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Results of the Archbold Expeditions. No. 78 Frogs of the Papuan Hylid Genus *Nyctimystes*

By Richard G. Zweifel

Many specimens of the hitherto little-known genus of tree frogs *Nyctimystes* are included in the extensive herpetological material obtained by the five Archbold Expeditions to New Guinea. The study of this material and other important specimens obtained in central New Guinea by E. Thomas Gilliard makes it possible to redefine the genus *Nyctimystes* and to add several new species to the known fauna of New Guinea. In addition to the specimens in the collection of the American Museum of Natural History, I have examined specimens in the Carnegie Museum through the generosity of Dr. M. Graham Netting, and the *Nyctimystes* in the collection of the Museum of Comparative Zoölogy through the courtesy of Mr. Arthur Loveridge. I am grateful to Mrs. Frances W. Zweifel, who prepared figures 1, 2, 4, 7, 11, 14, and 16, and aided in the preparation of most other illustrations. Mr. Charles M. Bogert is due thanks for reading and helpfully criticizing the manuscript.

For catalogued specimens, the following abbreviations are used:

A.M.N.H., the American Museum of Natural History
B.M.(N.H.), British Museum (Natural History)
C.M., Carnegie Museum
M.C.Z., Museum of Comparative Zoölogy of Harvard College

THE GENUS *NYCTIMYSTES*

The hylid frogs of New Guinea have for many years been referred to two genera: *Hyla*, found in both Eastern and Western Hemispheres,

and *Nyctimystes*, restricted to New Guinea. The only feature that has been used to distinguish the two genera is the shape of the pupil—horizontal in *Hyla*, vertical in *Nyctimystes*. In 1897 Boulenger described a hylid with vertical pupils from New Guinea as *Nyctimantis papua*, and in 1914 he followed this paper with the description of *Nyctimantis granti*. The genus to which these new species were referred, *Nyctimantis*, was known previously from South America. It seemed to Stejneger (1916) that *N. papua* and *N. rugiceps* (the South American form) could not be phylogenetically related directly, as the latter has the skin of the head involved in the cranial ossification, while in *papua* there is no such fusion. So Stejneger proposed the generic name *Nyctimystes* for *Nyctimantis papua*. He did not discuss *N. granti*. Van Kampen (1923) used *Nyctimantis* for the Papuan frogs, and cited *Nyctimystes* as a synonym.

The next comment on *Nyctimystes* was that of Noble (1931, p. 513), who felt that pupil shape alone was not a sufficient criterion of genera in the Hylidae, as the vertical pupil seemed to have evolved independently in different groups of frogs. The two species of *Nyctimystes* known at that time seemed to differ sufficiently in characters other than the pupil shape that convergence was a strong possibility. Noble implied, but did not specifically state, that the two species of *Nyctimystes* known at that time belonged in the genus *Hyla*. However, in 1936 Parker was able to show that there were five species of hylids in New Guinea with vertical pupils and that these species seemed to form a natural group worthy of generic rank.

Little has been written about *Nyctimystes* in the more than 20 years since Parker's paper was published. Loveridge (1945) described *N. milneana;* Forcart (1953) described *N. flavomaculata;* Neill (1954) described *N. loveridgei;* and Brongersma (1953) suggested that *Hyla amboinensis* should be placed in the genus *Nyctimystes*. For reasons that are presented in paragraphs below, I consider all these recently described forms as belonging to the genus *Hyla*.

Though the generic name *Nyctimystes* has been in use for 40 years, there has never been a formal definition or diagnosis of the genus. Admittedly, the single character of vertical as opposed to horizontal pupil is a tenuous one for defining a genus. If the Papuan frogs truly constitute a natural group, it should be possible to find other characters that tie the species together and separate them from other hylid genera. One such character is the presence of a vein-like network, the palpebral reticulum, in the upper, otherwise pigmentless part of the lower eyelid (figs. 19, 20). This structure does not appear to be present in any

of the hylids of New Guinea that have horizontal pupils. All five species that Parker (1936) referred to the genus *Nyctimystes* show this character, though faintly in the case of one form. To these, I am able to add seven new species, and two species formerly referred to *Hyla*.

The solution to the problem of generic assignment of New Guinea hylids that I have adopted is to restrict the use of the name *Nyctimystes* to species that have both a vertically elliptical pupil and pigmented palpebral venation. This means that those forms with such a pupil, but without the reticulum, are referred back to *Hyla*. These species are dealt with in a subsequent section of this paper.

DEFINITION OF *NYCTIMYSTES*

The genus *Nyctimystes* Stejneger, 1916, may be defined as follows: hylid frogs in which the pupil when contracted forms a vertical slit; the transparent portion of the lower eyelid is provided with a pigmented, vein-like network; the tip of the first toe does not reach to or beyond the disc of the second toe; and the skin of the head is not coössified with the cranium.

Restriction of the name *Nyctimystes* to forms that have pigmented palpebral venation has the practical advantage of making it possible to place in the proper genus those specimens (usually in the majority) in which the pupil shape cannot be determined. At best this Papuan genus appears weakly differentiated from *Hyla* when compared to the degree of differentiation seen in several genera of tropical American hylids.

The geographic distribution of the genus is the Papuan region, including, as well as New Guinea, the Moluccas Islands on the northwest and the D'Entrecasteaux and Louisiade Islands on the southeast.

When more data become available, it may prove possible to include in the generic definition a statement of breeding habits and larval adaptation to stream life. Parker (1936) described peculiar, stream-type larvae that he referred to *N. montana* and *N. semipalmata*. He noted that tadpoles of this type may be characteristic of all species of *Nyctimystes*. There are many of these sucker-mouthed, depressed larvae in the collections of the American Museum, but unfortunately none of them can be associated with transformed frogs.

I have examined gravid females of 12 species that I consider to belong to the genus *Nyctimystes*. In 11 of these, the ovum is pale (white or yellowish orange), while in one (*N. rueppelli*) there is some darkening of the animal pole. Also, the ova are frequently large, often over 2 mm., and in one instance over 3 mm., in diameter. The presence of this

large, heavily yolked egg suggests that the embryo may undergo its development out of water, later to enter the swift streams to which the larvae are seemingly adapted. However, nothing is known of the breeding habits of *Nyctimystes* that might confirm or disprove this inference. The eggs of several species of *Hyla* in New Guinea are small (under 2 mm. in diameter), with dark brown or black animal hemispheres, but some do possess larger, unpigmented eggs similar to those seen in most *Nyctimystes.*

STRUCTURAL CHARACTERISTICS OF *NYCTIMYSTES*

The frogs of the genus *Nyctimystes* are rather generalized hylids in structure, at least as adults, and, with the exception of the palpebral venation and vertical pupil and a humeral spine in one species, have no peculiar characters. Differences between the species seem to lie mainly in the shape of the snout, in the form of the palpebral venation, in the degree of webbing of the hand, and in the size attained. Leg length varies somewhat, a useful character because in a few cases there are particularly long- or short-legged species. Very probably one who had the opportunity to study these animals in life would find characteristics of pigmentation, mating call, and habitat which would aid in discriminating among the species.

Vomerine teeth, except as an individual anomaly, are always present. The eyes are relatively large, the interorbital space being approximately equal to the greatest width of an upper eyelid. The palpebral venation may take several forms, but with some exceptions, all individuals of a species or at least a local population will show highly similar patterns. A common pattern is one in which the pigmented venation consists of a number of steeply sloping parallel lines, some of which may be forked. Relatively few of these near-vertical lines are joined to one another by horizontal interconnections. Some species show a true reticulum, with no obvious directional orientation of the lines. A third variant has a tendency to horizontal orientation, while one species has a weak, broken reticulum. The palpebral patterns of 12 species are shown in figures 19 and 20. The tympanum is almost always less than half of the diameter of the eye. A short, straight or curved, supratympanic fold is present. Finger and toe discs are present; the disc of the third finger is always larger than the tympanum. The relative lengths of the fingers are: $3>2>4>1$; of the toes: $4>5\geq3>2>1$. Webbing of the fingers varies from a scant basal web to nearly complete webbing (fig. 21). The toes, with the exception of the fourth, are usually webbed to the disc; the

fourth toe has part or all of the penultimate phalanx free. Distinct, rounded, subarticular tubercles are present on fore and hind feet; on occasion, a tubercle may be doubled (split), or even divided into three parts. A small inner metatarsal tubercle is present, and sometimes a tiny outer tubercle is seen as well. Tibial length varies from 45 per cent to 61 per cent of the snout to vent length (fig. 10, table 1). A dermal appendage may be absent on the heel, or may be present in sizes up to a prominent triangular fold of skin (fig. 18). The vocal sac, when present, is a median subgular structure, with slit-like openings on each side of the floor of the mouth.

METHOD OF DEALING WITH CHARACTERS

Differences in head proportions such as snout shape are difficult to express objectively. As a rule, a species with a long, flat snout has the nostrils placed closer together than a species with a short, high snout. I have sought to express this difference by means of the ratio of the distance from the anterior corner of the eye to the naris to the distance between the nares. Thus an individual with a long snout shows a relatively high ratio when compared to a broad-, short-snouted specimen. The abbreviation E-N/IN is used to designate this ratio (fig. 9, table 1). The measurements were made to the closest tenth of a millimeter with a vernier caliper seen through a binocular dissecting microscope.

In the computation of the ratio of the tibia length to the snout to vent length (TL/S-V), the tibia length was measured from the fold of skin at the knee to the heel.

COMPARISONS WITH OTHER GENERA

A genus that might be confused with *Nyctimystes* as here restricted is *Phyllomedusa* (including *Agalychnis*) of tropical America. These frogs have a vertical pupil, and some species have a well-developed reticulum. The more specialized species of *Phyllomedusa* have hands and feet highly adapted for grasping, so that the first toe is longer than the second and can be opposed to the others. Even in the more primitive members of the series, the first toe is proportionately longer than in other hylids and reaches at least to the disc of the second. This difference in toe proportions will serve to distinguish *Phyllomedusa* from *Nyctimystes*, which shows no such specialization of the hands or feet.

Some South American members of the genus *Hyla* possess a palpebral

reticulum, notably *H. boans*, *H. geographica*, and *H. maxima*, but do not combine this characteristic with a vertical pupil. New World *Hyla* that have a vertical pupil do not have a pigmented palpebral venation.

ACCOUNTS OF SPECIES

Nyctimystes avocalis, new species

Figure 1

TYPE: A.M.N.H. No. 56886, collected on the east side of Goodenough Island, D'Entrecasteaux Group, Territory of Papua, New Guinea, at an elevation of 900 meters (2950 feet) on October 25, 1953, by Kenneth M. Wynn.

DEFINITION: This species is characterized by the absence of both vocal sac and vocal-sac openings in the male, half-webbed outer fingers (fig. 21C), relatively long legs (TL/S-V averages 0.59), and palpebral veins that trend in a near-vertical direction (fig. 20D).

DESCRIPTION OF TYPE SPECIMEN: Adult male, with the following measurements (in millimeters): Snout to vent length, 35.0; tibia length, 20.4; head width, 13.4; head length, 12.9; diameter of tympanum (horizontal), 1.9; diameter of eye (horizontal), 4.7; internarial distance, 3.4; distance from eye to naris, 4.1.

The internarial distance is distinctly less than that from eye to naris (E-N/IN = 1.21). The loreal region is oblique and the canthus rostralis distinct. The tympanum is distinct and separated from the eye by a distance equal to the diameter of the tympanum. A fold of skin arises a bit behind the posterior corner of the eye and passes over the upper margin of the tympanum, concealing that margin, and then curves downward to disappear above the insertion of the forelimb. A series of light-colored tubercles is present on the outer edge of the forearm. On one arm several of these blend together to form a stretch of continuous fold. Only slight traces of corresponding tubercles are seen on the tarsus. A tiny tubercle is present on the heel. There are no vocal-sac openings. The skin of the throat resembles that of the remainder of the venter in being coarsely granulate; no evidence of an external vocal sac is present. The skin of the dorsal surface of the body is minutely granular.

The ground color above is gray. Lichen-like patches of tan are present on the body and the back of the head. The tibial region is banded irregularly with a similar color.

VARIATION: The three males and two females that make up the type series are all rather similar. The internal distance is distinctly smaller

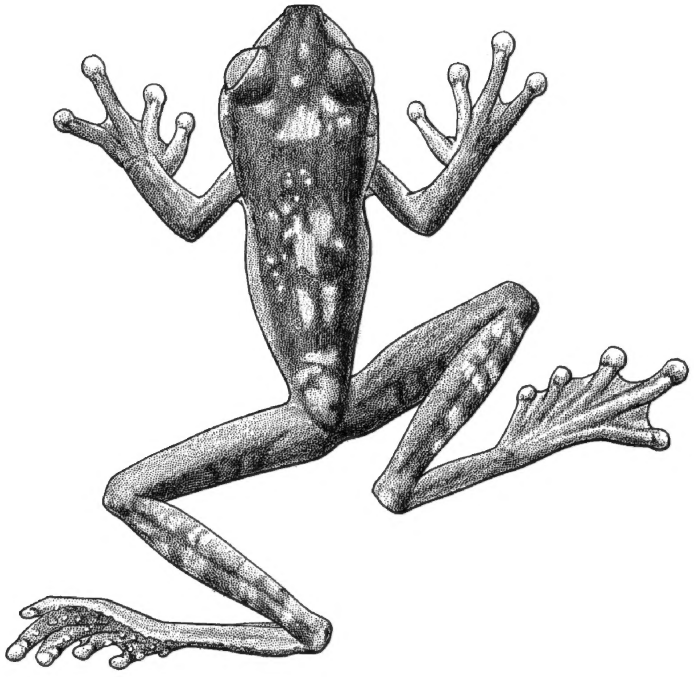

FIG. 1. *Nyctimystes avocalis*, type specimen, A.M.N.H. No. 56886. 1.5 times natural size.

than the distance from eye to naris in all (fig. 9, table 1). This species has, on the average, relatively longer legs than any other *Nyctimystes* (fig. 10, table 1). The outer fingers are half-webbed in all five specimens. Nuptial rugosities are not present on the first fingers of the males. The palpebral venation is similar in all. The tubercles of the forearm in some instances tend to fuse into a fold, as was noted for the type specimen. The tarsus shows only a very weak development of tubercles. A very small but distinct heel tubercle is present on all specimens. No vocal-sac openings or external vocal sacs are discernible in the males. This is probably a small species. The larger of the two female specimens is gravid and measures 47 mm. in snout to vent length. The three males measure 34, 34, and 35 mm.

Three specimens are gray and one is brown with no obvious darker or lighter markings such as the tan patches seen on the type specimen.

COMPARISON WITH OTHER SPECIES: Only one other species of *Nyctimystes*, *N. papua*, is known to be without vocal-sac openings in the male. Probably *avocalis* and *papua* are not closely related, as the latter is a larger species, with a different pattern of the palpebral venation

(fig. 19A) and scantly webbed fingers. Some difficulty might be experienced in distinguishing females of *avocalis* from those of *montana* and of *daymani*, species that have the same pattern of the palpebral venation. The ratio of tibia length to snout to vent length of *daymani* (range, 0.45–0.54) does not overlap that of *avocalis* (0.57–0.60; fig. 10, table 1). The situation is similar regarding the population of *montana* on Goodenough Island and *avocalis*, although one of the mainland populations of *montana* overlaps *avocalis* completely in TL/S-V ratio. On Goodenough Island, *montana* consistently shows less hand webbing than *avocalis*, but the difference is not great enough to be amenable to objective presentation.

DISTRIBUTION (FIG. 3): *Nyctimystes avocalis* is known only from the type locality, the east slope of Goodenough Island, Territory of Papua, at 900 meters. The description is based on A.M.N.H. Nos. 56486, 56886 (type specimen), 56892, 57342, and 57347 (paratypes).

