PAPUAN HYLID FROGS OF THE GENUS HYLA

by

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With 58 figures, 4 plates

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INTRODUCTION

The main objective of the present work is to present a taxonomic revision of the Papuan representatives of the hylid genus Hyla as a basis for further systematic studies. All relevant literature has been searched and available information on the biology, ecology and distribution included.

Deferring publication indefinitely in the hope that additional specimens of poorly represented species will be found is always an inviting and reasonable policy. To await the availability of topotypic specimens of such species as H. albolaris and H. obtusirostris would certainly enable them to be more readily defined and the limits of variation established. However, routine examination of thousands of unidentified specimens in museum
collections has not revealed the existence of any additional representatives of these species, and their re-discovery is not predictable.

The present studies have been undertaken over a period of six years, and the stage has been reached when to publish descriptions of additional new species would have merely complicated the task of identifying material. Ten new species are involved and it is evident that a revision of all Papuan members of the genus is necessary.

History of the Study of Papuan *Hyla*

In the course of reporting a collection of fifty species of reptiles and amphibians from New Guinea that included six new species, Parker (1936) commented, “This extraordinarily high percentage of undescribed forms is indicative of the present state of knowledge of the herpetological fauna of the region, and so meagre is our knowledge of even the described species that in many instances each additional specimen that comes to hand increases rather than diminishes the systematist’s perplexity.”

In the subsequent thirty years no less than thirty-nine new species of Papuan frogs have been described, and the majority of them within the last decade. Moreover, as ten more are described in the present paper and numerous additional species of other genera are known to lie in museum collections awaiting description, it is evident that Parker’s comments apply equally well to the present day knowledge of the Papuan herpetofauna.

Scientific study of the fauna of New Guinea commenced in the late eighteenth and early nineteenth centuries when European naval vessels sailed throughout the Pacific establishing administration and trading posts. Naturalists often accompanied these vessels obtaining specimens at the localities visited. Accompanying a voyage in 1771 Sonnerat (1776) was probably the first author of a scientific work devoted to material personally collected in New Guinea, and was primarily concerned with birds. The New Guinea birds, and particularly the Birds of Paradise, had attracted tremendous interest in Europe since the early sixteenth century when the first skins reached Spain. It is not surprising (to any but an herpetologist) that zoological collections, prior to as recently as 1860, were almost exclusively confined to birds and spectacular mammals and insects. This fact is illustrated by Sclater’s (1858) annotated list of birds enumerating 158 species and Bleeker’s contemporary (1859) list of reptiles and amphibians containing only six species of frogs. Lesson (1830) described the first frog from New Guinea (*Rana papua*) and Cope (1867) described the first hylid (*Hyla dolichopsis* from Amboina).
Establishing the frog fauna of New Guinea started in the period 1870-1885 when Boulenger, Doria, Macleay, Meyer, Muller, Peters and Ramsay received collections from the island and described or reported numerous species including twenty species of hylids. Boulenger (1882) established the systematic position of species formerly referred to Hyla, Hylella, Hyperolius, Litoria, Nyctimantis and Pelodryas, recognising three genera: Hyla, Hylella and Nyctimantis. At the turn of the century Boulenger, Méhély, Van Kampen and Werner were the most active workers; prolific writers, they published a large number of papers of which no less than thirty-five contained references to Papuan hylids and descriptions of new material.

Biological information about the species described was almost non-existent. The Hungarian explorer Lajos Biró may well have been the first to record field observations when he noted about Hyla thesaurensis, “At the end of the dry season they come out for after the first rains and begin to lay their eggs. These are dark brown on one side white on the other side. Their voice is a low creak, so feeble that it is only heard as far as ten stride.” (Méhély, 1898).

Van Kampen’s studies on Papuan frogs culminated in a major revision of the complete anuran fauna of the region published in 1923. He included forty-three species of Hyla but of this number nineteen were known solely from type specimens, most of which had not been examined by him. Nieden (1923) revised the entire genus and recognised forty-two Papuan species.

During the period 1923-1939 only one new species of Hyla was described and the majority of the papers published added little to the knowledge of Papuan Hyla.

The Second World War was indirectly responsible for initiating a new interest in the herpetofauna of New Guinea. Amongst the United States service personnel were several experienced collectors and they obtained numerous specimens of Hyla eventually reported by Loveridge (1945), Neill (1946, 1954), Tanner (1950, 1951a, 1951b). It would be a serious lapse to fail to draw attention to the work of Brongersma and Forcart independently reporting material obtained from other sources, but it was the wartime collections that led Loveridge (1948) to report all ‘New Guinean’ specimens in the Museum of Comparative Zoology and United States National Museum, expanding the paper into a valuable reference work by preparing a bibliography, gazetteer and checklists of all Papuan amphibians and reptiles. Loveridge listed only thirty-three species of Hyla, but the list did

1) In fairness to Méhély it must be pointed out that he may not have been responsible for the English translation of the text!
not include three species not occurring on the mainland, and many of the species appearing on Van Kampen's (1923) list were relegated to synonymy or altered to subspecific rank. Sixteen of the nineteen species known to Van Kampen from types or their descriptions had not been reported in the intervening period and, as less than half of the species on Loveridge's list had been examined by him, the status of the majority of forms remained uncertain.

In recent publications the status of many species has been resolved. Nine species have been removed from Hyla and four new species described (Zweifel, 1958, Tyler, 1962 et seq.). Of the species included in Hyla (as valid species or synonomys) by Van Kampen (1923) the following were referred to other genera:

- *Hyla brachypus* (Werner) = *Oreophryne brachypus* (Werner)
- *Hyla humeralis* Boulenger = *Nyctimystes humeralis* (Boulenger)
- *Hyla montana* Peters & Doria = *Nyctimystes montana* (Peters & Doria)
- *Hyla obsoleta* Lönnerg = *Nyctimystes obsoleta* (Lönnerg)
- *Hyla pulchra* Wandolleck = *Nyctimystes pulchra* (Wandolleck)
- *Hyla rueppeli* Boettger = *Nyctimystes rueppeli* (Boettger)
- *Hyla wolterstorffi* (Werner) = *Oreophryne wolterstorffi* (Werner)

Papuan *Hyla* appeared in a list of “Asian” species assembled by Gorham (1963) but none of the systematic changes proposed in the publications of Zweifel and Tyler were implemented for it was based on literature published prior to 1958.

The Papuan Frog Fauna

The Papuan frog fauna is composed of three distinct elements: a large group of endemic species occupying the New Guinea mainland and the northern and southern boundaries of the sub-region, a small group of Australian species predominant in southern New Guinea and an Oriental element which meets the Papuan in a broad zone of intergradation on the western boundary.

The land communication that existed between New Guinea and Australia until as recently as the Pleistocene permitted the interchange of a few species. On the basis of their relative predominance on one or other of the land masses it has been assumed that some of those occurring in New Guinea are of Australian origin and vice versa.

Six families of frogs are represented in the Papuan sub-region:

1. Bufonidae. — Numerous species occur throughout the Oriental Region and a few at the Papuan-Oriental boundary. There are no endemic
species on the New Guinea mainland but *Bufo marinus* was introduced into New Guinea (and Australia) before the Second World War, and is now well established at Lae, Bulolo, Popondetta, Port Moresby, Rabaul and at several localities in the Admiralty and Solomon Islands and New Ireland.

(2) Leptodactylidae. — This is the predominant family in Australia, but only three genera and six species are known to occur in New Guinea. Three of these (*Limnodynastes convexiusculus*, *Crinia signifera* and *Lechriodus fletcheri*) are probably confined to southern New Guinea, but are more widely distributed in Australia. The Papuan Leptodactylids are included in a revision of the Australasian representatives of the family by Parker (1940).

(3) Microhylidae. — This family is widely distributed throughout the Oriental region and is predominant on New Guinea. It extends as far east as New Britain and also occurs in north-eastern Australia. Parker (1934) recognised two Papuan sub-families composed of nine genera and sixty species. Zweifel (1956) lists eight genera and fifty-six species occurring on the New Guinea mainland and the D'Entrecasteaux Islands. At the present time approximately seventy Papuan species are recognised and many more are known to await description.

(4) Ranidae. — A revision of the Papuan Ranids is long overdue, and the status of many species is uncertain. *Rana*, the subject of a monograph by Boulenger (1920), is the most widespread genus, reaching the Solomon Islands and northern Australia. Loveridge (1948) listed three Ranid genera and twelve species in New Guinea. Brown (1952) reported seven genera and fourteen species from the Solomon Islands; of these three genera (*Batrachylodes*, *Ceratobatrachus* and *Palmatorappia*) and ten species were confined to the Solomon Islands. Brown (1965) in describing three new species of *Cornufer* from the Solomon Islands has increased the number of endemic species to thirteen.

(5) Rhacophoridae. — The Rhacophoridae are abundant in the Oriental region and have been recorded from islands on the western boundary of the Papuan sub-region. Their presence on New Guinea is known from two specimens collected at Lake Sentani near Hollandia (Sokarnopura). Described as *Hyla wirsi* by Roux (1927) it was referred to *Rhacophorus* by Forcart (1946) and may prove to be a synonym of the widely distributed *R. leucomystax*.

(6) Hylidae. — The Papuan Hylidae comprise two genera: *Hyla* which occupies the entire sub-region and extends westwards to Timor and the Talaud Islands within the Oriental region, and *Nyctimystes* which is distributed from Halmahera, throughout New Guinea to northern Australia.
Nyctimystes was revised by Zweifel (1958) who recognised fourteen Papuan species. Several additional species have since been described from or referred to the genus *Hyla* and the current total is twenty. Of the forty-four species of *Hyla* recognised in the present paper, allopatric populations of six occur in Australia. *Hyla everetti* is confined to Timor and nearby islands, *Hyla lutea* is confined to the Solomon Islands, and *H. capitula* to the Tenimber Islands. The remaining species have all been recorded on the New Guinea mainland.

**MATERIALS, METHODS AND TERMINOLOGY**

In the course of the present studies 5536 specimens have been examined. Of this total approximately 2500 were examined within two months of their collection whilst the remainder had been in preservative for up to one hundred years, and included representatives of most available type series. A total of 2375 tadpoles have also been examined.

The material is lodged in museum and university collections abbreviated in the following list. Letters in parentheses refer to departmental registration catalogues and precede the registration numbers of specimens cited in the text.

- A.N.U. Department of Zoology, Australian National University, Canberra.
- B.M. British Museum (Natural History), London.
- B.P.B.M. Bernice P. Bishop Museum, Honolulu.
- M.C.S.N. (CE.) Museo Civico di Storia Naturale, Genoa.
- M.M. Macleay Museum, University of Sydney, Sydney.
- M.Z.B. Museum Zoologicum Bogoriense, Bogor.
- N.M.B. Naturhistorisches Museum, Basle.
- N.M.M. National Museum of Victoria, Melbourne.
- N.M.V. Naturhistorisches Museum, Vienna.
- N.R. Naturhistoriska Riksmuseet, Stockholm.
- S.M.F. Senckenberg Museum, Frankfurt.
- U.M.Z. Museum of Zoology, University of Michigan, Ann Arbor.
- U.U. University of Uppsala, Uppsala.
Amongst the materials are the hitherto unreported collections of *Hyla* obtained by several major expeditions to New Guinea: The Third, Fourth, Fifth and Sixth Archbold Expeditions of 1938-39, 1953, 1956 and 1959 respectively (lodged in A.M.N.H.), Netherlands Star Mountains Expedition of 1959 (R.M.N.H. and S.A.M.) and the Australian Star Mountains Expedition of 1965 (S.A.M.). Specimens from Ambunti and Brugnowi, Sepik River, New Guinea were obtained by the Department of Microbiology, Australian National University during investigations into the epidemiology of arboviruses (supported in part by grants from the World Health Organisation).

Measurements of most specimens were estimated with a pair of Helios dial callipers and recorded to the nearest 0.1 mm. In the case of small species an eye-piece micrometer was employed. Definitions of the characters recorded are as follows:

- **Head length (HL).** — Distance between the tip of the snout and the posterior margin of the tympanum, including the tympanic annulus.
- **Head width (HW).** — The greatest width of the head, usually recorded at a level with the tympana.
- **Eye to naris distance (E-N).** — The distance between the anterior margin of the eye and the posterior margin of the naris.
- **Internarial span (IN).** — The minimum distance separating the nares.
- **Eye diameter.** — The distance between the anterior and posterior corners. The eye is probably liable to greater distortion than any other structure. It was therefore only measured when there was no evidence of damage or displacement within the orbit.
- **Tympanum diameter.** — In the vast majority of specimens the tympanum is circular and the horizontal diameter, measured to the outer margins of the tympanic annulus, was recorded. The tympanum was not measured when it was found to be obliquely oval.
- **Snout to vent length (S-V).** — The distance between the anterior tip of the snout and the superior margin of the cloacal aperture.
- **Tibia length (TL).** — The length of the tibia measured from the convex surface of the knee to the tibio-tarsal joint, with the knee held in the flexed position.

In the early stages of these studies it was observed that there were definite ontogenetic trends in certain characters. For example, juveniles tend to have relatively longer hind limbs and consequently higher TL/S-V ratios than
adults. Similarly, there are different rates of growth of the eye and tympanum. The definitions and descriptions in the systematic section of the paper are therefore based on adult specimens. The term adult has been applied in males to specimens exhibiting nuptial pads or, if these are absent, to specimens which are equal to or greater than the minimum size at which nuptial pads were observed in the same species. Females were considered adult when the oviducts were found to be greatly convoluted.

Intraspecific variation of external characters of adult specimens may be minimal (e.g. *Hyla infrafrenata* and *H. graminea*) or extensive (e.g. *H. angiana* and *H. arfakiana*). As the majority of species can be placed in the latter category it was considered preferable to present a generalised description based on all specimens examined, than to describe a single specimen and then report the ways in which the remainder diverged from it. Divergence from the characters of the types and topotypes and any geographical trends are discussed separately. A generalised description obviously cannot be applied to the description of new species, but the same format has been adopted.

Studies of the skeletal anatomy and musculature of Papuan *Hyla* have not reached the stage where it is possible to place all of the species in species groups. In certain instances the external characters are such that it is evident that close relationships exist between several species, but a large proportion consists of isolated forms of unknown affinities. For this reason keys have not been based on the customary species groups in the systematic section, and a discussion of species groups has been included later in the paper.

In view of the number of species involved a single key has been rejected in favour of three keys which separate them according to their vertical distribution. The existence of distinct montane and lowland faunae is discussed elsewhere. These are treated as separate units in the keys and there is an additional key for the altitudes at which they may overlap.

To date the tadpoles of only a few species have been identified and described and most of these are reproduced in the present paper. A standard format has been adopted for those described for the first time utilising the simplified staging tables of Gosner (1960). The only means of distinguishing *Nyctimystes* tadpoles from *Hyla* remains the difference in pupil shape and the presence or absence of pigmentation on the palpebrum. Therefore even the generic identity of isolated hylid tadpoles earlier than approximately stage 25 is at present indeterminable.

The synonymies and literature references cited under the adopted name
of each species are those based completely or at least partly on Papuan material. In those instances where allopatric populations occur in Australia, the synonyms and literature reporting the Australian populations have been synthesised by Copland (1957) and Moore (1961).

Geographical Nomenclature

There is unfortunately no uniformity in the uses of “New Guinea”, “Papua” and “Papuan” in the literature. “New Guinea” has been used to refer to the entire mainland, the entire mainland plus the Solomon Islands and the islands of the Bismarck Archipelago, or simply the mainland portion of the Australian Trusteeship Territory. Similarly “Papua” may refer to the Australian Territory of Papua alone or embrace both territories. The applications of “Papuan” are even more confusing: an indigene or an indigenous object in either of the preceding categories, or to the zoogeographical sub-region of which the mainland is only the major part. In the following pages “New Guinea” refers to the entire mainland, unless specifically qualified to indicate a distinct portion, and “Papuan” to the entire zoogeographical sub-region (fig. 1).

The boundary of the Papuan sub-region recognised here differs from that utilised by Gressitt (1956) in excluding the Cape York Peninsula of Queensland. Gressitt divided the Pacific into faunal regions, sub-regions, divisions and sub-divisions but did not divide or sub-divide the Papuan sub-region. The present study necessitates this step and it is essential to employ a nomenclature which does not permit ambiguity. (Use of the term “sub-division” is here purely a convenience and does not indicate similar zoogeographical status to the areas called sub-divisions by Gressitt).

Subdivisions involving distinctive geographical, climatological, floristic or faunistic boundaries are ideal. Some of the Papuan island groups (e.g. Solomon Islands and the Bismarck Archipelago) are already geographically defined and have long established names, but subdividing the mainland of New Guinea and finding acceptable names for the subdivisions presents a major problem.

The political boundary dividing New Guinea into eastern and western portions has not been employed as a point of reference in the present study. Instead the peninsulas have been treated as separate units and the remainder of the island divided up into predominantly lowland and predominantly highland areas. This has been adopted because the present data indicate that the range of vertical distribution of each species of Hyla rarely exceeds 3500 ft, and that the highland and lowland faunae are quite distinct from one another.
Fig. 1. The Papuan sub-region.
Ideally it would be necessary to delimit the lowland group at 3500 ft throughout the entire island, but on the peninsulas the coastal lowland strip is often so narrow that this is impractical on the scales required for reproduction in this publication.

The sub-divisions and their boundaries are recorded in fig. 1. Of the names applied to them, only the Huon and Vogelkop Peninsulas and Snow Mountains are current. Although the system adopted here has proved satisfactory for these studies it may be unacceptable to other contributors. Establishment of a standard method of sub-division and names for the respective parts will probably only be resolved by the collaboration of many investigators from different scientific fields. A symposium on such a topic would be of great benefit to the study of Papuan zoology.

All territorial names and the majority of the Papuan locality names have been changed at least once during the past century. Numerous names cited in the zoological literature are therefore no longer in use and do not appear on modern maps or in gazeteers.

Synonyms of the current territorial names are as follows:

<table>
<thead>
<tr>
<th>Former Name</th>
<th>Current Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>British New Guinea</td>
<td>Australian Territory of Papua</td>
</tr>
<tr>
<td>German New Guinea</td>
<td>Australian Trusteeship Territory of New Guinea,</td>
</tr>
<tr>
<td>Kaiser Wilhelmsland</td>
<td>Australian Trusteeship Territory of New Guinea,</td>
</tr>
<tr>
<td>Netherlands New Guinea</td>
<td>West Irian</td>
</tr>
</tbody>
</table>

In current Indonesian literature (e.g. in Somadikarta et al., 1964) the entire island of New Guinea is termed “Irian”.

For the area which was formerly Netherlands New Guinea the locality names utilised during the period of Netherlands administration have been retained in the present paper. That they have been used in preference to the current Indonesian names is due to consideration of two factors: (a) these are the names appearing in the literature cited; (b) the instability of the new Indonesian names.

The latitude and longitude references of the localities included in the following list have been compiled from several publications, the major sources being those of the United States Board on Geographic Names (Gazetteer No. 13, Indonesia, Netherlands New Guinea and Portuguese Timor; Gazetteer No. 29, Southwest Pacific). References to localities visited by early explorers were found in major works by Brigham (1900) and Wichmann (1912). In those instances where a locality name has alternative
spellings, that appearing in the United States Board on Geographic Names publications has been adopted for West Irian, and the Village Directory (1960 edition) compiled by the Department of Native Affairs (now the Department of District Administration), Territory of Papua and New Guinea for that region. The latitude and longitude of localities cited in the text but not appearing in the gazetteer are unknown.

<table>
<thead>
<tr>
<th>Locality Names</th>
<th>Lat. S.</th>
<th>Long. E.</th>
<th>Lat. S.</th>
<th>Long. E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aitape</td>
<td>3° 10'</td>
<td>142° 25'</td>
<td>Enarotali</td>
<td>3° 54'</td>
</tr>
<tr>
<td>Aitinjoe</td>
<td>1° 25'</td>
<td>132° 06'</td>
<td>Epo</td>
<td>9° 00'</td>
</tr>
<tr>
<td>Aiyura</td>
<td>6° 10'</td>
<td>145° 54'</td>
<td>Erokwer</td>
<td>1° 36'</td>
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<tr>
<td>Ajamaroe</td>
<td>1° 15'</td>
<td>132° 11'</td>
<td>Fakfak</td>
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</tr>
<tr>
<td>Alkmaar Bivak</td>
<td>4° 40'</td>
<td>138° 43'</td>
<td>Faro I.</td>
<td>6° 55'</td>
</tr>
<tr>
<td>Amboina</td>
<td>3° 40'</td>
<td>128° 10'</td>
<td>Ferguson I.</td>
<td>9° 30'</td>
</tr>
<tr>
<td>Ambon = Amboina</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>Ambunti</td>
<td>4° 14'</td>
<td>142° 50'</td>
<td>Finschaven</td>
<td>6° 30'</td>
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<td>Audai</td>
<td>0° 56'</td>
<td>134° 21'</td>
<td>Gariau</td>
<td>3° 44'</td>
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<td>Angabunga R.</td>
<td>8° 00'</td>
<td>133° 55'</td>
<td>Gebe</td>
<td>6° 05'</td>
</tr>
<tr>
<td>Angi Lakes</td>
<td>1° 25'</td>
<td>133° 55'</td>
<td>Geelvink Bay</td>
<td>2° 35'</td>
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<td>Ansus</td>
<td>1° 44'</td>
<td>135° 49'</td>
<td>Geelvink Bay</td>
<td>2° 35'</td>
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<tr>
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<td>Geelvink Bay</td>
<td>2° 35'</td>
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<td>143° 21'</td>
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<td>Arfak Mts.</td>
<td>1° 09'</td>
<td>133° 58'</td>
<td>Goodenough I.</td>
<td>9° 20'</td>
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<td>Aroa R.</td>
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<td>146° 55'</td>
<td>Goreda</td>
<td>3° 37'</td>
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<td>145° 50'</td>
<td>Goroka</td>
<td>6° 05'</td>
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<tr>
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<td>133° 25'</td>
<td>Guadalcanal</td>
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<td>144° 03'</td>
<td>Gumine</td>
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<td>Banz</td>
<td>5° 47'</td>
<td>144° 37'</td>
<td>Halmahera</td>
<td>1° 06'</td>
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<td>Barabuna</td>
<td>6° 25'</td>
<td>145° 57'</td>
<td>Hatam</td>
<td>1° 06'</td>
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<td>146° 14'</td>
<td>Hellwig Mts.</td>
<td>4° 30'</td>
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<td>Bena Bena</td>
<td>6° 05'</td>
<td>145° 30'</td>
<td>Herbertshohe = Kokopo</td>
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<td>Bernhard Camp</td>
<td>3° 30'</td>
<td>139° 12'</td>
<td>Hollandia</td>
<td>2° 32'</td>
</tr>
<tr>
<td>Betabib</td>
<td>4° 50'</td>
<td>140° 35'</td>
<td>Iamele</td>
<td>9° 28'</td>
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<tr>
<td>Biik I.</td>
<td>1° 00'</td>
<td>136° 06'</td>
<td>Ibaeso</td>
<td>2° 32'</td>
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<td>Bivak I.</td>
<td>5° 01'</td>
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<td>Jamoer L.</td>
<td>3° 35'</td>
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<td>Bougainville</td>
<td>6° 00'</td>
<td>155° 06'</td>
<td>Japen I.</td>
<td>1° 45'</td>
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<td>Bulolo</td>
<td>7° 12'</td>
<td>146° 39'</td>
<td>Joe Landing</td>
<td>11° 25'</td>
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<td>Buru</td>
<td>3° 24'</td>
<td>126° 40'</td>
<td>Kaileuma I.</td>
<td>8° 30'</td>
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<tr>
<td>Busilmin</td>
<td>4° 55'</td>
<td>141° 06'</td>
<td>Kainantu</td>
<td>6° 15'</td>
</tr>
<tr>
<td>Cape Vogel</td>
<td>9° 40'</td>
<td>150° 05'</td>
<td>Kaindi</td>
<td>8° 13'</td>
</tr>
<tr>
<td>Ceram</td>
<td>3° 00'</td>
<td>129° 00'</td>
<td>Kamboeja</td>
<td>1° 15'</td>
</tr>
<tr>
<td>Djamplong</td>
<td>10° 05'</td>
<td>123° 57'</td>
<td>Katak = Katow</td>
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<td>Kiet</td>
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<td>148° 20'</td>
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<td>146° 05'</td>
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<td>Kulumadau</td>
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<td>152° 45'</td>
<td>Noord R. = Lorentz R.</td>
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<td>Norcikova</td>
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<td>126° 01'</td>
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<td>Sepik R.</td>
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<td>Soe</td>
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<td>Mt. Rossell</td>
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<td>Mt. Wilhelm</td>
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<td>Tari</td>
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<tr>
<td>Mysol = Misol</td>
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<td>Tehak</td>
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<td>Tigi L.</td>
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1) Several specimens in the South Australian Museum collection were reputedly collected at "Mt. Parrington" by C. T. McNamara. This is believed to be a lapsus for Mt. Lamington q.v.
A brief generic diagnosis presented by Goin (1961) is as follows:

"Without teeth on mandible, palatine or parasphenoid; vocal pouch in male, if present, median and subgular; pupil horizontal; sacral diapophysis well expanded in all except some of the large forms; cranial derm not fused with skull except in a few West Indian species; neither eggs nor young carried on back of female; tympanum present and usually fairly distinct, tongue fairly well fused behind; a well-developed quadratojugal; no backward projecting process on ischium; no well-developed ventrolateral gland along each side."

As the diagnosis indicates, species are placed in *Hyla* rather through their lack of the specialised skeletal structures and/or breeding behaviour characterising most other hylid genera than by possession of unique characters or habits. Over two hundred species are currently recognised and their habitus is so varied, particularly in the Australian region, that even the homogeneity of the group may be regarded as suspect.

Interspecific variation in the Papuan members of the genus is extremely marked, and in certain respects diverges from the generic diagnosis.

**Size.** — The observed variation in size of sexually mature specimens of each species is depicted in figure 2, and the complete range of snout to vent lengths is from 20.5 mm (*H. dorsalis*) to 135 mm (*H. infrafrenata*).

**Habitus.** — Papuan *Hyla* vary from squat, short-legged species with relatively small heads, to extremely elongated species with long, narrow heads and exceptionally long hind limbs (in *H. nasuta* the length of the tibia may be equivalent to as much as 83% of the snout to vent length).

**Colour.** — The majority of species are cryptically marked and green, brown and grey are the predominant colours but virtually the entire spectrum is represented. Large bilobed or trilobed dorsal markings are common to approximately 25% of the species, whilst a similar percentage are completely immaculate. Mid-vertebral stripes are uncommon. Most lowland species are

<table>
<thead>
<tr>
<th>Lat. S.</th>
<th>Long E.</th>
<th>Lat. S.</th>
<th>Long E.</th>
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<td>Wau</td>
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<td>Uinba</td>
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<td>144° 36'</td>
<td>Wendessi</td>
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<td>Utakwa R. = Setikwa R.</td>
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<td>Wissel I.</td>
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<td>Wahai</td>
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<td>120° 30'</td>
<td>Woodlark I.</td>
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<td>Waidjewa</td>
<td>9° 30'</td>
<td>119° 20'</td>
<td>Yaramanda</td>
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<td>Waigeo</td>
<td>0° 14'</td>
<td>130° 45'</td>
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<td>Waikaiuna</td>
<td>10° 03'</td>
<td>150° 55'</td>
<td></td>
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</tbody>
</table>
Fig. 2. Size range of adult *Hyla*. Open bars males, solid bars females.
unpigmented ventrally whereas highland species are frequently heavily pigmented.

Inter-digital webbing and terminal discs. — Fully webbed hands (where the inter-digital webbing extends to the base of the discs of the third and fourth fingers) is exhibited by six arboreal species, and is usually associated with extremely dilated terminal discs. The complete absence of webbing between the fingers is associated with reduced development of terminal discs in species which are predominantly terrestrial and only occasionally scansorial (e.g. *H. nasuta*). Species frequently found in or near streams in highland areas lack or possess only vestigeal webbing between the fingers, but the terminal discs are often particularly well-developed in the larger species in this category (e.g. *H. arfakiana* and *H. micromembrana*).

Dermal appendages. — Prominent dermal bars or crenated lappets are exhibited by several Papuan species. Dorsal and lateral tubercles are common to several more and are particularly well-developed in *H. arfakiana* and *H. spinifera*. Similar structures are rare amongst Australian species.

Vomerine teeth. — The extent of development of vomerine teeth is apparently related to the adult size of the species involved, and presumably is associated with the range of food items ingested and the feeding mechanism. In the majority of species adult at less than approximately 30 mm the vomerine teeth are poorly developed and scarcely discernable (e.g. *H. brongersmai*) or even completely absent (e.g. *H. louisiadensis*).

Tongue. — The tongue is usually cordiform with a distinctive posterior indentation. There is frequently a posteriorly projecting process at the mandibular symphysis in large species causing a small anterior indentation on the tongue.

Tympanum. — The tympanum is frequently covered with skin and in several species is completely invisible externally.

Pupil shape. — In preserved material the pupil is more frequently dilated than constricted. When constricted it takes the form of a horizontal slit in most species. In preserved *H. amboinensis* the pupil is horizontal, rhomboidal or vertical, and is vertical or 'lozenge' shaped in life (Brongersma, 1953). In *H. caerulea* there are small, median, superior and inferior protrusions from a horizontal slit (Mann, 1931).

Secondary sexual characteristics. — Pigmented nuptial pads located on the outer surface of the thumbs have been found in adult males of each species examined, and there is considerable variation in their shape (see figure 3). Intraspecific variation is usually minimal, but in *H. infrafrenata* they are either in a single oval group or may be divided to form two separated and roughly circular groups.
Vocal sacs are present in all species and are median and subgular.

Fig. 3. Nuptial pads. a, *Hyla infrasrenata* Gunther; b, *Hyla thesaurensis* Peters; c, *Hyla graminea* Boulenger; d, *Hyla arfakiana* Peters & Doria; e, *Hyla spinifera* new species.
In the opinion of Copland (1962) the customary belief that *Hyla* should be regarded a feminine noun is erroneous. He maintained that as *Hyla* is derived from the masculine "hylas" it follows that *Hyla* is also masculine. Accordingly, Copland (1962, 1963) altered the terminations of numerous Australian species from the accepted feminine form to the masculine (e.g. *aurea* to *aureus; phyllochroa* to *phyllochrous*).

This interpretation is at variance with current universal practice and contrary to the 1961 International Code of Zoological Nomenclature: Article 30 (a) (i) (iii) states, "if a genus-group name is a Greek word latinized with a change of termination, it takes the gender appropriate to that termination."

The feminine gender has therefore been retained by the present writer.

Checklist of Papuan *Hyla*

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<tr>
<td><em>Hyla amboinensis</em></td>
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<tr>
<td><em>Hyla angiana</em></td>
<td>33</td>
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<tr>
<td><em>Hyla arfakiana</em> Peters &amp; Doria</td>
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<td><em>Hyla arvensis</em> Horst</td>
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<td><em>Hyla becki</em> Loveridge</td>
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<tr>
<td><em>Hyla bicolor</em> (Gray)</td>
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<tr>
<td><em>Hyla brongersmai</em> Loveridge</td>
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<tr>
<td><em>Hyla bulmeri</em> new species</td>
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<tr>
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<td><em>Hyla gemimaculata</em> Horst</td>
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<td><em>Hyla gracilentia</em> Peters</td>
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<tr>
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Summary of Taxonomic Changes

Species relegated to synonymy
Hyla angularis Loveridge = Hyla angiana Boulenger
Hyla loveridgei (Neill) = Hyla genimaculata Horst
Hyla mintima Tyler = Hyla angiana Boulenger
Hyla papuensis Werner = Hyla amboinensis Horst
Hyla trimiensis Ahl = Hyla infrarenata infrarenata Gunther
Hyla wollastoni Boulenger = Hyla arfakiana Peters & Doria

Species resurrected from synonymy
Hyla mystax Van Kampen

Changed synonymy
Hyla macgregori Ogilby is removed from the synonymy of H. thesaurensis Peters and transferred to the synonymy of H. congenita Peters & Doria.

Subspecies restored to specific status
Hyla dorsalis dorsalis (Macleay) = Hyla dorsalis (Macleay)

Key to Lowland Hyla (species occurring at 0-3,500 ft above sea level)

1. TL/S-V equal to or greater than 0.650 ........................................ nasuta, ................................................................. p. 148
TL/S-V less than 0.650 ......................................................... 2

2. Fingers fully or almost fully webbed ...................................... 3
Fingers no more than one-half webbed ........................................................... 5

3. Dorsum brown or grey ...................................................... amboinensis, ................................................................. p. 27
Dorsum uniform green in life and blue in alcohol ............................... 4

4. Prominent dermal folds on posterior surfaces of forearm and tibia; minimum adult body length 60 mm .................................................. graminea, ................................................................. p. 100
No dermal folds on posterior surfaces of forearm and tibia; maximum adult body length 45 mm ................................................................. aruensis, ................................................................. p. 43

5. Large irregular areas of pigment on abdomen .......................... albolabris, ................................................................. p. 24
Abdomen immaculate or pigmentation restricted to stippling ............ 6

6. E-N/IN less than 0.625 .......................................................... 7
E-N/IN greater than 0.625 ......................................................... 8

7. Conical heel tubercle present .............................................. arfakiana, ................................................................. p. 39
Conical heel tubercle absent .......................................................... 9

8. Vomerine teeth absent; tympanum invisible .................................... longicrus, ................................................................. p. 122
Vomerine teeth present; tympanum completely or partially visible ........... lousiadensis, ................................................................. p. 124

9. White stripe on lower lip extending posteriorly to tympanic region ................................. infrarenata, ................................................................. p. 103
Labial stripe absent or, if present, not confined to lower lip but extending superiorly to eye .................................
10. A row of small, triangular dermal appendages on posterior surface of forearm  .  
   No triangular dermal appendages on posterior surface of forearm  .  
   geminimaculata, p. 94  
11. Pale, lichen-like patches on dorsum  .  
   No pale, lichen-like patches on dorsum  .  
   napaea, p. 145  
12. Dorsum immaculate  .  
   Dorsum with lighter and/or darker markings  .  
   p. 94  
13. Fingers unwebbed  .  
   Fingers with at least basal webbing  .  
   vagabunda, p. 177  
14. Eye to naris distance less than internarial span  .  
   Eye to naris distance greater than internarial span  .  
   mystax, p. 142  
15. Fingers with broad lateral fringes  .  
   Lateral fringes narrow or absent  .  
   p. 16  
16. E-N/IN less than 1.050  .  
   E-N/IN greater than 1.050  .  
   caerulea, p. 60  
17. Maximum adult size less than 35 mm  .  
   Minimum adult size greater than 35 mm  .  
   bicolor, p. 50  
18. Bones of living and formalin preserved specimens pigmented; colour of dorsum not blue  .  
   Bones unpigmented; colour of dorsum blue  .  
   thesaurensis, p. 171  
19. Fingers unwebbed  .  
   Fingers with at least basal webbing  .  
   p. 20  
20. Maximum adult size less than 25 mm  .  
   Minimum adult size greater than 25 mm  .  
   dorsalis, p. 80  
   Back of thighs, if yellow, without black scriptiform markings  .  
   everetti, p. 90  
22. Dorsum predominantly blue in preservative (green in life)  .  
   Dorsum predominantly a colour other than blue  .  
   p. 23  
23. HL/HW greater than 1.200; fingers without broad lateral fringes  .  
   HL/HW less than 1.200; fingers with broad lateral fringes  .  
   migropunctata, p. 151  
24. Large, clearly defined white patches on entire dorsum  .  
   White absent or, if present as patches, confined to posterior third or in form of longitudinal stripes  .  
   p. 25  
25. Bones green in life and in formalin  .  
   Bones unpigmented  .  
   p. 26  
26. Fingers with broad lateral fringes  .  
   Fingers without broad lateral fringes  .  
   thesaurensis, p. 171  
27. E-N/IN less than 1.300  .  
   E-N/IN greater than 1.300  .  
   capitula, p. 64  
28. TL/S-V greater than 0.550  .  
   TL/S-V less than 0.550  .  
   napaea, p. 145  

Key to Submontane Hyla (species occurring at 3,000-5,000 ft above sea level)  

1. Fingers fully or almost fully webbed  .  
   Fingers no more than one-half webbed  .  
   eucnemis, p. 86  
2. Prominent dermal lappets on posterior surfaces of forearm and tibia  .  
   Dermal appendages on limbs in form of continuous ridge or completely absent  .  
   3  
3. Ground colouration of dorsum brown or grey  .  
   Ground colouration of dorsum blue (green in life)  .  
   5
4. Conspicuous black and yellow or black and orange markings on back of thighs
   No conspicuous markings on thighs
5. Large deep blue or violet spots on ventral surface of body
   No blue or violet spots on ventral surface of body
6. Fingers unwebbed or with only a trace of basal webbing
   Fingers at least one-third webbed
7. Canthus rostralis strongly curved
   Canthus rostralis slightly curved or straight
8. Row of conical tubercles on tarsus
   No conical tubercles on tarsus
9. E-N/IN less than 1.000
   E-N/IN greater than 1.000
10. Large sub-anal and heel tubercles present
    Neither sub-anal nor heel tubercles present
11. TL/S-V less than 0.610
    TL/S-V greater than 0.610
12. E-N/IN less than 1.300
    E-N/IN greater than 1.300
13. Dorsal surface immaculate blue (green in life)
    Dorsal surface not an immaculate blue
14. S-V less than 35 mm
    S-V greater than 35 mm
15. Head broader than long
    Head longer than broad
16. E-N less than IN
    E-N greater than IN
17. Occurring on New Guinea mainland
    Not occurring on New Guinea mainland
18. Back of thighs bearing scriptiform markings; bones unpigmented
    Back of thighs lack scriptiform markings; bones pigmented
19. Fingers with broad lateral fringes
    Fingers without broad lateral fringes
20. Back of thighs variegated with black and yellow or brown and yellow
    Back of thighs not variegated.
21. E-N/IN greater than 1.250
    E-N/IN less than 1.250
22. Males greater than 40 mm; females greater than 55 mm
    Males less than 40 mm; females less than 55 mm
23. Dorsal surface blue with darker and occasionally lighter markings
    Dorsal surface predominantly a colour other than blue
24. Maximum adult size less than 30 mm
    Minimum adult size greater than 30 mm

Key to Montane Hyla (species occurring at over 5,000 ft above sea level)

1. Fingers fully or almost fully webbed
   Fingers no more than one-half webbed
2. Dorsal surface predominantly blue
   Dorsal surface predominantly grey or brown
3. E-N/IN greater than 1.300
   E-N/IN less than 1.300
4. E-N/IN greater than 1.000 ........................................ 5
e-N/in less than 1.000 ........................................ 8
5. HL/HW less than 0.370 ........................................ 6
   HL/hw greater than 0.370 ........................................ 7
6. Dorsal surface immaculate blue ........................................ 7
dorsal surface not an immaculate blue ........................................ 7
7. TL/S-V less than 0.485 ........................................ 7
   TL/s-v greater than 0.485 ........................................ 7
8. Large conical tubercles on heel ........................................ 9
   No large tubercles on heel ........................................ 10
9. Canthus rostralis straight ........................................ 10
   Canthus rostralis strongly curved ........................................ 10
10. Minimum size 40 mm (males); 55 mm (females)................. 10
    males less than 40 mm; females less than 55 mm ......................... 11
11. Dorsal and dorso-lateral surfaces immaculate blue .............. 11
    Dorsal and dorso-lateral surfaces not immaculate blue .............. 12
12. TL/S-V less than 0.500 ........................................ 12
    TL/S-V greater than 0.500 ........................................ 13
13. E-N/IN greater than 0.750; TL/S-V less than 0.580 .............. 13
    E-N/IN less than 0.750; TL/S-V greater than 0.580 .............. 13
14. Back of thighs variegated with black and yellow .............. 14
    Back of thighs not variegated with black and yellow .............. 15
15. Fingers unwebbed or with only a minute vestige of basal webbing ...... 15
    Distinct webbing between the fingers ........................................ 20
16. Canthus rostralis very strongly curved ........................................ 20
    Canthus rostralis slightly curved or straight .............. 20
17. Black cantho-rostral stripe present ........................................ 20
    No black cantho-rostral stripe present .............................. 20
18. Eye diameter greater than internarial span .............................. 18
    Eye diameter less than internarial span .............................. 19
19. E-N/IN less than 0.600; males larger than 33 mm ....................... 19
    E-N/IN greater than 0.600; males smaller than 33 mm ............... 19
20. Dorsal surface blue marked with black and occasionally pale orange ....... 20
    Dorsal surface brown or grey with darker or lighter (but not orange) markings ....... 21
21. Fingers one-half webbed; dorsum with or without pale veins ............ 21
    Fingers less than one-half webbed; dorsum without pale veins ............ 22
22. E-N/IN greater than 0.830 ........................................ 22
    E-N/IN less than 0.830 ........................................ 22

ACCOUNT OF SPECIES

**Hyla albolabris** Wandolleck


_Hyla montana_ Nieden, 1923 : 215 (part).

