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## Two New Hylid Frogs from Papua New Guinea and a Discussion of the *Nyctimystes papua* Species Group

RICHARD G. ZWEIFEL<sup>1</sup>

### ABSTRACT

*Nyctimystes papua* has been recorded from a wide area of New Guinea, but evidence developed here suggests that the only specimens that can be referred with confidence to the species are some of those in the syntype series. A lectotype is proposed for *N. papua* and the *papua* species group

is characterized. Members include *N. papua*, *N. disrupta*, *N. trachydermis*, and *N. tyleri*, the last two described as new. Attention is called to several samples of *papua* group populations that are too poorly known for allocation to described species or naming.

### INTRODUCTION

Hylid frogs make up more than 40 percent of the species of frogs known from New Guinea, and are outnumbered only by microhylids (Zweifel and Tyler, 1982). Only two genera of the Hylidae are recognized in New Guinea, *Litoria* with 52 species and *Nyctimystes* with 19. New Guinean *Litoria* (then referred to *Hyla*) were revised by Tyler (1968) and *Nyctimystes* by Zweifel (1958). Studies by Tyler (e.g., 1963a, 1963b, 1965) subsequent to Zweifel's publication resulted in the description of several new species of *Nyctimystes* and the transfer of some species to *Nyctimystes* from *Hyla*, with the concomitant recognition that *Nyctimystes* occurs in Australia as well as in New Guinea. Much remains to be learned of the systematics of

*Nyctimystes*, this later work notwithstanding. These frogs are associated with streams in mountainous or upland regions. The habitats are often difficult of access and much of montane New Guinea is inadequately explored for its anuran fauna. Also, existing collections in many cases lack pertinent—even essential—information, such as color in life and recordings of mating calls. The number of species of *Nyctimystes* recognized can be expected to increase substantially as better information accrues.

The present work deals with *Nyctimystes papua* (type species of the genus) and some related species. *Nyctimystes papua* is redefined and a lectotype designated, two new species are described and a species is treated

<sup>1</sup> Curator, Department of Herpetology, American Museum of Natural History.

in detail for the first time; samples of specimens not yet assignable to species are also discussed.

### METHODS

Measurements (in millimeters) were made as follows (abbreviations used are in parentheses): body length, from snout to vent (SV); length of tibia, from heel to outer side of flexed knee (TL)<sup>2</sup>; distance from anterior edge of eye opening to center of external naris (EN); internarial distance, between centers of external nares (IN); head width, at jaw articulation (HW); head length, from tip of snout to posterior edge of jaw angle (HL); diameter of eye opening, measured between anterior and posterior edges (Eye); horizontal diameter of tympanum, including ring (Ear). Statistics are given in the format: mean  $\pm$  standard error of mean (range) N.

### ACKNOWLEDGMENTS

Curators in several museums generously made specimens available for my study. Museums, curators, and abbreviations follow: American Museum of Natural History, New York (AMNH); Australian Museum, Sydney, H. Cogger (AM); British Museum (Natural History), London, B. Clarke (BMNH); Bernice P. Bishop Museum, Honolulu, A. Ziegler (BPBM); Museum of Comparative Zoology, Harvard University, Cambridge, E. Williams and P. Alberch (MCZ); National Museum of Natural History, Washington, G. Zug (USNM); Yale Peabody Museum of Natural History, New Haven, F. Sibley (YPM). Dr. Allen Allison, Wau Ecology Institute, Papua New Guinea, kindly lent color transparencies of BPBM specimens he collected. Mr. Angus Hutton provided housing at Garaina for me in 1968 and for the Alpha Helix party in 1969. I thank Dr. William E. Duellman for his critical review of the manuscript. Mrs. Frances Zweifel assisted with the illustrations. My fieldwork on which the new species were collected was supported by the National Geographic Society (1968) and by the National Science Foundation through the R/V Alpha Helix Expedition (1969).

<sup>2</sup> A more standard measurement than the shorter span used in my 1958 study.

### DEFINING AND DIAGNOSING SPECIES OF *NYCTIMYSTES*

Characters useful in the species-level systematics of *Nyctimystes* are for the most part the same as those that serve for other anuran taxa. Here I briefly discuss those characters that have been useful in this study and I mention those found wanting.

**BODY SIZE AND MATURITY:** All species of *Nyctimystes* known from adequate samples are sexually dimorphic in size; females attain larger sizes than males. Maturity of females can be assessed by the presence of enlarged ova or of large, convoluted oviducts if ova have been shed, but maturity in males is not so readily determined. Nuptial pads on the first fingers indicate maturity, but in the species treated here these often are poorly developed or absent, possibly due to the stage of the individual's sexual cycle or to loss after preservation. In species that possess a vocal sac, the presence of openings to the sac is an indication of sexual maturity, but evidently all the species treated here lack a vocal sac. Size at maturity and maximum size, which vary in tandem, are useful characters when they can be determined.

**SNOUT SHAPE AND NARIAL PLACEMENT:** The shape of the snout in *Nyctimystes* varies between rather long, low, and flattened to short, high, and blunt. Distance between nares and between naris and eye often are useful in quantifying snout shape—a long-snouted species typically has the nostrils relatively close together and far from the eyes, compared with more widely spaced nostrils closer to the eyes. The measurements conveniently are expressed as a ratio of one to the other (EN/IN) or as of each to body length (EN/SV, IN/SV). The first ratio has the advantages that the two measurements are of similar magnitude and that it appears little affected by ontogeny (i.e., ontogenetic change is similar in the two measurements, so the ratio is not greatly affected). The other two ratios suffer more from spurious variation because of difficulty in measuring the quantities with comparable accuracy, but are useful in revealing interspecific differences where species could produce similar EN/IN ratios though the actual measurements might be rather different at a given body size. Ratios of narial

measurements are useful in some of the present interspecific comparisons. Figures 4 and 5 illustrate variation in IN and EN measurements relative to SV length in a large sample with good size distribution.

**PALPEBRAL PIGMENTATION:** The transparent upper half of the lower eyelid, unmarked in most frogs, is variously pigmented in *Nyctimystes*. The pigmentation ranges from a few scattered flecks, scarcely visible to the unaided eye, to an orderly veinlike arrangement dense enough to cover most of the area. Species treated here have little palpebral pigmentation and similar ranges of variation, so the character is of little use.

**TYMPANUM SIZE AND VISIBILITY:** In *Nyctimystes* the tympanum typically is small and inconspicuous, with the upper edge concealed beneath a postocular fold. Sexual dimorphism is lacking. Rarely, as in one of the species described here, is there no external indication of the tympanum, there being no difference in the character of the skin adjacent to and covering it.

**CHARACTERISTICS OF HANDS AND FEET:** Relative sizes of digital discs, relative lengths of fingers and toes, and the nature of the subarticular and other tubercles do not differ significantly among the species studied. Webbing of the fingers has been useful in distinguishing among species of *Nyctimystes*; it has limited use here because of the small range of variation and individual variation. Toe webbing does not differ significantly among the species studied. The nuptial pads located on the inner sides of the first fingers are small, fine grained, and inconspicuous in the species studied (figs. 7, 13) and do not appear to provide any characters of systematic significance (pads of different character are found in some other species).

**LEG LENGTH:** This character, generally expressed as the ratio of tibia length to length from snout to vent, is useful in some interspecific comparisons but not among the species studied here. Figure 9 shows variation in a large sample with good size distribution.

**SKIN TEXTURE AND DERMAL APPENDAGES:** Dorsal skin varies from smooth to rough. To some extent this may be influenced by the means of killing and preserving the specimen. However, the nature of the roughness—distinctly pointed asperities as opposed to more

rounded elevations—characterizes one of the species studied. A dermal appendage in the form of a heel lappet is seen in some species of *Nyctimystes* but not in any of those treated here.

**COLOR AND PATTERN:** Inadequacy of information on colors in life, individual variation and postmortem changes limit the usefulness of color and pattern but do not prevent their use completely.

**EYE COLOR:** Experience with living *Nyctimystes* indicates that species may differ markedly in the color of the iris. Unfortunately, nothing of the color in life can be inferred from preserved specimens. Where colors are known I have made use of them in coming to taxonomic decisions. Iris colors may prove to vary ontogenetically and geographically, but there is as yet no evidence for such variation in *Nyctimystes*.

**INTERNAL ANATOMY:** I have not studied the skeleton or musculature of the species investigated. Tyler and Davies (1979) surveyed the skull of *Nyctimystes* and reported some differences among species, but more knowledge of individual variation will be required before the significance of the differences can be assessed.

**LARVAL MORPHOLOGY:** Nothing is known of the larvae of the species treated here, and scarcely anything more about the remainder of the genus except that the tadpoles are sucker-mouthed and otherwise adapted to streams.

**VOCALIZATION:** Males of the species discussed lack vocal sac openings, and if they call this has not been reported.

#### THE *NYCTIMYSTES PAPUA* SPECIES GROUP

In my 1958 revision I referred all *Nyctimystes* with sparse palpebral pigmentation and lacking vocal sac apparatus to *N. papua*. The descriptions of *N. disrupta* (Tyler, 1963b) and of two new species here, as well as the evidence for additional undescribed but possibly related forms, raise the question of the existence of a monophyletic group. Characteristics that appear to tie the species together are: palpebral pigmentation sparse or at least much reduced compared with other *Nyctimystes*; males lacking vocal sac (inferred for

*N. papua*); snout relatively short, high and rounded, EN/IN usually 1.10 or less; outer finger one-half or less webbed; size moderate to large (males 50 to 80+ mm. SV). In order to demonstrate convincingly that the species concerned form a natural group, it would be necessary to show that the shared characters (or some of them) are derived, attributable to common ancestry. As is so often the case with frogs, determining character polarities is chancy, and convergence is a distinct possibility.

Palpebral pigmentation is well developed in most *Nyctimystes* and absent in the probable sister group, *Litoria*. On this basis, reduced pigmentation might be thought to be primitive within *Nyctimystes* and hence not of use in grouping species, but it might as reasonably be considered as a loss of pigmentation from the more typical condition.