The specimens were collected on October 25 and 26, 1953, near a small creek in oak-rain-forest transition.

Nyctimystes daymani, new species

Figure 2

TYPE: A.M.N.H. No. 57070, collected on the north slope of Mt. Dayman, Territory of Papua, New Guinea, at an elevation of 700 meters (2300 feet), on July 22, 1953, by G. M. Tate.

DEFINITION: This species has the veins of the palpebral reticulum oriented largely in a near-vertical direction, with few horizontal interconnections (fig. 20B). The internarial distance is distinctly less than the distance from the eye to the naris (E-N/IN averages 1.30). The legs are relatively short; the ratio of tibia length to snout to vent length averages 0.51. The size is relatively small; the largest of 25 males measures 42 mm. from snout to vent.

DESCRIPTION OF TYPE SPECIMEN: Adult male, with the following measurements (given in millimeters): Snout to vent length, 37.8; head width, 14.0; head length, 12.7; tibia length, 19.8; tympanum diameter (horizontal), 1.8; eye diameter (horizontal), 4.3; internarial distance, 3.0; distance from eye to naris, 4.3.

The snout is relatively long and narrow; the canthus rostralis is distinct and slightly curved, and the loreal region not vertical, but with a slight slope. A strong skin fold passes from the posterior corner of the eye over the upper margin of the tympanum and down, terminating above the axilla. The tympanum is small but distinct and is slightly

FIG. 2. *Nyctimystes daymani*, type specimen, A.M.N.H. No. 57070. 1.5 times natural size.

less than its own diameter from the posterior corner of the eye. The veins of the palpebral reticulum are very distinct and are oriented in a near-vertical direction, with very few horizontal interconnections. The vomerine teeth are in two patches between the internal nares. The skin is very minutely granular above, much coarser below. The outer fingers are about one-half webbed; the outer toe is webbed to the base of disc. A small tubercle is present on the heel. A row of light-colored tubercles is present on the outer edge of the forearm. Slit-like, vocal-sac openings are present in the floor of the mouth. A small patch of very fine horny tubercles is found on the first finger.

The ground color (in alcohol after formalin preservation) dorsally is dark brown. On the body and head this color is broken up by lichen-like patches of pale brown, each patch in turn spotted with dark brown. The tibia has irregular bands of dark and light brown, the light brown areas spotted with darker brown. The forelimbs and femora are unicolor gray-brown. The under surfaces are pale yellowish tan, without marking.

VARIATION: Variation in two proportions (TL/S-V and E-N/IN) is summarized in table 1 and illustrated in figures 9 and 10. The fold of skin on the forearm may be a series of tubercles as in the type, or may be a crenulated fold or even a straight fold. There is considerable vari-

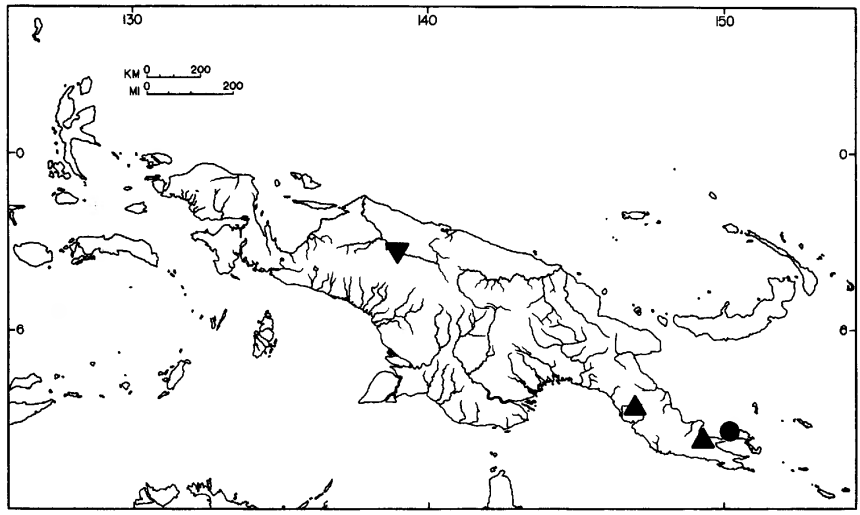

FIG. 3. Distribution of *Nyctimystes avocalis* (dot), *N. daymani* (triangles), and *N. fluviatilis* (inverted triangle).

ation in dorsal color pattern. Occasional individuals are gray-brown and virtually patternless. One is brown, with several white spots on the head and body, while another combines some of this white spotting with a pattern otherwise similar to that of the type specimen. The form of the palpebral reticulum is quite constant throughout the series, as is the degree of finger webbing.

COMPARISON WITH OTHER SPECIES: The high ratio of internarial distance to eye-naris distance seen in *daymani* distinguishes it from all other species except *fluviatilis, semipalmata, perimetri,* and *avocalis. Nyctimystes semipalmata* is a much larger species, with longer legs (fig. 10) and a prominent heel tubercle (fig. 18). *Nyctimystes avocalis* is similar in size to *daymani,* but lacks vocal-sac openings in the male and has longer legs. *Nyctimystes perimetri* is similar in proportions, but is a larger species. Comparison with *fluviatilis* is made in the account of that species.

Nyctimystes daymani exists sympatrically with *N. montana* on Mt. Dayman. The two species are similar, but *montana* is larger, with more widely spaced nostrils (see account of *montana*). The presence of relatively small but gravid females in the sample of *daymani* assures that what is called *daymani* is not merely the young of *montana.*

DISTRIBUTION (FIG. 3): *Nyctimystes daymani* is known from 35 specimens (type and paratypes) from the type locality. An additional individual from Mafulu is tentatively assigned to this species. It has long

legs, at the extreme for topotypic *daymani* (TL/S-V = 0.54), but falls well within the *daymani* range of the ratio of eye to naris to internarial distance (E-N/IN = 1.23).

LOCALITY RECORDS: *Territory of Papua:* North slope, Mt. Dayman, 700 meters (A.M.N.H. Nos. 56379, 56595–56598, 56600, 57060, 57065, 57070 [type], 57071, 57081, 57098, 57111, 57113, 57117, 57121, 57126–57129, 57136, 57138–57140, 57155–57157, 57171–57172, 57208, 57227–57230, 57359); Mafulu, 1250 meters (A.M.N.H. No. 60376).

The type series was collected by G. M. Tate on July 18 through 24, 1953. All specimens were noted to have been found at the banks of a rocky stream in the forest. Among several other species of frogs found in the same habitat were *Nyctimystes montana* and *N. semipalmata.*

Nyctimystes fluviatilis, new species

Figure 4

TYPE: A.M.N.H. No. 49567, collected at Bernhard Camp, Idenburg River, Netherlands New Guinea, in April, 1939, by W. B. Richardson.

DEFINITION: A relatively small species (S-V 50 mm.) with a high ratio of internarial distance to eye-naris distance (1.41) and a very tiny heel tubercle.

DESCRIPTION OF TYPE SPECIMEN: Adult female (gravid), with the following measurements (in millimeters): Snout to vent length, 50.3; tibia length, 26.4; head width, 17.5; head length, 15.7; tympanum diameter (horizontal), 2.0; eye diameter (horizontal), 5.7; internarial distance, 3.4; distance from eye to naris, 4.8.

The snout is relatively flat and depressed, with internarial distance distinctly less than distance from eye to naris (E-N/IN = 1.41). The canthus rostralis is distinct, the loreal region oblique. The palpebral venation consists of a relatively few heavy veins, nearly vertical, with very few horizontal interconnections (fig. 20F). There is a relatively weak fold of skin which passes from the posterior corner of the eye over the upper edge of the tympanum and becomes obscure immediately after leaving the tympanum. A series of light-colored tubercles is present on the outer edge of the forearm and another similar series along the corresponding surface of the tarsus and outer metatarsals. A very small heel tubercle is present. The outer fingers are about one-half webbed, and the outer toes, with the exception of the fourth, are webbed to the disc. The skin of the dorsum is smooth, that of the venter granulate.

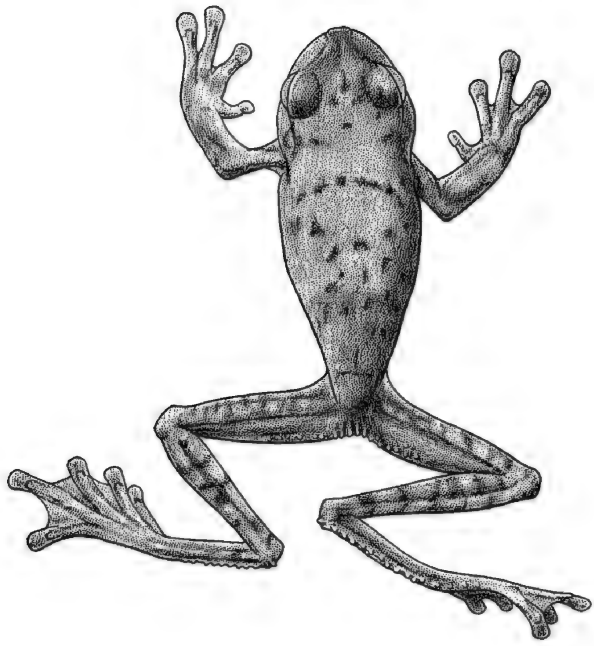

FIG. 4. *Nyctimystes fluviatilis*, type specimen, A.M.N.H. No. 49567. Natural size.

The dorsal color (in preservative) is light brown, with scattered spots 1 to 2 mm. in diameter on the body and head. The hind limbs bear some irregular dark cross bars. The ventral surfaces are pale tan without markings.

COMPARISON WITH OTHER SPECIES: The type is the only specimen of *fluviatilis* in the American Museum collections. The ratio of internarial distance to eye to naris distance of this specimen, 1.41, is the second highest among all specimens of *Nyctimystes* examined, exceeded only by a single *N. semipalmata*, with a ratio of 1.54. The mean in six *semipalmata* is 1.34. Otherwise the ratio of *fluviatilis* is approached by *daymani* (maximum 1.38 among 20 specimens, mean 1.30) and *perimetri* (maximum 1.39 among six specimens, mean 1.31). The type of *fluviatilis* is a gravid female with a snout to vent length of 50 mm. It is probably safe to assume that this is a much smaller species than *semipalmata* which attains a length of over 80 mm. Also, the large, triangular, heel tubercle of *semipalmata* (fig. 18) is not seen in *fluviatilis*. There is considerable similarity between *daymani* and *fluviatilis* in both size and proportions. The two differ in ways additional to the ratio mentioned above: head relatively slightly wider in *fluviatilis*, head length to head

width equal to 0.90, as contrasted to a mean of 0.99, minimum 0.93, for 21 *daymani;* webbing of fingers slightly more extensive in *fluviatilis.* These differences are relatively slight, and additional specimens of *fluviatilis* will be needed before we can be certain that the characters apparent in the type specimen will be consistent enough to differentiate the species.

Nyctimystes perimetri of Sudest Island is evidently a larger species than *fluviatilis,* as the only gravid female measures 66.5 mm. from snout to vent, and males measure up to 52 mm. Possibly the species differ in eye size, too, as the five specimens of *perimetri* show a range in the ratio of eye length to head width of 0.34 to 0.39, mean 0.36, while the single *fluviatilis* has a ratio of 0.33.

As an individual specimen, *fluviatilis* is reasonably distinct from other known *Nyctimystes,* but the possibility that additional specimens will destroy this distinctness is recognized.

DISTRIBUTION (FIG. 3): *Nyctimystes fluviatilis* is known only from the type specimen (A.M.N.H. No. 49567) from Bernhard Camp, Idenburg River, Netherlands New Guinea. Although no specific data as to elevation accompanied the specimen, the elevation of the camp was 50 meters.

Nyctimystes granti Boulenger

Nyctimantis granti BOULENGER, 1914, p. 249, pl. 27, fig. 2. VAN KAMPEN, 1923, p. 23.

Nyctimystes granti, PARKER, 1936, p. 77.

TYPE: No catalogue number was cited by Boulenger in his original description of the species. The specimen is in the British Museum (Natural History) and was collected by the Wollaston Expedition at an elevation of 3000 feet on the Utakwa River in Netherlands New Guinea.

DEFINITION: A very large species (100 mm. in snout to vent length) without a heel tubercle, and with a dorsal pattern of black vermiculations on body and limbs.

DESCRIPTION: The female type specimen was described by Boulenger (1914, p. 249) as follows: "Tongue circular, nicked and slightly free behind. Vomerine teeth in two transverse series between the large choanae. Head moderate, much broader than long, the skin free from the skull; snout rounded, shorter than the orbit, with obtuse canthus and very oblique, slightly concave loreal region; interorbital space as broad as the upper eyelid; tympanum very indistinct, about one-third the diameter of the eye. Fingers much depressed, outer one-third webbed, disks two-thirds the diameter of the eye. Toes webbed to the

disks of the third and fifth and to the penultimate phalanx of the fourth; a very small inner metatarsal tubercle; subarticular tubercles moderate. The tibio-tarsal articulation reaches the tip of the snout. Skin smooth above, granular on the belly and under the thighs; a strong curved fold above the tympanum. Purplish grey above, vermiculate with black; flanks and sides of thighs lilac; lower parts whitish."

In a synopsis of the species of *Nyctimystes*, Parker (1936, p. 77) added the following details: "Snout about as long as the eye, high, with vertical lores; distance between the anterior corners of the eyes much longer than the snout; no papilla on heel. A palpebral reticulum."

COMPARISON WITH OTHER SPECIES: This species is known only from the type specimen, which I have not seen. Among the large species of *Nyctimystes*, the dorsal pattern should distinguish *granti* from *humeralis*, which is unicolored. The large heel tubercle of *semipalmata* will differentiate this form from *granti*, which lacks a tubercle.

DISTRIBUTION (FIG. 17): *Nyctimystes granti* is known only from the type locality, Utakwa River, 3000 feet, Netherlands New Guinea.

Nyctimystes gularis Parker

Nyctimystes gularis PARKER, 1936, p. 78.

TYPE: B.M.(N.H.) No. 1935.3.9.173, collected at Mondo, Papua, 5000 feet, in January, 1934, by Miss L. E. Cheesman.

DEFINITION: The palpebral venation is distinct and forms a reticulum without obvious directional orientation of the lines (fig. 20A). The legs are relatively long, TL/S-V averages 0.58. The outer fingers about one-quarter webbed, as in figure 21A. The male has vocal-sac openings and a vocal sac. The internarial distance averages about the same as the eye-naris distance, E-N/IN = 0.98.

DESCRIPTION (BASED ON A.M.N.H. No. 60300): The head is broader than long; length/width ratio equal to 0.92. The internarial distance is equal to the eye-naris distance. The loreal region is very slightly oblique, nearly vertical, the snout high. The outer fingers are about one-quarter webbed. The legs are long; the tibia length equals 60 per cent of snout to vent length. The skin of the dorsal surfaces is nearly smooth but becomes granular on the sides and ventral surfaces. A crenulated ridge is present on the outer side of the forearm, but there is no similar ridge on the tarsus. No tubercle is present on the heel. In preservative the dorsal surface of the body and limbs is dark gray, with faint traces of both darker and lighter markings. The ventral surfaces are brownish yellow, with no markings. The snout to vent length is 56 mm. The specimen is an adult female.