Syntypes. — As reported by Tyler (1965), only two of the original series of 'many specimens' reported by Wandolleck are now extant: N.M.V. 16976,
S.A.M. R.4947, collected at Aitape, Northern Lowlands, New Guinea by O. Schlaginhaufen.

Definition. — A small coastal species (male snout to vent length approximately 20.0-22.0 mm), characterised by scant webbing between the fingers, broadly spaced nares and extensive brown markings on the ventral surface of the body and limbs. In preservative the dorsal surface is dark blue sparsely marked with pale blue.

Material examined. — Both syntypes.

Description of syntypes. — Both syntypes are extremely dehydrated, distorted and brittle. The limbs of one specimen (S.A.M. R.4947) are detached from the body and portions of several digits are missing. There is a slight dorsal curvature of each specimen and accurate measurements cannot be obtained. The description is therefore inevitably a generalised one.

The head is not flattened and is longer than broad; its length equivalent to approximately one-third of the snout to vent length. The snout is not prominent; rounded when viewed from above and in profile. The nostrils are more lateral than superior, their distance from the end of the snout approximately equal to the distance from the eye. The distance between the eye and the naris is very much greater than the internarial span. The canthus rostralis is moderately defined and slightly curved. The eye is large and prominent, its diameter greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to approximately two-fifths of the diameter of the eye. The vomerine teeth are in two small, round series situated directly between the small rounded choanae. The tongue is small and cordiform with a slightly indented posterior margin.

The fingers are long and slender and appear to lack lateral fringes. The webbing on the fourth finger reaches to a point slightly below the sub-articular tubercle at the base of the penultimate phalanx. In decreasing order of length probably $3 > 4 > 2 > 1$. The terminal discs are prominent.

The hind limbs are long and slender with a TL/S-V > 0.500 and ± 0.550. Toes in decreasing order of length probably $4 > 5 > 3 > 2 > 1$. On the fourth toe the webbing reaches the sub-articular tubercle at the base of the penultimate phalanx. The remaining toes are webbed to points just below the terminal discs. There is a small oval inner but no outer metatarsal tubercle.

The skin on the dorsal surface of the body and limbs is smooth with the exception of a tubercular area on the posterior halves of the upper eyelids. There is a moderately pronounced supra-tympanic fold extending from the
posterior corner of the eye to a point above the insertion of the forearm. A narrow tarsal ridge is present but may be an artefact brought about by excessive dehydration. The throat and chest are smooth and the abdomen and lower femora granular.

There is a small nuptial pad at the base of the first finger and an internal vocal sac with paired openings at the angles of the jaws.

In preservative the dorsal surface of the head, body and limbs is dark blue with very faint pale blue markings. N.M.V. 16976 bears a pale blue patch on the anterior portion of the head, bounded by the canthus rostralis and terminating posteriorly on a level with a line crossing the anterior one-quarter of the upper eyelids. The remainder of the dorsum of this specimen is very finely dotted with very small circular spots of a similar colour. The head marking is not present in R.4947 but the pale blue spots extend on to the dorsal surface of the head. On the upper portion of the jaw, beneath the posterior one-third of the eye of N.M.V. 16976 are clear cream patches. In S.A.M. R.4947 the patches are dull yellow and less conspicuous. Both specimens are marked with poorly defined patches of dull yellow on the head and distal third of the humerus and on the sides of the body. The ventral surface of the throat, body and limbs is a dull yellow with irregular markings and spotting of brown. In N.M.V. 16976 the throat is marbled with chocolate and the abdomen and femora heavily marked with large irregular spots. The markings are very much paler and less noticeable in the other syntype.

Comparison with original description. — Wandolleck stated that he originally considered that the specimens forming the type series represented three distinct species, but was able to demonstrate by means of skeletal preparations and further examination that they were different stages of a single species. This discovery led Wandolleck to comment that the comparative morphology of the skeleton should not be overrated in its value for systematic study. However, examination of Wandolleck’s data indicates that his initial conclusion might have been correct.

Wandolleck’s largest specimens were up to 40 mm in length whilst the remaining adult male syntypes have snout to vent lengths of approximately 20-22 mm (approximately 22-24 mm ‘total length’). Assuming the 40 mm specimens were females, the ratio of male to female size is high for a single species to be involved. Individuals occur in almost every population which are outside the ‘normal’ adult size range, but even so the disparity in the present situation could hardly be attributed to gigantism. Wandolleck mentioned that three size groups were included and drew attention to four
large specimens which he originally identified as *H. dolichopsis* (*H. infrafrenata*). As a total length in the vicinity of 30 mm would be the anticipated female size of a species whose males measure in the range of 20-25 mm, Wandolleck’s 40 mm specimens could be assumed to have been a distinct species.

The brown ventral markings exhibited by the existing syntypes were apparently confined to those specimens in the medium of the three size groups, and the smaller and larger ones were a uniform pale yellow. The possibility that the smaller group was also distinct cannot be excluded, for a small distinct *Hyla* species fitting this definition does occur at the type locality (reported as *H. bicolor* by Loveridge, 1948).

In the absence of freshly preserved topotypic specimens of green *Hyla*, alizarin preparations cannot be made to compare with Wandolleck’s figures of the bones. Wandolleck’s observations on variation appear to be unduly pessimistic and as the variation in the form of the head of the scapular in two preparations figured is far greater than in any single species known to the present author, support for the belief that two or more distinct species are involved may be forthcoming.

Taxonomy. — Tyler (1965) discussed the taxonomic status of this and other species at one time synonymised with *Nyctimystes montana* (Peters & Doria).

Comparison with other species. — *Hyla bicolor*, *H. mystax*, and *H. nigropunctata* are lowland species of a similar size as *H. albolabris* and basically similar in their dorsal colouration. With the exception of a dark patch near the angles of the jaws of *H. nigropunctata*, the ventral surface of each of the compared species is immaculate. The extensive brown markings on the venter of *H. albolabris* thus distinguish the species. *Hyla dorsalis* is a smaller species than *H. albolabris* but shares a densely pigmented venter. The more slender habitus, elongated snout, reduced webbing between the toes and unwebbed fingers are characters exhibited by *H. dorsalis* distinguishing it from *H. albolabris*. As stated in the preceding description of the syntypes, their condition precludes more detailed comparisons based on measurements and ratios.

**Hyla amboinensis** Horst


*Hyla papuensis* Werner, 1901a, Zool. Anz. 24 (637) : 99, 1901b : 613; Van Kampen,


Types. — 3 syntypes, R.M.N.H. 4418, 2 specimens (an adult male and an adult female, not “an adult and a young one”, as reported in the original description) collected at Ambona by D. S. Hoedt in 1866, and R.M.N.H. 4419 collected at Misool by D. S. Hoedt in 1866.

Definition. — A moderately sized species (females attain a maximum snout to vent length of 64 mm, and males 54 mm). The fingers are webbed to the base of the discs. The dorsal colouration is grey or brown and the majority of specimens bear a rhomboid-shaped marking on the dorsal surface of the head.

Material examined. — The syntypes and 599 additional specimens.

Ceram: M.C.Z. 2433 (H. kampeni holotype), Wahai.


Huon Peninsula: N.M.V. 5942, Sattelberg; Z.M. 16497 (T. papuensis holotype), "German New Guinea".


Description. — The head is flattened and as long as or longer than broad (HL/HW 1.000-1.158), its length less than or greater than one-third of the snout to vent length (HL/S-V 0.327-0.355). The snout is prominent, when viewed from above and in profile it is strongly rounded. The nostrils are more lateral than superior, their distance from the end of the snout less than from the eye. The distance between the eye and the naris is slightly less than or greater than the internarial span (E-N/IN 0.957-1.148). The canthus rostralis is curved and sharply defined. The eye is large, its diameter greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to two-thirds of the eye diameter. The vomerine teeth are in two small, oblique series situated between the choanae. The tongue is cordiform with a slightly indented posterior border.

The fingers are fully webbed; the webbing reaching the base of the disc on the fourth and second fingers (fig. 4). In decreasing order of length 4>3>2>1.

The hind limbs are long and slender (TL/S-V 0.510-0.611). Toes in decreasing order of length 4>5 = 3>2>1. The webbing between the toes reaches the base of the terminal discs on all toes excepting the fourth where
it extends slightly above the sub-articular tubercle at the base of the penultimate phalanx.

The skin on the dorsal surface is either completely smooth or distinctly

Fig. 4. *Hyla amboinensis* Horst. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
tubercular. There are tubercles or traces of a weak skin fold on the posterior surface of the forearm. There is a curved supra-tympanic fold extending from the posterior corner of the eye to the shoulder.

In preservative the colouration of the dorsal surfaces is grey or pale brown with darker marbling. The majority of specimens exhibit a rhomboid-shaped marking on the posterior portion of the head, bisected by a narrow median line. Occasional specimens are marked with very small, faint blue spots on the head and body. The posterior surface of the thighs is pale grey or pale yellow, with or without indistinct brown marbling. The anal region is brown and marked with irregular white spots.

The ventral surface of the body is white and the throat usually marked with brown.

The colour in life has been reported by Brongersma (1953).

Geographic variation. — Consideration of geographic variation is hampered by the availability of limited material from all localities except Mabilabol in the Southern Lowlands. This locality lies approximately in the middle of the range of the species. The snout to vent length of 341 adult individuals from a total sample of 539 collected there during a three month period have been recorded in the form of a histogram in figure 5. Male individuals from the western limit of the geographic range (the male syntypes of H. amboinensis and the holotype of H. kampeni) vary from 41.5-43.7 mm, and therefore lie in the centre of the peak.

External characteristics such as the extensive webbing between the fingers and the colouration are not apparently subject to geographic trends.

Biological and ecological notes. — *Hyla amboinensis* has been recorded at altitudes up to 4000 ft above sea level, but details of its habitat are unknown.

Ova dissected from gravid females are up to 1.5 mm in diameter and pigmented. The tadpole was described by Mertens (1930), translated as follows:

“Body twice as long as deep, tail nearly one and one half times longer than the body, and nearly four times longer than deep, nares nearer the tip of the snout than the eye; eye situated laterally midway between the tip of the snout and spiracle; the latter situated in an oblique cleft left of the ventral midline, situated approximately midway between the tip of the snout and the anus; distance between the eyes twice as great as the internarial span; anal opening to the right, on the outer edge of the subcaudal dermal fringes; these as high as or slightly lower than the upper, reaching the base of the tail; tail acuminate. Lips with a papillary margin, absent only from
the median portion of the upper lip; horny beak with narrow black rims; dental formula $1'\ 1/3$, the lowest row on the lower lip is the shortest. — Upperside light brown, underside white; sides of the tail each with two bright longitudinal stripes; between each of these is a light brown band; the upper caudal stripe commences on the posterior portion of the back.”

A total of 230 tadpoles from Mabilabol have been examined by the writer (R.M.N.H. 12088-94; S.A.M. 5112). The specimens were collected between May 14th and August 30th, 1959 and vary from early stage to metamorphosing juveniles. The largest specimen has a snout to vent length of 26 mm and a total length of 63 mm. The material closely conforms to Mertens’ description, and it may be noted that all metamorphosing juveniles exhibit the rhomboid head marking common to many adults. The mouthparts are depicted in fig. 6.

Distribution. — This species is predominant in the western half of the sub-region. Its distribution has been plotted in fig. 7.

Taxonomy. — *Hyla papuensis* Werner has hitherto been considered a valid species. The type of the species is a male with a snout to vent length

Fig. 5. Histogram of adult *Hyla amboinensis* Horst collected at Mabilabol. Vertical axis = frequency; horizontal axis = snout to vent lengths in millimetres.
Fig. 6. Tadpole mouthparts. a, *Hyla wissevensis* new species; b, *Hyla amboinensis* Horst.
of 54 mm and agrees perfectly with similarly sized specimens from south-western New Guinea.

*Hyla kampeni* Barbour was synonymised with *H. amboinensis* by Loveridge (1948). The holotype has been examined and the species is clearly also a synonym of *H. amboinensis*.

Brongersma (1953) referred *H. amboinensis* to *Nyctimystes* on the grounds of its possession of a vertical or rhomboidal-shaped pupil. Zweifel (1958) referred the species back to *Hyla* drawing attention to the absence of a palpebral venation.

Colloquial names. — The names “Kol jaran” and “Kol wopwor” were recorded by the Netherlands Star Mountains Expedition at Mabilabol. “Aag ajoj” is used at Komara on the Vogelkop Peninsula.

Comparison with other species. — *Hyla amboinensis* shares the characteristic of fully webbed fingers with *H. aruensis*, some individuals of *H. darlingtoni*, *H. eucnemis*, *H. graminea* and *H. multiplica*. Of these species only *H. darlingtoni* and *H. eucnemis* have a grey or brown dorsal colouration. The dorsal markings of *H. amboinensis* and *H. darlingtoni* are variable, but individuals share a diamond-shaped marking on the head, frequently bisected by a median paler line. In their size and proportions the species are similar, but *H. amboinensis* lacks the vivid black and yellow markings present on the thighs, groin and axilla of *H. darlingtoni*, and *H. darlingtoni* lacks the dermal appendages present on the limbs of *H. amboinensis*. Distribution records indicate that the species are allopatric, with *H. amboinensis* predominant below 3500 ft and *H. darlingtoni* occupying the highland valleys and lower slopes of the mountains at a minimum altitude of 4000 ft.

*Hyla eucnemis* is distinguished from *H. amboinensis* by having larger and obtusely pointed (not rounded) lappets on the limbs, a much more pronounced canthus rostralis and usually a higher E-N/IN ratio (0.957-1.148 in *H. amboinensis* and 1.020-1.500 in *H. eucnemis*).

**Hyla angiana** Boulenger


*Hyla montana montana*, Loveridge, 1948: 396 (part).


Definition. — The species is characterised by broadly spaced nares (E-N/IN 0.509-0.780) and a moderate to high TL/S-V ratio of 0.524-0.647. The tympanum is small with a diameter equivalent to approximately one-quarter of the eye diameter. This species is polymorphic in its colour pattern. The snout to vent length of males ranges from 40.1-65.9 mm and of females 56.2-77.5 mm.

Material examined. — The syntypes + 685 additional specimens.


Fig. 8. *Hyla angiana* Boulenger. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.

South-east Peninsula: A.M.N.H. 66994-9, Kaindi.

Description. — The head is high and usually broader than long (HL/HW 0.878-1.012), its length usually less than one-third of the snout to vent length (HL/S-V 0.300-0.347). The snout is not prominent; when viewed from above it is evenly rounded or obtusely angular; in profile it is rounded or acutely angular. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is considerably less than the internarial span (E-N/IN 0.509-0.780). The canthus rostralis is very slightly curved or straight and only slightly defined. The eye is moderate, its diameter greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to one-third to one-quarter of the eye diameter. The vomerine teeth are in two short oblique series situated between the choanae. The tongue is cordiform with a slightly indented posterior border.

The fingers (fig. 8) are moderately long and are equipped with narrow lateral fringes; in decreasing order of length 3>4>2>1; the webbing is not extensive, not reaching the sub-articular tubercle at the base of the penultimate phalanx on the fourth finger. The terminal discs are moderate.

The hind limbs are long with a moderate to high TL/S-V ratio (0.524-0.647). Toes in decreasing order of length 4>3>or = 5>2>1. The toes are webbed to the discs with the exception of the fourth which is webbed to the sub-articular tubercle at the base of the penultimate phalanx.

The skin on the dorsal surfaces is smooth or slightly tubercular. The throat is smooth and the chest, abdomen and lower femora granular. There is a prominent, curved supra-tympanic fold extending from the posterior corner of the eye to the shoulder. On the posterior surface of the forearm are tubercles which are widely separated from one another, in juxtaposition in a distinct row, or replaced by a continuous fold. There is a poorly defined dermal ridge on the posterior surface of the heel and tarsus.

The colouration is very highly variable, and in the absence of any genetic studies it is uncertain whether the most distinctive forms can be regarded as polymorphs. Certainly sexual dimorphism occurs at most localities and it is possible to separate the majority of specimens in collections into at least four groups, with the remainder representing intergrades between the groups.
The characteristic features of each variant (a term of convenience) and the names applied to them are as follows:

"Type Variant" (figured by Boulenger, 1915).

The dorsal surface is pale blue with or without a few indistinct black spots or marbling. There is a dark (usually black) patch at the end of the snout, dividing on a level with the nares and continuing as a broad stripe along the canthus rostralis to the eye and continuing behind the eye as a short stripe to the insertion of the forearm. There are brilliant, white longitudinal stripes on the posterior surface of the forearm, heel and tarsus, and a broad, curved, white supra-anal bar. The lateral surfaces of the body are dull crimson marked with large, irregular white spots. The ventral surfaces of the body are a paler crimson with white spots which are particularly dense on the throat.

"Brown Variant"

A uniform brown dorsally and laterally. The only markings are a triangular, pale blue patch behind the eye and a white supra-anal bar. The ventral surfaces vary from white to a very pale brown.

"Mintima Variant"

The dorsal and lateral surfaces are uniformly a very deep slate and lack markings of any kind. The ventral surfaces are pale slate.

"Dull Variant"

Basically similar to the type variant but with extensive black marking on the dorsal and lateral surfaces. The white limb and supra-anal markings are absent or replaced by poorly defined pale grey patches. The ventral surfaces are dull grey.

Intergrades

Many specimens exhibit large white spots on the dorsal surfaces and some the hour-glass shaped marking on the posterior portion of the head and anterior portion of the body (a marking common to other species such as *H. genimaculata*). These markings are not seen in any of the variants described above.

Distribution and relative abundance of the variants. — Although representatives of each of the described variants apparently co-exist throughout the geographic range of the species, the relative abundance of each variant in each sample is highly variable. Of 109 adult specimens collected at Okapa (S.A.M. 5211), 30 are females of the Type Variant and 79 are males of the Dull Variant. Of 92 males and 5 females from Telefomin (S.A.M. 5419), 91 males
are of the Dull Variant and 4 females of the Type Variant. This suggestion of sexual dimorphism towards these variants is supported by samples from other localities, but in a previous sample of 9 males and 2 females from Telefomin, the males form a complete range of intergrades between the Dull Variant and the Mintima Variant.

Mintima and Brown Variants occur with far less frequency than Type and Dull Variants and are not confined to either sex.

It is not yet known whether the microenvironmental niches occupied differ from variant to variant. Field observations by the writer prompted the description of the Mintima Variant as a new species (*Hyla mintima*), and the identification of the Dull Variant as *Hyla montana*. However, at that time there was no appreciation of the extensive variation in colour pattern and the unreliable characteristics. It is the writer’s opinion that only a field investigation will resolve the question of whether more than one species is involved, and the wish to provide a basic taxonomic structure for field studies is fulfilled by recognising only one at the present time.

Biological and ecological notes. — *Hyla angiana* is an arboreal, montane species occurring at altitudes of 4000-9000 ft. Most of the specimens reported were found amongst dense vegetation near fast-flowing streams in moss forests. Juveniles have been found on the leaves of sweet potato plants in native gardens.

The ova in gravid females are unpigmented and up to 2.8 mm in diameter. The tadpole is unknown but in transforming juveniles the remnant larval mouthparts are ventral and suctorial. The smallest juvenile examined had a snout to vent length of 23 mm.

Distribution. — This species occurs throughout the mountains of New Guinea from the Vogelkop Peninsula to the South-east Peninsula (fig. 9).

Taxonomy. — There are two synonyms — *H. mintima* Tyler based on the exceptionally dark variant discussed earlier, and *H. angularis* Loveridge.

Comparison with other species. — Of the montane species whose maximum adult size is within the range of *H. angiana* (*H. arfakiana, H. darlingtoni, H. eucnemis, H. micromembrana, H. multiplica* and *H. spinifera*), only *H. arfakiana, H. spinifera* and *H. micromembrana* have broadly spaced nares. The limited extent of the webbing between the third and fourth fingers of *H. angiana* readily distinguishes it from *H. multiplica* which has fully webbed fingers. The remaining species lack webbing between the fingers and in each case are further distinguished by the sharply pronounced canthus rostralis and, in most individuals, by the proportions of the head — broader than long or as broad as long in *H. angiana*, and longer than broad in the remainder.
**Hyla arfakiana** Peters & Doria


*Hyla angularis*, Tyler, 1963: 113; Mann & Tyler, 1963: 1224.


Definition. — This species is characterised by a prominent pointed snout with a sharp canthus rostralis, and a conspicuous, straight supra-tympanic fold. Large sub-anal tubercles are exhibited by all specimens and conical heel tubercles are usually present. The S-V length of adult males varies from approximately 35 mm to 45 mm and from 45 mm to 65 mm in females.

Material examined. — 3 paralectotypes (M.C.S.N. C.E. 29723 B, R.M.N.H. 4241) and 303 additional specimens.
Huon Peninsula: S.A.M. 4254, Finschaven; N.M.V. 18229:3-6, Sattelberg.
South-east Peninsula: M.C.Z. 23297-9, Mt. Missim; N.M.V. 18229:1-2, Astrolabe Mts.

Description. — The head is flattened and longer than broad (HL/HW 1.077-1.152), its length slightly more than one-third of the snout to vent length (HL/S-V 0.340-0.373). The snout is projecting; when viewed from above its shape may be acutely pointed (males) (fig. 10) or obtusely pointed (most large females); in profile the snout is acutely pointed in both sexes. The nostrils are lateral, their distance from the tip of the snout slightly less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.600-0.760). The canthus rostralis is very slightly curved and extremely sharply defined. The loreal region is concave and oblique. The eye is large, its diameter greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to one-third to one-half of the eye diameter. The vomerine teeth are in two, short oblique series situated between the rounded choanae. The tongue is cordiform with a slightly indented posterior border.

The fingers are long and slender and lack lateral fringes; in decreasing order of length 3>4>2>i; unwebbed or with a trace of webbing at the base of the third and fourth fingers (fig. 10). The terminal discs are extremely prominent.

The hind limbs are slender and there is considerable variation in the TL/S-V ratio (range 0.554-0.712, mean 0.645). The extreme individuals in most samples differ by approximately 10%. Toes in decreasing order of length 4>5>3>2>i. The webbing between the outer and fourth toes extends to the sub-articular tubercle at the base of the penultimate phalanx or to approximately half way up the penultimate phalanx on the fifth, whilst the penultimate phalanx of the fourth may be free or webbed to slightly above the sub-articular tubercle.

The skin on the dorsal surfaces is roughened. Conical tubercles are distributed as follows: on the upper eyelid (usually confined to the posterior half), and on the heel and beneath the vent. Throat lightly granular, abdomen and lower femur coarsely granular. There is a conspicuous, straight supra-tympanic fold extending from the eye to the shoulder, an irregular, slightly raised tubercular ridge above the vent and rows of small tubercles on the posterior surface of the forearm and the tarsus.
The colouration is highly variable, in preservative the majority of specimens are grey, brown or dull blue. A narrow, black transverse V-shaped line usually divides the dorsal surface of the head into two portions. The anterior portion is frequently paler than the remainder of the dorsum, and

Fig. 10. *Hyla arfakiana* Peters & Doria. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
the line also may form the anterior border of an hour-glass marking on the back. The canthus rostralis and the skin fold behind the eye are usually darker than the surrounding areas and may be surrounded by a narrow white line. The pre-anal fold is white, and the backs of the thighs are red or dull brown. The ventral surfaces vary from cream to pale brown, and there are frequently small darker spots on the posterior half of the body and the lower surfaces of the thighs.

In life the dorsum varies from shades of brown, sandy yellow or dull orange to green. Occasionally the anterior portion of the head is a conflicting colour and more frequently a paler shade. The back of the thighs may be green, yellow, orange, red or brown, and the anal warts white, cream or pink.

Males possess a sub-gular vocal sac. The nuptial pad has been included in fig. 3.

Biological and ecological notes. — Hyla arfakiana lives amongst low vegetation near streams in montane forest at altitudes of approximately 2500-6000 ft.

Ova dissected from gravid females are unpigmented so the spawn is presumably not exposed to the sunlight. The spawn and early stages of development are unknown, but tadpoles with well developed hind limbs were collected in one of the fast flowing rivers draining the Wahgi — Sepik Divide in May 1960, and described and figured by Tyler (1963a) as H. angularis. The major features are the dorso-ventral flattening of the body, and the large, suctorial, ventral mouth. There are two upper and three lower rows of labial teeth and the horny beak is unusual in being reduced to four small lateral portions.

Hyla arfakiana is usually found in association with Hyla micromembrana. That these species share the same environmental niche may be assumed from the evidence that they are by far the most common hosts of the endoparasitic leech Batrachobdella (Mann & Tyler, 1963; Tyler, Parker & Bulmer, 1966).

Distribution. — Hyla arfakiana occurs in the highlands throughout the entire New Guinea mainland, with a range of over 1200 miles between the type locality on the Vogelkop Peninsula and Lucas' (1898) record from Fife Bay in the South-East (fig. 11).

Taxonomy. — H. wollastoni Boulenger (1914) is here considered synonymous with H. arfakiana. It was described from a conspicuously pigmented adult male taken at 2500 ft on the Octakuia River (B.M. 1913.11. 1.151 = 1947.2.23.59). Measurements and detailed notes of this specimen provided by Dr. Zweifel and the figure accompanying the type description agree in every respect with H. arfakiana.
Comparison with other species. — The Papuan species with E-N/IN ratios within or approaching the range of *H. arfakiana* are *H. angiana*, *H. becki*, *H. bulmeri*, *H. dorsivena*, *H. iris*, *H. leucova*, *H. longicrus*, *H. micromembrana*, *H. multiplica*, *H. mystax*, *H. pratti*, *H. napaea*, *H. spinifera* and *H. louisadiensis*. Of these species the size of adult female *H. leucova*, *H. longicrus*, *H. mystax* and *H. napaea* is approximately 30 mm, and *H. louisadiensis* (known solely from males) is predictably only slightly larger. The size range of adult female *H. arfakiana* is approximately 45-65 mm.

*Hyla angiana* has a more robust habitus than *H. arfakiana* and can be readily distinguished by comparison of the HL/HW ratios (0.878-1.012) for *H. angiana* and 1.077-1.152 for *H. arfakiana*), and the shape of the snout (very bluntly rounded in *H. angiana* and projecting and pointed in *H. arfakiana*).

The only species sharing conical dermal tubercles on the heels is *H. spinifera*. In that species these are accompanied by a series of prominent, similarly shaped tubercles on the posterior surface of the tarsus and frequently the tibia, whereas the tarsus and tibia of *H. arfakiana* are smooth.

**Hyla aruensis** Horst


*Hyla infrafrenata*, Boulenger, 1912: 214 (part); Nieden, 1923: 205 (part).

Fig. 11. Distribution of *Hyla arfakiana* Peters & Doria. Open circles = literature records; closed circles = specimens examined.
Types. — 3 syntypes, R.M.N.H. 4416 (two specimens), collected in the Aru Islands by C. B. H. von Rosenberg, and R.M.N.H. 4417 collected at Misool, by D. S. Hoedt. The date of collection of the latter specimen was probably April, 1867.

Definition. — This species is characterised by short, broadly fringed and almost completely webbed fingers and the absence of dermal folds on the limbs. In the small series examined the S-V lengths of the largest males and females were 38 mm and 43 mm respectively.

Material examined. — The syntypes and 11 additional specimens.
Southern Lowlands: A.Z.M. 5687, Alkmaar.

Description. — The head is flattened and usually broader than long (HL/HW 0.922-1.105), its length more than one-third of the snout to vent length (HL/S-V 0.330-0.382). The snout is not prominent; when viewed from above it is slightly rounded or almost truncate, and rounded in profile. The nostrils are more lateral than superior, their distance from the tip of the snout approximately half that from the eye. The distance between the eye and the naris is equal to or greater than the internarial span (E-N/IN 1.000-1.225). The canthus rostralis is straight and slightly defined. The loreal region is concave and oblique. The eye is large, its diameter greater than the distance separating it from the nostril. The tympanum is poorly defined, at least the superior half being covered by skin; the tympanal diameter is from slightly more than one-half to two-thirds of the eye diameter. The vomerine teeth are in two small, round series between the obliquely oval choanae. The tongue is very small, extremely thick and cordiform in shape.

The fingers are short with broad lateral fringes (fig. 12); in decreasing order of length 3>4>2>1; extensively webbed, the webbing on the fourth finger reaching a point slightly above the sub-articular tubercle at the base of the penultimate phalanx. The terminal discs are large but do not extend laterally much beyond the fringes.

The hind limbs are moderately long, with a TL/S-V ratio of 0.522-0.578 and mean of 0.548. Toes in decreasing order of length 4>5>3>2>1. The webbing reaches the discs of all toes except the first. There is a flattened, broadly oval inner metatarsal tubercle.

The skin on the dorsal surface is completely smooth; the lateral surfaces of the body, the back of the thighs and the anal region are weakly granular.
Fig. 12. *Hylo aruensis* Horst. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
Fig. 13. Distribution of *Hyla aruensis* Horst.

The throat is smooth and the remainder of the ventral surface of the body granular. The supra-tympanic fold is scarcely discernable. There is neither a tarsal ridge nor a dermal appendage on the heel.

The colouration varies only slightly: in preservative all specimens exhibit pale blue or greyish-blue dorsal body surfaces. The colour is confined to a narrow strip on the femur and is absent from the humerus. There is a trace of a narrow white stripe on the canthus rostralis and upper eyelid on one specimen (R.M.N.H. 4417), and distinct white stripes on the posterior surfaces of the forearm and tarsus in all specimens. The posterior surface of the femur is a very pale violet. The ventral surfaces of the body and limbs are dull creamy yellow.

The only information on the colour in life is the brief field note recorded by M. Boeseman: "Bright green above. Yellow beneath".

Males possess a sub-gular vocal sac and nuptial pads on the first fingers.

Distribution. — The only representatives of this species previously reported are the types. The additional material reported here extends the range to the Vogelkop Peninsula and to the Louisiade Archipelago. The specimen from Alkmaar partly bridges the gap, but the appearance of the species in the Louisiades remains an unexpected occurrence. (See fig. 13).
Taxonomy. — Boulenger (1912) considered *H. aruensis* a synonym of *H. infrafrenata*. Barbour (1912) stated in a footnote that he would have accepted this opinion and excluded *H. aruensis* from his check-list, but did not see Boulenger's paper until his own work was in page proof. Van Kampen (1923) examined the syntypes and resurrected *H. aruensis*. With the exception of a brief reference to the name by Kinghorn (1928) no subsequent mention of *H. aruensis* occurred in the literature until it was cited by Gorham (1963).

Comparison with other species. — The combination of adult size greater than 35 mm, a uniform blue (green in life) dorsal colouration and fully or almost fully webbed fingers is shared with *H. graminea* and occasional specimens of *H. multiplica*.

*Hyla graminea* is a considerably larger species than *H. aruensis*, attaining a maximum size of approximately 80 mm and it possesses prominent dermal ridges on the lateral surfaces of the forearm and tibia, lacked by *H. aruensis*. The internarial span of *H. multiplica* is less than the eye to naris distance (E-N/IN 0.775-0.956) whereas in *H. aruensis* it is as great as or greater than the eye to naris distance (E-N/IN 1.000-1.225). Furthermore *H. multiplica* possesses extremely prominent dermal ridges on the limbs, and the lateral and ventro-lateral surfaces of the body are brilliantly marked with large spots of dark blue. *Hyla aruensis* lacks these markings.

*Hyla multiplica* is a montane species occurring at altitudes above 4500 ft. *Hyla aruensis* apparently inhabits the coastal lowlands and the only sympatric species with which it has been confused is *H. infrafrenata*. The latter attains a much larger size, has a considerably higher E-N/IN range of 1.143-1.531, and far less extensively webbed fingers.

**Hyla becki** Loveridge


Types. — Holotype M.C.Z. 25900 collected at an altitude of 7500-10000 ft on Mt. Wilhelm, Eastern Mountains, New Guinea in October 1944, and 39 paratypes: M.C.Z. 25901-9 + 30 uncatalogued specimens taken at the same locality. The series was collected by P. J. Darlington. There is no record at the Museum of Comparative Zoology of the number of uncatalogued paratypes and the figure quoted is that appearing in the original description. Six uncatalogued paratypes remain at M.C.Z. and six others are known to have been distributed to other museums and catalogued there as follows: A.M.N.H. 58662-3, 58671, B.M. 1947.3.1.4-5, U.M.M.Z. 107610.

Definition. — A moderately sized highland species (males 37-38 mm)
characterised by very broadly spaced nares (E-N/IN 0.500-0.553), a TL/S-V ratio of 0.565-0.576, very slightly curved or straight canthus rostralis and basally webbed fingers.

Material examined. — The holotype and 15 of the paratypes (M.C.Z. 25901-9, M.C.Z. uncat. (6)).

Description. — The head is longer than broad (HL/HW 1.015-1.034), its length equivalent to or slightly more than one-third of the snout to vent length (HL/S-V 0.334-0.353). The snout is evenly rounded when viewed from above and bluntly rounded in profile. The nostrils are more lateral than superior, equidistant from the end of the snout and the eye. The distance between the eye and the naris is equivalent to one-half of the internarial span (E-N/IN 0.500-0.553). The canthus rostralis is well defined and very slightly curved. The eye is large and conspicuous; its diameter is greater than the eye to naris distance and less than the internarial span. The superior one-third of the tympanum is hidden beneath the supra-tympanic fold. The diameter of the typanum is equivalent to two-fifths to three-fifths of the eye diameter. The vomerine teeth are in two oblique series whose anterior borders are on a level with the anterior borders of the choanae, with the posterior borders extending beyond the posterior border of the choanae. The tongue is cordiform with an indented posterior border.

