (n = 21), was any possible deviation found, where the HL/HW and HW/HB ratios deviated significantly from normal. In all other groups, where the sample size was large enough to be valid, all variables appeared to be normally distributed. Unfortunately, *Nyctimystes oktediensis* could not be fitted into this figure as the number of specimens for which I had data (n = 2) was much too small.

So there may be more than one species masquerading as *Nyctimystes disruptus* but, at present, there is no supporting evidence for this, and the apparent lack of voice these male frogs is a distinct handicap in separating species. Interestingly, the Kalam people of the Schrader Mountains recognise two kinds of *Nyctimystes disruptus* by colour and altitude (Bulmer and Tyler 1968). A light variety (Kwyos) is "Normally found in water but sometimes in pandanus and other vegetation." The dark variety (Gepgep) is "seldom found in the lower altitude cultivation zone, overlapping with Kwyos in bush fallow". Both are said to make a whistling call but they also have a very pungent odour, which may be species specific.

With the addition of more specimens of *Nyctimystes papua*, the difference between that species and *N. disruptus* has become clearer though sample sizes (for *N. papua*) are still small. Currently, there is no evidence to support *Nyctimystes oktediensis* or for more than one species in what is known as *N. disruptus*. Elucidation may also have to wait for more data and possibly molecular investigation.

The two very large species, *Nyctimystes trachydermis* and *N. tyleri* appear to be quite distinct but it would certainly be good to have more examples of *N. tyleri*.

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APPENDIX 1

Statistics

Table A1. Complementary statistics of figure 2: *t*-test (assuming equal variances)

	Females				Males			
	Difference	*t*	*df*	Prob. > [*t*]	Difference	*t*	*df*	Prob. > [*t*]
Estimate	13.8234	10.397	77	<0.0001	11.0046	10.254	115	<0.0001
SE	1.3295				1.032			
lr. 95%	11.1760				8.8787			
up. 95%	16.4707				13.1304			

Table A2. Complementary statistics of figure 2:.means for one-way ANOVA (SE uses a poled estimate of variance).

	Females					Males				
level	*n*	mean	SE	lr. 95%	up. 95%	*n*	mean	SE	lr. 95%	up. 95%
N. disruptus	69	68.7854	0.4730	67.843	69.727	102	56.2106	0.3843	55.449	56.972
N. papua	10	54.9620	1.2425	52.488	57.436	15	45.2060	1.0021	43.221	47.191

Table A3. Complementary statistics of figure 7: *t*-test (assuming equal variances)

	TL/HB				EN/IN			
	Difference	*t*	*df*	Prob. > [*t*]	Difference	*t*	*df*	Prob. > [*t*]
Estimate	0.0157	2.795	201	0.0057	0.0947	4.850	200	<0.0001
SE	0.0056				0.0195			
lr. 95%	0.0046				0.0562			
up. 95%	0.0268				0.1332			

Table A4. Complementary statistics of figure 8: *t*-test (assuming equal variances)

	TL/HB				HW/HB			
	Difference	*t*	*df*	Prob. > [*t*]	Difference	*t*	*df*	Prob. > [*t*]
Estimate	-0.0034	-0.302	34	0.9646	-0.0133	-1.870	34	0.0700
SE	0.0114				0.0071			
lr. 95%	-0.0265				-0.0288			
up. 95%	0.0197				0.0012			

	TY/HB				EN/IN			
	Difference	*t*	*df*	Prob. > [*t*]	Difference	*t*	*df*	Prob. > [*t*]
Estimate	-0.0133	-1.870	34	0.6515	-0.0452	-1.457	34	0.1542
SE	0.0024				0.03606			
lr. 95%	-0.0060				-0.1067			
up. 95%	0.0039				0.0176			

	EY/HB				HL/HW			
	Difference	*t*	*df*	Prob. > [*t*]	Difference	*t*	*df*	Prob. > [*t*]
Estimate	-0.0170	-2.794	34	0.085	-0.0064	-0.395	34	0.6954
SE	0.0061				0.0162			
lr. 95%	-0.0293				-0.0394			
up. 95%	-0.0046				0.0266			

Table A5. Complementary statistics of figure 11 (eight groups): variables in the analysis

step	var.	Tolerance	*F* to remove	Wilk's lambda
1	HW	1.000	233.618	
2	HW	0.213	543.539	0.608
	HL	0.213	70.627	0.104
3	HW	0.186	515.399	0.441
	HL	0.206	24.021	0.041
	IN	0.406	83.530	0.029

Table A6. Complementary statistics of figure 11 (eight groups): Wilk's lambda.

step	No. of vars	Lambda	*df*1	*df*2	*df*3	Exact *F*	
						statistic	*df*1
1	1	0.104	1	7	190	233.618	7
2	2	0.29	2	7	190	132.133	14
3	3	0.022	3	7	190		

Table A7. Complementary statistics of figure 11 (eight groups): Pairwise comparisons (*F*-value followed by *p*-value).