COMPARISON WITH OTHER SPECIES: The original description of this species was based on two male specimens very similar to *N. papua* but differing from that species in the possession of vocal sac and slits and in having a strong rather than a very weak palpebral venation. A third specimen, a female, was tentatively referred to this species (Parker, 1936, pp. 79–80). The reticulate nature of the palpebral venation will distinguish *gularis* from all species except *humeralis* and *kubori*. *Nyctimystes humeralis* is a larger form, with uniform green coloration (in life), more finger webbing, and a humeral spine in the male. *Nyctimystes kubori* also has more webbing and on the average has shorter legs. There is similarity in proportions and general appearance among *papua, narinosa, persimilis,* and *gularis,* all species with low ratios of eye-naris to internarial distance and scantly webbed fingers. *Nyctimystes papua* is distinguished by its very weak palpebral venation and by the absence of a vocal sac in the male. *Nyctimystes narinosa* has a lower E-N/IN ratio than *gularis* (mean 0.84) and has a palpebral venation with a definite tendency to horizontal orientation of the lines. *Nyctimystes gularis* is compared to *N. persimilis* in the account of the latter species.

The specimen described above (A.M.N.H. No. 60300) is from the west slope of Mt. Tafa, less than 10 kilometers from the type locality. Two female specimens from Mt. Dayman, 2230 meters, seem to represent the species *N. gularis.* They agree with the Mt. Tafa specimen in having relatively long legs, the ratios of the tibia length to the snout to vent length for the two being 0.58 and 0.57. The palpebral reticulum is similar in form to that of the Mt. Tafa specimen, but in one individual is absent on the posterior half of the eyelid. Finger webbing is scanty, as in the Mt. Tafa specimen and the type. The holotype male measures 37 mm. from snout to vent (Parker, 1936, p. 79); the three female specimens in the American Museum measure 56 mm. (Mt. Tafa), 42 mm., and 43 mm. (Mt. Dayman).

DISTRIBUTION (FIG. 12): *Nyctimystes gularis* is known only from the mountains of southeastern Papua, where it has been taken between the elevations of 5000 and 7900 feet.

LOCALITY RECORDS: *Territory of Papua:* Mondo, 5000 feet (type locality, Parker, 1936, p. 79); west slope of Mt. Tafa, 2400 meters (A.M.N.H. No. 60300); north slope of Mt. Dayman, 2230 meters (A.M.N.H. Nos. 56800, 56935).

There is almost no information on the natural history of this species. The specimen from Mt. Tafa was found at night a few feet up in shrubbery on August 25, 1933, by Richard Archbold.

FIG. 5. *Nyctimystes humeralis*, left humerus of male in ventral aspect to show humeral spine.

Nyctimystes humeralis Boulenger

Hyla humeralis BOULENGER, 1912, p. 216. VAN KAMPEN, 1923, p. 56.

TYPE: "*Hyla humeralis, sp. n.* is based on two male specimens (one of which has been made into a skeleton) from Madew [= Madiu], St. Joseph River, British New Guinea, between 2000 and 3000 feet, collected by the late W. W. Stalker in 1908" (Boulenger, 1912, p. 216).

DEFINITION: A large species (males to 100 mm. in snout to vent length) of uniform dorsal coloration (green in life, purple in alcohol-preserved specimens) in which the male bears a spine-like process on the anterior surface of the proximal part of the humerus (fig. 5).

DESCRIPTION: The head is broader than long, with the loreal region nearly vertical, slightly oblique. The internarial distance averages slightly less than the eye to naris distance (E-N/IN averages 1.04; fig. 9, table 1). The hind legs are relatively long; the tibia length is 56 to 58 per cent of the snout to vent length (fig. 10, table 1). The two outer fingers are about one-half webbed or slightly more (as in fig. 21C, D). The skin of the dorsal body surface is minutely granular, that of the ventral surface more coarsely so. A smooth, light-colored fold is present along the outer side of the forearm and fourth finger, and a similar fold on the heel, tarsus, and fifth toe. There is no tubercle on the heel. The palpebral venation forms a strong reticulum in some specimens (fig. 20C), while in others the veins are oriented vertically (see discussion).

A subgular vocal sac with slit-like openings in the floor of the mouth is present in the male. The first finger (thumb) of the male is provided with two black, spiny, nuptial pads. The apparently unique character of the species, at least as far as *Nyctimystes* is concerned, is the spine on the humerus of the male, which protrudes as a sharp point beneath the skin of the breast at the base of the foreleg. The humerus is shown in figure 5. This drawing was evidently made for or by G. K. Noble and

must represent the skeletonized cotype of the species, as the cotypes were the only specimens of the species known during Noble's time.

A color photograph (Gilliard, 1953, p. 460) of a specimen from the Kubor Mountains near Kup shows a uniform, bright green color to the dorsal surfaces of the head, body, and limbs. The side of the body and parts of the limbs that are concealed when the frog is resting are lilac. The upper lip, skin folds on the forearm and tarsus, and anal region are yellow. In preservative the green changes to purple and the lilac and yellow to dirty white. The ventral surfaces are immaculate.

COMPARISON WITH OTHER SPECIES: Only two other species of *Nyctimystes* reach or exceed the size of *humeralis: N. granti* and *N. semipalmata.* The uniform dorsal coloration of *humeralis* will serve to distinguish females from those of *granti,* the only known specimen of which has vermiculate dark markings on the dorsal surface of the body. *Nyctimystes semipalmata* does not possess the humeral spine characteristic of the male *humeralis.* Also, the presence of a large heel tubercle (fig. 18) separates *semipalmata* from *humeralis,* which has no tubercle.

DISCUSSION: One of the American Museum specimens, that from Matsika, is nearly topotypic, being from only about 6 kilometers from the type locality. It is a male and agrees with Boulenger's description of the type in all pertinent characters. A male and two females from the Idenburg River region of Netherlands New Guinea also certainly represent the same form. The male bears a prominent humeral spine, and all specimens agree also in less important characters. I am slightly less certain of the identification of the specimens from the intermediate localities in North-east New Guinea, Kubor Mountains, and Telafolmin. All specimens are females, hence the important humeral spine character cannot be employed. The dorsal coloration is uniform purple as in *humeralis* from the southeastern and northwestern localities, except that the Telafolmin specimen shows some slight mottling on the femur. The upper lip of both Kubor and Telafolmin specimens bears a distinct light-colored margin. While this is not true of the individual from Matsika, it is true of the Idenburg River specimens. The palpebral venation forms a reticulum in the Matsika, Idenburg, and Telafolmin specimens (fig. 20C), but is oriented into more vertical lines in those from the Kubor Mountains. The upper extremes of the ratio of the head length to head width and that of the eye-naris distance to internarial distance represent the figures for the Telafolmin specimen. If this specimen does not belong to the species *humeralis,* it is closer to that form than to any other.

When Boulenger described *Hyla humeralis,* he noted the palpebral

reticulum but evidently was not aware of the vertical pupil. He considered *humeralis* to be most closely related to *Hyla infrafrenata* and *Hyla caerulea,* species that are similar in being both large and green.

DISTRIBUTION (FIG. 6): *Nyctimystes humeralis* is found along the central mountainous ridge of New Guinea. Records accompanying the specimens indicate an altitudinal range of from 2000 to 3000 feet up to at least 5000 feet.

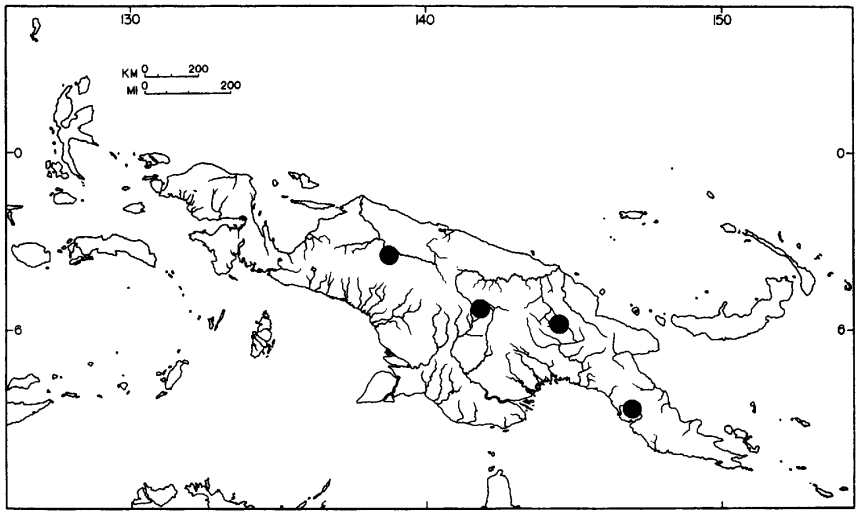

FIG. 6. Distribution of *Nyctimystes humeralis.*

LOCALITY RECORDS: *Territory of Papua:* Madiu, 2000–3000 feet, St. Joseph's River (type locality, Boulenger, 1912, p. 216); Matsika, 980 meters (A.M.N.H. No. 58700). *North-east New Guinea:* Kubor Mountains near Kup, 5000–8000 feet (A.M.N.H. Nos. 55880, 55910–55912); Telafolmin, north flank of Victor Emanuel Mountains (A.M.N.H. No. 57923). *Netherlands New Guinea:* Four kilometers southwest of Bernhard Camp, 850 meters (A.M.N.H. Nos. 49695, 49697); 6 kilometers southwest of Bernhard Camp, 1200 meters (A.M.N.H. No. 49691).

Nyctimystes kubori, new species

Figure 7

TYPE: A.M.N.H. No. 55913, collected in the Kubor Mountains near Kup at an elevation of between 5000 and 8000 feet, North-east New Guinea, in 1952, by E. Thomas Gilliard.

DEFINITION: A moderate-sized species of *Nyctimystes* reaching a snout to vent length of 59 mm., with outer fingers one-third to one-half webbed (fig. 21B, C) and a heavy palpebral venation forming a reticulum (fig. 19D).

DESCRIPTION OF TYPE SPECIMEN: Adult female (gravid), with the following measurements (in millimeters): snout to vent length, 56.5; tibia length, 29.1; head width, 18.6; head length, 16.6; diameter of tympanum (horizontal), 2.4; diameter of eye (horizontal), 5.9; internarial distance, 4.8; distance from eye to naris, 4.5.

The snout is relatively short, blunt, and high (E-N/IN = 0.94), with distinct canthus rostralis and oblique loreal region. The vomerine teeth are in two patches between the posterior edges of the choanae. The palpebral venation forms a heavy reticulum. The tympanum is distinct and is separated from the eye by approximately the diameter of the tympanum. A fold of skin passes from the posterior corner of the eye, over the upper edge of the tympanum and down, becoming indistinct above the insertion of the forelimb. The skin of the dorsum is minutely roughened, that of the venter coarsely granular. A row of tubercles is present along the outer edge of the forearm, and there is a similar row on the tarsus. There is only a slight suggestion of a heel tubercle. The outer fingers are approximately half-webbed, the toes (except the fourth) webbed to the disc.

The body and head are light brown dorsally, with irregular dark brown blotches. The legs have a similar ground color, with irregular darker spots and bands present on the tibia.

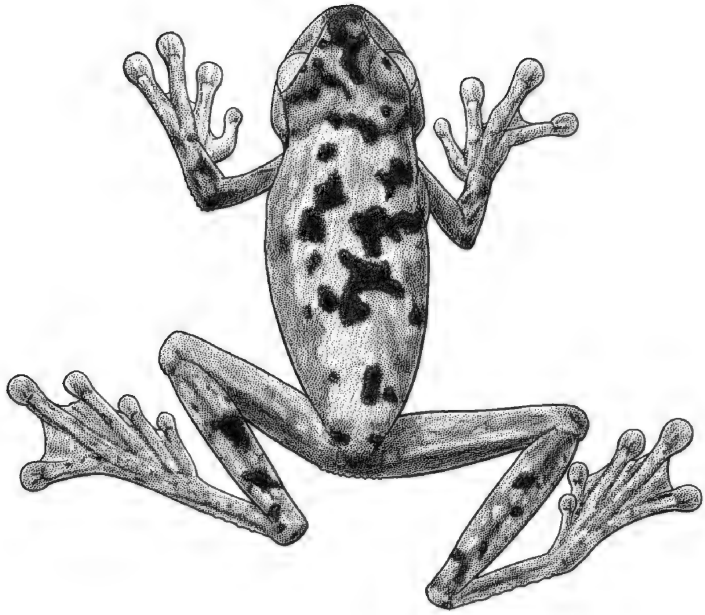

FIG. 7. *Nyctimystes kubori*, type specimen, A.M.N.H. No. 55913. Natural size.

VARIATION: In table 1 and figures 9 and 10 statistics on variation in the proportions E-N/IN and TL/S-V are presented. Two specimens bearing the same locality data as the type specimen are available, one a gravid female 59 mm. in snout to vent length, and the other a female, apparently post-breeding to judge by the enlarged oviducts and tiny ova, 47 mm. in length. The larger of these is gray-brown dorsally, with no pattern discernible. The smaller has traces of pattern, but nothing so distinct as the type specimen. As has the type specimen, these two have a heavy palpebral reticulum and a row of tubercles on the forearm and tarsus.

A small individual from Kondiu, near Kup (A.M.N.H. No. 58699), may represent this species or may be *N. humeralis*. In dorsal color it resembles *humeralis*, but it lack the light border to the upper lip seen in *humeralis* from this geographic region.

COMPARISON WITH OTHER SPECIES: No other species of *Nyctimystes* of the size of *kubori* (gravid females, 56 and 59 mm. from snout to vent) shares the heavy, reticulated, palpebral venation and half-webbed fingers with *kubori*. The relatively short snout is common to several species: *gularis, papua, narinosa,* and *humeralis*. The first three of these have only scant finger webbing; *papua* has a very weak palpebral venation, and *narinosa* an even lower ratio of eye to naris distance to internarial distance than *kubori*. There is considerable similarity in proportions and finger webbing between *humeralis* and *kubori*. Also, the palpebral venation may be similar. *Nyctimystes humeralis* is evidently a much larger species and reaches a snout to vent length of 100 mm., while females of *kubori* are adult at less than 60 mm. in snout to vent length. Probably the humeral spine of the male *humeralis* will distinguish the species, though no males of *kubori* are at present available. Compared with specimens of *humeralis* of similar size from the same locality, *kubori* differs in several respects with regard to color and pattern. The preserved *humeralis* are purple dorsally (green in life) and immaculate, while *kubori* is gray-brown, with or without darker markings. *Nyctimystes humeralis* in the area of overlap with *kubori* possesses a distinct light border to the upper lip, while this region in *kubori* shows no light margin, or a much narrower light edge, with irregular upper margin.

Nyctimystes narinosa, N. papua, and *N. humeralis,* three species to which *N. kubori* bears a resemblance, are found in the same immediate region as *kubori*. Two of these (*papua* and *humeralis*) were found in the Kubor Mountains, while the type locality for *narinosa* is nearby Mt. Hagen.

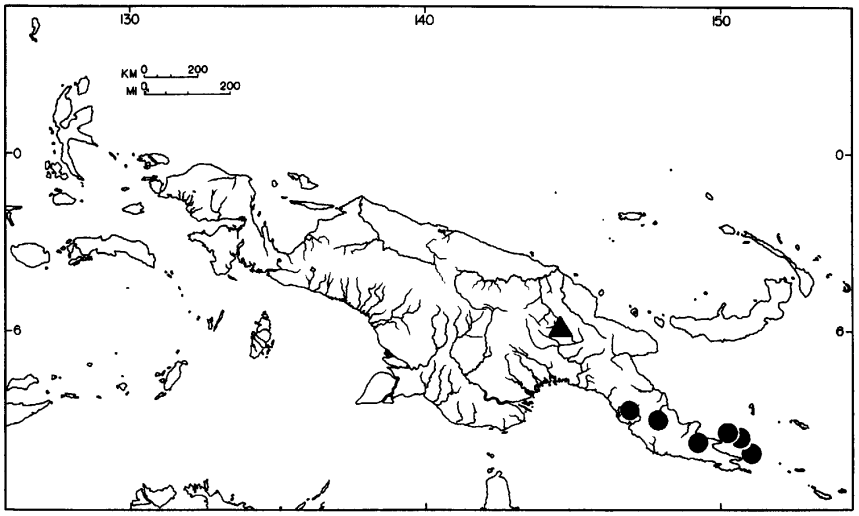

FIG. 8. Distribution of *Nyctimystes kubori* (triangle) and *N. montana* (dots).