The fingers are long and lack lateral fringes (fig. 14); in decreasing order of length 3>4>2>1. There is no webbing between the fingers. Terminal discs are prominent.

The hind limbs are moderately long (TL/S-V 0.565-0.576). Toes in decreasing order of length 4>5>3>2>1. On the fifth toe the webbing reaches to a point slightly above the sub-articular tubercle at the base of the penultimate phalanx, whilst on the fourth the penultimate and next phalanx are free.

The dorsal surface of the head, body and limbs and posterior surface of the thighs is smooth but for a few flattened and indistinct tubercles on the posterior halves of the upper eyelids. The throat is smooth, the abdomen granular and the lower surface of the thighs very slightly granular.

In preservative the dorsal surface of the head, body and limbs is dull slate, and the back of the thighs a paler shade of the same colour (flecked in one specimen with dull whitish spots). Beneath the eye is a small and obscure unpigmented patch. The ventral surface is a dull cream heavily suffused or slightly stippled with slate.

Discussion. — The specimens reported as H. becki by Tyler (1963) and Mann & Tyler (1963) are distinct from that species but cannot be confidently
Fig. 14. *Hyla becki* Loveridge. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
referred to any other. Topotypic collections have contained numerous *H. micromembrana* which is quite distinct from *becki*, but no specimens agreeing with the *H. becki* types in all respects. In the circumstances the description has been based solely on the types. The reference to *H. becki* in Reichenbach-Klinke & Elkan (1965) is based on the data of Mann & Tyler (1963), whilst the species figured by Tyler, Parker & Bulmer (1966) is *H. micromembrana*.

Comparison with other species. — Of the highland species with unwebbed or basally webbed fingers only *H. arfakiana*, *H. bulmeri*, *H. micromembrana*, *H. modica*, *H. pratti* and *H. spinifera* have E-N/IN ratios overlapping or near the range of *H. becki*. *Hyla becki* is distinguished from *H. arfakiana* by its rounded (not pointed) snout, lack of conical tubercle on the heel and lower E-N/IN ratio. In *H. micromembrana* and *H. spinifera* the canthus rostralis is very strongly curved and the TL/S-V ratios are higher. The latter feature also distinguishes *H. bulmeri* which is further separated by its possession of a conspicuous dorso-lateral stripe not present in *H. becki*. *Hyla modica* is a much smaller species than *H. becki* (males 23.4-30.0 mm, females 27.4-35.4 mm; smallest adult male *H. becki* 36.8 mm). Males of *H. pratti* are also smaller than those of *H. becki* (29.5-31.4 mm) and the species differs from *H. becki* in the following respects: E-N/IN higher (0.758-0.848 compared with 0.500-0.553); eye diameter slightly greater than the internarial span (much less than internarial span in *H. becki*); canthus rostralis straight and not slightly curved.

**Hyla bicolor** (Gray)

*Hylella bicolor*, Werner, 1901b: 613.


Holotype. — B.M. 1947.2.22.59 collected at Port Essington, Northern Territory, Australia, by Gilbert (initials of collector and date of collection unknown).

Definition. — A small and slender lowland species characterised by its very narrow head (HL/HW 1.243-1.254) and uniform dorsal colouration (green in life and blue in preservative). Females attain a maximum snout to vent length of 33 mm and males 28 mm.
Fig. 15. *Hyla bicolor* (Gray). a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
Material examined. — 7 specimens.

Aru Islands: N.M.B. 3715-6, S.M.F. 2337-41, Naiguli, Terangan.

Description. — The head is distinctly longer than broad (HL/HW 1.243-1.254), its length less than or equal to one-third of the snout to vent length (HL/S-V 0.295-0.333). The snout is projecting; when viewed from above it is obtusely pointed or rounded, and in profile the end of the snout extends considerably beyond the tip of the lower jaw. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.136-1.158). The canthus rostralis is straight and moderately defined. The eye is small, its diameter slightly greater than the eye to naris distance. The tympanum is visible, its diameter equal to approximately two-thirds the diameter of the eye. There are no vomerine teeth. The tongue is broadly oval and slightly indented on its posterior border.

The fingers are long and slender with very narrow lateral fringes (fig. 15); in decreasing order of length 3 > 4 > 2 > 1. The webbing extends to the sub-articular tubercles at the base of the penultimate phalanx on the third and fourth fingers. The terminal discs are relatively small.

The hind limbs are long and slender with a low TL/S-V ratio (0.471-0.514). Toes in decreasing order of length 4 > 5 = 3 > 2 > 1. The webbing between the toes reaches the base of the discs of all except the fourth, where it extends to a point midway between the disc and the sub-articular tubercle at the base of the penultimate phalanx.

The skin on the dorsal surfaces is smooth or minutely pitted. The throat and chest are smooth, the abdomen and lower femora coarsely granular. There is a very weak supra-tympanic fold extending from the posterior corner of the eye to a point above the insertion of the forelimb.

In preservative the dorsal surfaces of the body and limbs are dull blue. There are a few scattered chromatophores on the lateral surfaces of the body, and there is a distinctive white stripe commencing beneath the eye and extending almost to the groin. There is a dark cantho-rostral stripe continuing for a short distance behind the eye above the white stripe.

The groin, anterior surface of the thigh and distal half of the posterior surface of the thigh is brownish or pale maroon.

Distribution. — Hyla bicolor occurs along the northern and north-eastern Australian coastline, and has been reported from several coastal localities in the southern lowlands of New Guinea and the Aru Islands. Loveridge (1948) reported a series from Aitape, but the specimens (M.C.Z. 35853-61, 26036-40) are in such a poor condition that the identification is suspect.
The present author has examined specimens from localities as widely separated as Keravat in New Britain and Jamoer Lake which closely resemble *bicolor* in all respects except relative head width. Specimens in the South Australian Museum from the Northern Territory consistently tally with the Aru Islands material and so the remainder have been excluded from consideration in the above account of variation.

A.K. Lee states (in litt.) that the Australian *H. bicolor* consists of two distinct species: one occupying the northern and the other the southern portion of the range, and corresponding to Copland's (1957) *H. b. bicolor* and *H. b. glauerti* subspecies respectively. Elucidation of the status of the New Guinea populations must await publication of these observations and the collection of more material.

One of the *H. rueppelli* paratypes from Halmahera (S.M.F. 39260) is a gravid female which clearly represents a species closely resembling *bicolor*.

Taxonomy. — Correspondence in the Australian Museum reveals that Fry wrote to Douglas Ogilby querying whether *H. bicolor* was valid for the Australian species since it was preoccupied in *Hyla* by *H. bicolor* Latreille (= *Phyllomedusa bicolor*). Ogilby replied (12.3.1912) that it was not valid. Moore (1961) drew attention to the same matter and stated that he hoped that no one would contemplate proposing a new name.

Comparison with other species. — There are ten Papuan species sharing with *H. bicolor* a uniform or almost uniform blue dorsal colouration in preservative, and an immaculate venter: *H. aruensis, H. chloronota, H. contrastens, H. graminea, H. gracilenta, H. infrafrenata, H. leucova, H. longicrus, H. mystax* and *H. sanguinolenta*. Of these the minimum size of adult *H. graminea, H. infrafrenata* and *H. sanguinolenta* is so much greater than maximum size attained by *H. bicolor* that further comparison is unnecessary. The size range of *H. aruensis* approaches that of *H. bicolor*, but the former is readily distinguished by its possession of fully webbed fingers.

*Hyla chloronota* has been collected at an altitude of 8000 ft above sea level and possesses a broader head (as broad as long in *H. chloronota*, as opposed to being distinctly longer than broad in *H. bicolor* which has an HL/HW ratio of 1.243-1.254). The head proportions also distinguish *H. contrastens* (HL/HW 1.027-1.189) and *H. gracilenta* (0.913-0.940). *Hyla leucova* has unpigmented ova (they are pigmented in *H. bicolor*) and broad transverse folds on the ventral surface of the body (granular in *H. bicolor*). The hind limbs of *H. longicrus* (TL/S-V 0.623-0.628) are much longer than those of *H. bicolor* (0.471-0.514). *Hyla mystax* can be distinguished by its lower E-N/IN ratio (0.769 compared with 1.136-1.158 in *bicolor*).
**Hyla brongersmai** Loveridge


Holotype. — M.C.Z. 15203 collected at Panara Valley, near Doorman Top, Snow Mountains, New Guinea, by P. Wirz in 1922.

Definition. — A small species (males have a snout to vent length of 23.9-24.3 mm) characterised by an eye to naris distance only slightly less than the internarial length, scantily webbed fingers and a very dark dorsal body surface with a contrasting pale dorsal surface of the thighs.

Material examined. — 3 specimens — the holotype and two topotypes (N.M.B. 3618-9).

Description. — The head is moderately flattened and longer than broad (HL/HW 1.064-1.076), its length more than one-third of the snout to vent length (HL/S-V 0.342-0.359). The snout is not prominent; when viewed from above and in profile it is rounded. The nostrils are more lateral than superior, their distance from the end of the snout considerably less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/N 0.852-0.923). The canthus rostralis is straight and slightly defined. The eye is inconspicuous, its diameter slightly greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to approximately three-fifths of the diameter of the eye. The vomerine teeth are in two very slightly raised circular series situated between the choanae. The tongue is oval with a slightly indented posterior margin.

The fingers are short and equipped with narrow lateral fringes (fig. 16); in decreasing order of length 3>4>2>1. The webbing between the third and fourth fingers reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth.

The hind limbs are comparatively short with a TL/S-V ratio of 0.519-0.544. Toes in decreasing order of length 4>5>3>2>1. The webbing reaches the base of the disc of all toes except the fourth where it reaches the subarticular tubercle at the base of the penultimate phalanx.

The skin on the dorsal surface of the head, body and forelimbs is minutely pitted, and of the hind limbs smooth but for a few scattered and flattened tubercles. The throat is smooth and the abdomen and lower surface of the thighs coarsely granular. There is a conspicuous, curved supra-tympanic fold extending from the posterior corner of the eye to a point above the insertion of the forearm.
Fig. 16. *Hyla brongersmai* Loveridge. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
In preservative the dorsal surface of the head, body and forelimbs is an intensely dark brown with a slate like tinge. The dorsal and posterior surfaces of the thighs are paler than the remainder of the dorsum and the tubercles upon them paler still. The throat and chest are dull cream with a broad, brown mandibular border. The granules on the remainder of the ventral surface are creamish yellow with dense brown stippling at the base of the granules.

All specimens have sub-gular vocal sacs and nuptial pads on the first fingers. These pads are unpigmented in the holotype and pigmented in the topotypes.

Comparison with type description. — The major point of divergence in the present composite description concerns the vomerine teeth, absent in the holotype according to Loveridge. They are present but poorly developed and difficult to detect.

Distribution. — Known solely from the type locality which, as reported by Forcart (1953a), was erroneously spelt in the original description. A small adult male (S-V 21.2 mm) in the Amsterdam collection (A.Z.M. 5681) may be a representative of this species. Collected on the middle or upper reaches of a river which discharges on the east coast of Geelvink Bay, it is rather distorted and can be only tentatively referred to H. brongersmai.

Comparison with other species. — Of the species within the size range of H. brongersmai only H. leucova, H. napaea and some individuals of H. iris share similar E-N/IN ratios. In the case of H. napaea the shape of the snout is quite distinct, being pointed and slightly projecting when viewed from above whereas the snout of H. brongersmai is rather truncate and only slightly rounded. Hyla napaea also has longer hind limbs than H. brongersmai — the TL/S-V ratio being 0.590-0.679 as opposed to 0.519-0.544 in H. brongersmai.

The distinctive colouration of H. iris distinguishes it from the dull H. brongersmai and most adults are larger than H. brongersmai. Hyla leucova is known from a single specimen and that differs from H. brongersmai in its colouration, in having a smaller head (HL/S-V 0.326 in comparison with 0.342-0.359 in H. brongersmai), and by the nature of the skin covering the abdomen (broad transverse ridges present in H. leucova and absent in H. brongersmai).

**Hyla bulmeri** new species (pl. 1, a)

Definition. — This species is characterised by its small size (males 29-34 mm), broadly spaced nares (E-N/N 0.605-0.641) and distinctive colouration.

Fig. 17. *Hyla bulmeri* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
The dorsal surface is blue and there is a broad, black lateral stripe extending from the naris to a point at least midway along the body.

Description of holotype. — The head is high and longer than broad (HL/HW 1.065), its length equivalent to slightly more than one-third of the snout to vent length (HL/S-V 0.366). The snout is abrupt, broadly rounded when viewed from above, projecting and almost pointed in profile. The nostrils are more lateral than superior, their distance from the end of the snout less than one-half that from the eye. The distance between the eye and the naris is very much less than the internarial span (E-N/IN 0.605). The canthus rostralis is slightly defined and gently rounded. The eye is not prominent, its diameter is considerably greater than the eye to naris distance. The tympanum is covered with skin and the annulus only slightly defined. The tympanum diameter is equivalent to one-third of the eye diameter; separated from the eye by a distance equivalent to half its own diameter. Only the left series of vomerine teeth is present. It is small and round and situated near the upper margin of the choana. The choanae are very widely spaced. The tongue is small and broadly cordiform with a slightly indented posterior border.

The fingers are very long and slender with narrow lateral fringes (fig. 17); in decreasing order of length 3 > 4 > 2 > 1. There is no webbing between the fingers. The terminal discs are prominent.

The hind limbs are long and slender (TL/S-V 0.618). Toes in decreasing order of length 4 > 5 = 3 > 2 > 1. The webbing between the toes reaches the base of the disc on the fifth and slightly below the sub-articular tubercle at the base of the penultimate phalanx on the fourth. There is a small depressed inner metatarsal tubercle.

The dorsal surface of the head and body is smooth. There is a very weak supra-tympanic fold extending from the posterior corner of the eye to above the insertion of the forearm. Above and at the sides of the anus is a row of tubercles. The throat and chest are smooth, and the abdomen and lower surface of the thighs coarsely granular.

Dimensions: snout to vent length 31.4 mm; tibia length 19.4 mm; head length 11.5 mm; head width 10.8 mm; eye to naris distance 2.6 mm; internarial span 4.3 mm; eye diameter 3.9 mm; tympanum diameter 1.4 mm.

There is a nuptial pad on the first finger.

In preservative the dorsal surfaces of the head, body and limbs are dull blue. The lateral surface of the head and body are a similar colour. There is a conspicuous black, lateral line commencing at the naris and extending to a point approximately midway along the body. There is a short black,
horizontal line beneath the eye and a smaller marking beneath it on the margin of the upper jaw. The anterior and posterior surfaces of the thigh are pale yellow and the anal region pale brown. The throat is white, finely stippled with pale blue. The chest and lower surfaces of the thighs are dull yellow and the abdomen cream. On the abdomen and lower surfaces of the thighs are small indistinct spots of pale brown. The plantar surface is a very dark brown and there is a very fine white line at the margin of the plantar surface and the lateral blue colouration.

Variation. — The two paratypes (S.A.M. R. 5624, 8107) are both males and were collected at an altitude of approximately 7500 ft at Glkm by R. N. H. Bulmer on November 17th, 1963. An additional two male specimens are also referred to this species (A.M.N.H. 74157-8, taken at an altitude of 8300 ft at Mt. Kominjin, Schrader Mountains by the late E. T. Gilliard). As all specimens are rather distorted, measurements and ratios quoted in the following account are approximations only.

The snout to vent length range of the material is 29-34 mm, the head is consistently longer than broad with a range 1.030-1.160, and the head length less than or greater than one-third of the snout to vent length. The nares are widely spaced and the E-N/IN ratio varies from 0.605-0.641. The hind limbs are long and slender and the TL/S-V range is 0.590-0.665.

The black lateral stripe reported in the holotype description is distinctive in all specimens and may be rendered more conspicuous by the presence of a very narrow white superior border. The brown anal patch is darker and most distinctive in the paratypes, and in A.M.N.H. 74158 the stippled throat is replaced by a uniform brown pigmentation. The proximal half of the posterior surface of the thigh is usually dull brown.

Field notes. — Bulmer collected the holotype in a stream and the paratypes by moonlight at the side of a stream. The colloquial name was “Kogop” but this was also applied to some specimens of *H. angiana* bearing a superficial resemblance to *H. bulmeri*.

Comparison with other species. — The following species share with *H. bulmeri* the combination of broadly spaced nares with E-N/IN ratios within or overlapping the range of 0.550-0.650, and relatively long limbs (TL/S-V ratios greater than 0.550): *H. angiana, H. arfakiana, H. becki, H. longicrus, H. micromembrana, H. pratti* and *H. spinifera*. Of these *H. angiana* is a considerably larger species (the smallest adult male recorded having a snout to vent length of approximately 45 mm, whereas the range of the male *H. bulmeri* is 29-34 mm).
Hyla arfakiana and H. spinifera are also larger but are more readily distinguished by their pointed snouts — prominent and pointed in these species, and abrupt and broadly rounded in H. bulmeri. The conspicuous broad, lateral stripe exhibited by H. bulmeri is not shared by H. becki, H. longicrus, H. micromembrana and H. pratti.

**Hyla caerulea** (White)

*Calamita cyanea*, Cope, 1867: 404.  

Holotype. — The whereabouts of the type (if extant) is unknown. The type locality is believed to be New South Wales.

Definition. — A large squat species characterised by an extremely broad head, glandular supra-tympanic folds, large discs, broad lateral fringes on the fingers and a uniform dorsal colouration. Females may attain a maximum snout to vent length of slightly more than 100 mm and males approximately 80 mm.

Material examined. — 16 specimens.


Description. — The head is usually broader than long (HL/HW 0.845-1.022, mean 0.994), its length usually more than one-third of the snout to vent length (HL/S-V 0.324-0.381, mean 0.353). The snout is high; when viewed from above it is truncated and when viewed in profile it is truncated or slightly rounded. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is almost equal to or greater than the internarial span (E-N/IN 0.927-1.171, mean 1.041). The canthus rostralis is very slightly curved. The eye is large, its diameter greater than the distance separating it from the nostril. The tympanum is large, its diameter equivalent to two-thirds to three-quarters of the eye diameter. The superior one-third of the
tympanum is covered by the supra-tympanic fold. The vomerine teeth are in two large series on prominent elevations; their posterior borders extend well beneath the posterior margins of the choanae. The tongue is broadly cordiform with a slightly indented posterior border.

Fig. 18. *Hyla caerulea* (White.) a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
The fingers are short and flattened with extremely broad lateral fringes; in decreasing order of length $3 > 4 > 2 > 1$; the webbing between the fingers is scant (fig. 18), rarely reaching the sub-articular tubercle at the base of the penultimate phalanx on the fourth. The terminal discs are large, but do not extend laterally much beyond the margins of the fringes.

The hind limbs are short and stocky, the TL rarely more than half the S-V length ($\text{TL}/\text{S-V} 0.441-0.502$, mean 0.475). Toes in decreasing order of length $4 > 5 = 3 > 2 > 1$. The webbing between the outer and fourth toes extends half way up the penultimate phalanx on the fifth and reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth.

The skin on the dorsal surfaces is glandular with numerous pores, particularly on the parotoid region. There is an extremely prominent, glandular supra-tympanic fold extending from the eye to the shoulder and indistinct dermal ridges on the posterior surfaces of the forearm and tarsus. The throat is smooth and the abdomen and lower femur granular.

In preservative the dorsal surface is dull slate blue and the ventral surface dull cream. Living Australian specimens are green or greenish-brown dorsally and white ventrally.

Males possess a large sub-gular vocal sac and nuptial pads.

Biological and ecological notes. — Moore (1961) has reviewed the literature on the habitat preferences, call, breeding habits and habits in captivity of Australian specimens. There is no information on the biology of this species in New Guinea.

Distribution. — *Hyla caerulea* is widely distributed throughout northern and eastern Australia, and has been reported from widely separated localities in the Papuan sub-region. As the Australian portion of its distribution has recently been discussed and plotted by Moore (1961) current attention is devoted to the distribution north of the Australian mainland.

In the literature there are numerous records of the collection of *H. caerulea* on islands west and south-east of New Guinea between approximately 1840 and 1880; the majority referring to the species by its synonym *H. cyanea* (Daudin). However, for the major portion of this period *H. caerulea* and *H. cyanea* were considered to be the only large green *Hyla* species occurring in the Papuan sub-region. Peters & Doria (1878) report *H. caerulea* from fifteen localities outside Australia and express what was clearly the popular belief at that time, “Species comune in tutta la Papuasia e nelle Isole che ne dipendono”. The specimens reported by them from Ternate, Katau, Amboina,
Aru Islands and Buru have been examined and found to represent *H. infrafrenata infrafrenata* and, where details of specimens are provided by authors in the same period the same species is clearly involved in most instances (see literature references to *H. infrafrenata infrafrenata* on p. 104).

*Hyla caerulea* has been reported from islands in the Torres Straits (Macleay, 1877; Gunther, 1884; Boulenger, 1912), and has been taken on several occasions at Merauke (Van Kampen, 1909; Roux, 1920). The material reported in the present paper extends the known distribution to the north coast of New Guinea and the Vogelkop Peninsula.

**Taxonomy.** — The authorship of this species has been a subject of debate. Although attributed to Shaw, the description appears in a work by White (1790), and current authors associate White's name with the species. There are no synonyms based on specimens of Papuan origin.

Comparison with other species. — The presence of distinct parotid glands is a character which will distinguish *H. caerulea* from all other Papuan species. Only three of the species that are uniformly green in life and blue or brownish in alcohol have adults attaining approximately the same size as *H. caerulea*. *Hyla infrafrenata* is usually more slender than *H. caerulea* with a longer head and relatively longer limbs. However there is an overlap of the HL/HW ratios (0.845-1.022 for *H. caerulea* and 0.901-1.087 for *H. infrafrenata*). The basic difference in the shape of the snout is expressed in the E-N/IN ratios (*H. caerulea* 0.927-1.171, *H. infrafrenata* 1.143-1.531). *Hyla caerulea* lacks the conspicuous white stripe found on the margin of the upper jaw of *H. infrafrenata* and possesses very broadly fringed fingers (weakly fringed in *H. infrafrenata*).

Adult *H. graminea* are within the size range of *H. caerulea* but the former have much longer limbs (TL/S-V 0.441-0.502 for *H. caerulea* and 0.558-0.602 for *H. graminea*) and the forearm and tibia bear prominent lateral dermal ridges not exhibited by *H. caerulea*.

The particularly slender habitus of *H. sanguinolenta* enables it to be readily distinguished from *H. caerulea*, and the long snout of *H. sanguinolenta* with an E-N/IN range of 1.212-1.400 is sufficiently distinct to prevent any confusion of the two species.

Occasional specimens of *H. angiana* are uniformly green dorsally, but the E-N/IN range of 0.509-0.780 is well outside the range of *H. caerulea*. 
**Hyla capitula** new species (pl. 1, b)


Definition. — This species is characterised by its very small head (HL/S-V 0.299), short limbs (TL/S-V 0.496) and high E-N/IN ratio (1.476).

Description of holotype. — The head is flattened and longer than broad (HL/HW 1.020), its length equivalent to less than one-third of the snout to vent length (HL/S-V 0.299). The snout is not prominent; blunt and slightly rounded when viewed from above, and rounded in profile. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is considerably greater than the internarial span (E-N/IN 1.476). The canthus rostralis is poorly defined and very slightly rounded. The eye is small and inconspicuous, its diameter equal to the distance separating it from the naris. The tympanum is visible, its diameter equal to three-fifths of the eye diameter. The vomerine teeth are in two small, wedge-shaped series close together near the midline and completely below the choanae. The tongue is broadly oval with a very weak posterior indentation.

The fingers are short; in decreasing order of length 3>4>2>i. The webbing between the third and fourth fingers just reaches the sub-articular tubercle at the base of the penultimate phalanx (fig. 19). The terminal discs and sub-articular tubercles are prominent.

The hind limbs are short with a TL/S-V ratio of 0.496. Toes in decreasing order of length 4>5>3>2>i. The toes are equipped with broad lateral fringes. On the fifth toe the webbing reaches the base of the disc, and on the fourth it reaches the sub-articular tubercle at the base of the penultimate phalanx.

The dorsal and lateral surfaces of the body are smooth. The throat and chest are weakly granular and the abdomen and lower surface of the thighs coarsely granular. There is a weak supra-tympanic fold extending from the posterior corner of the eye, crossing the superior margin of the tympanic annulus, and extending to a point above the insertion of the forelimb. A prominent skinfold crosses the chest.

Dimensions: snout to vent length 34.1 mm; tibia length 16.9 mm; head length 10.2 mm; head width 10.0 mm; eye to naris distance 3.1 mm; internarial span 2.1 mm; eye diameter 3.1 mm; tympanum diameter 1.9 mm.

In preservative the dorsal surface of the head, body and limbs is a very
Fig. 19. *Hyla capitula* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
pale brown. There is a minute pale spot above the insertion of the forelimb and a distinctive, broad, very pale cream stripe above the groin. A similarly coloured mark occurs above the vent, another on the heel extending on to the proximal portion of the tibia, and a series of markings along the tarsus. The ventral surface of the body and limbs is a dull creamish colour.

Distribution. — *Hyla capitula* is known solely from the holotype collected at Samlakki, Tenimber Island (Timorlaut). Van Kampen (1909b) in an account of specimens in the Buitenzorg (Bogor) Museum reported an individual (as *H. rubella*) from Larat on Tenimber which was probably based on a specimen of *capitula*. However, this supposition cannot be confirmed for S. Kadarsan states (in litt.) that neither the frog nor any record of it ever being deposited at Bogor can be traced. Furthermore, M. Boeseman states (in litt.) that it is not included in the Leiden collection.

Rensch (1936) based his record of *H. rubella* at Timorlaut on the reports of Van Kampen (1909b) and Mertens (1930). The source of his report of the occurrence of *H. rubella* on Timor has not been traced in the literature and, if the record is valid, it remains uncertain whether *H. rubella* or *H. capitula* is involved.

Comparison with other species. — *Hyla capitula* is superficially similar to *H. congenita* and the Australian species *H. rubella*. From *H. rubella* it is readily distinguished by its very much longer legs (TL/S-V 0.496 in *H. capitula* and 0.335-0.432 in *H. rubella*) and high E-N/IN ratio, and by the absence of the dark dorso-lateral stripes on the head and body. *Hyla congenita* has longer legs than *H. rubella* (TL/S-V 0.477-0.520) but has a considerably lower E-N/IN ratio than *H. capitula* (0.941-1.148 in *H. congenita* and 1.476 in *H. capitula*). The markings of *H. congenita* are highly variable but the conspicuous markings in the groin and on the heel of *H. capitula* are quite distinct from the pattern and type of markings of *H. congenita*.

**Hyla chloronota** (Boulenger)


*Hyla chloronotus* (sic), Van Kampen, 1919: 52.

*Hyla chloronota* (sic), Condit, 1964: 89.

Types. — Two syntypes, B.M. 1947.2.31.40-41, collected at an altitude of 8000 ft in the Arfak Mountains, Vogelkop Peninsula, New Guinea, by A. E. Pratt.
Definition. — A small species (males adult at 27 mm) characterised by a uniform green colouration in life, short limbs (TL/S-V < 0.500) and the absence of vomerine teeth.

Material examined. — 1 syntype (B.M. 1947.2.31.49).

Description. — Both syntypes are completely dehydrated and shrivelled, so it is not possible to prepare an accurate description. The only additional specimen reported in the literature is a juvenile collected by the Wollaston Expedition at Camp 3, Utakwa River, Southern Lowlands and reported by Boulenger (1914). As the anterior portion of the head of this specimen is damaged, and the characteristics of juveniles often differ from adults, a description based on that specimen could prove misleading, particularly as comparison of the juvenile with the original description leads the writer to regard the identification as suspect.

The original description is as follows: "Tongue oval, slightly nicked. Head as broad as long; snout rounded, scarcely prominent, as long as orbit; canthus rostralis distinct; loreal region nearly vertical; interorbital space broader than the upper eyelid; tympanum distinct, about half the diameter of the eye. Outer fingers one-third webbed; toes nearly entirely webbed; discs of fingers as large as the tympanum; subarticular tubercles moderate. The tibio-tarsal articulation reaches the tip of the snout; tibia not quite half the length of head and body. Skin smooth above; throat, belly and base of lower surface of thighs very coarsely granulate; no fold across the chest. Green above, white beneath, the green colour forming a narrow stripe along the upper surface of the thighs. Males with an internal vocal sac and brown nuptial rugosities on the inner finger.

From snout to vent 27.0 mm."

Comparison with other species. — Species which are green in life and adult at around 27.0 mm are *H. bicolor*, *H. contrastens*, *H. gracilenta*, *H. iris*, *H. leucova*, *H. longicrus* and *H. mystax*. The fact that the hind limbs of *chloronota* are short (a tibia length slightly less than half the body length would result in a TL/S-V ratio within the range of 0.450-0.500), distinguishes the species from *H. leucova* (0.584), *H. longicrus* (0.623), and possibly *H. gracilenta* (0.507-0.560) and *H. mystax* (0.539).

In *H. gracilenta* the head is distinctly broader than long whereas the head of *H. chloronota* is stated to be as broad as long. Head proportions also distinguish *H. bicolor*, where the length is distinctly greater than the breadth.

The absence of vomerine teeth in *H. chloronota* (not mentioned in the type description, but implied by Boulenger's action in referring the species to
Hylella), distinguishes the species from *H. contrastens* and the majority of specimens of *H. iris*. *Hyla chloronota* lacks the distinctive colouration of *H. iris*, and the throat, belly and lower surface of the thighs of *H. chloronota* are all coarsely granular, whereas in *H. iris* the throat is quite different from the remainder of the ventral surface in being only slightly granular.

**Hyla congenita** Peters & Doria


*Hyla macgregorii* (sic), Werner, 1901a: 101.

*Hyla thesaurensis*, Méhély, 1897: 414 (part); Van Kampen, 1914: 368; Loveridge, 1948: 400.

*Hyla mcgregori* (sic), Neill, 1946: 258.


Definition. — A small species (males 32 mm S-V; females <41 mm). The characteristic features are very short hind limbs with a TL/S-V mean of 0.498, short fingers and a brown dorsal colouration, frequently marked with irregularly defined longitudinal stripes.

Material examined. — One paralectotype (M.C.S.N. C.E.29722B) and 93 additional specimens.

Aru Islands: N.M.B. 2717-8, S.M.F. 2373-5, Naiguli.


Description. — The head is flattened and longer than broad or broader than long (HL/HW 0.969-1.061), its length less than or equal to one-third of the snout to vent length (HL/S-V 0.309-0.336). The snout is not prominent; when viewed from above it is truncate or slightly rounded, and slightly rounded in profile (fig. 20). The nostrils are more lateral than superior, their distance from the tip of the snout less than that from the eye. The distance between the eye and the naris is less than or greater than the internarial span (E-N/IN 0.941-1.148). The canthus rostralis is very
Fig. 20. *Hyla congenita* Peters & Doria. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
slightly curved and extremely sharply defined. The eye is large and prominent, its diameter greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to two-thirds of the eye diameter. The vomerine teeth are in two small rounded or oblique series between or slightly beneath the choanae. The tongue is broadly oval with a slightly indented posterior border.

The fingers are short and possess narrow lateral fringes; in decreasing order of length \( 3 > 4 > 2 > 1 \); the webbing between the third and fourth fingers is about one-third (fig. 20). The terminal discs are prominent.

The hind limbs are very short with a TL/S-V range of 0.477-0.520 and a mean of 0.498. Toes in decreasing order of length \( 4 > 5 > 3 > 2 > 1 \). The webbing between the outer and fourth toes extends to the base of the disc on the fifth and the base of the penultimate phalanx on the fourth.

The skin on the dorsal surfaces is smooth. There is an inconspicuous supra-tympanic fold extending from the posterior corner of the eye to the insertion of the forelimbs. The throat and chest are smooth and the abdomen and lower surfaces of the thighs granular.

In preservative all specimens are brown dorsally with variable markings. The most common of these are darker canthal stripes and irregularly defined, broad, pale dorsolateral stripes on the body. A pale mid-dorsal stripe is present on the body of a few specimens in addition to or without the dorsal lateral stripes. The ventral surfaces are white or pale grey. Occasionally the abdomen and lower femora are dull mustard. The posterior surface of the thighs is brown.

Biological and ecological notes. — Roux (1910) reported the collection of a series of tadpoles in a small pond at Naiguli in the Aru Islands. A translation of his description of the material is as follows:

"Body somewhat longer than broad. Tail one and two-thirds times longer than the body. Nostrils nearer the tip of the snout than the eye. Eye visible from beneath, rather small; its distance from the tip of the snout less than that from the spiracle. The distance between the eyes one and one-half times greater than that between the nostrils, and equal to two-thirds the breadth of the mouth, (including the lips). Spiracle situated on the left, almost vertical, in this form a vertical slit, its distance from the mouth equal to the distance from the hind limbs. Anus situated to the right, near to the free border of the fin.

Body three and one-third times longer than high, back longitudinally and very finely tapered to the end of the fin. The two fins almost equally high. Muscular portion strong, high. The upper fin extends along the dorsum,
increasing into a crest, and reaching a point above the base of the hind limbs. Jaws bordered with black. The labial papillae absent from the middle portion of the upper lip. Teeth rows two thirds (sometimes the inner, upper and lower disrupted), of the three lower rows the outer is the shortest. The numerous papillae standing in many rows, particularly on the lower lip and on the sides of the mouth.

Colour. Back dark brown with black spots. On the individuals with well-developed tails, the handsome, bright latero-dorsal stripes of the adults are visible. Frequently the larvae have a very thin mid-dorsal white line from the tip of the snout to the base of the tail. Sides of the body rather brighter coloured because the dark dots are less numerous. In the case of all transforming examples the muscular portion of the tail is provided with a dark median stripe. Upper half a light yellow band. The upper portion of the muscles brown, the lower grey with brown markings. The black stripe becoming narrower and reaching half way along the tail. The fins are marked with numerous black dots. Abdomen white, the throat and sides with black spots.

Size: total length 41 mm; body length 14 mm; tail length 27 mm.

The juveniles, with four limbs and the remains of a tail already exhibit the adult markings and are 12 mm long. The forelimbs measure 9 mm the hindlimbs 20 mm.”

Neill (1946) reported the presence of large congregations of specimens (*H. mcgregori*) in epiphytic egg plants.

Fig. 21. Distribution of *Hyla congenita* Peters & Doria. Open circles = literature records; closed circles = specimens examined.
Distribution. — *Hyla congenita* is confined to the coastal lowlands of southern New Guinea and islands between New Guinea and Australia (fig. 21).

Taxonomy. — *Hyla macgregori* Ogilby was referred to the synonymy of *H. thesaurensis* by Loveridge (1948). This decision probably arose from the superficial similarities of the colour pattern of some of the juveniles of these species. However, *H. macgregori* is clearly synonymous with *H. congenita*.

Comparison with other species. — *Hyla congenita* can be readily distinguished from all other coastal lowland species except *H. caerulea* and *H. capitula* by its short hind limbs. The TL/S-V ratio of *H. congenita* (0.477-0.520) overlaps that of *H. caerulea* (0.441-0.502), but this is about the only feature that they have in common. *Hyla caerulea* is a large species with a maximum S-V length of 110 mm, whilst the largest specimen of *H. congenita* recorded has an S-V length of only 41 mm.

*Hyla congenita* bears a superficial resemblance to the Australian species *H. rubella*, as has been noted by Peters & Doria (1878) and Roux (1920). In addition to the differences in colour pattern noted by these and other authors (*H. rubella* exhibits a very broad, dark stripe on the side of the head and body not found in *H. congenita*, and *H. congenita* has pale regular or irregular stripes or patches on the dorsal surface of the body not exhibited by *H. rubella*), the limbs of *H. rubella* are very much shorter, and comparison of the TL/S-V ratios provides a means of distinguishing the species (0.335-0.432 for *H. rubella* and 0.477-0.520 for *H. congenita*).

*Hyla congenita* is compared with *capitula* on p. 66.

**Hyla contrastens** new species (pl. 2, a)


Definition. — The characteristic features of this species are its small size (females 32-36 mm, males 25-30 mm), short limbs with a TL/S-V ratio of 0.448-0.544, and an E-N/IN ratio of 0.893-1.172. The dorsal surface is a uniform blue in preservative and green in life.

Description of holotype. — The head in flattened and longer than broad (HL/HW 1.142), its length equivalent to slightly more than one-third of the snout to vent length (HL/S-V 0.344). The snout is prominent; almost
Fig. 22. *Hyla contrastens* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
pointed when viewed from above and strongly projecting in profile. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.067). The canthus rostralis is slightly defined and gently rounded. The eye is small and inconspicuous, its diameter less than the eye to naris distance. The tympanum is visible, its diameter equivalent to slightly more than one-half the eye diameter; separated from the eye by a distance equivalent to two-thirds of its own diameter. There are no vomerine teeth. The tongue is oval with a weakly indented posterior margin.

The fingers are short and equipped with narrow lateral fringes; in decreasing order of length 3 > 4 > 2 > i. The webbing between the third and fourth fingers reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth (fig. 22).

