PHILIPPINE ZOOLOGICAL EXPEDITION

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ROBERT F. INGER

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The Philippine Expedition: Amphibia

INTRODUCTION

Prior to the work of Taylor (1920, 1922a, b, 1923), the Philippine Amphibia were known only through miscellaneous papers of Günther, Peters, Boulenger, Boettger, and Stejneger (see References). These authors received their material from such collectors as Hugh Cuming, F. Jagor, Carl Semper, A. H. Everett, O. F. Moellendorff, and E. A. Mearns. With the exception of Cuming, who collected on most of the larger islands, each of these men worked on one or a few islands only. None of them was interested primarily in reptiles and amphibians. Cuming, for example, made a general natural history collection, Semper was primarily interested in invertebrates, and Mearns in mammals.

It was not, therefore, until Taylor began his work in 1913 that a herpetologist conducted extensive field operations in the Philippines. Taylor worked on the majority of the large islands and collected in parts of some that previously had been unexplored herpetologically. In his first compilation, Taylor (1920) recognized sixty-six species, of which nineteen were described as new. Subsequent papers by Taylor (1922a, b, 1923) described twenty-two additional species. In collaboration with Noble (Taylor and Noble, 1924), he described one more species.

Between 1924 and the present, no taxonomic papers devoted in large part to Philippine species have appeared, although ecological studies by Villadolid and Rosario (1930) and Cendaña and Fermin (1940) have been published.

The collections made by the Philippine Zoological Expedition, 1946–1947, of Chicago Natural History Museum in co-operation with the Philippine National Museum (see Hoogstraal, 1951), include over 1,800 amphibians, principally from Mindanao, the Calamian Islands, and Palawan. Additional material from other parts of the Philippines—notably Luzon, Mindoro, Leyte, and Mactan—has been received by various American museums from members of the United States Armed Forces that were stationed in the Philippines during World War II. Subsequent to 1947, Mr. D. S. Rabor of Silliman University, Dumaguete City, Negros, has sent specimens from southern Negros to Chicago Natural History Museum. This large accumulation of fresh material presented an excellent opportunity for a review of the Philippine Amphibia.

It was at the suggestion of Dr. Karl P. Schmidt, Chief Curator, Department of Zoology, Chicago Natural History Museum, that this study was undertaken. It is not possible to express adequately my appreciation of his constant inspiration and helpful criticism. I am also indebted to my colleagues of the staff of Chicago Natural History Museum for advice and varied assistance; the aid of Dr. Rainer Zangerl and Messrs. D. Dwight Davis, Harry Hoogstraal, Clifford H. Pope, and Loren P. Woods was especially appreciated. Miss Margaret Bradbury, also of Chicago Natural History Museum, made all of the illustrations.

Material was borrowed from various institutions, and types have been examined as far as available. For the many courtesies extended me I wish to thank the following: American Museum of Natural History, Mr. C. M. Bogert, and Mrs. M. Hecht; British Museum (Natural History), Dr. H. W. Parker, Dr. M. A. Smith, Mr. J. C. Battersby; California Academy of Sciences, Mr. J. R. Slevin; Carnegie Museum, Mr. M. G. Netting and Dr. G. L. Orton; Museum of Comparative Zoology, Messrs. Arthur Loveridge and Benjamin Shreve; Museum d'Histoire Naturelle, M. Jean Guibé; Raffles Museum, Mr. M. W. F. Tweedie; University of Michigan, Museum of Zoology, Dr. Norman Hartweg; United States National Museum, Dr. D. M. Cochran.

Dr. E. H. Taylor, University of Kansas, and Mr. Robert Roecker, Cornell University, kindly lent me specimens from their private collections. Dr. W. H. Stickel, United States Fish and Wildlife Service, graciously permitted me to use his field notes, made on Mindoro.

Finally, I am grateful to my wife, Mary Lee Inger, for typing parts of the manuscript and for her patient editorial assistance.

GEOGRAPHIC NOTES

The physical geography of the Philippine Islands has frequently been described. Although this paper has no new information to offer, a brief outline is presented here for use in connection with the discussions of species ranges and ecological notes.

The Philippine archipelago (fig. 28), situated between 5° and 22° N. Lat. and 117° and 127° E. Long., includes more than 7,000

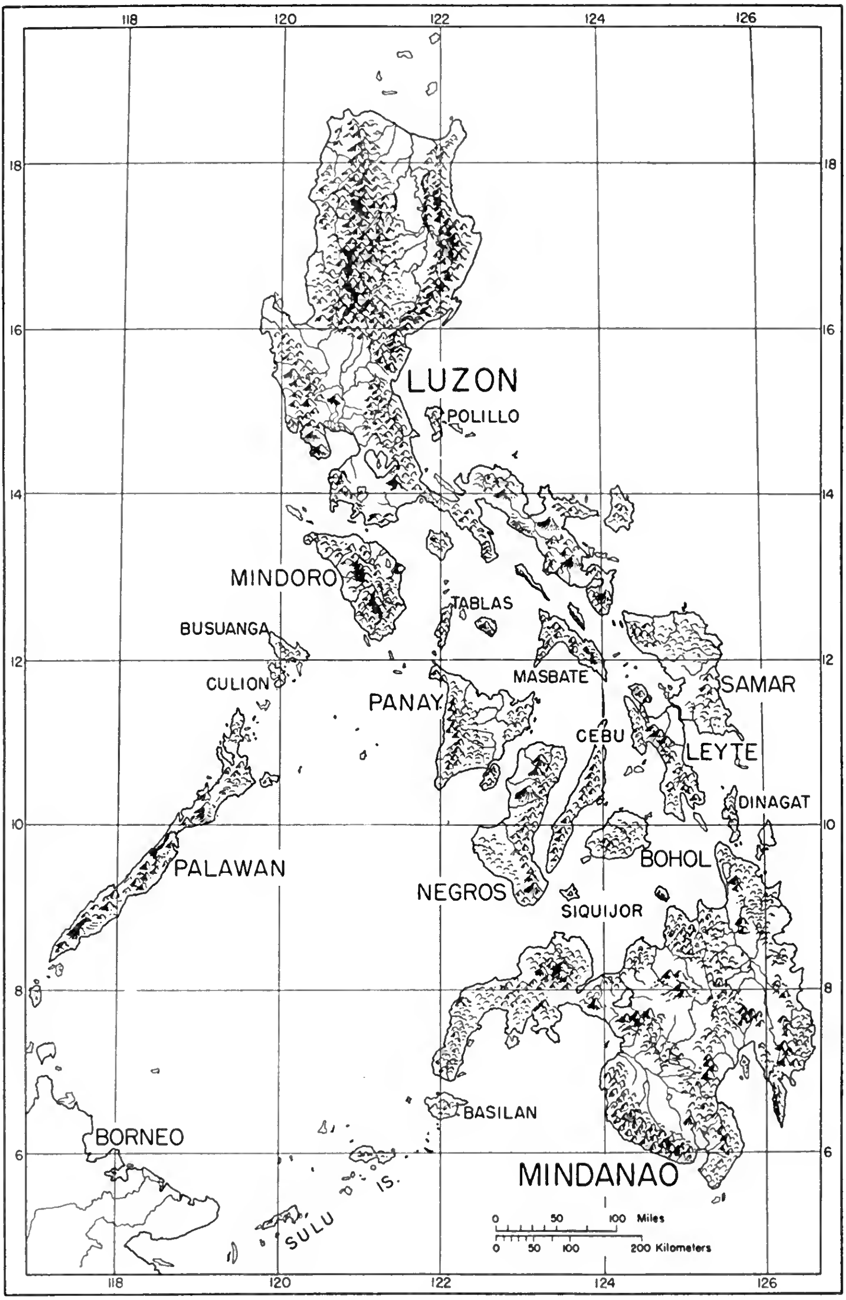


FIG. 28. The Philippine Islands. Topography adapted from King and McKee (1949).

islands, of which only slightly more than 450 exceed 2.5 square kilometers in area. The two largest, Luzon and Mindanao, have areas of 105,708 and 95,587 square kilometers, respectively. The latter is approximately equal in area to Hungary or to the state of Indiana. The central islands of Panay, Negros, Cebu, Bohol, Siquijor, Leyte, and Samar are often referred to as the Visaya Islands. The small islands between Borneo and Mindanao are grouped under the term Sulu Islands or Sulu Archipelago.

Generally, the islands are mountainous. Luzon, Mindoro, Palawan, Mindanao, Negros, Panay, and Sibuyan have elevations greater than 1,500 meters. Broad plains occur in central Luzon, western Negros, and northeastern Leyte. In the eastern part of the archipelago, the mountain ranges have a northwest–southeast trend, whereas in the west the trend is northeast–southwest.

The east border of the archipelago is formed by the Mindanao Trench, which attains depths in excess of 10,000 meters. Most of the Celebes Sea, on the southern border, is below the 4,000 meter isobath. The South China Sea on the west is a shallow basin for the most part, although it, too, reaches the 4,000 meter isobath. The Sulu Sea, surrounded by Borneo and the Philippines, contains large areas that are over 4,000 meters deep. Of the waters completely enclosed by the Philippine Islands only a small area, in the Mindanao Sea north of Mindanao, is more than 2,000 meters deep.

Large areas of the enclosed waters are less than 200 meters deep. The flanks of the Sulu Sea are formed by two submarine ridges, running from Borneo northward to include Palawan and the Calamian Islands and from Borneo northeastward to the Sulu Archipelago and western Mindanao. Only the second of these has small strips lying below 100 meters. A third submarine ridge, which is forked, passes southward from eastern Mindanao. Both branches run toward Celebes, one indicated by the Sangihe and Sarangani Islands and the other by the Talaud Islands. Except where these islets emerge, this forked ridge does not rise above the 200 meter isobath.

Major topographic features are illustrated in figures 28 and 29.

NOTES ON THE ENVIRONMENT OF THE PHILIPPINE AMPHIBIA

A discussion of the Philippine Islands as an environment is worthy of a separate volume. This section is offered not as a substitute for such a discussion but merely as a compendium of miscel-

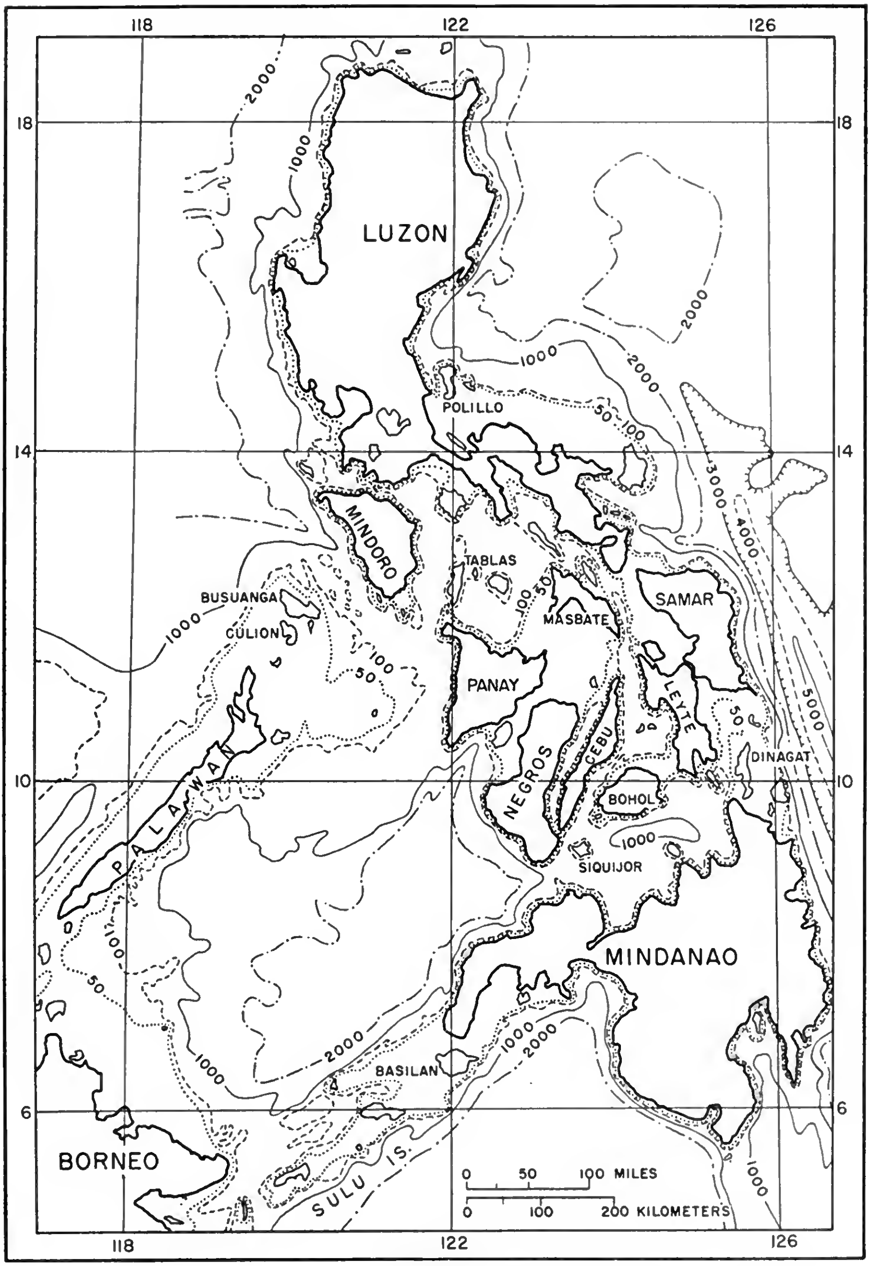


FIG. 29. The submarine topography of the Philippine Islands.

laneous information that may serve as a background against which the ecological notes of the individual species can be considered.

Climate.—The climate of the Philippine archipelago is tropical—temperature and rainfall are generally high. The notes that follow are taken from Coronas (*in* Merrill, 1926), Maso (1914), and Selga (1935). Average annual temperature for fifty stations situated near sea level from the Batan Islands north of Luzon to Palawan, southern Mindanao, and the Sulu Islands ranges only from 25.8° to 27.9° C. The range of mean monthly temperatures is slight but varies geographically from south to north. The range is 3° C. at Jolo in the Sulu Islands and 8° C. at Aparri on the north coast of Luzon. Not many observations are available for high altitudes. At 1,500 meters on Mount Mirador, Mountain Province, Luzon, mean temperature over a sixteen-year period was 17.9° C. In the mountains of northern Luzon, light frosts and snows are not uncommon during December and January.

Both the amount and the seasonal distribution of rainfall vary geographically. The mean annual rainfall for 350 stations ranges from 963 mm. at Padada, Davao Province, Mindanao, to 4,436 mm. at the City of Baguio, Luzon; over the entire archipelago the mean is in excess of 2,000 mm. With regard to the seasonal distribution of rainfall, the Philippines may be divided into three climatic zones. The western faces of the western islands are characterized by sharply contrasting wet and dry seasons. Approximately 90 per cent of the annual rainfall is carried to these areas in the period from June to October by winds originating in the southwest. The second climatic zone coincides with the eastern border of the archipelago from Polillo southward. This region has no dry season but has a pronounced maximum rainfall period from November to February; northeast monsoon winds bring the rains of this period. The third climatic zone is characterized by relatively uniform rainfall throughout the year, although there may be a short dry season lasting from one to three months. The climatic zones are shown in figure 30.

Prevailing winds, as implied above, are from the southwest from June to October and from the northeast during the remainder of the year. Typhoons, which may be important to animal dispersal, are common during the summer and autumn. They originate over the Pacific and generally cross the archipelago north of central Samar in a northwesterly direction, although occasional tracks have a west-southwest bearing.

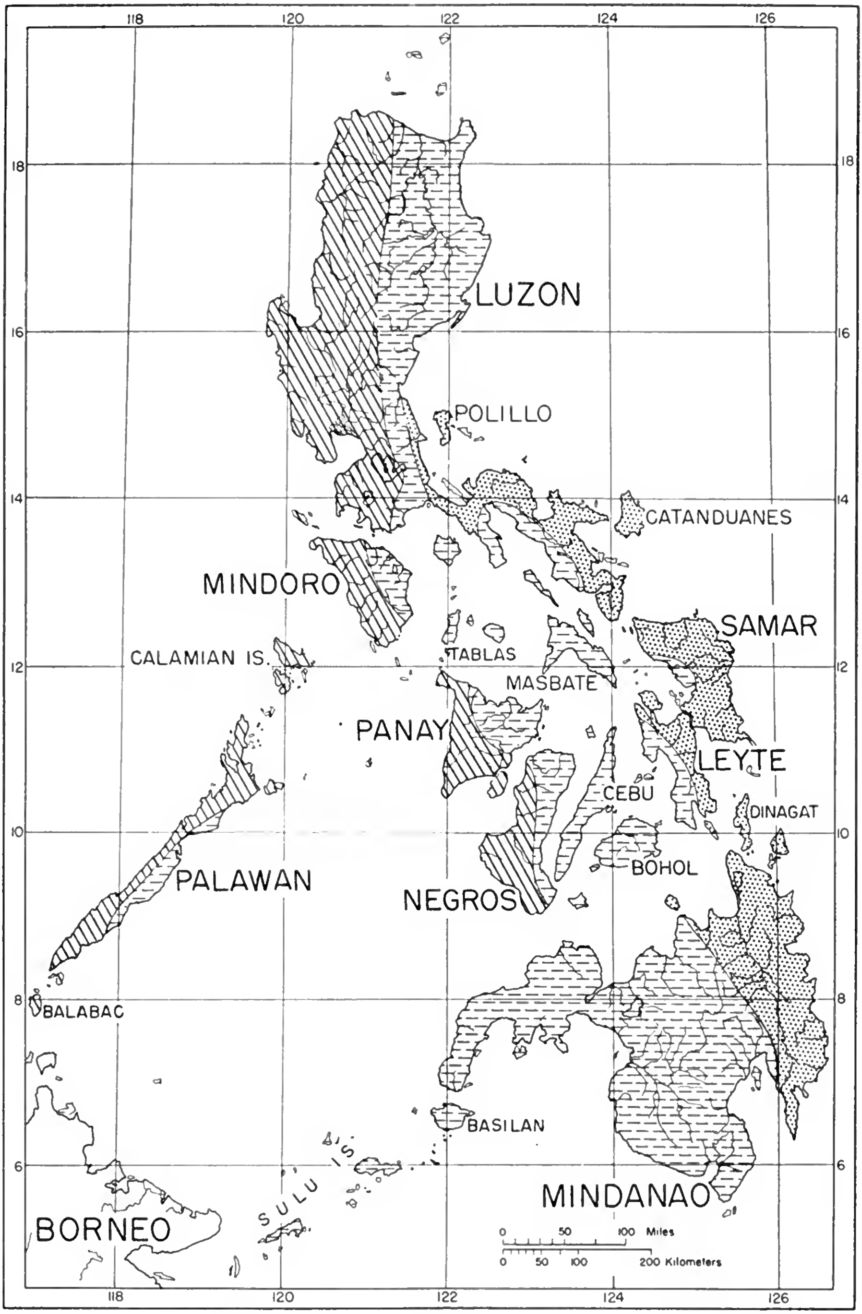


FIG. 30. The climatic zones of the Philippine Islands. Slanting lines = sharply contrasting wet and dry seasons; dots = no dry season, but a distinct period of maximum rainfall from November to February; broken lines = rainfall throughout the year. Adapted from Coronas *in* Merrill (1926).

Vegetation (adapted from Merrill, 1926).—The original vegetation of the Philippine Islands was composed of three major associations: the lowland rain forest, the montane mossy forest, and the mangrove swamps. The first was (and is) dominated by large trees of the family Dipterocarpaceae, although the forest is exceedingly mixed. The dipterocarpous forests are characterized by a thick canopy formed by the crowns of the largest trees. Relatively little sunlight penetrates the canopy. Beneath it develop two other stories of trees. Humidity and temperature are high and vary but little (see p. 474).

This lowland forest gradually merges with the montane forest near an altitude of 750 meters, the actual zone of change being determined by seasonal distribution of rainfall, among other factors. The montane forest lacks the tall trees found at lower altitudes. The trees become stunted with increasing elevation and finally give way to shrubs. Mosses, lichens, and epiphytes are extremely abundant in the montane forest. The mangrove swamps are the only relatively homogeneous natural association; they were originally distributed in bays and in the tidal zones of rivers.

The activities of man have, of course, materially altered the vegetation cover. Three important associations have been introduced. The development of two originates with primitive shifting agriculture. A section of original forest is felled and burned, and the area is used to grow food for a very few years, after which it is abandoned; if it is not burned repeatedly, secondary forest generally appears. This consists of a dense tangle of trees and vines that belong to species usually not occurring in the interior of the primary forest. It is presumed that, as soon as the proper conditions of humidity, temperature, and light develop in the secondary forest, it would be invaded and gradually dominated by species from adjacent primary forest.

Frequently, however, coarse grasses such as lalang (*Imperata*) take over the abandoned fields. The grasslands are usually burned periodically. Under these circumstances, reforestation is prevented, since all tree seedlings are destroyed. Fire does not affect the buried rhizomes of the perennial grasses.

The third introduced association—large, uniform, cultivated areas—developed with the advent of modern agricultural techniques. The copra and abaca plantations are of greater extent and permanence than the fields of shifting agriculture.

Merrill (1926) believes that before the arrival of man the three types of original forest covered the entire archipelago. Estimates of the present extent of forest cover in the Philippines vary. Merrill states that 50 per cent of the land is covered by forest (33 per cent original forest and 17 per cent secondary), 40 per cent by grassland, and 10 per cent by cultivated fields. Tamesis (1940) estimates that 60 per cent of the land area is in forest and 22 per cent in cultivated fields; presumably the remaining 18 per cent is waste grassland.

Faunal environment.—Insects, which are the chief item of the diet of frogs, are especially abundant in the Philippines, as in all humid tropical regions. Ants and termites, important in the economy of burrowing frogs (for example, *Kaloula*), occur in great numbers. Except for the predaceous aquatic larvae of certain insect groups (for example, the Odonata) and a few aquatic spiders, which probably prey on tadpoles, invertebrates are not important as predators of amphibians.

The principal predators of frogs are to be found among the bony fishes and all classes of terrestrial vertebrates. The fishes are of especial importance during the aquatic larval stages of amphibians. In the Philippines the dominant fresh-water fishes are the carnivorous gobies and related families, of which approximately 50 are fresh-water species (Herre, 1927). According to Herre (1924a, b), the remainder of the Philippine fresh-water fish fauna is composed of 4 species of catfishes, 29 species of cyprinids, and 4 species of labyrinthicine fishes. This fauna contrasts sharply with that of Borneo, which includes 63 species of fresh-water catfishes, 101 species of cyprinids, and 23 species of labyrinthicines (Weber and de Beaufort, 1913, 1916, 1922). The gobies of Borneo are not well known, but it is clear that they are not the dominant fresh-water group.

The Philippine snake fauna includes representatives of the principal families, with the exception of the Leptotyphlopidae and Viperidae (Taylor, 1928). The fauna is well balanced relative to that of Borneo, no group having a disproportionate number of species, as was noted in fishes. The five families of lizards (Gekkonidae, Agamidae, Varanidae, Scincidae, and Dibamidae) that occur in the Philippines (Taylor, 1928) include the most important faunal elements of the Indo-Australian archipelago (de Rooij, 1915).

From the standpoint of amphibian ecology the snakes are probably the most important group of predators. The water snakes of the genus *Natrix* have particular significance, as frogs constitute one of their two chief food items. Eight species of *Natrix* are found in the Philippines (Taylor, 1922b, d). Other Philippine snakes probably preying on frogs are *Sibynophis* (one species), *Lycodon* (three species), and *Ahaetulla* (four species) (Taylor, 1922d). The zoogeographic relations of Philippine lizards and snakes are discussed below (pp. 465 ff.).

Representatives of the major mammalian orders, with the exception of the marsupials, lagomorphs, proboscideans, and perissodactyls, are included in the Philippine fauna. The forms are distributed as follows (the number of species is taken from Taylor [1934] and the generic arrangement from Raven [1935]):

Order	Species	Genera
Pholidota	1	1
Insectivora	16	5
Dermoptera	1	1
Chiroptera	77	23
Primates	9	5
Carnivora	11	10
Rodentia	75	19
Artiodactyla	21	3

In comparing this fauna with the mammals of Borneo and the Malay Peninsula, the difference of greatest interest here is the reduction in variety and numbers of carnivores in the Philippines. The southern Malay Peninsula has 32 species of Carnivora distributed in 16 genera (24 per cent of total number of mammalian genera) and Borneo 45 species and 21 genera (27 per cent of total number of mammalian genera) (Raven, 1935). Carnivores account for only 15 per cent of the Philippine mammalian genera.

Most of the families of birds present in other parts of Malaysia are also found in the Philippines (Delacour and Mayr, 1946). The groups of most importance in the ecology of amphibians occur in the following numbers: 21 species of herons, 17 hawks, one crane, 10 owls, 10 kingfishers, and 4 shrikes. All of these groups are potential predators of frogs.

TAXONOMIC BACKGROUND

In any extensive study of the taxonomy of one of the larger groups of animals the problem of generic definition arises. In the Salientia the history of a pair of related genera is often one of alternate lumping and splitting by successive herpetologists. Examination of such cases shows that the argument revolves around the "significance" of characters. "Significance" is usually related merely to extent of variation, implicitly if not explicitly. Almost without exception the definitions of frog genera are based entirely on morphological characters, with no attempt made to elucidate their ecological importance or other meaning.

The concept of natural selection leads to the conclusion that every species is more or less adapted to its environment and implies that the difference between closely related sympatric species is a matter of differential adaptation. It also follows that the difference between any two related sympatric groups, regardless of taxonomic level, is one of adaptation.

Simpson (1944) visualizes the organic world as divided into a hierarchy of ecological zones and subdivisions that shift in time. He illustrates his "adaptive grid" with the fissipede and pinnipede carnivore major zones, the canid and felid zones, and the machairodont (saber-tooth) and feline sub-zones. This example emphasizes that each taxonomic level is adapted to exploit a particular way of life; therefore, the differences between groups at any single level are adaptational, reflecting these different modes of life. Furthermore, the ecological latitude diminishes downward in the hierarchy. Consequently, the differences become less fundamental at successively lower levels. It follows that the differences at the generic level are of a more fundamental nature than those at the species level.

Adaptation is a relationship between structure, behavior (in a broad sense), and environment. Consequently, to attempt to assess "significance," using a purely descriptive morphological approach, will not bring about understanding of adaptation, which is the key to a classification reflecting evolution. I believe that the failure to emphasize the ecological implications of morphology is one of the two cardinal causes for difficulty at the generic level of amphibian taxonomy.

Although this is not the place for a comprehensive demonstration of an ecological-morphological approach, it is hoped that the comments that follow will serve the dual purpose of focusing attention on this general problem and of explaining the taxonomic position adopted here.

Among the genera of Philippine amphibians, three groups provide useful examples. The genera of Ranidae constitute one such group. As delimited in this report, the genus *Rana* (=subgenera

Rana and *Hylarana* of Boulenger, 1920) is a group of species in which the outer metatarsals are separated by a web, at least in their distal halves, the toes are extensively webbed, and the eggs are small and pigmented. These species inhabit a variety of aquatic situations, although some are less restricted to water than others.