DISTRIBUTION (FIG. 8): *Nyctimystes kubori* is known only from the Wahgi Valley region of North-east New Guinea, where the type series was captured at an elevation of between 5000 and 8000 feet in the Kubor Mountains near Kup (A.M.N.H. Nos. 55886, 55908 [paratypes], 55913 [type]). A juvenile from Kondiu, near Kup (A.M.N.H. No. 58699), is provisionally assigned to this species.

Nyctimystes montana Parker

Nyctimystes montana PARKER, 1936, p. 80, fig. 4 (tadpole). LOVERIDGE, 1948, p. 406.

TYPE: B.M.(N.H.) No. 1935.3.9.176, a male collected at Mondo, Territory of Papua, New Guinea, 5000 feet, in February, 1934, by Miss L. E. Cheesman.

DEFINITION: A moderate-sized species reaching a snout to vent length of 63 mm., with palpebral venation oriented largely in a near-vertical direction (fig. 19B), outer fingers one-third to one-half webbed (as in fig. 21B, C), a small heel tubercle usually present, and E-N/IN ratio averaging about 1.10.

DESCRIPTION: The head is usually slightly broader than long, with moderately distinct canthus rostralis and oblique loreal region. A curved supratympanic fold is present. The tympanum is relatively small (less than one-half of the diameter of the eye), but distinct. The veins of the palpebrum are oriented in steeply sloping, nearly parallel

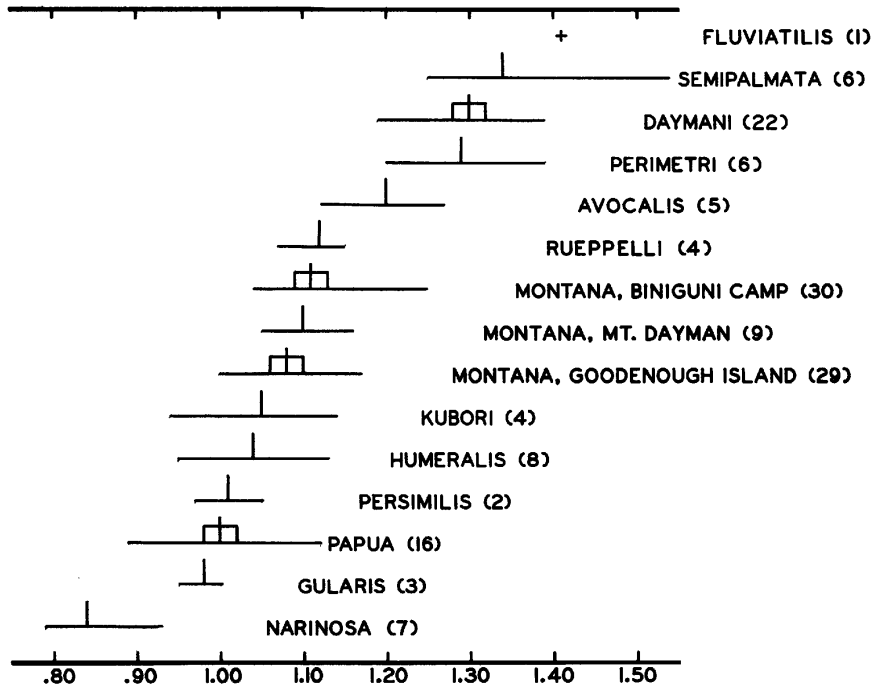

FIG. 9. Ratio of distance from eye to naris to internarial distance in *Nyctimystes*. The horizontal line indicates the range of variation; the vertical line, the mean. For larger samples, two times the standard error of the mean is indicated on each side of the mean by a rectangle. Sample size is given in parentheses following the species name.

lines, with few horizontal interconnections (fig. 19B). The outer fingers are one-third to one-half webbed, the toes (except the fourth) webbed to the base of the disc. The forearm usually bears a row of light-colored tubercles, though in a few specimens there is a straight or crenulated fold there, or the region is smooth. A very small tubercle is usually present on the heel, though there may be none. The skin is relatively smooth dorsally, more granular on the ventral surfaces. The male is provided with a subgular vocal sac, with paired, slit-like openings in the floor of the mouth.

In preservative, most specimens are gray or gray-brown dorsally and pale gray ventrally. Indistinct darker mottling of the body is sometimes detectable, and the legs show traces of barring. A specimen from Goodenough Island has the top of the head and the back much lighter than the flanks and the side of the head. The line of demarcation is

TABLE 1

RATIOS OF TIBIA LENGTH TO SNOUT TO VENT LENGTH AND OF EYE TO NARIS DISTANCE TO INTERNARIAL DISTANCE IN THE GENUS *Nyctimystes*

Species	TL/S-V				E-N/IN			
	Mean	σ_m	Range	*N*	Mean	σ_m	Range	*N*
avocalis	0.587	—	(0.57–0.60)	5	1.20	—	(1.12–1.27)	5
daymani	0.507	±0.004	(0.45–0.54)	27	1.30	±0.01	(1.19–1.38)	22
fluviatilis	0.525	—	—	1	1.41	—	—	1
gularis	0.584	—	(0.57–0.60)	3	0.98	—	(0.95–1.00)	3
humeralis	0.572	—	(0.56–0.58)	8	1.04	—	(0.95–1.13)	8
kubori	0.539	—	(0.51–0.57)	4	1.05	—	(0.94–1.14)	4
montana								
Biniguni Camp	0.559	±0.003	(0.52–0.61)	33	1.11	±0.01	(1.04–1.25)	30
Mt. Dayman	0.527	—	(0.49–0.55)	10	1.10	—	(1.05–1.16)	9
Goodenough Is.	0.527	±0.004	(0.48–0.58)	30	1.08	±0.01	(1.00–1.17)	29
narinosa	0.563	—	(0.54–0.61)	7	0.84	—	(0.79–0.93)	7
papua	0.550	±0.004	(0.51–0.58)	21	1.00	±0.01	(0.89–1.12)	16
perimetri	0.531	—	(0.50–0.56)	6	1.29	—	(1.20–1.39)	6
persimilis	0.555	—	(0.55–0.56)	2	1.01	—	(0.97–1.05)	2
rueppelli	0.500	—	(0.48–0.53)	4	1.12	—	(1.07–1.15)	4
semipalmata	0.586	—	(0.56–0.61)	6	1.34	—	(1.25–1.54)	6

abrupt and wavy on the body. The dorsal surface of the snout is dark.

Specimens from localities on the mainland of New Guinea consistently have the outer fingers about one-half webbed (as in fig. 21C), while those from Goodenough Island are just as regular in having less webbing, about one-third (as in fig. 21B). In leg length, specimens from Goodenough Island and Mt. Dayman (on the mainland) agree closely, but those from Biniguni Village, only about 5 miles in airline distance from Mt. Dayman, are conspicuously longer-legged (fig. 10, table 1).

Most samples of *Nyctimystes* are very poorly balanced as regards to the sex of the specimens comprising the sample. However, the series of *montana* from Goodenough Island includes enough adult males and females that the possibility of sexual variation in proportions could be checked. The ratio of tibia length to snout to vent length for 18 males averages 0.527, range 0.48–0.56. The corresponding ratio for 12 females ranges from 0.48 to 0.58, mean 0.527. A statistical test to verify the lack of sexual dimorphism in this character scarcely seems necessary. The ratio of eye to naris distance to internarial distance averages 1.10 ± 0.01 for 18 males (range 1.00–1.17) and 1.06 ± 0.01 for 11 females (range 1.00–1.14). Here there is a suggestion of a statistically significant difference, but a slight one if true. The extent of the possible difference

is sufficiently small that I have not hesitated to pool male and female samples in computing the averages and ranges for the several species.

The largest of 52 male specimens measures 53 mm. in snout to vent length. The largest of 21 females measures 63 mm.

None of the male specimens from the mainland or Goodenough Island shows a dark nuptial pad on the first finger, though this structure may be subject to seasonal variation. However, one of the males from Fergusson Island does have such a pad. Parker (1936, p. 81) mentions the presence of a "diffuse nuptial pad" on the type specimen.

COMPARISON WITH OTHER SPECIES: Among the species of *Nyctimystes* from the mainland of southeastern New Guinea in the collection of the American Museum are two partly sympatric but distinct forms to which Parker's description of *montana* might apply. *Nyctimystes daymani* is a small species, usually brown above, with lighter variegations, and with a more vertical loreal region than the specimens here referred to *montana*. Size may be used effectively to compare the two forms: The largest of 25 male *daymani* is 42 mm. in snout to vent length, while *montana* males are almost all longer than this, and range up to 52 mm. The type of *montana* measures 49 mm. (Parker, 1936, p. 81). Without having actually seen the type specimen of *montana*, I cannot say for certain that the name is properly applied here. However, three paratypes in the Museum of Comparative Zoölogy (M.C.Z. Nos. 21327–21329) agree in pertinent characters with the frogs here referred to *montana*.

Several species other than *daymani* possess a pattern of the palpebral venation that is similar to, and might be confused with, that of *montana*. The single specimen of *N. fluviatilis* has a higher ratio of eye to naris to internarial distance than any specimen of *montana*. *Nyctimystes perimetri*, a species of a size similar to that of *montana*, has a higher average ratio of eye to naris to internarial distance and a larger heel tubercle. *Nyctimystes avocalis* is of smaller size and lacks vocal sac and openings in the male. *Nyctimystes rueppelli* is probably a smaller form and has more extensive finger webbing.

DISTRIBUTION (FIG. 8): *Nyctimystes montana* is known from the mountains of southeastern Papua and the D'Entrecasteaux Islands. Specimens from Goodenough Island, while deviating slightly from the mainland specimens, clearly belong to the same species. With only two specimens from Fergusson Island and one from Normanby, the status of these insular populations cannot be fixed, and the allocation of the three individuals to *montana* must be regarded as tentative.

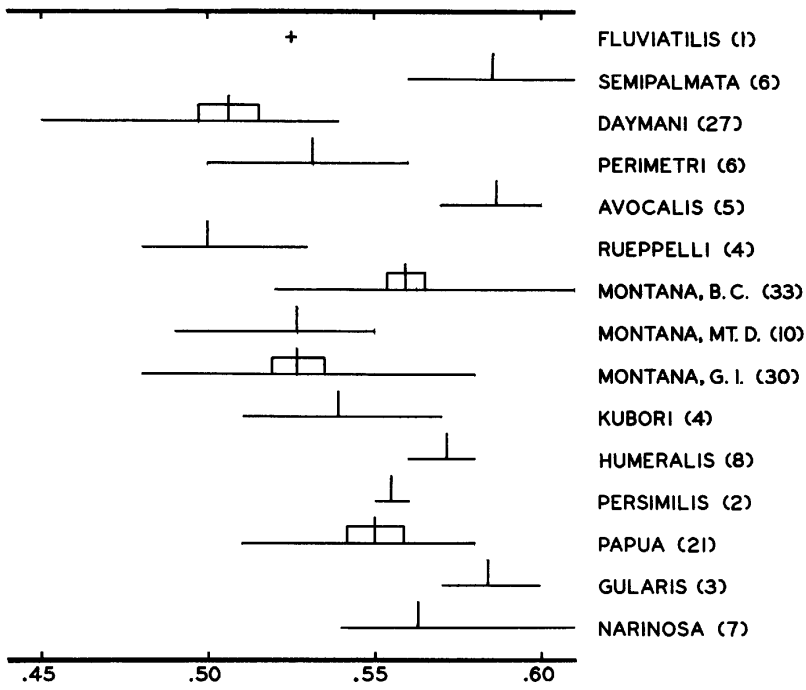

FIG. 10. Ratio of tibia length to snout to vent length in *Nyctimystes*. Method of presentation as in figure 9.

LOCALITY RECORDS: Where a specimen number is cited, the specimen has been seen by me; all localities are in the Territory of Papua. Mondo, 5000 feet (type locality, Parker, 1936, p. 80); Kokoda, 1200 feet (M.C.Z. Nos. 21327–21329); Biniguni Village, Gwariu River, 145–190 meters (A.M.N.H. Nos. 56372–56374, 56410–56431, 56435–56456, 56458–56482, 56488–56494, 56496–56511, 56539–56541, 56543, 56546–56551, 56556–56563, 56565–56575, 56578–56582, 56585, 56715); Mt. Dayman, 700 meters (A.M.N.H. Nos. 57114, 57137, 57143–57145, 57153, 57174–57175, 57337–57338); east slope of Goodenough Island, 1600 meters (A.M.N.H. Nos. 56725–56736, 56894, 56905–56906, 56911, 56936, 56941, 56943–56947, 56956–56957, 56964–56967, 57264, 57268, 57270, 57349–57352); Mt. Pabinama, Normanby Island (A.M.N.H. No. 60182); Agamoia, Fergusson Island (A.M.N.H. Nos. 59944–59945).

The specimens from Biniguni Village were collected between July 30 and August 11, 1953, by G. M. Tate. Field notes record that most individuals were found along the banks of the Gwariu River, some

"among stones and reeds." Others were found on low trees near a stream, in forest about 100 yards from the river, and in scrub about 100 yards from the river. Almost all specimens are adults, and most are males. The specimens from the 700-meter camp on Mt. Dayman were all found on the banks of a rocky stream in forest on July 21 and 22, 1953. Those collected on Goodenough Island were taken by K. M. Wynn and H. M. Van Deusen between October 9 and 22, 1953. Several were found in trees at night, while others were caught on the ground in traps set for small mammals.

Nyctimystes narinosa, new species

Figure 11

TYPE: A.M.N.H. No. 60372, collected on Mt. Hagen in the Wahgi Valley region of North-east New Guinea at an elevation of over 8000 feet by E. Thomas Gilliard in 1950.

DEFINITION: Veins of palpebral reticulum oriented largely in a horizontal direction, with relatively few vertical interconnections (fig. 19C); the internarial distance is relatively great, always greater than the distance from eye to naris (E-N/IN averages 0.84); the hands have little webbing; the outer fingers are about one-quarter webbed (fig. 21A).

DESCRIPTION OF TYPE SPECIMEN: Adult female, with the following measurements (given in millimeters): snout to vent length, 64; head width, 22.7; head length, 21.1; tibia length, 39.0; tympanum diameter (horizontal), 2.3; eye diameter (horizontal), 6.4; internarial distance, 6.4; distance from eye to naris, 5.3.

The head is broad, the snout high and blunt, the canthus rostralis distinct, and the loreal region nearly vertical. A strong, slightly curved, supratympanic fold begins at the posterior corner of the eye and disappears above the insertion of the forelimb. The tympanum is small but distinct. The veins of the palpebral reticulum are distinct, with largely horizontal orientation. The vomerine teeth are in two patches between the internal nares, nearly on a line connecting the posterior margins of the nares. The skin is minutely granular above, coarser beneath. The fingers have only a basal web; the toes are about three-quarters webbed; webbing does not reach the disc of any toe. There is no tubercle on the heel. A nearly straight, very slightly crenulated fold of skin is present on the outer surface of the forearm.

The color is uniform gray-brown above, pale brown beneath. Probably it is much modified by preservation in formalin.