Group	1	2	3	4	5	6	7
2	3.930; 0.004						
3	0.168; 0.955	2.173; 0.074					
4	7.330; 0.000	1.881; 0.115	1.626; 0.169				
5	0.109; 0.979	1.514; 0.200	0.233; 0.919	1.909; 0.111			
6	1.858; 0.120	7.145; 0.000	0.584; 0.674	9.596; 0.000	0.826; 0.510		
7	0.420; 0.794	3.114; 0.016	0.467; 0.760	5.226; 0.001	0.113; 0.978	2.593; 0.036	
8	1066.315; 0.000	675.211; 0.000	429.826; 0.000	1421.424; 0.000	320.849; 0.000	879.116; 0.000	701.732; 0.000

Table A8. Complementary statistics of figure 11 (eight groups): Eigenvalues and Wilks' lambda.

Functions	Eigenvalue	% variance	Cumulative %	Canonical correlation	Test of Functions	Wilk's Lambda	Chi-square	*df*	sig.
1	33.457*	99.1	99.1	0.985	1-3	0.022	732.223	21	0.000
2	0.269*	0.8	99.9	0.460	2-3	0.753	54.368	12	0.000
3	0.047*	0.1	100.0	2.11	3	0.955	8.761	5	0.119

* first three canonical discrimant functions were used in the analysis

Table A9. Complementary statistics of figure 11 (eight groups): classification results (40% of original grouped cases correctly classified).

		Predicted group membership								
Group		1	2	3	4	5	6	7	8	total
Count	1	2	1	3	6	7	9	11	0	39
	2	0	6	0	4	0	1	1	0	12
	3	0	0	3	0	2	1	1	0	7
	4	3	23	6	27	6	9	5	0	79
	5	0	1	0	0	3	1	0	0	5
	6	0	0	1	5	3	9	3	0	21
	7	0	0	0	3	2	2	7	0	14
	8	0	0	0	0	0	0	0	0	25

Table A10. Complementary statistics of figure 11 (seven groups): variables entered/ removed

step	entered	Wilk's lambda						
		statistic	*df*1	*df*2	*df*3	Exact *F*		
						statistic	*df*1	*df*2
1	TL	0.722	1	6	170	10.887	6	170

Table A11. Complementary statistics of figure 11 (seven groups):. Wilk's lambda.

step	No. of vars	Lambda	*df*1	*df*2	*df*3	Exact *F*			
						statistic	*df*1	*df*2	sig.
1	1	0.729	1	6	165	10.204	6	165	0.000

Table A12. Complementary statistics of figure 11 (seven groups): variables in the analysis

step	var.	Tolerance	*F* to remove
1	TL	1.000	10.887

Table A13. Complementary statistics of figure 11 (seven groups): Pairwise comparisons (*F*-value followed by *p*-value).

Group	1	2	3	4	5	6
2	15.390; 0.000					
3	0.058; 0.810	6.328; 0.013				
4	29.219; 0.000	0.586; 0.445	5.916; 0.016			
5	0.048; 0.826	6.914; 0.009	0.120; 0.729	6.354; 0.013		
6	1.973; 0.162	21.430; 0.000	1.204; 0.274	34.307; 0.000	0.307; 0.580	
7	0.024; 0.878	11.654; 0.001	0.100; 0.752	14.541; 0.000	0.012; 0.914	0.927; 0.337

Table A14. Complementary statistics of figure 11 (seven groups): classification results (24.3% of original grouped cases correctly classified).

		Predicted group membership							
Group		1	2	3	4	5	6	7	total
Count	1	5	6	1	2	4	19	2	39
	2	0	9	0	0	1	1	1	12
	3	0	0	1	1	0	2	3	7
	4	0	37	1	8	7	8	19	80
	5	0	0	0	1	1	3	0	5
	6	0	2	0	3	0	15	1	21
	7	0	1	0	1	1	3	3	9

APPENDIX 2

Geographical coordinates (°S, °E) of places mentioned in the text.

Papua, Indonesia

Ok Minam, 4.87, 140.87
Mistkamp, 3.58, 139.05

Papua New Guinea

Central and Milne Bay Provinces

Mt. Victoria, 8.88, 147.53
Avios, Mt. Albert Edward, 8.31, 147.21
Woitape, 8.52, 147.35
Agaun, 9.5, 147.62
Bonenau, 9.88, 149.4
Efogi, 9.13, 147.67

Eastern Highlands and Simbu Provinces

Andandara, SE Kainantu
Chuave, 6.13, 145.13
Dumun, 6.11, 145.08
Goroka; 6.07, 145.38
Igindi, nr. Goroka
Kainantu, 6.28, 145.87'
Lafoiyufa, WSW Goroka
Menyamya, 7.23, 146.02
Okapa, 6.52, 145.65
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