The morphological characters tie in with ecological observations. It is of obvious importance to an aquatic frog that the surface area of the foot be large, relative to total size. Both the webbing of the toes and the wide separation of the metatarsals increase surface area. About half of the species have flaps of skin along the inner edge of the first and the outer edge of the fifth toes, further adding to the surface of the foot.

The free-swimming larvae develop in standing or flowing water. The broods are large (usually much in excess of 150 eggs per clutch), and, as a consequence, the ova are small relative to the female (see Table 35, p. 349). One hemisphere of the egg is black; presumably the pigment absorbs heat from the light incident in the relatively open site of oviposition, thus increasing the rate of development. The pigment may also protect the ova from harmful radiations such as ultra-violet (Sergeev and Smirnov, 1939).

The section or subgenus *Hylarana* is distinguished by the presence of a circummarginal groove around the end of the dilated digit tip. Some Malaysian species of *Rana* (*sens. str.*) have swollen digit tips, but none has the broad disks and grooves common in species of *Hylarana* (fig. 33). Noble and Jaeckle (1928) demonstrated that the appearance of the groove around the end of the digital disk is an indicator of histological specialization of this region. These disks, though usually referred to as scansorial, may also function as devices for clinging to stones and other objects in water currents. In addition to the enlarged disks all the Malaysian species of *Hylarana* that I have examined have an extra subarticular tubercle at the base of each finger (fig. 33, B). These, too, probably function as gripping devices.

Despite the development of these specialized structures, it is not possible at present to recognize *Hylarana* as a distinct genus. The difference noted does not by itself indicate an ecological shift of sufficient magnitude to warrant that step. *Rana* (*Hylarana*) *erythraea*, for example, is found in flooded rice fields along with *Rana* (*Rana*) *cancrivora; Rana* (*Hylarana*) *nicobariensis* occurs along small streams and ditches but spends some time away from water in grass (Mertens, 1930)—behavior corresponding to that of *Rana* (*Rana*) *limnocharis.* Some species of *Hylarana,* for example, *everetti,* are most abundant around hill streams, whereas others, like *signata,* wander about the forest floor or occasionally climb onto low vegetation. The significance of the disks in this group of species seems to be that they permit the group to occupy a variety of habitats and may in the past have been the structures enabling the shifts from one sub-zone to another by other genera of ranids.

As a matter of fact, Noble (1931) places *Hylarana,* which he accords full generic status, in the subfamily Cornuferinae in which it is associated with nine genera (according to Noble), all of which have specialized digit tips and all but one of which are known to have made important ecological shifts relative to *Rana* (*sens. str.*). Three of these groups (equivalent to four of Noble's genera) occur in the Philippines. *Cornufer* (including *Platymantis* of Noble and others) consists of a group of species in which the web is greatly reduced or absent and the outer metatarsals are bound together for almost their entire lengths. Both of these characteristics reduce the surface area of the foot and would place these species at a disadvantage in an aquatic but not in a terrestrial life. The morphological deductions coincide with field observations, as *Cornufer* is typically an inhabitant of the forest floor. It is illuminating to compare the feet of a *Cornufer* (fig. 34) and an aquatic *Rana* (fig. 35).

Cornufer is also characterized by the absence of free-swimming larvae. The eggs are large, few in number, and apparently laid on land (see p. 348). The large amount of yolk provides sufficient food for the pre-metamorphic period. Sites of oviposition are not known. It we may judge from the behavior of other land-breeding frog genera (for example, *Eleutherodactylus*), it is probable that *Cornufer* deposits its ova under debris of the forest floor and in crevices and holes in plants. Such situations would offer some protection from predation and desiccation. They would also shield the ova from light, making dark pigment superfluous.

Thus the morphological characteristics of *Cornufer* have clear relations to behavior and the environment occupied by its species. The general ecology of *Cornufer* represents a shift to a different sub-zone. Certainly the differences between the modes of life of *Cornufer* and *Rana* (in either a broad or limited sense) are of an entirely different order from the distinctions between species within each group or between *Hylarana* and *Rana* (*sens. str.*). It is for this reason that *Cornufer* should be recognized as a genus while *Hylarana* should not.

Staurois, the second genus of "Cornuferinae" represented in the Philippines, has been distinguished from *Rana* by the morphology of its larvae. Tadpoles of *Staurois* are adapted to life in a mountain brook habitat. A suctorial abdominal disk enables these larvae to cling to the rocky substrate in strong currents. Additional larval modifications for the torrent habitat are the reduction of the lungs (Noble, 1929), the depressed body form, strong tail muscle, and low tail fin (Liu, 1950). Noble (1931) maintains that adult *Staurois* cannot be distinguished from adult *Rana* (*Hylarana*), but he retains the generic status of the former because of the larval morphology. These striking modifications denote an adaptive shift with clear and important ecological consequences.

The third cornuferine genus found in the Philippines is *Micrixalus.* This is a group of small Oriental ranids with enlarged digital disks similar to those of *Rana* (*Hylarana*) and extensive webbing between the toes. There is little to distinguish this group from *Hylarana;* indeed Noble (1931) refers to them as "a group of small species of *Hylarana* lacking vomerine teeth." The Philippine species tentatively placed in *Micrixalus* (p. 344) has vomerine teeth. But, even assuming that this latter form is not to be associated with *Micrixalus,* a genus based upon the presence or absence of vomerine teeth does not satisfy the requirement of shift of ecological emphasis suggested above. No explanation of the role of the vomerine teeth in the economy of a species has been advanced. Reliance on this particular character has resulted in confusion in other groups, as will be pointed out below. Unfortunately the species of *Micrixalus* are so poorly known, both ecologically and morphologically, that a definitive opinion on the status of the genus is not possible. I have retained *Micrixalus* solely in the interests of conservative nomenclature.

The family Bufonidae affords another useful example of the morphological-ecological approach. The cosmopolitan genus *Bufo* consists chiefly of heavy-bodied, short-legged toads. These species are terrestrial and breed in quiet water. The thick tuberculate skin of the adults protects them from desiccation and permits them to wander far from water. The toes are usually about one-half webbed; the web is generally thick and does not resemble the membranous web of aquatic frogs. These characters are additional evidence of the dissociation of adult *Bufo* from the aquatic habitat. Another group of bufonids is characterized by complete and membranous webs, slim bodies, and long legs. These species, placed here in the genus *Ansonia* Stoliczka, have been collected beside and in swift rocky streams in the forests of Malaysia. Clearly, the morphological differences between adult *Bufo* and *Ansonia* are connected with the known ecological differences.

The larvae of the two groups broaden the area of morphological and ecological differences. *Bufo* larvae have subspherical bodies, high tail fins, and generalized oral disks; in short, they have the characteristics common to benthic tadpoles of the standing or slowly moving water they inhabit. By contrast, larval *Ansonia* have depressed bodies, reduced fins, and sucker-like oral disks; in other words, they are typical torrent tadpoles (see description of *Staurois* larvae above). Thus the fundamental adaptations of adult and larval *Bufo* and *Ansonia* are associated with different modes of life (see also pp. 239 ff.).

The last example is a negative one. The two Oriental genera of Rhacophoridae, *Rhacophorus* and *Philautus*, have been distinguished on the basis of the presence or absence of vomerine teeth. Authors have questioned this distinction because of intraspecific variation of this character; the lack of evidence of the functional significance of vomerine teeth has been noted above. At present there is no known ecological difference between them. The dichotomy of these groups of species is one of the least satisfactory in the Amphibia of the Malaysian region. Recognition of two genera in this instance can not be justified even on grounds of convenience, for some species have been moved back and forth between the two (see van Kampen, 1923, and Wolf, 1936). Nevertheless, both genera are retained here because a satisfactory decision must be based upon a study of a large proportion of the forms, a task beyond the scope of this report.

The second cardinal cause for taxonomic difficulties at the generic level is the practice of defining a genus on the basis of one or a few morphological characters and of arbitrarily insisting that all the species agree in these characters. One of the principal defects of this practice is that it ignores what may be called the independent variation of species. Our concept of a classification reflecting genetic relationship implies that the species grouped in a genus have a common ancestry, which in turn implies a certain amount of common genetic make-up. Common genetic backgrounds may result in parallel modification in several species. However, a particular change in one species need not be accompanied by a similar change in the other. As soon as populations become isolated from one another their subsequent variation is independent in this limited sense.

Genetics has brought forward abundant evidence for the mutability, either through gene and chromosome mutation or through recombination, of all kinds of characters. Accepting the theses that any character may be modified and that the variation of isolated populations is independent, there is no reason for rigidly maintaining that a given character is a "generic character" in which all the species of the genus must agree (Schmidt, 1948).

The idea that the important differences between genera are generally differences in the basic adaptations of the groups is pertinent here. An adaptive pattern is built up by a number of characters, although all characters may not be of equal importance in an adaptive morphological complex. Some characters may merely represent steps in progressive specialization. The absence of a character of this type, despite its appearance in most of the species of a given genus, should not be taken as evidence that a species does not belong to the genus.

The case of *Rhacophorus* vis-à-vis *Philautus* is illustrative. As noted earlier, the only distinction between these genera is the presence of vomerine teeth (*Rhacophorus*) or their absence (*Philautus*). The most recent revision of *Rhacophorus* (Wolf, 1936) recognizes *Philautus* on this basis but also admits the weakness of the distinction. Indeed, Wolf includes the species *spinosa* Taylor and *edentulus* Müller, both of which lack vomerine teeth, in the genus *Rhacophorus*. Obviously the presence of vomerine teeth cannot be an absolute criterion of generic affinity. However, if a group of characters defining a shift of ecological emphasis could be found to distinguish these two genera, the vomerine tooth character might be ignored.

Smith (1931) separated *Ooeidozyga lima* from *O. laevis* and other species of the genus because only *lima* has a pointed tongue, those of the other species being rounded posteriorly. The over-all agreement in adult morphology and the distinctive tadpoles common to these species are thus considered less important than a single character of unknown functional or phylogenetic significance. Smith's action is even less understandable in view of the ecological similarity of *lima* and *laevis*. Both species are thoroughly aquatic, although Siamese specimens of *laevis* seem to be less so than East Indian individuals (see Smith, 1916, and Mertens, 1930).

Cornufer provides the final example of the difficulties imposed by a rigid character diagnosis. The species of *Cornufer* have reduced webbing. *Rana glandulosa* may have as little web as some species of *Cornufer*, for example, *guentheri*. But no one would recommend placing *glandulosa* in *Cornufer*. The extent of the fusion of outer metatarsals varies in *Rana* and *Cornufer* with the low extreme of the former approaching the upper limit of *Cornufer*. The omosternum of *Cornufer* is forked; that of *Rana* is not except in a very few species, for example, *cancrivora*, which clearly belongs in *Rana*. If any one of these characters is considered singly or if all species of each genus must conform to a generic pattern in all characters, no distinction between *Rana* and *Cornufer* would be possible. On the other hand, the characters of the species of *Cornufer* and *Rana*, viewing each group as a unit, contribute to distinctive adaptive patterns that permit the recognition of two genera.

Thus, if every genus is characterized by an assemblage of morphological features contributing to an adaptive pattern that can be shown to have a fundamental ecological significance, the genera will coincide with natural groups and many of our present difficulties will disappear.

As noted above, Taylor (1920) recognizes 66 species in his review of the Philippine amphibians and adds 23 species in later papers. Fully 29 of these are placed in synonymy in this report. An additional 15 are treated as subspecies of other forms. Three more are omitted from this report; they represent misidentifications or incorrect localities in the old literature. A fourth, *Halophila jagori* Peters, is of indeterminate status (p. 354). By contrast only three new species are described here. A total of 56 species is recognized in this study.

The great discrepancy between Taylor's work and the present study results partly from differences in concepts of the species. Although species were originally treated as "kinds," they are now largely thought of as populations. A "biological" species concept is acquiring increasingly wider acceptance. The cardinal points of this type of approach are that species are natural populations or groups of natural populations and that these populations (or groups) are isolated, the isolation resting upon physiological or genetic bars to reproduction.

However, a number of practical difficulties beset the biological species concept. One of these, discussed at length by Mayr (1942), is the fact that all populations are not in spatial contact, with the consequence that it is not possible to tell with certainty whether bars to interbreeding actually exist. Obviously this point is of particular importance when dealing with the fauna of an archipelago. Mayr proposes the following as a practical working definition: species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups. This recognizes both the biological viewpoint and the uncertainty occasioned by isolated populations. It is the definition applied in this paper.

Apparently Taylor did not think of species in terms of populations. Rather, he seemed to define species as morphologically distinct specimens at his disposal; for example, he described two specimens from Mindanao as two distinct species. I refer to *Rana philippinicus* and *R. grandocula.* Certainly these individual frogs differed from one another. If the species may be defined as a "kind" of organism, logically one cannot dispute Taylor's arrangement. Indeed, logically the number of species could have been multiplied indefinitely. But as species are populations, the differences between Taylor's frogs will be recognized as the differences to be expected between individuals of sexually reproducing organisms. Museum specimens must be understood to be samples of the *populations* in nature; "collecting" is a sampling technique.

Whether spatially isolated populations are potentially capable of interbreeding is not always easy to determine. The systematist in these cases can only make appraisals based upon morphological and ecological observations of the group to which the questioned populations belong. One cannot arbitrarily apply the rule that all isolated populations exhibiting some differences are distinct species. This treatment frequently obscures the essential similarity of the populations involved, and assumes that there is no exchange of genes over a long time interval. On the other hand, to refer to all such populations as subspecies is to assume that none of them has attained reproductive isolation. Mayr (1943) associates morphological differences and reproductive isolation within a group so that for a given genus (or other supra-species category) a certain level of morphological distinction can be used as a gauge of reproductive isolation in questionable cases.

This procedure has been utilized in this report. If the differences between two insular populations do not reach the level characteristic of unquestioned specific gaps within a genus, the populations are treated here as subspecies. Comparison of the diagnoses of *Rhaco-*

phorus pardalis, R. leucomystax, and *R. appendiculatus* will demonstrate the magnitude of gaps between distinct species in this genus. Differences between *leucomystax* and *linki* Taylor are not at the same level; therefore, I regard the latter as a subspecies of *leucomystax.*

The different interpretations of this case illustrate another cause of part of the discrepancy between Taylor's systematic arrangement and mine. Many of the population differences that Taylor evaluated at the species level are considered here as subspecific. Actually Taylor did not refer to any groups of populations as subspecies, but this may be explained in part by the dates of his publications.

METHODS AND TERMINOLOGY

With the exception of some live material collected in North Borneo, all specimens examined were preserved in alcohol. The material varied in age; some specimens had been collected in the middle of the nineteenth century, others as recently as 1950.

The descriptive terms employed are those in common herpetological usage. For the benefit of the non-herpetologist who may use this report explanations of some terms frequently appearing in keys and diagnoses follow.

Canthus rostralis: juncture of the side and top of the head anterior to the eye.

Dorso-lateral fold: fold or ridge of skin running along the juncture of side and back.

Disks of digit: swellings at tips of digits; also referred to as pads, terminal disks, or simply disks.

Subarticular tubercles: swellings on ventral surfaces of digits, confined to phalangeal region; usually one on each of first two fingers and toes, two on each of third and fourth fingers and third and fifth toes, and three on fourth toe.

Metatarsal tubercles: tubercles at tarsal-metatarsal joint of foot; usually one laterad ("outer") and one mesad ("inner").

Supernumerary tubercles: tubercles on metacarpals (see fig. 33, B) and those on metatarsals in addition to ones described above.

Sexual maturity, as used here, is determined in males by the presence of secondary sex characters—vocal sacs, nuptial pads, and other excrescences. In females the presence of enlarged, convoluted oviducts or maturing ova are used as criteria. Generally, all specimens of one sex larger than the smallest individual satisfying these criteria are considered mature.

The muscle terminology is that of Gaupp (1896).

Except for a few special cases explained in the text, only four measurements were used: snout-vent length; head width, taken at temporal region; head length, measured from posterior rim of tympanum to tip of snout; and lower leg length, measured from convex surface of knee to convex surface of tibio-tarsal joint with leg flexed. Measurements were taken with a vernier caliper reading to 0.1 mm. Most of the samples were small. When large series were available usually only the first twenty-five individuals of each sex drawn from the containers were measured. The formulae for statistical tests come mainly from Tippett (1941). Unless otherwise stated *t* is understood to be that of Student. The tables of Davenport and Ekas (1936) and Fisher and Yates (1948) were used.

To test errors of measurement twenty-five *Rana macrodon* were remeasured after an interval of one month. The average error of the snout-vent dimension was 0.95 per cent, of head width 0.70 per cent, and of lower leg length 0.60 per cent.

Mode of preservation and length of time in preservative probably affect size. The amount of shrinkage in amphibians resulting from either of these factors is unknown. Klauber (1937) estimates that shrinkage of snakes upon being preserved in alcohol approximates 2 per cent. Presumably discrepancies arising from differences in preservation would not exceed that amount. I assume that this applies roughly to amphibians. Inasmuch as all statistically significant differences exceeded 5 per cent of the dimension, errors introduced by differential shrinkage can probably be ignored.

Preservation also affects coloration. Certain hues, for example green and red, disappear rapidly in formalin or alcohol. However, the pattern of light and dark tones remains relatively clear except in unusual circumstances. As the color descriptions are based almost entirely on preserved material, the actual hues cited often will not match living specimens. Only the distribution of light and dark tones can be relied upon for field identification.

An attempt has been made to give a complete list of localities in the ranges. Specimens were examined from all localities not followed by a literature citation. The *Gazetteer of the Philippine Islands* (United States Coast and Geodetic Survey, Washington, D.C., 1945) is the authority for the spelling adopted.

The following abbreviations refer to source collections:

AMNH: American Museum of Natural History
BM: British Museum (Natural History)
CAS: California Academy of Sciences
CM: Carnegie Museum
CNHM: Chicago Natural History Museum
EHT: Edward H. Taylor

MCZ: Museum of Comparative Zoology
MHNP: Museum d'Histoire Naturelle, Paris
RM: Raffles Museum
RR: Robert Roecker
UMMZ: University of Michigan Museum of Zoology
USNM: United States National Museum

The keys in this work are intended only as aids to species identification. Identifications made by use of these keys should be checked against the diagnosis provided for each species. It must be emphasized that good preservation is essential to rapid and accurate identification; many dermal characters—such as granulation, webbing, skin folds, etc.—become obscured if preservation is poor.

FIG. 31. Ventral view of *Megophrys monticola* (A) and *M. hasselti* (B), showing axillary glands; × 1.

KEY TO GENERA OF METAMORPHOSED PHILIPPINE AMPHIBIA

1a. Limbless, body snake-like; eyes covered by skin.............*Ichthyophis*
1b. With limbs; frogs and toads.......................................2
2a. Tongue adherent around entire margin; toes webbed to tips (fig. 36, B) *Barbourula*
2b. Tongue not adherent...3
3a. Upper jaw toothless...4
3b. Upper jaw with teeth..10
4a. Fingers with fleshy web; first finger very short (fig. 40); size not over 25 mm. *Pelophryne*
4b. Fingers without fleshy web..5
5a. Conspicuous parotoid glands behind eyes (fig. 38)................*Bufo*
5b. No parotoid glands..6
6a. All toes except fourth webbed to terminal disks (fig. 42, B).......*Ansonia*
6b. Toes not webbed to disks..7
7a. A small pointed dermal projection at heel; belly and thighs with bold yellow and brown network................................*Chaperina*
7b. No such dermal projection; no ventral network.....................8
8a. No web on foot; not over 25 mm. in length.....................*Oreophryne*
8b. Foot webbed at least to proximal subarticular tubercle of fifth toe; adults over 25 mm..9

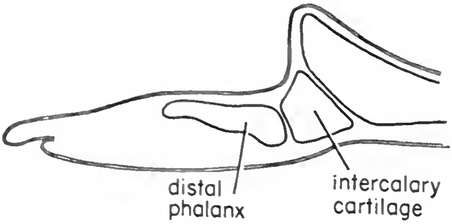


FIG. 32. Diagrammatic sagittal section through end of digit of *Rhacophorus*, showing intercalary cartilage.

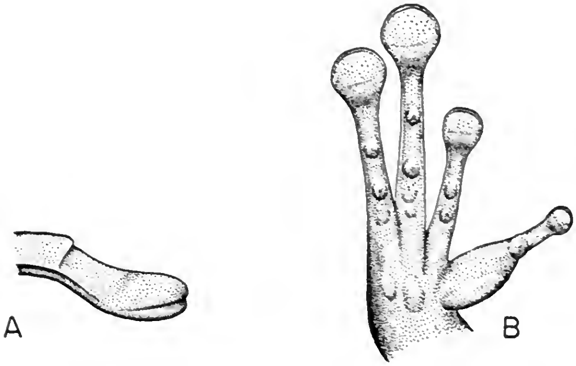


FIG. 33. *Rana everetti*. A, enlarged digit tip showing circummarginal groove of disk; B, ventral view of hand; × 2.

FIG. 34. Ventral view of foot of *Cornufer corrugatus;* × 3. Compare outer metatarsal region with that of *Rana erythraea* (fig. 35).

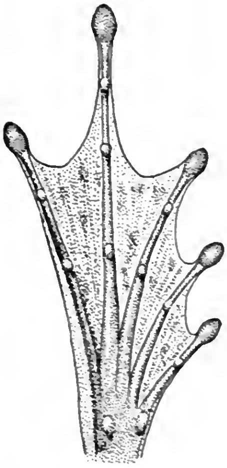


FIG. 35. Ventral view of foot of *Rana erythraea;* × 1.3.

9a. A black inguinal spot almost always present (fig. 73); entire rim of tympanum distinct..*Kalophrynus*
9b. No black inguinal spot; at least posterior rim of tympanum hidden..*Kaloula*
10a. Conspicuous gland in ventral axillary region (fig. 31)...........*Megophrys*
10b. No such gland..11
11a. Intercalary cartilage present in all digits (fig. 32);* abdomen coarsely granular; large disks at tips of digits...............................12
11b. No intercalary cartilage; abdomen various; digits with or without enlarged disks..13
12a. Vomerine teeth present...................................*Rhacophorus*
12b. Vomerine teeth absent.....................................*Philautus*
13a. Vomerine teeth absent..14
13b. Vomerine teeth present...16
14a. Fourth finger with at least three tubercles on ventral surface between palmar tubercles and finger tip (fig. 33, B)................*Cornufer* (part)
14b. Fourth finger with at most two tubercles on ventral surface............15
15a. Digit tips with circummarginal grooves (fig. 33, A)..............*Staurois*
15b. Digit tips without circummarginal grooves...................*Ooeidozyga*
16a. Outer metatarsals united for at least two-thirds of lengths (fig. 34)......17
16b. Outer metatarsals separated for at least two-thirds of lengths (fig. 35)...18
17a. Fourth finger with at most two tubercles on ventral surface between palmar tubercle and terminal disk................................*Rana* (part)
17b. Fourth finger with at least three such tubercles (fig. 33, B).*Cornufer* (part)
18a. Tips of toes without circummarginal grooves................*Rana* (part)
18b. Tips of toes with circummarginal grooves (fig. 33, A).................19
19a. Fourth finger with at least three tubercles on ventral surface between palmar tubercle and terminal disk (fig. 33, B)...............*Rana* (part)
19b. Fourth finger with less than three such tubercles..............*Micrixalus*

* The presence of the intercalary cartilage can be determined by splitting the end of the longest toe and comparing the cut surface with figure 32.

CAECILIIDAE

Ichthyophis monochrous Bleeker

Epicrium monochrous Bleeker, 1858, Nat. Tijdschr. Ned.-Indië, **16:** 188—Singkawang, Borneo.

Ichthyophis monochrous Boulenger, 1882, Cat. Batr. Grad. Brit. Mus., p. 91, pl. 4, figs. 1–1c; 1890, Fauna Brit. India, Rept., p. 517; 1912, Vert. Fauna Malay Pen., Rept. and Batr., p. 286; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 3.

Ichthyophis weberi Taylor, 1920, Phil. Jour. Sci., **16:** 227—Malatgan River, Palawan.

Ichthyophis glandulosus Taylor, 1923, Phil. Jour. Sci., **22:** 516—Abungabung, Basilan.

Material examined.—Mindanao, 21 (CNHM).

Taxonomic notes.—*Ichthyophis weberi* Taylor, described from a single specimen, was distinguished on the basis of having only one row of mandibular teeth. In view of the reduction of the inner row of mandibular teeth in *monochrous*, Taylor's action appears to be hasty. I follow van Kampen (1923) in considering *weberi* a synonym of *monochrous*.

Mindanao specimens at hand agree with the original description of *glandulosus* Taylor. The "dorsolateral glandular fold" noted by Taylor is not glandular. It is a ridge of prominent muscles; the skin at this point is not distinguishable from that above or below the ridge. The prominence may result from shrinkage of the skin in preservative. *Ichthyophis glandulosus* Taylor is probably conspecific with *monochrous* Bleeker. I am unable to find distinguishing characters.

Diagnosis.—Body cylindrical or slightly depressed, elongate; numerous annuli around body; eye small, covered with skin; tail short, pointed; anal opening a longitudinal slit.

Description.—Head posteriorly equal to width of body; snout obtusely pointed, projecting; nostrils above end of mandible, distance between nostrils one-half interocular distance; eyes small, visible through skin; distance between eyes approximately equal to length of snout; tentacle just above mouth, anterior to eye; tentacle twice as far from nostril as from eye; two rows of teeth in upper jaw; one (rarely) or two rows of mandibular teeth, inner row always shorter than outer; two grooves on ventral surface of neck, continuous or not on dorsal surface; Philippine specimens with 273–324 annuli on body, some annuli incomplete; anal opening a longitudinal slit; tail short, pointed; total length of Philippine adults 250–280 mm.

Color (in alcohol) plumbeous or brown, slightly lighter beneath; lips and anal region lighter than body.

Larvae.—Eighteen of the specimens collected by the Philippine Zoological Expedition are larvae. These vary in length from 65 to 231 mm.

Head as wide as body; snout blunt; lateral line system visible on head; no tentacle or tentacular aperture; tentacular canal present in skull; no external gills or spiracle; tail compressed, with a dermal fin around the margin.

Ecological notes.—*Ichthyophis monochrous* has the burrowing habit typical of caecilians. Specimens have been collected at shallow depths in soil and under logs (Taylor, 1923) and other debris of the forest floor. The larvae inhabit small streams.

Philippine specimens have been found from sea level to 900 meters. A record from the Malay Peninsula increases the altitudinal range to 1,200 meters (Boulenger, 1912).

Range.—Mindanao: Davao Province (Todaya on Mount Apo). Basilan (Abungabung [Taylor, 1923]). Palawan (Malatgan River [Taylor, 1920]).

Outside the Philippines this species is known from Sumatra, Borneo, Java, and the mainland of southeastern Asia from India to the Malay Peninsula (van Kampen, 1923).

DISCOGLOSSIDAE

Barbourula busuangensis Taylor and Noble

Barbourula busuangensis Taylor and Noble, 1924, Amer. Mus. Nov., no. 121, p. 1—Busuanga; Myers, 1943, Copeia, **1943**: 148.

Material examined.—Busuanga, 31 (CNHM).

Taxonomic notes.—Taylor and Noble (1924) consider *Barbourula* most closely related to *Bombina*—an opinion in which Myers (1943) concurs. The present study indicates that *Barbourula* is intermediate between *Bombina* and *Discoglossus*. Elsewhere, Noble (1922, 1924) points out that *Bombina* is the most primitive of the Discoglossidae by virtue of the single condyle on the coccyx and the absence of the adductor longus from the thigh musculature. *Discoglossus* has a coccyx with a double condyle and an adductor longus. *Barbourula* combines the characters of coccyx with a single condyle and the presence of the adductor longus.