VARIATION: Variation in the proportions E-N/IN and TL/S-V is summarized in table 1 and illustrated in figures 9 and 10. The fold of

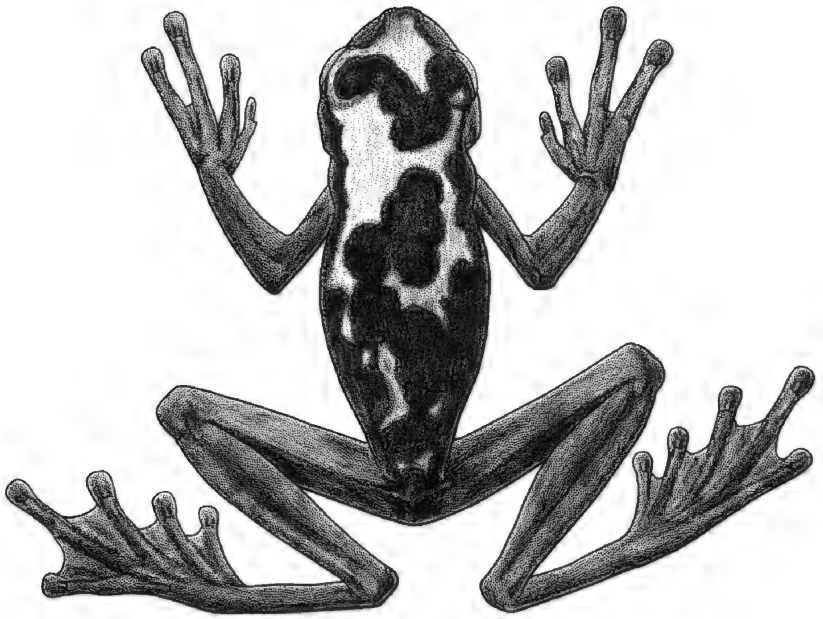

FIG. 11. *Nyctimystes narinosa*, paratype, A.M.N.H. No. 55335. Natural size.

skin on the forearm is continuous (not broken into tubercles) in all specimens, but in one individual is very weak. None of the specimens shows a heel tubercle. Finger webbing is very reduced in this species, all specimens showing only a slight basal web (fig. 21A). The orientation of the palpebral reticulum is similar in the type and other specimens. The tendency to longitudinal orientation of the veins is strongest in the upper part of the palpebrum, where one or two veins usually continue the entire length of the eyelid (fig. 19C). The veins may rarely be broken into short segments, but even here the horizontal orientation is evident. The males possess vocal slits in the floor of the mouth and a subgular sac.

Five specimens show the same patternless gray dorsum of the type. One large female has a light-colored nape region, with the light color extending along the back where it forms a border to large, asymmetrically placed blobs of darker pigment (fig. 11). Another specimen exhibits a similar pattern, but with less contrast, possibly an artifact of preservation.

COMPARISON WITH OTHER SPECIES: The high, relatively blunt snout

of this species, together with the scant webbing of the hand, brings a resemblance to *N. papua* and *N. gularis.* The form of the palpebral venation will serve to differentiate the species: horizontally oriented in *narinosa,* a reticulum without distinct orientation in *gularis,* greatly reduced in *papua.* The most distinctive feature of *N. narinosa* is the wide placement of the nostrils relative to the eye to naris distance. The very low ratio of internarial distance to eye to naris distance of the *narinosa* sample (mean 0.84, range 0.79–0.93) overlaps the range of only one other species, *papua,* a species that occurs in the same general region as *narinosa.* If more specimens of the several forms become available, more overlap in range of the ratios may be expected, but it seems unlikely that the extensive differences among the means will be significantly changed.

DISTRIBUTION (FIG. 12): Specimens are known only from mountains in the Wahgi Valley region of central New Guinea, North-east New Guinea. All were collected by E. Thomas Gilliard in 1950.

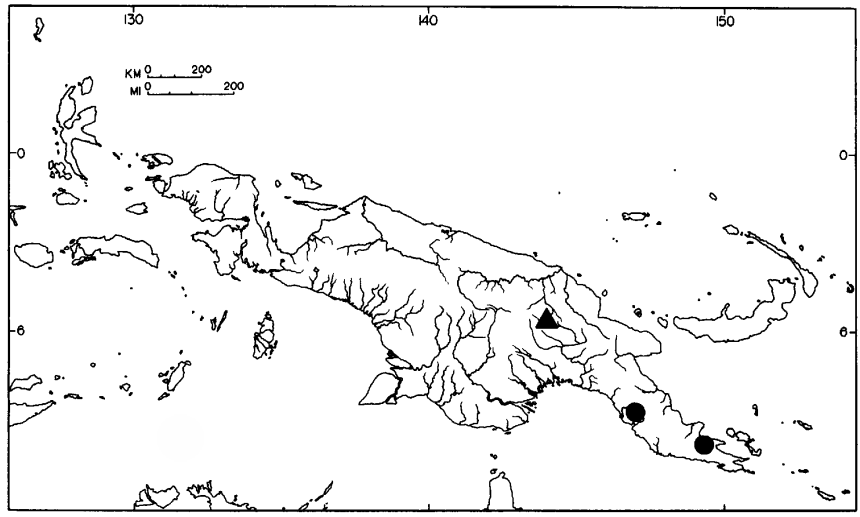

FIG. 12. Distribution of *Nyctimystes gularis* (dots) and *N. narinosa* (triangle).

LOCALITY RECORDS: *North-east New Guinea:* Mt. Hagen, 8000+ feet (A.M.N.H. Nos. 60372 [type specimen], 60370–60371 [paratypes]); Wahgi Valley region, between 5200 and 11,500 feet (A.M.N.H. Nos. 55335–55336, 56269–56270 [paratypes]).

Nyctimystes papua Boulenger

Nyctimantis papua BOULENGER, 1897, p. 12, pl. 1, fig. 5. PROCTOR, 1921, p. 207. VAN KAMPEN, 1923, p. 22.

Nyctimystes papua, STEJNEGER, 1916, p. 85. PARKER, 1936, p. 77, fig. 2. LOVERIDGE, 1948, p. 405. GRIFFITHS, 1954, p. 41.

[*Hyla*] *papua*, NOBLE, 1931, p. 513.

TYPE: Boulenger described the species from "several specimens" from Mt. Victoria, Owen Stanley Range, Territory of Papua. Parker (1936, p. 77) states that of five specimens in the British Museum, four females represent *papua*, while a male is tentatively referred to *N. semipalmata*. No museum numbers have been cited in the literature for the British Museum cotypes. One of the original cotype series is M.C.Z. No. 12838.

DEFINITION: A moderate-sized species of *Nyctimystes* with much reduced and indistinct palpebral venation (fig. 19A), scantily webbed fingers (as in fig. 21A), and no vocal sac or vocal-sac openings in the male.

DESCRIPTION: The head is broad, the length averaging 90 per cent of the width. The snout is high, with the loreal region nearly vertical, only slightly oblique. The internarial distance averages the same as the distance from eye to naris (fig. 9, table 1). The tympanum is less than half the diameter of the eye and has its upper margin partly concealed by the supratympanic fold. The outer fingers are less than one-third webbed, usually about one-fourth. A narrow fold of skin or a row of indistinct tubercles may be present on the outer side of the forearm, but this structure is not emphasized by the presence of light pigment seen in many species. There is no tubercle on the heel. The skin of both the dorsal and ventral surfaces of the body is granular, that of the ventral surfaces more so. The palpebral venation is represented only by lines of pigment spots (fig. 19A) or by a reticulum with frequent breaks in the continuity of the lines.

Dorsal coloration appears to be highly variable. Some specimens are dull gray-brown, with faint, irregular, darker blotches, while others show contrasting light spotting and mottling on the back and flanks. The legs are banded, though not conspicuously. The ventral surfaces are dirty yellow or gray. Darker markings are present in the gular region of most specimens.

In a series of 34 male specimens, Parker (1936, p. 78) found the length to vary from 46 to 51 mm., mode 49 mm. One giant specimen (A.M.N.H. No. 58701) measures 77 mm. and appears to be a male. The next largest male seen by me (M.C.Z. No. 23294) measures 60 mm. The largest females are two that measure 69 and 70 mm. The ratio of male to female size seen in the last three mentioned specimens is typical of

other *Nyctimystes,* suggesting that the 77-mm. individual may be abnormal or perhaps even a different species.

COMPARISON WITH OTHER SPECIES: The greatly reduced palpebral venation of *papua* will immediately distinguish it from other species of *Nyctimystes.* The species that appear most similar to *papua* are *gularis, narinosa,* and *persimilis;* all have a relatively low ratio of eye to naris distance to internarial distance and much-reduced finger webbing. In addition to the reduced palpebral venation, *papua* is distinguished from these by the lack of vocal sac and sac openings in the male.

DISTRIBUTION (FIG. 13): *Nyctimystes papua* has been found at several localities along the central mountainous ridge of New Guinea from southeastern Papua to the Idenburg River. All records are for relatively high elevations, the limits being approximately 5000 and 7000 feet.

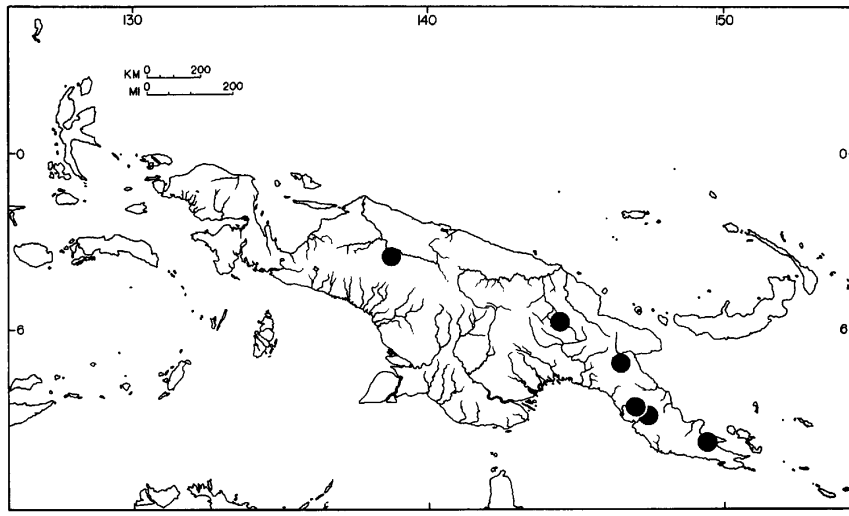

FIG. 13. Distribution of *Nyctimystes papua.*

LOCALITY RECORDS: The citation of a museum number indicates a specimen that I have examined. *Territory of Papua:* Mt. Victoria (type locality, cotype, M.C.Z. No. 12838); Mondo, 5000 feet (M.C.Z. Nos. 21816–21820); north slope, Mt. Dayman, 1550 meters (A.M.N.H. Nos. 56749, 56837); east slope, Mt. Tafa, 2070 meters (A.M.N.H. Nos. 58701–58703). *North-east New Guinea:* Mt. Misim, Moroke District (M.C.Z. Nos. 23293–23296; these specimens were recorded by Loveridge [1948, p. 398] as *Hyla arfakiana*); Kubor Mountains near Kup, 5000–7000 feet (A.M.N.H. Nos. 55881–55884). *Netherlands New Guinea:* Fifteen kilometers southwest of Bernhard Camp, Idenburg River, 1800 meters (A.M.N.H. Nos. 49671, 49694).

There is no published information on the natural history of *N. papua*. The three specimens from the east slope of Mt. Tafa, 2070 meters, were collected by A. L. Rand on June 6, 1933. They were found along with a number of arboreal microhylid frogs (*Oreophryne anthonyi*) in pandanus trees. One was found "in the cool damp space at the base of a leaf where water collects" (field notes of A. L. Rand on file in the American Museum).

Nyctimystes perimetri, new species

Figure 14

TYPE: A.M.N.H. No. 60081, obtained by R. F. Peterson at an elevation of 250–350 meters (830–1170 feet) on the west slope of Mt. Riu, Sudest (Tagula) Island, Louisiade Archipelago, Territory of Papua, New Guinea, between August 23 and September 5, 1956.

DEFINITION: A moderate-sized species (up to 67 mm. in snout to vent length) with a very high ratio of eye to naris distance to internarial distance ratio (mean ± 1.29), and relatively short legs (TL/S-V averages 0.53).

DESCRIPTION OF TYPE SPECIMEN: Adult male, with the following measurements (in millimeters): snout to vent length, 51; tibia length, 27.7, head width, 19.6; head length, 18.4; eye diameter (horizontal), 7.2; tympanum diameter (horizontal), 2.6; distance from eye to naris, 6.2; internarial distance, 4.6.

The loreal region is oblique, the canthus rostralis distinct, and the internarial distance distinctly less than the distance from eye to naris (E-N/IN = 1.35). The palpebral venation is arranged in oblique to near-vertical lines, with very few horizontal interconnections (fig. 19F). The tympanum is small, but distinct, and is separated from the posterior corner of the eye by a distance slightly less than the diameter of the tympanum. A curved supratympanic fold is present. The outer fingers are about one-half webbed, the web reaching to the penultimate subarticular tubercle. Webbing reaches the discs of the third and fifth toes and the disc of the second toe on the outside. There is less extensive webbing on the fourth toe and between the first and second. A copulatory excrescence formed of very minute spines is present on the first finger. The skin is minutely granular dorsally, coarsely so beneath. Slit-like vocal-sac openings are present in the floor of the mouth. A very indistinct row of low tubercles is present on the outer edge of the forearm. There is no corresponding row on the tarsus. A moderate-sized triangular heel tubercle is present.

FIG. 14. *Nyctimystes perimetri*, type specimen, A.M.N.H. No. 60081, natural size.

In preservative, the type specimen is lead-colored dorsally. There is almost no trace of pattern on the body, but there is indistinct spotting on the femur, and faint, irregular bands are present on the tibia. On the flanks, the dark dorsal color gives way along an irregular border to the unpigmented chest and abdomen. The chin and margin of the lower jaw are peppered with dark pigment cells most abundant along the periphery. There is no light margin to the upper lip, but dark pigment is less abundant there than on the rest of the head. Dark mottling is present on the lower surfaces of the hind legs.

VARIATION: Four topotypic specimens agree in pertinent features with the type. All show similar patterns of the palpebral venation. Vocal-sac openings are present in the three males (48–52 mm. in snout to vent length), and dissection of one individual reveals a single, subgular, vocal sac. The female topotype (67 mm. from snout to vent) contains numerous relatively large (*ca.* 2.3 mm. in diameter), unpigmented eggs. The tubercles on the forearm are slightly more distinct than in the type in some specimens, but are not prominent in any. There are no striking variations in color or pattern. Some yellow pigment is present on the throat and chest of two individuals.

The single individual from Rossel Island is sufficiently like those from Sudest Island that it must be considered as belonging to the same species. In all proportions, however, it represents an extreme when compared to the ratios computed for the Sudest Island frogs, but the

differences are too slight to warrant serious consideration with such a small sample.

COMPARISON WITH OTHER SPECIES: Species with a high ratio of eye to naris distance to internarial distance that might be confused with *perimetri* are *daymani, semipalmata,* and *fluviatilis. Nyctimystes avocalis* shows some overlap with *perimetri* in the ratio in question, but is easily distinguished by the smaller adult size and lack of vocal-sac openings in the male.

Nyctimystes daymani is evidently a much smaller species than *perimetri,* as the largest of 25 males measures only 42 mm. from snout to vent, while the four male *perimetri* measure between 48 and 54 mm. *Nyctimystes daymani* has slightly shorter legs and a less prominent heel tubercle.

Nyctimystes semipalmata attains a snout to vent length of 84 mm. and is thus probably a much larger species than *perimetri,* of which the largest individual measures 67 mm. *Nyctimystes semipalmata* is longer-legged than *perimetri,* there being a minimum of overlap in the ranges of the ratios of tibia length to snout to vent length for the two forms (fig. 10, table 1). Also, the heel tubercle of *semipalmata* is relatively larger, though this character is not amenable to objective presentation.