The hind limbs are short with a TL/S-V ratio of 0.520. Toes in decreasing order of length 4 > 5 = 3 > 2 > i. The webbing of all toes except the fourth reaches the base of the discs; on the fourth toe the webbing reaches the sub-articular tubercle at the base of the penultimate phalanx.

The dorsal and lateral surfaces of the body are smooth. There is an inconspicuous, flattened supra-tympanic fold. The throat and chest are smooth, and the abdomen and lower surface of the thighs coarsely granular.

Dimensions: snout to vent length 32.3 mm; tibia length 16.8 mm; head length 11.1 mm; head width 9.8 mm; eye to naris distance 3.2 mm; internarial span 3 mm; eye diameter 3.1 mm; tympanum diameter 1.8 mm.

The ova are small and pigmented.

In preservative the dorsal surfaces of the head, body and limbs are dull blue and unmarked. There is a narrow and poorly defined white stripe on the upper jaw extending from a point below the eye to above the insertion of the forelimbs. The ventral surfaces of the body and limbs are an immaculate white and there is an abrupt demarcation on the dorso-lateral surface of the body.

Variation. — There are thirteen paratypes: M.C.Z. 54412-54423, S.A.M. R. 6450, collected with the holotype at Barabuna by F. S. Parker on 16th August, 1964.

The paratype series consists of eight adult males, four adult females and one juvenile. The snout to vent lengths of the males range from 26.3 mm to 30.2 mm; and the females 32.7 mm to 36.4 mm. The head is consistently longer than broad (HL/HW 1.027-1.189). In twelve of the paratypes the head
length is more than one-third of the snout to vent length, but in one is distinctly less. The complete range of HL/S-V ratios is 0.312-0.358. The tip of the snout is particularly subject to post mortem distortion and the range of E-N/IN ratios is based on undistorted material (0.893-1.172).

The extent of the webbing between the fingers and toes of the paratypes is similar to that of the holotype. The hind limbs are short, six specimens having TL/S-V ratios of less than 0.500. The complete range is 0.448-0.544.

Variation of colour in the paratype series is mainly confined to the tone of blue of the dorsum. Indistinct dark markings on the dorsal surface are apparently not pigmentation but evidence of bruising. In some specimens the white stripe along the side of the head merges laterally with the ventral colouration so that the dorsal and ventral colourations are more clearly demarcated on the sides of the body than in those in which the lateral stripe is inconspicuous in preservative.

Parker reports that in life the dorsal surface is usually bright green but a single specimen collected by him was a dull khaki. The ventral surface is white and the anterior and posterior surfaces of the hind limbs bright red. The green upper surface of the thighs is occasionally spotted with black.

Distribution. — An additional 131 specimens of H. contrastens have been examined: A.M. uncat. (11), Kapukamariki, Bena Bena via Goroka; A.M.N.H. 66800-68009, Kassam, Kratke Mountains; M.C.Z. 54424-54466, Noreikova (adjacent to the type locality); M.C.Z. 55201-2. These localities are situated at altitudes of approximately 4000-5500 ft and the species ranges throughout a small portion of the Eastern Mountains.

Biological and ecological notes. — The specimens collected by Parker at Barabuna and Noreikova were taken in the vicinity of swamps surrounded by flat grasslands at 5400 ft. He reports: “The frogs live in clumps of grass and reeds. By night they are found in the grass, by day many are found in the axils of leaves of cultivated banana plants in gardens, in or near the swamps. Lives communally. The call a deep “crrrrk”, the note uttered once at 3-5 second intervals.”

Comparison with other species. — The species which are within the size range of H. contrastens, and similarly coloured are H. bicolor, H. chloronota, H. gracilenta, H. leucova, H. longicrus and H. mystax. The TL/S-V ratio of H. longicrus (0.623) is so far outside the range of H. contrastens (0.448-0.548) that this single characteristic will separate the species. Hyla leucova is distinguished by the broad transverse folds on the venter (absent in H. contrastens), by the pale and spotted dorsal surface of the thighs.
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The HL/HW range of *H. contrastens* (1.027-1.189) is quite distinct from that of *H. bicolor* (1.243-1.254) and *H. gracilenta* (0.913-0.940). *Hyla chloronota* is reported to have a head as broad as long, and is found at an altitude of 8000 ft, whereas *H. contrastens* occurs at 4000-5500 ft. *Hyla mystax* has been taken at a lower altitude than *H. contrastens* and has broadly spaced nares with an E-N/IN ratio of 0.769 which is outside the range of *H. contrastens* (0.893-1.179). The HL/S-V ratios of *H. mystax* and *H. contrastens* are also quite distinct (0.386 and 0.312-0.358 respectively).

**Hyla darlingtoni** Loveridge


Holotype. — M.C.Z. 25890 collected at an altitude of 5000-8000 ft on Mt. Wilhelm, Bismarck Range, Eastern Mountains, New Guinea by P. J. Darlington Jr. in October, 1944.

Definition. — An arboreal species of moderate size (largest female 58 mm; largest male 49 mm, snout to vent length). The dorsal surfaces are brown with irregular darker marbling and occasionally a pale mid-dorsal stripe. The backs of the thighs are vividly marked with black and yellow. The webbing between the fingers is highly variable: on the fourth finger, extending from as far as the base of the disc to just below the sub-articular tubercle.

Material Examined. — 451 specimens.


Description. — The head is flattened and usually broader than long (HL/HW 0.985-1.038), its length equivalent to approximately one-third of
the snout to vent length (HL/S-V 0.317-0.344). The snout is not prominent; when viewed from above and in profile it is rounded. The nostrils are more lateral than superior, their distance from the end of the snout considerably

Fig. 23. Hyla darlingtoni Loveridge. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
less than that from the eye. The distance between the eye and the naris is less than or greater than the internarial span \( (E-N)/IN \ 0.973-1.275 \). The canthus rostralis is gently curved and slightly defined. The eye is large, its diameter equal to or slightly greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to two-thirds to three-fifths the eye diameter. The vomerine teeth are in two rounded series between and slightly below the choanae. The tongue is broadly oval with a slightly indented posterior border.

The fingers are long and possess or lack lateral fringes; in decreasing order of length \( 3>4>2>1 \). The extent of the webbing between the fingers is highly variable, reaching from the base of the discs of the third and fourth to points slightly beneath the sub-articular tubercles (fig. 23).

The hind limbs are comparatively short \( (TL/S-V \ 0.496-0.565) \). Toes in decreasing order of length \( 4>5 = or>3>2>1 \). The webbing reaches the base of the discs of all toes except the fourth.

The skin on the dorsal surfaces is smooth or tubercular. The throat and chest are slightly tubercular, and the abdomen and lower surfaces of the thighs coarsely granular. On the posterior surfaces of the forearm, hand and tarsus are rows of poorly developed tubercles.

In preservative the dorsal surfaces vary from grey to brown with darker and lighter markings. The darker markings usually comprise an indistinct diamond shaped patch on the head and a poorly defined broad mid-dorsal patch. In some specimens the darker markings take the form of irregular and indistinct marbling. The most commonly occurring lighter marking is a narrow mid-dorsal line bisecting the diamond patch on the head, and occasionally continuing posteriorly along a mid-vertebral path to the sacrum. The posterior surfaces of the thighs are yellow, variegated with black. The extent of the black pigmentation is very highly variable. Similar markings of black on a yellow background may occur on other parts of the body — on the posterior surface of the tibia, anterior surface of the tarsus, anterior surface of the thigh, in the inguinal and axillary regions and on the lateral surfaces of the body. The supra-tympanic fold is edged with black. The throat is dark brown and the remainder of the body surfaces pale brown or dull cream. The black markings on the hind limbs may extend on to the ventral surfaces.

In life the dorsal surfaces vary from grey to a brown with an orange tinge. The gular region may also be dull orange. The ground colouration of the back of the thighs is a bright orange.

Biological and ecological notes. — *Hyla darlingoni* is an arboreal species
occurring at altitudes of 4000-6500 ft in the highlands of Eastern New Guinea. It is abundant in the deforested valleys and extends into the fringe areas between the valley floors and the sub-tropical rain forests. The upper altitudinal limit of its distribution is probably determined by the availability of static or slow moving water in which the spawn is laid. In this respect it is probably unique amongst the highland species, and over much of the area in which it occurs does not co-exist with any other *Hyla* species.

Tyler (1962a, 1962b) has reported the habitat preferences, call and diet of this species and described the ova, larval mouthparts and larval feeding habits. Predation by the Colubrid snake *Ahaetulla calligaster calligaster* and small fish (*Gambusia* sp. — Poeciliidae) and endoparasitism by leeches are also reported in the latter paper.

Distribution. — *Hyla darlingtoni* is restricted to the Eastern Mountains of New Guinea between Telefomin and Okapa (fig. 24).

Comparison with other species. — Of the species occurring above 4000 ft only *H. angiana, H. arfakiana, H. eucnemis, H. micromembrana, H. multiplica, H. spinifera* and possibly *H. pratti* are within the size range of *H. darlingtoni*. In addition *H. jeudei* must be included because the type locality is unknown. The elongate fingers and the vestigeal or complete absence of webbing between them, as exhibited by *H. arfakiana, H. jeudei, H. micromembrana, H. pratti* and *H. spinifera* readily distinguish these

![Fig. 24. Distribution of *Hyla darlingtoni* Loveridge.](attachment:image)
species from *H. darlingtoni*. From *H. angiana* and *H. multiplica* it can be distinguished by difference in the E-N/IN ratios: 0.509-0.780 (*H. angiana*), 0.775-0.956 (*H. multiplica*) and 0.973-1.275 (*H. darlingtoni*).

*Hyla darlingtoni* lacks the dermal appendages that occur on the limbs of *H. eucnemis* and bears vivid black and yellow or black and orange markings on those surfaces of the limbs hidden when the animal is in the normal resting position. These markings are not exhibited by *H. eucnemis* or any of the other species with which it is being compared.

**Hyla dorsalis** (Macleay)


Holotype. — As reported by Fry (1913) and subsequent contributors, the whereabouts of the type is unknown. The specimen was obtained by W. Macleay at Katow near the mouth of the Binaturi River in the Southern Lowlands of New Guinea in 1875.

Definition. — An extremely small species of slender habitus (snout to vent length of gravid female 20 mm). The fingers are unwebbed and webbing between the toes does not reach the subarticular tubercle at the base of the penultimate phalanx on the fifth. The dorsal surface is brown, with the lateral portions darker than the median.

Material examined. — 1 specimen.  
Southern Lowlands: M.C.Z. 28389, Omati.

Description. — The head is distinctly longer than broad (HL/HW 1.153), its length equivalent to one-third of the snout to vent length (HL/S-V 0.332). The snout is prominent, pointed when viewed from above and pointed and projecting in profile. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.313). The canthus rostralis is slightly defined and straight. The eye is not prominent, its diameter slightly greater than the eye to naris distance. The tympanum is visible, its diameter equivalent to one-half of the eye diameter. The vomerine teeth are in two small, obliquely oval series between the choanae. The tongue is oval and without a posterior indentation.

The fingers are long and slender and unwebbed (fig. 25); in decreasing order of length 3>4>2>1. The terminal discs are large.
Fig. 25. *Hyla dorsalis* (Macleay). a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
The hind limbs are relatively long with a TL/S-V ratio of 0.566. Toes in decreasing order of length 4>5>3>2>1. The webbing between the toes reaches the sub-articular tubercle at the base of the penultimate phalanx.

The dorsal surfaces are smooth but for a few scattered tubercles on the upper eyelids. The throat is smooth and the abdomen coarsely granular.

In preservative the dorsal surface is brown with the dorso-lateral portions darker than the median. There is an inconspicuous dark brown supra-tympanic stripe. The posterior surfaces of the thighs are brown flecked with white. The ventral surfaces are creamy yellow, densely stippled with brown on the throat, chest and anterior one-quarter of the abdomen.

Dimensions: snout to vent length 20.5 mm; tibia length 11.6 mm; head length 6.8 mm; head width 5.9 mm; eye to naris distance 2.1 mm; inter-narial span 1.6 mm; eye diameter 2.2 mm; tympanum diameter 1.1 mm.

Taxonomy. — The status of this minute species has been the subject of debate for the whereabouts of the type is unknown, and the original description was extremely brief. Cogger (1966) has reviewed the matter in such detail that a complete account here would involve considerable repetition of recently published data. However, since there is only limited agreement between Cogger's conclusions and those of the writer it is necessary to include a brief discussion.

There are now three issues involved. One is the status of *H. dorsalis* (determined from an inadequate description), the second the identity of the specimen collected at Omati and reported by Loveridge (1956), and the third the status of the population occurring at Cairns in Queensland and described by Cogger (1966). An additional Papuan specimen was reported by Cogger but it is a juvenile and does not contribute much to the knowledge of the species.

If the original description is taken literally the generic disposition of the type is uncertain. If it is assumed that Macleay was in error in presuming the specimen to be a juvenile, that his description of toe webbing was inappropriate and misleading, and that the feature, “a broad central whitish band from the snout to the anus”, is not necessarily shared by all members of the species, then the *Hyla* specimen reported by Loveridge could well represent *H. dorsalis*. Rejection of the hypothesis necessitates a new name for the Omati frog, for it is quite distinct from all other Papuan species. Assumption of conspecificity is therefore at least the most convenient action.

Cogger maintained that to recognise the Australian population as a separate species would obscure the affinity that the specimens were presumed to share with those from New Guinea. He therefore considered them a subspecies
which he named *H. dorsalis microbelos*. This recognition of subspecies is, as Cogger points out, purely a means of indicating the presumed affinities. Since the available data are insufficient to support the action, the present contributor considers that the populations should be recognised as distinct species until a closer relationship can be demonstrated. The morphological affinities of *H. dorsalis* and *H. microbelos*, and the indication that their habitus is unlike that of the other Papuan and Australian species known at the present time, is indicated in the present contribution by placing them in a separate species group.

Comparison with other species. — The minute size of *H. dorsalis* readily distinguishes the species from other Papuan and Australian species except *H. microbelos* from Queensland. Cogger (1966) distinguishes the latter by its lack of vomerine teeth and reduced ventral pigmentation.

**Hyla dorsivena** new species (pl. 2, b)


Definition. — A moderately sized highland species (males 26.4-29 mm; females 41-48 mm) characterised by its straight canthus rostralis, broadly spaced nares (E-N/IN 0.600-0.764), long limbs (TL/S-V 0.582-0.637) and half-webbed fingers.

Description of holotype. — The head is flattened and slightly longer than broad (HL/HW 1.027), its length equivalent to less than one-third of the snout to vent length (HL/S-V 0.326). The snout is prominent and rather angular when viewed from above, and projecting and angular in profile. The nares are lateral, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.635). The canthus rostralis is well defined and straight. The eye is small and inconspicuous, its diameter greater than the eye to naris distance but less than the internarial span. The tympanum is prominent, its diameter equivalent to slightly more than one-third of the eye diameter; separated from the eye by a distance equivalent to its own diameter. The vomerine teeth are in two prominently raised and slightly oblique series between the choanae. The tongue is cordiform with an indented posterior border.

The fingers are long and equipped with narrow lateral fringes (fig. 26); in decreasing order of length 3>4>2>1. The webbing between the third and fourth fingers reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth. The terminal discs are large.
The hind limbs are long with a TL/S-V ratio of 0.589. Toes in decreasing order of length 4>5>3>2>1. The webbing reaches the base of the disc on

Fig. 26. *Hyla dorsivena* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
the fifth toe, and the sub-articular tubercle at the base of the penultimate phalanx on the fourth.

The dorsal surfaces are smooth but for scattered and poorly developed tubercles on the rim of the upper eyelid. On the posterior surface of the forearm is a scarcely detectable ridge on which are a few very small tubercles. There is a group of small tubercles on the heel and a larger patch below the anus extending onto the proximal halves of the posterior surfaces of the thighs. The ventral surface of the head and body is granular, with the granules most conspicuous on the abdomen.

Dimensions: snout to vent length 46.2 mm; tibia length 27.2 mm; head length 15.1 mm; head width 14.7 mm; eye to naris distance 3.3 mm; internarial span 5.2 mm; eye diameter 4.7 mm; tympanum diameter 1.7 mm.

In preservative the dorsal surface is dull grey with lighter and darker markings. The superficial cutaneous vessels are unpigmented and visible so that dorsum bears an irregular pattern of branched white lines. A narrow white line extends from the tip of the snout along the canthus rostralis to the posterior border of the upper eyelids. The sides of the body are creamish and sparsely marked with scattered circular black spots up to 1.5 mm in diameter. There are also a few smaller and less intense black spots extending on to the posterior surfaces of the hind limbs.

The ventral surface is a paler shade of grey than the dorsal. The ova are cream and can be seen through the wall of the abdomen.

Variation. — The paratype series consists of five females (S.A.M. R. 7902-6) and five males (S.A.M. R.7907-11) collected with the holotype by B. Craig. Measurements in the following account of variation are confined to the paratype series, but variation in colouration includes reference to the following 56 additional specimens: S.A.M. 5876, 7896, 7920-3, B.P.B.M. (uncat.), Telefomin; S.A.M. 7882-95, Ofekaman near Telefomin.

The size range of the males is 26.4-28.0 mm and of the females 41.0-46.4 mm. The head is longer than broad in nine specimens and the complete HL/HW range 0.980-1.100. There is a distinct sexual difference in the HL/S-V ratios. The females conform to the holotype description in that their head lengths are less than or only slightly greater than one-third of the snout to vent length (HL/S-V 0.318-0.339). However, in the males the HL/S-V ratio is much higher (0.364-0.390). A further sexual difference occurs in the eye diameters, with the eye less than the internarial span in females, as opposed to being equal to or very slightly greater than the internarial span in males. These points of divergence initially suggested that the material
was not entirely conspecific, but in all other respects the males and females are uniform and their homogeneity is no longer considered suspect.

The E-N/IN range of the paratypes is 0.600-0.764 (both extreme individuals are females) and the TL/S-V range is 0.582-0.637. In several specimens the length of the fifth toe is equal to the third and not greater than the third as in the holotype.

In preservative the ground colouration of the dorsum varies from dull grey to dark brown or almost black. Scattered black spots occur on the sides of some individuals, and in a few the dorso-lateral surfaces are distinctly lighter than the dorsal. In these specimens the hand is much paler than the forearm, or the forearm is uniformly pale but for a broad band of dark pigment on the wrist. Pale veins are common to approximately 20% of the specimens examined and the light head stripe to about 10%. In those specimens which exhibit very dark dorsal surfaces the ventral surfaces are densely suffused with slate.

Comparison with other species. — Of the species occurring at elevations above 5000 ft the following are about as large or larger than *H. dorsivena*: *H. angiana*, *H. arfakiana*, *H. becki*, *H. brongersmai*, *H. bulmeri*, *H. darlingtoni*, *H. micromembrana*, *H. multiplica*, *H. pratti* and *H. spinifera*. Of these *H. arfakiana*, *H. becki*, *H. brongersmai*, *H. bulmeri*, *H. micromembrana*, *H. pratti* and *H. spinifera* have unwebbed or only basally webbed fingers and therefore are readily distinguished from the one-half webbed *H. dorsivena.*

*Hyla angiana* is a considerably larger species (the smallest males and females examined have snout to vent lengths of 40.1 and 56.2 mm respectively), and the finger webbing is never as extensive as in *H. dorsivena*. In *H. multiplica* the fingers are fully or almost fully webbed; there are very well developed dermal fringes on the limbs (not present in *H. dorsivena*), and the colouration is quite different being predominantly blue. *Hyla darlingtoni* has conspicuous markings on the back of the thighs, whereas this area in *H. dorsivena* is similar to the dorsal surface of the thighs or paler but unmarked. A further difference between *H. darlingtoni* and *H. dorsivena* is that ova are pigmented in the former and unpigmented in the latter.

Colloquial names. — At Telefomin Craig recorded the following: “Atem, Degok, Neen, Nen, Okfin” and “Sisil”. Most of these are also applied to the sympatric species *H. arfakiana*.

**Hyla eucnemis** Lönnberg


Definition. — Hyla eucnemis is a large species (males 38-48 mm, females 51-71 mm) with fully webbed fingers and toes, high E-N/IN and TL/S-V ratios, triangular dermal flaps on the heels and crenulated dermal ridges on the back of the forearm and tarsus.

Material examined. — The syntypes and an additional 38 specimens.


South-east Peninsula: A.M.N.H. 6664, Oomsis Creek, Morobe District.

Description. — The head is flattened and as long as or longer than broad (HL/LW 1.000-1.219), its length less than or greater than one-third of the snout to vent length (HL/S-V 0.327-0.410). The snout is prominent, rounded when viewed from above and in profile. The nostrils are more lateral than superior, their distance from the tip of the snout about half that from the eye. The distance between the eye and the naris is greater than the inter-narial span (E-N/IN 1.020-1.500). The canthus rostralis is prominent, angular and slightly curved. The loreal region is concave and oblique. The eye is large, its diameter approximately equal to the distance separating it from the nostril. The tympanum is visible its diameter equivalent to one-half to three-fifths of the eye diameter. The vomerine teeth are in two, prominently raised series in juxtaposition or separated between the choanae. The tongue is broadly cordiform with a deeply indented posterior border.

The fingers are long, flattened with broad lateral fringes; in decreasing order of length 3>4>2>i; fully webbed, the webbing reaching the disc of the fourth and two-thirds up the penultimate phalanx of the third (fig. 27).

The hind limbs are long and muscular. The TL/S-V range is 0.538-0.639. Toes in decreasing order of length 4>5 = or>3>2>i. The webbing reaches the discs of all toes except the fourth which is broadly fringed.

The skin on the dorsal surfaces is granular or distinctly tubercular. There are crenulated ridges on the outer edge of the tarsus and fifth toe and the forearm and fourth finger. A horizontal row of triangular dermal flaps is usually present beneath the anus, and a single, large dermal flap on the heel. There is a narrow supra-tympanic fold extending from the eye to the
Fig. 27. *Hyla eucnemis* Lönnberg. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
shoulder. The throat and chest are slightly tubercular, and the abdomen and lower femur coarsely granular.

The colouration is highly variable; in preservative the dorsal surfaces are brown with or without darker or lighter markings. The basic pattern of these markings are a trilobate marking on the head and back and pale transverse bars on the hind limbs. Variation in colouration has been discussed at length and figured by Tyler (1965). The only information on the colour in life is the field note that the back of the thighs and tibia of R.M.N.H. 12025 (a juvenile) were “orange-red”.

Males possess a sub-gular vocal sac. The nuptial pad has been described by Tyler (1965).

Ecological notes. — *Hyla eucnemis* inhabits sub-tropical rain forests and has been collected at altitudes of up to 4000 ft.

Distribution. — This species has been reported from widely separated localities in New Guinea and also occurs on the Cape York Peninsula of northern Queensland.

Since publication of the distribution map by Tyler (1965) additional specimens have been examined from Mabilabol and Betabib, localities on the Ok Sibil, a tributary of the Digoel River in the Southern Lowlands.

Taxonomy. — Tyler (1965) synonymised *H. rhacophorus* Van Kampen from Etna Bay and the Australian species *H. serrata* Andersson with *H. eucnemis*. The reader is referred to that publication for further details.

Comparison with other species. — All specimens of *H. eucnemis* examined exhibit fully or almost fully webbed fingers — the webbing reaching the base of the terminal discs on the third and fourth fingers, to the disc on the third and a point above the sub-articular tubercle on the fourth. Comparisons are therefore confined to those species sharing this characteristic: *H. amboinensis*, *H. aruensis*, *H. darlingtoni*, *H. graminea* and *H. multiplica*. In each case the extent of the webbing is variable and only a few individuals have fully webbed fingers.

*Hyla amboinensis* and *H. aruensis* are both confined to lowland localities. The former may be distinguished from *H. eucnemis* by comparison of the heads of the two species, that of *H. eucnemis* being distinctly flattened with a long, curved and very prominent canthus rostralis. *Hyla aruensis* is green in life and blue in preservative and, together with *H. amboinensis*, may be further distinguished from *H. eucnemis* by the absence of dermal lappets on the limbs.

Of the remaining species *H. multiplica* and *H. graminea* are green in life
and blue in preservative. Dermal appendages on the limbs take the form of folds and not triangular lappets. *Hyla darlingtoni* lacks dermal appendages and exhibits vividly contrasting black and orange markings on the thighs — a feature not found in *H. eucnemis.*

**Hyla everetti** Boulenger


Types. — 8 syntypes, B.M. 1947.2.23.60-67. Collected at Savu and Sumba Islands, Lesser Sunda Islands by A. E. Everett during the period August-December, 1896.

Definition. — A moderately sized species (males 37-41 mm, females 41-49 mm). Confined to Timor and the Lesser Sunda Islands and characterised by an E-N/IN ratio of 1.030-1.242 and an eye diameter equal to the eye to naris distance. The dorsal colouration is grey or brown with darker marbling and the back of the thighs is yellow with brown or black markings.

Material examined. — 2 syntypes (B.M. 1947.2.23.61 from Savu; B.M. 1947.2.23.66 from Sumba) and 33 additional specimens.

Timor: M.C.Z. 13513-22, Djamplong; M.C.Z. 13523-34, Soe; N.M.B. 4914-5, Mollo, Fatoe, Menassi; S.A.M. 5808, Manatuto; S.A.M. 5811, Lospalos.

Sumba: N.M.B. 5895, Waimangura, Waidjewa; N.M.B. 5896, Pogobina.

Alor: M.C.Z. 11653.

Description. — The head is flattened and as long as or longer than broad (HL/HW 1.000-1.130), its length slightly more than or less than one-third of the snout to vent length (HL/S-V 0.305-0.376). The snout is not prominent; when viewed from above and in profile it is rounded. The nostrils are more lateral than superior, their distance from the tip of the snout considerably less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.030-1.242). The canthus rostralis is gently curved and slightly defined. The eye is large, its diameter equal to or slightly greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to approximately two-thirds of the eye diameter. The vomerine teeth are in two circular or broadly oval series situated between the choanae. The tongue is cordiform with a slightly indented posterior border.

The fingers are short and possess broad lateral fringes; in decreasing
Fig. 28. *Hyla everetti* Boulenger. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
order of length $3 > 4 > 2 > 1$. The webbing between the third and fourth fingers reaches the subarticular tubercle at the base of the penultimate phalanx of the fourth (fig. 28).

The hind limbs are comparatively short (TL/S-V $0.495-0.547$). Toes in decreasing order of length $4 > 5 = or > 3 > 2 > 1$. The webbing reaches the base of the terminal discs of all toes.

The skin on the dorsal surfaces is smooth or distinctly tubercular. The throat is tubercular and the abdomen and lower femur are coarsely granular. There is a conspicuous, slightly curved supra-tympanic fold extending from the eye to the shoulder. On the posterior surface of the forearm and tarsus are poorly developed tubercles.

In preservative the dorsal surfaces vary from grey to brown with darker and lighter irregular marbling. The inferior margin of the supra-tympanic fold is dark brown or black. The tubercles on the posterior surface of the forearm and the tarsus are white. The backs of the thighs are yellow with brown (or black — vide Boulenger, 1897) markings. These markings are scriptiform in most specimens but occasionally consist of a median brown lateral stripe widening near the anus. The throat is uniformly brown or pale cream marked with irregular brown patches particularly near the angles of the jaws. The remainder of the ventral surfaces are pale cream or white.

Males possess a sub-gular vocal sac. There is a small nuptial pad at the base of the first finger.

The variation in adult size, E-N/IN and TL/S-V ratios of the insular populations is recorded in table 1.

<table>
<thead>
<tr>
<th>Locality</th>
<th>S-V length in mm</th>
<th>E-N/IN</th>
<th>TL/S-V</th>
</tr>
</thead>
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<tr>
<td>Sumba</td>
<td>males 36.1-41.9 (2)</td>
<td>females —</td>
<td>$1.071-1.200$</td>
</tr>
<tr>
<td>Savu</td>
<td>—</td>
<td>44.0 (1)</td>
<td>$1.242$</td>
</tr>
<tr>
<td>Timor</td>
<td>35.4-42.8 (17)</td>
<td>40.3-45.5 (7)</td>
<td>$0.971-1.321$</td>
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<tr>
<td>Alor</td>
<td>—</td>
<td>48.8 (1)</td>
<td>$1.242$</td>
</tr>
</tbody>
</table>

Biological and ecological notes. — *Hyla everetti* has been collected at altitudes of 350-4500 ft in a wide variety of habitats. Smith (1927) reported that he collected the species in small temporary ponds at Djamplong and Soe, Timor, and stated that at the later locality it occurred "in such diverse situations as the open hillside, among rocks, and on the tops of high trees".
The frogs were reported to be particularly active during a heavy storm. Reporting material from Prai Jawang, Sumba, Forcart (1953b) stated that newly metamorphosed frogs were collected on the leaves of shrubs and bushes in damp palm forest.

Ova dissected from gravid females are pigmented. Smith (1927) stated that the tadpole is "large and very similar to that of H. infrafrenata", and described it as follows:

"Length of head and body twice its breadth, body rounded; nostrils nearer to the tip of the snout than the eyes, which are lateral; spiraculum on the left side of the medioventral line, midway between the lower lip and the end of the body, semitubular in form, the external opening being a transverse slit; vent dextral, the opening being above the lower border of the subcaudal crest. Tail about one and a half times as long as high, acutely pointed; crests convex, the upper starting just behind the head, not as high as the lower.

Mouth subterminal; lips bordered with a single fringe of papillae, except in the middle of the upper lip, where there is a gap; jaws broadly edged with black; upper lip with two rows of teeth, the inner broadly interrupted by the beak; lower lip with three rows, the innermost narrowly interrupted and a little shorter than the second, the outer very short, often absent.

Colour. — Olivaceous with darker spots and markings.

Dimensions of a specimen with the hind limbs well developed — Total length 63 mm.; length of head and body (to base of muscular part of tail) 23 mm.; height of tail 15 mm."

A single tadpole has been examined by the present author (M.C.Z. 13522). The horny beak is proportionately larger in relation to the size of the mouth than in Smith's figure, and the outermost row of lower labials is absent.

Distribution. — Hyla everetti occurs on Timor and adjacent Lesser Sunda Islands. A common feature of these islands is a very marked dry season for approximately four months of the year and in this period there are fewer than ten days on which rain falls (Lam, 1934).

Comparison with other species. — The only other Hyla species reported from the islands on which H. everetti occurs is H. infrafrenata, and that probably based on a record by Duménil & Bibron (1841). The colouration, size and appearance of H. infrafrenata and H. everetti are so dissimilar that no detailed comparison is needed.

The distribution data of the other species occurring to the south-west of the New Guinea mainland are scant, but it seems unlikely that any of them are sympatric with everetti.
Hyla genimaculata Horst


_Hyla papua_ Van Kampen, 1909, Nova Guinea 9: 33, pl. 2 fig. 2; Barbour, 1912: 175; Van Kampen, 1913: 457 (part); 1919: 52; Nieden, 1923: 213; Tyler, 1964b: 266; Daan & Hillenius, 1966: 120.

_Hyla montana_, Boulenger, 1914: 248 (part); Van Kampen, 1923: 33 (part).


Holotype. — R.M.N.H. 4420, collected at Gebe (Gebeh) Island (West of Waigeo Island), New Guinea, by H. A. Bernstein (probably in 1866).

Definition. — The characteristic features of _Hyla genimaculata_ are a very high E-N/IN ratio (1.250-1.585), crenated dermal folds on the posterior surfaces of the forearms and tarsus and a very small, triangular dermal appendage on the heel. Adult males have a snout to vent length of 30-41 mm and adult females 40-52 mm.

Material examined. — The holotype and 74 additional specimens.


Description. — The head is flattened and longer than broad (HL/HW 1.055-1.103), its length more than one-third of the snout to vent length (HL/S-V 0.350-0.404). The snout is high; when viewed from above and in profile it is truncate or very slightly rounded. The nostrils are lateral, their distance from the end of the snout considerably less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.250-1.585). The canthus rostralis is prominent and slightly curved. The eye is large, its diameter slightly greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to from one-quarter to almost two-thirds of the eye diameter. The vomerine teeth are in two oval series situated between and extending slightly below the level of the choanae. The tongue is small and broadly cordiform, with a slightly indented posterior border.

The fingers are long and slender with very narrow lateral fringes. In decreasing order of length, 3>4>2>1. The webbing on the fourth finger
Fig. 29. *Hyla genimaculata* Horst. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
reaches the sub-articular tubercle at the base of the penultimate phalanx (fig. 29). The terminal discs are conspicuous.

The hind limbs are long and slender with a TL/S-V ratio of 0.516-0.613. Toes in decreasing order of length 4 > 5 = or > 3 > 2 > 1. The fourth and first toes are webbed to the sub-articular tubercles at the base of the penultimate phalanx, and the remainder are webbed to the base of the terminal discs.

The skin on the dorsal surfaces is smooth or very finely tubercular. There is a very narrow supra-tympanic fold extending from the eye to a point above the insertion of the forelimbs. The upper margin of the tympanic annulus is occasionally hidden beneath this fold. On the posterior surfaces of the forearm and tarsus are single rows of triangular dermal appendages. These are acutely pointed on the forearm and obtusely pointed on the tarsus. There is a very small triangular dermal appendage on the heel, and a few prominent tubercles around the anus. The throat is tubercular, and the chest, abdomen and the lower surface of the thighs granular.

In preservative the dorsal surfaces of the body and limbs are dull blue in most specimens and marked with irregularly shaped spots and marbling of darker pigments. There is usually an hour-glass shaped brown marking commencing on the head on a level with a line running across the anterior one-third of the upper eyelids. The narrowest portion of this marking occurs behind the head, and expands posteriorly beyond the sacrum. When the limbs are adpressed a broad brown band occupying the major portion of the femur is confluent with a similar band on the tibia. Some specimens are a uniform dark brown dorsally. The dermal appendages on the limbs are white. The mandibular margin is creamish with obscure dull brown stippling. The under surfaces of the body and limbs are a greyish cream and the granular portions of the skin are dull yellow.

The colour in life has been reported by Neill (1954) as mottled with light green, dull brown and dark greyish black dorsally, and marked with transverse bands of lighter and darker pigment. The striking pattern of markings in Neill's field illustration of the holotype are not visible in any of the preserved specimens examined.

Males possess a sub-gular vocal sac and there is a small nuptial pad on the inner surface of the first finger.

Distribution. — The geographic range of this species extends from Gebeh, to the west of New Guinea, to the South-east Peninsula, and has been plotted in fig. 7.

Comparison with other species. — The lowland species whose adults are within the size range of adult *H. genimaculata* are *H. amboinensis*, *H.*
Hyla amboinensis, H. aruensis and H. lutea are readily distinguished by the extensive webbing between their fingers. Head proportions distinguish H. genimaculata from H. caerulea and H. vagabunda (HL/HW 1.055-1.103 in H. genimaculata, 0.845-1.022 in H. caerulea and 0.951 in H. vagabunda). Differences in the E-N/IN ratios separate it from H. everetti and H. nasuta (1.250-1.585 in H. genimaculata, 1.030-1.242 in H. everetti and 1.000-1.200 in H. nasuta). Hyla sanguinolenta and H. thesaurensis share with H. genimaculata high E-N/IN ratios. The first species is distinguished by its immaculate blue dorsal colouration and the absence of dermal appendages on the limbs, whilst H. thesaurensis lacks dermal appendages and has pigmented bones (unpigmented in H. genimaculata).

Hyla obtusirostris is reported to have a warty skin, a short snout and a broad head. These are major points of divergence from H. genimaculata which has a smooth skin, an exceptionally long snout and a head which is distinctly longer than broad.

Hyla jeudei is evidently a smaller species than H. genimaculata (the S-V length of the unique female holotype is 33.2 mm, whereas the range for female H. genimaculata is 40-52 mm). In addition H. jeudei differs in lacking webbing between the fingers, and by the absence of the dermal folds on the limbs and dermal appendage on the heel that characterise H. genimaculata.

Taxonomy. — Hyla loveridgei (Neill) is here referred to the synonymy of H. genimaculata.

Hyla gracilenta Peters (pl. 1, c)


Holotype. — Z. M. 6618, collected at Bowen (formerly Port Mackay), Queensland, Australia by Godefroy. Date of collection unknown.

Definition. — The characteristic features of this species are its small size (males 27.0-28.0 mm) and broad head (HL/HW 0.913-0.940). The dorsal surfaces of the head and body are blue with a cantho-rostral stripe of a paler shade. On the upper surface of the thigh, pigment is restricted to a few medial chromatophores.

Material examined. — 3 specimens.

Eastern Mountains: S.A.M. 6307-9, Hoiebia near Tari.

Description. — The head is flattened and broader than long (HL/HW 0.913-0.940), its length equivalent to one-third of the snout to vent length (HL/S-V 0.337-0.347). The snout is not prominent; truncate when viewed
Fig. 30. *Hyla gracilenta* Peters. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
from above and abrupt and slightly rounded in profile. The nostrils are more lateral than superior, their distance from the end of the snout less than one-half that from the eye. The distance between the eye and the naris is greater than the internarial span \((E-N/IN 1.042-1.238)\). The canthus rostralis is slightly defined and gently rounded. The eye is large and extremely prominent, its diameter greater than the eye to naris distance. The tympanum is covered with skin, its site indicated by the protruding annulus. The tympanum diameter is equivalent to slightly less than half the diameter of the eye; separated from the eye by a distance equivalent to half its own diameter. The vomerine teeth are in two small round series lying close together on each side of the midline, between and below the posterior borders of the small rounded choanae. The tongue is small and oval with a very slightly indented posterior border.