Other characters of indeterminate phylogenetic significance show resemblances to *Bombina* in some instances and to *Discoglossus* in others. Illustrative of the latter class are the absence of aposematic coloration and the presence of a tympanic annulus. The pterygoid of *Barbourula* has a large, ventrally directed lateral flange at the juncture of the three rami. Boulenger's figure (1897–98) of the skull of *Discoglossus pictus* shows a slight projection at the same point. The pterygoids of the other discoglossids have smooth lateral curves.

Myers first noted the presence of a suborbital papilla in *Barbourula*. According to Gaupp (1896) the nasolacrimal duct opens posteriorly by means of two pores that lie in the anterior half of the juncture of the pigmented and non-pigmented portions (the transparent and non-transparent portions) of the lower eyelid. In both *Bombina maxima* and *B. orientalis* there is a low but distinct elongate elevation along the anterior third of this juncture. At the posterior end of the elevation are the two openings of the duct. In *Barbourula* there is a corresponding suborbital elevation, but it

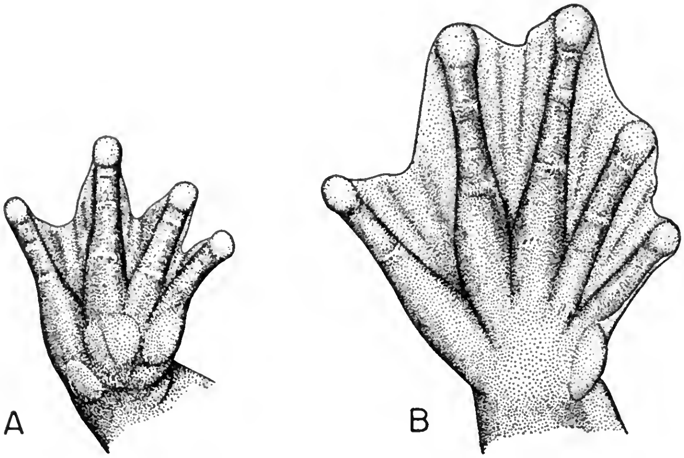


FIG. 36. Ventral views of hand (A) and foot (B) of *Barbourula busuangensis*; × 2.

ends in the heavily pigmented papilla, which is about 2 mm. long and 1 mm. wide and bears two openings at its tip. The two pores open on the eyelid in *Bombina variegata*, *Discoglossus*, and *Alytes*, but no elevation was found in these. Although the nasolacrimal duct of *Barbourula* probably passed through a stage similar to that observed in *Bombina maxima*, it does not necessarily follow that *maxima*, or the stock from which it arose, is the ancestor of *Barbourula*. The evolution of the suborbital papilla appears to require only increase in growth of the nasolacrimal duct, a structure present in all salientians. If this is true then, conceivably, the immediate ancestor of *Barbourula* might have exhibited no greater specialization in the region under question than does *Discoglossus*.

Finally there remain several specializations of *Barbourula* that have no apparent bearing on the relationship to the other living discoglossids. The first of these is the elongate squamosal. In *Barbourula* this bone extends forward as far as the pterygomaxillary suture, and is roughly twice as long as that of any other member of the family. The highly developed squamosal and the flange of the pterygoid seem to be related functionally through their serving for muscle attachment, but their significance is unknown.

The second specialization involves the ova. In *Discoglossus* and *Bombina* the ova have almost black animal hemispheres and are small. In *Alytes* the eggs are non-pigmented and large in correlation with oviposition on land. The ova of *Barbourula* are practically without pigment and are relatively large.

Diagnosis.—A large-sized frog, about 85 mm. snout to vent; fingers extensively webbed (fig. 36); toes webbed to tips; third and fourth toes of approximately equal length; nostrils superior; a distinct, dark papilla below eye; tongue circular, adherent around entire margins.

Description.—Habitus stocky, depressed; head wider than long; snout broadly rounded; nostrils superior; a dark papilla below eye; tympanum completely hidden by skin. Skin above rough; upper eyelid with pustules; scattered light tubercles over most of dorsal surfaces; tubercles on hind limbs tipped with black spinules; skin below smooth.

Limbs stout; tips of fingers blunt, not expanded; web reaching tips of fingers as a fringe, excised deeply between fingers; no subarticular tubercles; usually two large palmar tubercles, the one at base of first finger strongest. Tips of toes rounded, larger than those of fingers; third and fourth toes approximately equal in length; fifth toe shorter than second; all toes webbed to tips; web not excised; a fold of skin along median edge of first toe; subarticular tubercles absent; a strong, oval inner metatarsal tubercle; no outer one.

Color (in alcohol) dark slate or brown above, more or less uniform; below dirty white, the gular region suffused with brown.

Secondary sex characters.—Black spinules are characteristic of the males of *Discoglossus* and *Bombina*. Such asperities are also present in *Barbourula* though not in as great numbers. In *Barbourula* the males have black spinules on the lores, lips, chin, and, less densely, on the arms. There are no clusters of asperities on the fingers; the males lack nuptial pads. As noted in the description both sexes have black spinules on the hind limbs.

True vocal sacs are not found in the other species of Discoglossidae (Liu, 1935) nor are they present in *Barbourula*.

Apparently there is no difference between the snout-vent lengths of the sexes. The smallest male possessing the black spinules measured 69.7 mm., snout to vent; the next smaller male, which did not have these secondary sex characters, measured 66.0 mm. Among females examined the smallest containing mature ova or enlarged oviducts was 68.7 mm.; another female, measuring 70.1 mm., had neither enlarged ova nor enlarged oviducts.

Some sexual dimorphism appears to be present in head width, the males having slightly larger heads (see Table 1).

Table 1. Adult Male and Female *Barbourula busuangensis*

Nine males and ten females

	Mean±SE	Range
Snout-vent length		
Males	84.80±3.33	69.7–100.7
Females	85.30±3.02	68.9–98.2
Head width/snout-vent		
Males	0.376±0.007	0.337–0.397
Females	0.356±0.005	0.336–0.390

$t=2.498$; $n=17$; $P=0.03$

Ecological notes.—From all indications, *busuangensis* is thoroughly aquatic. Myers (1943) reports that all but one of twenty-three specimens were collected in a small creek flowing through the timber at an elevation of 150 to 185 meters. Similarly, specimens collected by the Philippine Zoological Expedition were found in a small creek, but near sea level. According to the collector's field notes (Myers, 1943), *Barbourula* frequently floats with only eyes and nostrils above the surface. When disturbed, the frog dives to the bottom and hides under stones.

The depressed body, dorsally placed nostrils, extensively webbed fingers and toes, and strong legs certainly seem to adapt this species to an aquatic existence in moderate currents. Furthermore, the stomach contents suggest that *Barbourula* feeds in the water. The stomachs of three of the specimens seen contained crab fragments, including entire claws, another contained a minnow 45 mm. long, and a fifth one contained fragments of a large ant.

The eggs of *busuangensis* are large, few in number, and almost lacking in pigment. A female (89.7 mm. snout to vent) contained a total of 78 ripe ova. Ten of the latter varied in diameter between 5.5 and 6.0 mm., with a mean of 5.9 mm. It is known that frog eggs deposited out of water tend to be relatively larger (Lutz, 1948) and to have less pigment than those laid in water. But *busuangensis* probably does not deposit its ova on land. A possible explanation for the loss of pigment may be that the ova are placed under rocks in streams. This habit would make dark pigment functionless and would tend to release the eggs from the selection pressure that maintains the pigment in other aquatic frog ova. *Rana graminea* is an example of a species that deposits non-pigmented ova under stones in streams (Pope, 1931). But even assuming the validity of this highly speculative hypothesis, the large relative size of the eggs—approximately 0.065 of the female's length as compared to 0.020 in *Discoglossus* and 0.035 in *Bombina* (calculations from data in Boulenger, 1897–98)—remains unexplained.

Range.—Busuanga (Dimaniang, San Nicolas [Myers, 1943]).

PELOBATIDAE

Megophrys Kuhl and van Hasselt

No dermal projection from edge of upper eyelid; no longitudinal folds on back. *M. hasselti*

Conspicuous dermal projection from edge of upper eyelid; longitudinal folds present.

- No vomerine teeth ....*M. monticola stejnegeri*
- Vomerine teeth present ....*M. monticola ligayae*

Megophrys hasselti Müller

Leptobrachium hasseltii Müller, *in* Tschudi, 1838, Mem. Soc. Sci. Neuchâtel, **2**: 81—Java.

Megophrys hasseltii Smith, 1930, Bull. Raffles Mus., no. 3, p. 134; Pope, 1931, Bull. Amer. Mus. Nat. Hist., **61**: 450, fig. 5; Mertens, 1934, Arch. Hydrobiol., **12**, Suppl. (Trop. Binnengew.), **4**: 678.

Megalophrys hasseltii Boulenger, 1908, Proc. Zool. Soc. London, **1908**: 425, pl. 25, fig. 3; Taylor, 1920, Phil. Jour. Sci., **16**: 355, pl. 8, figs. 4–4a; 1922, op. cit., **21**: 184; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 13; Noble, 1927, Ann. New York Acad. Sci., **30**: 74, figs. 13A–B.

Material examined.—Mindoro, 2 (1 MCZ; 1 USNM); Mindanao, 68 (66 CNHM, mostly larvae; 2 USNM); Basilan, 1 (MCZ); Palawan, 43 (41 CNHM, including larvae; 2 MCZ); Borneo, 7 (6 MCZ; 1 UMMZ); Java, 5 (4 BM; 1 USNM).

Diagnosis.—A moderate-sized species of *Megophrys;* no dermal projections either on upper eyelid or at commissure of jaws; snout projecting only slightly; the line from nostrils to symphysis of mandible sloping forward; no longitudinal folds on back; inner metatarsal tubercle round, much less than one-half length of first toe.

Description.—Head large, body tapering to groin (except gravid females); head wider than long; snout obtusely pointed, barely projecting beyond lower jaw; no vomerine teeth; tongue heart-shaped, notched posteriorly; canthus rostralis distinct, angular; tympanum obscured by skin but usually visible, about one-third diameter of eye; eyes large and projecting from sides of head. Skin granular or with raised network above; ventrally granular except on chest; conspicuous supratympanic fold; no longitudinal folds on back; no dermal "horns" on upper eyelid or at commissure of jaws; a round, flat gland at median border of axilla (fig. 31, B); a smaller gland, usually white, in distal half of posterior surface of thigh.

Finger tips rounded but not dilated; first finger longer than second; subarticular tubercles of fingers weak or absent; two large, conspicuous palmar tubercles. Tips of toes resembling fingers; first toe with fleshy web almost to tip; second and third toes with fleshy web at base; no web between fourth and fifth toes; subarticular tubercles weak or absent; a small, round inner metatarsal tubercle, much less than one-half length of first toe; no outer metatarsal tubercle.

Color (in alcohol) gray, dark brown or black above; on lighter specimens an irregular dark mark commencing in frontal region and continuing length of back; ventrally light gray or brownish, uniform or with varying amounts of darker infusion or spotting; limbs usually with dark crossbars dorsally.

Secondary sex characters.—Males of *hasselti* have median subgular internal vocal sacs with round or oval openings a short distance behind the corners of the mouth. There are no nuptial pads or other glands that distinguish the sexes.

The females are probably larger than the males, but the evidence is incomplete and conflicting. Boulenger (1908) gives the snout-vent lengths of a male and a female as 47 mm. and 74 mm., respectively. However, there is no assurance that the difference in these two is representative of a sex dimorphism in his specimens. The largest specimens in my samples are females from Java, Mindanao, and Borneo. Yet the presence within the Palawan sample of larger males than females prevents any conclusion based on the present data (Table 2).

Ecological notes.—Information about the habits of *hasselti* is fragmentary and, in the case of adults, vague. Adults are terrestrial inhabitants of forests. At least the relatively weak legs and reduced webbing suggest that the species is neither a strong swimmer nor a good climber. Five of the twelve adults collected by the Philippine Expedition are from the ground in original forests; six others were collected on rocks and logs along small streams. I have collected adults along the banks of forest streams in North Borneo.

Observations on the ecology of the larvae are more complete and permit some generalizations. Most of the reports (Annandale, 1917; Smith, 1917; Mertens, 1934) agree that the tadpoles are benthonic and that they are found in pools of streams, usually swift streams of forested hills or mountains. The field notes of the Philippine Expedition support these observations.

The vertical distribution of *hasselti* is extensive when the entire geographic range is considered. Mertens (1934) maintains that *hasselti* is a strictly montane species. He gives 500 meters as its lower limit on Sumatra, Java, and Bali. Similarly, reports of *hasselti* in Burma (Annandale, 1917) and the Malay Peninsula (Boulenger, 1912) are from mountainous districts. Smith (1925a, b, 1931) records *hasselti* from high elevations (up to 1,675 meters) on Borneo; my own Bornean material is from near sea level. Philippine records indicate that, at least on Mindanao and Palawan, *hasselti* may occur almost at sea level. An adult (CNHM 14893) has been collected at San Ramon, Mindanao, and larvae have been found at Mauyon, Palawan, both within 40 meters of sea level. Nevertheless, most Philippine specimens have been collected above 450 meters, the highest locality being at 1,340 meters.

Inter-island variation.—There is some evidence of geographic variation in coloration: none of the seven specimens from Borneo has dark bars on the antero-dorsal face of the thighs, whereas these bars are present on all Philippine specimens. The single specimen from Java had the bars. Additional material is necessary to substantiate this difference between Bornean specimens and others.

Table 2. Snout-vent lengths and relative head widths in various samples of *Megophrys hasselti*

Snout-vent length

	Males			Females		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Mindoro	—	—	—	2	52.60	47.0-58.2
Mindanao ..	7	47.77±1.49	43.0-52.7	2	62.30	56.6-68.0
Palawan....	4	56.23	54.0-60.5	2	48.90	45.4-52.4
Borneo.....	4	45.93	43.4-52.4	3	57.10	44.4-64.5
Java........	2	41.35	37.2-45.5	3	58.33	47.0-77.2

Head width/snout-vent

Males

	No.	Mean±SE	Range	Difference of means	*t*	*n*	P
Mindanao ..	6	0.449±0.004	0.436-0.464	0.034	5.645	8	<0.001
Palawan ...	4	0.415±0.005	0.402-0.424	0.034	4.377	6	0.008
Borneo.....	4	0.449±0.006	0.431-0.458				

Inter-island variation was also observed in body length and the ratio of head width to body length. The Palawan males examined were larger and had relatively narrower heads than those from Mindanao and Borneo. The Mindanao and Borneo samples do not differ in these respects. Although the differences between the Palawan sample and the others are statistically significant, the value of the observations is limited because of the small number of individuals involved (Table 2).

Range.—Mindoro (near Lake Naujan). Mindanao: Cotabato Province (Burungkôt near Upi); Davao Province (Mount Apo, Mount McKinley); City of Zamboanga (San Ramon). Basilan (Abungabung). Palawan (Lapulapu near Iwahig, Mauyon, Mount Balabag, Thumb Peak).

Known also from the Malay Peninsula, Burma, Siam, Sumatra, Java, Bali, and Borneo.

Megophrys monticola Kuhl and van Hasselt

Taxonomic notes.—Megophrys stejnegeri Taylor (type locality Mindanao) and *M. ligayae* Taylor (type locality Palawan) are both clearly related to *monticola* Kuhl and van Hasselt (type locality Java). The relationship is evident in many characters: habitus, dermal projections of the head, coloration, skin characteristics, and secondary sex characters. There are several distinctions to be made among the three forms: *stejnegeri* lacks vomerine teeth, whereas the others have them; the number and length of the dorsal skin folds differ in the three; the size differs. The three are evidently conspecific and represent separate subspecies. However, these remarks pertain to *monticola* of Java only and the discussion of this group of forms would not be complete without considering all of the populations that have been referred to *monticola.*

Megophrys nasuta Schlegel (type locality Sumatra) and *monticola* have been thought to be very similar and closely related by all authors dealing with them since Boulenger (1908). The tadpoles are indistinguishable; Mertens (1934), for example, was unable to find differences between the two larvae and associated them with the adult most common on the particular island. Boulenger (1908) points out that his own descriptions of the two adults are almost identical and that the only differences to be found are the greater development of dermal projections on the snout and upper eyelid of *nasuta* and the absence of vocal sacs in the males of *monticola.*

Boulenger includes Java, Sumatra, Borneo, and the Malay Peninsula in the range of *montana* (=*monticola*). His Philippine specimens belong either to *stejnegeri* or *ligayae*. For the range of *nasuta* Boulenger lists the Malay Peninsula, Sumatra, Borneo, and the Natuna Islands. Smith (1926) states that all of the mainland specimens identified as *monticola* actually belong to *aceras* Boulenger. Mertens notes that *monticola* is rare on Sumatra, although *nasuta* is abundant. On Borneo, *monticola* is known from only two localities, whereas *nasuta* has been reported from at least eight localities, including the two of *monticola* (van Kampen, 1923; Smith, 1931); this difference could be taken to indicate a difference in abundance on Borneo also.

This distribution pattern may be summarized as follows: *monticola* is common on Java but exists only in small numbers on Sumatra and Borneo; *nasuta* is abundant on Sumatra and Borneo but absent on Java. I believe that the reports of a few specimens of *monticola* on Sumatra and Borneo stem from the failure to recognize the possibility of variation in length of the dermal appendages of the head within a population; that is, that individual frogs with no snout projection or with at most a vestige of one, have been called *monticola* and those with long ones *nasuta*. Boulenger and subsequent authors agree that on Java *monticola* may have a small dermal projection on the snout. Conversely, it is at least theoretically possible that on Borneo and Sumatra a population recognizable as *nasuta* may contain individuals with poorly developed nasal appendages. This is exactly the situation in a sample of ten specimens from Mount Kina Balu, Borneo (MCZ 22630–32, 22634–37, 22640–42) that I have identified as *nasuta;* in this group the snout appendage varies from a mere nubbin to a projection 3.5 mm. long. The same comments apply in the case of identifications based on the length of the orbital dermal appendage.

There is also doubt as to the difference in secondary sex characters used to separate *nasuta* and *monticola*. The one male *monticola* from Java examined by myself (AMNH 24790) had vocal sacs, contrary to Boulenger's statement. It is not at all clear how many males Boulenger examined nor what was their geographic origin. Moreover, it is worthy of note that no author subsequent to Boulenger (1908), in reporting on *monticola*, from whatever island, has even stated that he examined males. If there is variation in this respect, it has not been critically studied.

In summary, there is little reason to recognize two sympatric forms on Borneo and Sumatra on the basis of any character thus far suggested. On the other hand the evidence indicates that the two forms, *monticola* and *nasuta,* act as geographic replacements, the former inhabiting Java and the latter Borneo and Sumatra. As the concept is applied in this report, *nasuta* Schlegel must be considered a subspecies of *monticola* Kuhl and van Hasselt. The differences distinguishing the four forms, *monticola monticola, m. nasuta, m. ligayae,* and *m. stejnegeri,* are dealt with in greater detail below.

Diagnosis.—A moderate- to large-sized form of *Megophrys;* conspicuous dermal projections from edge of upper eyelid and at commissure of jaws; snout projecting beyond lower jaw, profile sloping down and backwards; one or two pairs of longitudinal folds on back (fig. 37); inner metatarsal tubercle elongate, at least one-half length of first toe.

Description.—Head large; body stout, tapering but slightly to groin; head much wider than long; snout obtusely pointed; snout (exclusive of dermal appendage) projecting beyond lower jaw; with or without vomerine teeth; tongue round, only rarely with shallow notch posteriorly; canthus rostralis sharp; lores concave; tympanum faintly visible or hidden by skin, one-third to one-half diameter of eye. Skin smooth above, usually with a few large black tubercles anteriorly, occasionally small spinules posteriorly; skin of head involved in ossification of skull in larger animals; granular ventrally; bony ridge from eye to above tympanum curving down to axilla; transverse occipital fold; one or two pairs of longitudinal folds on back; a large dermal projection from edge of upper eyelid and a smaller one at commissure of jaws; nasal dermal appendage of varying length present or absent; conical, tubercle-like gland at lateral edge of breast (fig. 31, A); flatter white gland in distal half of postero-ventral face of thigh.

Tips of fingers slightly swollen; first finger longer than second; subarticular tubercles of fingers absent; elongate swollen tubercle at base of first finger. Tips of toes similar to those of fingers; toes webbed at base only; subarticular tubercles indicated by faint swellings or absent; a large, elongate inner metatarsal tubercle, exceeding one-half length of first toe; no outer metatarsal tubercle.

Color (in alcohol) above dark purplish gray or brown; a dark triangular mark with angles on the eyelids and occiput usually visible; several dark spots anteriorly; sides occasionally light tan-gray;

ventral surfaces dirty white with many black spots, some specimens gray with black spots; a broad black band from eye to mouth, continued ventrally as a longitudinal black band reaching chest; dorsal surface of limbs somewhat lighter than back; thigh and lower leg with dark crossbars; a black spot on ventral surface of forearm from wrist midway to elbow; ventral surface of leg black from tibiotarsal joint to tips of toes.

Secondary sex characters.—Dissection confirms Liu's statement (1935) that males of this species (Liu lists *nasuta* and *ligayae*) have median subgular internal vocal sacs. The round openings lie midway between the commissure of the jaws and the posterior of the base of the tongue. It has been pointed out above that the single Javanese male seen had vocal sacs.

Males of *monticola* also differ from the females in having nuptial pads on the first two fingers and light-colored spinules on both jaws. These spinules may be tipped with horn. The females are larger (see Table 3), and, in the case of *monticola nasuta* from Borneo, the nasal projection of the males is longer. This appendage varied from 0 to 2.0 mm. (average 0.5 mm.) in the four females available and from 1.5 to 3.5 mm. (average 2.1 mm.) in six males. No differences in body proportions were observed.

Ecological notes.—Like other species of the same genus, *monticola* is a terrestrial amphibian found only occasionally in water. Only three out of twenty specimens were collected in streams by the Philippine Expedition. According to Boulenger (1912) *monticola* is nocturnal and, according to field notes of the Philippine Expedition, an inhabitant of forests.

Tadpoles of *monticola* occur in either standing or rapidly moving water (Dunn, 1928; Mertens, 1934) on Java and Sumatra. The Philippine Expedition found larvae only in pools.

The known altitudinal distribution of *monticola* varies over its geographic range. On Java, for example, *monticola* has not been recorded from below 900 meters and has been found as high as 2,050 meters (van Kampen, 1923; Mertens, 1934). On Sumatra it has been found between 300 and 2,000 meters (Mertens, 1934). Smith (1931) records the species from 900 to 1,675 meters on Borneo. In the Philippines the range seems to lie between 400 and 1,825 meters (CNHM 51031 and 50950) although Taylor (1920) reports a single specimen from Zamboanga, Mindanao, and one from Cabalian, Leyte, both at sea level. However, the land rises imme-

Table 3. Snout-vent lengths of male and female *Megophrys monticola*

	Females			Males		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Java	7	83.14±2.55	75.1- 94.8	1	44.3	—
Borneo	4	111.68±2.59	104.8-117.6	9	92.04±1.99	83.5-102.0
	Difference of means = 19.64; t = 5.592; P = <0.001					
Palawan	1	90.00	---	3	64.33	60.4-69.0
Mindanao	9	67.06±2.55	57.0-77.8	7	46.34±1.55	40.6-52.5
	Difference of means = 20.72; t = 6.455; P = <0.001					

diately behind both cities so that the two specimens may have been caught at higher elevations.

Inter-island variation.—Of the characters showing geographic variation in *monticola* perhaps the most striking is that observed in the dermal appendages of the head (fig. 37). These structures are most highly developed in the populations of Sumatra and Borneo and are least conspicuous in the population of Java. As noted earlier, the length of the snout projection in the Bornean sample (ten specimens) varied from 0 to 3.5 mm. (mean 1.5). In no other specimen seen did this appendage exceed 1 mm. in length, and in most cases it was present only as a small swelling.

The orbital appendage is also largest in the Bornean population (*nasuta*). In the series available, this projection varied from 3.5 to 7.0 mm. in specimens from Borneo, 2.0 to 3.0 in those from Palawan, 1.5 to 3.5 in those from Mindanao, and from 1.0 to 3.0 in those from Java. Because of systematic variation in snout-vent lengths, comparison of these samples was made on the basis of the ratio of appendage length to snout-vent length. Statistical tests indicate the significance of the inter-island differences in this ratio. The data are presented in Table 4.

Additional variation is evident in the size of adults. Individuals from Borneo are the largest, those from Mindanao the smallest, and those from Java and Palawan intermediate (see Table 3). Analysis demonstrates the statistical significance of the differences in every instance in which sufficient material was available (see Table 4).

Vomerine teeth are absent in all specimens known from Mindanao, Basilan, Leyte, Dinagat, and Samar. (Information on specimens from Dinagat and Samar was very kindly sent to me by Dr.

H. W. Parker of the British Museum.) By contrast all specimens examined from Java, Borneo, and Palawan have vomerine teeth. However, Dr. Parker informs me that of the British Museum material one specimen from Borneo (BM 94.6.30.162) and one from Palawan (BM 1903.4.30.13) lack these structures.

Table 4. Geographic variation of certain characters of *Megophrys monticola*

Orbital appendage/snout-vent

	No.	Mean±SE	Range		No.	Mean±SE	Range
Mindanao...	15	0.042±0.001	0.033-0.052	Borneo..	10	0.055±0.003	0.038-0.070
Palawan....	4	0.041	0.036-0.047	Java.....	8	0.034±0.002	0.029-0.045

	Difference of means	*t*	*n*	P
Mindanao—Borneo	0.013	4.220	23	<0.001
Mindanao—Java	0.008	3.248	21	0.006
Java—Borneo	0.021	5.391	16	<0.001

Snout-vent lengths[1]

	Sex	Difference of means	*t*	*n*	P
Mindanao—Borneo	♀	44.62	10.524	11	<0.001
Mindanao—Borneo	♂	45.70	17.027	14	<0.001
Mindanao—Java	♀	16.08	4.418	14	<0.001
Borneo—Java	♀	28.54	7.279	9	<0.001

[1] Means and extremes presented in Table 3

Finally, there is inter-island variation in the number and lengths of the longitudinal skin folds on the back. One or two pairs of these may be present (fig. 37). The lateral fold when present is a continuation posteriorly of the ridge proceeding from the eye over the tympanum; this fold runs in a line half-way down the side of the body. The median fold is invariably present; it begins on the occiput roughly in line with the nostril and has a slight outward curve. Both folds are found in all of the Bornean and Palawan specimens seen, but in the latter specimens neither fold continues more than two-thirds the length of the body, whereas in those from Borneo the median fold, at least, usually extends the entire length of the trunk. In the sample from Java all but one individual have only the median pair of folds, and in all but one the folds reach the end of the body. The Mindanao sample shows more variation than the others; nevertheless, it may be characterized as having only the median pair of folds, and these are usually short. In the table "long" means that at least the median fold reaches the end of the body, and "short" that no folds extend more than two-thirds the length of the trunk.