In proportions, *perimetri* and *fluviatilis* are very similar. As three of the four male specimens of *perimetri* are larger than the gravid female

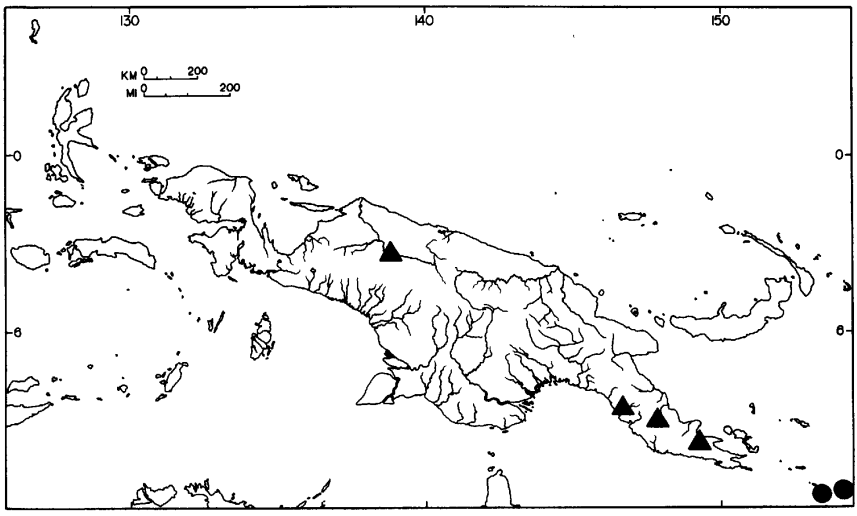

FIG. 15. Distribution of *Nyctimystes perimetri* (dots) and *N. semipalmata* (triangles).

holotype of *fluviatilis*, it may tentatively be assumed that *perimetri* is a larger species. The heel tubercle of *perimetri* is larger than that seen in *fluviatilis*.

DISTRIBUTION (FIG. 15): *Nyctimystes perimetri* is known only from Sudest and Rossel Islands in the Louisiade Group, Territory of Papua, New Guinea. Specimens (paratypes) have been examined from the west slope of Mt. Riu, Sudest Island, 250–350 meters (A.M.N.H. Nos. 60079–60083) and the south slope of Mt. Rossel, 700 meters, Rossel Island (A.M.N.H. No. 60132).

Nyctimystes persimilis, new species

Figure 16

TYPE: A.M.N.H. No. 56838, collected on the north slope of Mt. Dayman, Territory of Papua, New Guinea, at an elevation of 1370 meters (4570 feet) on July 2, 1953, by G. M. Tate.

DEFINITION: Veins of palpebral reticulum oblique, with few horizontal interconnections (fig. 20E). The internarial distance is approximately equal to the distance from naris to eye (E-N/IN = 0.97 and 1.05 in two specimens). The fingers have only a basal web (as in fig. 21A).

DESCRIPTION OF TYPE SPECIMEN: Adult male, with the following measurements (in millimeters): Snout to vent length, 40; head width, 14.5; head length, 13.5; tibia length, 22.1; tympanum diameter (horizontal), 2.1; eye diameter (horizontal), 5.6; internarial distance, 3.8; distance from eye to naris, 4.0.

The head is relatively broad and short-snouted. The vomerine teeth are in two patches between the internal nares. The eyes are large (eye length to head width ratio equals 0.36–0.39). The palpebral reticulum consists largely of oblique lines, with few horizontal interconnections. The canthus rostralis is slightly curved; the loreal region is oblique. The tympanum is distinct and smooth and is separated from the posterior corner of the eye by a distance approximately equal to the horizontal diameter of the tympanum. A curved fold of skin passes from the posterior corner of the eye over the upper edge of the tympanum and curves downward, to disappear above the insertion of the forelimb. The skin of the dorsal surface of the body is only slightly roughened, but that of the venter is coarsely granulate. The webbing of the fingers is slight, with only a basal web on the outer fingers. The webbing of the toes fails to reach the disc of any toe. There is no heel tubercle. A row of light-colored tubercles is present on the outer surface of the forearm. The first finger is swollen basally and bears numerous minute

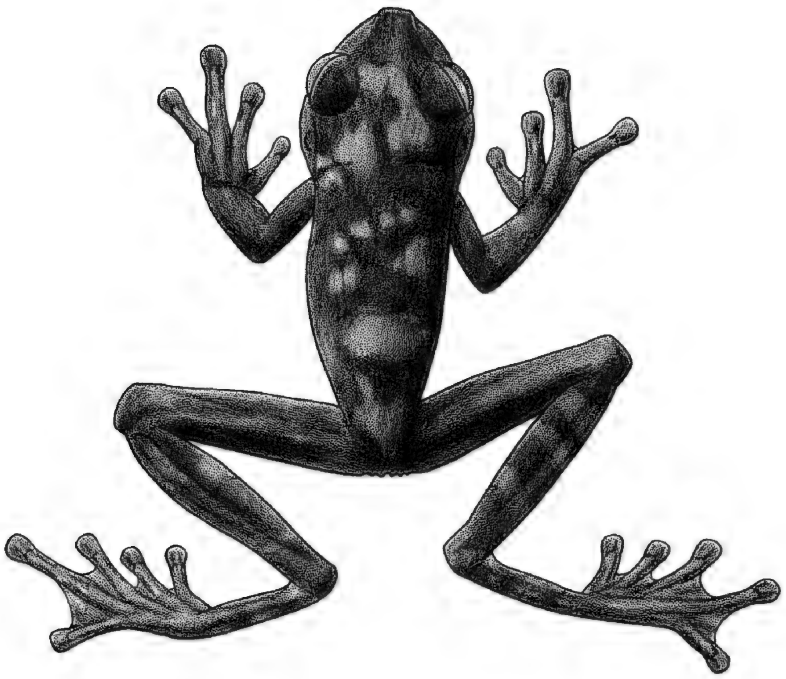

FIG. 16. *Nyctimystes persimilis*, type specimen, A.M.N.H. No. 56838. 1.5 times natural size.

brown spines. Slit-like vocal-sac openings are present in the floor of the mouth.

The dorsal color (in preservative) is dark purplish brown, with irregular patches and spots of lighter color showing through. Owing to darkening caused by preservative, it is difficult to make out details of pattern. The tibia was evidently banded and spotted. The ventral surfaces are brownish, there being considerable melanic pigment present. For the most part this is in the form of a continuous wash, though there is some tendency to the formation of indistinct vermiculations, particularly on the throat.

VARIATION: The only other specimen of *persimilis* is a male 37 mm. in snout to vent length which resembles the type specimen closely. It is slightly more rugose, especially in the lateral and postero-dorsal regions, but otherwise shows no significant departure from the type.

COMPARISON WITH OTHER SPECIES: The relatively short snout and scant finger webbing of *persimilis* seem to ally this species with *papua*, *gularis*, and *narinosa*. The distinct palpebral reticulum of *persimilis* will serve to distinguish it from *papua*. Also, the males of *papua* lack

vocal-sac openings. The much broader spacing of the nostrils separates *narinosa* from *persimilis*. The two species are also distinguished by differences in the pattern of the palpebral reticulum (figs. 19C and 20E).

There is close similarity between *gularis* and *persimilis*. Two of the three specimens I refer to *gularis* are from the same locality as *persimilis*, Mt. Dayman, but at a higher elevation. These two *gularis* are of approximately the same size as the specimens of *persimilis*, but both are females. Hence the possibility exists that some of the differences to be mentioned may merely reflect sexual dimorphism. In *gularis*, the dorsal skin is considerably more roughened than in *persimilis*. The tympanum of *gularis* is indistinct and roughened, not smooth and distinct. The palpebral venation of *persimilis* includes more parallel, oblique veins than *gularis*, and is less of a reticulum (fig. 20A, E). Relative eye size is larger in *persimilis*. The ratio of eye length to head width in the two specimens of *persimilis* is 0.386 and 0.364, compared to 0.312, 0.304, and 0.316 in three *gularis*. The difference here is not related to absolute size of the individuals involved, as the *persimilis* and the two Mt. Dayman *gularis* are similar in size, 37 to 43 mm. from snout to vent. The two specimens of *persimilis* are slightly shorter-legged than the three *gularis*. Ratios of tibia length to snout to vent length are: *persimilis*, 0.55 and 0.56; *gularis*, 0.58, 0.57, 0.60. Much larger samples would be necessary to verify the slight differences in leg length suggested here. The loreal region of *gularis* appears to be somewhat more vertical than that of *persimilis*.

DISTRIBUTION (FIG. 17): *Nyctimystes persimilis* is known only from the type locality, north slope of Mt. Dayman, 1370 meters (4570 feet), Territory of Papua, New Guinea. The two specimens representing the species are A.M.N.H. Nos. 56738 (type specimen) and 56838 (paratype).

Geoffrey M. Tate collected both specimens of the new species. They were found on the bank of a small stream in heavy forest on July 2 and 9, 1953.

Nyctimystes rueppelli Boettger

Hyla rueppelli BOETTGER, 1895, p. 137; 1900, p. 373, pl. 16, figs. 12–12c. VAN KAMPEN, 1923, p. 35. BRONGERSMA, 1948, p. 306.

DEFINITION: Palpebral venation usually distinct, oriented largely in a near-vertical direction, with few horizontal interconnections. Fingers with much webbing, the outer finger webbed almost to disc (fig. 21D). A very small tubercle may or may not be present on the heel.

DESCRIPTION: The head is broader than long; the canthus rostralis is not distinct; the loreal region is oblique; the internarial distance is less

than the distance from eye to naris (fig. 9, table 1). The palpebral venation is distinct in three specimens, but is reduced to individual pigment spots in one; the lines are oriented largely in a vertical direction, with few horizontal interconnections. The outer finger is webbed almost to disc. The heel is without a tubercle, or has a very small one. The skin is smooth above, granular below. A weak, wavy fold is present on the outer surface of the forearm. The legs average shorter than those of other *Nyctimystes* (TL/S-V averages 0.50). Vocal-sac openings and a vocal sac, as well as nuptial pads on the first finger, are present in the males. This does not appear to be a large species. Boettger (1895, p. 138) recorded a male 48 mm. in length. One of the cotypes in the American Museum is a gravid female with a snout to vent length of 40 mm.

Boettger (1900, p. 374) described this frog as follows (translation from Van Kampen, 1923, p. 35): "Upper parts in life yellow above, sometimes powdered with blackish; in spirit yellowish, greyish or blackish brown, uniform or spotted and marbled with lighter, sometimes light grey with two indistinct, darker, rhombic spots on head and back; usually an indistinct lighter spot on the upper lip, or the whole upper lip yellowish, powdered and spotted with blackish; greyish white beneath." The specimens I have examined fall within the range of variation encompassed in Boettger's description.

COMPARISON WITH OTHER SPECIES: The discovery that this species has a palpebral reticulum necessitates its removal from the genus *Hyla* where it has reposed since its description. In the four specimens available to me, the pupil is too expanded for one to be certain that it would be vertically elliptical when closed. However, the association of palpebral venation with the vertical pupil seen in other species argues for a similar relationship here. The extensive webbing of the fingers and lack of a strong heel tubercle form a combination of characters that will distinguish *N. rueppelli* from most other *Nyctimystes*. The above-mentioned characters are shared with some *N. humeralis*, a much larger species with longer legs, a humeral spine in the male, and uniform dorsal coloration.

DISTRIBUTION (FIG. 17): The localities of collection for this species are on Halmahera and Morotai Islands in the Moluccas Islands. This species has the most northern and western distribution of any in the genus.

LOCALITY RECORDS: *Halmahera Island:* Kau (A.M.N.H. Nos. 23759–23760, cotypes); Soah Konorah (Boettger, 1900, p. 373); Galela (Boettger, *loc. cit.*). *Morotai Island:* No exact locality (C.M. Nos. 25554–25555); between Bilowoh and Goegoeti (Brongersma, 1948, p. 306).

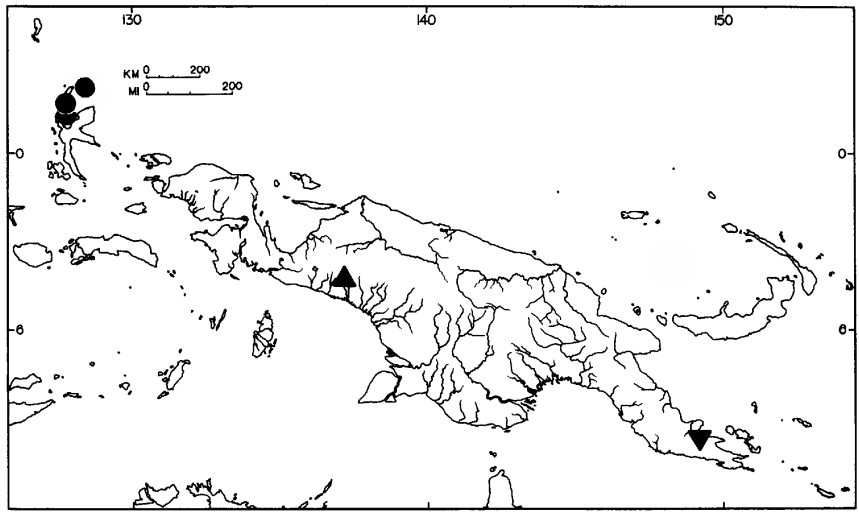

FIG. 17. Distribution of *Nyctimystes granti* (triangle), *N. persimilis* (inverted triangle), and *N. rueppelli* (dots).

Nyctimystes semipalmata Parker

Nyctimystes semipalmata PARKER, 1936, p. 83, figs. 5–6.
Nyctimantis papua, BOULENGER, 1897 (part), p. 12.

TYPE: B.M.(N.H.) No. 1935.3.9.198, a female from Kokoda, Territory of Papua, 1200 feet, secured by Miss L. E. Cheesman.

DEFINITION: In a synopsis accompanying the description of *N. semipalmata*, Parker (1936, p. 77) characterized the species as having "Outer fingers half-webbed. . . . Snout longer than the eye; a palpebral reticulum; heel with a large lappet." In the collections of the American Museum there are no specimens that agree completely with this diagnosis. However, there are several specimens that, except for having less finger webbing, fit the diagnosis and Parker's (1936, pp. 83–84) more detailed description fairly well. If the American Museum specimens truly represent *semipalmata*, the species may be redefined as follows: size large (females to 84 mm. in snout to vent length); internarial distance distinctly smaller than distance from eye to naris (E-N/IN averages 1.34); a relatively large, triangular dermal appendage on the heel (fig. 18).

DESCRIPTION: (Based on A.M.N.H. No. 56396, Mt. Dayman, Territory of Papua). Female, snout to vent length, 80 mm.; tibia length, 47.1; head width, 32.7; head length, 28.8; internarial distance, 6.3; distance from eye to naris, 9.7; eye diameter, 8.3; tympanum diameter (horizontal), 3.5.

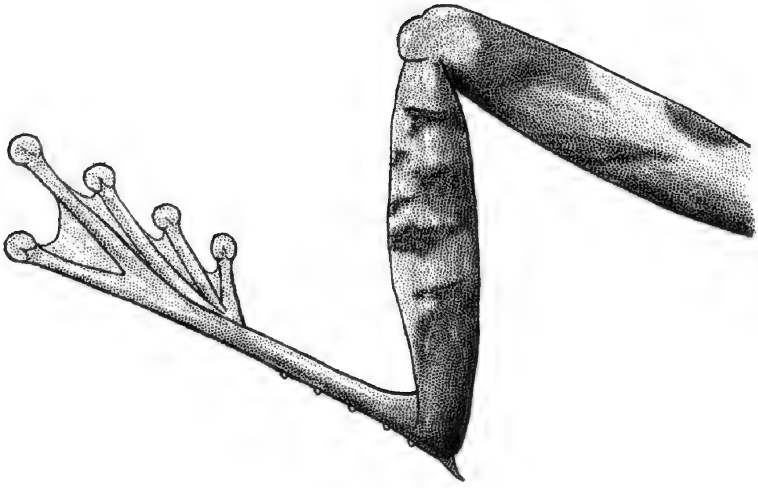

FIG. 18. Left hind leg of *Nyctimystes semipalmata* (natural size) to show the large, triangular, heel tubercle.