The presence of vocal sac apparatus is so widespread in hyloid frogs (as among frogs in general) that I can confidently treat its absence in some *Nyctimystes* as a derived condition. This does not, however, assure monophyly: at least two species—*N. avocalis* Zweifel and *N. tympanocryptis* (Anderson), *vide* Tyler and Davies (1979)—with no other indication of close relationship to the species considered, lack a vocal sac.

Similarity in size, snout shape, and finger webbing are characters whose polarity cannot reliably be inferred and whose possibly convergent attainment cannot be refuted.

I conclude that the absence of the vocal sac has the most likelihood of being a shared derived character indicative of monophyly among the species considered and that the other characters, unsatisfactory as they are, tend to support this hypothesis. (It is unfortunate that the absence of the vocal sac in *N. papua* must be inferred, since there are no males certainly referable to the species; however, the females are much like the other species in pertinent morphology.) Comparative studies of the skeleton such as initiated by Tyler and Davies (1979)<sup>3</sup> and of the musculature may eventually prove useful in identifying natural groups.

<sup>3</sup> These authors used "*Nyctimystes papua*" as their standard for osteological comparisons. Almost certainly this is not *papua* as I restrict the name.

I assign four species to the *Nyctimystes papua* species group: the nominate species, *N. disrupta*, *N. trachydermis*, and *N. tyleri*. The last two are described herein, and evidence is presented for the existence of related undescribed forms. Among species not included within the *papua* group, the one most similar morphologically is *Nyctimystes narinosa* Zweifel, which has more palpebral pigmentation than is usual in the group, but less than in many other species, moderately large size, sparse finger webbing, and an EN/IN ratio of less than 1.0. It differs in possessing a vocal sac.

#### *Nyctimystes papua* (Boulenger)

*Nyctimantis papua* Boulenger, 1897, p. 12 (type locality, "Mount Victoria, Owen Stanley Range, New Guinea"; "several" syntypes, lectotype [by present designation], BMNH 96.10.31.50, adult female, collected by A. S. Anthony, presumably between April and June 1896). Van Kampen, 1923, p. 22.

*Nyctimystes papua*: Stejneger, 1916, p. 85 (new generic name, *Nyctimantis* restricted to a South American species). Parker, 1936, p. 77 (part). Loveridge, 1948, p. 405 (part). Zweifel, 1958, p. 28 (part).

TYPE LOCALITY: The type locality given in the synonymy is taken from the title of Boulenger's paper, which provides no other information. Wichmann (1912, p. 608) indicates that Anthony collected on Mt. Victoria between April and June 1896, and since Anthony operated out of Port Moresby, it is likely that collections were made on the western rather than the eastern side of the Owen Stanley Range in what is now the Central Province of Papua New Guinea. The title of a paper by Rothschild and Hartert (1896) treating birds collected by Anthony on the same trip (Wichmann, 1912) includes the phrase "mostly at elevations of from 5000 to 7000 feet."

APPLICATION OF THE NAME *Nyctimantis papua*: Boulenger (1897) described *papua* on the basis of "several specimens" without specifying a type specimen, though a frog was figured. Parker (1936), as the first to deal with the genus *Nyctimystes* at any length, stated that "of the five specimens still in the British Museum four are females and one a male." He noted several differences between the male

and the others, and "tentatively" referred the former to *Nyctimystes semipalmata* which he described in the same paper. Nothing more of pertinence to the status of *papua* appeared until my revision (Zweifel, 1958), in which I diagnosed the species on the basis of its greatly reduced palpebral pigmentation, moderate size, and absence of vocal sac, and recorded specimens from over a wide area of montane New Guinea.

My assessment of *papua* was made without benefit of examination of the type series except for syntype MCZ 12838, received on exchange at Harvard before Parker did his study. Tyler (1963a) examined the type series in the British Museum (and MCZ 12838 as well) and concluded that of the four syntypes that Parker retained in *papua*, one (designated specimen D by Tyler) was not conspecific with the others. This specimen (BMNH 96.10.31.51) possesses well-developed palpebral pigmentation, a fact that I confirmed upon examination of the British Museum syntypes in 1964. Tyler also gave reasons for supposing that two of the remaining BMNH syntypes (A and B, BMNH 96.10.31.52–53) differed from the third (C, BMNH 96.10.31.50). Thus, though it is agreed that the syntype series of *N. papua* includes more than one species, and Parker and subsequent authors have concurred in using the name *papua* for *Nyctimystes* with reduced palpebral pigmentation, a lectotype has not been designated. The situation is complicated not only by the apparent heterospecificity of the type series, but also by the description of a similar species, *N. disrupta* Tyler (1963b) that at least one author (Woodruff, 1972) thought was of questionable validity, by the discovery of two new species described here, and by evidence presented here for the existence of additional species possibly related to *N. papua*.

With the exclusion of the syntype that Parker (1936) referred to *N. semipalmata* (BMNH 1947.2.24.46, formerly 1896.10.31.54), and excluding also the syntype Tyler (1963a) called specimen D, there remain three syntypes of *N. papua* in the British Museum and one in the Museum of Comparative Zoology. I regard these four as conspecific. Tyler considered one of the three BMNH syntypes (specimen C) different from the other two (A

and B), citing differences in color, skin texture and EN/IN ratios. I do not consider the differences cited as trenchant, and attribute more significance to the similarities among these specimens and to the MCZ syntype. Also, I find the EN/IN ratio of specimen C to fall between those of specimens A and B, rather than outside that range. (This is not to say that my measurements are more accurate than Tyler's; the disagreement merely emphasizes how slight are the differences among the specimens; see also fn. 4.

Woodruff (1972) quite reasonably suggested that the specimen illustrated by Boulenger (1897, plate 1, fig. 5) should be designated lectotype. The specimen loaned to me upon my request for the syntype illustrated by Boulenger, BMNH 96.10.31.50 (evidently Tyler's specimen C), resembles the illustration in boldness of pattern but differs in details. My notes on the other two BMNH syntypes (examined more than a decade ago) record dorsal patterns of faint darker mottling on a reddish brown background. The illustration depicts the form of *N. papua* excellently, but cannot be cited as an accurate representation of the lectotype's color pattern. Whether the illustration represents a specimen no longer in the British Museum or was intended merely as a generalized representation cannot be determined.

**DIAGNOSIS:** As here defined, the name *papua* is restricted to *Nyctimystes* of moderate size—females are mature at about 52 mm. snout-vent length and reach at least 64 mm.—with greatly reduced palpebral pigmentation and scant webbing on the fingers; males presumably lack a vocal sac. Other species with reduced palpebral pigmentation are larger (mature females 64 to 80 mm. SV) and have more extensive finger webbing. See below for additional comparisons.

**DESCRIPTION OF LECTOTYPE:** Adult female with short snout, subacute viewed from above, high and slightly rounded seen laterally; canthus distinct, slightly curved, loreal region slightly concave, and nearly vertical; nostrils directed laterally, scarcely visible from above, much closer to tip of snout than to eye, internarial distance slightly greater than distance from eye to naris (EN/IN 0.933). Eye and snout about equally long, interocular distance greater than width of upper eyelid; pal-

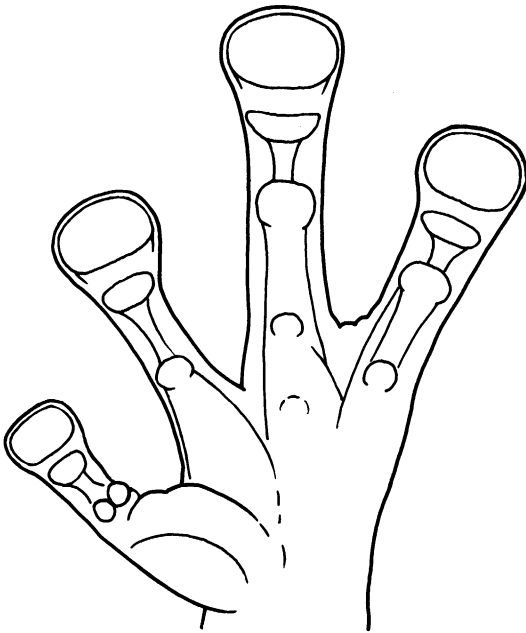


FIG. 1. Left hand of *Nyctimystes papua* in palmar view. Based on MCZ 12838 (paralectotype); webbing of the lectotype is virtually identical.

pebrum with only a few pigment spots in anterior corner; pupil vertical. Tympanum smooth and moderately distinct, upper edge covered by curved postocular fold. Vomerine teeth in two short diagonal rows between internal nares and behind their posterior borders.

Relative lengths of fingers  $3 > 4 > 2 > 1$ ; webbing sparse, reaching halfway between proximal and distal tubercles on fourth finger, to proximal tubercle on third, and not so far as proximal tubercles on second and third; prominent discs on fingers two to four, disc on first finger scarcely wider than fringed edges of finger; prominent single subarticular tubercles; smaller, less distinct tubercles on palm; an elongate, rounded inner metacarpal tubercle. Relative lengths of toes  $4 > 5 = 3 > 2 > 1$ ; webbing to the distal tubercle of fourth toe, slightly more extensive but not to disc on adjacent sides of third and fifth toes, less extensive between second and third and between first and second toes; rounded subarticular tubercles, rounded inner metatarsal tubercle, no outer metatarsal tubercle, discs well developed on all toes. Legs long (TL/SV

0.607). Dorsal body surfaces largely smooth between isolated small tubercles; chin much smoother than granular chest and abdomen; no fold on forearm, no heel tubercle.

Dorsum brown with large, irregular, darker brown blotches, much as illustrated by Boulenger (1897); similar irregular crossbars, faintly light edged, on lower legs; posterior thigh with irregular vertical dark and light markings in basal region, giving way to uniform brown toward the knee; anterior of thigh and groin uniform brown; side of body light gray beneath prominent brown mottling; upper lip mottled.

MEASUREMENTS OF LECTOTYPE: SV 63.6; HW 24.7; HL 23.9; TL 38.6; IN 6.0; EN 5.6; snout 9.6; Eye 8.0; Ear 2.7; width of third finger disc 4.0, width of penultimate phalange 2.1; width of fourth toe disc 3.3, width of penultimate phalange 1.9.