	One pair of folds		Two pairs of folds		
	Long	Short	Long	Short	
	Observed frequency				Total
Mindanao	4	10	2	1	17
Palawan	0	0	0	7	7
Java	15	1	1	0	17
Borneo	0	0	8	2	10
	Calculated frequency				
Mindanao	6.3	3.7	3.7	3.3	17.0
Palawan	2.6	1.5	1.5	1.4	7.0
Java	6.3	3.7	3.7	3.3	17.0
Borneo	3.7	2.2	2.2	2.0	10.1

Chi square=80.1; n=9; P=<0.001

The high value of chi square is evidence of a significant departure from random distribution and, therefore, of statistical significance for the geographic variation observed.

As stated above, four subspecies should be recognized.

1a. No vomerine teeth . . . . *monticola stejnegeri* Taylor
1b. Vomerine teeth present 2
2a. One pair of longitudinal folds of skin on the back. *monticola monticola* Kuhl and van Hasselt
2b. Two pairs of longitudinal skin folds 3
3a. Median pair of folds usually continued to end of trunk; dermal appendage of snout usually well developed . . . . *monticola nasuta* Schlegel
3b. Median pair of folds usually not extending more than two-thirds the length of the trunk; appendage of snout usually absent . . . . *monticola ligayae* Taylor

Megophrys monticola monticola Kuhl and van Hasselt

Megophrys monticola Kuhl and van Hasselt, 1822, Isis, **1822**: 475—Java; Mertens, 1934, Arch. Hydrobiol., **12**, Suppl. (Trop. Binnengew.), **4**: 679 (part).

Megalophrys montana Boulenger, 1908, Proc. Zool. Soc. London, **1908**: 411 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 8 (part); Smith, 1926, Proc. Zool. Soc. London, **1926**: 983.

Material examined.—Java, 20 (7 AMNH; 13 USNM).

Diagnosis.—A moderate-sized form of *monticola;* adult females about 83 mm. from snout to vent, males smaller (see Table 3); dermal appendage of snout absent or present only as a rudiment; orbital dermal appendage small to moderate (1 to 3 mm. in length);

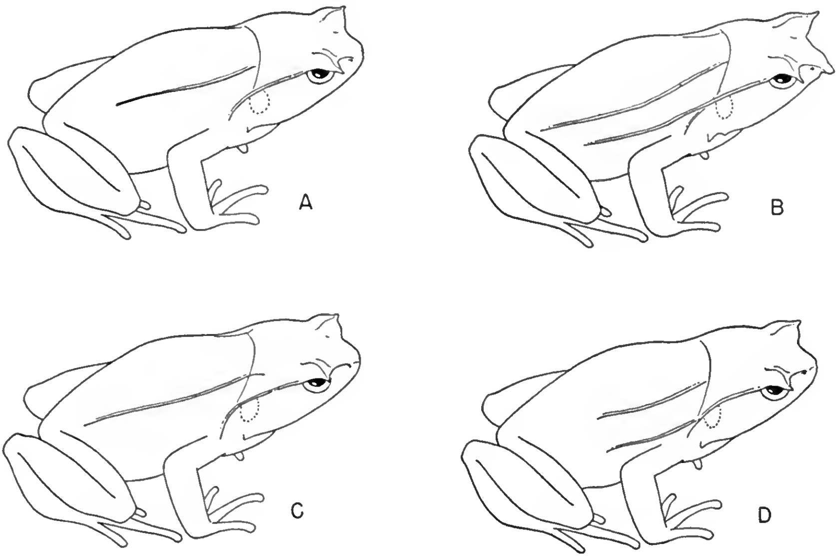


FIG. 37. A, *Megophrys monticola stejnegeri* (× 0.6); B, *M. m. nasuta* (× 0.4); C, *M. m. monticola* (× 0.5); D, *M. m. ligayae* (× 0.5).

one pair of longitudinal dermal folds on back; folds reaching end of trunk (fig. 37).

Range.—Java.

Megophrys monticola nasuta Schlegel

Ceratophryne nasuta Schlegel, 1858, Handl. Dierk., **2**: 57, pl. 4, fig. 72—Sumatra.

Megophrys nasuta Smith, 1930, Bull. Raffles Mus., no. 3, p. 132; 1931, op. cit., no. 5, p. 9; Mertens, 1934, Arch. Hydrobiol., **12**, Suppl. (Trop. Binnengew.), **4**: 680.

Megalophrys nasuta Boulenger, 1908, Proc. Zool. Soc. London, **1908**: 413, pl. 22; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 10, fig. 2.

Megalophrys montana Boulenger, 1908, Proc. Zool. Soc. London, **1908**: 411 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 8 (part).

Megophrys monticola Smith, 1931, Bull. Raffles Mus., no. 5, p. 12; Mertens, 1934, Arch. Hydrobiol., **12**, Suppl. (Trop. Binnengew.), **4**: 679 (part).

Material examined.—Borneo, 13 (10 MCZ; 3 UMMZ).

Diagnosis.—A large form of *monticola;* adult females about 110 mm., males 90 mm. (see Table 3); dermal appendage of snout usually well developed (up to 3.5 mm.), occasionally present only as a small projection; orbital appendage large (3.5 to 7.0 mm.); two pairs of longitudinal skin folds on the back, the median pair usually reaching the end of the body (fig. 37, B).

Range.—Malay Peninsula, Sumatra, Natuna, and Borneo.

Megophrys monticola ligayae Taylor

Megalophrys ligayae Taylor, 1920, Phil. Jour. Sci., **16**: 350, pl. 10, figs. 2, 2a—northern Palawan; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 8; Noble, 1927, Ann. New York Acad. Sci., **30**: 75.

Megalophrys montana (part) Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat., (3), **2**: 163; Boulenger, 1908, Proc. Zool. Soc. London, **1908**: 413.

Material examined.—Palawan, 18 (1 CM, paratype; 14 CNHM, including 9 larvae; 3 MCZ).

Diagnosis.—A medium-sized form of *monticola;* adult males about 64 mm., females at least up to 90 mm. (see Table 3); dermal appendage of snout usually absent, rarely present as a small projection; orbital appendage moderate in length (2.0 to 3.5 mm.); two pairs of longitudinal skin folds on the back, the median pair not more than two-thirds the length of the trunk (fig. 37, D).

Remarks.—In size and number of longitudinal skin folds *ligayae* appears to be more closely related to *nasuta* than is *stejnegeri*. *Megophrys m. nasuta* is the largest of the three with *ligayae* and *stejnegeri* following in that order. Both *ligayae* and *nasuta* have two pairs of skin folds, whereas *stejnegeri* has but one. There are no characters in which *stejnegeri* is more similar to *nasuta* than is *ligayae.*

Range.—Palawan (Kabalnecan near Brooke's Point, Mount Balabag, Thumb Peak). Balabac should probably be included in the range. The only specimens from that island known to me are those reported by Boulenger (1908). From the fact that Boulenger identified them as *montana* rather than *nasuta* I surmise that the snout lacked a dermal projection and, hence, that the specimens are *ligayae.*

Megophrys monticola stejnegeri Taylor

Megalophrys stejnegeri Taylor, 1920, Phil. Jour. Sci., **16**: 347, pl. 10, figs. 1, 1a—Bunawan, Agusan Province, Mindanao; 1922, op. cit., **21**: 281; Noble, 1927, Ann. New York Acad. Sci., **30**: 75.

Megalophrys montana (part), Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 36; Boulenger, 1882, op. cit., p. 442; 1908, Proc. Zool. Soc. London, **1908**: 411; Fischer, 1885, Jahrb. Hamburg Wiss. Anst., **2**: 80; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 125; 1892, Kat. Batr. Mus. Senck. Naturf. Ges., p. 49.

Material examined.—Leyte, 1 (MCZ); Mindanao, 151 (1 AMNH; 145 CNHM, including 121 tadpoles; 5 USNM); Basilan, 1 (USNM).

Diagnosis.—A small form of *monticola;* adult females about 67 mm., males 46 mm. (see Table 3); dermal appendage of snout usually absent, occasionally present as a small projection never exceeding 1 mm. in length; orbital appendage moderate in length (1.5 to 3.5 mm.); usually one pair of longitudinal folds on the back, folds rarely continuing more than two-thirds the length of the trunk (fig. 37, A).

Range.—Leyte (Cabalian, Ormoc [Boettger, 1892]). Samar (Boulenger, 1908). Dinagat (Boulenger, 1882). Mindanao: Agusan Province (Bukidnan, Bunawan [Taylor, 1920]); Cotabato Province, (Burungkôt near Upi); Davao Province (Mainit, Meran, and Todaya on Mount Apo, Mount McKinley, Padada River); Surigao Province (Taylor, 1922b); City of Zamboanga (Zamboanga). Basilan.

BUFONIDAE

Bufo Laurenti

Parietal and supraorbital crests continuous and conspicuous (fig. 38, A). *Bufo biporcatus philippinicus*

Parietal crest absent (fig. 39) .... *Bufo marinus*

Bufo biporcatus philippinicus Boulenger

Bufo philippinicus Boulenger, 1887, Ann. Mag. Nat. Hist., (5), **19**: 348, pl. 10, fig. 5—Puerto Princesa, Palawan; 1894, op. cit., (6), **14**: 88; Taylor, 1920, Phil. Jour. Sci., **16**: 344, pl. 9, fig. 5; 1922, op. cit., **21**: 281; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 86.

Bufo divergens Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat., (3), **2**: 158.

Material examined.—Busuanga, 18 (12 CNHM; 6 MCZ); Culion, 3 (CNHM); Palawan, 68 (CNHM); Dumaran, 1 (MCZ); Balabac, 6 (CNHM).

Taxonomic notes.—The close relationship of *B. philippinicus* (type locality Palawan) to *biporcatus* Gravenhorst (type locality Java) was recognized by Boulenger (1887) who distinguished them primarily on the basis of a difference in the cranial crests. In the type of *philippinicus,* the only specimen available to Boulenger, the supraorbital ridge was separated from the parietal, unlike *biporcatus,* in which the two crests are continuous. Several specimens of *philippinicus* in the topotypic series of Chicago Natural History Museum have between the supraorbital and parietal crests the same small gap that was figured by Boulenger in the original description;

however, the majority of the topotypic series have the two crests continuous, as in *biporcatus*. Taylor (1920) also refers to variation in arrangement of the cranial ridges in *philippinicus*.

Similarly, other distinctions implicit in Boulenger's description are weakened or modified by individual variation within both *biporcatus* (including specimens from Java, Bali, and Borneo) and *philippinicus*. To be sure there is geographic variation in certain characters, but the over-all morphological agreement of *philippinicus* and *biporcatus* and the juxtaposition of their ranges (fig. 82) are such as to leave no doubt that we are dealing with subspecies of a single wide-ranging species.

Diagnosis.—A moderate- to large-sized species of *Bufo* (body about 70 mm.); cranial crests present; supraorbital and parietal ridges well developed; tympanum distinct; fingers long, without web; toes not webbed beyond distal subarticular tubercles of third and fifth toes; web thick, margined with horn-tipped spinules; no tarsal fold or ridge.

Description.—Habitus bufoniform, heavy; head broader than long; snout obtusely pointed, not projecting beyond mandible; cranial crests well developed; supraorbital and parietal crests strong, usually continuous; tympanum distinct, one-half to three-fourths diameter of eye. Skin above with tubercles, some spinose; skin below coarsely granular; parotoid subtriangular or oval; a string of enlarged tubercles continuous with end of parotoid present or absent.

Tips of fingers blunt; first finger shorter or longer than second; no web at base of fingers; subarticular tubercles distinct; numerous smaller tubercles on palm and fingers. Tips of toes blunt; web not reaching tips of any toes; third and fifth toes with web to outer subarticular tubercles; web thick, its margin with horn-tipped spinules; two metatarsal tubercles, the outer one half the size of the inner; numerous small tubercles on sole and toes; no tarsal fold.

Color (in alcohol) brown or grayish above, uniform or with several large dark spots; ventral surfaces somewhat lighter than dorsal ground color, usually uniform; leg with or without dark crossbar.

Secondary sex characters.—As described by Liu (1935), male *Bufo biporcatus* have median subgular vocal sacs. Liu considers the vocal sac of *biporcatus* to be external and that of *philippinicus* (treated by Liu as a separate species) to be internal. According to my observations some males of *b. philippinicus* appear to have modified gular skin, whereas others do not.

Liu also noted that *biporcatus* (=*biporcatus* and *philippinicus* of Liu) may have either one or two slit-like openings to the vocal sacs. Approximately five-sixths of the males examined in this study have a single opening, which may be either on the right or on the left side of the mouth.

Males of *biporcatus* have nuptial pads consisting of masses of black spinules. The pads are usually present on the dorsal surface of both first and second fingers, that of the second finger being much smaller. Van Kampen (1923) states that the nuptial pad appears only on the first finger in *biporcatus*. Unfortunately, I have examined only one male of *biporcatus biporcatus*, and this individual has nuptial pads on both fingers. Three of thirty-nine males from the Philippines have the pad on the first fingers only.

Differences between males and females are also evident in size. The statistical analysis of snout-vent lengths presented in Table 5 demonstrates conclusively that the females are larger. There is weak evidence that the parotoid glands of males are wider relative to parotoid length than in females. The pertinent data are given in Table 5. It will be noted that, although the sex difference in the Busuanga sample is not statistically significant, the males do have slightly broader parotoids. Mertens (1930) comments that among males from Sangsit, Bali, the parotoid is only slightly longer than broad, whereas in the females the gland is almost twice as long as broad.

Ecological notes.—Like many other species of *Bufo*, *biporcatus* is terrestrial and eurytopic. Mertens (1930) notes that the type sub-

Table 5. Comparison of adult males and females of *Bufo biporcatus philippinicus*

Snout-vent length

	Sex	No.	Mean±SE	Range	Difference of means	*t*	*n*	P
Busuanga.......	♀	5	80.32±3.11	69.3-85.6	9.93	3.805	15	0.003
Busuanga.......	♂	12	70.39±1.13	62.9-77.8				
Palawan........	♀	20	66.38±1.05	58.5-75.5	8.54	6.671	38	<0.001
Palawan........	♂	20	57.84±0.74	52.0-64.5				

Parotoid width/parotoid length

Busuanga.......	♂	12	0.644±0.015	0.58-0.75	0.012	0.46	15	0.65
Busuanga.......	♀	5	0.632±0.017	0.60-0.69				
Palawan........	♂	20	0.594±0.012	0.50-0.72	0.035	2.229	38	0.03
Palawan........	♀	20	0.559±0.010	0.50-0.67				

species as well as *biporcatus cavator* Barbour is found in many biotopes, including the vicinity of human habitations. The only biotope in which Mertens did not observe *biporcatus* was the true original rain forest. These observations are supported by the field notes of the Philippine Zoological Expedition, which collected *b. philippinicus* in the following situations: dry open pasture land (11), second growth forest (6), dry creek bed (9), rice paddies (9), swampy coconut grove (39), and in a house (1). This variety of biotopes indicates that *biporcatus* is not bound to moist situations.

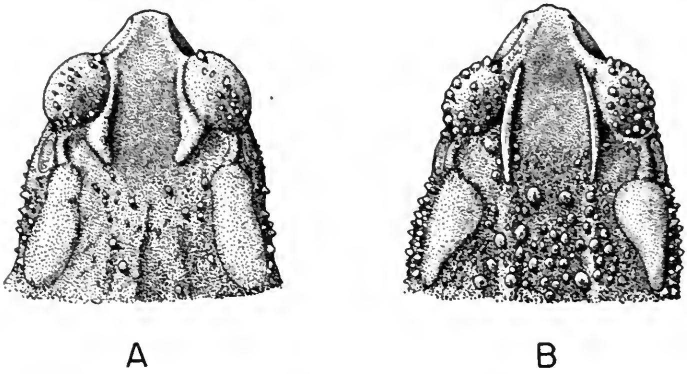


FIG. 38. Heads of *Bufo biporcatus philippinicus* (A) and *B. b. biporcatus* (B); × 1.6.

The altitudinal range of *biporcatus* extends from sea level to about 1,500 meters, although it is much more common at lower elevations. On Java it has been recorded up to 1,500 meters (van Kampen, 1923), on Borneo to 1,200 meters (van Kampen, 1923), and on Bali and Lombok to 700 meters (Mertens, 1930). Taylor (1920) mentions collecting specimens in low mountains on Palawan and Busuanga. All other known Philippine material has been collected within 100 meters of sea level.

Inter-island variation.—Boulenger (1887) indicated that the parietal crests of *philippinicus* are thicker than those of *biporcatus* (=*b. biporcatus*). My observations support this conclusion (fig. 38). The increase in crest thickness seems to take place in Balabac. The development of the crests is not independent of body size within samples. Nevertheless, even the smaller individuals (ca. 55 mm.) of the Balabac series (CNHM 51391–95, 51460) have heavier parietal crests than do any of the six seen from Java, Bali, or Borneo (50 to 75 mm., snout to vent). The parietal crests of specimens from the Calamian Islands are on the average thicker than those on material from Palawan and Balabac. This difference is correlated with differences in body lengths and may not indicate a change in growth relations.

Another characteristic of the supraorbital-parietal crest showing geographic variation is the position of its highest point. In the specimens from Java, Bali, and Borneo the high point is opposite the posterior third of the eye; in all specimens from the Philippines the high point is behind the eye, that is, on the parietal portion of the crest.

The parotoid glands of the two subspecies are different in shape. Specimens of *biporcatus* from Java, Borneo, and Bali have subtriangular parotoids, the hind end being decidedly narrower than the front end (fig. 38, B). Occasionally the parotoid in these is atten-

Table 6. Geographic variation of characters in adult *Bufo biporcatus*

Snout-vent length

	Males			Females		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Culion	2	79.90	79.2-80.6	1	84.8	---
Busuanga	12	70.39±1.13	62.9-77.8	5	80.32±3.11	69.3-85.6
Palawan	20	57.84±0.74	52.0-64.5	20	66.38±1.05	58.5-75.5
Balabac	5	57.92±1.63	53.9-63.0	---	---	---

	Difference of means	*t*	*n*	P	Difference of means	*t*	*n*	P
Busuanga—Palawan	12.55	9.728	30	0.001	13.94	5.403	23	0.001
Palawan—Balabac	0.08	0.05	23	0.9	---	---	--	---

Parotoid width/parotoid length

	Males			Females		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Culion	2	0.61	—	1	0.62	—
Busuanga	12	0.644±0.015	0.58-0.75	5	0.632±0.017	0.60-0.69
Palawan	20	0.594±0.012	0.50-0.72	20	0.559±0.010	0.50-0.67
Balabac	5	0.524±0.010	0.50-0.55	—	—	—
Java	1	0.47	—	1	0.56	—

	Difference of means	*t*	*n*	P	Difference of means	*t*	*n*	P
Busuanga—Palawan	0.050	2.538	30	0.017	0.073	3.364	23	0.004
Palawan—Balabac	0.070	2.767	23	0.011	—	—	--	—

uate. By contrast the parotoid glands in all Philippine specimens are oval, both ends being approximately equal in width (fig. 38, A).

Within the subspecies *philippinicus* there is inter-island variation in the relation of parotoid width to parotoid length. The northern populations appear to have relatively wider glands than the southern ones. This may be seen in the statistical analysis of the ratio of parotoid width to parotoid length (Table 6). The difference between populations is probably independent of body size. The difference between the ratios of the Palawan and Balabac series is greater than that between the means of the Busuanga and Palawan series, thus contrasting with the relation of the populations with respect to mean snout-vent length (Table 6).

Behind and continuous with the parotoids is an oblique row of enlarged spiny tubercles. These are highly developed and appear in all *b. biporcatus* seen. However, they are present in only seven of 44 specimens from Palawan, five of 17 from Busuanga, and not at all in three from Culion or in six from Balabac. Even in those specimens from Palawan and Busuanga in which the row of tubercles is present, they are not as conspicuous as in *b. biporcatus.*

One of the distinctions between *philippinicus* and *biporcatus* implied by Boulenger (1887) involved the difference in the size of the first finger relative to the second. According to Boulenger the first finger of *philippinicus* is much larger than the second, whereas in *biporcatus* the first finger is generally shorter than the second (Boulenger, 1882). All of the *philippinicus* I have examined have the first finger longer than the second. Only one of the Java (USNM 43207) and none of the Bornean or Bali specimens have the first finger shorter.

Inadequate material limits the discussion of geographic variation in size to the Philippine subspecies (for statistical analysis see Table 6). The populations of Culion and Busuanga are obviously larger than those of Palawan and Balabac. The difference within the Calamian Island populations could not be tested because of the few specimens from Culion on hand.

To summarize, populations of *b. biporcatus* from Java, Borneo, and Bali are characterized by the lower and narrower parietal crest, subtriangular parotoid gland, and conspicuous lateral row of enlarged tubercles; in the populations of *b. philippinicus* from Balabac, Palawan, Culion, and Busuanga, the parietal crests are higher and thicker, the parotoids oval, and the rows of enlarged tubercles weak or absent. Within the subspecies *philippinicus* there is geographic variation in size and in the ratio of parotoid width to parotoid length.

Range.—Busuanga (Coron). Culion (San Pedro). Palawan (Babuyan, Brooke's Point, Puerto Princesa, Santa Teresa, Taytay [Taylor, 1920]). Dumaran (Dumaran). Balabac (Balabac). (Fig. 82.)

Bufo marinus Linnaeus

Rana marina Linnaeus, 1758, Syst. Nat., 10th ed., **1**: 211—America.

Bufo marinus Schneider, 1799, Hist. Amph., Fasc. 1, p. 219; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 315.

Material examined.—Panay, 3 (CNHM); Negros, 1 (CNHM).

Diagnosis.—A large-sized species of *Bufo* (often in excess of 100 mm.); cranial crests present; no parietal ridge (fig. 39); tympanum distinct; fingers long, without web; toes webbed beyond distal subarticular tubercles; tarsal ridge present.

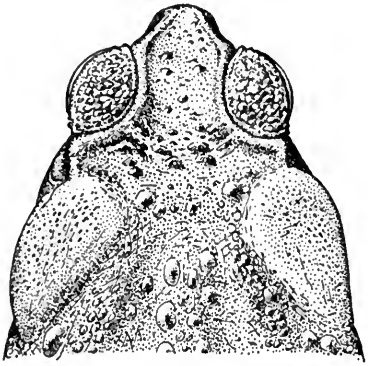


FIG. 39. Head of *Bufo marinus;* × 0.8.

Description.—Habitus bufoniform, heavy; head broader than long; snout rounded, not projecting beyond mandible; cranial crests well developed; no parietal crest; tympanum distinct, two-fifths to one-half diameter of eye. Skin above irregularly tubercular, some of tubercles spinose; skin below coarsely granular; parotoid large, subrhomboidal; usually a skin fold bearing large tubercles continuous with tip of parotoid.

Tips of fingers blunt or rounded; first finger longer than second; no web at base of fingers; subarticular tubercles distinct; numerous small supernumerary tubercles on hand. Tips of toes rounded; web reaching between subarticular tubercle and rounded tip of first and second toes, between distal tubercle and tip of third and fifth, to middle subarticular tubercle of fourth toe; edge of web crenulate but without spinules; two metatarsal tubercles, inner elongate and about twice the size of rounded outer one; subarticular tubercles distinct; numerous small supernumerary tubercles on foot; a strong tarsal ridge.

Color (in alcohol) brown above with black spots enclosing one or several tubercles; ventral surfaces dirty cream or light brown variously spotted with dark brown or black; limbs with or without dark crossbars dorsally.

Secondary sex characters.—The males at hand confirm Liu's statement (1935) that *marinus* has median subgular vocal sacs with a slit-like opening on each side of the mouth. Adult males also have nuptial pads composed of clustered horn-tipped spinules. On the first finger the pad extends from the base to the articulation of the two phalanges on the dorsal and median surfaces. A smaller round pad is usually present over the metacarpal of the second finger.

Males of *marinus* are further differentiated from females by the presence of numerous spinules scattered over the entire dorsal surface, including the tubercles and parotoids. By contrast the females are smooth. Noble (1931) suggested that spinules of this sort might function in sex recognition but he doubted this, because in some species, for example, *marinus*, the male was spinose, whereas in others, for example, *B. terrestris* and *B. bufo*, the female was. There is no theoretical reason why a stimulus-response relationship cannot change from species to species as well as a morphological character. Sex recognition remains a good suggestion for the function of the spinules.

Females appear to reach a larger size than males. Not enough specimens were available to determine the extent of sex dimorphism in the Philippines, but some idea may be gained from a small collection of Colombian material in Chicago Natural History Museum. Ten individuals of both sexes were measured (snout-vent length) with the following results:

	Mean ± SE	Range	Difference of means	*t*	P
Females.....	103.37±3.52	87.0–117.6	5.38	1.257	0.23
Males.......	97.99±2.44	86.3–107.8			

The difference is not statistically significant. Of the Philippine material examined the single male measured 96.6 mm.; the three females ranged from 110.9 to 132.0 mm. snout to vent.

Ecological notes.—The following information is taken from Rabor (1952). *Bufo marinus* was introduced into the Philippines in 1934. Where breeding populations have become established, the toad is common along streams, in cultivated areas, in secondary growth, and about human habitations. The eggs are laid in ditches, swamps, flooded fields, and slowly moving streams. The food consists primarily of insects, although Rabor has found remnants of the blind snake, *Typhlops*, and rat fur in a few *marinus* stomachs.

Rabor suggests that in the vicinity of Dumaguete, Negros, *marinus* is driving out the formerly abundant native species, *Rana cancrivora, R. erythraea, Ooeidozyga laevis,* and *Kaloula conjuncta.* The processes involved in these population changes are not known, but it is noteworthy that *marinus* deposits its myriad spawn in the sites utilized by the larvae of the native species.

Range.—Luzon: Laguna Province (Rabor, 1952). Panay: Iloilo Province (Ajuy). Negros: Occidental Province (Rabor, 1952); Oriental Province (Dumaguete, Santa Catalina [Rabor, 1952]). ?Mindanao (Rabor, 1952).

Originally occurring only in tropical America, *B. marinus* is now found, thanks to man, in such widely separated places as Bermuda, the Hawaiian Islands, the Marianas, the Solomons, the Admiralty Islands, and the Philippines.

Pelophryne Barbour

Throat uniform cream or yellow	*Pelophryne albotaeniata*
Throat with black spots	*Pelophryne brevipes*

Pelophryne albotaeniata Barbour

Pelophryne albotaeniata Barbour, 1938, Proc. Biol. Soc. Washington, **51**: 194, fig.—Thumb Peak, Palawan.

Material examined.—Palawan, 8 (7 CNHM; 1 MCZ, type of *albotaeniata*).

Taxonomic notes.—The comparison of *albotaeniata* with related forms made here is based on the literature (van Kampen, 1923; Smith, 1931; Barbour, 1938) except in the case of the Philippine species.

Of the eight species of *Pelophryne* listed by Barbour, one, *lighti* Taylor, is reduced to synonymy; a second, *maculata* Mocquard, differs radically from the others in the appearance of hand and foot; and a third, *misera* Mocquard, is distinguished by the arrangement of dorsal tubercles into rows. The remaining species (*albotaeniata* Barbour, *brevipes* Peters, *guentheri* Boulenger, *macrotis* Boulenger, *signata* Boulenger) seem to be very similar and are distinguished by minor characters only.

Pelophryne albotaeniata differs in coloration from the species with which it is bracketed above. The throat is uniform cream, contrasting thereby with *brevipes*, *guentheri*, and *macrotis*, in which the throat is spotted. The comparison with *signata* is uncertain at this point. However, *signata* is figured by Boulenger (1894b) with an X-shaped mark on the back, whereas in *albotaeniata* the sides of the mid-dorsal pattern are subparallel. In *brevipes*, which resembles *signata* somewhat at this point, the mid-dorsal mark flares out at both ends. Apparently *guentheri* and *macrotis* lack a defined mid-dorsal mark, having small spots instead.