The fingers are short and equipped with narrow lateral fringes; in decreasing order of length \(3>4>2>1\). The webbing between the third and fourth fingers reaches the top of the sub-articular tubercle at the base of the penultimate phalanx on the fourth. The terminal discs are prominent (fig. 30).

The hind limbs are moderately long and slender \((TL/S-V 0.507-0.560)\). Toes in decreasing order of length \(4>5>3>2>1\). The webbing of all toes except the fourth reaches the base of the discs. On the fourth toe the webbing extends to a point slightly above the sub-articular tubercle at the base of the penultimate phalanx. There is a small oval inner but no outer metatarsal tubercle.

The dorsal and lateral surfaces of the head and body are finely granular. There are very narrow and inconspicuous dermal folds on the posterior surfaces of the forearm and tarsus. There is a prominent and very slightly curved supra-tympanic fold extending from the eye to slightly behind the tympanum. The throat and chest are smooth and the abdomen and lower surface of the thighs are tubercular.

There is a nuptial pad on the first finger extending proximally to a point midway up the penultimate phalanx.

In preservative the dorsal surface of the head, body and tibia and the side of the head are pale blue. There is an indistinct stripe of a paler shade commencing between the nares and continuing as a cantho-rostral stripe to the eye, continued posteriorly on the supra-tympanic fold. The dorsal surface of the thigh is pale, creamy yellow with a few pale blue chromatophores scattered on the median line. The upper portion of the arm is pale yellow and devoid of blue markings. The dermal ridges on the forearm and tarsus are white.
Distribution. — This is the first record of this species in New Guinea. Moore (1961) has discussed its distribution in Australia, demonstrating that it extends along a narrow coastal strip from New South Wales to the tip of the Cape York Peninsula in Australia. Its presence in the Southern Lowlands of New Guinea could not therefore be surprising, but the specimens reported here were collected on the southern flanks of the Eastern Mountains. The locality (Hoiebia) is 250 miles from the portion of the coast opposite to Australia. Morphologically the specimens agree favourably with examples from Australia and although differences in habitat would strongly suggest the likelihood of biological differentiation, such information is lacking and the populations must at the present time be regarded conspecific.

Comparison with other species. — Hyla bicolor, H. chloronota, H. contrastens, H. leucova, H. longicrus and H. mystax are all small species adult at approximately the same size as H. gracilenta, sharing an immaculate or only slightly marked blue dorsal surface. Hyla gracilenta is readily distinguished by having a head which is broader than long, the HL/HW range being 0.913-0.940. In all other species the head is as broad as long or longer than broad: H. bicolor 1.243-1.254, H. chloronota “as long as broad”, H. contrastens 1.027-1.189, H. leucova 1.010, H. longicrus 1.000 and H. mystax 1.086. From all but one of the species whose E-N/IN ratios are closest to H. gracilenta, it is further distinguished by the TL/S-V ratios (0.507-0.560 in H. gracilenta, 0.623 in H. longicrus and less than 0.500 in H. chloronota). From H. leucova it is distinguished by differences in the E-N/IN ratios: 0.857 in H. leucova and 1.042-1.283 in H. gracilenta.

**Hyla graminea** Boulenger


Holotype. — B.M. 1947.2.23.31, collected in “British New Guinea” at an altitude of 900 ft by E. Gerrard. Date of collection unknown.

Definition. — A large species (males 65 mm) usually a uniform green dorsally in life and blue in alcohol, characterised by fully or almost fully webbed fingers, prominent white dermal folds on the outer edge of the forearm and fourth finger, and on the knee, tarsus and fifth toe. The head is as broad as or broader than long and the ventral surface of the body immaculate.

Material examined. — 3 specimens.

Fig. 31. *Hyla graminea* Boulenger. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
Description. — The head is flattened and as broad as long or broader than long (HL/HW 0.904-1.027), its length greater than one-third of the snout to vent length (HL/S-V 0.337-0.362). The snout is not prominent; when viewed from above it is truncate or slightly rounded; when viewed in profile it is obliquely truncate, the anterior face sloping backwards meeting the superior face at an oblique angle. The nostrils are more lateral than superior, their distance from the tip of the snout less than that from the eye. The distance between the eye and naris is greater than the internarial span (E-N/IN 1.091-1.189). The canthus rostralis is straight or very slightly curved. The eye is not prominent, its diameter slightly greater than the distance separating it from the nostril. The tympanum is visible, the superior margin of the tympanic annulus touching or slightly hidden by the supra-tympanic fold; the tympanal diameter varies from two-thirds to four-fifths of the eye diameter. The position of the vomerine teeth is variable. They may be in two small series, nearer the choanae than the mid-line and extending posteriorly to the posterior margins of the choanae, or a larger series nearer the mid-line than the choanae, and extending considerably below the posterior margins of the choanae. The tongue is broadly cordiform, indented on its anterior and posterior borders. The anterior indentation is caused by a small projection on the posterior border of the mandibular symphysis.

The fingers are short, with broad lateral fringes; in decreasing order of length 3>4>2>1. The webbing between the fingers is extremely extensive, reaching the base of the disc or at least halfway up the penultimate phalanx (fig. 31).

The hind limbs are moderately long, with a TL/S-V ratio of 0.558-0.602. Toes in decreasing order of length 4>5>3>2>1. The webbing reaches the discs of all toes except the first. There is a flattened broadly oval outer and no inner metatarsal tubercle.

The skin on the dorsal surfaces of the head, body, limbs and the lateral surfaces of the body are weakly granular. The throat is smooth and the abdomen and back of the thighs coarsely granular. The supra-tympanic fold is scarcely discernable. There is a prominent thin dermal fold on the posterior surface of the forearm and fourth finger and a more conspicuous fold extending from the posterior surface of the knee along the tibia, tarsus and fifth toe.

The basic colouration is extremely uniform: in preservative all specimens are dark blue dorsally, but on the thighs it is restricted to a narrow longitudinal stripe on the superior aspect, and this colour is not present on the concealed surfaces of the femora. The back of the thighs vary from a yellowish
brown to pale lilac. The dermal folds on the limbs are an immaculate white and the ventral surfaces of the body and limbs pale cream. Boulenger states that the upper eyelid has a white edge, but this feature has not been noticed in the specimens examined.

In life the dorsal surfaces are green and the concealed surfaces of the femora and upper arms bright yellow (Parker, 1936).

Males possess a sub-gular vocal sac and a narrow nuptial pad on the first finger (fig. 3).

Distribution. — *Hyla graminea* is widely distributed on the New Guinea mainland, extending from the Vogelkop Peninsula to south-east New Guinea. In view of the superficial similarity to *H. infrafrenata* it is possible that some of the literature records of that species are based on specimens of *H. graminea*.

Notes. — One specimen (R.M.N.H. 12377) was found to be infested with a larva of the dipterous parasite *Batrachomyia* sp.

Comparison with other species. — *Hyla infrafrenata* is as large as or larger than *H. graminea* and shares a similar dorsal colouration. However it has far less webbing between the fingers than *H. graminea*, lacks prominent dermal ridges on the lateral surfaces of the forearm and tarsus and possesses a conspicuous white labial stripe not exhibited by *H. graminea*.

Of the species sharing fully webbed fingers and a uniform blue dorsal colouration, *H. aruensis* may be distinguished by the absence of lateral dermal ridges, and its smaller size. *Hyla multiplica* is a montane species with fully webbed fingers distinguished from *H. graminea* by the presence of dark spots on the lateral and ventral surfaces of the body (unpigmented in *H. graminea*), and by the E-N/IN ratio (1.091-1.189 in *H. graminea* and 0.775-0.956 in *H. multiplica*).

**Hyla infrafrenata** Gunther

Holotype. — B.M. 67.5.6.92 collected on Cape York Peninsula, Queensland, Australia. The name of the collector and the date of collection are unknown.

Definition. — The largest species of *Hyla* known, females attaining a maximum snout to vent length of 135.0 mm, and males 115.0 mm. The dorsal surfaces of the body and limbs are an immaculate green in life and blue in preservative. There is a brilliant white labial stripe extending posteriorly to the tympanic region.

Subspecies. — Two subspecies are recognised — *H. infrafrenata infra-
frenata and H. infrafrenata militaria. They may be distinguished as follows:

- Projecting rudiment of pollex present . . . . . . . . . . infrafrenata militaria
- No projecting rudiment of pollex . . . . . . . . . . infrafrenata infrafrenata

**Hyla infrafrenata infrafrenata** Gunther

*Calamita cyanea*, Tschudi, 1839: 73 (part).


*Pelodryas dolichopsis*, Meyer, 1874: 140.

*Pelodryas coerules*, Doria, 1874: 357; Peters & Doria, 1878: 428; Boettger, 1900: 327.

*Pelodryas caerulea*, Meyer, 1875: 140.


*Hyla infralineata* Rensch, 1936: 244 (lapsus for *infrafrenata*).


Material examined: — 316 specimens.

Amboina: M.C.S.N. 29688.

Aru Islands: M.C.S.N. 29695, Wokan; S.M.F. 6275, Dobo; S.M.F. 6500-1, Mangil; N.M.B. 2721, Naiguli.

Buru: M.C.S.N. 29688.

Doom Island: R.M.N.H. 12208, 12241.

Gag Island: R.M.N.H. 12235.

Misool: R.M.N.H. 12236.

Ternate: M.C.S.N. 29688.
Description. — The head is flattened and either longer than broad or broader than long (HL/HW 0.901-1.087), its length less than or greater than one-third of the snout to vent length (HL/S-V 0.302-0.364). The snout is high; when viewed from above and in profile it is rounded. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.143-1.531). The canthus rostralis is prominent and slightly curved. The eye is large, its diameter less than or slightly greater than the eye to naris distance. The tympanum is visible, its diameter equivalent to from two-thirds to four-fifths of the eye diameter. The vomerine teeth are in two large oblique series between the choanae, their posterior borders extending beyond the posterior margins of the choanae. The tongue is very large and broadly cordiform, with a deep posterior indentation and a slightly indented anterior border.
Fig. 32. *Hyla infrarrenata* Gunther. a, hand of *Hyla i. infrarrenata* Gunther in ventral view; b, first digit of *Hyla i. militaria* (Ramsay); c, head in lateral view; d, head in dorsal view; e, foot in ventral view.
The fingers are long and equipped with lateral fringes; in decreasing order of length \(3 > 4 > 2 > 1\). The webbing between the fingers is scant, on the fourth finger rarely extending as far as the sub-articular tubercle at the base of the penultimate phalanx (fig. 32). The terminal discs are large and the sub-articular tubercles are large and depressed. The nuptial pad is depicted in fig. 3.

The hind limbs are long and slender with a TL/S-V ratio of \(0.510-0.627\). Toes in decreasing order of length \(4 > 5 > 3 > 2 > 1\). The fourth toe is webbed to the sub-articular tubercle at the base of the penultimate phalanx, continuing to the discs via a broad fringe and the other toes are webbed to the base of the terminal discs.

The skin on the dorsal surfaces is smooth or glandular. There is a narrow supra-tympanic fold extending from the eye to a point behind the insertion of the forelimbs. On the posterior surfaces of the forearm and tarsus are very narrow, inconspicuous dermal folds. The lateral surface of the body is coarsely granular. The ventral surfaces of the body vary from weakly to coarsely granular.

The dorsal colouration in preservative varies from slate blue to a very deep reddish blue and is devoid of markings. The dermal ridges on the posterior surfaces of the limbs are white. There is a conspicuous white stripe extending from the mandibular symphysis along the lower jaw and continuing posteriorly to the tympanic region. This stripe is occasionally bordered inferiorly by a very narrow violet or crimson stripe. The throat is slate blue or greyish blue, and the remainder of the ventral surface pale yellowish, or dull cream. The anterior and posterior surfaces of the thigh are suffused with crimson.

In life this species is bright green dorsally and the white labial stripe is particularly conspicuous. The throat is green and the chest, abdomen and lower surfaces of the limbs are creamish or almost white. The posterior surface of the thighs is frequently suffused with dull crimson or grey.

Biological and ecological notes. — This subspecies inhabits the coastal lowlands, and extends into the highlands to a maximum altitude of slightly less than 3500 ft.

Several authors have mentioned the tadpole and Van Kampen (1906, 1923) has published descriptions. The latter is as follows:

"Length of body twice its width; tail somewhat more than one and a half the length of the body, about twice and a half as long as deep. Nostril nearer the tip of the snout than the eye; eyes lateral, as far from the tip of the snout as from the spiraculum; the distance between them about twice and
Fig. 33. Distribution of *Hyla infrafrenata* Gunther. Open circles = literature records; closed circles = specimens examined; half closed symbols indicate the distribution of *Hyla i. militaria* (Ramsay) based on specimens examined.
a half that between the nostrils, which equals the width of the mouth; spiraculum without tube; it is a transverse slit on the left side, near the medioventral line, equally distant from tip of snout and base of tail, or nearer the latter; when dextral, above the lower border of the subcaudal crest. Tail acutely pointed, the crests high, with convex border, the lower distinctly higher than the upper, which reaches forward to above the spiraculum.

Lips bordered with papillae, which are absent only on the middle part of the upper lip; jaws, especially the lower one, broadly edged with black; series of teeth i1/i2 or i1/i3, the outer one of lower lip short.

Grey above, lighter beneath, with a median and a pair of lateral light longitudinal dorsal streaks. Length 62 mm.”

Merten's (1930) notes on tadpoles from Ambon add little to the above description, other than that the dental formula of a specimen from Saparoea was i1/i2'2'.

Distribution. — This subspecies extends from Queensland throughout New Guinea to the Talaud Islands in the North-West and Timor in the South-West. Barbour (1912) includes the Solomon Islands but this is clearly erroneous. An isolated population occurs on Java, apparently introduced by man according to Van Kampen (1907a) and recorded there as early as 1857 by Bleeker. The distribution of *H. infrafrenata* is presented in fig. 33.

Taxonomy. — The taxonomy of *H. infrafrenata* has been discussed by Boulenger (1912), Loveridge (1948), Copland (1957) and Moore (1961). The only additional synonym recorded here is *H. trinilensis* Ahl (1929) of Java, considered a probable synonym by Mertens (1930) but apparently not examined by subsequent authors according to Darlington (1957). The three syntypes have been examined by the present author and are clearly referable to *H. infrafrenata*.

**Hyla infrafrenata militaria** (Ramsay)


*Hyla dolichopsis calcarifera* Vogt, 1912a: 10 (attributed to Werner but probably a lapsus for *H. dolichopsis pollicaris*).


*Hyla pollicaris*, Noble, 1931: 118.

*Hyla infrafrenata*, Hediger, 1934: 484.


Material examined. — The holotype and an additional 18 specimens.


Biological and ecological notes. — Werner (1900) briefly described and provided outline drawings of the tadpole and published the field notes of F. Dahl. The loud bass call is remarkably like the deep-throated barking of a large dog. On New Britain the species breeds in permanent swamps and flooded depressions. Amplexal pairs were collected in January and February. When handled *H. infrafrenata* releases a copious flow of secretions with an odour which is similar to that of dried thyme.

Distribution. — This subspecies is confined to the Bismarck Archipelago. It is abundant in New Britain and the Duke of York Island and probably throughout New Ireland (Ramsay's holotype is the only frog taken there). It has not been reported from New Hanover and is replaced in the Admiralty Islands by the nominate subspecies.

Comparison with other species. — The large size and presence of a conspicuous white stripe on the upper jaw distinguish this species from all other Papuan congeners. *Hyla sanguinolenta* bears a strong resemblance to *H. infrafrenata* and, with the exception of the labial stripe often exhibits a virtually identical colouration. The TL/S-V range of *H. sanguinolenta* (0.554-0.605) lies within the range of *H. infrafrenata* (0.510-0.627) as does the E-N/IN range (1.212-1.400 for *H. sanguinolenta* and 1.143-1.531 for *H. infrafrenata*). *Hyla infrafrenata* tends to have a shorter head than *H. sanguinolenta* as exemplified by the HL/HW and HL/S-V ratios (HL/HW 0.901-1.087 for *H. infrafrenata* and 1.016-1.132 for *H. sanguinolenta*; HL/S-V 0.302-0.364 for *H. infrafrenata* and 0.364-0.414 for *H. sanguinolenta*). As revealed by comparison of fig. 53 with fig. 32 the canthus rostralis is far more prominent in *H. sanguinolenta* than *H. infrafrenata*, and the tip of the snout truncate in profile, as opposed to being gently rounded in *H. infrafrenata*. *Hyla sanguinolenta* is a much smaller species with females attaining a maximum recorded snout to vent length of 55 mm and males 40 mm.

The HL/HW, HL/S-V, E-N/IN and TL/S-V ratios of *H. aruensis* overlap those of *H. infrafrenata*, but the former species has far more extensively webbed fingers and attains a maximum snout to vent length of only 43 mm.
(females) and 38 mm (males). *Hyla graminea* also exhibits ratios overlapping those of *H. infrarena* and is larger than *H. aruensis*. However, it is also separated from *H. infrarena* by almost fully webbed fingers and by possession of prominent dermal fringes on the lateral surfaces of the forearm and tibia.

Large specimens of *H. caerulea* may be distinguished from *H. infrarena* by possession of broadly fringed fingers, broad head and a lower E-N/IN range (0.927-1.171 in *H. caerulea* and 1.143-1.531 in *H. infrarena*).

**Hyla iris** Tyler


Definition. — A small montane species (males 25.3-34.1 mm; females 30.1-38 mm). In preservative the dorsal surface is blue, usually with darker and occasionally lighter markings. There is usually a deep violet patch in the groin and similarly coloured markings occur on the axilla, posterior surface of the thighs, tibia and tarsus.

Material examined. — The type series and 101 additional specimens.


Description. — The head is as broad as long or longer than broad (HL/HW 1.000-1.192), its length less than or greater than one-third of the snout to vent length (HL/S-V 0.328-0.384). The shape of the snout is highly variable, being from prominent to inconspicuous and strongly or only slightly rounded when viewed from above and in profile. The nostrils are lateral in specimens with prominent snouts and more lateral than superior in specimens with inconspicuous snouts. The nares are very much nearer
Fig. 34. *Hyla iris* Tyler. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
the eye than the tip of the snout in the latter individuals and almost equidistant in the former. The distance between the eye and the nares is less than the internarial span (E-N/IN 0.667-0.965). The canthus rostralis is curved and slightly or well defined. The eye is large and prominent, its diameter greater than the distance separating it from the nostril. The tympanum is covered with skin, its diameter equivalent to from one-third to slightly less than one-half the eye diameter. Vomerine teeth are present in the majority of specimens, and confined to small circular series on slight elevations between the choanae. The tongue is broadly cordiform with a slightly indented posterior margin.

The fingers are short and equipped with very slight lateral fringes; in decreasing order of length 3>4>2>1. The webbing reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth finger. The terminal discs are prominent (fig. 34).

The hind limbs are variable with a TL/S-V ratio of 0.485-0.587. Toes in decreasing order of length 4>5>3>2>1. The webbing between the toes reaches the base of the disc of all toes, except the fourth where it reaches the tubercle at the base of the penultimate phalanx.

The skin on the dorsal surface of the head, body and limbs is minutely roughened. The throat and chest are slightly granular. There are a row of tubercles on the posterior surface of the forearm, and conspicuous tubercles below the anus. Femoral tubercles are usually present. The supra-tympanic fold is inconspicuous.

In preservative the dorsal surface may be immaculate dark blue or densely stippled with black. Occasional specimens are a paler shade of blue, spotted with white and darker blue. Dull orange patches may extend on to the dorsum in the axillary region and a single specimen taken at Tari was dark brown (same colour in life and possibly due to a dermal lipid deficiency affecting the carotenoid distribution).

The lateral surfaces of the body are frequently heavily pigmented with black or deep violet, marked with large white patches. There is invariably a violet patch in the groin and the same colouration may be present in the axilla and on the posterior surface of the tibia and tarsus. There is a white patch beneath the eye extending to the angle of the jaws or on the lateral surfaces of the body. The ventral surface of the body is cream with or without sparse blue stippling on the throat near the angle of the jaws. The lower surface of the hind limbs is creamish yellow or dull yellow.

This species is often beautifully pigmented in life being marked with cream, orange, yellow, green, violet and black (Tyler, 1962). The colouration of a juvenile specimen is reported in the same paper.
Biological and ecological notes. — *Hyla iris* is a scansorial species found amongst low vegetation at altitudes of 4500-7500 ft. A single specimen has been collected on a moss-covered slope at 9500 ft, but there are no intermediate records. The maximum altitude record was in a catchment area considerably above the site of free flowing water. The breeding habits are such that it seems unlikely that the species could breed much above 7500 ft.

Tyler (1963) described the ova, site of deposition of spawn, early development and tadpole mouthparts and provided a field sketch of the tadpole. In view of the unusual spawning habits of this species, a precis of these data follows:

The ovum is pale green in colour and has a diameter of approximately 2.5 mm. The ova are laid in groups of from 4 to 37 (mean 14) on the leaves of trees overhanging water, and around the stems of vegetation at the edge of the water. The ova are surrounded by a very large mass of clear albumen. A period of approximately fourteen days is spent within the spawn clump, and the tadpole emerges possessing internal gills and capable of coordinated movements.
The mouth is anterior in position, and surrounded by a band of papillae on the inferior and lateral borders. There are two upper and three lower rows of labial teeth.

Ova dissected from gravid, preserved females are cream in colour and are marked with a circular patch of scattered pigment. In an ovum with a diameter of 2.3 mm, the patch had a diameter of 1.7 mm.

Distribution. — This species is abundant over a small portion of the Snow- and Eastern Mountains (fig. 35).

Comparison with other species. — Montane species within or approximating the size range of \( H. \) \( \text{iris} \) are \( H. \) \( \text{brongersmai} \), \( H. \) \( \text{bulmeri} \), \( H. \) \( \text{contrastens} \), \( H. \) \( \text{gracilenta} \), \( H. \) \( \text{leucova} \), \( H. \) \( \text{longicrus} \), \( H. \) \( \text{multiplica} \) and \( H. \) \( \text{wisselensis} \).

\( Hyla \) \( \text{brongersmai} \) is smaller than \( H. \) \( \text{iris} \) (S-V range 23.9-24.3 mm as opposed to 25.3-34.1 mm). A superficial character providing a means of distinguishing the species is the colour of the dorsal surface of the body and thighs. In \( H. \) \( \text{brongersmai} \) the body is an intensely dark brown with a slate tinge, and the thighs very much paler. In \( H. \) \( \text{iris} \) the body is dark blue with or without darker and/or lighter markings. There is a broad median band of a similar pigment on the thighs, usually bounded anteriorly and posteriorly by irregular violet markings.

\( Hyla \) \( \text{bulmeri} \) exhibits a dark lateral stripe (not occurring in \( H. \) \( \text{iris} \)), has longer limbs with a TL/S-V range of 0.592-0.618 (0.485-0.587 in \( H. \) \( \text{iris} \)), and more broadly spaced nares with an E-N/IN range of 0.605-0.641 (as opposed to 0.667-0.965 in \( H. \) \( \text{iris} \)).

The proportions of the head separate \( H. \) \( \text{gracilenta} \) from \( H. \) \( \text{iris} \) (HL/HW 0.913-0.940 in \( H. \) \( \text{gracilenta} \) and 1.000-1.192 in \( H. \) \( \text{iris} \)), whilst \( H. \) \( \text{multiplica} \) is separated by possessing conspicuous lateral dermal fringes on the limbs (lacking in \( H. \) \( \text{iris} \)) and fully webbed fingers (not fully webbed in \( H. \) \( \text{iris} \)).

\( Hyla \) \( \text{contrastens} \), \( H. \) \( \text{leucova} \) and \( H. \) \( \text{longicrus} \) all lack the vivid flash markings of \( H. \) \( \text{iris} \); \( H. \) \( \text{leucova} \) is further distinguished from \( H. \) \( \text{iris} \) by its unpigmented ova, and \( H. \) \( \text{contrastens} \) in having the animal hemispheres completely pigmented.

\( Hyla \) \( \text{wisselensis} \) has shorter hind limbs than \( \text{iris} \) (TL/S-V 0.402-0.478 in \( H. \) \( \text{wisselensis} \) and 0.485-0.587 in \( H. \) \( \text{iris} \)), and more narrowly spaced nares (E-N/IN 1.045-1.225 in \( H. \) \( \text{wisselensis} \) and 0.667-0.965 in \( H. \) \( \text{iris} \)).

There is a very marked similarity between \( H. \) \( \text{iris} \) and \( H. \) \( \text{nigropunctata} \). The latter species is distinguished by its higher E-N/IN ratio (1.091) and by its very broad lateral fringes on the fingers (no prominent in \( H. \) \( \text{iris} \)). The unusual breeding habits of \( H. \) \( \text{iris} \) are particularly suitable to montane conditions, and the species has been found at altitudes of 4500-9500 ft. \( Hyla \)
nigropunctata has been taken solely at coastal localities a few feet above sea level.

**Hyla jeudei** Werner


Holotype. — Z.M. 16498. A gravid female collected in “German New Guinea” by E. Tappenbeck. The exact type locality and date of collection are unknown.

Definition. — A very high E-N/IN ratio (1.435), short limbs with a low TL/S-V ratio (0.482), unwebbed fingers and incompletely webbed toes characterise this species.

Material Examined. — The holotype.

Description of holotype. — A gravid female. The head is long and flattened and longer than broad (HL/HW 1.073), its length more than one-third of the snout to vent length (HL/S-V 0.355). The snout is rather prominent, gently rounded when viewed from above and strongly rounded in profile. The nostrils are more superior than lateral, their distance from the end of the snout about one-half that from the eye, and separated from each other by a distance which is equivalent to approximately two-thirds of the eye to naris distance (E-N/IN 1.435). The canthus rostralis is straight and inconspicuous and the loreal region oblique. The eye is small, its diameter less than the eye to naris distance. The tympanum is visible, its diameter equivalent to two-thirds of the eye diameter and separated from the eye by a distance equivalent to approximately one-half its own diameter. The vomerine teeth are in two obliquely oval series in juxtaposition on the midline between the small, obliquely oval choanae. The tongue is small, triangular and very feebly indented on its posterior border.

The fingers are long, slender and unwebbed (fig. 36). The terminal discs are large and the sub-articular tubercles prominent. The fingers in decreasing order of length 3>4>2>i.

The hind limbs are short with a TL/S-V ratio of 0.482. The toes are incompletely webbed, the webbing reaching the base of the penultimate phalanx on the fourth toe, and half-way up the penultimate phalanx of the fifth. Toes in decreasing order of length 4>5 = 3>2>i. The skin on the dorsal surfaces of the head and body is smooth but for a few flattened tubercles on the back. The throat is smooth and the chest, abdomen and
Fig. 36. *Hyla jeudei* Werner. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
back of the thighs are coarsely granular. There is an inconspicuous supratympanic fold and a pronounced skin fold across the chest. There is neither a tarsal ridge nor a dermal appendage on the heel.

Dimensions: snout to vent length 33.2 mm; tibia length 15.8 mm; head length 11.8 mm; head width 11.0 mm; eye to naris distance 3.3 mm; inter-narial span 2.3 mm; eye diameter 3.1 mm; tympanum diameter 2.0 mm.

The dorsal surfaces of the head and body and limbs are a very pale brown with indistinct darker and lighter marbling. Marbling is present and most conspicuous on the dorsal surface of the thigh and tibia. The ventral surfaces of the body and limbs are dull cream with an irregular brown patch on the throat.

Distribution. — This species is known solely from the type locality. At the time of its collection (1900 or earlier) exploration of this territory had been extended from a few isolated coastal localities in the vicinity of Madang to the Bismarck Mountains and the Markham River headwaters. The Eastern Mountains had not been visited by European explorers. On this basis it therefore seems reasonable to assume that the site of collection is east of long. 144° and within 75 miles of the coast.

Taxonomy. — Three terminations appear in the literature (jeudii, jeudei and jeudi). In accordance with the recommendations of the 1961 Code, the genitive singular case-ending, i, is here added to the entire name of the zoologist it honours in preference to removal of the terminal vowel and addition of ii.

Comparison with other species. — *Hyla jeudei* exhibits a unique combination of characters: a rather elongated body, slender and unwebbed fingers and short limbs. The first two features are common to the majority of *Hyla* species that are only occasionally scansorial, and are invariably associated with long hind limbs. *Hyla jeudei* is therefore unusual in possessing hind limbs which are not long but in fact rather short (TL/S-V 0.482). The only species which may have as short or shorter limbs are *H. caerulea* (TL/S-V 0.441-0.502), *H. congenita* (0.447-0.520), *H. iris* (0.485-0.587) and *H. wis-selensis* (0.402-0.478). All may be distinguished by the presence of webbing between the fingers.

The high E-N/IN ratio of *H. jeudei* (1.435) is surpassed by five species: *H. eucnemis* (1.020-1.500), *H. genimaculata* (1.250-1.585), *H. infrarenata* (1.143-1.531), *H. lutea* (1.106-1.533) and *H. thesaurensis* (1.257-1.485). The presence of webbing between the fingers will also distinguish this series of species from *H. jeudei*.
**Hyla leucova** new species (pl. 3, a)


Definition. — A small species characterised by an immaculate dark blue dorsal colouration, stippled pigmentation on the dorsal surface of the thighs; eye to naris distance less than the internarial span, the absence of vomerine teeth, an immaculate unpigmented ventral surface, no flash markings in the axilla, groin or the posterior surface of the thighs, and unpigmented ova.

Description of holotype. — The head is flattened and slightly longer than broad (HL/HW 1.010), its length equivalent to slightly less than one-third of the snout to vent length (HL/S-V 0.326). The snout is not prominent; rounded when viewed from above and truncate in profile. The nostrils are almost entirely lateral, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.857). The canthus rostralis is slightly defined and quite straight. The eye is moderate in size and not prominent, its diameter only a fraction larger than the eye to naris distance. The tympanum is visible, its diameter equivalent to half the diameter of the eye; separated from the eye by a distance equivalent to half its own diameter. There are neither vomerine teeth nor vomerine elevations. The tongue is oval with a strongly indented posterior border.

The fingers are short and broadly fringed; in decreasing order of length $3>4>2>1$. The webbing on the fourth finger reaches the sub-articular tubercle at the base of the penultimate phalanx (fig. 37). The terminal discs are prominent.

The hind limbs are long and slender (TL/S-V 0.536). Toes in decreasing order of length $4>5>3>2>1$. The webbing of all toes except the fourth reaches the base of the discs. On the fourth toe the webbing reaches midway up the penultimate phalanx and is connected to the disc by a broad lateral fringe. There is a small oval inner but no outer metatarsal tubercle.

The dorsal surface of the head, body and limbs is smooth except for the upper eyelids which are weakly tubercular. There is a prominent curved supra-tympanic fold extending from the posterior corner of the eye, covering the upper rim of the tympanic annulus. The throat is smooth and the chest and anterior portion of the abdomen bear broad, flattened, transverse ridges. On the posterior portion of the abdomen the ridges are broken to form separate flattened granules in transverse rows. The skin covering the
Fig. 37. *Hyla leucova* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
posterior portion of the ventral surface of the thighs is similarly granular, but the granules are not distributed in a regular pattern. Beneath the anus is a large area of prominent tubercles.

Dimensions: snout to vent length 30.4 mm; tibia length 16.3 mm; head length 9.9 mm; head width 9.8 mm; eye to naris distance 3.0 mm; inter-narial span 3.5 mm; eye diameter 3.2 mm; tympanum diameter 1.8 mm.

The ovarian eggs are completely unpigmented and approximately 2 mm in diameter.

In preservative the dorsal surface of the head, body and tibia is an immaculate dark blue. The dorsal surface is pale creamish yellow — very finely stippled with dark blue. The stippling is absent from numerous small circular areas so that ground colouration appears in the form of circular spots. The dorsal surface of the tarsus and foot are also stippled with blue and on the tarsus there are poorly defined areas where there is no stippling. On the lateral surfaces of the body the dorsal colouration merges to a pale cream on an irregular and undulating border.

The ventral surface of the throat and body and the subanal tubercles are a pale creamish white.

Comparison with other species. — *Hyla bicolor*, *H. chloronota*, *H. contrastens*, *H. gracilenta*, *H. longicrus* and *H. mystax* are all green in life (blue in preservative) and similar in size to *H. leucova*.

A character, apparently unique to *H. leucova*, is the presence of broad, transverse dermal ridges on the ventral surface of the body.

From *H. bicolor*, *H. leucova* may also be distinguished by differences in the HL/HW ratios (1.243-1.254 in *H. bicolor* and 0.857 in *H. leucova*). In *H. chloronota* the tibia length is said to be equivalent to less than one-half of the body length (greater than one-half in *H. leucova*), and the colour of the dorsal surface of the body is said to extend along the thighs in the form of a narrow stripe. The pigmentation of the dorsal surface of the thighs of *H. leucova* is conspicuously different from the rest of the dorsum, and is not simply an extension of the pigmentation of the body.

In *H. contrastens* and *H. mystax* the colour of the dorsal surface of the thighs is similar to the rest of the dorsum, but in *H. gracilenta* there are only a few scattered chromatophores in the midline. *Hyla gracilenta* and *H. leucova* are distinguished by head proportions (HL/HW 0.913-0.940 in *H. gracilenta*; 1.010 in *H. leucova*) and by E-N/IN ratios (1.042-1.238 in *H. gracilenta* and 0.857 in *H. leucova*). The thighs of *H. longicrus* are completely unpigmented and this species has far longer legs than *H. leucova* (TL/S-V 0.623 in *H. longicrus* and 0.536 in *H. leucova*).
Hyla longicrus (Boulenger)


Types. — Two syntypes, B.M. 1947.2.22.60 collected at Fakfak and B.M. 1947.2.22.61 collected at Wendessi, Vogelkop Peninsula, New Guinea by A. E. Pratt.

Definition. — A small species characterised by its exceptionally long hind limbs (TL/S-V 0.623-0.628), widely spaced nares (E-N/IN 0.579-0.616) and uniform dorsal colouration. Snout to vent lengths — 31.8 mm (female), 27.4 mm (male).

Material examined. — 2 specimens, B.M. 1947.2.22.60 (syntype) and 1 additional specimen.

Eastern Mountains: S.A.M. 6482, Kawolabib.

Description. — The head is flattened and as long as broad (HL/HW 1.000), its length equivalent to slightly less than or more than one-third of the snout to vent length (HL/S-V 0.321-0.358). The snout is not prominent; rounded when viewed from above and in profile. The nostrils are more lateral than superior, their distance from the end of the snout about one-half that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.579-0.616). The canthus rostralis is slightly defined and gently curved. The eye is large and conspicuous, its diameter equivalent to one and one-half the eye to naris distance. The tympanum is visible, its diameter equivalent to slightly less than one-half the eye diameter. The vomerine teeth are in two very small, circular series on a line directly between the choanae. The tongue is oval with a weakly indented posterior margin.

The fingers are short and equipped with narrow lateral fringes; in decreasing order of length $3>4>2>1$. The webbing between the third and fourth fingers reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth (fig. 38).

The hind limbs are extremely long with a TL/S-V ratio of 0.623-0.628. Toes in decreasing order of length $4>5>3>2>1$. The webbing of all toes except the fourth reaches the base of the discs. On the fourth toe the webbing reaches the sub-articular tubercle at the base of the penultimate phalanx.

The dorsal and lateral surfaces of the body are smooth. There is an inconspicuous, flattened supra-tympanic fold. The throat and chest are
Fig. 38. *Hyla longicrus* (Boulenger). a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
smooth, and the abdomen and lower surface of the thighs are granular.

In preservative the dorsal surface of the body of the syntype is dull blue and unmarked. The limbs with the exception of the thighs, are a similar colour; the thighs are unpigmented. There is a short white bar below the eye extending posteriorly to the angle of the jaws. The ventral surfaces of the body and limbs are cream. In the original description the dorsum is said to be green and the throat and belly white. The S.A.M. specimen referred to H. longicrus differs from the holotype in having pigment on the dorsal surface of the thigh and in lacking the white bar below the eye.

Comparison with other species. — The species sharing with H. longicrus small size and green colouration in life (blue in preservative) are H. bicolor, H. chloronota, H. contrastens, H. gracilenta, H. leucova and H. mystax.

Hyla longicrus has a higher TL/S-V ratio (0.623-0.628) and lower E-N/IN (0.579-0.616) than any of these species: H. bicolor 0.471-0.514 and 1.136-1.158 respectively; H. contrastens 0.448-0.544 and 0.893-1.172; H. gracilenta 0.507-0.560 and 1.048-1.238; H. leucova 0.536 and 0.857; H. mystax 0.539 and 0.769. In the case of H. chloronota the E-N/IN ratio is unknown but the TL/S-V ratio is less than 0.500.

**Hyla louisiadensis** new species (pl. 4, a)


Definition. — A small species (adult males 25.8-29.2 mm) characterised by broadly spaced nares (E-N/IN 0.657-0.758), the absence of vomerine teeth and the tympanum completely covered with skin.