VARIATION: The only specimens that can be assigned to *N. papua* with confidence are the lectotype and three paralectotypes, BMNH 96.10.31.52–53 and MCZ 12838. The three paralectotypes are adult females measuring approximately 53–54 mm. snout to vent. The four specimens have the following proportions: TL/SV 0.594 (0.585–0.607); EN/IN 0.881 (0.774–0.936); EN/SV 0.083 (0.077–0.088); IN/SV 0.094 (0.087–0.099). Finger webbing (fig. 1) is similarly scanty in all four, and all exhibit only the faintest trace of palpebral pigmentation. The iris of the holotype is golden with a black network; that of MCZ 12838 shows a black network on a paler background, but the ground color is not pale gold. The dorsal surfaces of MCZ 12838 are more uniformly granular than in the lectotype. I did not make note of the iris pigmentation or the degree of skin granularity in the other two paralectotypes. The paralectotypes are less boldly patterned than the lectotype, being reddish brown dorsally with indistinct darker mottling.

Parker (1936) reported 34 male specimens of *N. papua* from Mondo, elevation 5000 feet (1524 m.) on the north slope of Mt. Tafa about 60 km. northwest of Mt. Victoria. I have examined five specimens of this series now in the Museum of Comparative Zoology (MCZ 21816–21820). The size range in this group is 48–51 mm. At least three are sexually mature, judged by their nuptial pads;

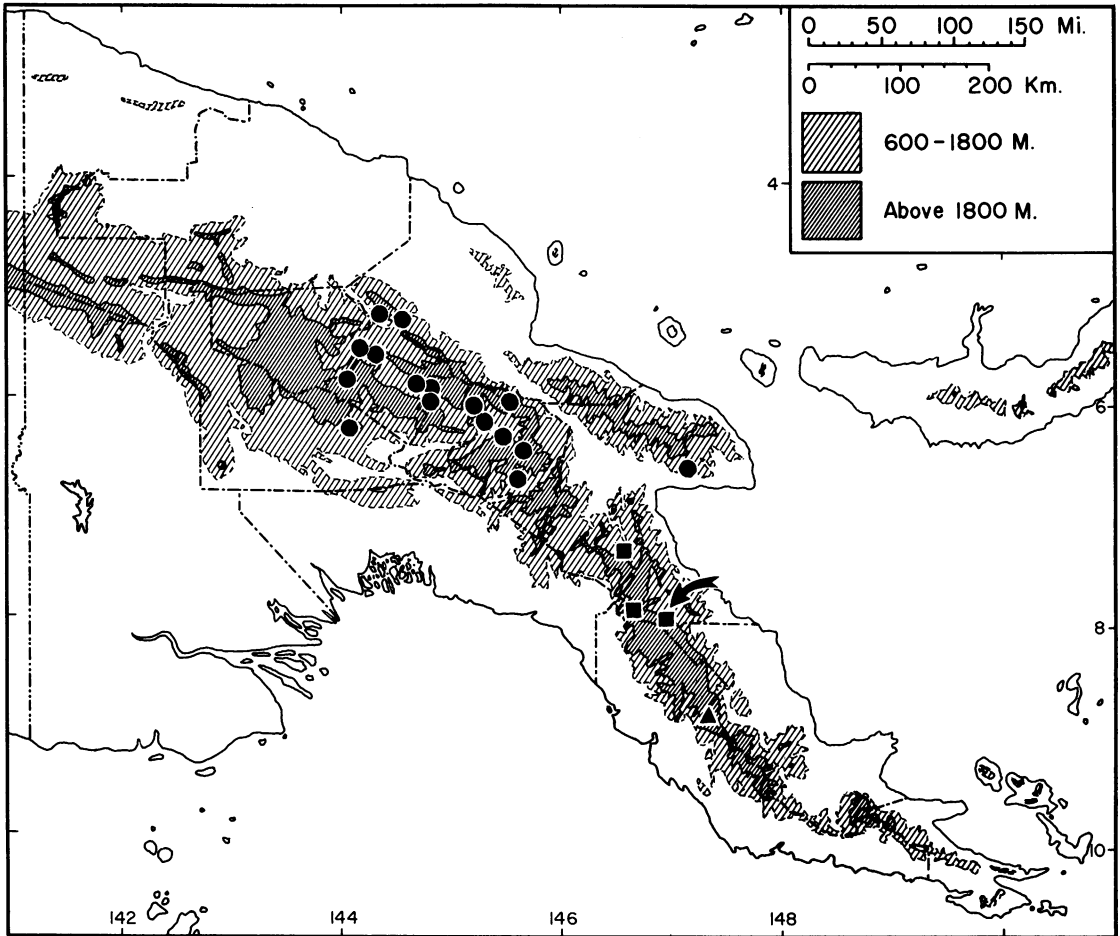


FIG. 2. Distribution of species of the *Nyctimystes papua* group in Papua New Guinea: triangle, *N. papua*; circles, *N. disrupta*; squares, *N. trachydermis*; square with arrow, type locality of *N. trachydermis*, type and only locality of *N. tyleri*. See figure 17 for distribution of *papua* group samples not assigned to species.

all lack vocal sac openings. Values for EN/IN average 0.995 (0.917–1.040), for EN/SV 0.094 (0.086–0.096), and for TL/SV 0.574 (0.555–0.586). Palpebral pigmentation is variable. Two specimens approach the condition in syntypic *papua* closely, having only a few scattered flecks of pigment in the anterior two thirds of the area. One has a distinct pigmentation, with diagonal lines, occasionally interconnected, over three-quarters of the palpebral area, whereas the remaining two specimens are intermediate, with scattered, isolated short lines of pigment. Finger webbing ranges from identical with that in

the syntypes (one specimen) to distinctly more, but not so extensive as in *N. disrupta*.

In size and general appearance these frogs match expectations for the male of *N. papua*, but some details make me suspect that they may not be that species. The males are relatively shorter legged, with almost no overlap in the ranges of the TL/SV ratio between the two samples. Similarly, there is little overlap in the EN/IN ratios. In this instance the difference is due wholly to the relatively greater EN distance in the males. Though these ratios can change with growth, the average sizes of the male and female samples (49 and 56 mm.



FIG. 3. *Nyctimystes disrupta*, AMNH 74820 from Koko, Eastern Highlands Province; male, SV 74 mm.

SV, respectively) are too close to favor this explanation. Palpebral pigmentation in the males, though not extensive, is slightly greater than in the females in most and considerably so in one specimen. Likewise, the finger webbing of four of five males exceeds that of the syntypes. For the present I prefer to consider the Mondo series of males as *Nyctimystes* sp.

**COMPARISON WITH OTHER SPECIES:** Though *Nyctimystes papua* can be characterized reasonably well in its combination of moderate size, sparse palpebral pigmentation, and scanty finger webbing, adequate interspecific comparison is hampered by scarcity of specimens and of information on appearance in life. Without male specimens the absence of a vocal sac can only be inferred. With only four specimens confidently assigned to the species, knowledge of the extent of variation is quite limited. The crucial character of iris color remains to be known.

*Nyctimystes disrupta* is represented by a large series of specimens. Eighteen adult females measure 66 to 81 mm. SV, whereas the four adult female *N. papua* are 52 to 64 mm., the size of male *disrupta*. The apparent slight difference in palpebral venation (sparser in *papua*) may appear less distinctive when the range of variation in *papua* is better known, and overlap in the amount of finger webbing may also be anticipated. The EN/IN ranges of the two forms show little overlap (*papua* 0.77–0.94, *disrupta* 0.90–1.15) and may be useful for differentiating them.

*Nyctimystes trachydermis* and *N. tyleri* are so much larger than *N. papua* (even larger than *N. disrupta*) that their status as species distinct from *papua* is assured. The concealed tympanum of *trachydermis* would segregate any juvenile compared with *papua*, but further comparisons with *tyleri* would best await acquisition of more specimens of the latter.

In a separate section following the last species account I discuss the status of specimens of the *papua* group presently unassignable to species.

**DISTRIBUTION AND SPECIMENS EXAMINED:** *Nyctimystes papua* is known only from the type locality, Mt. Victoria, Papua New Guinea, probably on the western slope in Central Province: BMNH 96.10.31.50 (lectotype), 96.10.31.52–53 (paralectotypes), MCZ 12838 (paralectotype).

#### *Nyctimystes disrupta* Tyler

##### Figure 3

*Nyctimystes papua*: Zweifel, 1958, p. 28 (part).

Tyler, 1963a, p. 111. Duellman, 1967, p. 42.

*Nyctimystes disrupta* Tyler, 1963b, p. 118 (type locality, "at an elevation of 6,000 feet in the Kaironk Valley, Schrader Mountains, Australian Trusteeship Territory of New Guinea [Madang Province, Papua New Guinea]"; holotype female, AM R15923, collected by R. N. H. Bulmer on February 4, 1960). Woodruff, 1972, p. 59. Zweifel, 1980, p. 398.

**DIAGNOSIS:** A moderately large species of *Nyctimystes* (males to 68 mm. SV or exceptionally to 74 mm., females to 80 mm.) with indistinct, usually disrupted palpebral pigmentation, males lacking a vocal sac, outer fingers about one-half webbed, tympanum visible externally, and iris green in life. No other species of *Nyctimystes* is known to have a green iris. Among species with similar palpebral pigmentation, preserved specimens may be distinguished as follows: *N. trachydermis* is much larger (males to 85 mm. SV compared to normally less than 70 mm. in *disrupta*) with completely hidden tympanum and much lower EN/IN ratio (typically greater than 0.90 in *disrupta*, less than 0.85 in *trachydermis*); *N. tyleri* is larger (the only *tyleri*, a male, measures almost 78 mm. SV) with the underside of the lower leg heavily spotted (uniform in *disrupta*); *N. papua* is smaller (mature females 52 to 64 mm. SV vs.