Additional distinctions between the two Philippine species may be noted. The tympanum is distinct in *albotaeniata* (as in *guentheri*, *macrotis*, and *signata*) and not covered with skin as in *brevipes*. Furthermore, males of *albotaeniata* have nuptial pads, whereas these structures are absent in *brevipes*. Other differences in the secondary sex characters are pointed out below (p. 238).

According to Barbour, "a small, round, rather ill-defined parotoid gland" is present above the insertion of the arm in *albotaeniata*. Dissection of the material at hand indicates Barbour to have been in error. No parotoid is present; there are not even any conspicuously enlarged tubercles in the neighborhood of the arm. There is a slight swelling above the insertion of the arm, but this bulge merely represents the angle in the scapula and its overlying muscle.

Diagnosis.—A small bufonid; fingers short, first and second extensively webbed; no parotoids or cranial crests; tympanum distinct, not covered with skin; throat without dark spots.

Description.—Habitus moderately slender, trunk not wider than head; head as wide as long; snout short, not protruding beyond mandible, profile vertical; cranial crests absent; tympanum distinct, not covered, one-third to one-half diameter of eye. Skin above with irregularly distributed tubercles interspersed with small spinules; gular region rugose; abdomen with coarse granules; no parotoid.

Limbs slender; fingers short; web fleshy, indistinguishable from palm; first finger projecting as small nubbin from web; finger tips truncate, not dilated; subarticular tubercles similar to supernumerary tubercles of hand (as in fig. 40). Foot with fleshy web to tips of first, second, and third toes; web reaching level of subarticular tubercle of fifth toe; first, second, and third toes short, the last much shorter than the fifth; tips of toes rounded, smaller than finger tips; usually two flat subcircular metatarsal tubercles, occasionally one or both indistinct; subarticular tubercles indistinct; supernumerary tubercles absent.

Color (in alcohol): a dark-edged brown mid-dorsal band, and a similar lateral band, the two separated by a dorso-lateral light tan stripe; throat and chest uniform cream; belly cream with dark brown spots; dorsal surfaces of limbs light tan with dark-edged crossbars.

Secondary sex characters.—The males of *albotaeniata* have the elongate testes typical of the bufonids. Bidder's organ is present as a light cap on the antero-ventral tip of the testis.

The vocal sac is median, subgular, and external. The sac itself is long and extends backward beyond the submaxillaris muscle (=mylohyoid of Liu), overlapping the coraco-radialis. The sac opens into the mouth via a pair of slits.

Males of *albotaeniata* have nuptial pads covering the entire medio-dorsal surface of the first finger. The pad is composed of a cluster of small cream-colored pustules. In addition, three of the four males examined have a row of well-separated larger pustules running the length of the second finger on its upper surface.

On the chins of the males there are cream-colored or white spinose tubercles arranged in four or five rows near the symphysis and tapering to one row laterally along the ventral side of the mandible. The distinction between the sexes is not sharp in this character, for the largest of the three adult females examined also had several such asperities. In no other way did this female (CNHM 51371) show a tendency towards intersexuality.

Finally, there appears to be a difference in size between the sexes, the females averaging larger. For the three adult females, the range of snout-vent length is 19.2–22.8 mm. (mean 21.0); for four adult males the corresponding values are 18.2–19.9 mm. (mean 18.7).

Ecological notes.—Most of the species of *Pelophryne* come from high-altitude forests, and the present species is no exception. The type (MCZ 23291) was collected at 1,370 meters on Thumb Peak and the specimens in Chicago Natural History Museum were taken at 1,550 meters on Mount Balabag. The latter were found on the floor of a mossy forest.

Breeding behavior undoubtedly differs from that of *Bufo* (see p. 239), for the eggs are relatively large and very few in number. Each ovary of the largest female at hand (length 22.8 mm.) contained six enlarged, non-pigmented ova and about twice as many small white immature ova. The large eggs vary in diameter from 1.5 to 2.5 mm. with a mean of 2.0 ± 0.13. The extremely swollen condition of the oviducts and the size of the ova indicate the approach of oviposition and may be taken as evidence that the full complement of mature eggs was present.

Range.—Palawan (Mount Balabag, Thumb Peak).

Pelophryne brevipes Peters

Hylaplesia brevipes Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**: 34—Zamboanga, Mindanao.

Pelophryne brevipes Barbour, 1938, Proc. Biol. Soc. Washington, **51**: 194.

Bufo brevipes Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 287; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 125; Taylor, 1920, Phil. Jour. Sci., **16**: 340.

Nectophryne lighti Taylor, 1920, Phil. Jour. Sci., **16**: 338, pl. 7, figs. 3, 3a—Bunawan, Agusan Province, Mindanao.

Material examined.—Basilan, 1 (EHT); Mindanao, 8 (CNHM).

Taxonomic notes.—Taylor (1920) apparently did not realize the close relationship between his *Nectophryne lighti* and *brevipes*. In his key to the genera of bufonids, Taylor separated *Nectophryne* from *Bufo*, in which genus he placed *brevipes*, largely on the basis of the webbing of the fingers in *Nectophryne*. However, it might have been noted that the original description of *brevipes* states that the first finger projected only as a small nubbin: "Der erste Finger tritt nur als ein kleines Knötchen hervor. . . ." The inference is clearly that the first finger is webbed.

The only differences between *lighti* and *brevipes*, according to Taylor's description of the former, lie in the smoothness of the skin of the belly in *lighti* and in its coloration. The type of *lighti* was described as having a yellowish brown belly spotted with white; the belly of adult *brevipes* is cream or white spotted with black. On Mount McKinley, larvae of *brevipes* with developed fore and hind limbs were collected together with adults by the Philippine Expedition. These larvae have smooth yellowish bellies without any spots, thus approaching *lighti* very closely. When it is also considered that *lighti* is known only from a juvenile (15 mm.) and that, like *brevipes,* its type locality is Mindanao, the distinction between the two seems very weak. *Nectophryne lighti* Taylor is here placed in the synonymy of *brevipes* Peters. It is unfortunate that the type of *lighti* has been lost, making a further check impossible unless two species are found on Mindanao at a later date.

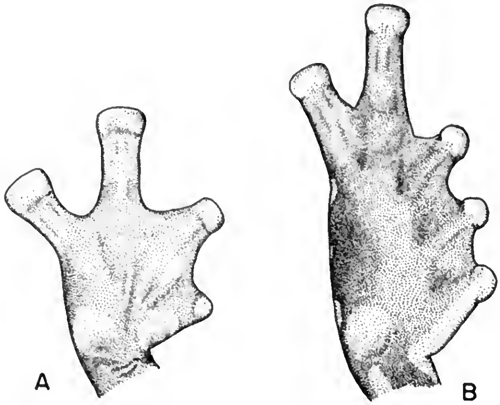


FIG. 40. Ventral views of hand (A) and foot (B) of *Pelophryne brevipes;* × 7.

Pelophryne brevipes resembles *signata* Boulenger of Borneo especially in coloration. As noted above (p. 234) both species have dorsal patterns that are somewhat cruciform and white venters spotted with black. The comparison cannot be carried further because of the lack of specimens of *signata.* A comparison with *albotaeniata* has been made above.

Diagnosis.—A small bufonid; fingers short, first finger extensively webbed (fig. 40); no parotoids or cranial crests; tympanum obscured by skin; throat with black blotches.

Description.—Habitus moderately slender, trunk not wider than head; head as wide as long; snout short, projecting slightly beyond mandible, profile sloping downward and backward; tympanum obscure, covered with skin, slightly less than one-half diameter of eye. Skin above with irregularly distributed tubercles, interspersed with spinules; chest and abdomen coarsely granular in adults; no parotoid.

Limbs slender; fingers short; first finger webbed almost to tip, other fingers at base; web fleshy; scarcely distinguishable from palm; tips of fingers truncate, slightly dilated; a few indistinct tubercles present on hand, subarticular tubercles absent. Foot with fleshy web to tips of first, second, and third toes; fourth and fifth toes about half webbed; first, second, and third toes short, the last much shorter than fifth; tips of toes truncate, smaller than finger tips; a flat round inner metatarsal tubercle and an indistinct flat outer one present or absent; no subarticular or supernumerary tubercles present (fig. 40).

Color (in alcohol) above light tan or gray with a dark-edged brown hourglass figure mid-dorsally, the figure frequently broken at the constriction; a dark-edged lateral band extending forward over lores; ventrum cream or white with large black blotches scattered over entire surface; dorsal surfaces of limbs tan or gray with dark-edged crossbars.

Secondary sex characters.—The males of *brevipes* agree with those of *albotaeniata* in the possession of elongate testes and in the position and size of Bidder's organ.

The vocal sac is median subgular with a pair of slit-like openings. As in *albotaeniata* the vocal sac extends caudad beyond the edge of the submaxillaris, but the sac of *brevipes* is longer than that of *albotaeniata* and overlaps the portio epicoracoidea of the pectoralis muscle.

Asperities are found on the chins of the males, recalling *albotaeniata*. But in *brevipes* the asperities are small tubercles, rounded rather than spinose; furthermore, the tubercles are arranged in a single row all the way around the ventral side of the mandible instead of in four rows at the tip of the chin. Neither of the two females seen had these asperities.

The males do not have nuptial pads.

No evidence of sexual dimorphism in size could be gathered from the small sample examined. The two females measured 16.6 and 17.4 mm., snout to vent. The smaller contained only immature ova and did not have an enlarged oviduct; it may have been immature. The larger one, however, was adult, having enlarged ova and oviducts. Five males, possessing vocal sacs and mandibular tubercles, and, hence, adult, varied from 16.0 to 17.7 mm., snout to vent (mean 17.1 mm.).

Ecological notes.—*Pelophryne brevipes*, like *albotaeniata*, is an inhabitant of forest floors though occasionally it climbs onto lower vegetation. Four of the specimens collected by the Philippine Zoological Expedition were found on leaves about one meter above the ground.

The known altitudinal distribution of *brevipes* is more extensive than that of *albotaeniata*. Most of the specimens have come from high elevations, that is, between 1,000 and 1,400 meters, but Taylor collected specimens at about 300 meters. The extreme low is represented by the type of *lighti*, collected below 150 meters.

Range.—Mindanao: Agusan Province (Bunawan [Taylor, 1920]); Davao Province (Mount McKinley); Zamboanga Province (Peters, 1867). Basilan (Abungabung).

Ansonia Stoliczka

A consideration of the morphological and ecological characteristics of both larva and adult of *Bufo muelleri*, *B. penangensis*, and *B. leptopus* not only brings out their close relationship but also suggests that they require separate generic status. The generic name *Ansonia* Stoliczka (type species *penangensis* Stoliczka) is available for these species. The characters of the adults of these three forms that distinguish them from true *Bufo* of Malaysia are as follows: parotoids absent, cranial crests absent (see figs. 39, 41), subarticular tubercles of the fingers poorly developed or absent, no small supernumerary tubercles on the feet, web membranous and well developed. Generally, adults of *Ansonia* are less than 60 mm. snout to vent, whereas adults of Indo-Australian *Bufo* (*sens. str.*) are larger.

Bufo spinulifer Mocquard and *B. fuligineus* Mocquard (both from Borneo) agree with the *penangensis* group in most of the above characters; but *spinulifer* recalls *Cacophryne borbonica*, especially in the presence of a dorso-lateral ridge of very large and confluent tubercles, and may belong in the genus *Cacophryne*. However, both *fuligineus* and *spinulifer* are known only from the types, and their generic assignment must wait for additional material. All the remaining *Bufos* from Malaysia differ from the *penangensis* group in the characters listed above, with the exception of *valhallae* Meade-Waldo and *sumatranus* Peters, which lack cranial crests. Other characters of these last two species leave no doubt that they should be associated with the remainder of the genus *Bufo*.

The life cycle within the genus *Bufo* shows remarkably little variation (Noble, 1927). Regardless of geographic distribution the ova are generally heavily pigmented, small, and deposited in large numbers. Table 7 presents a short summary of quantitative data for representative species of *Bufo*. It may be seen that the species of *Bufo* usually have broods that number in the thousands, with rare exceptions (in the smallest species) of over five hundred. Also, the eggs have a maximum diameter of 2.0 mm. even including those of the giant species *marinus.*

Contrasting sharply with this picture, the females of *Ansonia penangensis* and *muelleri* lay large non-pigmented eggs (average diameter over 2.0 mm.) in relatively small numbers. Although I have data (see Table 7) only for *muelleri,* the large egg size of *penangensis* would indicate that it, too, would have a small clutch size, not exceeding 250 ova per clutch.

The larvae of *Bufo* are generalized, with little specialization of any sort. The tadpoles have subspherical bodies, moderately developed tails, high fins, and generalized oral disks. These last are ordinarily equipped with well-developed horny jaws and papillae at the sides. The habitat is, most frequently, slowly moving or standing water. In habits, *Bufo* tadpoles are benthic.

Ansonia penangensis and *muelleri* differ radically from this pattern. The larvae of both species have depressed bodies, strong muscular tails, reduced fins, and sucker-like oral disks (fig. 43). As in other, unrelated frog larvae with sucking mouth parts, the jaws are somewhat reduced; the two halves of the lower jaw are barely in contact and those of the upper jaw are separated by a distance equal to the length of one half. Furthermore, the oral disk has a border of papillae broken only along the anterior margin.

Only one species of *Bufo* (*sens. str.*) is reported to have a tadpole with such specialized mouth parts. According to van Kampen (1910) the larvae of *B. asper* have sucker-like oral disks. There is some reason to doubt van Kampen's identification. A tadpole with this modification undoubtedly lives in torrents. Yet the very large, unmodified body of the *asper* is singularly poorly adapted to breeding in rapidly flowing water. Furthermore, the identification rested upon the observation that the larvae had fully webbed toes and the fact that *asper* is the only *Bufo* known from Java with a complete web. The possibility remains that these larvae belong to a species of *Ansonia.* The identification of van Kampen's larvae certainly requires confirmation.

The habitat of *muelleri* and *penangensis* is also of interest. The adults of the former and the larvae of both are found in rapidly moving mountain streams (Boulenger, 1912; Taylor, 1922a; field notes of Philippine Zoological Expedition). The depressed body, strong tail, reduced fins, and sucker-like mouth of the tadpole of both species suit them to their habitat. Similarly, the depressed

Table 7. Egg and clutch sizes in some species of *Bufo* and *Ansonia*

Species	Egg size Mean and Range	Clutch size	Snout-vent length Females
Bufo			
Asiatic species			
raddei	1.5 (Liu, 1950)	---	58-72 (Pope, 1931)
bufo gargarizans	1.5 (Liu, 1950)	---	64-106 (Okada, 1931)
melanostictus	1.38 (1.0-1.5)[1]	2000+[2]	80
biporcatus philippinicus	1.40 (1.25-1.5)[1]	2000+[2]	66
biporcatus philippinicus	1.48 (1.25-1.5)[1]	2000+[2]	85
European species (all data from Boulenger, 1897-98)			
bufo bufo	1.5-2.0	4,900-6,800	94-130
viridis viridis	1.0-1.5	10,000-12,000	79-93
calamita	1.0-1.5	3,000-4,000	65-75
North American species			
quercicus	0.8-1.0[3]	600-760[3]	20-32[4]
terrestris americanus	1.0-1.4[3]	20,000[5]	56-110[4]
woodhousei fowleri	1.0-1.4[3]	25,000[5]	58-118[4]
South American species			
marinus	1.78 (1.5-2.0)[1]	30,000[5]	200
Ansonia			
muelleri	2.15 (1.5-2.5)[1]	162[6]	31
muelleri	2.13 (1.75-2.0)[1]	158[6]	31
penangensis	2.0 (Noble, 1927)	—	40 (Boulenger, 1912)

[1] The long diameters of 10 eggs chosen at random in each case.

[2] A conservative estimate based on a count of over 500 ova in the surface layer of one ovary.

[3] Wright and Wright (1924).

[4] Wright and Wright (1949).

[5] Cited by H.M. Smith (1947) as large broods.

[6] Based on the total count of the ova in one ovary.

body, full swimming web, and swollen digit tips of the adults are adaptations to aquatic life in strong currents.

In summary, then, the distinctive habitat and the modifications of the adults and larvae to that habitat set *muelleri* and *penangensis* off from the species of the genus *Bufo*. The species *leptopus*, though not as well known as the other two, is so similar morphologically to *penangensis* that little doubt is attached to placing it in the genus *Ansonia*.

Ansonia muelleri Boulenger

Bufo muelleri Boulenger, 1887, Ann. Mag. Nat. Hist., (5), **20**: 52—Mindanao; Taylor, 1920, Phil. Jour. Sci., **16**: 341; Davis, 1936, Field Mus. Nat. Hist., Zool. Ser., **20**: 118.

Bufo mcgregori Taylor, 1922, Phil Jour. Sci., **21**: 182—Pasonanca, Zamboanga, Mindanao.

Material examined.—Mindanao, 120 (1 BM, type of *muelleri;* 112 CNHM, including 25 larvae; 7 MCZ, including 6 paratypes of *mcgregori*).

Taxonomic notes.—Bufo mcgregori (type locality Zamboanga, Mindanao) was distinguished by Taylor (1922a) from *muelleri* on the basis of four characters. It is difficult to understand how Taylor arrived at his conclusions, for nowhere does he indicate that he had comparative material available. Indeed, he states (1920, p. 341) that *muelleri* was known only from the type at that time. It must be assumed that Taylor relied solely on the original description of *muelleri*. The distinctive characters designated by Taylor are: the presence of a constriction in the neck region of *mcgregori* (supposedly absent in *muelleri*); the strongly tubercular dorsal skin of *mcgregori* (nearly smooth in *muelleri* according to Boulenger's description); the presence of three instead of two metatarsal tubercles in *mcgregori;* and the lesser extent of webbing in *mcgregori*.

The bulk of the evidence suggests that the differences mentioned by Taylor represent individual variation rather than species differentia. As a matter of fact, even within the paratypic series of *mcgregori* there is sufficient variation in the neck region and in the metatarsal tubercles to warrant ignoring these points. There is also minor variation within both the paratypic series and a sample from Davao Province in the matter of webbing, but no distinction between the two samples is possible. No specimen had the fourth toe broadly webbed to the tip. The same is true of the type of *muelleri*, though Boulenger states "toes . . . webbed to tips."

Within the Davao Province sample and within the paratypic series of *mcgregori*, there is similar individual variation in the degree of tuberculation. The tubercles of the type of *muelleri* are not as prominent as those of most specimens in the two series. Nevertheless, there is no reason for believing that this supposed difference between *muelleri* and *mcgregori* represents anything but individual variation. In the absence of significant evidence to the contrary, *mcgregori* must be considered conspecific with *muelleri*.

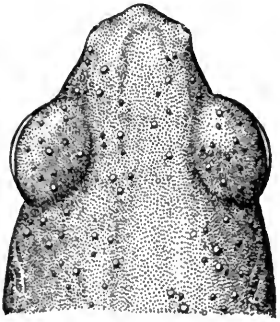


FIG. 41. Head of *Ansonia muelleri;* × 4.

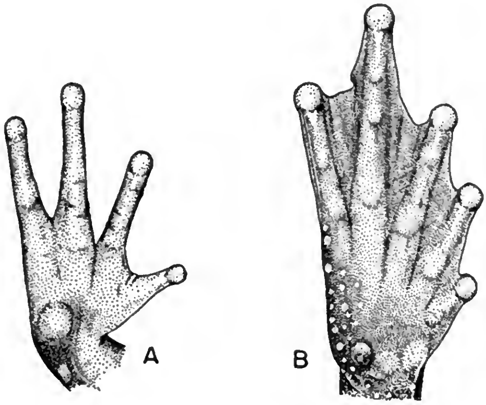


FIG. 42. Ventral views of hand (A) and foot (B) of *Ansonia muelleri;* × 4.

Although displaying close affinities with *A. penangensis* and *A. leptopus*, *muelleri* differs from these in certain characters. A tympanum is absent in *muelleri* and present in both of the others; all toes, except the fourth, are broadly webbed to the disks in *muelleri*, only the first and second toes of the other forms; the nuptial pad of *muelleri* lacks horn, which is present on the pads of *leptopus* and *penangensis*.

Diagnosis.—A small bufonid; cranial crests absent; no parotoids (fig. 41); tympanum absent; fingers long, webbed at base (fig. 42, A); toes, except fourth, webbed to distal swellings; web membranous (fig. 42, B).

Description.—Habitus moderately slender; head depressed, as broad as long; snout obtusely pointed or truncate, projecting beyond mandible; cranial crests absent; tympanum absent; skin of back with irregularly distributed tubercles of varying sizes; skin below coarsely granular; no parotoids.

Tips of fingers with round swellings, these only slightly wider than penultimate phalanges; first finger shorter than second; web at bases of inner fingers; subarticular tubercles faintly indicated or absent; no supernumerary tubercles. Tips of toes with swellings as in fingers; all toes except fourth broadly webbed to distal swelling; web membranous, smooth; two or three metatarsal tubercles; subarticular tubercles faintly visible or absent; supernumerary tubercles usually absent, occasionally a few weak ones near tarsal-metatarsal articulation.

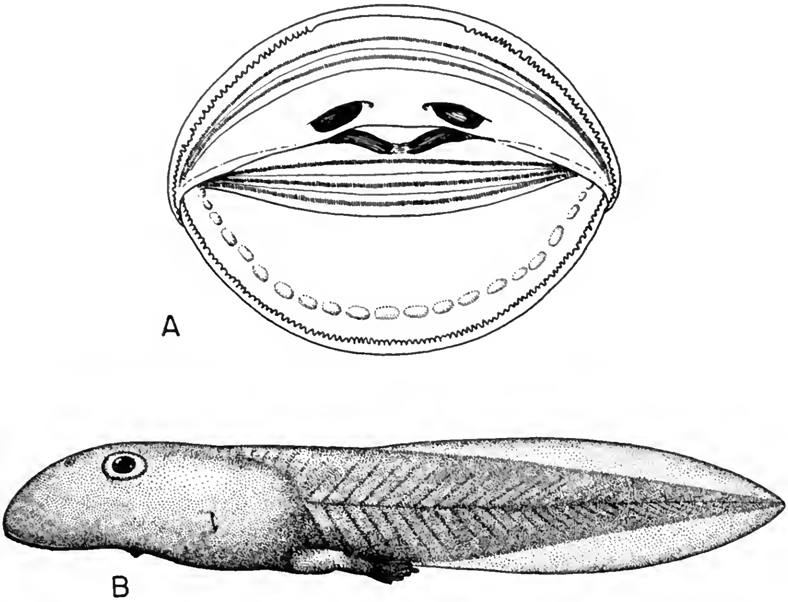


FIG. 43. Tadpole of *Ansonia muelleri*. A, mouth parts (× 10); B, lateral view (× 4).

Color (in alcohol) above brownish gray with irregular darker markings; gular region cream or black; abdomen uniform cream or with suffusion of black on breast; dorsal surfaces of limbs with dark crossbars.

Description of tadpole.—Specimen without hind limbs (CNHM 50904): body (fig. 43) depressed; eyes about midway between tip of snout and anus; spiracle low on left side; anus median; tail one and one-third times length of body, muscular portion well developed; fins narrow, upper fin on distal half of tail only, lower fin entire length of tail; total length 17 mm. Oral disk ventral, sucker-like; lips expanded; labial borders with one row of small papillae, interrupted on anterior edge opposite gap between separated halves of anterior beak; a row of low thick papillae on posterior lip two-thirds of distance from beak to labial border; beaks with serrated, black edges, white basally; both beaks divided, the two halves of anterior beak separated by distance equal to length of one half; halves of posterior beak less widely separated; two long continuous tooth rows anterior to mouth, three continuous ones posteriorly. Color almost uniform black on back and tail, slightly lighter ventrally.

Specimen (CNHM 50904) with well-developed hind limbs and erupted forelimbs, tail fully developed; mouth parts as in younger specimen except that less horn is present on beaks; foot almost completely webbed, toes with rounded tips; fingers long relative to palm, first shorter than second; skin with fine punctations dorsally; limbs barred with black and white; abdomen with small black spots laterally; total length 25 mm., body 13 mm.

A complete developmental series terminating with individuals with adult-like mouths and largely resorbed tails was collected by the Philippine Expedition. Comparison of the most advanced members of this series with adult *muelleri* leaves no doubt as to their identity. Adults and larvae were found in the same stream.

Secondary sex characters.—Males of *muelleri* have nuptial pads composed of coarse white or cream-colored pustules on the mediodorsal surface of the first finger. There is apparently no horny covering on the pustules. The extent of the pads shows much individual variation. At the maximum they occupy a large round area at the articulation of metacarpus and proximal phalanx and extend distad as a narrow projection to the articulation of the two phalanges; at the minimum they are present only as a small cluster of five or six pustules situated at the articulation of metacarpus and phalanx. This variation, plus the absence of nuptial pads in three males that appear to be mature so far as vocal sacs and size are concerned, suggests that the nuptial pads regress between breeding periods.

The males also have median subgular vocal sacs opening in the floor of the mouth through a single elongated slit, which may be on either the right or left side. The skin external to the vocal sac is stretched and, therefore, somewhat thinned in most of the males examined. Dissection of specimens from the sample at hand confirms Davis' (1936) statement that Bidder's organ is present in *muelleri.*

Sexual dimorphism is further evident in size and in coloration of the throat. Adult females from Davao Province average about 5 mm. larger, snout to vent, than adult males, the difference in the sample being statistically significant ($t = 11.61$; $P = < 0.001$).

	Sex	No.	Mean ± SE	Range
Davao Province.....	♀	18	33.06±0.47	30.4–36.8
Davao Province.....	♂	25	27.72±0.20	25.6–29.7

The coloration of the gular region may be uniform cream or black; in approximately one-fifth of the Davao Province specimens the color is intermediate, or grayish. With a few exceptions the males have black throats and the females cream. The data are as follows:

	Observed				Calculated		
	Cream	Gray	Black	Total	Cream	Gray	Black
Males....	2	3	20	25	6.4	4.7	13.9
Females..	9	5	4	18	4.6	3.3	10.0

Treating the above as a contingency table, chi square equals 14.95. With 2 degrees of freedom, P equals less than 0.001, indicating statistical significance for the difference between the sexes. The Zamboanga series was not included in the calculations because the coloration over the entire body had faded too much.

Geographic variation.—The mean snout-vent length of twenty-five adult males from Davao Province is 27.72±0.20 mm., that of seven from the Zamboanga Peninsula is 37.17±0.56 mm. The value of *t* for this difference is 19.98, and P equals less than 0.001. This represents the only distinction I can make between the two samples (cf. *Rana microdisca,* p. 298).

Ecological notes.—As indicated above (p. 240), the larvae of *muelleri* are found in forest streams with swift currents. The Philippine Expedition found tadpoles on and under rocks in rapids and swift channels of mountain streams. A few specimens were clinging to rocks just above the surface of the water.

Nine adults were collected in the same streams and under similar circumstances as the larvae. However, 28 adults were also collected along the banks of streams and nine were found on the forest floor away from water. Taylor (1922a) reports on a number of adults clinging to "spray-moistened" stones in a stream. "When disturbed they dove into the swift-flowing water and took refuge under stones at the bottom."