Description of holotype. — The head is slightly longer than broad (HL/HW 1.031), its length equivalent to more than one-third of the snout to vent length (HL/S-V 0.356). The snout is not prominent; abrupt and truncate when viewed from above and very slightly rounded in profile. The nostrils are lateral, their distance from the end of the snout slightly less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.694). The canthus rostralis is well defined and very slightly curved. The eye is large and conspicuous, its diameter greater than the eye to naris distance. The tympanum is covered with skin and very small, its diameter equivalent to one-third of the eye dia-
Fig. 39. *Hyla* *louisiadensis* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
meter; separated from the eye by a distance greater than its own diameter. There are no vomerine teeth. The tongue is broadly cordiform with a weakly indented posterior border.

The fingers are short and equipped with narrow lateral fringes. In decreasing order of length \( 3 > 4 > 2 > 1 \). The webbing between the third and fourth fingers extends to a point slightly below the paired sub-articular tubercles at the base of the penultimate phalanx on the fourth (fig. 39). The terminal discs are prominent.

The hind limbs are long and slender with a TL/S-V ratio of 0.584. Toes in decreasing order of length \( 4 > 5 = 3 > 2 > 1 \). The webbing of all toes except the fourth reaches the base of the discs, on the fourth toe the webbing reaches the sub-articular tubercle at the base of the penultimate phalanx and continues to the disc via a narrow fringe.

The dorsal and lateral surfaces of the body are finely pitted and striated. There is an inconspicuous supra-tympanic fold. The throat and chest are smooth, and the abdomen and proximal halves of the ventral surface of the thighs are coarsely granular.

There is a small pigmented nuptial pad at the base of the first finger. The vocal sac openings are exceptionally long — extending from the base of the tongue to the angles of the jaw.

Dimensions: snout to vent length 28.4 mm; tibia length 16.6 mm; head length 10.1 mm; head width 9.8 mm; eye to naris distance 2.5 mm; internarial span 3.6 mm; eye diameter 4.0 mm; tympanum diameter 1.3 mm.

In preservative the dorsal and lateral surfaces of the head, body and limbs are very dark chocolate brown, with obscure, faint, irregular patches where the chromatophores are less densely distributed. The ventral surface is a pale creamish colour, stippled with dark brown on the throat.

Variation. — There are fifteen paratypes, A.M.N.H. 60069-60078, 77017-77021 collected at Mount Riu, Sudest Island, Louisiade Archipelago during the period August 23rd-September 5th, 1956, by R. F. Peterson.

All of the paratypes are adult males with a snout to vent length range of 25.8-30.3 mm. None of the specimens possess vomerine teeth or any trace of vomerine elevations. The hind limbs are slightly shorter than those of the holotype, the TL/S-V range being 0.511-0.575. Since the holotype is the only specimen available from Rossel Island it is uncertain whether this is a significant difference of these insular populations. The E-N/IN range is 0.657-0.771 and the snout shape consistently abruptly truncate when viewed from above. A portion of the tympanic annulus is discernable in eight specimens and invisible in the remainder. Measurements
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of head length are difficult to obtain and for this reason HL/HW and HL/S-V ratios have been omitted.

All of the paratypes are a very dark chocolate brown, but the pale areas depicted by the holotype are absent.

Ecological notes. — Brass (1959) states that the collecting activities of the Fifth Archbold Expedition on Mt. Rossell (where the holotype was taken) were from a camp established at 2300 ft, “close under the peak” (2750 ft). The topotypes were evidently collected at a similar altitude on the slopes of the 2645 ft Mt. Riu. Botanical notes on Rossell Island and a photograph from the peak of Mt. Rossell are provided by Brass.

Comparison with other species. — The only species within the size range of *H. louisiadensis* and having E-N/[IN] ratios as low as or lower than this species are *H. bulmeri*, *H. iris*, *H. longicrus* and *H. mystax*. Each of these species is distinguished in being basically blue in preservative (*H. louisiadensis* is dark chocolate brown), and in having a visible tympanum (covered with skin and usually invisible in *H. louisiadensis*). *Hyla bulmeri*, *H. longicrus*, *H. mystax* and most *H. iris* have vomerine teeth, whereas these are not present in *H. louisiadensis*.

It is considered highly unlikely that *H. louisiadensis* will be found to be sympatric with any of the above species. *Hyla bulmeri* is known solely from localities in the Schrader Mountains at altitudes of 7300-8200 ft. *Hyla iris* is more widespread at elevations of 4500-9500 ft and *H. longicrus* and *H. mystax* are known from localities which, although lower than the preceding ones, are 2000 and 1000 miles distant respectively from the *H. louisiadensis* type locality.

**Hyla lutea** Boulenger


*Hyla thesaurensis*, Kinghorn, 1928a : 134 (part); Burt & Burt, 1932 : 488 (part); Tanner, 1951b : 78.

*Corunfer guppyi*, Burt & Burt, 1932 : 489 (part).

Types. — Three syntypes, B.M. 1947.2.23.50-52. Collected at Faro Island, Solomon Islands by C. M. Woodford.

Definition. — A large species confined to the Solomon Islands. Females attain a maximum snout to vent length of 73.0 mm and males 65.0 mm. This species is characterised by high E-N/[IN] and TL/S-V ratios and green bones.
In alcohol most specimens are a very pale creamish brown dorsally with or without white spots.

Fig. 40. *Hyla lutea* Boulenger. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
Material examined. — 57 specimens.

Solomon Islands: S.A.M. R.4219-4220, 4419-4420, 4918, 4932, 5155, 5160, 5165, Kunua, Bougainville; 4269, unspecified locality; S.A.M. 4931, Kieta, Bougainville; N.M.B. 4274-4275, New Georgia.

Description. — The head is flattened and usually longer than broad (HL/HW 0.986-1.156) its length equal to or greater than one-third of the snout to vent length (HL/S-V 0.333-0.360, mean 0.348). The snout is prominent; when viewed from above and in profile it is rounded. The nostrils are more lateral than superior, their distance from the end of the snout is less than half the distance between eye and naris. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.106-1.533, mean 1.296). The canthus rostralis is curved and prominent. The loreal region is concave and oblique. The eye is large, its diameter equal to the distance separating it from the nostril. The tympanum is visible, its diameter

Fig. 41. Distribution of Hyla spp. in the Solomon Islands. Hatching indicates the presence of Hyla thesaurenensis Peters alone, chequering indicates the presence of Hyla thesaurenensis Peters and Hyla lutea Boulenger.
equivalent to one-half to two-thirds of the eye diameter. The vomerine teeth are in two oblique series between the rounded choanae. The tongue is broadly cordiform with a slightly indented posterior border.

The fingers are long and possess broad lateral fringes; in decreasing order of length 3>4>2>1; almost fully webbed, the webbing reaching above the paired sub-articular tubercles at the base of the penultimate phalanx on the fourth finger. The terminal discs are large (fig. 40).

The hind limbs are usually extremely long and the TL/S-V ratio high (0.530-0.609, mean 0.572). Toes in decreasing order of length 4>5>3>2>1. The webbing between the outer and fourth toes reaches the disc of the fifth, and midway up the penultimate phalanx of the fourth, continuing to the disc as a broad fringe.

The dorsal and dorso-lateral surfaces of the body are smooth or finely granular. The throat is finely granular and the abdomen and posterior surfaces of the thighs coarsely granular. There is a broad, curved supratympanic fold extending from the eye to the shoulder, frequently covering the posterior margin of the tympanic annulus, and there are indistinct dermal folds on the posterior surfaces of the forearm and tarsus.

In preservative the dorsal surfaces of the head, body and limbs are pale sandy-brown. A few small white spots are occasionally present. The ventral surfaces are dull cream. The bones are bluish-green and the limb bones are clearly visible on the ventral surface.

In life the dorsal surfaces are dull green, yellowish-green or pale brown with white spots. The dermal folds on the posterior surfaces of the limbs are white. The ventral surfaces are dull white.

Distribution. — *Hyla lutea* is confined to north-western islands of the Solomon Islands group (fig. 41). In view of the close similarity of this species to *H. thesaurensis* it is possible that some records of the latter species from the Solomon Islands are based on *H. lutea*.

Comparison with other species. — As *H. thesaurensis* is the only sympatric species, it is the only species compared with *H. lutea*.

There is considerable overlap of all ratios. Both species have pigmented bones and highly variable dorsal colouration, and they have been synonymised by several workers. The most satisfactory means of distinguishing *H. lutea* and *H. thesaurensis* involves a comparison of the hands. In *H. lutea* the fingers are equipped with extremely broad, lateral fringes, and the webbing on the fourth finger reaches a point above the paired sub-articular tubercles situated at the base of the penultimate phalanx. Lateral fringes on the fingers of *thesaurensis* are scarcely detectable; there is a single sub-articular
tubercle at the base of the penultimate phalanx, in that species, and the webbing does not extend above it.

**Hyla micromembrana** Tyler

_Hyla montana pratti_, Loveridge, 1948: 397.


Definition. — A moderately sized species (males 30.2-35.9 mm; females 43.9-52.7 mm) characterised by the combination of the following characteristics — a high TL/S-V ratio of 0.581-0.689; a low to moderate E-N/IN ratio of 0.571-0.884. The eye is larger than the internarial span and the canthus rostralis is strongly curved (particularly in females).

Material Examined. — The type series and 715 additional specimens.


Description. — The head is usually longer than broad (broader than long in two specimens), the HL/HW range being 0.900-1.056. The head length varies from slightly less than to considerably more than one-third of the snout to vent length (HL/S-V 0.328-0.368). The snout is high; rounded when viewed from above and rounded or rarely very obtusely angular in profile. The nostrils are more lateral than superior, their distance from the end of the snout equal to or slightly more than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.571-0.884). The canthus rostralis is well defined and strongly curved. The eye is large and prominent; its diameter is greater than the eye to naris distance and approximately equal to the internarial span. The tympanum is completely visible or a portion of the annulus may be obscured by the supra-tympanic fold (most commonly the latter condition). The
Fig. 42. *Hyla micromembrana* Tyler. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
diameter of the tympanum varies from one-third to two-fifths of the eye diameter. The vomerine teeth are in two transverse or oblique series between the choanae. The tongue is very broadly cordiform with a strongly indented posterior border.

The fingers are long and equipped with extremely narrow lateral fringes (fig. 42); in decreasing order of length 3>4>2>1. The fingers are completely unwebbed or there may be a minute trace of basal webbing between the third and fourth fingers. The terminal discs are extremely prominent.

The hind limbs are very long and slender (TL/S-V 0.581-0.689). Toes in decreasing order of length 4>5 = or>3>2>1. The toes are webbed to midway up the penultimate phalanges with the exception of the fourth where it rarely reaches above the base of the penultimate phalanx.

The dorsal surfaces of the head, body and limbs are smooth or tubercular. The tubercles may be scattered over the entire surfaces or confined to the posterior halves of the upper eyelids. There is an extremely prominent supra-tympanic fold extending from the posterior corner of the eye to a point above the forearm. The throat is smooth or slightly granular, the abdomen granular and the lower surfaces of the thighs smooth or granular.

In preservative the dorsal surface of the head, body and limbs varies from light grey to dark brown or slate with irregular lighter or darker markings.

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Fig. 43. Distribution of Hyla micromembrana Tyler.
These may take the form of large spots or irregular and usually longitudinal bands. In most of the specimens with a pale ground colouration conspicuous dark brown spots are present on the lateral surfaces of the body, and the anal region is a similar colour. The ventral surface is a very dull cream, light grey or pale brown with dark spots which may be indistinct and only slightly darker than the surroundings, or conspicuous and deep violet or black.

The colouration of the dorsal surfaces in living *H. micromembrana* varies from an extremely dark green to dark chocolate with brown or pale green markings. The ventral surface is creamish or light grey with or without slate and/or violet and/or brown markings.

**Distribution.** — *Hyla micromembrana* occurs at altitudes of 4000-8000 ft in the Snow Mountains and Eastern Mountains (fig. 43). The Western limit of its distribution may extend beyond the present record of Mabilabol, for that locality is virtually the limit of intensive collecting activities. In the Eastern Mountains it is evidently abundant, but no specimens have been taken east of Okapa.

**Comparison with other species.** — The highland species sharing with *H. micromembrana* unwebbed or basally webbed fingers and E-N/IN ratios of less than 0.900 are *H. arfakiana*, *H. becki*, *H. bulmeri*, *H. modica*, *H. pratti* and *H. spinifera*. *Hyla arfakiana* is readily distinguished from *H. micromembrana* by comparison of the heads: *H. arfakiana* has a perfectly straight canthus rostralis whereas in the latter species it is very strongly curved. In *H. bulmeri* the canthus rostralis is only slightly curved and that species exhibits a distinctive dark stripe on the canthus rostralis and continuing along the dorso-lateral surfaces of the body. This marking does not occur in *H. micromembrana*.

*Hyla becki* has a lower TL/S-V ratio than *H. micromembrana* (0.565-0.576 against 0.581-0.689) and a lower E-N/IN ratio (0.500-0.553 against 0.571-0.884). The diameter of the eye of *H. becki* is very much less than the internarial span, whereas in *H. micromembrana* it is as great as or greater than the internarial span.

In *H. pratti* the canthus rostralis is straight or very slightly curved and the TL/S-V ratio (0.534-0.564) lower than that of *H. micromembrana*. *Hyla modica* is a smaller species than *H. micromembrana* (males 23.4-30.4 mm against 30.2-35.9 mm; females 27.4-35.4 mm against 43.9-52.7 mm), and the eye diameter is consistently less than the internarial span.

Males of *H. spinifera* are larger than those of *H. micromembrana* (38.4-42.3 mm against 30.2-35.9 mm) but females are within the range of *H. micromembrana*. When tubercles are present on the body of *H. micromembrana*
brana they are less abundant and of a different form to those on H. spinifera (rounded and not conical). Hyla micromembrana lacks the particularly prominent conical tubercles on the tarsus, and sub-anal tubercles, if present, are small and unlike the prominent appendages on H. spinifera.

**Hyla modica** new species (pl. 3, b)


Definition. — This species is characterised by its small size (males 23.4-30.0 mm, females 27.4-35.4 mm), moderate to relatively long limbs (TL/S-V 0.522-0.604) and broadly spaced nares (E-N/IN 0.611-0.818). The colouration is highly variable.

Description of holotype. — The head is longer than broad (HL/HW 1.132), its length equivalent to more than one-third of the snout to vent length (HL/S-V 0.350). The snout is evenly rounded when viewed from above and projects slightly in profile. The nostrils are more lateral than superior, their distance from the tip of the snout less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.727). The canthus rostralis is well defined and distinctly curved. The eye is prominent, its diameter greater than the eye to naris distance and less than the internarial span. The superior one-third of the tympanum is hidden beneath the supra-tympanic fold. The diameter of the tympanum is equivalent to slightly more than one-third of the eye diameter. The vomerine teeth are in two small oblique series between the choanae. The tongue is almost circular and lacks a posterior indentation.

The fingers are long and lack lateral fringes; in decreasing order of length 3>4>2>1. There is a small vestige of webbing between the third and fourth fingers. The terminal discs are not prominent (fig. 44).

The hind limbs are relatively long with a TL/S-V ratio of 0.558. Toes in decreasing order of length 4>5 = 3>2>1. On the fifth toe the webbing extends two-thirds up the penultimate phalanx of the fifth and to the base of the penultimate phalanx on the fourth.

The skin on the dorsal surface of the head, body and limbs is smooth but for a few small and only slightly developed tubercles on the scapular region. The throat, abdomen and lower surface of the thighs are very weakly granu-
lar. There is a row of small tubercles extending posteriorly from the angle of the jaws, and a patch of similar sized tubercles beneath the anus.

Fig. 44. *Hyla modica* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
Dimensions: snout to vent length 29.4 mm; tibia length 16.4 mm; head length 10.3 mm; head width 9.1 mm; eye to naris distance 2.4 mm; inter-narial span 3.3 mm; eye diameter 2.9 mm; tympanum diameter 0.9 mm.

The dorsal surface of the head, body and limbs is a pale sandy colour darkened by the presence of very dense, minute, dark brown stippling. The anterior portion of the head bordered laterally by the canthus rostralis, and posteriorly to a line between the anterior portions of the upper eyelids is an immaculate pale blue. Of the tubercles at the angles of the jaws those anterior to the tympanum are pale blue, whilst those posterior to it are white. The scapular tubercles are pale blue, and the lateral surfaces of the body between the axilla and the groin are liberally spotted with white. The ventral surfaces are creamish with less dense stippling than appears on the dorsum. The greatest density of groups of chromatophores on the ventral surface appears on the throat and particularly towards the mandibular margins.

Variation. — There are six paratypes, M.C.Z. 52857-52861, S.A.M. R. 8108 collected with the holotype by F. S. Parker, and an additional 101 specimens obtained by him — M.C.Z. X05826, 05828-9, 05831-7, Gomgale; 05875-6, 05878-9, 05881-2, 05892-4, 05896, 05900-1, 05903-4, 05906, 05908-9, 05911-2, Dege; 05998, 06000, 06006-9, 06011-3, 06015-7, 06019, 06022-3, 06024-8, 06030, 06032, 06035-6, 06040-1, 06044, 06048-51, 06053, 06060, 06063, 06065, 06068, 06072, Oruge; 06374, 06378, 06380-1, 06383, 06385, 06388, 06390-1, 06394, 26501-4, 26508, 26514, 26516-20, 26522, 26524-5, 26527, 26529, 26533, 26542, 26544, 26548-50, 26552, 26555-8, 26561-2, 26564-70, 26572, 26574, 26577-9, 26582, 26584-5, 26588, 26590-1, Elmagale.

The following account of variation is based on that of the paratypes and a random sample of 22 specimens from the above series.

Males vary in size from 23.4 mm to 30.0 mm and females from 27.4-35.4 mm. The head length is consistently longer than broad (HL/HW 1.028-1.155) and the head length varies from one-third (1 specimen) to considerably more than one-third of the snout to vent length, the complete HL/S-V range being 0.333-0.404. The E-N/IN range is 0.611-0.818 and the eye diameter is consistently smaller than the inter-narial span. The TL/S-V range is 0.522-0.604.

There is considerable variation in the colouration, with some specimens resembling the holotype very closely, others lacking the dorsal and lateral spots and varying from a pale sandy brown to dark chocolate, and yet others with far more extensive blue markings on the head and body than exhibited by the holotype. The ventral surfaces are frequently densely pigmented with areas of pale brown on a lighter background.
Distribution. — The localities cited above are all situated in the Kubor Range at the following elevations: Elmagale 4500 ft, Dege and Oruge 5000 ft, Gomgale 7000 ft. Twelve further representatives of *H. modica* are lodged in the South Australian Museum from three of these localities: 6175, Dege; 6181 Oruge; 6172, Gomgale. An additional 16 S.A.M. specimens are from other localities: 6578, 6584, 6589, Dumun; 6591, Mintima; 6825, 6832, Tumia. The currently known range of the species is therefore completely within the Eastern Mountains.

Comparison with other species. — The sub-montane and montane species within the size range of *H. modica* and having similarly webbed fingers are *H. brongersmai*, *H. chloronota*, *H. contrastens*, *H. gracilenta*, *H. iris*, *H. jeudei*, *H. leucova*, *H. longicrus*, *H. pratti* and *H. wisselensis*. Of these, *H. chloronota*, *H. contrastens*, *H. gracilenta*, *H. leucova* and *H. longicrus* are green in life and blue in preservative and, with the exception of a pale cantho-rostral stripe in *H. gracilenta*, immaculate dorsally and quite unlike any specimens of *H. modica*.

*Hyla brongersmai* is known from three specimens with snout to vent lengths of 23.9-24.3 mm which are within the range of *H. modica* (23.4-30.0 mm). *Hyla modica* has a lower E-N/IN ratio (0.611-0.818 compared with 0.852-0.923 in *H. brongersmai*) and the dorsal surface of the body and thighs are similarly coloured (the dorsal surface of the thighs is very much paler than the body in *H. brongersmai*).

The range of colouration of *H. iris* is totally unlike the range of *H. modica*, whilst *H. jeudei* has shorter limbs (TL/S-V 0.482 against 0.522-0.604), a significantly higher E-N/IN ratio (1.435) and pigmented ova (unpigmented in *H. modica*)

Male *H. pratti* overlap the size range of male *H. modica* (29.5-31.4 mm) but the female at 48.7 mm is well outside the range of female *H. modica* (27.0-35.4 mm). Comparison of relative eye sizes distinguish the species: in *H. pratti* the eye diameter is greater than the internarial span, whilst in *H. modica* the eye diameter is consistently less than the internarial span.

*Hyla wisselensis* has a variable colouration but the various patterns exhibited are quite distinct from the range of *H. modica*, and the species are readily distinguished by a comparison of the TL/S-V ratios (0.402-0.478 in *H. wisselensis* and 0.522-0.604 in *H. modica*).

*Hyla micromembrana* occasionally closely resembles *H. modica* in its colouration, but is a larger species (males 30.0-36.0 mm, females 44.0-53.0 mm) in which the TL/S-V is usually higher (0.581-0.689) and the eye diameter is most commonly very much greater than the internarial span.
TYLER, PAPUAN HYLID FROGS OF THE GENUS HYLA

Hyla multiplica Tyler


Definition. — The species is characterised by fully webbed outer fingers, a large rounded head with inconspicuous eyes, well developed dermal folds on the posterior surface of the forearm, anus, tibia, tarsus and fifth toe, and (in preservative) a distinctive colouration in which blue and violet are the predominant pigments. Hyla multiplica is a moderately sized species, for females attain a maximum snout to vent length of 48.0 mm and males 42.0 mm.

Material examined. — The type series and 44 additional specimens.


Description. — The head is large, broadly rounded and broader than long or longer than broad (HL/HW 0.993-1.058), its length equivalent to one-third or less than one-third of the snout to vent length (HL/S-V 0.302-0.337). The snout is very high; rounded when viewed from above and rounded or truncate in profile. The nostrils are oblique, their distance from the end of the snout about one-half that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.775-0.956). The canthus rostralis is slightly defined and gently rounded. The eye is small, inconspicuous and surrounded by a loose fold of skin which extends beyond the margin of the orbit. The eye diameter is less than or greater than the eye to naris distance. The tympanum is completely covered with skin. Its site may be indicated by a depression or by protrusion of a portion of the tympanic annulus. The diameter of the tympanum is equivalent to approximately two- to three-fifths of the eye diameter. The vomerine teeth are in two small, rounded series situated between the choanae. The tongue is cordiform, its posterior border free and slightly indented.

The fingers are short; in decreasing order of length 3>4>2>1. The webbing reaches the disc or at least half way up the penultimate phalanx on the fourth finger, whilst the remaining fingers are at least half-webbed. The terminal discs are large (fig. 45).

The hind limbs are long and there is considerable variation in the TL/S-V ratio (0.533-0.635). The upper portion of this range is occupied by the
Fig. 45. *Hyla multiplica* Tyler. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
largest females examined but in the absence of sexually immature specimens it is not possible to establish whether there is a distinct ontogenetic trend.

Toes in decreasing order of length 4 > 5 > 3 > 2 > 1. The webbing between the toes reaches the discs of all but the fourth, where it extends as far as the base of the penultimate phalanx and continues to the disc as a fringe. There is a distinct oval inner but no outer metatarsal tubercle.

The skin on the dorsal surfaces of the head and body is minutely glandular. There is a narrow, prominent dermal fold on the outer surface of the forearm and fourth finger, and a more conspicuous fold extending from the knee, along the tibia, tarsus and fifth toe. There is an extremely prominent bilobed dermal flap beneath the anus and large round or conical tubercles on the undersurfaces of the thighs particularly numerous proximally. There is a poorly defined, flattened supra-tympanic fold. The sides of the body, the throat and chest are minutely granular, and the abdomen more conspicuously granular.

The colour in preservative is extremely uniform. The dorsal and lateral surfaces of the head and body and the dorsal surface of the limbs are dark blue marked with numerous very small patches of a paler shade. These patches are particularly numerous on the body. On the thighs this colouration is confined to a narrow median strip, and on the forearm it terminates abruptly at the wrist. The anterior and posterior surfaces of the thighs are maroon and a maroon patch is often present on the posterior surfaces of the humerus near the axilla. The lateral and ventral surfaces of the body and limbs are cream and the throat cream or a pale pearl. The mandibular margin is pale blue, and the abdomen and tibia (and occasionally femur) are marked with irregularly shaped spots of brilliant violet. These violet spots extend on to the lateral surfaces of the body and occasionally reach a point above the insertion of the forearm. The dermal ridges on the limbs and below the anus are an immaculate white.

A colour transparency of a living specimen provided by F. Parker depicts a rich lime green dorsal surface with small isolated spots of a paler shade of green.

Distribution. — Apparently confined to the Eastern Mountains.

Comparison with other species. — No Papuan Hyla species shares with H. multiplied a blue dorsal colouration in preservative, fully or almost fully webbed outer fingers, prominent dermal ridges on the outer surface of the forearm and tibia and large spots of blue pigment conspicuous on the lateral body surfaces and extending to the ventral.

Hyla graminea shares the above characters except the spots of pigment
on the lateral and ventral surfaces of the body. The E-N/IN and HL/S-V ratios also distinguish the species (E-N/IN 0.775-0.956 in *H. multiplied* and 1.091-1.189 in *H. graminea*; HL/S-V 0.302-0.337 in *H. multiplied* and 0.337-0.362 in *H. graminea*). Some *Hyla aruensis* exhibit a similar dorsal colouration and finger webbing, but the prominent dermal folds on the limbs and the distinctive ventral and lateral body pigmentation are absent.

*Hyla eucnemis* has fully webbed fingers and bears dermal appendages on the limbs (but in the form of crenulated ridges). Although the dorsum may be marked with blue, the predominant colour of preserved *H. eucnemis* is brown. A further distinguishing character is the E-N/IN ratio which, as that of *H. graminea*, is higher than in *H. multiplied* (1.020-1.500).

Some *H. iris* bear a superficial resemblance to *H. multiplied*, and the largest female *H. iris* examined has a snout to vent length of 38.0 mm, which is just within the range of *H. multiplied*. Dense pigmentation occurs on the lateral body surfaces of *H. iris*, and may extend on to the ventral surface. However, that species lacks the dermal ridges on the limbs and has less webbing between the fingers.

**Hyla mystax** Van Kampen

*Hyla mystax* Van Kampen, 1906, Nova Guinea 5 (17): 173, pl. 6 fig. 6, 1907b: 415; Barbour, 1912: 177; Van Kampen, 1919: 52; Nieden, 1923: 211.

*Hyla bernsteini*, Van Kampen, 1923: 31 (part).

Holotype. — R.M.N.H. 4632 collected at Moaif, Northern Lowlands, New Guinea by the Netherlands New Guinea Expedition of 1903, during the period 26th June to 4th July.

Definition. — A small species with a large head (HL/S-V 0.386), widely spaced nares (E-N/IN 0.769), prominent eyes and a uniform dark blue dorsal colouration.

Material examined. — The holotype.

Description. — The head is prominent, high and longer than broad (HL/HW 1.086), its length equivalent to considerably more than one-third of the snout to vent length (HL/S-V 0.386). The snout is high; abrupt and gently rounded when viewed from above and slightly rounded in profile. The nostrils are lateral, their distance from the end of the snout equivalent to approximately half the distance from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.769). The canthus rostralis is prominent and strongly curved. The eye is large and conspicuous, its diameter greater than the eye to naris distance. The inferior
Fig. 46. *Hyla mystax* Van Kampen. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
three-quarters of the tympanum are visible, its diameter equivalent to two-fifths of the eye diameter. The vomerine teeth are in two small circular series on slight elevations between the choanae. The tongue is broadly oval with a very slightly indented posterior margin.

The fingers are short and equipped with narrow lateral fringes; in decreasing order of length $3 > 4 > 2 > 1$. The webbing between the third and fourth fingers reaches the sub-articular tubercle at the base of the penultimate phalanx on the fourth (fig. 46).

The hind limbs are short with a TL/S-V ratio of 0.539. Toes in decreasing order of length $4 > 5 = 3 > 2 > 1$. The webbing of all toes except the fourth reaches the base of the discs. On the fourth toe the webbing reaches the sub-articular tubercle at the base of the penultimate phalanx.

The dorsal and lateral surfaces of the body are very slightly granular. There is an inconspicuous, flattened supra-tympanic fold covering the superior one-quarter of the tympanum. The ventral surface of the body and lower surface of the thighs are granular. There is an inconspicuous dermal ridge on the posterior surface of the forearm, and a further ridge on the tarsus, foot and fifth toe. There is a broadly flattened dermal ridge beneath the anus and a few conspicuous tubercles below it.

Dimensions: snout to vent length 29.5 mm; tibia length 15.9 mm; head length 11.4 mm; head width 10.5 mm; eye to naris distance 3.1 mm; internarial span 3.9 mm; eye diameter 3.6 mm; tympanum diameter 1.5 mm.

In preservative the dorsal surfaces of the head, body and limbs are dark blue and unmarked. There is a broad white bar beneath the eye, broken below the posterior corner and then extending posteriorly to a point in front of the insertion of the forearm. The dermal ridges are white. The posterior surface of the thighs and tarsi, and the anterior surface of the thighs are maroon. The ventral surfaces of the body and limbs are a pale yellowish cream colour.

The specimen has evidently faded since it was described. In the original description Van Kampen stated that the dorsal surfaces were greenish-blue, the posterior surface of the thighs black, and the underside (of the body) yellowish brown.

Taxonomy. — Van Kampen (1923) referred *H. mystax* to the synonymy of *H. bernsteini* a species in turn relegated to the synonymy of *H. nigropunctata* by Loveridge (1948).

Distribution. — Van Kampen (1907) includes Australia within the range of *H. mystax*. There is no evidence of literature references to any specimens other than the holotype, and the record is clearly erroneous.
Comparison with other species. — The species which are green in life (blue in preservative) and within or near to the size range of *H. mystax* are *H. bicolor*, *H. chloronota*, *H. contrastens*, *H. gracilenta*, *H. leucova* and *H. longicrus*. The head of *H. mystax* is very much longer than in any of the other species, the HL/S-V ratio of *H. mystax* being 0.386 and *H. bicolor* 0.295-0.333, *H. contrastens* 0.312-0.358, *H. gracilenta* 0.337-0.347, *H. leucova* 0.326 and *H. longicrus* 0.321.

Of the coastal species possibly sympatric with *H. mystax*, *H. nigropunctata* is distinguished by its distinctive colouration and higher E-N/IN ratio (0.769 in *H. mystax* and 1.091 in *H. nigropunctata*).

**Hyla napaea** new species (pl. 3, c)

Holotype. — A.M.N.H. 49659, a gravid female collected at an altitude of 2830 ft at Camp 2, 3-4 miles south-west of Bernhard Camp, Idenburg River, Snow Mountains, New Guinea by W. B. Richardson of the Third Archbold New Guinea Expedition, in March 1939.

Definition. — A small species, males 19.0-23.0 mm, females 25.0-28.0 mm with long limbs (TL/S-V 0.590-0.679), broadly spaced nares (E-N/IN 0.818-0.931) and vomerine teeth which are not or only slightly elevated. The dorsal colouration consists of cryptic lichen-like markings on a pale background.

Description of holotype. — The head is as long as broad (HL/HW 1.000), its length equivalent to more than one-third of the snout to vent length (HL/S-V 0.366). The snout is rather prominent; slightly projecting and obtusely pointed when viewed from above, and slightly projecting in profile. The nostrils are more lateral than superior, their distance from the end of the snout approximately two-thirds that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.900). The canthus rostralis is well-defined and strongly rounded. The eye is large and prominent, its diameter greater than the eye to naris distance. The tympanum is covered with skin, only the inferior half of the annulus being visible. The tympanum diameter is equivalent to two-fifths of the eye diameter; separated from the eye by a distance greater than its own diameter. The vomerine teeth are on two straight, very slightly raised ridges commencing at the superior margins of the choanae and extending obliquely downwards for a distance equivalent to the diameters of the choanae. The tongue is rather distorted and roughly cordiform in shape with a very slightly indented posterior margin.
Fig. 47. *Hyla napaea* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
The fingers are long and slender with lateral fringes; in decreasing order of length $3 > 4 > 2 > 1$. The webbing between the third and fourth fingers reaches a point slightly below the sub-articular tubercle at the base of the penultimate phalanx on the fourth. The terminal discs are not prominent (fig. 47).

The hind limbs are very long and slender ($\text{TL}/\text{S-V} 0.679$). Toes in decreasing order of length $4 > 3 > 5 > 2 > 1$. The webbing of all toes except the fourth reaches the base of the discs. On the fourth toe the webbing reaches the sub-articular tubercle at the base of the penultimate phalanx. There is a small flattened, kidney-shaped inner but no outer metatarsal tubercle.

The dorsal and lateral surfaces of the head and body are smooth but for a few, widely scattered, flattened tubercles. There is a weak and very slightly curved supra-tympanic fold extending from the posterior corner of the eye to slightly behind the tympanum. The throat and chest are smooth and the abdomen and proximal halves of the lower surface of the thighs are coarsely granular.

Dimensions: snout to vent length 26.8 mm; tibia length 17.8 mm; head length 9.8 mm; head width 9.8 mm; eye to naris distance 2.7 mm; internarial span 3.0 mm; eye diameter 3.5 mm; tympanum diameter 1.3 mm.

In preservative the dorsal surfaces of the head, body and limbs are pale grey marked with black marbling and irregular variegations. Around the variegated markings there are areas of black stippling, each dot of which stands in the centre of a small unpigmented circular spot. The ventral surfaces of the body and limbs are a dull creamish colour with scattered black stippling on the throat, the posterior ventro-lateral surface of the thighs and on the tarsus and foot.

Variation. — There are six paratypes: A.M.N.H. 49657, 49573, 49575, 77022-4 collected at the type locality by Richardson during the period March-April, 1939.

The male paratypes vary in size from 18.8-22.7 mm and the females 25.1-28.3 mm. They conform closely to the description of the holotype, variation in the ratios being as follows: $\text{HL}/\text{HW} 1.000-1.128$, $\text{HL}/\text{S-V} 0.336-0.398$, $\text{E-N}/\text{IN} 0.818-0.931$, $\text{TL}/\text{S-V} 0.590-0.679$. The unusual condition of the vomerine teeth of the holotype is shared by two of the paratypes, and there is no trace of any vomerine elevations in the remainder. Ovarian eggs are unpigmented.

The marbling, variegations and stippling on the dorsum of the paratypes is extremely variable and follows no distinct pattern. The ground colouration is brownish or greyish.
Habitat. — The type locality is situated in an enclosed valley drained by a tributary of the Sahoeweri River and named the Araucaria River. Archbold, Rand & Brass (1942) described the type locality and published plates of the camp site and surrounding vegetation. They noted rain forest occupied the floor of the valley, and described the presence of an unusual amount of moss on trees and on the ground. This occurrence led them to conclude that the frequent fogs and mists which they experienced were more than a seasonal occurrence. The ranges of temperature recorded during the expedition's stay (March 6th-April 5th, 1939) were: maximum range 22.5-28°C (mean 25°C); minimum 16.5-19°C (mean 18°C).

Comparison with other species. — The only species which are adult within the size range of *H. napaea* are *H. brongersmai*, *H. pygmaea*, and *H. wisselensis*.

*Hyla brongersmai* shares with *H. napaea* a brown dorsal colouration but is darker and lacks the markings of *H. napaea*, and is readily distinguished by its blunt snout (somewhat pointed and slightly projecting in *H. napaea*) and shorter limbs (TL/S-V ratio 0.519-0.544 in *H. brongersmai* and 0.590-0.679 in *H. napaea*).

*Hyla pygmaea* is vividly marked with white or brown, has shorter limbs (TL/S-V 0.495-0.564) and a higher E-N/IN ratio (1.029-1.143 in *H. pygmaea* and 0.818-0.931 in *H. napaea*).

Although the colouration of *H. wisselensis* is very highly variable it does not bear any resemblance to that of *H. napaea*, and it is readily distinguishable in having exceptionally short legs with a TL/S-V ratio of 0.402-0.478.

**Hyla nasuta** (Gray)


Holotype. — B.M. 1947.2.22.81. Collected at Port Essington, Northern Territory, Australia by “Gilbert”. Date of collection unknown.

Definition. — A slender terrestrial species with an elongated head and body, and extremely long hind limbs (TL/S-V 0.649-0.826, mean 0.754). Females attain a maximum snout to vent length of 55.0 mm and males 45.0 mm. The fingers are unwebbed and the toes scantily webbed; on the fourth toe two phalanges are free.
Fig. 48. *Hyla nasuta* (Gray). a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
Material examined. — 78 specimens.


Description. — The head is very much longer than broad (HL/HW 1.280-1.374), its length considerably greater than one-third of the snout to vent length (HL/S-V 0.397-0.419). The snout is projecting; when viewed from above and in profile it is rounded. The nostrils are more lateral than superior, their distance from the tip of the snout less than that from the eye. The distance between the eye and the naris is usually greater than the inter-narial span (E-N/IN 1.000-1.200). The canthus rostralis is straight and inconspicuous. The eye is not prominent, its diameter equal to the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to approximately three-quarters of the eye diameter. The vomerine teeth are in two oblique series between the rounded choanae. The tongue is oval.