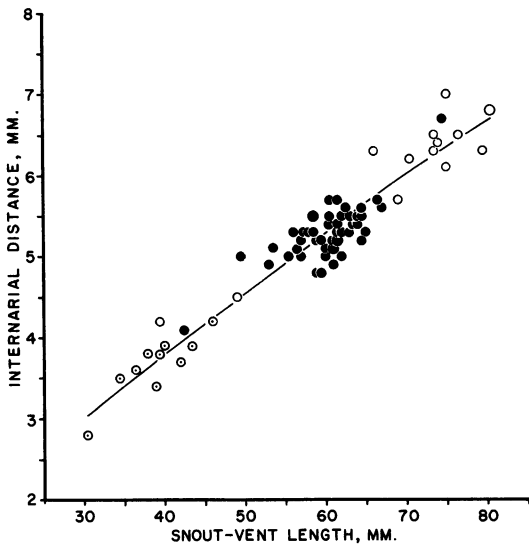


FIG. 4. Relationship of internarial distance to snout-vent length in 74 *Nyctimystes disrupta*. Open circles, females; closed circles, males; circles with dot, not sexed. Females greater than 65 mm. SV are adult. Regression formula,  $Y = 0.190X^{0.811}$ ,  $r = 0.962$ .

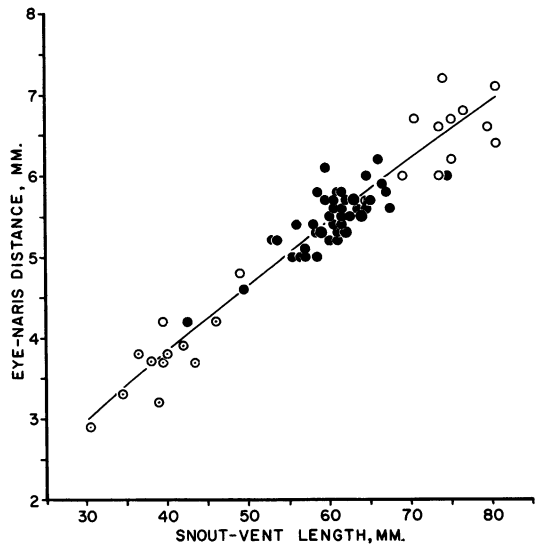


FIG. 5. Relationship of eye-naris distance to snout-vent length in 74 *Nyctimystes disrupta*. See figure 4 for symbols. Regression formula,  $Y = 0.161X^{0.859}$ ,  $r = 0.961$ .

66 to 80 mm. in *disrupta*) with slightly less finger webbing and often a lower EN/IN ratio (less than 0.90 in 3 of 4 *papua*).

**DESCRIPTION AND VARIATION:** A moderately large species, males typically to 68 mm. SV or less, but one exceptional individual 74 mm. ( $N = 52$ ), females mature at about 66 mm. and reach 80 mm. ( $N = 19$ ). Snout short and high, slightly rounded in both dorsal and lateral views; internarial distance virtually equal to distance from eye to naris, mean EN/IN in four geographically segregated samples 0.99, 1.01, 1.01 and 1.06 (total range 0.90–1.15)<sup>4</sup>; relative internarial distance decreases with growth (measured by regression line, mean IN/SV reduces from 0.100 to 0.083, range 0.079–0.106, fig. 4); relative eye-naris distance decreases with growth (mean EN/SV reduces from 0.100 to 0.087, range 0.081–0.106, fig. 5), canthus rostralis curved, loreal region sloping and slightly concave. Eyelid

<sup>4</sup> Tyler (1963b) reported a somewhat higher mean EN/IN for the type series (1.20), a consequence, I think, of his measuring the internarial distance between the inner margins of the nares rather than from the centers as I do.

narrower than interorbital space; palpebral pigmentation typically in spots and thin broken lines over anterior 40 to 60 percent of area, rarely a more continuous pattern thinly covering most of area (fig. 6). Tympanum small and indistinct but with annulus visible, about one-third diameter of eye, no sexual dimorphism evident. Male without vocal sac. Small nuptial pad on body side of first finger composed of microscopic points, about 700 per square millimeter (fig. 7), colored light brown; many males without evident pad development. Relative lengths of fingers,  $3 > 4 > 2 > 1$  (2 and 4 almost the same length); webbing between third and fourth fingers reaches to distal subarticular tubercle of fourth and halfway between distal and proximal tubercles on third (fig. 8); terminal discs well developed on all fingers and toes. Relative lengths of toes  $4 > 5 > 3 > 2 > 1$  (3 and 5 almost the same length); webbing extends to distal subarticular tubercle of fourth toe and almost to base of disc on adjacent sides of third and fifth toes; an elongate outer metatarsal tubercle, but no inner tubercle. Hind legs moderately long, mean TL/SV (as measured by regression line, fig. 9) decreasing from about 0.58 in juveniles to 0.56 in large adults, range 0.51 to 0.65.

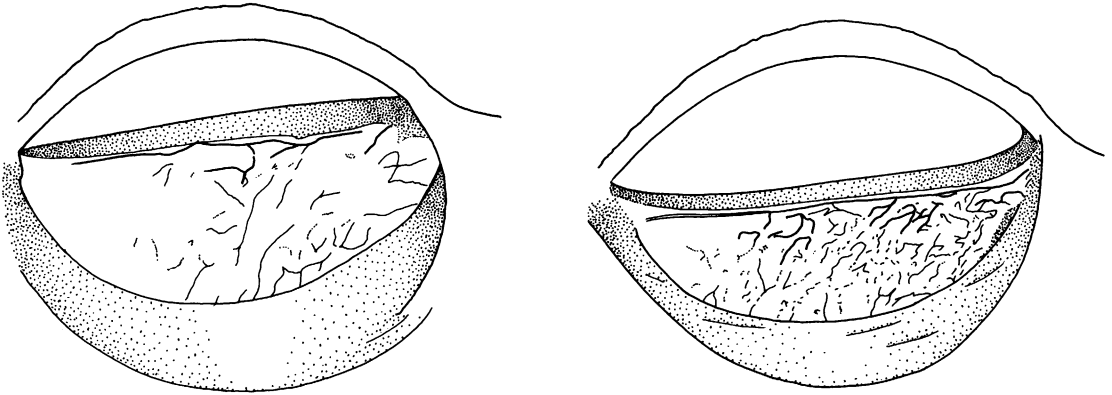


FIG. 6. Right eyes of *Nyctimystes disrupta* to show palpebral pigmentation. Based on individuals from the same locality (AMNH 81035, left, and 81031) with typically sparse pigmentation and with unusually heavy pigmentation.

Dorsal surfaces smooth to somewhat granular, ventral surfaces granular; a curved skin fold from posterior corner of eye across upper margin of tympanum; a low, smooth to slightly crenulate fold on outer side of forearm; no heel lappet.

The majority of preserved specimens have a dark reddish purple ground color through which an underlying darker mottled or spot-

ted pattern can be discerned. The ground color of a few individuals is paler and the darker pattern more pronounced, sometimes incorporating small light spots. The undersides from chin to lower hind legs are essentially uniform reddish purple, paler than the dorsal surfaces. If the dorsal surfaces are boldly marked, some of this pattern may extend slightly down into the groin and slightly onto the anterior and posterior surfaces of the thighs, but these areas typically are pigmented the same as the venter.

My color notes (partly paraphrased and rearranged for ease of comparison) on living adult frogs from three parts of the range illustrate some similarities over a wide area. AMNH 81029–81036 (Western Highlands Prov.): dorsal color dark gray-green with a black reticulum faintly visible; underside of body reddish purple, same color present in webbing; iris green with a grayish tint. AMNH 74820 (Eastern Highlands Prov., fig. 3): dorsal color light green with black markings and pale green spots; anterior and posterior surfaces of thigh and underside of shank yellowish brown; all ventral surfaces and finger and toe webs dull purple; iris greenish tan. R. Zweifel 5475 (field no., specimen lost, from Huon Peninsula, Morobe Prov.): dark green dorsally with reddish brown flecks; dorsal surfaces of hind limbs dark green, mottled and banded with reddish brown; chin pale green with reddish brown markings; chest

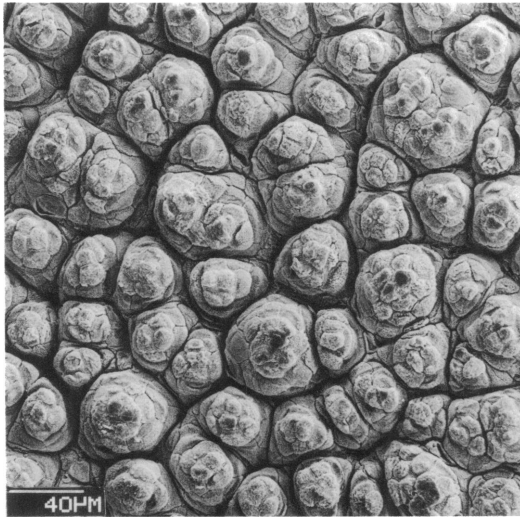


FIG. 7. Magnified view of part of nuptial pad of *Nyctimystes disrupta* (SEM photograph). Area covered measures approximately 0.28 mm. on a side.

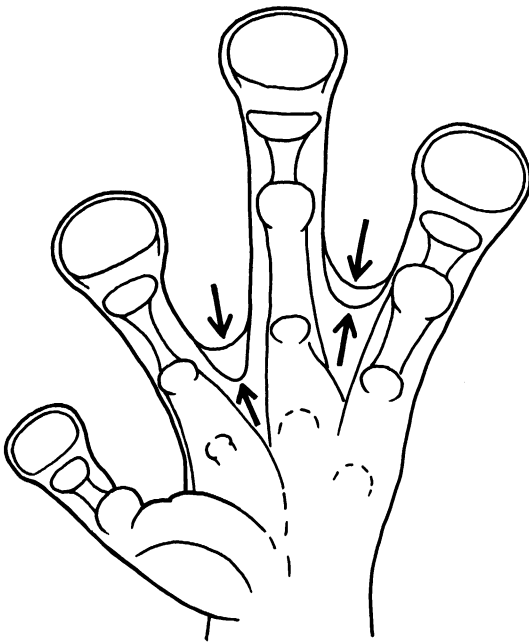


FIG. 8. Left hand of *Nyctimystes disrupta* in palmar view to show variation in webbing. Arrows indicate maximum and minimum amounts of webbing in a sample of 12 adult specimens; average is closer to the maximum.

similar, but abdomen, lower surfaces of hind limbs, groin, anterior and posterior surfaces of thighs, and webbing of hands and feet purplish red; iris green.