It may be questioned whether these mountain streams constitute the habitat utilized by *muelleri* for most of its post-metamorphic functions. As an alternative one might suggest that the forest floor, upon which some adults were collected, is the most utilized habitat and that the mountain streams are merely breeding sites. This is an attractive proposal in view of the terrestrial rather than aquatic habits of most bufonids. Nevertheless, in addition to the contrast in numbers collected in different situations, other evidence, such as the morphology of the adult and the presence of aquatic insects in the stomach of an adult, points to the mountain stream as the usual habitat.

The altitudinal distribution of *muelleri* extends from slightly below 600 meters to at least 1,950 meters. The lower limit is probably dependent upon availability of streams with suitable current and substrate qualities.

Range.—Mindanao: Bukidnon Province (near Agusan, Misamis Oriental Province); Davao Province (Mainit and Todaya on Mount Apo, Mount McKinley); City of Zamboanga (near Pasonanca).

HYLIDAE

Hyla sp.

Material examined.—Negros, 1 (CM).

Taxonomic notes.—This specimen was included in the type series of *Cornufer hazelae* Taylor. The field tag attached to it associates it with Canlaon Volcano, the type locality of *hazelae*.

The distribution of the genus *Hyla* is noteworthy for the large gap of uninhabited territory between Yunnan, Hainan, and Formosa in the north and west, and Sumba, Boeroe, and Halmaheira on the south and east. In view of this gap a record from the central Philippine Islands is unexpected. The frequently erroneous catalogue of Casto de Elera (1895) lists *Hyla chinensis* from Luzon and Basilan, but no preserved specimens are extant nor have these records been confirmed. Taylor (1920) doubts the validity of de Elera's report.

The present case probably belongs in the doubtful category also, but certain circumstances make it more difficult to dispose of. In the first place, the specimen does exist. In the second place, the collector's number (307) is very close to the numbers of the type of *hazelae* (293) and some of its paratypes (e.g., 304 and 306). Finally, the *Hyla* differs from all of the Asiatic and Papuan forms, though resembling *Hyla montana* Peters and Doria (range, New Guinea) and *H. rubella* Gray (range, Timorlaut and Australia).

This surprising record, if proved accurate, would establish a parallel in the distributions of *Hyla* and *Cornufer*. Both genera are found on Halmaheira and the islands to the southeast, then again in the Philippines. Neither genus is known from Celebes.

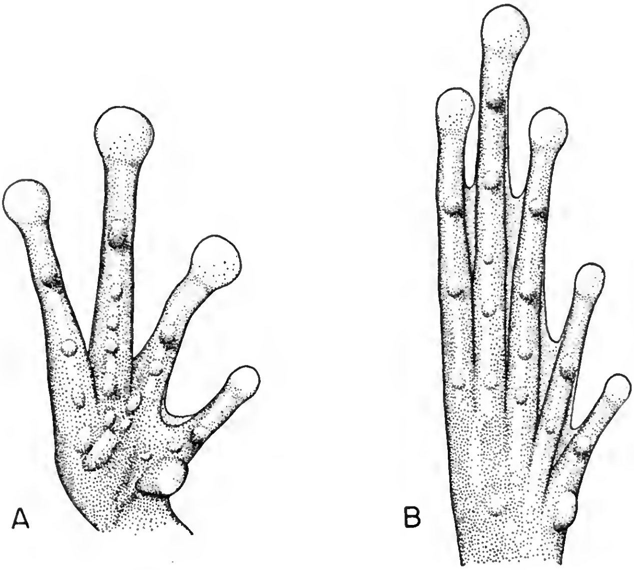


FIG. 44. Hand (A) and foot (B) of *Hyla* sp.; × 6.5.

I refrain from naming this form until fresh material confirms the locality.

Diagnosis.—Epicoracoids overlapping; intercalary cartilages present in digits; maxillary teeth present; pupil horizontal.

Description.—Head as long as broad; snout broadly rounded, projecting, slightly longer than eye; nostril near tip of snout, directly above tip of mandible; canthus rostralis rounded; lores sloping, slightly concave; interorbital space depressed, wider than upper eyelid; vomerine teeth present, between hind rims of choanae; tympanum distinct, two-fifths diameter of eye. Skin above smooth except upper eyelid, which is weakly tubercular; throat indistinctly granular; chest and belly coarsely granular; weak skin fold across chest; skin of head free from skull; a row of light tubercles along lateral edge of lower arm.

Digits with dilated terminal disks; disks of outer fingers and toes subequal, slightly smaller than tympanum; disks with horizontal circummarginal grooves; first finger shorter than second; latter shorter than fourth; base of fingers with rudimentary web; subarticular tubercles distinct; numerous supernumerary metacarpal tubercles (fig. 44, A). First and second toes webbed to distal edge of subarticular tubercle, third and fifth to distal tubercle, and fourth to middle tubercle; subarticular tubercles distinct; several supernumerary tubercles on each metatarsal; an oval inner metatarsal tubercle and a feeble, round outer one; a dermal ridge on median edge of tarsal segment (fig. 44, B); tibio-tarsal joint reaching front edge of eye.

Snout to vent 18.0 mm.; head width 6.5 mm.

Color (in alcohol) cream above, uniformly speckled with dark chromatophores; uniform cream below; no white stripes on head or trunk; no crossbars on legs.

RANIDAE

Ooeidozyga Kuhl and van Hasselt

All toes completely webbed; nostrils superior	*Ooeidozyga laevis*
Toes incompletely webbed; nostrils lateral	*Ooeidozyga diminutiva*

Ooeidozyga laevis laevis Günther

Oxyglossus laevis Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 7, pl. 1, fig. A—Philippine Islands; Boulenger, 1882, op. cit., p. 6; 1897, Proc. Zool. Soc. London, **1897**: 228; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 121; Taylor, 1920, Phil. Jour. Sci., **16**: 230, pl. 1, fig. 1; 1922, op. cit., **21**: 258; 1922, Phil. Agriculturist, **11**: 128; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 230, fig. 26.

Ooeidozyga laevis Smith, 1927, Proc. Zool. Soc. London, **1927**: 204.

Oxydozyga laevis laevis Mertens, 1931, Abh. Senck. Naturf. Ges., **42**: 209.

Phrynoglossus laevis Smith, 1931, Bull. Raffles Mus., no. 5, p. 16.

Material examined.—Luzon, 13 (9 CM; 2 RR; 2 USNM); Mindoro, 7 (CM); Panay, 4 (CNHM); Siquijor, 7 (CNHM); Samar, 6 (CNHM); Negros, 198 (190 CNHM; 8 CM); Mindanao, 47 (7 CM; 40 CNHM); Basilan, 1 (CNHM); Busuanga, 7 (CNHM); Culion, 22 (CNHM); Palawan, 9 (4 CNHM; 5 USNM); Balabac, 10 (CNHM); Borneo, 4 (CNHM).

Taxonomic notes.—In the absence of material from the continent, critical examination of the subspecific status of the continental populations (*O. laevis martensi* Peters) is not possible in this report. I am following the arrangements of Mertens (1930) and Pope (1931).

Diagnosis.—A medium-sized, heavy-bodied frog; tongue round or oval, not notched posteriorly; no vomerine teeth; nostrils dorsal; toes completely webbed to disks.

Description.—Habitus stout; head somewhat broader than long; snout rounded; lores rounded; nostrils superior; vomerine teeth absent; tongue subcircular or oval, not notched posteriorly; tympanum hidden, position frequently indicated by a light temporal spot; no dorso-lateral fold; a weak temporal fold from posterior corner of eye to just caudad of angle of jaws.

Fingers without web; tips slightly swollen; first finger equal to or longer than second; a prominent subarticular tubercle at base of each finger; two prominent, oval palmar tubercles. Hind limbs short, very stout; tips of toes with distinct round disks larger than those of fingers; toes webbed to disks; a dermal ridge along inner side of first toe and metatarsal and one along outer edge of fifth toe and metatarsal; a tarsal ridge; an elongate inner but no outer metatarsal tubercle.

Skin smooth above except for white spinules appearing on posterior portion of back and on dorsal surface of legs; abdomen smooth, occasionally wrinkled in preservative.

Color (in alcohol) brownish to gray or olive above variously spotted with darker color; occasional individuals with a mid-dorsal band and/or a thin vertebral line; gular region varies from cream with a few dark spots or irregular mottling to almost solid black; abdomen and ventral surfaces of legs cream, immaculate or variously mottled and spotted with black; limbs with dark crossbars or spots.

Secondary sex characters.—Liu (1935) states that the males of *laevis* have median subgular internal vocal sacs, with somewhat elongated openings. My observations on Philippine material agree with Liu's. A nuptial pad extending from the last joint of the finger to the wrist covers the entire dorsal and median surfaces of the first finger in males.

In addition to these structures adult males have small white spinules on the gular region. There is considerable individual variation in the area occupied by these asperities. They are always found at the very tip of the chin. As they become more numerous the area occupied spreads laterally along the rim of the mandible and posteriorly down the mid-line of the throat. At their maximum development the spinules cover the entire gular region. With only the few exceptions to be noted below, the females lack these small asperities, but usually have instead two longitudinal rows of larger tubercles running the entire length of the center of the throat.

The females are larger than the males (see Table 8). Of the specimens included in the table, all males over 23.8 mm., with one exception, had the secondary sex characters developed. The exceptional male measured 27.4 mm. One female containing pigmented eggs measured 32.7 mm. (snout to vent), the only one under 35 mm.

Table 8. Sex dimorphism in snout-vent length in *Ooeidozyga laevis*

	Females			Males		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Mindanao......	14	44.85±1.92	37.2-60.8	11	32.55±1.21	26.8-37.4
Negros.........	25	43.02±1.12	32.7-61.6	25	33.20±0.67	28.1-41.6
Luzon	9	37.49±1.31	32.4-44.5	1	31.8	—
Mindoro........	—	—	—	4	30.08	25.5-32.8
Busuanga......	6	36.28±0.95	31.6-37.8	--	—	—
Culion..........	2	35.45	33.7-37.2	5	29.12±1.27	25.8-31.9
Palawan........	—	—	—	3	29.77	27.4-33.6
Balabac........	7	45.19±0.38	43.5-46.3	2	30.65	27.6-33.7

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes..........	282.80	1	282.80
Within sexes............	113.45	11	10.31
Total......................	396.25	12	

F (1,11) = 27.43; P = 0.01

Reference was made above to certain "exceptional" females. These individuals, all from Negros (CNHM 57195–96, 57201), had the gular asperities normally found in males but lacked the gular tubercles usually found in females. Furthermore, these three specimens had nuptial pads of the same nature as those of males. Internally they had the characteristics of mature females: masses of large pigmented ova and swollen oviducts. I found no testicular material. With regard to size these individuals were definitely "female," varying from 49.1 to 52.6 mm. snout to vent (see Table 8).

A second group of five "females" had masculine characteristics. These individuals had normal ovaries, enlarged oviducts, and, in two cases, large, pigmented ova, with no evident testicular material; but they all had nuptial pads. Four of them were collected in Borneo (CNHM 14301–04) and one in Negros (CNHM 57197). The Bornean specimens ranged from 35.6 to 37.3 mm. in body length; the Negros specimen measured 45.4 mm.

Ecological notes.—Observations of *laevis* in the Philippines (Taylor, 1920) and East India (Mertens, 1930) agree with the field notes of the Philippine Expedition, which stated that this species is only rarely found out of water. The short, heavily muscled legs and complete webbing are certainly more adapted to swimming than to leaping. Taylor refers only to pools as the habitat of *laevis*. However, the Philippine Expedition collected specimens in streams and creeks as well. Mertens states that he collected specimens on Bali from slowly flowing water, rice paddies, and small mud puddles.

The altitudinal distribution of *laevis* in the Philippines extends from sea level to 1,800 meters. The latter elevation is based on a single specimen from Mountain Province, Luzon (Taylor, 1920). The collection of Chicago Natural History Museum from Davao Province, Mindanao, includes 10 from 825 meters and 16 from sea level. The other high altitude records of which I have knowledge are 1,070 meters on the Horns of Negros (CNHM 54060) and 915 to 1,070 meters in the neighborhood of Lake Balinsasayo, Negros Oriental (CNHM 61221–61250).

Inter-island variation.—Geographic variation is most pronounced in coloration. As stated in the description some individuals have mid-dorsal light markings that take the form of a band or a thin line. Table 9, in which band and line are grouped, presents the observed and calculated distribution of the light marks in the various samples.

Chi square computed from this table is 17.01. With 7 degrees of freedom, P equals 0.018, a statistically significant figure, indicating that light-marked individuals were not distributed at random with respect to samples. The samples from Palawan, Culion, and Busuanga are very similar in the proportions of light-marked individuals. One would anticipate this similarity on geologic and geographic bases, but one would also expect the Balabac sample to be included in this natural grouping. If the three similar samples are combined into a "Calamian Group" sample and the chi square test applied to the new contingency table, the degrees of freedom are reduced to 5, chi square to 15.44 and P to slightly less than 0.01, somewhat stronger confirmation of geographic variation.

Table 9. Distribution of Light Mid-Dorsal Marking in Philippine Samples of *Ooeidozyga laevis*

	Observed frequencies			Calculated frequencies	
	With light marks	Without light marks	Total	With light marks	Without light marks
Balabac	0	10	10	2.36	7.64
Palawan	2	2	4	0.95	3.05
Culion	7	12	19	4.48	14.50
Busuanga	4	3	7	1.66	5.35
Mindanao	10	28	38	8.98	29.00
Negros*	6	44	50	11.81	38.20
Mindoro	3	3	6	1.42	4.58
Luzon	3	11	14	3.31	10.68
Total	35	113	148	34.97	113.00

* Only the first 50 individuals removed from the container were used in this and the succeeding table.

There are also indications of inter-island variation in the coloration of the ventral surface of the lower leg. This surface may be uniformly cream (in alcohol) or cream set with dark spots of varying sizes. The distribution of spotted legs in the samples is set forth in Table 10. Chi square computed from this table equals 35.82; with 7 degrees of freedom, P is less than 0.001. As in the case of the mid-dorsal markings, the samples from Busuanga, Culion, and Palawan have similar frequencies, only in this instance the Balabac sample is in agreement with the others. If, then, these four are combined into a "Calamian" sample and the contingency table test is applied, the results are identical to the first test, chi square equaling 34.56 and P again less than 0.001. Thus in this character also there is geographic variation within the Philippines.

Table 10. Distribution of Spotting on Ventral Surface of Leg in Philippine Samples of *Ooeidozyga laevis*

	Observed frequencies			Calculated frequencies	
	With spots	Without spots	Total	With spots	Without spots
Balabac	0	10	10	2.75	7.25
Palawan	0	4	4	1.10	2.90
Culion	2	17	19	5.23	13.77
Busuanga	0	7	7	1.93	5.07
Mindanao	6	30	36	9.91	26.09
Negros	27	20	47	12.94	34.06
Mindoro	2	4	6	1.65	4.35
Luzon	1	8	9	2.48	6.52
Total	38	100	138	37.99	100.01

However, the situation is not as simple as just stated. There is distinct evidence of *intra*-island geographic variation in this character, at least on Negros, and this is hidden by lumping the data from each island; for instance, the Negros sample in the table is divided almost equally between specimens from Dumaguete, on the eastern coast of southern Negros, and from the vicinity of Amio, in the western foothills of the mountains of southern Negros. The following is an analysis of leg spotting in the Negros samples.

	With spotting	Without spotting	Total
Amio	9	16	25
Dumaguete	18	4	22
Total	27	20	47

Applying Yates' correction for small samples and treating the data as a contingency table, one obtains a chi square value of 8.263, which, with one degree of freedom, yields a probability of 0.007. Thus the difference between the Amio and Dumaguete series is statistically significant.

Now suppose only the Amio specimens had been available. Would the results of Table 10 be different? If the four "Calamian" samples are grouped, chi square of such a table would be 11.71, giving P equal to 0.02 with 4 degrees of freedom. If the "Calamian" samples are not grouped, chi square equals 12.57, there are 7 degrees of freedom, and P equals 0.09—not statistically significant. The grouping of the samples from Balabac, Palawan, Culion, and Busuanga is justified, I believe, both because these islands form a natural unit and because the frequencies in these samples are almost identical. Accordingly I conclude that there is inter-island as well as intra-island variation.

The only other sample that can be examined approximately in the same fashion is that from Mindanao. The 36 specimens listed in Table 10 can be broken down as follows:

	With spotting	Without spotting	Total
Agusan	4	1	5
Davao (Mount McKinley)	1	9	10
Davao (Tagum)	1	11	12
Cotabato	0	4	4
Zamboanga	0	5	5
	6	30	36

Chi square=17.23; n=4; P=0.003

Finally, geographic variation is found in snout-vent lengths. The Busuanga and Culion females are handled as a unit ("Calamian") in the following discussion and in Table 11. The data in Table 8 suggest that this treatment has only the effect of increasing the sample size. The mean of this Calamian sample is 36.08±0.78.

Table 8 reveals that the samples of the area from Luzon through Palawan are characterized by smaller snout-vent lengths than are those from Balabac, Mindanao, and Negros. Table 11 presents the statistical comparisons of the samples.

Table 11. Comparison of Snout-Vent Lengths in Samples of *Ooeidozyga laevis* (Means given in Table 8)

	Difference of means	*t*	*n*	P
Mindanao-Negros ♂	0.65	0.507	34	0.61
Mindanao-Negros ♀	1.83	0.887	37	0.38
Negros-Luzon ♀	5.53	2.728	32	0.01
Luzon-Calamian ♀	1.41	0.895	15	0.41
Calamian-Balabac ♀	9.11	10.022	13	0.001
Calamian-Negros ♀	6.94	3.405	31	0.003
Mindanao-Balabac ♀	0.34	0.123	19	0.9

The geographic variation present does not permit taxonomic distinction between these island populations.

Range.—Luzon: Bataan Province (Mariveles, Mount Mariveles [Taylor, 1922b]); Laguna Province (Mount Maquiling [Taylor, 1922b]); City of Manila; Rizal Province (Las Piñas, Philippine University); Mountain Province (Banaue [Taylor, 1920], Kalinga Subprovince [Taylor, 1922b]); Tayabas Province (Mount Banahao [Taylor, 1922b]). Polillo (Taylor, 1922b). Mindoro. Samar (Catarman). Leyte (Taylor, 1920). Panay: Iloilo Province (Ajuy). Siquijor. Negros: Negros Occidental (Hinigaran, Isabella); Negros Oriental (Amio, Canlaon Volcano, Cuernos de Negros, Dumaguete, Lake Balinsasayo, Luzuriaga, Pagyabunan, Pamoat, Sicopon River). Dinagat (Taylor, 1920). Mindanao: Agusan Province (Bunawan); Cotabato Province (Bugasan, Burungkôt near Upi, Conel near Buayan); Davao Province (Mount McKinley, Tagum); City of Zamboanga (San Ramon). Busuanga (Dimaniang). Culion (San Pedro, Siuk). Palawan (Malinao River at Mantaquin Bay, Mauyon, Puerto Princesa). Balabac (Balabac).

Taylor (1920) originally included Sulu Archipelago in the range of *laevis*, but later (1922b) doubted his report because he was unable to find any other reference to its occurrence there or to discover any specimens on Jolo Island.

Outside the Philippine Islands, *O. laevis* is found on Borneo, Java, Sumatra, Celebes, Bali, Sumbawa, and Flores (Mertens, 1930) (fig. 89).

Ooeidozyga diminutiva Taylor

> *Micrixalus diminutiva* Taylor, 1922, Phil. Jour. Sci., **21**: 267, pl. 1, figs. 3–4, pl. 2, figs. 2–3—Pasonanca, Zamboanga, Mindanao; Smith, 1923, Jour. Nat. Hist. Soc. Siam, **6**: 211; Myers, 1942, Proc. Biol. Soc. Washington, **55**: 73.

Material examined.—Mindanao, 1 (CAS); Jolo, 6 (MCZ).

Taxonomic notes.—Both Smith (1923) and Myers (1942) have presented objections to the generic allocation given *diminutiva* by Taylor. Smith called attention to the lack of circummarginal grooves on the digit tips. The digit tips of the species of *Micrixalus* present a uniform, highly specialized pattern (see p. 346). Comparison of the finger tips of *diminutiva* (fig. 45) and *Micrixalus mariae* (fig. 61) will illustrate how great is the divergence of *diminutiva* from *Micrixalus.*

The possibility that *diminutiva* belonged to the genus *Ooeidozyga* was considered and rejected by Taylor (1922b). Taylor specifically pointed to the slightly bifid tongue of *diminutiva,* the "character" of its toes, and the single tooth-like process at the tip of the mandible as excluding the species from *Ooeidozyga.* But *O. lima* has a tongue that is pointed behind and *laevis* one that is rounded. Thus the form of the tongue in *Ooeidozyga* is variable. It is true that Smith (1931) placed *lima* in one genus and the rest of the species of *Ooeidozyga* in another on the basis of tongue shape. However, such fragmentation is objectionable, both because it is based on a single character of unknown significance and because it obscures the natural grouping of related species (as evidenced by larval characteristics, ecology, etc.).

The "character" of the toes does not serve to distinguish *diminutiva.* Slightly swollen toe tips are found in *O. laevis, O. semipalmata* Smith, and *diminutiva;* an incomplete web is found in *semipalmata* and *diminutiva;* and a fringe of skin on the outer side of the fifth toe occurs in *semipalmata* and *diminutiva;* in short, I find no character of the toes of *diminutiva* that prohibits its union with other species of *Ooeidozyga.* As for the process at the tip of the mandible, a similar prominence is to be found in *O. lima.*

My reasons for placing *diminutiva* in *Ooeidozyga* are based on the following characters: the forked omosternum, the absence of vomerine teeth, the fact that the tongue is only slightly bifid instead of deeply notched, the short snout, and the habitus. Considered together these add up to a definite association. Conclusive proof concerning the generic allocation of *diminutiva* must wait upon the discovery of the larva.

Diagnosis.—A small stocky frog (not over 30 mm. in body length); tongue slightly notched; no vomerine teeth; nostrils lateral rather than dorsal; only first and second toes webbed to disks; males with a nuptial pad (see fig. 45) and internal subgular vocal sacs.

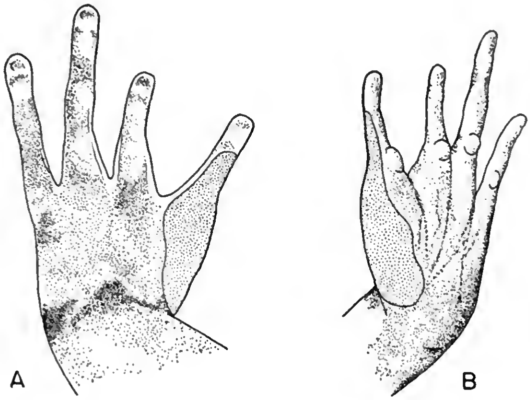


FIG. 45. Dorsal and medio-ventral views of hand of male *Ooeidozyga diminutiva;* × 10.

Description.—Body short, moderately heavy; head slightly longer than broad; snout short, rounded or truncate, scarcely projecting beyond lower jaw; no vomerine teeth; tongue narrow, only slightly notched behind; tympanum completely hidden or only anterior rim visible; a thin dorso-lateral skin fold from eye ending approximately halfway to the groin; a straight skin fold from posterior corner of eye to insertion of arm.

First, second, and fourth fingers equal; third finger longer, equal to length of palm; tips of fingers rounded. Hind leg short; first and second toes broadly webbed to disk on outer side; third toe broadly webbed to distal subarticular tubercle on outer side, fifth toe similarly webbed on inner side, last two phalanges of fourth toe with only a fringe of web; a prominent elongate inner metatarsal tubercle, no outer metatarsal tubercle (although the original de-

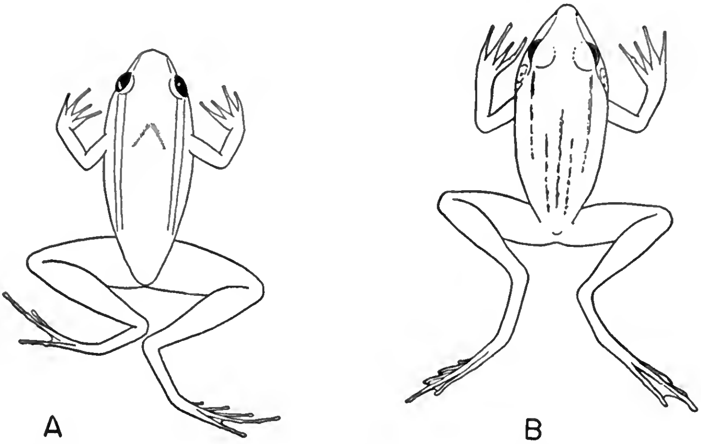


FIG. 46. A, *Rana micrixalus* (× 1); B, *Rana microdisca leytensis* (× 0.7).

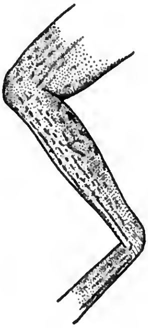


FIG. 47. Lower leg of *Rana erythraea;* × 0.8.

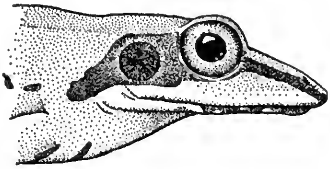


FIG. 48. *Rana sanguinea;* × 1.

scription cites a "very dim" one); a ridge or fold of skin along the outer side of the fifth metatarsal.

Skin of back and head smooth or faintly shagreened; upper eyelid with one or two small pustules; sides with scattered tubercles; gular region smooth in females, with spinules in males; abdominal region smooth.

Color (in alcohol) dark brown on dorsal surfaces with indistinct darker markings; a dark V pointing forward between shoulders; ventral surfaces cream except for gular region, which is uniform brown or cream densely spotted with brown; hind limb with dark crossbars; a light mid-dorsal band or line occasionally present.

Secondary sex characters.—The males have paired subgular vocal sacs the openings of which lie very close to the jaw at the corners of the mouth. A nuptial pad (fig. 45) covers the dorsal and lateral surfaces of the first finger up to the last phalanx. The gular region of the males bears small, uniformly scattered white asperities. Sex dimorphism in size is uncertain; however, the one presumably adult female measures 26.4 mm. snout to vent as compared to an average of 18.6 mm. for four adult males.

Range.—Mindanao: City of Zamboanga (Pasonanca). Basilan (Abungabung [Taylor, 1922b]). Sulu Archipelago: Jolo Island.