The fingers are long and slender, and lack lateral fringes. In decreasing order of length $3>4>i>or = 2$. There is no webbing between the fingers. The terminal discs are extremely small (fig. 48).

The hind limbs are slender and extremely long with a very high TL/S-V ratio (0.649-0.826, mean 0.754). The toes are extremely long; in decreasing order of length $4>3>5>2>i$. The webbing of the toes is scant with the disc and two phalanges of the fourth toe free. The sub-articular tubercles are rounded and prominent, and the inner metatarsal tubercle oval and projecting.

The skin on the dorsal surface of the body is disrupted by the presence of longitudinal, raised skin folds and flattened tubercles. The throat and chest are smooth, and the abdomen and lower surface of the thigh minutely granular. There is a skin fold across the chest, and an inconspicuous supratympanic fold.

In preservative the basic colouration of the dorsal surface of the body is brown with lighter and darker markings. The most commonly occurring lighter markings are a broad, pale tan mid-dorsal stripe from the tip of the snout to the end of the body, with or without a broad longitudinal stripe on each side of the mid-line commencing behind the head and continuing to the end of the body. The dorso-lateral surfaces of the body are brown with darker spots and there is a broad stripe on the side of the head anterior to the eye. The posterior surface of the thighs is marked with brown and
cream. Throat and chest are white and the abdomen and lower surfaces of the thighs pale yellow. The throat of males is stippled with brown.

Distribution. — *Hyla nasuta* is widely distributed in the lowlands of the southern portion of New Guinea and occurs in a wide arc along the coast of eastern and northern Australia (Moore, 1961). The New Guinea population extends from Milne Bay in the South-east Peninsula to Kawakit on the upper reaches of the Digul River approximately 760 miles to the west. It probably occurs further west in the unexplored swamplands.

Taxonomy. — *Hyla semoni* Boettger from Milne Bay was synonymised with *H. nasuta* by Van Kampen (1909a). The writer has examined a photograph of the holotype of *H. semoni* (S. M. F. 2625) and measurements of the specimen taken by Dr. K. Klemmer, and supports Van Kampen’s opinion.

Comparison with other species. — Elongation of the head, body, hind limbs and digits are more pronounced in this species than in any other Papuan species.

The HL/HW range of 1.280-1.374 is exceptionally high, the nearest approaching the range being a single specimen of *H. eucnemis* with a ratio of 1.219. The high HL/S-V range of 0.397-0.419 is overlapped by *H. eucnemis* (0.327-0.410), *H. genimaculata* (0.350-0.404) and *H. sanguinolenta* (0.364-0.414). All of these species possess webbing between the fingers, lacking in *H. nasuta*.

The extremely high TL/S-V ratio of 0.649-0.826 is overlapped by only two species: *H. arfakiana* (0.554-0.712) and *H. spinifera* (0.612-0.693), and nearly overlapped by *H. angiana* (0.524-0.647). *Hyla angiana* has webbed fingers and broadly spaced nares with an E-N/IN range of 0.509-0.570 which is well outside the range of *H. nasuta* (1.000-1.200). *Hyla arfakiana* and *H. spinifera* lack webbing between the fingers, but also have much lower E-N/IN ranges (0.600-0.760 for *H. arfakiana* and 0.604-0.783 for *H. spinifera*).

**Hyla nigropunctata** (Meyer)


Hyla ouwensi, Van Kampen, 1923: 37.


Type. — The holotype was collected at Jobi Island, Geelvink Bay, New Guinea by A. B. Meyer in 1873. The specimen was lodged in the Dresden Museum (Schüz, 1929) and lost when the museum was destroyed during the Second World War.

Definition. — A small coastal species attaining a maximum snout to vent length of approximately 34.0 mm. The fingers are short and equipped with broad lateral fringes and extensive webbing. E-N/IN ratio is 1.091 (single specimen). In preservative the dorsal surfaces are dull blue with lighter and darker markings, and the groin and posterior surface of the thigh is a brownish violet.

Material examined. — 2 specimens.

Jobi Island: M.C.Z. 2434 (H. ouwensi holotype), Pom.

Gebe Island: R.M.N.H. 4421 (H. bernsteini syntype).

Description. — The head is moderately flattened and longer than broad (HL/HW 1.033-1.077), its length slightly or considerably more than one-third of the snout to vent length (HL/S-V 0.334-0.366). The snout is not prominent; when viewed from above and in profile it is gently rounded. The nostrils are lateral, their distance from the tip of the snout less than that from the eye. The distance between the eye and the naris is greater than the internarial span (one specimen), E-N/IN 1.091. The canthus rostralis is curved and only slightly defined. The eye is large and prominent, its diameter greater than the distance separating it from the nostril. The tympanum is covered with skin, its diameter equivalent to from one-quarter to one-half of the eye diameter. The vomerine teeth are reduced to a single or pair of teeth near each choana, and are not elevated. The tongue is broadly cordiform with a slightly indented posterior margin.

The fingers are short and equipped with fairly prominent lateral fringes and paired sub-articular tubercles; in decreasing order of length 3>4>2>i. The webbing reaches midway up the terminal phalanx on the fourth finger. The terminal discs are prominent (fig. 49).

The hind limbs are moderate with a TL/S-V ratio of 0.526-0.566. Toes in decreasing order of length 4>5>3>2>1. The webbing reaches the
Fig. 49. *Hyla nigropunctata* (Meyer). a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
base of the disc of all toes, except the fourth where it extends to a point midway between the disc and the sub-articular tubercle at the base of the penultimate phalanx.

The skin on the dorsal surfaces of the head, body and limbs is minutely roughened. The throat and chest are smooth but for a few flattened tubercles. The abdomen and lower femora are coarsely granular. There is a short row of tubercles on the outer surface of the fourth finger. A more conspicuous dermal ridge extends along the outer surface of the tarsus and fifth toe. There are numerous tubercles below the anus, and two extremely prominent femoral tubercles. The supra-tympanic fold is inconspicuous.

In preservative the dorsal surfaces of the head, body and limbs are a pale greyish blue marked with numerous, small, indistinct darker spots, and a few white spots. The backs of the thighs are a deep brownish violet. There are similarly coloured patches in the groin and on the posterior surface of the tibia. The dermal ridges are white and there is a white patch around the anus and beneath the eye. The throat is white, sparsely stippled with black at the angle of the jaws. The chest is creamish and the abdomen and lower surface of the limbs dull yellow.

Taxonomy. — Although the exact type locality was not reported by Meyer, the short duration of his visit to Jobi indicates that it may be safely assumed that the holotype was collected within the vicinity of Ansus, the only locality mentioned in his paper. (Although at least a portion of the published account of Meyer’s travels within Geelvink Bay has been proved fictitious by Wichmann (1912), there is no evidence to indicate that the specimens purported to have been collected at Jobi were not found there).

*Hyla ouwensi* Barbour was collected at Pom, a coastal locality on Jobi very near to Ansus, and conforms to the brief description sufficiently to support Loveridge’s (1948) step of synonymising the species with *H. nigropunctata*. *Hyla bernsteini* was also considered a synonym by Loveridge (1948) and re-examination of one of the syntypes confirms this opinion.

The secondary homonym *Hyla nigropunctata* Boulenger of South America has been referred to the synonymy of *Phrynokyas spilomma* (Cope) by Duellman (1956).

Comparison with other species. — The lowland species within the size range of *H. nigropunctata* are *H. capitula*, *H. congenita*, *H. longicrus*, *H. loisiadensis*, *H. mystax* and *H. pygmaea*. *Hyla capitula* and *H. congenita* are rather squat species and have short limbs with TL/S-V ratios of 0.496 and 0.477-0.520 respectively, whereas *H. nigropunctata* is more...
slender and has longer limbs with a TL/S-V range of 0.526-0.566. In preservative the ground colouration of the dorsal surface of *H. capitula* and *H. congenita* is invariably pale brown whereas *H. nigropunctata* is blue.

*Hyla longicrus*, *H. louisiadensis* and *H. mystax* share broadly spaced nares (E-N/IN ratios being 0.579, 0.657-0.691 and 0.769 respectively), whereas in *H. nigropunctata* the distance between the eye and the naris is slightly greater than the internarial span (E-N/IN 1.091). *Hyla longicrus* is further distinguished in having longer limbs and in being immaculate dorsally. *Hyla mystax* has a very much longer head and *H. louisiadensis* may be distinguished by the fact that the tympanum is covered with skin and is not a prominent feature.

*Hyla pygmaea* is an extremely distinctive species bearing (in preservative) large white spots against a brown background, therefore contrasting with the appearance of *H. nigropunctata*. The fingers of *H. pygmaea* lack lateral fringes exhibited by *H. nigropunctata*.

The characters distinguishing *H. nigropunctata* from the montane species *H. iris* are discussed in the account of the latter species.

**Hyla obtusirostris** (Meyer)


The holotype was collected at Anus on the south coast of Jobi (Japan) Island, Geelvink Bay, by A. B. Meyer in 1873 and lodged in the Dresden Museum. Its presence there was confirmed by Schüz (1929) and the specimen was lost when the museum was destroyed during the Second World War. No further specimens have been reported and there is an urgent need for topotypic material.

A translation of Meyer's original description is as follows: "Webbing complete, discs rather large. Typanic diameter half as large as the eyes, tympanum rather deeply set. Short snout, frenal region feebly concave, nearly even. Canthus rostralis very feeble. Head broad. Heel of hind extremity reaches more than 8.0 mm beyond the tip of the snout. Vomerine teeth are in two round groups between and behind the choanae. The skin finely warty over the entire body. On greyish blue background are small yellowish warts so that the complete pigmentation has a bluish tinge. Under-
side pale, without any pattern. Total length 37.0 mm, head length 15.0 mm, head breadth 14.0 mm, forelimb 26.0 mm, hand with third finger 12.0 mm, hind limb 68.0 mm, foot with fourth toe 29.0 mm."

There is one point at which there is a divergence from previous translations. Boulenger (1882) and Van Kampen (1923) describe the fingers as “free” and the toes “entirely webbed”. Meyer (1875) stated “Schwimmhäute vollständig”, but, as he did not qualify this statement in any way, it is uncertain whether he was referring solely to the webbing of the feet or to the hands and feet. His action of referring the species to the genus *Litoria* Tschudi indicates that it lacked webbing between the fingers but there is no explicit statement in the original description.

Comparison with other species. — *Hyla obtusirostris* is evidently a long limbed species. For the heel of a specimen with a total length of 37.0 mm to extend more than 8.0 mm beyond the tip of the snout, a TL/S-V ratio greater than 0.600 is indicated.

Of the lowland species adult at a similar or greater total length, *H. nasuta* is the only one with a TL/S-V ratio consistently higher than 0.600, but individuals of *H. amboinensis*, *H. genimaculata*, *H. infralateralis* and *H. thesaurensis* occasionally reach or exceed that figure. The only one of these with an occasionally warty skin is *H. amboinensis* which has not been collected on Jobi Island but does occur on the nearby Vogelkop Peninsula. If it is assumed that the type of *H. obtusirostris* had fully webbed fingers, *H. amboinensis* differs from the description of *H. obtusirostris* in the following respects: the tympanum is equivalent to two-thirds of the eye diameter (not one half) and is not rather deeply set. The snout is not short and the canthus rostralis is prominent (not feeble). The vomerine teeth are between the choanae (not between and behind them) and there are further points of divergence in the colouration and in the measurements of a 37.0 mm specimen with those quoted for *H. obtusirostris*.

There is no doubt that *H. obtusirostris* is distinct from those *Hyla* species which take priority by date of publication (*H. bicolor*, *H. caerulea*, *H. infralateralis* and *H. nasuta*).

Distribution. — Although the only reported specimen of this species is the holotype, Van Kampen (1906) stated that *H.obtusirostris* occurs at Jobi and Australia, and Barbour (1912) lists Jobi and Queensland. In a card index compiled by Dene B. Fry at the Australian Museum is a note that after the latter publication Fry wrote to Barbour querying the presence of *H. obtusirostris* in Australia. In a letter dated December 23, 1913, Barbour replied that the inclusion of Queensland was an error. As
Van Kampen (1923) cited only Jobi for the distribution of *H. obtusirostris*; it is concluded that his 1906 statement was also an error.

**Hyla pratti** Boulenger


*Hyla prattii* (sic), Barbour, 1912: 177.

Types. — 5 syntypes, B.M. 1947.2.23.54-56 collected at Wendessi, Vogelkop Peninsula, New Guinea; B.M. 1947.2.23.57-58 collected at an altitude of 8000 ft in the Arfak Mountains, Vogelkop Peninsula. A. E. Pratt obtained the entire series.

Definition. — This species is characterised by its rather broadly spaced nares (E-N/IN 0.758-0.848), moderately long limbs (TL/S-V 0.534-0.564), basally webbed outer fingers and straight or only very slightly curved canthus rostralis. The female syntype has a snout to vent length of 48.7 mm, and male syntypes vary from 29.5 mm to 31.4 mm.

Material examined. — The type series.

Description. — The head is longer than broad (HL/HW 1.019-1.071), its length equal to or greater than one-third of the snout to vent length (HL/S-V 0.333-0.356). The snout is not prominent; when viewed from above it is evenly rounded or obtusely angular; in profile it is rounded. The nostrils are more lateral than superior, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is less than the internarial span (E-N/IN 0.758-0.848). The canthus rostralis is straight or very slightly curved and only slightly defined. The eye is moderate, its diameter greater than the distance separating it from the nostril. The tympanum is only partially visible — the posterior half being hidden beneath the supra-tympanic fold. The diameter of the tympanum is equivalent to one-half or one-third of the eye diameter. The vomerine teeth are in two transverse, oval series between the choanae, or oblique oval series between and extending behind the posterior margins of the choanae. The tongue is cordiform with a slightly indented posterior border.

The fingers are long and slender; in decreasing order of length $3 > 4 > 2 > 1$; the webbing between the fingers is confined to a minute basal membrane between the third and fourth (fig. 50).

The hind limbs are of moderate size, the TL/S-V ratio being 0.534-0.564. The toes are webbed to the base of the discs or midway up the penultimate phalanges, with the exception of the fourth which has the penultimate and half of the adjacent phalanx free.
Fig. 50. *Hyla pratti* Boulenger. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
The skin on the dorsal surface is smooth with a few slightly raised tubercles on the posterior halves of the eyelids. The throat and chest are smooth or slightly granular and the abdomen conspicuously granular. There is a prominent, curved supra-tympanic fold extending from the posterior corner of the eye to above the insertion of the forelimb.

In the female syntype (B.M. 1947.2.23.54) the dorsal surfaces are a pale greyish-blue sparsely spotted with black. The upper lip is creamish stippled with blue and bears black spots. The ventral surfaces are dull cream, fading on the throat where there are a few small, faint markings. The male syntypes are brown dorsally with or without indistinct darker markings and ventrally vary from dull yellow to creamish with or without brown spots or stippling on the throat.

Distribution. — Specimens reported in the literature as *H. pratti* have without exception proved erroneously identified. The current knowledge of the distribution is therefore based solely on the type localities which are on the Vogelkop Peninsula.

Comparison with other species. — Of the montane species only *H. micromembrana*, *H. modica* and *H. spinifera* overlap the size range of *H. pratti* and have basally webbed or unwebbed fingers and similar E-N/IN ratios. *Hyla micromembrana* and *H. spinifera* have long hind limbs (TL/S-V 0.581–0.689 in *H. micromembrana* and 0.602–0.603 in *H. spinifera* compared with 0.534–0.564 in *H. pratti*), whilst the canthus rostralis is strongly curved in the first two and straight or only very slightly curved in *H. pratti*. Curvature of the canthus rostralis is not pronounced in *H. modica*, but the eye diameter is less than the internarial span in that species (larger than the internarial span in *H. pratti*).

**Hyla pygmaea** (Meyer)


*Hylella pygmaea*, Meyer, 1887: 16; Van Kampen, 1907b: 415.

*Hylella boulenieri* Méhély, 1897, Természet. Fuz. 20 (3): 414, pl. 10 fig. 8; Werner, 1901b: 613; Vogt, 1912b: 359.


*Hyla pygmea* (sic), Barbour, 1912: 177.


Types. — The two syntypes were lodged in the Dresden Museum and their presence there confirmed by Schüz (1929). They were lost when the Dresden Museum was destroyed during the Second World War. The syntypes were juveniles collected at Jobi by A. B. Meyer in 1873.

Definition. — This distinctive species is characterised by its small size (the S-V of males is 24.0-30.0 mm and females 28.0-38.0 mm), and conspicuous dorsal colouration of large white spots on a dark brown background. The fingers are slender with large terminal discs and are approximately half-webbed.

Material examined. — 19 specimens.


Southern Lowlands: U.S.N.M. 119204-8, Toem; R.M.N.H. 5258, Jamoer Lake; B.M. 1913.11.1.152-3 (H. fallax syntypes), Katow; M.C.Z. 9384, “New Guinea”.

Description. — The head is small, longer than broad (HL/HW 1.012-1.145), its length greater than one-third of the snout to vent length (HL/S-V 0.338-0.361). The snout is not prominent; when viewed from above and in profile it is evenly rounded. The nostrils are more lateral than superior, their distance from the tip of the snout is considerably less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.029-1.143). The canthus rostralis is very slightly curved and inconspicuous. The loreal region is concave and oblique. The eye is prominent, its diameter greater than the distance separating it from the nostril. The tympanicum is covered with skin, and only the anterior and posterior portions of the tympanic annulus are visible in most specimens; the tympanic diameter varies from one-third to one-half of the eye diameter. The vomerine teeth are in two very small, circular series between or beneath the choanae. The tongue is broadly oval or almost circular with a weakly indented posterior border. In some specimens the anterior half of the tongue is covered with small, conical papillae.

The fingers are long and slender and lack lateral fringes; in decreasing order of length 4>3>2>1; the webbing between the third and fourth fingers does not reach the sub-articular tubercle at the base of the penultimate phalanx (fig. 51). The terminal discs are prominent.

The hind limbs are short with a TL/S-V range of 0.495-0.564. Toes in decreasing order of length 4>5>3>2>1. The webbing between the outer and fourth toe extends almost to the disc of the fifth toe and the base of the penultimate phalanx of the fourth.
Fig. 51. *Hyla pygmaea* (Meyer). a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
The skin on the dorsal surfaces is smooth, and there is a curved supratympanic fold extending from the eye to the insertion of the forelimbs.

In preservative the colouration of the dorsal surface of the body is dark with large, irregularly shaped white markings. The distribution of the white markings is highly variable, but most specimens exhibit a broad canthal stripe or pre-ocular bar, post-ocular bar, three or four paired, longitudinally distributed patches on the body and a coccygeal patch. The limbs are dark brown with pale cream flecks or mottling. The ventral surfaces of the body and limbs are pale cream.

There is no information on the colour in life.

Males possess a sub-gular vocal sac and a small nuptial pad on the first finger.

Ecological notes. — *Hyla pygmaea* is known from a few specimens almost invariably collected singly. The only information on the habitat preferences of this species is a field note that one of the uncatalogued B.P.B.M. specimens was collected in a *Pandanus* sp.

Distribution. — This species occurs at coastal localities and lowland river deltas on the New Guinea mainland (fig. 52).

Taxonomy. — There has been considerable confusion regarding the valid name of this species. It was originally described as *Hyperolius pygmaeus* by Meyer and transferred to *Hylella*, as *H. pygmaea*, by the same author (1887). Méhely (1897) described *Hylella boulengeri* and Boulenger (1898) *Hyla fallax*. These species were considered synonymous but distinct from *H. pygmaea* by Van Kampen (1909a), and later (1913a) he again reported specimens of *H. boulengeri*. Boulenger (1914) maintained that as *H. boulengeri* was preoccupied by *Scytopsis boulengeri* Cope, *H. fallax* remained valid. Van Kampen appeared not to accept this opinion for in subsequent publications he utilised the name *H. boulengeri* as a synonym of *H. fallax* and queried whether *H. pygmaea* might also be a synonym.

Nieden (1923) proposed the new name *H. mehelyi* for *H. boulengeri* and no further contributions were made until Loveridge (1948) resurrected *H. pygmaea* as the oldest available name for what he recognised to be a single valid species. Cochran (1952) has since drawn attention to the existence of a secondary homonym (the Brazilian species *Hyla pygmaea* Weiner) and proposed for it the new name *Hyla werneri*.

Although the type specimens of *Hyla pygmaea* (Meyer) and *H. boulengeri* (Méhely) have been destroyed, their descriptions tally with the *H. fallax* syntypes and other material examined, and the writer shares Loveridge's opinion that a single species is involved.
*Hyperolius pygmaeus* Ahl (1931b) is a primary homonym.

Comparison with other species. — The only lowland species with individuals sharing with *H. pygmaea* a dorsal colouration of distinctive light areas against a darker ground colouration are *H. congenita* and *H. thesaurensis*.

*Hyla thesaurensis* is a larger species with green bones (unpigmented in *H. pygmaea*) and although the presence of light markings on the dorsum is common to all juveniles they are exhibited by only a few adults and always take the form of a transocular bar and narrow longitudinal stripes extending along the entire length of the body. In *H. congenita* the light markings are variable but smaller and far less distinctive and it also differs from *H. pygmaea* in having a shorter head (HL/S-V 0.309-0.336; 0.338-0.361 in *H. pygmaea*).

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Fig. 52. Distribution of *Hyla pygmaea* (Meyer). Open circles = literature records; closed circles = specimens examined.
Hyla sanguinolenta Van Kampen

Hyla infrafrenata, Boulenger, 1912: 214 (part).
Hyla sanguineolenta (sic), Barbour, 1912: 175; Kinghorn, 1928b: 289.

Types. — Lectotype, A.Z.M. 5676 collected at Sabang, Lorentz River and 2 paralectotypes, A.Z.M. 5674 from Bivak Island, Lorentz River and A.Z.M. 5675, Lorentz River (exact locality unspecified), Southern Lowlands by Lorentz in 1907.

Definition. — A moderately sized species in which females attain a maximum snout to vent length of 55.0 mm and males 40.0 mm. The species is characterised by a long curved canthus rostralis, a high E-N/IN and TL/S-V ratio and an immaculate blue dorsal colouration of the body.

Material examined. — The type series and 3 additional specimens.

Description. — The head is flattened and longer than broad (HL/HW 1.016-1.132, mean 1.067) its length approximately two-fifths of the snout to vent length (HL/S-V 0.364-0.414, mean 0.391). The snout is prominent; when viewed from above it is truncated; in profile slightly rounded. The nostrils are more lateral than superior, their distance from the end of the snout less than half the distance between eye and naris. The distance between the eye and naris is considerably greater than the internarial span (E-N/IN 1.212-1.400, mean 1.337). The canthus rostralis is strongly curved and extremely prominent. The loreal region is concave and oblique. The eye is large, its diameter greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to at least two-thirds of the eye diameter. The vomerine teeth are in two round or oblique series directly between the rounded choanae. The tongue is cordiform with a slightly indented posterior border.

The fingers are long and possess lateral fringes; in decreasing order of length 3>4>2>1; less than half-webbed, the webbing not reaching the sub-articular tubercle at the base of the penultimate phalanx on the fourth finger. The terminal discs and sub-articular tubercles are large and prominent (fig. 53).

The hind limbs are extremely long and slender with a high TL/S-V ratio (0.554-0.605, mean 0.582). Toes in decreasing order of length 4>5>3>2>1. The webbing between the outer and fourth toes reaches almost to the disc
Fig. 53. *Hyla sanguinolenta* Van Kampen. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
of the fifth, and to midway up the penultimate phalanx of the fourth and continuing to the disc as a broad fringe.

The dorsal and lateral surfaces of the body and limbs are finely granular. The throat is finely granular and the abdomen and lower surface of the thighs coarsely granular. There is a narrow supra-tympanic fold extending from the eye to the shoulder, and indistinct skin folds on the posterior surfaces of the forearm and tarsus.

The dorsal colouration in preservative of five of the six specimens examined is a rich dark blue; the exception is a very pale blue. The colour of the dorsum terminates abruptly on the dorso-lateral surfaces of the body. The ventral and ventro-lateral surfaces of the body and limbs are cream. The cream extends onto the dorsal surface of the hind limbs and meets the blue colour in an irregular line. As Van Kampen (1909) mentions, the specimen from Sabang (A.Z.M. 5676) exhibits wine-red flecks on the sides of the limbs and, to a lesser extent, on the abdomen.

Distribution. — The locality records of Van Kampen (1909a, 1914, 1923) are all in Western New Guinea and centralised in the Southern Lowlands. In view of the superficial similarity of this species to *H. infraplenata* some of the numerous literature records of the latter may be based on *H. sanguinolenta*.

Taxonomy. — Boulenger (1912) synonymised *H. sanguinolenta* with *H. infraplenata* but it was resurrected by Van Kampen (1923) who drew attention to distinctions between the species. No further specimens have been reported since that date.

Comparison with other species. — The species with similarly pigmented dorsal surfaces and whose adult snout to vent length ranges overlap or approximate that of *H. sanguinolenta* are *H. aruensis*, *H. caerulea* and *H. graminea*. *Hyla aruensis* and *H. graminea* can be readily distinguished from *H. sanguinolenta* by the extent of the webbing between the fingers (reaching the base or near to the base of the discs in these species, and not reaching as far as the sub-articular tubercle at the base of the penultimate phalanx in *H. sanguinolenta*). *Hyla caerulea* is a robust and rather squat species contrasting sharply with the elongated habitus of *H. sanguinolenta*. This difference is indicated by comparison of the HL/HW and E-N/IN ratios (0.845-1.022 and 0.927-1.171 respectively in *H. caerulea* and 1.016-1.132 and 1.212-1.400 respectively in *H. sanguinolenta*).

*Hyla sanguinolenta* is superficially similar to *H. infraplenata*. The latter is a considerably larger species readily distinguished by the presence of a
white labial stripe (absent in *H. sanguinolenta*). A detailed comparison of these two species is presented on page 110.

**Hyla spinifera** new species (pl. 3, d)

Holotype. — M.C.Z. 54510. An adult male collected at an altitude of approximately 5000 ft at Oruge, Eastern Mountains, New Guinea by F. S. Parker on 18th April, 1965.

Definition. — This species is characterised by its sharply defined canthus rostralis, prominent pointed snout, long hind limbs and conspicuous conical tubercles on the outer edge of the tarsus and foot. The size range of the adult males examined is 38.0-42.0 mm S-V and females 48.0-50.0 mm.

Description of holotype. — The head is flattened and longer than broad (HL/HW 1.112), its length equivalent to more than one-third of the snout to vent length (HL/S-V 0.372). The snout is extremely prominent; obtusely pointed when viewed from above and in profile. The nostrils are lateral, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is very much less than the internarial span (E-N/IN 0.750). The canthus rostralis is extremely sharply defined and strongly curved. The eye is large and prominent, its diameter greater than the distance separating it from the nostril. The tympanum is just visible, its diameter equivalent to slightly less than half the diameter of the eye; separated from the eye by a distance equivalent to approximately one and one-half its own diameter. The vomerine teeth are in two oblique series situated between and below the rounded choanae. The tongue is broadly cordiform with a very slightly indented posterior border.

The fingers are very long and slender and lack lateral fringes and interdigital webbing. In decreasing order of length 3>4>2>1. The terminal discs are prominent (fig. 54).

The hind limbs are long and slender (TL/S-V 0.623). Toes in decreasing order of length 4>5 = 3>2>1. On the fourth toe the webbing reaches the sub-articular tubercle at the base of the terminal phalanx. The remaining toes are webbed to a point midway up the penultimate phalanx. There is a small oval inner but no outer metatarsal tubercle.

The dorsal and lateral surfaces of the head, body and limbs bear conspicuous tubercles. These tubercles are particularly densely aggregated on the posterior halves of the upper eyelids. There is an extremely prominent supra-tympanic fold. On the posterior surface of the forearm, tibia and foot are rows of prominent tubercles. These are particularly well developed on the tarsus where each tubercle is conical in shape and sharply pointed.
Fig. 54. *Hyla spinifera* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
at the apex. Beneath the anus is a clump of prominent rounded tubercles. The throat and chest are smooth, and the abdomen and lower femora coarsely granular.

Dimensions: snout to vent length 40.1 mm; tibia length 25.0 mm; head length 14.9 mm; head width 13.4 mm; eye to naris distance 3.9 mm; inter-narial span 5.2 mm; eye diameter 4.2 mm; tympanum diameter 2.0 mm.

In preservative the dorsal surface of the head, body and limbs is pale blue with darker markings and irregular marbling of a similar shade. There is a dark trans-ocular bar uniting the posterior halves of the eyelids. Behind this bar, and partly superimposed upon it is an X marking extending posteriorly on to the scapular region. On the sacral region is a broad and less clearly defined transverse bar. The posterior surface of the thighs is a dull yellow and the subanal tubercles are white. The ventral surface of the body and limbs is a very pale grey, and there is indistinct, pale brownish mottling on the throat and on the femora.

Variation. — There are thirty-one paratypes, M.C.Z. 54467-54470, 54490-54511, S.A.M. R.6298-6301. The paratype series was collected with the holotype at Oruge by F. S. Parker on 18th April, 1965. A further twenty-three specimens taken by the same collector at nearby localities have also been examined: M.C.Z. 54471-5, S.A.M. 6297, collected at Dege on 17th April 1965 and M.C.Z. 54476-54489, S.A.M. 6295-6, collected at Bomai on 30th May, 1965.

Adult males vary in size from 38.4-42.3 mm snout to vent length, whilst the two females collected measure 47.8 and 49.8 mm respectively.

In one specimen (M.C.Z. 54511) the head length and head breadth measurements are equal. All other specimens share with the type HL>HW with a range of 1.010-1.136. The head length is consistently greater than one-third of the snout to vent length with a range of 0.347-0.394. The broadly spaced nares is another characteristic feature of this species, the range of the E-N/IN ratio being 0.604-0.783. The canthus rostralis is a conspicuous feature in all specimens examined, and the tympanum varies in size only slightly, being from slightly more than one-third to one-half of the eye diameter.

The fingers are elongated, unfringed and unwebbed in all specimens. The hind limbs are very long with a TL/S-V ratio range of 0.602-0.693. The relative lengths of the third and fifth toes is variable. In the majority of specimens they are of equal length, but in some the fifth is slightly longer than the third. The nuptial pad is depicted in fig. 3.

The size and density of the dorsal tubercles are variable. The row of
conical tubercles on the posterior surfaces of the limbs is present in all specimens, but is more conspicuous in some than in others.

The ground colouration of the dorsal surfaces of the head, body and limbs varies from pale blue to a dull greenish brown. The trans-ocular bar and other markings exhibited by the holotype are present in all specimens having a pale blue ground colouration. The brown mottling on the throat is common to all specimens and is particularly conspicuous in the specimens collected at Bomai, where the brown forms a clearly defined variegation on a white background.

Parker reports the colour of living specimens to be mottled with green and brown above. Many of the numerous dorsal tubercles are tipped with a reddish colour. The ventral surfaces are white and mottled with a translucent greyish. The iris is golden yellow, with brown areas at the ends of the horizontal pupil.

Biological and ecological notes. — The habitat of this species is dense rain forest at altitudes of 3500-5000 ft. All specimens were collected in the vicinity of small waterways. During the daytime the species was found among leaves near the water, and at night on leaves overhanging water.

Distribution. — All specimens were collected at localities south of Kundiawa. Latitude and longitude readings are unknown, but Parker has provided the following information: Dege area — about 14 miles south, 12 miles west of Kundiawa, on the southern slopes of the eastern end of the Kubor Ranges. Oruge area — about 3 miles due west of Dege. Bomai area — about 3 miles south and 1 mile west of the summit of Mt. Au, on the Tive Plateau between the Kubor Ranges and the Tua River. Main collections around the airstrip at Unani, about 6 miles south and 8 miles west of Oruge.

Comparison with other species. — The montane species in which inter-digital webbing of the hands is absent or reduced to a remnant at the base are *H. arfakiana*, *H. becki*, *H. bulmeri*, *H. micromembrana*, *H. modica* and *H. pratti*. With the exception of *H. micromembrana* these may be distinguished by differences in the shape of the head, and particularly of the canthus rostralis (very strongly curved in *H. micromembrana* and *H. spinifera*, and straight or bearing only a slight curvature in the remainder).

The males of *H. spinifera* are larger than those of *H. micromembrana*, the snout to vent length ranges being 38.4-42.3 mm and 30.2-35.9 mm respectively. However, the females lie within the range of female *H. micromembrana*. Tarsal tubercles, so well developed in *H. spinifera*, are not exhibited in *H. micromembrana*, and the sub-anal tubercles of the former
are far more prominent than in the latter species. *Hyla spinifera* tends to be a more elongate species than *H. micromembrana* as indicated by a comparison of the HL/HW and HL/S-V ratios (1.016-1.136 and 0.347-0.394 respectively in *H. spinifera*; 0.900-1.056 and 0.328-0.368 respectively in *H. micromembrana*). The species are further distinguished by comparison of their pigmentation.

Of the species separated from *H. spinifera* by the shape of the canthus rostralis, only *H. arfakiana* possesses tubercles. The sub-anal tubercles are similarly well-developed in the latter species, whilst on the limbs there is a single tubercle on the heel but none on the tarsus.

**Hyla thesaurensis** Peters


Types. — Two syntypes, Z.M. 9121, collected at Treasury Island, Solomon Islands, by Brazier. Date of collection unknown.

Definition. — A very highly variable species characterised by a high E-N/N ratio, reduced webbing of the fingers and green bones. Adult size varies from population to population with a maximum snout to vent length of 65.0 mm (females) and 50.0 mm (males).
Material examined. — 304 specimens.

Solomon Islands (Bougainville): S.A.M. 4430, Kieta; S.A.M. 4222-4235, 4425, 4765, 4759-60, 4919, 4923, 5156, 5175, Kumua.

New Britain: S.A.M. 5789, 7120, 7141, 6794, 6802, 6983, 7759-63, 8020-1, 8307, Keravat.

New Hannover: N.M.B. 4518-21, Neingi.

South-east Peninsula: M.C.Z. 11652 (Nyctimystes milneana holotype), Milne Bay; M.C.S.N. C.E. 29719 B (H. impura paralectotype), Yule Island; M.C.Z. 28411, Gemeheng; S.A.M. 5851, 5878, Popondetta; B.P.B.M. (uncat.), Wau.


Description. — The head is flattened and longer than broad (HL/HW 1.023-1.200), its length greater than one-third of the snout to vent length (HL/S-V 0.340-0.373). The snout is prominent, when viewed from above and in profile it is slightly rounded. The nostrils are more lateral than superior, their distance from the end of the snout approximately half that from the eye. The distance between the eye and the naris is very much greater than the internarial span (E-N/IN 1.257-1.485). The canthus rostralis is curved and slightly defined. The eye is large and prominent, its diameter less than, equal to, or greater than the distance separating it from the nostril. The tympanum is visible, its diameter equivalent to two-thirds of the eye diameter. The vomerine teeth are in two large, oblique series between the upper margins of the choanae. The tongue is broadly oval with a slightly indented posterior border.

The fingers are long and slender with large terminal discs and very narrow lateral fringes. In decreasing order of length $3>4>2>i$. The webbing between the fingers is scant, just reaching the sub-articular tubercle at the base of the penultimate phalanx of the fourth (fig. 55).

The length of the hind limbs is highly variable, differing markedly between different samples. The range of TL/S-V is from 0.528-0.629. Toes in decreasing order of length $4>5 = 3>2>i$. The webbing reaches the base of the disc on the fifth toe and the sub-articular tubercle at the base of the penultimate phalanx on the fourth.

The skin on the dorsal surface is smooth. In occasional specimens the upper eyelids are slightly granular. A row of tubercles on the posterior surface of the forearm vary from well developed to being scarcely detectable. There is a very weak supra-tympanic fold extending from the posterior
Fig. 55. *Hyla thesaurensis* Peters. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
corner of the eye to a point above the insertion of the forearm. A very small portion of the superior margin of the tympanic annulus is usually hidden beneath the supra-tympanic fold. There are a few flattened tubercles on the throat. The chest is smooth, and the abdomen and lower surfaces of the thighs coarsely granular.

The male possesses a sub-gular vocal sac and an exceptionally elongate nuptial pad on the first finger (fig. 3).

In preservative the ground colouration of the dorsal surfaces is usually pale grey, buff, brown or cream with or without lighter or darker markings. The lighter markings almost invariably consist of three longitudinal stripes situated mid-dorsally and dorso-laterally. The darker markings are commonly in the form of irregularly shaped brown or black spots. A white bar is present beneath the eye of most specimens. The backs of the thighs are brown with or without numerous, very small, circular white or cream spots. The bones are green. Pigmentation is not confined to the periosteum but is present throughout the bone and persists in specimens preserved in formalin for at least thirty years (S.A.M. collection).

The nature of the pigment in this species is unknown but Barrio (1965) attributes the green appearance of the bones, muscles and ova of several South American anurans (including hylids) to hyperbiliverdinaemia. The presence of biliverdin has been found to be the cause of the green appearance of a wide variety of vertebrate structures and presumably has been deposited in the bones of *H. thesaurensis*.

In life the colouration is very highly variable, with the dorsal surfaces bright yellow, green or virtually any shade of grey or brown. The longitudinal stripes mentioned in the preceding paragraph are usually pale yellow. Tanner (1951b) has reported the colour of living specimens in the Solomon Islands.