In addition to the specimens described above, I examined a living juvenile (SV 31 mm.), AMNH 81027, taken at Ialibu, Southern Highlands Province, that appears to be *disrupta*. The head and anterior dorsal body surface was light green, replaced posteriorly by mottling of light greenish gray. The iris too was light greenish gray, in marked contrast to the brown irises of two adult *Nyctimystes* sp. taken at the same locality (see following discussion of specimens not assigned to species). The palpebral pigmentation was in very fine disconnected golden lines.

Menzies (1976, pl. 8e) illustrates in color as *disrupta* a *Nyctimystes* with a greenish eye crossed by a brown streak. Possibly this is the same species as *disrupta* in the sense I define it. Tyler (1963b, p. 120) mentioned that a specimen from Yaramanda, Western

Highlands Province, had the iris light olive in life.

REMARKS: Tyler (1963b) diagnosed *Nyctimystes disrupta* on the basis of more extensive finger webbing and more pronounced palpebral pigmentation than in *N. papua*. The differences remain valid, though individual variation is greater than was evident in Tyler's sample. My concept of *N. disrupta* is based on close resemblance in morphology and pigmentation among preserved specimens from over a rather wide area (fig. 2) and from knowledge of colors in life, especially the color of the iris. I have listed below as *disrupta* specimens examined and recorded from the general area in which green-eyed frogs are known to occur; records of *N. papua* from this area (Zweifel, 1958; Tyler, 1963a; Duellman, 1967) are no longer tenable. Quite possibly the true distribution of *disrupta* may be more extensive, and it also is possible that more than one species of the *papua* group exists among the specimens I refer to *disrupta*. One instance of sympatry of green- and brown-eyed frogs is known (see above and following section on specimens not assigned to species).

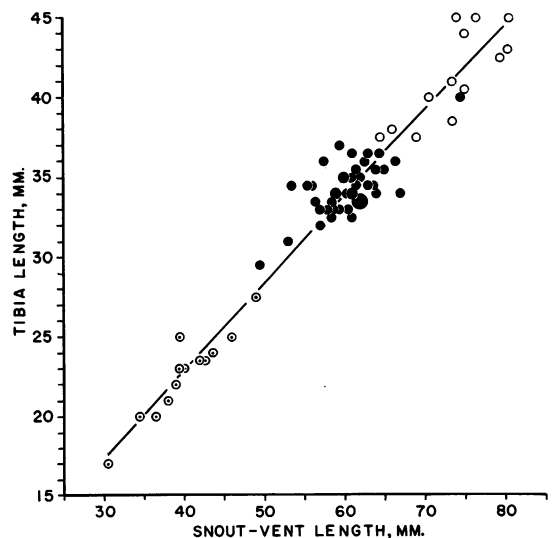


FIG. 9. Relationship of tibia length to snout-vent length in 74 *Nyctimystes disrupta*. See fig. 4 for symbols. Regression formula,  $Y = 0.681X^{0.954}$ ,  $R = 0.976$ .

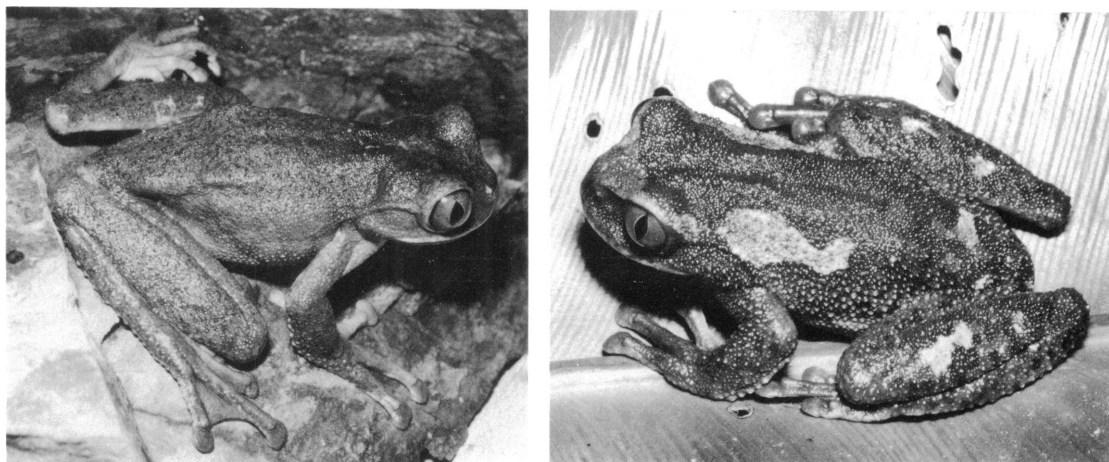


FIG. 10. *Nyctimystes trachydermis*. Left, paratype AMNH 82876, Edie Creek Road, Mt. Kaindi, Morobe Province; male, SV 85 mm. Right, holotype AMNH 82866, Gapaia Creek, Morobe Province; male, SV 76 mm.

**DISTRIBUTION AND SPECIMENS EXAMINED:** A conservative estimate of the range of *Nyctimystes disrupta* is the highlands of central Papua New Guinea from the Schrader Mountains in western Madang Province and from Ialibu in Southern Highlands Province southeastward to Purosa, Eastern Highlands Province, with a disjunct population in the mountains of the Huon Peninsula, Morobe Province (fig. 2).

Chimbu Province: Kup, Kubor Mtns., 1520–2130 m. (AMNH 55881–55884). Eastern Highlands Province: Watabung (AMNH 76724–76732); Orumba, 13 km. S, 10 km. W Goroka, 2130 m. (AMNH 76733); Lafoiyufa (AMNH 76734, 76735); Rintibe (AMNH 76736); Koko, 10 km. W, 8 km. S Goroka, 2190 m. (AMNH 74820–74823); Kotuni, Mt. Otto, 2130–2740 m. (AMNH 66221); northeast slope of Mt. Michael, 1980 m. (AMNH 66432–66479, 100935–101017); Purosa, 1950 m. (AMNH 66602–66610); Moife, 8 km. E, 14 km. N Okapa (AMNH 114819, BPBM 1053–1055). Madang Province: Kaironk Valley, Schrader Mtns., 1420–1830 m. (AMNH R15923, holotype); Mt. Kominjim, Schrader Mtns., ca. 2440 m. (AMNH 74165); Simbai (Woodruff, 1972, p. 59). Morobe Province: Gang Creek, Mt. Rawlinson, 1310–1370 m. (AMNH 74818, 74819, 74824, 75991–75993); Mt. Rawlinson near Zangaren, 1370 m. (AMNH 75994–75999); Num-

but, Mt. Rawlinson, 1220 m. (AMNH 76000–76002); Kotkin, Mt. Rawlinson, 1220 m. (AMNH 76003). Southern Highlands Province: Ialibu, 1900 m. (AMNH 81027); Western Highlands Province: Tigi Plantation, 32 km. N Mt. Hagen (town), 1340 m. (AMNH 81028–81036); Banz (AMNH 68149); Yaramanda, 1520 m., west side of Baiyer River (Tyler, 1963b, p. 120); Nondugl, Ahl Valley (BPBM 1115, 1116); Wahgi-Sepik Divide, vicinity of Nondugl between 1920 and 2290 m. (Tyler, 1963a, p. 111); Mt. Hagen, 2100 m. (BPBM 3030); Tomba, Mt. Hagen, 2500 m. (BPBM 5333).

***Nyctimystes trachydermis*, new species**

Figure 10

**HOLOTYPE:** AMNH 82866 (field no. RZ 8912), adult male, collected by R. G. Zweifel, Robert Storez and Papuan assistants at an elevation of about 1280 m. at Gapaia Creek, on the trail between Garaina and Saureli, Morobe Province, Papua New Guinea, on September 1, 1969.

**PARATYPES** (all from Morobe Province, Papua New Guinea): AMNH 82860–82865 and YPMA5435 and A5436, collected at the same time and place as the holotype; AMNH 81038–81042, collected by R. G. Zweifel and Papuan assistants at the type locality on June

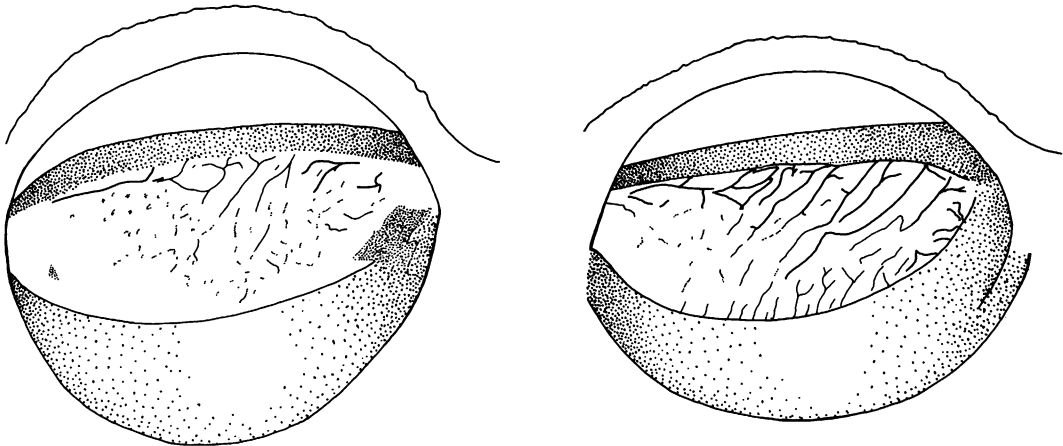


FIG. 11. Right eyes of *Nyctimystes trachydermis* to show palpebral pigmentation. Based on individuals from the same locality (holotype AMNH 82866, left, and paratype 82863) with sparse pigmentation and with pigmentation heavier than usual.