The head is broad, with depressed snout, closely spaced nares, and oblique loreal region. Palpebral venation is in oblique lines (more vertical than horizontal), with a few horizontal interconnections. A heavy dermal fold passes from the posterior corner of the eye over the upper edge of the tympanum and down to the insertion of the forelimb. The outer fingers are approximately half-webbed (as in fig. 21C), the third and fifth toes webbed to the disc. A light-colored dermal ridge extends from the elbow to the disc of the fourth finger. A similar but less distinct ridge occupies the outer edge of the tarsus and fifth toe. There is a relatively large, triangular, dermal appendage on the heel (as in fig. 18).

This specimen is gray-brown in preservative. The top of the snout, head, and body are somewhat darker than the loreal region, side of head, and flanks. The line of demarcation is abrupt along the canthus rostralis, but less so elsewhere. The forelimbs and tibial and tarsal segments are colored dorsally as are the more lateral body parts, light gray-brown. The femora are clouded with darker pigment on both dorsal and anterior surfaces. Numerous tiny black specks are scattered over the body and limbs and are particularly evident on the side of the head. The upper and lower lips are narrowly margined with light color. The under surfaces are grayish yellow and unmarked except for some flecks of darker color bordering the light margin of the lower lip and spotting the under side of the tibia.

VARIATION: In addition to the specimen described above, I assign to this species a male from Papua and four females from Netherlands New Guinea. All these specimens agree in having a prominent heel tubercle, broad head, narrowly spaced nostrils, large size, and fingers about one-half webbed.

The male from Diene, Papua (A.M.N.H. No. 60389), is much darker than the Mt. Dayman example described above and shows traces of banding on the tibia, probably items of little significance. Other than in features of pigmentation, this specimen is closely similar to the large female from Mt. Dayman. This male has slit-like, vocal-sac openings and measures 65 mm. from snout to vent.

The four females from the region of the Idenburg River (A.M.N.H. Nos. 49627, 49672, 49673, 49675) are similar in size to the Mt. Dayman specimen, 80–84 mm. in snout to vent length. Two of the four specimens have the palpebral venation somewhat more of a reticulum, especially anteriorly (fig. 19E). If these northern specimens do not represent the same species as those from Papua, they certainly are more closely related to the species from Diene and Mt. Dayman than to any other known form.

There remain to be discussed the differences between the animals I have examined and the type description of *semipalmata*. The length of the type specimen, a female, is given as 59 mm. In the absence of a topotypic series that would give some idea of maximum size and size at sexual maturity, the matter of size difference must be held in abeyance. Where adequate data are available, differences in size attained serve as useful taxonomic characters. The somewhat more extensive webbing of the hand of the type specimen of *semipalmata* (Parker, 1936, fig. 5) is another apparent difference. In at least one species (*N. montana*), where specimens are available from several scattered localities, there are consistent differences in webbing between populations. So the greater degree of webbing of the type does not necessarily indicate specific distinctness. Weighed against these possible significant differences are the many similarities. Without actually having examined the type specimen, I cannot be sure of its conspecifity with those I rank with it, but I think it the best solution to regard them as representing the same species.

COMPARISON WITH OTHER SPECIES: The only species that resemble *semipalmata* in size are *humeralis* and *granti*. The humeral spine of the male, the lower ratio of eye to naris distance to internarial distance, and the lack of a tubercle on the heel will distinguish *humeralis* from *semipalmata*. *Nyctimystes granti* lacks a heel tubercle. I have not meas-

TABLE 2

MAXIMUM SNOUT TO VENT LENGTH (IN MILLIMETERS) ATTAINED BY THE SPECIES OF *Nyctimystes*

Species	Sex	*N*	Length
avocalis	♂	3	35
	♀	2	47
daymani	♂	25	42
	♀	2	45
fluviatilis	♀	1	50
granti	♀	1	100
gularis	♂	1	37
	♀	3	56
humeralis	♂	4	100
	♀	7	83
kubori	♀	3	59
montana	♂	52	53
	♀	21	63
narinosa	♂	3	50
	♀	4	64
papua	♂	10	60 (77)[a]
	♀	11	70
perimetri	♂	5	54
	♀	1	67
persimilis	♂	2	40
rueppelli	♂	3	48
	♀	2	47
semipalmata	♂	1	65
	♀	5	84

[a] See page 29.

ured the type and unique specimen, so have no direct information on possible proportional differences. However, Parker (1936, p. 77) states that the snout is high, with vertical lores, which contrasts with the low snout with more oblique lores seen in *semipalmata.*

DISTRIBUTION (FIG. 15): *Nyctimystes semipalmata* is known from the region of the Idenburg River in Netherlands New Guinea and from the southeastern end of the island in the Territory of Papua.

LOCALITY RECORDS: *Netherlands New Guinea:* Four kilometers southwest of Bernhard Camp, 850 meters, Idenburg River (A.M.N.H. Nos. 49672, 49673, 49675); 6 kilometers southwest of Bernhard Camp, 1200 meters, Idenburg River (A.M.N.H. No. 49627). *Territory of Papua:* Kokoda, 1200 feet (type locality, Parker, 1936, p. 83); Mt. Victoria (male cotype of *N. papua* tentatively assigned to *semipalmata* by

Parker); Diene, 480 meters (A.M.N.H. No. 60389); north slope of Mt. Dayman, 700 meters (A.M.N.H. No. 56396).

The specimen from Mt. Dayman was found on the bank of a rocky stream in forest on July 19, 1953, by G. M. Tate. Tate also collected *N. montana* and *N. daymani* in the same habitat. Elevations at which *semipalmata* has been captured range from 1200 feet (360 meters) to 4000 feet (1200 meters).

SPECIES REMOVED FROM THE GENUS *NYCTIMYSTES*

In accord with the restricted definition of the genus *Nyctimystes* that I have adopted, it is necessary to refer four forms back to the genus *Hyla*. Two of these forms described as *Nyctimystes* prove to be based on specimens referable to species of *Hyla* that had already been described.

Hyla amboinensis Horst

Hyla amboinensis HORST, 1883, p. 239.
Nyctimystes amboinensis, BRONGERSMA, 1953, p. 579.

This species has been known from Amboina, Misool, and Ceram Islands and was reported from the mainland of New Guinea (Vogelkop Peninsula) by Brongersma (1953). He noted that in life the "pupil was neither horizontal nor vertical, but lozenge-shaped" (1953, p. 580). This difference of pupil shape from the horizontal pupil usually encountered in *Hyla* led Brongersma to refer the species to the genus *Nyctimystes*. Examination of specimens of this species from Ceram in the collection of the American Museum reveals that pigmented palpebral venation is lacking; hence the species must be referred to *Hyla*.

Hyla darlingtoni Loveridge

Hyla darlingtoni LOVERIDGE, 1945, p. 53.
Nyctimystes flavomaculata FORCART, 1953, p. 63, pl. 1a–c.

In the collections of the American Museum of Natural History there are over 100 specimens of this species collected at Kondiu near Kup by Father O. Shelly and in the Kubor Mountains by E. Thomas Gilliard. Specimens from this series have been compared directly with the type of *darlingtoni* (M.C.Z. No. 25890), and there is no question as to their specific identity. Forcart's description and illustrations of *N. flavomaculata* (1953) make it clear that the same species is involved.

There is no trace of a palpebral reticulum in this species; hence I refer it to the genus *Hyla*. In most specimens, the pupil is sufficiently expanded that its orientation cannot be determined. There are some well-preserved individuals in which the contracted pupil appears

plainly vertical, and others in which it appears horizontal. The true pupil shape will have to be confirmed with living frogs.

The eggs of *darlingtoni* are small and have a dark animal hemisphere, unlike the large unpigmented eggs seen in most *Nyctimystes*. The tadpole of *darlingtoni* is typical of *Hyla* and lacks the specializations of at least some *Nyctimystes*.

Hyla loveridgei Neill

Nyctimystes loveridgei NEILL, 1954, p. 83, fig. 1.

Neill, in his original description of this species, specifically mentioned the lack of a palpebral reticulum. He noted that while in preservative the pupil of the type specimen appeared circular; when the living individual was exposed to bright sunlight the pupil formed a vertical slit.

A series of 191 frogs from Peria Creek Crossing, Kwagira River, Territory of Papua, in the collection of the American Museum of Natural History appears to represent this species. The locality is about 130 miles east of the type locality (Taburi, near Rouna Falls) across the narrow southeastern tip of New Guinea. Comparison of frogs from this series with the type specimen of *loveridgei* (M.C.Z. No. 27823) satisfies me that the type and the Peria Creek frogs represent the same species, inasmuch as they are closely similar in pigmentation, size, and proportions.

The distinctive cross-banded color pattern illustrated by Neill (1954, fig. 1) and emphasized in the specific diagnosis has faded on the type specimen so that it is only dimly visible. Traces of the same pattern, as distinct as now in the type, can be seen in many of the frogs from Peria Creek. The illustration of the specimen accompanying the original description shows the digits about one-half too short.

The eggs of *loveridgei* are typical of *Hyla*, being small, with a dark animal hemisphere.

Hyla thesaurensis Peters

Hyla thesaurensis PETERS, 1877, p. 421.
Nyctimystes milneana LOVERIDGE, 1945, p. 57.

The type specimen of *N. milneana* was said to have a pupil with "a basal nick indicating that it would be vertical when contracted" (Loveridge, 1945, p. 58). I have been unable to differentiate between the type specimen of *milneana* (M.C.Z. No. 11652) and specimens in a long series from Menapi on Cape Vogel which I think represent *Hyla thesaurensis*. For example, the ratio of tibia length to snout to vent length

of the type of *milneana* is 0.50; the same ratio for 26 females of similar size from Menapi averages 0.50. There is no palpebral reticulum in the type specimen of *milneana,* so it cannot be retained in the genus *Nyctimystes.* The evidence for a vertical pupil is very weak. I prefer to recognize *milneana* as a synonym of *thesaurensis.*

COMMENTS ON GEOGRAPHIC DISTRIBUTION

With many of the species known from only one or two localities, it is evident that much remains to be learned of the distribution of the species of *Nyctimystes.* A glance at the distribution maps will show that the locality records for the genus on the mainland of New Guinea are concentrated along the central mountainous ridge. Records for lower elevations are few, although the lowlands of New Guinea have been more thoroughly explored than the higher elevations. The absence of *Nyctimystes* from the Vogelkop Peninsula and the Huon Peninsula is probably more apparent than real, and a careful examination of collections of *"Hyla"* from these regions might well disclose additional *Nyctimystes.*

It is noteworthy that in several localities more than one species has been found. From Mondo, Papua, Parker (1936) recorded *N. papua, N. gularis, N. montana,* and *N. semipalmata.* On Mt. Dayman, Territory of Papua, collectors on the Fourth Archbold Expedition found the following species: *daymani* (700, 1250 meters); *montana* (700 meters); *semipalmata* (700 meters); *persimilis* (1370 meters); *papua* (1550 meters); and *gularis* (2230 meters). In the vicinity of Bernhard Camp, Idenburg River, Netherlands New Guinea, *fluviatilis, humeralis* (850, 1200 meters), *semipalmata* (850, 1200 meters), and *papua* (1800 meters) were collected. These data are suggestive of some altitudinal stratification, but there are as yet too few records to verify the suggestion.

On the most recent (Fifth) Archbold Expedition to New Guinea, Russell Peterson collected *Nyctimystes* on Rossel and Sudest Islands, but failed to find the genus on Woodlark, although that island has other typical Papuan frogs. I find no *Nyctimystes* among the frogs collected by the Archbold Expedition to Cape York Peninsula (1948) and doubt if the genus occurs in Australia. In occurring west to the Moluccas Islands but not beyond (not past "Weber's Line"), *Nyctimystes* conforms to the pattern of distribution of many other genera and species of Papuan animals. The Aru Islands have a dominantly Papuan fauna, and *Nyctimystes,* although not yet known there, may possibly be present on this ill-explored group.

The vast majority of localities from which specimens of *Nyctimystes*

in the American Museum have been collected are described in detail in several reports published by the Museum. The 1933–1934 Archbold Expedition to Papua was covered in the paper by Archbold and Rand (1935). The 1935–1937 Archbold Expedition to the Fly River region was described by Rand and Brass (1940). The 1938–1939 Archbold Expedition to Netherlands New Guinea is covered in the report by Archbold, Rand, and Brass (1942). The Fourth (1953) Archbold Expedition, to southeastern New Guinea and adjacent islands, is described by Brass (1956). Collecting sites in central New Guinea are described by Mayr and Gilliard (1954).

Each of these publications contains a wealth of information on the habitat conditions met at each collecting station; hence I repeat little of such information in the present paper. Detailed locality maps also accompany each of the above-mentioned papers.

KEY TO THE SPECIES OF *NYCTIMYSTES*

The following key to *Nyctimystes* is offered only as a tentative guide to the species. Not only are some species known from a single or very few specimens, but the characteristics that distinguish species are often not amenable to expression as key characters. Anyone attempting to use this key will, of course, find it necessary to labor through the species accounts in order to verify the identification suggested by the key. Variation in the key characters selected has necessitated that some species appear more than once in the key.