Rana Linnaeus

1a.	Tips of toes, or of fingers and toes, with circummarginal grooves (fig. 33)	9
1b.	Tips of digits without such grooves	2
2a.	Tips of toes expanded into disks wider than penultimate phalanges (fig. 51)	4
2b.	Tips of toes blunt or pointed, not wider than penultimate phalanges (fig. 49)	3
3a.	A free flap of skin along outer edge of fifth toe and metatarsal.	*Rana cancrivora cancrivora*
3b.	No flap of skin along fifth toe and metatarsal	*Rana limnocharis vittigera*
4a.	Second and third toes webbed to disk on both sides (fig. 51)	5
4b.	Second and third toes not webbed to disk on both sides	6
5a.	A continuous dorso-lateral fold	*Rana woodworthi*
5b.	No dorso-lateral fold	*Rana macrodon*
6a.	A continuous or partially interrupted dorso-lateral fold	8
6b.	No dorso-lateral fold	7
7a.	Broad web not reaching second subarticular tubercle of fourth toe (fig. 54).	*Rana parva*
7b.	Broad web reaching at least to second subarticular tubercle of fourth toe (fig. 53)	*Rana microdisca*
8a.	Dorso-lateral fold broad (fig. 46, A)	*Rana micrixalus*
8b.	Dorso-lateral fold thin (fig. 46, B)	*Rana microdisca*
9a.	Posterior third of belly coarsely granulate	*Rana everetti*
9b.	Belly without coarse granulation	10
10a.	A distinctly raised dorso-lateral fold	13
10b.	No distinct dorso-lateral fold	11
11a.	Dorso-lateral light lines present (fig. 58, C)	*Rana signata*
11b.	No dorso-lateral light lines	12
12a.	Throat black, with or without small white spots	*Rana melanomenta*
12b.	Throat not black	*Rana signata*
13a.	Lower leg with longitudinal markings (fig. 47)	*Rana erythraea*
13b.	Lower leg without longitudinal markings	14
14a.	A dark, sharply delineated rhomboid temporal spot (fig. 48).	*Rana sanguinea*
14b.	No sharply delineated temporal spot	*Rana nicobariensis*

Rana cancrivora cancrivora Gravenhorst

Rana cancrivora Gravenhorst, 1829, Delic. Mus. Zool. Vratisl., **1**: 41—Java; Boulenger, 1920, Rec. Ind. Mus., **20**: 23; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 170; Smith, 1927, Proc. Zool. Soc. London, **1927**: 205.

Rana cancrivora cancrivora Dunn, 1928, Amer. Mus. Nov., no. 315, p. 5.

Rana tigrina (part) Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 9; Boulenger, 1882, op. cit., p. 25.

Rana moodiei Taylor, 1920, Phil. Jour. Sci., **16**: 234, pl. 1, fig. 5—Manila, Luzon; 1923, op. cit., **22**: 519.

Material examined.—Luzon, 78 (4 CM; 74 USNM); Mindoro, 25 (2 MCZ; 1 USNM; 22 RR); Lubang, 58 (USNM); Tablas, 25 (MCZ); Samar, 1 (CNHM); Leyte, 11 (1 CM; 2 CNHM; 8 USNM); Negros, 33 (8 CAS; 19 CNHM; 6 USNM); Panay, 127 (USNM); Cebu, 1 (USNM); Mactan, 28 (CM); Camiguin, 1 (USNM); Siquijor, 1 (CNHM); Basilan, 2 (CNHM); Mindanao, 28 (CNHM); Cuyo, 25 (CNHM); Culion, 2 (CNHM); Busuanga, 1 (CNHM); Palawan, 29 (CNHM); Borneo, 98 (CNHM); Java, 4 (USNM).

Taxonomic notes.—The Philippine population was described by Taylor as a distinct species. As pointed out by Smith (1927), *moodiei* Taylor can not be distinguished from typical *cancrivora.* The differences between the Luzon frogs and those from the Greater Sundas or between the latter and the Mindanao frogs are not as pronounced as, for example, the differences between Philippine and Greater Sunda *limnocharis.* I do not think that the distinctions are sufficient to designate any Philippine populations of *cancrivora* as a separate subspecies.

Diagnosis.—Medium- to large-sized frog; tips of digits not expanded, without groove separating dorsal and ventral surfaces; dark interorbital bar pointing backward; no enlarged mandibular processes; no outer metatarsal tubercle; a distinct flap of skin on the outer side of the fifth toe and metatarsal; irregular longitudinal skin folds on the back.

Description.—Body stocky; head as broad as or slightly broader than long, snout broadly rounded or obtusely pointed; lores sloping; tympanum distinct, one-half to two-thirds diameter of eye; no dorso-lateral fold; irregular skin folds on back; supratympanic fold present.

First finger longer than second and fourth; third finger about one and one-half times length of palm; tips of fingers blunt, not expanded; fingers without a fringe of skin. Hind limb moderately short, heavily muscled; webbing on outer side of first and inner side of fifth to

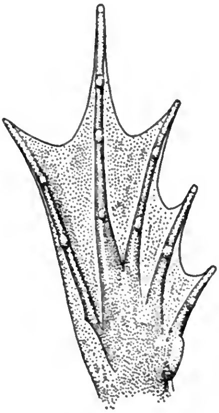


FIG. 49. Ventral view of foot of *Rana cancrivora cancrivora*; × 1.7.

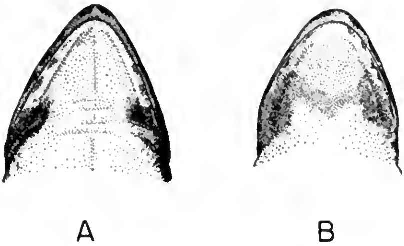


FIG. 50. Ventral view of heads of male (A) *Rana cancrivora cancrivora* (× 1.2) and (B) *R. limnocharis vittigera* (× 1).

tips of toes; webbing to tips on outer side of second and third toes in males, slightly less in females; web reaching slightly beyond middle subarticular tubercle of fourth toe; web usually deeply excised between toes; an elongate inner but no outer metatarsal tubercle; a deep fold of skin along outer side of fifth toe and metatarsal (fig. 49).

Skin between longitudinal folds shagreened; skin of throat and abdomen smooth except in males; occasional individuals with slightly rugose bellies.

Color (in alcohol) gray or brown dorsally with irregular darker markings; ground color of ventral parts cream or pale yellow, immaculate or with dark mottling; lips barred; limbs with dark crossbars or spots.

Secondary sex characters.—The males have median external subgular vocal sacs. The modified skin is limited to the sides of the throat. Approximately co-extensive with the modified skin is a pair of triangular or rectangular black spots (fig. 50, A). Though variable in extent, these marks are never confluent across the throat as in *limnocharis* (see fig. 50, B). The nuptial pad reaches the last phalanx on the median side of the first finger and extends proximally a short distance up the radial border of the arm. As in *limnocharis* (p. 269) the venter in males is covered with small pale asperities. In *limnocharis* the spinules are absent on the throat and mid-line of the belly, but in *cancrivora* they extend down the center of the throat in a narrow band that expands posteriorly to include the

Table 12. Comparison of snout-vent lengths in adult male and female *Rana cancrivora*

	Female			Male		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Luzon..........	23	55.66±1.60	46.1-78.0	19	53.25±1.05	44.8-64.1
Mindoro........	10	73.98±1.18	68.8-79.0	15	60.04±0.92	53.7-65.6
Tablas	11	59.73±1.88	53.4-72.0	13	49.45±0.89	44.5-54.2
Leyte...........	4	68.05	53.4-84.6	5	52.90±2.41	44.7-58.5
Mactan..........	6	59.21±2.54	51.9-69.7	8	49.43±1.07	46.0-53.9
Negros..........	10	65.55±1.22	58.8-70.6	7	60.90±3.00	52.3-74.9
Panay	23	66.41±1.99	51.8-88.1	24	56.23±0.68	49.6-63.4
Cuyo	9	67.17±3.03	55.7-81.6	12	56.38±1.53	49.7-64.8
Palawan	9	64.66±2.09	56.6-74.0	16	58.99±0.73	54.7-66.2
Mindanao......	11	61.50±1.93	51.0-72.3	9	55.37±1.56	49.2-62.0
Borneo.........	16	68.00±2.42	48.6-82.0	25	58.75±0.84	52.0-70.9

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes..........	426.40	1	426.40
Within sexes.............	447.57	20	22.37
Total......................	873.97		

$F(1,20) = 19.054;\ P = <0.01$

entire width of the abdomen immediately behind the arms. The asperities are of uniform density all over the abdomen posterior to the axillae.

The throat spot, the nuptial pad, and the spinules apparently undergo regression between successive breeding seasons. Of eight adult males from Dumaguete, Negros, collected November 25, only two had nuptial pads. The same two had faintly indicated throat spots. None of the eight had the ventral spinules. Much the same picture is obtained from thirteen male *cancrivora* from Tablas Island, collected in January and February. Only two individuals had fully developed nuptial pads and throat spots. Two others had these structures barely detectable. None of nine males collected in December on Mactan Island had pads or throat markings. On the other hand, males collected between the end of March and the end of July from various other Philippine Islands had the secondary sex characters well developed.

Sex dimorphism is also shown by snout-vent lengths, the females being larger. The smallest adult female (from Luzon) measured 46.1 mm. and the largest 88.1 (from Panay). The smallest adult male measured 44.5 mm. (from Leyte) and the largest 74.9 (from Negros). Table 12 summarizes the data. It is apparent from the analysis of variance that the difference between the sexes is statistically significant.

No sex dimorphism was observed in body proportions.

Ecological notes.—*Rana cancrivora* seldom leaves the vicinity of standing or very slowly moving water. Practically all Philippine specimens for which I have habitat data were found in ditches, rice fields, ponds or swamps. This is in agreement with Mertens' findings (1930) in the Lesser Sundas. The most remarkable habitat in which *cancrivora* occurs is brackish water (Boulenger, 1920; Mertens, 1930; Pearse, 1911; field notes, Philippine Zoological Expedition). Annandale (*in* Boulenger, 1920) has even seen a specimen leap into the sea and swim to shore apparently unaffected. Pearse (1911) made observations indicating that the tadpoles of *cancrivora* are able to live in water that has a salt content of 2.6 per cent by weight (sea water 3.5 per cent). The capacity to withstand salty water is of obvious advantage to an animal inhabiting an archipelago and, in the case of *cancrivora,* may be a partial explanation of its wide range.

The altitudinal distribution of *cancrivora* is limited. In the Philippines it is not known to occur higher than 150 meters above sea level. Mertens (1930) found a few specimens as high as 500 meters in the Lesser Sundas.

Inter-island variation.—Geographic variation in Philippine *cancrivora* was found in size, in body proportions, and in coloration. Among the females, those from Mindoro had the largest average size and those from Luzon the smallest. Of the males, the largest mean was found in those from Negros and Mindoro and the smallest in those from Tablas and Mactan (see Table 12). Statistical evaluation of the differences between successive samples is presented in Table 13; only those pairs in which at least one sex showed statistically significant differences are listed. Inter-island differences were also found in the ratios of head width to snout-vent and lower leg length to snout-vent. Statistical analyses of the data of these ratios are also given in Table 13; only those differences approaching or attaining a significant level are listed.

The lower leg in *c. cancrivora* has from three to five dark crossbars or bands. Of the material examined only one specimen from Panay and several from Borneo had five bands. Only one specimen from Palawan and one from Borneo had three bands. The data are summarized in Table 13, with only the statistically significant differences listed.

Table 13. Geographic variation in size, body proportions and banding of lower leg in Philippine samples of *Rana cancrivora cancrivora*

Snout-vent length[1]

	Males				Females			
	Difference of means	*t*	*n*	P	Difference of means	*t*	*n*	P
Luzon—Mindoro	6.79	4.714	32	<0.001	18.32	7.138	31	<0.001
Luzon—Tablas	3.80	2.573	30	0.02	4.07	1.484	31	0.16
Mindoro—Panay	3.81	3.402	37	0.003	7.57	2.403	31	0.02
Mindoro—Tablas	10.59	8.190	26	<0.001	14.25	6.280	18	<0.001
Mindoro—Cuyo.........	3.66	2.140	25	0.04	6.81	2.183	17	0.05
Mindoro—Palawan	1.05	0.898	29	0.38	9.32	3.981	17	<0.001
Tablas—Panay	6.78	6.000	35	<0.001	6.68	2.024	31	0.05
Panay—Negros	4.67	2.323	29	0.03	0.86	0.273	31	0.78
Panay—Palawan	2.76	2.706	38	0.01	1.75	0.506	30	0.62
Negros—Mactan	11.47	3.798	13	0.004	6.34	2.536	14	0.03
Mactan—Mindanao	5.94	3.061	15	0.009	1.29	0.401	15	0.70
Mindanao—Borneo	3.38	2.012	32	0.05	6.50	1.951	25	0.07
Palawan—Mindanao..	3.62	2.386	23	0.03	3.16	1.108	18	0.29

[1] Means and their standard errors as well as total observed ranges are listed in Table 12.

Head width/snout-vent

(Sexes combined)

	No.	Mean±SE	Range		No.	Mean±SE	Range
Luzon......	42	0.357±.002	0.321-0.379	Panay......	44	0.354±0.003	0.320-0.396
Mindoro....	26	0.336±.003	0.308-0.390	Negros.....	17	0.357±0.004	0.332-0-394
Tablas.....	24	0.359±.002	0.339-4.387	Mactan.....	17	0.345±0.002	0.328-0.364
Palawan...	24	0.362±.003	0.336-0.405	Leyte	9	0.352±0.003	0.338-0.362
Borneo.....	41	0.330±.002	0.302-0.366	Mindanao..	21	0.348±0.003	0.324-0.374
Cuyo	21	0.348±.004	0.315-0.383				

	Difference of means	*t*	*n*	P
Luzon-Mindoro	0.021	6.024	66	<0.001
Mindoro-Panay	0.018	4.251	68	<0.001
Mindoro—Tablas	0.023	5.761	48	<0.001
Mindoro—Cuyo........	0.012	2.491	45	0.02
Mindoro—Palawan ...	0.026	5.694	48	<0.001
Negros—Mactan	0.012	2.605	32	0.015
Mindanao—Borneo ...	0.018	4.954	60	<0.001
Palawan—Borneo	0.032	8.540	63	<0.001
Palawan—Cuyo	0.014	2.863	43	0.009
Palawan—Mindanao..	0.014	3.131	43	0.005

Table 13. Geographic variation in size, body proportions and banding of lower leg in Philippine samples of *Rana c. cancrivora (continued)*

Lower leg/snout-vent

(Sexes combined)

	No.	Mean±SE	Range
Luzon	38	0.459±0.003	0.398-0.484
Mindoro	26	0.446±0.003	0.403-0.477
Tablas	24	0.434±0.004	0.399-0.472
Palawan	25	0.460±0.004	0.396-0.487
Borneo	37	0.451±0.002	0.423-0.486
Cuyo	20	0.436±0.004	0.402-0.475
Panay	47	0.450±0.003	0.418-0.502
Negros	17	0.472±0.005	0.436-0.505
Mactan	17	0.472±0.004	0.449-0.506
Leyte	9	0.456±0.005	0.431-0.475
Mindanao	21	0.430±0.005	0.403-0.484

	Difference of means	*t*	*n*	P
Luzon—Mindoro	0.013	2.847	62	0.008
Luzon—Tablas	0.025	4.973	60	< 0.001
Mindoro—Tablas	0.012	2.298	48	0.03
Mindoro—Palawan ...	0.014	2.868	49	0.008
Tablas—Panay	0.016	3.203	69	0.003
Panay—Cuyo	0.014	2.717	65	0.009
Panay—Palawan	0.010	2.019	70	0.05
Panay—Negros	0.022	3.806	62	0.001
Negros—Mindanao ...	0.042	5.722	36	< 0.001
Mactan—Leyte	0.016	2.519	24	0.02
Mactan—Mindanao ...	0.042	6.476	36	< 0.001
Mindanao—Leyte	0.026	3.122	28	0.006
Mindanao—Borneo ...	0.021	4.364	56	< 0.001
Palawan—Borneo	0.009	2.065	60	0.04
Palawan—Cuyo	0.024	4.114	43	< 0.001
Palawan—Mindanao..	0.030	4.699	44	< 0.001

Banding of lower leg

	No.[1]	Mean±SE	No. of bands				No.	Mean±SE	No. of bands		
			3	4	5				3	4	5
Luzon.....	71	3.6±0.06	27	46	0	Panay.........	72	3.7±0.06	23	47	2
Mindoro...	46	3.3±0.07	33	13	0	Negros........	35	3.4±0.08	20	15	0
Tablas....	42	3.2±0.07	32	10	0	Mactan........	42	3.6±0.08	17	25	0
Palawan..	31	4.0±0.03	1	30	0	Leyte	18	3.3±0.11	12	6	0
Borneo....	76	4.2±0.05	1	62	13	Mindanao.....	42	3.5±0.08	21	21	0

[1] Legs rather than individuals. In a few instances one leg had faded to such an extent that the count could not be made.

	Chi Square	*n*	P		Chi Square	*n*	P
Luzon—Mindoro.......	12.69	1	< 0.001	Panay—Negros........	13.53	2	0.001
Luzon—Tablas........	15.41	1	< 0.001	Panay—Palawan......	6.44	2	0.03
Luzon—Leyte	4.79	1	0.03	Mindanao—Borneo....	45.50	2	< 0.001
Mindoro—Panay.......	28.23	2	< 0.001	Palawan—Borneo.....	6.33	2	0.04
Mindoro—Palawan....	35.24	1	< 0.001	Palawan—Mindanao..	18.18	1	< 0.001
Tablas—Panay........	31.34	2	< 0.001				

Table 14 summarizes the inter-island differences for the above four characters. Two features brought out in this table are of interest: (1) the populations do not fall into obvious groups on the basis of the characters; (2) the Mindoro population exhibits the greatest amount of divergence from neighboring samples. The Leyte population, on the other hand, shows the least amount of divergence.

Table 14. Summary of Inter-Island Differences in Samples of *Rana c. cancrivora*
+, significant difference; ○, difference not significant; –, no information

	Snout-vent ♂	Snout-vent ♀	Head width ratio	Lower leg ratio	Banding of lower leg
Luzon-Mindoro	+	+	+	+	+
Luzon-Tablas	+	○	○	+	+
Luzon-Leyte	○	–	○	○	+
Mindoro-Panay	+	+	+	○	+
Mindoro-Tablas	+	+	+	+	○
Mindoro-Cuyo	+	+	+	○	–
Mindoro-Palawan	○	+	+	+	+
Tablas-Panay	+	+	○	+	+
Panay-Cuyo	○	○	○	+	–
Panay-Palawan	+	○	○	+	+
Panay-Negros	+	○	○	+	+
Negros-Mactan	+	+	+	○	○
Negros-Mindanao	○	○	○	+	○
Mactan-Leyte	○	–	○	+	○
Mactan-Mindanao	+	○	○	+	○
Mindanao-Leyte	○	–	○	+	○
Mindanao-Borneo	+	○	+	+	+
Palawan-Borneo	○	○	+	+	+
Palawan-Cuyo	○	○	+	+	–
Palawan-Mindanao	+	○	+	+	+

Range.—Luzon: Laguna Province (Molawin Creek [Taylor, 1922c]); City of Manila (Manila); Rizal Province (Las Piñas). Lubang. Mindoro (San José, Sumagui). Tablas (Odiongan). Samar (Catarman). Leyte (Carigara, Inayupan near Abuyog, Tacloban, Tarragona). Mactan. Cebu (Río Kotkot). Negros: Negros Oriental (Dumaguete). Panay: City of Iloilo (Iloilo); Iloilo Province (Ajuy). Cuyo. Busuanga (Dimaniang). Culion (San Pedro). Palawan (Brooke's Point, Puerto Princesa). Camiguin (Mahinog). Siquijor. Mindanao: Agusan Province (Cabadbaran); City of Davao (Davao); Misamis Occidental (Bonifacio); Misamis Oriental (Cagayan); City of Zamboanga (Zamboanga); Zamboanga Province (Katipunan). Basilan.

Outside the Philippine Islands, *c. cancrivora* is known from the Lesser Sundas as far east as Flores (Dunn, 1928), and from Java, Sumatra, Borneo, and the Malay Peninsula.

Rana limnocharis vittigera Wiegmann

Rana limnocharis Boie *in* Wiegmann, 1835, Nova Acta Acad. Leop. Carol., **17**, pt. 1, p. 255—Java; Boulenger, 1920, Rec. Ind. Mus., **20**: 28; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 167, fig. 23.

Rana vittigera Wiegmann, 1835, Nova Acta Acad. Leop. Carol., **17**, pt. 1, p. 255, pl. 21, fig. 1—Laguna de Bay, Luzon; Taylor, 1920, Phil. Jour. Sci., **16**: 236, pl. 2, fig. 3; 1923, op. cit., **22**: 518; Smith, 1927, Proc. Zool. Soc. London, **1927**: 207.

Rana cancrivora (part) Boulenger, 1920, Rec. Ind. Mus., **20**: 23.

Material examined.—Luzon, 97 (32 CM; 20 CNHM; 9 RR; 36 USNM); Mindanao, 62 (CNHM); Palawan, 65 (CNHM); Borneo, 13 (MCZ); Java, 48 (7 MCZ; 41 USNM).

Taxonomic notes.—There can be no doubt of the close relationship of this Philippine frog to Asiatic and East Indian *limnocharis*. The remarkable similarities in the secondary sex characters, even down to such details as the distribution of the white spinules of the male venter, prohibit consideration of the Philippine frogs as a distinct species. The agreement in habitus, webbing, and ecological relations emphasize the essential identity. There are, however, some minor differences between Philippine and non-Philippine *limnocharis*. Taylor (1923) points out that Philippine specimens do not have an outer metatarsal tubercle, which is present in individuals from other parts of the range. Also, Philippine specimens do not have a ridge of skin bordering the fifth metatarsal as do most non-Philippine *limnocharis*, and the Philippine frogs attain a much larger size. On the basis of these differences, the Philippine form should be recognized as a subspecies for which Wiegmann's name, *vittigera*, is available.

From time to time questions have arisen concerning the name *limnocharis*. The name has been credited to Wiegmann, to Boie *in* Wiegmann, or to Kuhl *in* Gravenhorst. Schlegel (1826, Isis, **20**: 281–295) supplies the following information: Kuhl and van Hasselt made their Javanese collections under the direction of the Netherlands Museum. Their specimens were turned over to Heinrich Boie, who was to include the descriptions of new species in his projected Herpetology of Java. Schlegel indicated that there would be a delay in the publication of Boie's work and that, in the meantime, specimens of Boie's species, under his manuscript names, were being sent to various European museums. Boie was dogged by a series of misfortunes (for some of which see Schlegel, loc. cit.) and his manuscript was never published. The first adequate description of *limnocharis* is found in Wiegmann (1835), who accredited it to Boie. I am indebted to Dr. L. D. Brongersma for the sheet of Boie's longhand manuscript notes, in German, unfortunately in a script no longer readily legible. With the aid of Miss Lenel, of the Newberry Library in Chicago, enough of the description has been deciphered to make it entirely clear that Boie was describing the Javanese frog now known under the name *limnocharis.* I see no reason for regarding this name as a nomen nudum, or for crediting it otherwise than to Boie.

Diagnosis.—Medium- to large-sized frog; tips of digits not expanded; no groove separating dorsal and ventral surfaces of tip of digits; irregular longitudinal skin folds scattered over back; interorbital bar usually pointing backward; no paired enlargements of mandible; no outer metatarsal tubercle; no flap of skin on outer edge of fifth toe and metatarsal; during the breeding season, males with black figure on throat (fig. 50, B).

The only species in the Philippines with which *limnocharis* may be confused is *R. cancrivora,* from which it may be separated by the absence of a flap of skin on the outer side of the fifth metatarsal. Breeding males of these two species are easily distinguished by differences in the black patterns of the throat (fig. 50). The present form differs from *l. limnocharis* by the absence of the outer metatarsal tubercle, by the absence of the ridge of skin on the outer side of the fifth metatarsal, and by its large size.

Description.—Body stocky; head as long as or slightly longer than broad; snout obtusely pointed; tympanum visible, one-half to two-thirds diameter of eye; dorso-lateral fold absent; many irregular, scattered longitudinal skin folds on dorsum; supratympanic skin fold present.

First finger longer than second and fourth; third finger one and one-half times length of palm; tips of fingers not expanded; fingers without distinct fringe of skin. Hind limb moderately long, heavily muscled; webbing to tips of first and second toes on outer side, short of tips on outer side of third, and inner side of second, third, and fifth; web reaching last subarticular tubercle of fourth toe as narrow membrane; web between third and fifth toes excised to level of second subarticular tubercle of fourth toe; an oval inner but no outer metatarsal tubercle; no flap of skin on outer side of fifth metatarsal.

Skin between folds of back smooth, occasionally with very small pustules; skin of ventral regions smooth except for wrinkles posteriorly in some individuals; skin of throat of males modified, at least during breeding season.

Color (in alcohol) gray above with a black interorbital bar pointing backward and with variously shaped black spots scattered over the back; usually a W-shaped mark across the back between the arms; a dark loreal streak; a black tympanic spot; lips barred with black; throat of females usually immaculate cream, some specimens with brown spots; throats of males black; entire abdomen of both sexes immaculate cream; limbs with dark crossbars dorsally. Some individuals with a light mid-dorsal band or line and with a light longitudinal line on inner edge of calf.

Secondary sex characters.—Males of *limnocharis* have a median external subgular vocal sac. The skin of the entire throat is modified, although in a few cases the modified skin is limited to the sides of the throat. A distinctive feature of the males is the black M-shaped gular mark that is roughly coincident with the modified skin (fig. 50, B). The nuptial pad, at least in Philippine specimens, is limited to the first finger and extends on the dorso-median edge of the finger to the distal end of the penultimate phalanx.

One character of these males that has apparently escaped notice thus far is the presence of white spinules in large numbers on the ventral surface. These structures are most dense on the chin anterior to the black gular mark and in two transversely elongated ovals between the arms. Posterior to this level they are present laterally in reduced density and are almost absent in the mid-line of the belly. There are no spinules on the skin covering the vocal sac. Similar concentrations are found in males from various parts of China and the Riukiu Islands. A few of these spinules are present around the insertion of the arms in some females. Similar structures are present in the males of *R. cancrivora,* but in that species the distribution of the spinules is different (see p. 261).

The male secondary sex characters mentioned thus far seem to be evident only during the breeding season. None of twelve mature males from Las Piñas, Rizal Province, Luzon, collected at the end of November show the secondary sex characters. Yet all males collected within 25 miles of Las Piñas in the months of July, August, and September have these structures fully developed. Taylor (1920) states that the breeding in this section of Luzon begins around the first of July. Mertens (1930) reports analogous results from his investigations in the Lesser Sunda Islands. From March to July he found no males with well-developed sexual characters; the first males with indications of the secondary sex characters were found in August. The breeding season in the Lesser Sundas is initiated with the rainy season in September or October.

The sexes also differ in body length, the females being larger (see Table 15). This relationship holds true over most parts of the range (Inger, 1947).

Table 15. Sexual Dimorphism in Size of Adult *Rana limnocharis vittigera*

	No.	Mean±SE	Range	Difference of means	*t*	*n*	P
Luzon ♀	25	54.22±1.96	39.8–75.1	3.74	1.651	48	0.11
Luzon ♂	25	50.48±1.14	37.3–60.1				
Palawan ♀	24	55.69±1.41	38.8–69.9	6.27	3.212	45	0.004
Palawan ♂	23	49.42±1.35	39.2–66.6				
Mindanao ♀	17	68.11±2.65	48.5–80.6	8.74	3.494	40	0.001
Mindanao ♂	25	59.37±1.01	48.2–66.1				

Although the difference in the Luzon sample is not statistically significant, the relationship is the same as in other samples. I found no consistent sex dimorphism in body proportions.

Ecological notes.—*Rana limnocharis* is the common frog of the rice fields of southern and eastern Asia. In the Philippines it is associated primarily with quiet water in rice fields, ditches, and ponds, although it may also be found around streams. The frogs collected by the Philippine Expedition showed the following relation to current: standing water (swamp or rice field), Mindanao 34, Palawan 39, Luzon 8; moving water (stream, creek, or river), Mindanao 13, Palawan 26, Luzon 0. Mertens (1930) states that *limnocharis* may wander some distance from water, unlike *cancrivora.* Only one specimen was collected away from the vicinity of water by the Philippine Expedition.