29, 1968; AMNH 82422–82425, from an elevation of about 2300 m. on the Ono River, collected by Angus Hutton in June 1969; AMNH 82867, from the Edie Creek Road on Mt. Kaindi, about 10 km., from Wau, collected by R. G. Zweifel on September 7, 1969; BPBM 7373, from Mt. Kaindi, 1600–2000 m., collected by Nixon Wilson on October 6, 1968; BPBM 5191, from Mt. Kaindi at about 1950 m., collected by W. Winter on July 10, 1967; USNM 197473, 197473A, 197474, from Maori Creek, Mt. Kaindi, 1890–1920 m., collected by George Zug on November 16 and 19, 1971.

**DIAGNOSIS:** *Nyctimystes trachydermis* is distinguished from all other known species of the genus in the following combination of characters: tympanum completely concealed; palpebral pigmentation relatively sparse; large size—males to 88 mm. SV length, maximum size of females unknown; dorsal skin roughened by tiny, conical asperities rather than by variable sized and more rounded irregularities as seen in some other species; iris brown in life, vertical pupil distinct; males without vocal sac.

**DESCRIPTION OF HOLOTYPE:** Adult male with snout short and rounded, high and sloping in profile and only slightly longer than eye; canthus rostralis distinct, slightly curved, loreal region concave and sloping; nostrils directed largely laterally (scarcely evident in

dorsal aspect), internarial distance distinctly greater than distance from eye to naris (EN/IN 0.781). Upper eyelid slightly narrower than interorbital space; palpebral pigmentation of dots and short unconnected lines, growing progressively weaker posteriorly until virtually absent from posterior part of area (fig. 11). Tympanum not visible externally. No vocal sac openings. Vomerine teeth in two small patches between the posterior borders of the nares.

Relative lengths of fingers  $3 > 4 > 2 > 1$ ; scanty webbing between third and fourth fingers reaching not quite to level of distal subarticular tubercle on fourth finger, barely past proximal tubercle on third, fingers somewhat fringed; subarticular tubercles single; discs of fingers two to four large, greater than one-half of eye length, that of first finger smaller. A small, inconspicuous, finely granular and unpigmented nuptial rugosity on inside (body side) of base of first finger. Relative lengths of toes  $4 > 5 > 3 > 2 > 1$ , fifth very little longer than third; all toes except fourth webbed to base of disc, fourth toe webbed to distal subarticular tubercle but with broad fringe to disc; subarticular tubercles rounded, single; a low, rounded inner metatarsal tubercle but no outer one.

All dorsal surfaces roughened with small, mostly conical and white tipped asperities, those on outer surface of arm in an indistinct

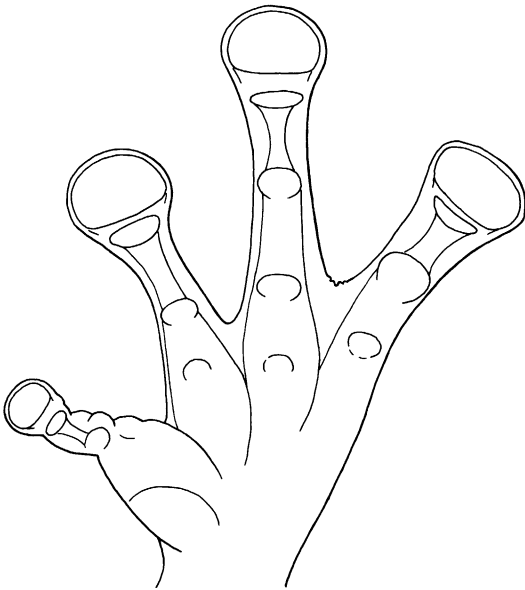


FIG. 12. Left hand of *Nyctimystes trachydermis* (paratype AMNH 81038) in palmar view.

row. A strong fold from posterior corner of eye to above arm insertion. Ventral surfaces granular. No heel lappet.

Dorsal ground color brown in life (fig. 10), with a pale tan area on the top of the snout continuous along the outer edge of the eyelids with an elongate patch of the same color on the right side and slightly separated from a similar, shorter patch on the left. Smaller, irregularly shaped areas of the same light color were present on the hind limbs and lower back. The upper lip was edged with yellowish tan, but with the upper edge of that color ill defined. The iris was reddish brown, with the conspicuous vertical pupil narrowly edged in yellow.

MEASUREMENTS AND PROPORTIONS OF HOLOTYPE: SV 75.9; HW 27.1; HL 28.6; TL 42.3; IN 7.3; EN 5.7; snout 11.1; Eye 8.1; width of third finger disc 4.7, width of penultimate phalange 2.4; width of fourth toe disc 4.4. TL/SV 0.557; HW/SV 0.357; EN/IN 0.781; IN/SV 0.096; EN/SV 0.075; Eye/SV 0.107.

VARIATION: All but one of the 23 adult specimens are male. They range in length from 71.6 to 88.0 mm. SV (the single female, gravid, is 76 mm. SV). The diagnostic characters

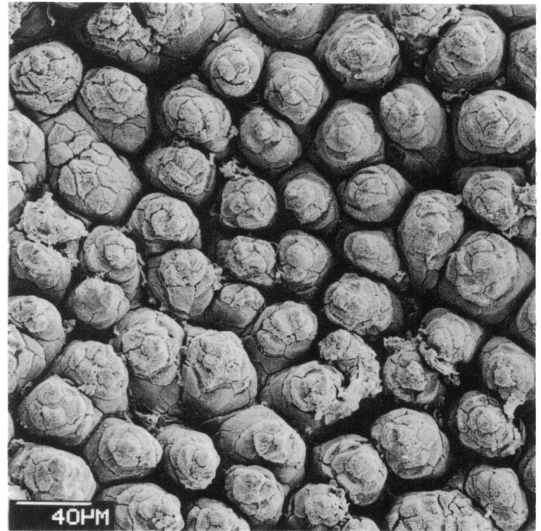


FIG. 13. Magnified view of part of nuptial pad of *Nyctimystes trachydermis* (SEM photograph, paratype AMNH 82861). Area covered measures approximately 0.28 mm. on a side.

of concealed tympanum and rugose dorsal surfaces are common to all specimens, including the only juvenile in the series (SV 41 mm.). The nuptial pad of the male occupies only a small area on the inside of the first finger and may be virtually colorless but more often is light brown. It is extremely fine-grained, with about 700 units per square millimeter (fig. 13). The amount of palpebral pigmentation is rather variable. An average individual has a pattern of spots and weak, disconnected lines over the anterior 40 to 50 percent of the area, whereas exceptional specimens have a better defined linear pattern (but of thin lines) over virtually the whole area (fig. 11). In living frogs, however, even the densest pigmentation is inconspicuous.

Variation of adults in selected proportions is as follows: TL/SV  $0.571 \pm 0.003$  (0.539–0.596) 19; HW/SV  $0.382 \pm 0.003$  (0.357–0.405) 19; EN/SV  $0.076 \pm 0.001$  (0.071–0.094) 20; IN/SV  $0.096 \pm 0.001$  (0.090–0.102) 20; EN/IN  $0.786 \pm 0.009$  (0.709–0.836) 20; Eye/SV  $0.110 \pm 0.001$  (0.100–0.123) 19.

The iris was brown in 15 living frogs that I examined; my notes refer to "light chestnut brown," "bright russet," and "rich reddish

brown." Figure 10 shows extremes of color pattern. The dorsal ground color of living frogs varied from dark greenish brown to gray, and virtually patternless individuals were more common than blotched ones such as the holotype. Finger and toe webbing, the groin and anterior and posterior surfaces of the thigh were bluish gray, paler than the dorsal ground color and much like the ventral surfaces. The upper lip was bordered with dull yellow.

COMPARISON WITH OTHER SPECIES: It is common for *Nyctimystes* to have the tympanum partly covered by the postocular fold, but only one known species other than *N. trachydermis* has the tympanum completely hidden: *Nyctimystes obsoleta* (Lönnerberg). I have not examined the holotype (and unique) specimen of *obsoleta*, but Tyler (1965) described it in detail in the course of transferring the species from *Hyla* to *Nyctimystes*. The two species differ in several respects to the extent that they may be considered only distantly related. Tyler described *N. obsoleta* as a male, snout-vent length 35 mm., with vocal sac openings, whereas *trachydermis* males lack a vocal sac and attain more than twice the length of *obsoleta*. The eye-naris distance of *obsoleta* is slightly greater than the internarial distance (EN/IN 1.097) and the legs long (TL/SV 0.643), whereas in *trachydermis* the internarial distance is considerably broader (mean EN/IN 0.786) and the legs relatively shorter (mean TL/SV 0.571). Tyler (1965, fig. 1) illustrates the palpebral pigmentation of *obsoleta* as in essentially vertical, occasionally bifurcating lines, in contrast to the more oblique trend in *trachydermis*. There is little likelihood that additional specimens of *obsoleta* will erase the observed distinctions between that species and *trachydermis*.

Large size is one of the distinctive features of *N. trachydermis*. Four other species commonly attain a snout-vent length of more than 80 mm: *granti*, *humeralis*, *pulchra* and *zweifeli*. All are smooth skinned species with the tympanum at least indistinctly visible, so should not be confused with *trachydermis*. Some additional features that distinguish these species from *trachydermis* are indicated in parentheses: *granti* (distinctive reticulate dorsal pattern, higher EN/IN ratio); *humer-*

*alis* (vocal sac and humeral spine in males, uniform green dorsum); *pulchra* (much higher EN/IN ratio, vocal sac in male, large triangular lappet on heel); *zweifeli* (vocal sac in male, dense reticulate palpebral pigmentation).

HABITAT NOTES: At the type locality at about 1280 m. elevation Gapaia Creek cascades amid boulders down a steep mountain slope. I collected there on the evenings of June 29, 1968, and September 1, 1969, in the company of a number of the local men and children and (in 1969) Mr. Robert Storez. Bushes and forest trees overhang the borders of the stream, and I captured my specimens on these; others may have come from boulders. The single frog I obtained on Mt. Kaindi was on a fern frond at night hanging over the middle of a stream little more than a meter wide that flowed rapidly over numerous cascades and through small pools.