1. Palpebral venation weak and disconnected, sometimes virtually absent (fig. 19A); outer fingers with only a basal web (fig. 21A); male without vocal-sac openings ..... *papua* (p. 28)
   Palpebral venation distinct, reticulate or in more or less parallel lines; fingers variously webbed; vocal-sac openings present or not.....2
2. Male with a humeral spine that forms a distinct projection on the side of the chest; dorsal color uniform (green in life); size large, up to 100 mm. from snout to vent; no papilla on heel ..... *humeralis* (p. 16)
   Male without humeral spine; coloration uniform or not; size large or small; papilla on heel present or absent 3
3. Size large, up to 100 mm. from snout to vent; dorsal pattern of dark vermiculations on lighter background; no papilla on heel (one specimen only) ..... *granti* (p. 13)
   Size large or small, but if large (80 mm. or greater), a triangular flap of skin present on heel (fig. 18); pattern variable 4
4. Palpebral venation consisting largely of parallel lines oriented in a near-vertical direction, with relatively few horizontal interconnections (figs. 19B, F, 20B, D, F) 5
   Palpebral venation partly or wholly a reticulum (figs. 19D, E, 20A, C) or in more or less horizontal lines (fig. 19C) 13

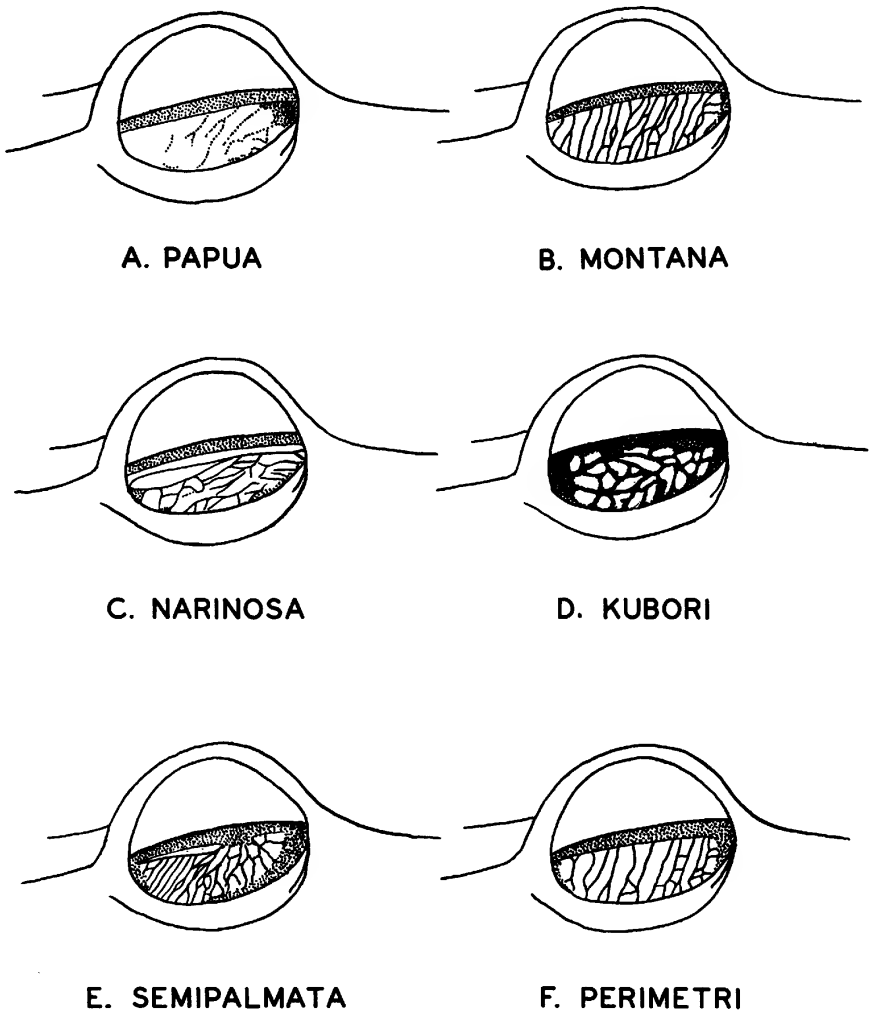

FIG. 19. Patterns of palpebral venation in *Nyctimystes*. The drawings are somewhat diagrammatic, and no effort is made to show differences in eye size.

5. Vocal-sac openings lacking in male; size small, less than 50 mm. from snout to vent; legs relatively long, tibia length/snout to vent length averages 0.59 ..... *avocalis* (p. 6)
   Vocal-sac openings present; size and leg length variable 6
6. Outer fingers with only a basal web (fig. 21A); internarial distance approximately the same as eye to naris distance ..... *persimilis* (p. 34)
   Outer fingers one-third or more webbed (fig. 21B, C, D); internarial distance usually distinctly less than distance from eye to naris 7
7. Hand webbing extensive, outer fingers more than one-half webbed (fig.

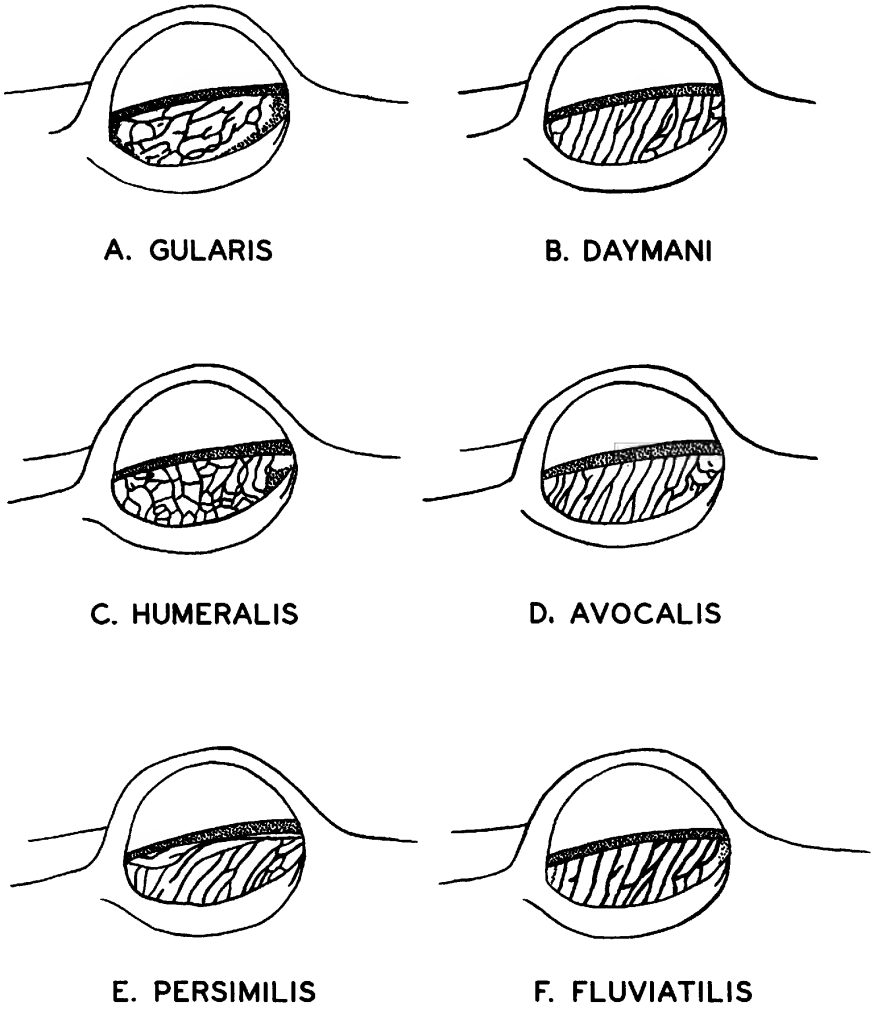

FIG. 20. Patterns of palpebral venation in *Nyctimystes*. See figure 19.

21D) 8

More than a basal web present, but outer fingers usually one-half or less webbed (fig. 21B, C) 9

8. A triangular dermal flap on heel (fig. 18); size large, up to 84 mm. from snout to vent ..... *semipalmata* (p. 38)

No flap or papilla on heel; size smaller, up to 48 mm. from snout to vent ..... *rueppelli* (p. 36)

9. Ratio of internarial distance to eye to naris distance (E-N/IN) usually less than 1.2 ..... *montana* (p. 21)

Ratio of internarial distance to eye to naris distance usually greater than

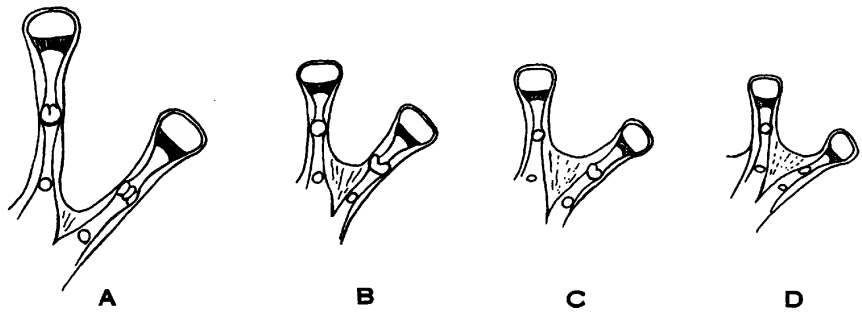

FIG. 21. Third and fourth fingers, in palmar view, of four species of *Nyctimystes* to show extent of webbing between these fingers. A. *N. narinosa* (basal web or one-quarter webbed). B. *N. kubori* (about one-third webbed). C. *N. avocalis* (one-half webbed). D. *N. rueppelli* (slightly more than one-half webbed).

1.2 10

10. Legs longer, TL/S-V = 0.56 or greater; a large triangular dermal flap on heel (fig. 18); size large, up to 84 mm. from snout to vent ..... *semipalmata* (p. 38)
    Legs shorter, TL/S-V usually less than 0.56; heel tubercle, if present, smaller; size smaller 11
11. E-N/IN 1.41 in single specimen ..... *fluviatilis* (p. 11)
    E-N/IN less than 1.4 12
12. Size larger, males to 54 mm. from snout to vent; heel tubercle prominent ..... *perimetri* (p. 31)
    Size smaller, males to 42 mm. from snout to vent; heel tubercle less prominent ..... *daymani* (p. 8)
13. E-N/IN greater than 1.2; a large, triangular, dermal flap on heel (fig. 18); size large, up to 84 mm. from snout to vent ..*semipalmata* (p. 38)
    E-N/IN less than 1.2; no tubercle on heel, or only a tiny one; maximum size under 80 mm. from snout to vent 14
14. Outer fingers more than one-quarter webbed ..... *kubori* (p. 18)
    Outer fingers with only a basal web 15
15. E-N/IN less than 0.95 (average 0.84); palpebral veins predominantly horizontal in orientation (fig. 19C) ..... *narinosa* (p. 26)
    E-N/IN 0.95 or greater; palpebral veins not predominantly horizontal 16
16. Palpebral venation composed of mostly parallel, oblique lines (fig. 20E) ..... *persimilis* (p. 34)
    Palpebral venation a somewhat broken reticulum, without obvious directional orientation (fig. 20A) ..... *gularis* (p. 14)

SUMMARY

The genus *Nyctimystes* (family Hylidae) is defined as including those species that combine the following characteristics: pupil forming a

vertical slit when closed, lower eyelid with pigmented venation, feet without elongate or opposable first digits. Fourteen species are recognized as belonging to the genus, seven of them described as new. Principal characters useful in distinguishing the species are the pattern of the palpebral venation, maximum size attained, amount of finger webbing, and ratio of distance from eye to naris to internarial distance. The species comprising the genus are:

N. avocalis, new species
N. daymani, new species
N. fluviatilis, new species
N. granti Boulenger
N. gularis Parker
N. humeralis Boulenger
N. kubori, new species
N. montana Parker
N. narinosa, new species
N. papua Boulenger
N. perimetri, new species
N. persimilis, new species
N. rueppelli Boettger
N. semipalmata Parker

The following changes in currently recognized generic and specific names are proposed:

Nyctimystes amboinensis Horst = *Hyla amboinensis* Horst
Nyctimystes flavomaculata Forcart = *Hyla darlingtoni* Loveridge
Nyctimystes loveridgei Neill = *Hyla loveridgei* Neill
Nyctimystes milneana Loveridge = *Hyla thesaurensis* Peters
Hyla humeralis Boulenger = *Nyctimystes humeralis* Boulenger
Hyla rueppelli Boettger = *Nyctimystes rueppelli* Boettger

The geographic range of the genus includes the entire Papuan region, from the Moluccas Islands on the northwest to the Louisiade Archipelago on the southeast.

BIBLIOGRAPHY

ARCHBOLD, RICHARD, AND A. L. RAND
1935. Results of the Archbold Expeditions. No. 7. Summary of the 1933–1934 Papuan Expedition. Bull. Amer. Mus. Nat. Hist., vol. 68, pp. 527–579.

ARCHBOLD, RICHARD, A. L. RAND, AND L. J. BRASS
1942. Results of the Archbold Expeditions. No. 41. Summary of the 1938–1939 New Guinea Expedition. Bull. Amer. Mus. Nat. Hist., vol. 79, pp. 197–288.

BOETTGER, O.
1895. Liste der Reptilien und Batrachier der Insel Halmaheira nach den

Sammlungen Prof. Dr. W. Kükenthal's. Zool. Anz., vol. 18, no. 472, pp. 129–138.

1900. Die Reptilien und Batrachier. *In* Kükenthal, W., Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. Abhandl. Senckenbergischen Nat. Gesell., vol. 25, no. 2, pp. 323–402.

BOULENGER, G. A.

1897. Descriptions of new lizards and frogs from Mount Victoria, Owen Stanley Range, New Guinea, collected by Mr. A. S. Anthony. Ann. Mag. Nat. Hist., ser. 6, vol. 19, pp. 6–13, pls. 1, 2.

1912. On some tree-frogs allied to *Hyla caerulea* with remarks on noteworthy secondary sexual characters in the family Hylidae. Zool. Jahrb., vol. 1, suppl. 15, pp. 211–218, 1 table.

1914. An annotated list of the batrachians and reptiles collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. Trans. Zool. Soc. London, vol. 20, pp. 247–274, 4 pls.

BRASS, L. J.

1956. Results of the Archbold Expeditions. No. 75. Summary of the Fourth Archbold Expedition to New Guinea (1953). Bull. Amer. Mus. Nat. Hist., vol. 111, pp. 77–152.

BRONGERSMA, L. D.

1948. Frogs and snakes from the island of Morotai (Moluccas). Zool. Meded. Leyden, vol. 29, pp. 306–310.

1953. Notes on New Guinean reptiles and amphibians. III. Proc. K. Nederlandse Akad. Wetensch., ser. C, vol. 56, pp. 572–583, figs. 1–2.

FORCART, LOTHAR

1953. Amphibien und Reptilien von Neuguinea, mit der Beschreibung eines neuen Laubfrosches, *Nyctimystes flavomaculata* n. sp. Verhandl. Naturf. Gesell. Basel, vol. 64, pp. 58–68, fig. 1.

GILLIARD, E. THOMAS

1953. New Guinea's rare birds and Stone Age men. Natl. Geogr. Mag., vol. 103, pp. 421–488.

GRIFFITHS, I.

1954. On the "otic element" in Amphibia Salientia. Proc. Zool. Soc. London, vol. 124, pp. 35–50, figs. 1–8, pls. 1–4, tables 1–3.

HORST, R.

1883. On new and little-known frogs from the Malayan Archipelago. Notes Leyden Mus., vol. 5, pp. 235–244.

LOVERIDGE, ARTHUR

1945. New tree-frogs of the genera *Hyla* and *Nyctimystes* from New Guinea. Proc. Biol. Soc. Washington, vol. 58, pp. 53–58.

1948. New Guinean reptiles and amphibians in the Museum of Comparative Zoölogy and United States National Museum. Bull. Mus. Comp. Zoöl., vol. 101, no. 2, pp. 305–430.

MAYR, ERNST, AND E. THOMAS GILLIARD

1954. Birds of central New Guinea. Results of the American Museum of Natural History expeditions to New Guinea in 1950 and 1952. Bull. Amer. Mus. Nat. Hist., vol. 103, pp. 315–374.

NEILL, WILFRED T.
1954. A new species of frog, genus *Nyctimystes*, from Papua. Copeia, no. 2, pp. 83–85, 1 fig.
NOBLE, G. KINGSLEY
1931. The biology of the Amphibia. New York and London, McGraw-Hill Book Co., xiii + 577 pp., 174 figs., frontispiece.
PARKER, H. W.
1936. A collection of reptiles and amphibians from the mountains of British New Guinea. Ann. Mag. Nat. Hist., ser. 10, vol. 17, pp. 66–93, figs. 1–6.
PETERS, W.
1877. Herpetologische Notizen. II. Bermerkungen über neue oder wenigen bekannte Amphibien. Monatsber. Akad. Wiss. Berlin, pp. 415–423.
PROCTOR, JOAN B.
1921. On the variation of the scapula in the batrachian groups Aglossa and Arcifera. Proc. Zool. Soc. London, pp. 197–214, figs.
RAND, A. L., AND L. J. BRASS
1940. Results of the Archbold Expeditions. No. 29. Summary of the 1936–1937 New Guinea Expedition. Bull. Amer. Mus. Nat. Hist., vol. 77, pp. 341–380.
STEJNEGER, LEONHARD
1916. New generic name for a tree-toad from New Guinea. Proc. Biol. Soc. Washington, vol. 29, p. 85.
VAN KAMPEN, P. N.
1923. The amphibians of the Indo-Australian Archipelago. Leiden, E. J. Brill, Ltd., xii + 304 pp.