The juvenile is dark brown and every specimen examined exhibits the three longitudinal stripes, united by a narrow trans-ocular bar. These stripes are cream in preservative and bright yellow in life.

Biological and ecological notes. — *Hyla thesaurensis* is one of the most abundant coastal species in the Papuan sub-region. It occurs in widely differing plant associations. Tanner (1951b) stated that the species is commonly found on the leaves of plants on the forest floor at Gaudalcanal, Solomon Islands.

A specimen imported into Australia from Bougainville, Solomon Islands laid approximately 1150 eggs in two large, shapeless clumps. Each of the
Fig. 56. Distribution of Hyla theravadekis Peters in New Guinea and the Bismarck Archipelago. Open circles = literature records; closed circles = specimens examined.

The distribution of this species in the Solomon Islands is depicted in fig. 47.
650 individuals which completed their development bore the characteristic longitudinal stripes on the dorsum.

The tadpole has been described by Brown (1952) as follows: "One of the younger larvae with the forelimbs rather well developed but still beneath the operculum, measures 58.0 mm in total length; vent to tip of tail 38.0 mm; width of body 12.0 mm (preserved condition); nostril to tip of snout 3.0 mm; eye to nostril 3.0 mm; interorbital space 6.0 mm; width of mouth 4.0 mm; greatest breadth of tail 9.0 mm. The mouth is antero-ventral in position. The lips are papillate except for the median third of the upper lip; the upper lip possesses two rows of horny teeth, the inner divided at the midline. The lower lip has three rows, the inner one also medianly divided. The edges of the jaws have a dark horny covering. The eyes are dorso-lateral in position. The spiracle forms a narrow slit-like opening (1.0 mm in length) slightly ventral to a line connecting the corner of the mouth and the groin on the left side and about equidistant from these two points of reference. The dorsal and ventral fins of the tail are of approximately equal width with the tip rounded, and heavily pigmented (dark greyish-brown in preservative)."

Distribution. — *Hyla thesaurensis* occurs at elevations below approximately 3500 ft along the southern and northern coasts of New Guinea east of the Vogelkop Peninsula, and on New Britain, New Hannover and the Solomon Islands. The species almost certainly occurs on New Ireland (figs. 56, 41).

Taxonomy. — The extensive synonymy of *H. thesaurensis* has been discussed at length by Parker (1939), Loveridge (1948) and Brown (1952). The only divergence in the present paper from that of Loveridge is that *H. macgregori* is removed from the synonymy of *H. thesaurensis* and referred to the synonymy of *H. congenita*. Early authors assumed that the differences observed between their material and existing descriptions were due to errors on the part of the previous authors. Thus Jeude (1897) redescribed *H. impura* because of the divergence from the description of Peters & Doria (1878), and Méhely (1898) prepared a further description because he thought Peters & Doria and Jeude had not examined specimens in breeding condition.

Brown (1952) suggested that the species might prove to be composed of at least two sub-species or to be undergoing such differentiation. Zweifel (1960) compared the maximum size and leg length of a large series of specimens collected at Menapi, New Guinea with a series from Guadalcanal in the Solomon Islands. He drew attention to the smaller size and shorter
TL:S-V ratios of the New Guinea specimens, and stated that he considered that a more detailed study of the species would probably indicate that the New Guinea population should be accorded separate taxonomic status.

On the basis of the conclusions of Brown and Zweifel, the present writer examined specimens of *H. thesaurensis* with the preconceived supposition that morphological criteria to distinguish the populations would be found. Even with this definite bias, conclusive evidence has not been forthcoming. The TL:S-V ratio varies considerably from locality to locality without any definite geographic trend. Maximum size may prove a means of distinguishing some of the island populations at the periphery of the range (e.g. New Hannover), but insufficient specimens are available.

In the Berlin Museum is a representative of *H. thesaurensis* said to be the type of "*Hyla niedeni*" and attributed to Vogt. The writer has been unable to trace a description or any reference to this name in the literature, and it is assumed to be an unpublished manuscript name.

Comparison with other species. — Of the lowland species similar to or approximating the size range of *H. thesaurensis*, only *H. genimaculata* and *H. lutea* exhibit any indication of a close relationship with that species. *Hyla genimaculata* is distinguished by the presence of crenulated dermal folds on the posterior surfaces of the forelimbs, and a very small, triangular lappet on the heel (neither being exhibited by *H. thesaurensis*), and by unpigmented bones (pigmented in *H. thesaurensis*).

*Hyla lutea* is the only other Papuan species with pigmented bones but has more extensive webbing between the fingers and broad lateral dermal fringes on the fingers.

The shape of the nuptial pad of *H. thesaurensis* is quite unlike that of any other species, in possessing a pronounced, narrow superior extension (% 3)

**Hyla vagabunda** Peters & Doria


Types. — Lectotype M.C.S.N. C.E. 29704 A, Wahai, Ceram, Moluccas, and allotype C.E. 29704 B, Sorong, Vogelkop Peninsula, New Guinea. Both types were collected by L. M. D'Albertis in 1872.

Definition. — The characteristic features of this species are a broad
head, short limbs, unwebbed fingers, a prominent fold of skin across the chest and dark blue dorsal colouration.

Material examined. — The allotype.

Description of allotype. — A gravid female. The head is broader than long (HL/HW 0.951), its length slightly less than one-third of the snout to vent length (HL/S-V 0.310). The snout is rounded when viewed from above and in profile. The nostrils are more lateral than superior, their distance from the end of the snout slightly less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.154). The canthus rostralis is straight and poorly defined. The eye is large, its diameter greater than the distance separating it from the nostril. Three-quarters of the tympanum is visible, the superior rim of the tympanic annulus is hidden beneath the supra-tympanic fold. The tympanal diameter is equivalent to two-thirds of the eye diameter. 1) The vomerine teeth are in two broadly oval series situated between the choanae. The tongue is broadly cordiform with a deeply indented posterior border.

The fingers are very long and slender with narrow lateral fringes; in decreasing order of length 3 > 4 > 2 > 1; unwebbed. The terminal discs and sub-articular tubercles are large and prominent (fig. 57).

The hind limbs are short and slender with a TL/S-V ratio of 0.513. Toes in decreasing order of length 4 > 5 > 3 > 2 > 1. The webbing between the outer and fourth toe reaches half-way up the penultimate phalanx on the fifth, and the sub-articular tubercle at the base of the penultimate phalanx on the fourth.

The skin on the dorsal surfaces is smooth with a few minute flattened tubercles. The throat and chest are slightly tubercular; the abdomen, sides of the body and lower surface of the thighs are extremely granular. There is a conspicuous curved supra-tympanic fold, and a prominent skin fold across the chest.

The dorsal surfaces are dark blue. There is a faint trace of a narrow white line above a broader brown line on the canthus rostralis, upper eyelid and supra-tympanic fold. The backs of the thighs are pale brown and marked with small irregularly-shaped, pale yellow spots. The backs of the tarsus and forearm are pale brown. The ventral surfaces are pale yellow with leaden blue patches at the angles of the jaws, and small faint brown spots on the remainder of the mandibular border and on the throat.

Dimensions: snout to vent length 37.4 mm; tibia length 19.2 mm; head length 11.6 mm; head width 12.2 mm; eye to naris distance 3.0 mm; inter-

1) The tympanum is slightly larger than depicted in fig. 57.
Fig. 57. *Hyla vagabunda* Peters & Doria. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
narial span 2.6 mm; eye diameter 3.7 mm; tympanum diameter 2.4 mm.

Distribution. — *Hyla vagabunda* is known solely from the type localities of Wahai on Ceram and Sorong on the Vogelkop Peninsula.

Comparison with other species. — The combination of long, slender and unwebbed fingers and relatively short limbs distinguishes *H. vagabunda* from all Papuan *Hyla* except *H. jeudei* and *H. dorsalis*. Whereas *H. vagabunda* has a head which is broader than long (HL/HW 0.951), the head of *H. jeudei* is longer than broad (HL/HW 1.073). The species are also clearly separated by the E-N/IN ratios (1.154 for *H. vagabunda* and 1.435 for *H. jeudei*). Although *H. vagabunda* is known from the existence of two specimens and *H. jeudei* from one, it is evident that they are quite distinct species. *Hyla jeudei* is brown in preservative with lighter and darker marbling on the dorsal surface of the head and body and on the back of the thighs. *Hyla vagabunda* is dark blue in preservative with the back of the thighs pale brown and marked with irregularly shaped yellow spots.

*Hyla dorsalis* is an exceptionally small species. The specimen examined is a gravid female with a snout to vent length of 20.5 mm. As the gravid female *H. vagabunda* allotype has a snout to vent length of 37.4 mm they are obviously quite distinctive.

**Hyla wisselensis** new species (pl. 4, b-d)


Definition. — This species is characterised by the combination of the following characters: small size (males 24.0-32.0 mm, females 29.0-37.0 mm), very short hind limbs (TL/S-V 0.402-0.478) and basal finger webbing. The colouration is highly variable.

Description of holotype. — The head is flattened and longer than broad (HL/HW 1.118), its length equivalent to more than one-third of the snout to vent length (HL/S-V 0.341). The snout is not prominent; rounded when viewed from above and in profile. The nostrils are oblique, their distance from the end of the snout about one-half that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.200). The canthus rostralis is slightly defined and gently rounded. The loreal region is concave and slightly oblique. The eye is large and extremely prominent, its diameter greater than the eye to naris distance. The tympanum is visible, its diameter equivalent to about two-thirds of the diameter of the eye, and separated from the eye by a distance
Fig. 58. *Hyla wisseleensis* new species. a, hand in ventral view; b, head in lateral view; c, head in dorsal view; d, foot in ventral view.
equivalent to about half its own diameter. The vomerine teeth are in two small, round series lying close together on each side of the mid-line, on a level with the anterior borders of the small, rounded choanae. The tongue is broadly oval, its posterior border free and very slightly indented.

The fingers are long and slender and lack lateral fringes; in decreasing order of length 3 \(>\) 4 \(>\) 2 \(>\) 1. There is only a trace of basal webbing between the third and fourth fingers. The terminal discs are extremely prominent (fig. 58).

The hind limbs are extremely short (TL/S-V 0.446). Toes in decreasing order of length 4 \(>\) 5 \(>\) 3 \(>\) 2 \(>\) 1. The webbing reaches the discs of all toes except the fourth where it extends half-way up the penultimate phalanx, continuing to the disc via a narrow fringe. There is a distinct oval inner but no outer metatarsal tubercle.

The skin on the dorsal surfaces is smooth but for a few inconspicuous tubercles on the head and upper eyelids. There is a row of prominent tubercles behind the forearm, a narrow tarsal ridge, a very small tubercle on the heel and a narrow supra-tympanic fold. The throat is granular and the abdomen and lower femur uniformly and finely granular.

Dimensions: snout to vent length 33.4 mm; tibia length 14.9 mm; head length 11.4 mm; head width 10.2 mm; eye to naris distance 3.0 mm; inter-narial span 2.5 mm; eye diameter 3.8 mm; tympanum diameter 2.4 mm.

Dorsally a pale brown colour with the following markings: a narrow pale cream mid-dorsal stripe extending from the tip of the snout to the sacral region, indistinctly defined canthal and supra-tympanic stripes, and dull slate streaks on the upper part of the head and behind the eyes. The throat is dull brown, the chest whitish with brown markings, and the abdomen and lower surfaces of the limbs pearly-grey.


The head is longer than broad in all specimens, the HL/HW ratio being 1.019-1.192, and the length of the head is consistently greater than one-third of the snout to vent length (HL/S-V 0.337-0.376). The distance
between the eye and the naris is greater than the internarial span in all specimens (E-N/IN 1.045-1.225). The hind limbs of this species are exceptionally short, the range of the paratype series being 0.402-0.478.

The position of the vomerine teeth in relation to the choanae, the distinctness of the tympanum and tympanic annulus and the extent of the webbing between the fingers and toes of the paratypes are similar to the holotype.

The colouration is highly variable. The dorsal surfaces of preserved specimens vary from blue to brown, with or without darker or lighter markings. The pale mid-dorsal stripe exhibited by the holotype is common to approximately forty per cent of the specimens examined, but varies in extent and contrast. The dark lateral head stripe is present in approximately ninety per cent of the specimens examined. The specimens appearing in Plate 4 have been selected to illustrate the range of dorsal pattern.

The following notes, based on field records prepared by Dr. H. Boschma, a member of the Netherlands New Guinea Expedition of 1939, indicate that the colour in life is equally variable:


R.M.N.H. 12288 — Head and body 'dark chocolate' with broad yellow lines extending along the body; one median and others commencing behind the eyes and running parallel to the median line. Dorsal surface of the limbs 'milk chocolate'. Ventral surfaces of body and limbs are brownish-grey.

Comparison with other species. — *Hyla wisselensis* has shorter limbs than any other Papuan species of *Hyla*. The TL/S-V ratio of 0.402-0.478 is partially overlapped by *H. caerulea* (0.441-0.545) but this is the only common characteristic for *H. caerulea* is a very much larger species with a broad head and broadly fringed fingers.

None of the montane species within the size range of *H. wisselensis* have short limbs. *Hyla iris, H. contrastens, H. gracilenta, H. chloronota, H. leucova* and *H. longicus* have TL/S-V ratios above the upper limit of *H. wisselensis*. Of these species only *H. iris* has not an immaculate colouration dorsally and that species is readily distinguished by the differences in the E-N/IN ranges (0.667-0.965 for *H. iris* and 1.045-1.225 for *H. wisselensis*). The remaining species are all unmarked dorsally.

*Hyla congenita* has relatively short limbs but the TL/S-V range of this species only slightly overlaps *H. wisselensis*. *H. congenita* has a narrower
head than *H. wisselensis* with an HL/HW range of 0.969-1.016 and occurs in the coastal lowlands.

Development. — 1025 tadpoles of this species have been examined: R.M.N.H. 12317, Waghte, Tigi Lake; R.M.N.H. 12318, Bobairo, Lake Paniai; R.M.N.H. 12319, 12320, Enarotali, Lake Paniai; S.A.M. 5651, R.M.N.H. 12322, 12336, Lake Paniai; R.M.N.H. 12321, Tage Mission, Lake Tage. The description of a specimen at stage 41 is as follows:

The body is not depressed. The eye is lateral, its distance from the anus about four times the distance between the eye and the tip of the snout. There is a single spiracle situated on the left ventro-lateral surface; distance between the tip of the snout and the spiracle is slightly less than half the distance between the snout and the anus. The length of the tail is almost twice the length of the body and the muscular portion is very well developed, the myotomes protruding and strongly convex. The fins are extremely narrow with the dorsal fin confined to the distal two-thirds of the tail, and the ventral extending along the entire length.

The mouth is ventral and extremely small. The lips are not expanded and are bordered by a fringe composed of rows of black-tipped papillae which do not completely surround the mouth being absent from the median portion of the superior margin. The horny beak is small, the distal halves black and finely serrated, and the proximal halves unpigmented. There are two rows of upper labial teeth, of which the outer is continuous, and the inner has a wide median gap. There are three rows of lower labial teeth on the tips of raised, muscular ridges: the innermost long and narrowly divided in the mid-line, the centre row long and continuous and the outer short and median (fig. 6).

The head and mid-dorsal surfaces of the body and tail are dark brown; the sides of the body and the tail myotomes are paler, and the ventral surface of the body pale cream.

Dimensions: length of body 22.8 mm; length of body and tail 61.0 mm.

Variation: the tadpoles examined consist of a series from stage 25 to 45. The longest specimen examined had a body length of 25.2 mm and a total length of 69.0 mm.

Variation of the mouthparts is confined to the pigmentation of the papillae, which is most conspicuous in tadpoles approaching transformation stage, and absent in some early stage specimens. The dorsal and lateral surfaces of the head, body and tail are frequently more extensively marked with dark brown than in the specimen described, and the ventral surfaces of the head and body may be densely spotted with brown.
In the specimens from stage 25 to 27 the anal orifice is dextral.

Habitat. — The majority of specimens were collected at an altitude of approximately 5800 ft at Enarotali on the shores of Lake Paniai, Wissel Lakes. The shores of Lake Paniai have been described by Boeseman (1963) as largely surrounded by steep calcareous rock. In places there are narrow stony beaches, and “large flat muddy areas are found near the river deltas covered with low vegetation”. The pH is reported to vary between 6.0 and 6.8.

Distribution. — *Hyla wisselensis* is apparently confined to and extremely abundant in montane lakes in the Snow Mountains.

Colloquial nomenclature. — The colloquial names of this species at Bobairo on Lake Paniai are “da” for the adult frog and “toba” for the tadpole.

Species of uncertain status

**Hyla javana** Ahl


Holotype. — Z.M. 29977. Type locality, “Java”. Date of collection and name of collector unknown.

Ahl's description was received with incredulity by his contemporaries and subsequent authors, for the type locality is isolated from the established range of other members of the genus. Parker (1929) described the status of the species as “doubtful”, and Mertens (1930) suggested that it might be based on *H. infrafrenata*, a species introduced into Java as reported by Van Kampen (1907a). S. S. Liem (Curator of Herpetology at the Museum Zoologicum Bogoriense) states (in litt.) that no additional representatives have been found in Java and queries whether the type locality was correct.

As the holotype is a unique specimen it has not been possible to undertake any major dissection to confirm that it is a *Hyla* species. Evidence obtained from radiographs tend to support its retention in the genus. It is clearly not based on *H. infrafrenata* or any other Papuan species.

Description of holotype. — The pectoral girdle is arciferal with the 'metasternal' portion of the sternum broad and partly ossified, and the 'xiphisternal' portion dilated with a large, posterior circular indentation so that it takes the form of two hook like prominences. Sacral diapophyses broadly dilated. Urostyle simple and articulating with the sacral vertebra by two condyles. Maxillary teeth present. Terminal phalanges short but roughly claw-shaped.
The head is flattened and very much broader than long (HL/HW 0.800), its length equivalent to less than one-third of the snout to vent length (HL/S-V 0.312). The snout is not prominent; rounded when viewed from above and in profile. The nostrils are slightly more superior than lateral, their distance from the end of the snout less than that from the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1.069). The canthus rostralis is slightly defined and gently rounded. The eye is small, its diameter greater than the eye to naris distance. The tympanum is completely covered with skin, its diameter slightly more than one-half the eye diameter. Vomerine teeth are present but there are no vomerine elevations. The tongue is circular and only slightly free behind.

The fingers are long, slender and unwebbed; in decreasing order of length 3>4>2>1. The terminal discs are small and circular.

The hind limbs are short with a TL/S-V ratio of 0.439. Toes in decreasing order of length 4>5>3>2>1. The webbing on the fifth toe reaches the sub-articular tubercle at the base of the penultimate phalanx and is connected to the disc by a narrow lateral fringe. There is a prominent oval inner but no outer metatarsal tubercle.

The dorsal and lateral surfaces are smooth and the ventral granular. There is a prominent supra-tympanic fold.

Dimensions: snout to vent length 41.0 mm; tibia length 18.0 mm; head length 12.8 mm; head width 16.0 mm; eye to naris distance 3.1 mm; internarial span 2.9 mm; eye diameter 4.4 mm; tympanum diameter 2.5 mm.

The specimen is a gravid female. Ova are small and pigmented.

In preservative the dorsal surface is a uniform, dark, slate blue and the ventral a dull cream.

**SUMMARY OF BIOLOGICAL DATA**

Although knowledge of the biology of Papuan species is extremely scant, summarising what is known indicates the presence of characteristics distinguishing most of the montane species from those occurring in the lowlands, and provides an opportunity to review the extent and variety of montane adaptations exhibited.

The presence or absence of pigmentation on the animal pole of the ovum is usually indicative of an exposed or unexposed spawning site. This association occurs in the few species whose spawn clumps have been examined in the field, and it is not unreasonable to anticipate that species whose ovarian eggs are unpigmented select unexposed spawning sites.

In table 2 the occurrence of pigmentation on the animal pole of the ova of
fourteen lowland and fourteen montane species has been recorded. (These are the only species in which the features of the ova have been noted. The fact that identical numbers are represented in each group is quite coincidental). With the exception of *H. iris* the pigment appears to be melanin and occupies the entire surface of the animal hemisphere.

Table 2

Pigmentation of animal pole of ova of lowland and montane species of *Hyla*.

<table>
<thead>
<tr>
<th>LOWLAND (0-3500 ft)</th>
<th>MONTANE (above 3500 ft)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Pigment</td>
</tr>
<tr>
<td><em>H. amboinensis</em></td>
<td>present</td>
</tr>
<tr>
<td><em>H. bicolor</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. caerulea</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. capitula</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. congenita</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. dorsalis</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. everetti</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. genimaculata</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. infrafrenata</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. jeudei</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. lutea</em></td>
<td>&quot;</td>
</tr>
<tr>
<td><em>H. napaca</em></td>
<td>absent</td>
</tr>
<tr>
<td><em>H. nasuta</em></td>
<td>present</td>
</tr>
<tr>
<td><em>H. thesaurensis</em></td>
<td>&quot;</td>
</tr>
</tbody>
</table>

Only one of the lowland species listed has unpigmented ova (*H. napaea*). Its inclusion in the list of 'lowland' species is simply due to the fact that it has only been collected at 2800 ft. On an island where the foot of a mountain is often only a few feet above sea level it is possible for a definite montane environment to exist at a relatively low altitude. Thus the inclusion of *H. napaea* amongst lowland forms is misleading and indicates a limitation in the system adopted.

Of the six highland species with pigmented ova one (*H. eucnemis*) may not occur above 4000 ft. Four of the remainder (*H. contrastens*, *H. darlingtoni*, *H. multiplica* and *H. wisselensis*) breed in static or slowly moving water. Their morphological characters suggest closer affinities to allopatric lowland than sympatric montane species, and their lowland-type breeding requirements have inhibited the extent to which they have become established in the highlands.

The only other highland species with pigmented ova is *H. iris*. Intra-uterine ova bear a small plate of pigment and when laid the ova appear entirely green. As discussed elsewhere, the species is well adapted to the montane environment.
The unpigmented ova are macrolecithal (a factor associated with breeding in cold waters according to Goin & Goin (1962)) and, in those instances where the spawn clump has been examined, the mucoid capsules are much smaller in relation to the diameter of the ovum than in lowland forms and are so gelatinous that it is possible to divide a clump into segments with a knife. In each case when spawn has been collected in the field the site of deposition has been beneath large flat stones on the beds of mountain torrents. The mucoid capsules therefore prevent the disintegration of the clump and protect the ova from the direct force of the current.

From the limited data it would appear that the majority of the lowland species breed in static or slowly moving water. *Hyla thesaurensis* in the Solomon Islands often deposits small clumps in the water that collects in the cut stems of bamboo, and in New Britain has been observed depositing in water lying in shallow depressions between the buttress roots of large forest trees. *Hyla infrafrenata* spawn has been seen in blocked drainage ditches, in swamps and in bomb craters in New Britain.

The tadpoles of the highlands species *H. arfakiana* and *H. dorsivena* are of the type referred to as mountain-stream type by Orton (1953), with prominent dorso-ventral flattening of the body and tail, and very large, ventral, suctorial mouths. Most of the highland species will probably prove to be similarly adapted. The type of horny beak in *H. arfakiana* is noteworthy in being medially divided. This represents an excellent modification to improve the efficiency of feeding on a smooth surface.

The few lowland tadpoles described are mostly of the generalised type. An exception is Van Kampen’s (1906) figure of a tadpole which he suggested might represent *H. bicolor*. It is clearly not that species and has a distinctly nektonic form.

It is not known whether there is any seasonal variation in the breeding condition of any of the Papuan *Hyla*. The predominance of sexually mature adults in breeding condition in the numerous collections received from the field over a period of several years, indicates a long and possibly continuous breeding season at least in the highlands. *Hyla congenita* and *H. everetti* are examples of lowland species inhabiting areas with very marked dry seasons, and it follows that they exhibit marked cyclic breeding activity.

**SPECIES GROUPS**

The morphological divergence exhibited by the Papuan and Australian species is far more marked than in any other genus occurring in the sub-
region. A large proportion of the genus consists of isolated individual forms without apparent close relationships to any of the other forms. The remainder exhibit definite affinities to one another forming associations regarded here as species groups. In several of the species groups there are Australian and Papuan representatives so it is undesirable to regard the latter as a separate unit.

The peroni group

The study of this group is complicated by the fact that *H. peroni* is composed of three distinct species awaiting detailed study. An undescribed species is known to occur near Brisbane whilst *H. rothi* De Vis from the Cape York Peninsula is undoubtedly distinct. (Biochemical evidence to support the recognition of *H. rothi* as a distinct species has recently been provided by Erspamer, Roseghini, Endean & Anastasi (1966)). The Australian members of the group collectively extend from the River Murray in South Australia, north-eastwards to the eastern seaboard and then, in what is almost a continuous crescentic arc, to the north-west of Western Australia. On Timor, Umboi, Savu and associated islands, the group is represented by *H. everetti* which is replaced by *H. amboinensis* on the islands of Amboina and Ceram. On the New Guinea mainland the group is represented by *H. amboinensis* in the lowland areas, and by *H. darlingtoni* in the central portion of the highlands. It is evident that the Papuan species are rarely sympatric with any other species of *Hyla* and in each case the population density is extremely high.

The dorsum of each of the members of the group is basically brown or grey. Dark, rhomboidal head markings are exhibited by some individuals of *H. amboinensis*, *H. darlingtoni* and *H. rothi*, whilst small, circular, light green spots and sparse black stippling are often present in *H. amboinensis* and *H. peroni*.

Brilliant black and yellow or black and orange markings occur on the posterior surface of the thighs of all except *H. amboinensis*, and are particularly conspicuous in *H. darlingtoni* and *H. rothi*. The extent of the markings, and the presence or absence of similar areas of pigment in the groin and axilla, and on the posterior surface of the tibia, varies from individual to individual. There is a definite interspecific variation in the shape of the black markings on the thighs: commonly reduced to small and usually roughly circular or oval spots in *H. peroni*; large variegations in *H. darlingtoni* and *H. rothi*, and most commonly narrow scriptiform markings in *H. everetti*. 
The *rubella* group

As in the case of the *peroni* group, study of the *rubella* group is complicated by the current compounding of two morphologically divergent populations as *H. rubella*. Confining to the northern half of Australia, one occupies the arid central portion and the other the peripheral coastal regions. The status of the populations has yet to be determined but they may well be distinct species.

In the lowlands of the New Guinea mainland (apparently the Southern Lowlands portion) the group is represented by *H. congenita*. The same species occurs in the Aru Islands, but is replaced by *H. capitula* on Tenimber Island. *Hyla wisselensis* is the only montane representative, and is currently known solely from the Wissel Lakes in the Snow Mountains.

All members of the group are small and squat (the snout to vent length rarely exceeding 35 mm), with short limbs and relatively small heads. The basic colouration is brown or grey in all except *H. wisselensis* and they exhibit irregular lighter markings or darker longitudinal stripes. In both populations of *H. rubella* the dark stripes take the form of broad lateral bands and there are also short sacral stripes. Pale sacral stripes are exhibited by *H. capitula*.

The *infrafrenata* group

The nominate member of the group is the most widespread occurring in Queensland and throughout the Papuan sub-region. *Hyla chloris* is possibly a member and is confined to Australia (New South Wales and Queensland) and *Hyla sanguinolenta* to a portion of the southern lowlands of New Guinea. *Hyla aruensis* is more widespread and occupies the Vogelkop Peninsula, southern lowlands, and islands to the south of the mainland, whilst *H. graminea* is known from localities in the southern lowlands and South-east Peninsula.

All species in the group are green in life and share (with the exception of *H. chloris*), broad white stripes on the posterior lateral surfaces of the forearm and foot.

The *micromembrana* group

Three montane species exhibit distinct affinities in sharing very long hind limbs, unwebbed or scarcely webbed fingers and irregular marbling dorsally.

*Hyla micromembrana* is widely distributed extending from the eastern end of the Snow Mountains and throughout the Eastern Mountains. Although
H. modica and H. spinifera occur in the same area, their geographic ranges have yet to be established.

The thesaurensis group

Two species (H. thesaurensis and H. lutea) share pigmented bones and are so similar morphologically that they are probably sibling species. A third (H. genimaculata) may well be closely related to them, but lacks bone pigment.

Hyla thesaurensis and H. lutea are sympatric in the Solomon islands. The former also occurs throughout the lowlands of the New Guinea mainland where it is sympatric with (but more abundant than) H. genimaculata.

The dorsalis group

The taxonomic problems involved are discussed elsewhere. If the Australian and Papuan populations are distinct species (and not subspecies as Cogger, 1966, contends) they form a distinct species group: H. dorsalis and H. microbelos. The characteristics of the group are the extremely small size at maturity (approximately 20.0 mm snout to vent length in females), unwebbed fingers and a reduction in the amount of webbing between the toes.

The bicolor group

As reported on page 53 there are two distinct species occurring in Australia compounded under the name of H. bicolor but recognised to merit separate taxonomic status by Copland (1957).

The specimens reported from New Guinea by several authors are in such a poor state of preservation that the identity as H. bicolor must be regarded as suspect in several instances. The conspecificity of northern Australian and Aru Islands populations has been confirmed in the present paper and there is little doubt that the same species occurs on the New Guinea mainland.

Hyla contrastens can be regarded as a member of the same species group.

DISTRIBUTION OF PAPUAN HYLID FROGS OF THE GENUS HYLID

Before providing faunal lists it is pertinent to present a brief outline of the various sites of origin of hylids that have been proposed, and the alternative routes of dispersal that have been suggested. The extent to which the genus has become established in the sub-region and the limi-
tions of the data from which the lists have been prepared are also discussed.

Parker (1929) drew attention to the disjunct distribution of *Hyla* and suggested that the simplest explanation would be to assume that the Hylidae are of northern (possibly North American) origin, with dispersals southwards into South America, westwards into Europe and eastwards into New Guinea and Australia via the Neotropical Region and the East Indian (Indonesian) islands. Beaufort (1951) queried whether *Hyla* reached the Australian region from Asia and raised the question of the existence of an Antarctic land bridge as a route for entry from South America. He stated that there is no proof that the genus ever existed in south-east Asia and commented, "... if *Hyla* was an old inhabitant of the Palaearctic Region, we should expect it to have split into different genera as it has in North America".

Darlington (1957) suggested that the predominance of hylids in South and Central America could indicate a primary radiation of hylids in Tropical South America. He considered that an alternative solution fitting the present distribution of *Hyla* would involve assuming that the primary radiation occurred elsewhere and that secondary radiations took place in America and the Australian Region. He also drew attention to the abundance of rhacophorids in much of the area where *Hyla* is absent, and suggested that in fact the Rhacophoridae might be replacing *Hyla* in the fringe areas where they meet.

There are modern workers who have expressed (in litt.) the opinion that Australian *Hyla* are possibly not true *Hyla*, and similar misgivings about the other major element of the Australian anuran fauna have appeared in print (Laurent, 1964, speaks of the "so-called Australian leptodactylids"). The extreme morphological divergence between such Australian *Hyla* species as *H. nasuta*, *H. aurea*, *H. caerulea*, *H. bicolor* and *H. rubella* is such that even the possibility that they are a polyphyletic assemblage cannot be excluded at this stage. Clearly, answers to these questions are required before the origin of the genus can be satisfactorily resolved.

As Bulmer & Tyler (in press) have pointed out, few herpetologists have visited the Papuan sub-region and the frog fauna of vast tracts of land remains completely unknown. Knowledge of the species occurring on some islands to the west of the New Guinea mainland is based solely on very small collections obtained by H. A. Bernstein during brief visits a century ago. To judge from the literature, the extensive and mountainous island of New Ireland, to the east of the mainland, has never been visited by a herpetologist and only ten specimens have been collected there. A faunal list is frequently only an index of faunal investigation and therefore may
contain only a minor portion of the total fauna. This is illustrated by
reference to Inger's (1954) revision of the frogs of the Philippines. Sum­
marising all data available at that time he listed three species occurring on
Bohol Island, and predicted that a further three widespread species would
be found there. As a result of a subsequent expedition Brown & Alcala
(1963) described a new species and increased the total to twenty. Even
when the extent of the fauna of an island apparently has been well
established, intensive collecting can prove otherwise. Numerous collections
have been obtained on Bougainville Island in the Solomons, resulting in
approximately twenty publications. However, Brown (1965) reports that
amongst the thousands of specimens obtained there by F. S. Parker during
the period 1960-64 were three new species, and at least a further three
new species are known to have been collected subsequently.

The broad zone of intergradation of faunae that forms the boundary
between the Oriental and Australian zoogeographical regions and is termed
‘Wallacea’ is virtually the western limit of the distribution of Papuan Hyla.
Species occur on all Wallacean islands with the exception of the Celebes
(Sulawesi), Lombok, Sumbawa and possibly Sula. With the possible
exception of a single specimen of Hyla recorded doubtfully from the Philip­
pines by Inger (1954) and H. javana of Java, the species occurring outside
Wallacea are clearly of Papuan origin.

North of the New Guinea mainland Hyla occurs on the Schouten Islands
in Geelvink Bay. There are no records of the genus occurring in Micro­
nesia, and few of the islands could be anticipated to provide an environ­
ment suitable for any frogs. To the north-east Hyla is found in the Purdy
Archipelago and southwards into the Solomon Islands. Frogs do not occur
in the New Hebrides (Baker, 1928) and the only frog recorded from New
Caledonia is the Australian species Hyla aurea (Sarasin, 1926), apparently
introduced there. In the more remote of the Pacific Islands there are few
species of frogs and the majority of these are not endemic (e.g. Bufo mari­
nus in the Gilbert Islands). There is in existence a single specimen of H.
infrafrenata purported to have been found amongst bananas imported into
Australia from Fiji in 1909. This species has not been reported in reviews
of the Fiji frog fauna by Barbour (1923) and Brown & Myers (1949),
but it has been so successful in colonising other Pacific islands, that the
presence of a population there, even of short duration and no longer extant,
cannot be completely discounted.

Hyla has therefore become established throughout the entire Papuan sub­
region and only the Ranids (mainly Platymantis, Cornufer and Rana)
extend further eastwards to the more remote Pacific islands.
Faunal Lists

Timor (T), Sumba (Su), Savu (Sa) and Alor (A) Islands: H. capitula or H. rubella (T), H. everetti (T, Su, Sa, A), H. infrafrenata (T).

Aru (A), Kei (K) and Tenimber (T) Islands: H. aruensis (A), H. bicolor (A, K), H. capitula (T), H. congenita (A, K), H. infrafrenata (A, K).

Vogelkop Peninsula (V) and associated islands: Amboina (A), Buru (B), Ceram (C), Halmahera (H), Misool (M), Talaud (Ta), Ternate (T) and Waigeo (W): H. amboinensis (A, C, M, V), H. angiana (V), H. arfakiana (V), H. aruensis (M, V, W), H. bicolor (V, W), H. caerulea (V), H. chloronota (V), H. eucnemis (?V), H. genimaculata (V), H. graminea (V), H. infrafrenata (all localities), H. longicrus (V), H. pratti (V), H. pygmaea (V), H. thesaurensis (V), H. vagabunda (V, C).

Aru (A), Kei (K) and Tenimber (T) Islands: H. aruensis (A), H. bicolor (A, K), H. capitula (T), H. congenita (A, K), H. infrafrenata (A, K).

Vogelkop Peninsula (V) and associated islands: Amboina (A), Buru (B), Ceram (C), Halmahera (H), Misool (M), Talaud (Ta), Ternate (T) and Waigeo (W): H. amboinensis (A, C, M, V), H. angiana (V), H. arfakiana (V), H. aruensis (M, V, W), H. bicolor (V, W), H. caerulea (V), H. chloronota (V), H. eucnemis (?V), H. genimaculata (V), H. graminea (V), H. infrafrenata (all localities), H. longicrus (V), H. pratti (V), H. pygmaea (V), H. thesaurensis (V), H. vagabunda (V, C).

Northern Lowlands (N) and associated islands: Biak (B), Japen or Jobi (J): H. albolabris (N), H. amboinensis (N), H. bicolor (N), H. caerulea (N), H. genimaculata (N), H. infrafrenata (all localities), H. jeudei (?N), H. mystax (N), H. nigropunctata (J, ?N), H. obtusirostris (J), H. thesaurensis (N).

Admiralty Islands: H. bicolor, H. infrafrenata, H. thesaurensis.

Purdy Archipelago: H. infrafrenata, H. thesaurensis.


Solomon Islands: H. lutea, H. thesaurensis.


D'Entrecasteaux and associated islands: H. infrafrenata, H. thesaurensis.


Acknowledgements

I am greatly indebted to the Director and Board of the South Australian Museum for providing laboratory, secretarial and other facilities, and a grant enabling me to visit New Britain to study several species in the field. Mr. F. J. Mitchell, the Senior Curator of Vertebrates, offered advice and support over a period of several years and it is a pleasure to record my indebtedness to him.

1) Amongst the Nyctimystes Rueppelli syntypes from Halmahera are two species of Hyla. One resembles H. bicolor and the other (represented by four juveniles: S.M.F. 2619-2622) is of uncertain identity and probably not included in the above list.

2) The specimen from New Britain reported to represent the Australian species H. nigrofrenata by Muller (1884) was re-identified as Rana kreffti by Roux (1918).
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