The type locality is notable for its concentration of stream hylids. I have five species of *Nyctimystes* and two of *Litoria* from there, in addition to a member of the *Rana grisea* complex and the riparian microhylid *Sphenophryne palmipes*. Besides *N. trachydermis* there are: *N. tyleri* (described below); a distinctively pigmented form close to *N. kubori* if not that species; a pale-eyed member of the *N. cheesmani* complex (Zweifel, 1980, p. 400); and a dimorphic (green and brown individuals) species that may be the true *N. gularis*. The other hylids are *Litoria angiana* and *L. micromembrana*. One wonders what circumstances permit (or promote) such extensive sympatry of relatively closely related species. At nearby Garaina, along low gradient forest streams at about 700 m., only two species of *Nyctimystes* and two of *Litoria* may be found: *N. cheesmani*, *N. semipalmata*, *L. eucnemis* and *L. wollastoni*.

ETYMOLOGY: The specific name, chosen for its descriptive quality, is an adjective derived from the Greek words *trachys* and *derma*, meaning rough and skinned.

DISTRIBUTION AND SPECIMENS EXAMINED: *Nyctimystes trachydermis* occurs at elevations of approximately 1280 to 2300 m. between Mt. Kaindi (near Wau) and Saureli (near Garaina), Morobe Province, Papua New Guinea (fig. 2). Specific localities and speci-

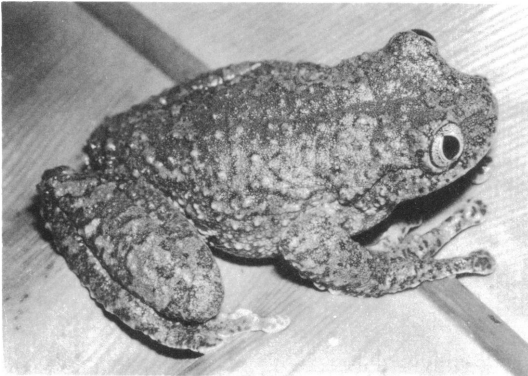


FIG. 14. *Nyctimystes tyleri*. Holotype AMNH 82876, Gapaia Creek, Morobe Province; male, SV 78 mm.

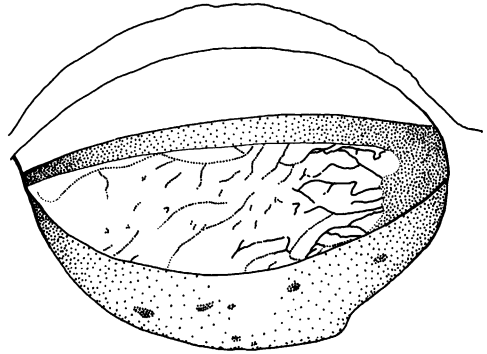


FIG. 15. Right eye of *Nyctimystes tyleri* (holotype AMNH 82876) to show palpebral pigmentation.

mens examined are given under Holotype and Paratypes, above).

#### *Nyctimystes tyleri*, new species

Figure 14

**HOLOTYPE:** AMNH 82867 (field no. RZ 8916), adult male, collected by R. G. Zweifel at an elevation of about 1280 m. at Gapaia Creek, on the trail between Garaina and Sauréli, Morobe Province, Papua New Guinea, on September 1, 1969. There are no other specimens of the species.

**DIAGNOSIS:** *Nyctimystes tyleri* is characterized by the combination of large size, absence of a vocal sac, weak palpebral pigmentation, and golden iris (in life). The species with which it most likely would be confused are *N. disrupta*, *N. trachydermis*, and *N. papua*. The iris is green in *disrupta*, brown in *trachydermis* and unrecorded in *papua*. *Nyctimystes disrupta* is a smaller species (SV of males typically less than 70 mm. but 78 mm. in the sole *tyleri*) with more finger webbing and the lower leg unspotted beneath. *Nyctimystes trachydermis* resembles *tyleri* in size but has the tympanum concealed and a much lower EN/IN ratio (maximum 0.84 vs. 0.96). *Nyctimystes papua* is considerably smaller (females mature at less than 60 mm.) and may also differ in its relatively longer legs and higher EN/IN value.

**DESCRIPTION OF HOLOTYPE:** Adult male with snout short, rounded and high, but longer than eye; canthus rostralis distinct, curved;

loreal region oblique, concave; internarial and eye-naris distances almost identical (EN/IN 0.96). Upper eyelid approximately equal in width to interorbital space; palpebral pigmentation weak, with broken lines in sloping orientation (fig. 15). Tympanum small, indistinct, partly covered by heavy, curved postorbital fold. No vocal sac openings. Vomerine teeth in two small patches between internal nares.

Relative lengths of fingers  $3 > 4 > 2 > 1$ ; webbing scanty, outer finger webbed short of distal subarticular tubercle; discs of second to fourth fingers large, more than one-half diameter of eye, that of first finger smaller (fig. 16); first finger appears swollen, but no obvious nuptial pad differentiated. Relative lengths of toes  $4 > 5 = 3 > 2 > 1$ ; first and fifth toes webbed to base of disc, fourth toe with less webbing but with broad fringe to disc on each side; large, single subarticular tubercles; a low, rounded inner metatarsal tubercle but no outer one.

All dorsal surfaces except for top of thigh extremely warty, but elevations mostly rounded rather than conical. Ventral surfaces except for shank more finely granular than dorsal. A crenulate fold along outer side of lower arm. Heel with small pointed warts but no enlarged tubercle or lappet.

In life (fig. 14) the dorsal ground color was dark green. Large blotches on the back were dark brown, not conspicuously differentiated from the ground color. A streak of brown occupied the central dorsal part of the thighs,



but the anterior and posterior surfaces were coarsely mottled with black on a blue-gray background. The ventral surfaces were gray with small spots of very dark brown on the chin, chest and abdomen, and larger spots of the same color on the legs. The webbing of the feet and hands was the same gray with brown spots. The palpebral pigmentation was golden and the iris bright yellow with black lines. The preserved specimen has a reddish purple ground color with darker purple markings. Under sides are pale tan with purple to gray markings. For an illustration in color, see Zweifel (1977, p. 33, middle figure).

MEASUREMENTS AND PROPORTIONS OF HOLOTYPE: SV 77.6; HW 28.8; HL 26.1; TL 42.3; IN 7.0; EN 6.7; snout 12.2; Eye 7.8; Ear 2.5; width of 3rd finger disc 5.6, width of penultimate phalange 3.2; width of 4th toe disc 4.8. TL/SV 0.545; HW/SV 0.371; EN/IN 0.957; IN/SV 0.090; EN/SV 0.086; Eye/SV 0.100.

ETYMOLOGY: This species, which is at least as handsome as *Nyctimystes zweifeli* Tyler, is named for Michael J. Tyler in recognition of his notable contributions to the systematics of Australo-papuan frogs.

HABITAT NOTES: I found the unique specimen at night as it sat on a tree branch several feet above the ground about 30 to 40 feet from a torrential mountain stream (see account of *N. trachydermis*).

DISTRIBUTION AND SPECIMENS EXAMINED: Known only from the type locality and the holotype specimen (fig. 2).

#### SPECIMENS NOT ASSIGNED TO SPECIES

My earlier assessment of *Nyctimystes* (Zweifel, 1958) included within *N. papua* specimens from as far afield as the Idenburg River of Irian Jaya and Mount Dayman near the southeastern tip of Papua New Guinea. Some specimens from intervening areas are now identified as *N. disrupta* and others as the new species *N. trachydermis* and *N. tyleri*. I have discussed in the foregoing section frogs that Parker (1936) identified as males of *N. papua* and have referred them to *Nyctimystes* sp. There remains, however, a substantial residue of specimens that do not fit comfortably into any of the taxa I now recognize

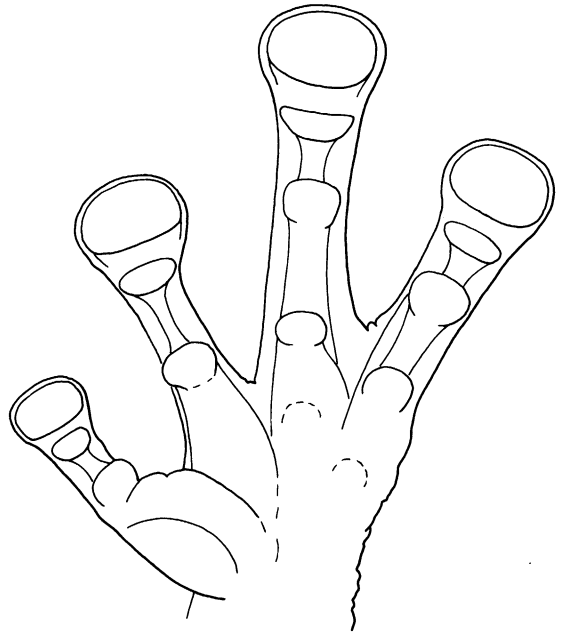


FIG. 16. Left hand of *Nyctimystes tyleri* (holotype AMNH 82876) in palmar view.

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*. Size ranges of adult males and females are mostly those of *disrupta*, not of *papua*. In several instances the iris color in life is known to be brown, rather than the green of *disrupta*, and I consider this adequate reason for doubting their conspecificity with *disrupta*. However, eye color is known from relatively few localities so I think it would be premature to describe additional species, especially when morphological evidence suggests that more than one species may be represented among the unassigned specimens. My purpose here is to call attention to the geographic distribution of these unassigned samples (fig. 17) and to comment on some pertinent aspects of morphology.

Irian Jaya; 15 km. SW Bernhard Camp, 1800 m.: The only *papua* group specimens I have examined from western New Guinea (AMNH 49671, 49674) are two adult females about 68 mm. SV that I earlier (Zweifel, 1958) referred to *N. papua*. Their principal distin-

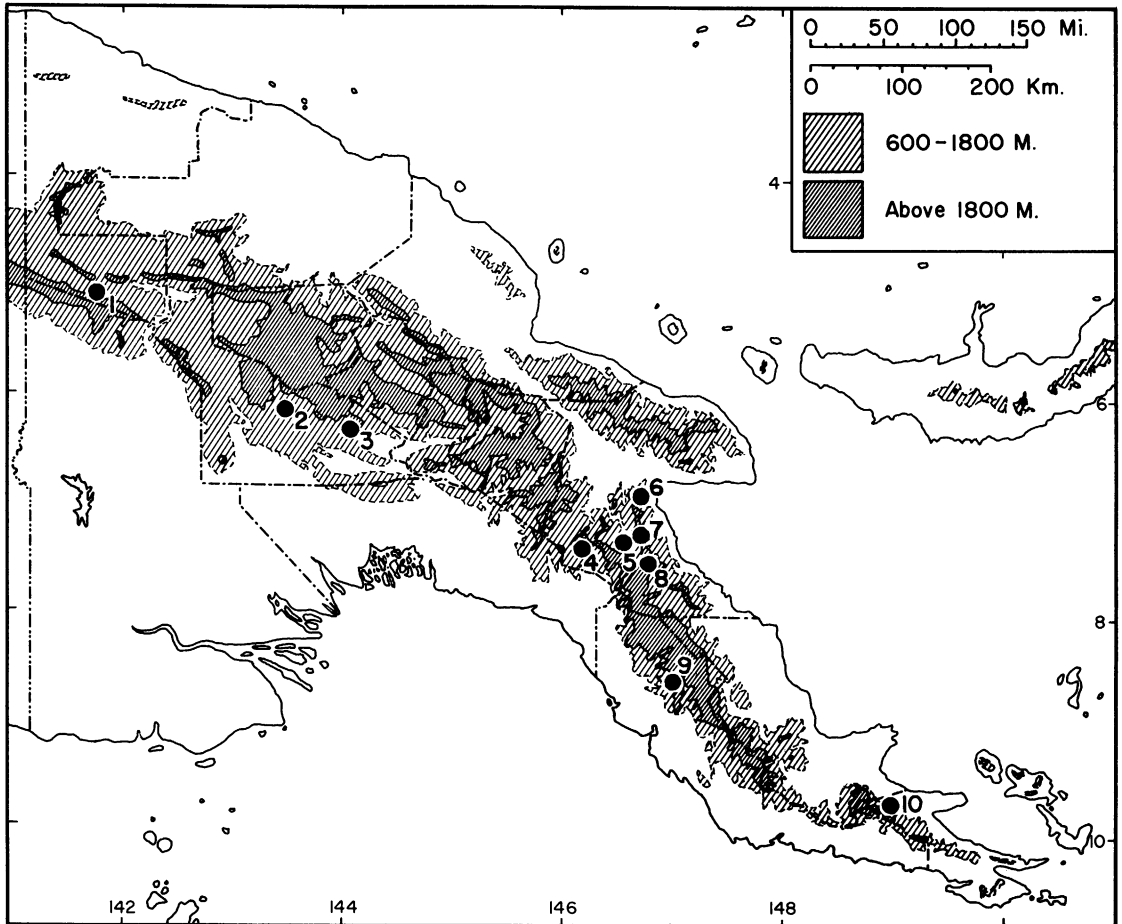


FIG. 17. Localities in Papua New Guinea for samples of *papua*-group *Nyctimystes* not assigned to species. 1, Telefomin and Ofekomin; 2, Nipa; 3, Ialibu; 4, Aseki; 5, 15 km. W Wau; 7, Mt. Missim; 8, 20–25 km. ESE Kaisenik; 9, Mt. Tafa; 10, Mt. Dayman. An additional locality not shown is in Irian Jaya, 340 km. WNW of Telefomin.

guishing feature amidst the general *disrupta*-like characters is an unusually low EN distance, resulting in an EN/IN value of about 0.85 in each specimen, well below the minimum of 0.90 for a large series of *disrupta*.

Telefomin and Ofekomin, 1400–1500 m., West Sepik Province: An adult male of 64 mm. SV and two adult females of 70 and 71 mm. (AMNH 114815–114817) closely resemble specimens from the Southern Highlands (below). The collector noted the dorsal color in life as dark green, but the iris color is unknown.

Nipa and Ialibu, Southern Highlands Province: The sample of eight specimens in-

cludes five males from Nipa (AMNH 103184–103188, 68 to 72 mm. SV), and two males (SV 64, 68 mm.) and an immature female (SV 55 mm.) from Ialibu (AMNH 79971, 81025, 81026). These frogs have the general appearance of *N. disrupta*, though the mean EN/IN value of 0.951 (0.90–0.98) is a bit low for that species and the finger webbing averages slightly less. Two males at 71 and 72 mm. SV are larger than all but one male *disrupta* in the large number examined. Two frogs from Ialibu that I examined alive were dark green dorsally with darker green markings (fig. 18). The sparse palpebral pigmentation of gold flecks was readily visible only



FIG. 18. Examples of brown-eyed *Nyctimystes* not assigned to species. Left, AMNH 81026, Ialibu, Southern Highlands Province; immature female, SV 55 mm. Right, BPBM 9413, Mt. Missim, Morobe Province; male, SV 58 mm. (Photo courtesy of A. Allison.)

under magnification. The iris was brown. Also taken at Ialibu was a juvenile 31 mm. SV with green eyes that I refer to *N. disrupta*. So far as I know this is the only instance where brown-eyed and green-eyed *Nyctimystes* of the *papua* group are recorded from the same locality.

Localities in Morobe Province: A series of 18 specimens taken at elevations ranging from 1100 to 2200 m. comprises mostly specimens from Mt. Missim, about 10 km. NE Wau (BPBM 9354, 9382–9384, 9391, 9407, 9413, 9660, 9786, 9787; MCZ 23293, 23294). Others come from Wagau (56 km. N Wau, AMNH 74816, 74817), from 20 to 25 km. ESE Kaisinik (30 km. ESE Wau, BPBM 6221, 6229), from the vicinity of Aseki (52 km. W Wau, BPBM 8539), and from 15 km. W Wau (BPBM 6263). There appear to be two forms within this group; I treat them separately.

Fifteen specimens (12 males 52 to 59 mm. SV, three females 69 to 74 mm.) have relatively high EN/IN ratios, mean  $1.05 \pm 0.014$  (0.96–1.15). In size and proportions these frogs resemble *disrupta*, though the finger webbing is rather less in some specimens. Two living specimens from Wagau that I examined, as well as four from Mt. Missim and another from 15 km. west of Wau I saw in color transparencies had the iris brown, not green as in *disrupta*. The dorsal ground color

of these frogs was brown rather than green as I have reported for *disrupta*. The specimens from Mt. Missim had bold black and white markings on the thighs and in the groin (fig. 18), whereas those from Wagau were more nearly uniform greenish gray in these areas. Earlier (Zweifel, 1980, p. 399) I identified the Wagau specimens as *N. disrupta*. Menzies (1976, pl. 8d) illustrated in color as *N. papua* a frog of the sort discussed here.

Three specimens segregated on the basis of low EN/IN ratio, mean 0.837 (0.81–0.88), are from Mt. Missim (MCZ 23293, 23294; BPBM 9786). Two females are 64 and 76 mm. SV, the male 62 mm. Palpebral pigmentation is variable, being fairly strong over much of the area in two specimens, weak and restricted to the anterior palpebral area in the other. There is no information on color in life, but the preserved specimens are rather boldly patterned, especially in the groin and on the anterior and posterior surfaces of the thighs. Finger webbing is less than typically seen in *disrupta*. Two of these specimens (MCZ) were identified as *Hyla angiana* by Loveridge (1948) and reidentified as *Nyctimystes papua* by Zweifel (1958).

Mt. Tafa, east slopes at 2070 m., Central Province: An unusually large male (SV 81 mm., AMNH 58701), an adult female (59 mm., AMNH 58703) and a smaller male (40

mm., AMNH 58702) may form a hetero-specific group. Palpebral pigmentation is rather sparse in the two larger specimens, whereas in the small male it forms weak, parallel diagonal lines over most of the area. Finger webbing is slightly less than in *disrupta*, but the EN/IN proportions are as in that species. The remarkable size of the large male (as large as the largest female *disrupta*) seems to divorce it from *disrupta*. It especially contrasts with the series of small males from nearby Mondo that Parker (1938) referred to *N. papua* (see foregoing account of that species).

Mt. Dayman, 1550 m., Milne Bay Province: Two adult females 64 and 67 mm. SV (AMNH 56749, 56837) have very little palpebral pigmentation and finger webbing a little less than is usual in *N. disrupta*. Proportions are as in *disrupta*.

REMARKS: The range in size of adult males and the sample differences in EN/IN values suggest that perhaps as many as four species may be confused among the samples discussed: two forms with low EN/IN values found many hundreds of kilometers apart in Papua New Guinea and Irian Jaya; a species represented by the giant male from Mt. Tafa; at least one species generally similar to *N. disrupta* but with brown eyes. Collection of topotypes of *Nyctimystes papua*—complete with information on color in life and size ranges of sexually mature males and females—will be basic to unraveling this tangle. Only then will it be possible to place any new information on other populations in the proper context.

SPECIMENS EXAMINED: Indonesia: Irian Jaya; 15 km. SW Bernhard Camp, Idenburg River, 1800 m. (AMNH 49671, 49694).

Papua New Guinea: West Sepik Province: Telefomin, ca. 1500 m. (AMNH 114817); Ofekomin, ca. 1400 m. (AMNH 114815, 114816). Southern Highlands Province: Nipa, Wage River (AMNH 103184–103188); Ialibu, 1900 m. (AMNH 79971, 81025, 81026). Morobe Province: Aiya Village, vic. Aseki, 1200 m. (BPBM 8539); Nupumanda Creek, ca. 15 km W Wau, 1200 m. (BPBM 6263); 20–25 km. ESE Kaisinik, 1700–2000 m. (BPBM 6221, 6229); Mt. Missim, 1550–1650 m. (BPBM 9354, 9382–9384, 9391, 9407, 9413, 9660); Mt. Missim, 2250 m. (BPBM

9786, 9787); Mt. Missim (MCZ 23293, 23294); Wagau, Herzog Mtns., 1100 m., 13 km. S, 21 km. W Lae (AMNH 74816, 74817). Central Province: Mt. Tafa, east slope, 2070 m. (AMNH 58701–58703). Milne Bay Province: Mt. Dayman, north slope, 1550 m. (AMNH 56749, 56837).

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