The altitudinal distribution of *limnocharis* is apparently restricted in the Philippines; for example, on Mindanao and Palawan the Philippine Expedition collected 135 specimens—all from elevations below 150 meters. All Luzon records known to me with one exception are from below 150 meters. It would appear that on Luzon also *limnocharis* is found only at very low elevations. However, the one exceptional record of eight specimens from Abra Province at 610 meters indicates that the apparent restriction of altitudinal range may be due to inadequate collecting. The collections made by the Philippine Expedition in the mountains of Mindanao shed some light on this question. Only eighty-two frogs of four species of *Rana* were caught above 305 meters. No *limnocharis* was found even though more than half of the eighty-two belong to species (*macrodon* and *microdisca*) showing habitat overlap with *limnocharis* at lower elevations. Thus on Mindanao, at least, there is good evidence that *limnocharis* is very rare above 150 meters. Mertens (1930) found *limnocharis* as high as 900 meters on Bali and up to 500 meters on Lombok. Pope (1931) records this species up to 1,200 meters in Fukien, China. The last height may be attained only by virtue of the suitable habitats produced by rice culture.

The collections of Chicago Natural History Museum hint at an interesting problem in the ecological relationship of *limnocharis vittigera* and *cancrivora*.

In the following chart are listed the localities that yielded more than three specimens of either *cancrivora* or *limnocharis* and the number of individuals of each species from particular habitat types.

	cancrivora	*limnocharis*
Palawan:		
Puerto Princesa	3 flowing water	26 flowing water 38 standing water
Brooke's Point	26 standing water	0
Cuyo Islands	25 (unknown habitat)	0
Mindanao:		
Misamis Oriental	10 standing water	0
Davao Province; Maco	0	23 standing water 4 unknown habitat
Davao Province; Madaum	0	11 standing water 12 flowing water 9 unknown habitat

All of the specimens listed were collected by the Philippine Expedition. It is obvious that one species or the other predominated in any given locality; indeed, with the one exception of Puerto Princesa, where one form was found the other was absent. The partial isolation was evidently not due to the type of habitat, nor was it due to the season, for all the collections of these species from Palawan were made during the last two weeks of April and the first week of May, 1947.

Isolation of this type was not observed by Taylor (1920) on Luzon. Taylor states that he found both species breeding in the same pools. Nevertheless, data such as are presented above indicate the possibility of strong competition between these closely related forms. Of course, much field work is needed before confidence can be placed in this hypothesis.

Inter-island variation.—In typical *limnocharis* the fifth metatarsal bears a flap or a prominently raised ridge of skin on its outer edge. There may be variation between these two conditions within a small population. However, in *limnocharis vittigera* there is only a light line marking the position of these dermal structures.

A small outer metatarsal tubercle is present in various degrees of development in *limnocharis limnocharis.* On the Asiatic mainland the tubercle is almost invariably prominently raised. In the East Indies, however, it may not be quite so prominent; nevertheless, it is present. The only indication of the tubercle in *limnocharis vittigera* is a light spot at the base of the fifth metatarsal in some individuals.

As has been indicated above, *limnocharis vittigera* attains a larger size than the typical form. The mean body length of twenty-five males from Java (type locality of *limnocharis limnocharis* Boie) is 34.8±0.40 mm. This is close to the figures for males from Indo-China (36.4), Szechwan (37.6), and Okinawa, Riukiu Islands (39.1) (see Inger, 1947). Seven males from Borneo average 41.3±1.22 mm. The difference between the two extremes (Java and Borneo) is less than the difference between the Borneo sample mean and the smallest mean of a Philippine sample (Palawan, 49.4±1.35 mm.). The maximum size of twenty-five males selected by Boulenger (1920) from various points in the range was 51 mm. This maximum is scarcely larger than the mean of the Palawan and Luzon males (Table 15) and is smaller than the mean of the Mindanao males. The same picture is obtained from an examination of the females. The maximum of fifty-five females given by Boulenger is 67 mm. This length is exceeded by 25 per cent of the Philippine females examined.

Within the Philippines, there is some variation in adult body length. As may be seen by consulting Tables 15 and 16 the Mindanao frogs exceed the others in length considerably. The Palawan and Luzon populations reach approximately the same body length.

One of the outstanding variables of *limnocharis* is the mid-dorsal color. Some individuals have a light vertebral line such as is found occasionally in other species of frogs. In addition to the line, some specimens of *limnocharis* have a light band or stripe of varying width either superposed on the line or alone. These two light marks either singly or in combination are found in various frequencies over the entire range of the species. In the East Indies and Philippine Islands only, a light line is found on the inner edge of the lower leg. The frequency of this character also varies from island to island. Of genetic significance is the fact that the lower leg line occurs only in combination with one or the other of the mid-dorsal variants. However, this is not to say that the leg line occurs in every individual with a mid-dorsal light mark.

Table 16. Inter-Island Variation in Size of *Rana limnocharis*

	Males				Females			
	Difference of means*	t	n	P	Difference of means	t	n	P
Luzon–Mindanao....	8.89	5.841	48	<0.001	13.89	4.302	40	<0.001
Luzon–Palawan.....	1.06	0.605	46	0.55	1.47	0.603	47	0.55
Mindanao–Palawan..	9.95	5.984	46	<0.001	12.42	4.447	39	<0.001
Palawan–Borneo.....	8.12	3.206	28	0.006				

*Borneo (males) mean=41.3±1.22; range=35.4–44.3; no.=7. Means of other samples in Table 15.

Mertens (1930) presents information on the frequency of these light markings in *limnocharis* from the Lesser Sunda Islands. Table 17 sets forth the frequency data of the mid-dorsal markings for the Philippine samples examined.

Table 17. Inter-Island Variation in Frequency of Mid-Dorsal Light Markings in *Rana limnocharis vittigera*

	No light markings	Mid-dorsal markings			
		Line	Band	Band and line	Total
Mindanao.........	23	21	4	11	59
Luzon.............	42	27	18	10	97
Palawan...........	37	15	2	5	59
Total.........	102	63	24	26	215

In testing to determine whether the distribution is the same in all three samples, a chi square value of 17.16 is obtained. With 6 degrees of freedom this value lies below P=0.01; hence the samples have significantly different distributions.

The lower leg line appears in 33 of the specimens from Mindanao, 48 of those from Luzon and 21 of those from Palawan. Apparently the frequency of the line does not vary significantly within these samples when the same type of test is used (chi square 5.20; 2 degrees of freedom; P greater than 0.05).

Range.—Polillo (Taylor, 1920). Luzon: Abra Province (Licuan); Bataan Province (Mariveles); Laguna Province (Mount Maquiling [Taylor, 1922c]); City of Manila; Nueva Vizcaya Province (Bayombong); Pangasinan Province (Umingan); Rizal Province (Barras, Las Piñas); Laguna de Bay (Wiegmann, 1835). Mindoro (Taylor, 1920). Negros (Taylor, 1920). Mindanao: City of Davao; Davao Province (Maco, Madaum, Sitio Taglawig). Palawan (Iwahig, Puerto Princesa) (fig. 88).

The absence of *limnocharis vittigera* from the other larger islands would seem to be apparent rather than real if one judged by its great abundance and extended range in the Greater Sunda Islands and southeastern Asia. However, as noted above (p. 271), there are hints of strong competition or other ecological relationship promoting isolation of *limnocharis vittigera* from *cancrivora.* This relationship may account for the failure of collectors to discover *vittigera* on Leyte, Panay, and other islands in the Philippines.

Rana woodworthi Taylor

Rana woodworthi Taylor, 1923, Phil. Jour. Sci., **22**: 519, pl. 1, figs. 1–2—Los Baños, Laguna Province, Luzon; 1922, Phil. Agriculturist, **9**: 129.

Material examined.—Polillo, 19 (7 CM; 2 MCZ, paratypes; 9 UMMZ; 1 USNM).

Taxonomic notes.—The relations of *woodworthi* are discussed below (p. 292).

Diagnosis.—Large frogs with round, slightly expanded digit tips that lack circummarginal grooves; terminal disks of toes with a dorsal groove; toes completely webbed; a flap of skin on outer edge of fifth toe and metatarsal; a narrow continuous dorso-lateral fold; a pair of bony projections at anterior end of mandible; a dark rhomboidal spot covering entire tympanum.

The complete webbing of the toes and the dark spot covering the tympanum serve to distinguish *woodworthi* from Philippine *microdisca.*

Description.—Body rather stocky; head as broad as long; snout obtusely pointed; tympanum distinct, one-half to two-thirds diameter of eye; a thin dorso-lateral fold present; a strong supratympanic fold from eye to insertion of arm.

Fingers long; tips slightly expanded, without circummarginal grooves; first finger longer than second, usually longer than fourth; third finger approximately twice length of palm; only two subarticular tubercles under third and fourth fingers; a distinct fringe of skin on both sides of second and third fingers. Tips of toes expanded into round disks; disks larger than those of fingers, without circummarginal grooves, with a groove on dorsal surface; all toes, except fourth, webbed to disk on both sides; fourth broadly webbed to distal subarticular tubercle; a distinct flap of skin on outer side of fifth toe and metatarsal; a narrow fringe along first toe; a strong elongate inner but no outer metatarsal tubercle.

Skin of back smooth or shagreened anteriorly, usually with spinules posteriorly; skin of ventral surface smooth.

Color (in alcohol) of back and head dark brown; a darker loreal streak and a rhomboidal temporal spot completely covering the tympanum; lips barred; venter cream or pale brown, the gular region usually mottled with darker brown; limbs with irregular spots or crossbars.

Secondary sex characters.—As in *microdisca* the males have paired internal vocal sacs that extend backward beyond the edge of the subhyoideus muscle at the sides of the throat. The openings are at the corners of the mouth. The males do not have humeral glands, nuptial pads, or distinctive asperities. Although the opinion is based on only four adults of each sex, there seems to be dimorphism in body length. Females 59.7–66.5 mm. (mean 63.9), males 42.8–60.2 mm. (mean 53.3).

Ecological notes.—Taylor (1922c) found *woodworthi* to be very common "along the mountain streams at low elevation." He also collected many specimens about stagnant pools of dry stream beds. The heavily muscled legs and extensive web indicate that *woodworthi* is a strong swimmer.

Range.—Polillo. Luzon: Laguna Province (Los Baños, Mount Maquiling [Taylor, 1923]).

Rana macrodon Duméril and Bibron

Taxonomic notes.—The populations considered to belong to this species, in addition to *macrodon* of the Malay Peninsula and the Sunda Islands, are *grunniens* Daudin of Celebes, and the Philippine frogs referred to by various authors as *magna*, *acanthi*, *macrodon*, and *modesta*. Several secondary sex characters are diagnostic of this complex of populations: The posterior portion of the head is enlarged in males, a development involving both a widening and a lengthening of the head behind the eyes; a pair of fleshy swellings is present on the occipital region of the males; and the pair of bony processes at the front of the mandible is almost twice as long in males as in females. The males do not have nuptial pads.

Other than these structures all members of the group have the toes completely webbed to the round disks and a conspicuous flap of skin along the outer side of the fifth toe and metatarsal. An elongate inner but no outer metatarsal tubercle is present. The tips of the fingers are slightly but distinctly enlarged into round disks. The body is stocky. There are no dorso-lateral folds of skin.

The largest form, *macrodon* (over 150 mm. in body length), is found in the Malay Peninsula and the Sunda Islands. The males are without vocal sacs. The snout is rather long when compared to the other forms. In large mature individuals the skin of the back is smooth. A large dark W-shaped mark is present on the back between the arms. Occasional individuals have a cream-colored mid-dorsal line or band and, less frequently, a light line on the lower leg.

Although no specimens were available for examination, a study of the literature reveals that *grunniens*, which is found on Celebes and New Guinea, is very similar to *macrodon*. Actually van Kampen (1923) states that it differs from the latter only by the shorter limbs. This form also reaches a body length of 150 mm. The males are without vocal sacs.

The Philippine form most closely related morphologically to *macrodon* appears to be the one occurring on the Calamian Islands. This form, *acanthi*, has the dark W on the back. Occasional individuals have a light vertebral marking as observed in *macrodon*, but the line on the leg does not appear. The skin of the back in mature specimens has elongate ridges and round tubercles. Adults rarely exceed 80 mm. snout to vent. A sharp distinction from *macrodon* is the presence of a pair of widely separated vocal sacs in males of *acanthi*. The snout is not as elongate as in *macrodon*.

Males of the Visayan sample have the same type of vocal sacs as *acanthi*. The body length is relatively small, only rarely exceeding 85 mm. The shape of the head and snout is as found in *acanthi*. The back is usually tuberculate. However, the populations of these islands differ from those of the Calamians in lacking the light mid-dorsal stripe and the dark W of the back, as well as in some body proportions.

The specimens from Balabac, Palawan, Culion, and Busuanga are referred to collectively in the foregoing discussion as the Calamian sample. Those from Panay, Negros, Bohol, Leyte, and Siquijor are referred to as the Visayan sample. The over-all similarity of the frogs within each of these samples is sufficient to warrant this treatment, which has the advantage of providing samples large enough for reliable statistical comparison.

The Luzon population is characterized by the large size attained by the individuals (frequently in excess of 100 mm.). As in *acanthi* the males have widely separated internal vocal sacs. This population differs from both *acanthi* and *macrodon* in not having either the W on the back or the light vertebral stripe. A light line is never present on the leg. Large specimens almost always have a rough skin, but only round tubercles are found. The snout is rather short and rounded.

On Mindanao and Basilan there occurs another large form occasionally attaining a body length of over 120 mm. This form, *magna,* is very similar to the one from Luzon. The vocal sacs, shape of snout, and absence of light mid-dorsal band, lower leg, line, and W on the back all recall the Luzon form. In large specimens, however, the skin on the back is usually smooth and the posterior third of the abdomen is densely spotted with dark brown or black, a condition not predominating in any other population.

Smith (1927) suggested that *magna* Stejneger was a subspecies of *modesta* Boulenger (type locality Celebes). Van Kampen (1923) placed *magna* in the synonymy of *modesta* without assigning the former to subspecies status. Certainly *modesta* Boulenger of Celebes resembles the *macrodon* group, especially young *magna,* in many characters. But *modesta* also closely resembles *Rana microdisca.* Unfortunately, not enough material of *modesta* was available (type series examined in the British Museum) to determine the presence of sex dimorphism in head proportions. Statistical analysis of these proportions will be necessary before the relationships of *modesta* Boulenger can be determined.

As indicated, the species *macrodon* is treated here as polytypic, including as subspecies *m. macrodon* Duméril and Bibron, *m. grunniens* Daudin, *m. magna* Stejneger, *m. acanthi* Taylor, another subspecies from Luzon, and one from the Visayas described below. If future investigations demonstrate that *modesta* Boulenger is as closely related to *magna* as *acanthi* is to *macrodon* and that *modesta* Boulenger is distinct from *grunniens,* two subspecies of *macrodon* (as here understood) will occur on Celebes. Other examples of two subspecies of a single polytypic species occupying the same area are known among vertebrates (see Mayr, 1942).

Diagnosis.—Large frogs with round expanded digit tips that lack a groove separating dorsal and ventral surfaces; toes fully webbed (see fig. 51); a flap of skin on outer edge of fifth toe and metatarsal; a narrow fringe of skin on both sides of second and third

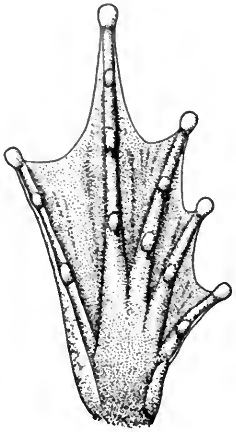
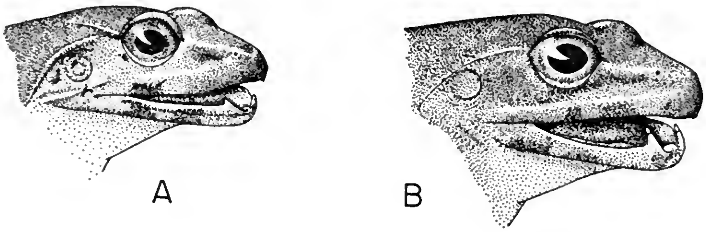


FIG. 51. Foot of *Rana macrodon;* × 1.

FIG. 52. Heads of female (A) and male (B) *Rana macrodon magna;* × 0.7. Compare eye–nostril distance with eye–tympanum.



fingers; no continuous dorso-lateral fold; a pair of bony projections at anterior end of mandible; projections larger in males than in females; males with internal vocal sacs.

Description.—Body stocky to very heavy; head large, in larger males much broader than long; snout rounded or obtusely pointed; a pair of bony projections at front of mandible; tympanum visible, two-fifths to four-fifths diameter of eye; supratympanic fold from eye to insertion of arm present; no dorso-lateral fold.

First finger longer than second; third finger less than twice the length of palm; tips of fingers expanded into distinct round pads that are less than twice the width of penultimate phalanges; second and third fingers with a distinct fringe of skin. Hind leg heavy, moderately long (tibia about one-half body length); all toes except fourth broadly webbed to disk; fourth toe broadly webbed to distal subarticular tubercle; third and fifth toes equal in length; an elongate inner metatarsal tubercle; no outer metatarsal tubercle; a flap of skin on outer edge of fifth toe and fifth metatarsal and one on inner edge of first toe.

Skin of back smooth or with tubercles; posterior part of back frequently with white spinules; entire ventral surface smooth.

Color (in alcohol) brown to dark slate on dorsal surfaces; lips barred with black; chin and throat cream-colored mottled with brown or black; pectoral and abdominal regions cream, mottled in varying degrees or immaculate; legs irregularly marked with black; soles and palms dark. Juveniles generally without spots on the abdomen and ventral leg surfaces.

Secondary sex characters.—The males of the Philippine forms have paired internal vocal sacs situated at the lateral edges of the throat. The sacs extend beyond the posterior edge of the subhyoideus muscle. The openings are at the posterior corners of the mouth. Nuptial pads and humeral glands are absent. Characteristic of the males of this group is the great enlargement of the bony mandibular processes and of the posterior portions of the head. Two features of the dimorphism in head proportions are outstanding: the distance between the eye and the tympanum relative to snout-vent length is greater in males (fig. 52), as is also the width of the head relative to snout-vent length. These sex differences, which reach a statistically significant level, are analyzed in Table 18.

The heads of large males are further distinguished by a pair of swellings in the occipital region caused by the extremely large temporal muscles. As for the bony mandibular processes it is of interest to note that the fleshy sheath that covers the small projections in females and young males is, in large males (fig. 52), commonly pushed down to the base, thus baring the bone. The exposure of these large processes seems to reflect the wearing away of the sheath by food, which consists of relatively large objects such as crabs and frogs.

Except for the Visayan population there is no significant size difference between the sexes. The females in the Visayan sample are larger than the males, the difference approaching statistical significance (mean of females=78.75 mm.; mean of males=68.69 mm.; t=2.258; n=19; P=0.04). The only sex dimorphism in body proportions is that of the head discussed above.

Ecological notes.—The frogs of this group are rarely found away from the immediate vicinity of water. This relationship to water can be shown by the following tabulation of the situations in which the 152 specimens of the Philippine Expedition were found: In water 69; immediate vicinity of water 64; away from water 7; unknown 12; total 152. "Immediate vicinity of water" includes such

Table 18. Sex dimorphism in head proportions of some samples of *Rana macrodon*

Eye-tympanum/snout-vent

	Males			Females		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Luzon........	15	0.065±0.006	0.014-0.103	11	0.046±0.002	0.035-0.060
Visayan.....	13	0.046±0.004	0.023-0.069	8	0.039±0.005	0.027-0.063
Mindanao....	25	0.059±0.003	0.030-0.084	25	0.037±0.002	0.020-0.055
Calamian....	23	0.040±0.001	0.029-0.051	24	0.032±0.001	0.018-0.048
Borneo.......	8	0.063±0.005	0.038-0.077	13	0.036±0.002	0.029-0.050

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes.............	689	1	689.00
Within sexes...............	591	8	73.88
Total......................	1280	9	

F (1, 8) = 9.33; P = 0.02

Head width/snout-vent

	Males			Females		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Luzon........	15	0.411±0.006	0.362-0.457	12	0.388±0.005	0.369-0.432
Visayan.....	13	0.381±0.005	0.357-0.414	8	0.370±0.005	0.354-0.389
Mindanao....	25	0.390±0.003	0.354-0.419	25	0.378±0.003	0.344-0.408
Calamian....	24	0.387±0.002	0.369-0.408	24	0.375±0.003	0.349-0.403
Borneo.......	9	0.414±0.004	0.400-0.430	14	0.378±0.004	0.354-0.413

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes....	883	1	883
Within sexes.......	1063	8	133
Total.............	1946	9	

F (1, 8) = 6.64; P = 0.04

field notes as "near stream," "near pool," "on the bank of stream," etc. Where no water but other situations were mentioned in the field notes, the specimens were listed "away from water." The relationship of these frogs to the presence or absence of current is shown in the following: In standing water 7; vicinity of standing water 21; total 28. In moving water 62; vicinity of moving water 43; total 105. Specimens associated with "pools," "ponds," or "rice paddies," according to the expedition field notes, are included in "standing water" categories; those associated with "stream," "creek," or "river" are included in "moving water" categories. The association with flowing water is even more pronounced than indicated above, for twenty of the twenty-one frogs listed as in "vicinity of standing water" were found on the edges of pools in dry stream beds. This particular habitat, of course, falls into the "moving water" category during wetter seasons.

The altitudinal distribution of the Philippine forms is extensive. On Mindanao *macrodon magna* was found by the Philippine Expedition from sea level to 855 meters; four specimens were collected at 2,135 meters on Mount Data, Luzon; on Balabac, Palawan, and the Calamian Islands all specimens (95) were collected below 150 meters.

According to Mertens (1930, 1934), in Java, Sumatra, and the Lesser Sunda Islands *macrodon* is primarily a montane form, being abundant at elevations over 400 meters but uncommon below that level. My own field observations in North Borneo indicate that *macrodon* may also be abundant within 100 meters of sea level.

Inter-island variations.—As noted above, this species shows considerable geographic variation. The characters involved include pigmentation, nature of skin, size, body proportions, and vocal sacs. All adult males from the Philippines have vocal sacs; none from the mainland or the Sunda Islands do.

Points of pigmentation that vary in this fashion are the marking of the back, spotting on the posterior part of the abdomen, and spotting on the ventral surface of the lower leg. A dark W-shaped mark occurs on the backs of specimens from Borneo and the Calamians but in no other Philippine specimens. Similarly restricted is a light vertebral line or band, only in this case the marking is not the same in both groups. A thin line is found in some Bornean specimens (4 of 24) and a broad band in the Calamian specimens (16 of 73).

The posterior part of the abdomen is densely spotted with brown or black in two-thirds of the specimens from Mindanao, in about one-fourth of those from Luzon, and in almost no others. The differences between all pairs of samples, except the Luzon-Visayan and Visayan-Calamian ones, reach statistically significant levels (Table 19). The ventral surface of the lower leg is spotted laterally but medially is usually free of dark pigment in specimens from the Visayans, the Calamians, and Borneo; however, this region is spotted in over four-fifths of the specimens from Luzon and Mindanao. Statistical comparison of the populations in these characters is pre-

Table 19. Analysis of some aspects of geographic variation in *Rana macrodon*

Spotting on ventral surface of lower leg

	No.	With spots	Without spots
Luzon	34	28 (82.4%)	6
Visayan	22	2 (9.1%)	20
Mindanao	54	47 (87.0%)	7
Calamian	57	9 (15.8%)	48
Borneo	23	5 (21.7%)	18

	Difference (%) ± SE[1]	Difference/SE	P
Luzon-Visayan	73.3±13.6	5.40	< 0.001
Luzon-Calamian	66.6±10.7	6.22	< 0.001
Visayan-Mindanao	77.9±12.1	6.44	< 0.001
Visayan-Calamian	6.7± 8.7	0.77	0.44
Mindanao-Calamian ...	71.2± 9.6	7.42	< 0.001
Mindanao-Borneo	65.3±11.7	5.58	< 0.001
Calamian-Borneo	5.9± 9.4	0.63	0.53

[1] The following test was carried out for each pair of samples:

	With spots	Without spots	Total
Luzon	28	6	34
Visayan	2	20	22
Total......	30	26	56

Difference (%) = 73.3

$$\text{SE difference} = \sqrt{\left(\frac{30}{56}\right) \times \left(\frac{26}{56}\right) \times \left(\frac{1}{34} + \frac{1}{22}\right)} = 13.6\%$$

Probability value (P) of quotient of difference/SE obtained from table of areas of normal curve.

sented in Table 19. Statistical significance is reached by the differences between all pairs of samples, except Visayan-Calamian, and Calamian-Borneo pairs.

Variation in tuberculation of the back has several aspects. Table 19 contains a statistical summary of geographic variation in the presence of tubercles on the anterior half of the back. The Luzon sample does not differ significantly from either the Visayan or Calamian samples in frequency; in all other compared sets the differences are statistically significant. What the table does not show, however, is a difference between the Luzon sample and the Visayan

Table 19. Analysis of some aspects of geographic variation in *Rana macrodon (continued)*

Spotting on posterior third of abdomen

	No.	With spots	Without spots
Luzon	35	8 (22.9%)	27
Visayan	22	1 (4.8%)	21
Mindanao	54	37 (68.5%)	17
Calamian	57	0	57
Borneo	23	0	23

	Difference (%) ± SE	Difference/SE	P
Luzon-Visayan	18.1± 9.9	1.828	0.067
Luzon-Calamian	22.9± 6.1	3.75	< 0.001
Visayan-Mindanao	63.7±12.6	5.06	< 0.001
Visayan-Calamian	4.8± 2.8	1.714	0.09
Mindanao-Calamian ...	68.5± 9.1	7.53	< 0.001
Mindanao-Borneo	68.5±12.4	5.52	< 0.001

Tuberculation of mid-dorsum in adults

	No.	With tubercles	Without tubercles
Luzon	35	33 (94.3%)	2
Visayan	22	18 (81.8%)	4
Mindanao	55	18 (32.7%)	37
Calamian	57	55 (96.5%)	2
Borneo	24	0	24

	Difference (%) ± SE	Difference/SE	P
Luzon-Visayan	12.5± 8.3	1.506	0.13
Luzon-Calamian	2.2± 4.4	0.500	0.62
Visayan-Mindanao	49.1±12.5	3.93	< 0.001
Visayan-Calamian	14.7± 6.7	2.195	0.03
Mindanao-Calamian ...	63.8± 9.0	7.09	< 0.001
Mindanao-Borneo	32.7±10.3	3.17	0.002
Calamian-Borneo	96.5±11.6	8.32	< 0.001

and Calamian series in the kind of tubercles: only round tubercles are found on Luzon specimens whereas both round and elongated ones occur in the other samples. Variation in the presence of tubercles with age is suggested by the Bornean material. The backs of young individuals (70 mm. or less snout to vent) are set with a few elongate and round tubercles. Yet all of the twenty-four adults examined had smooth backs.

Differences in snout-vent lengths have been mentioned above (pp. 276 ff.). None of the Philippine forms seems to attain the large size (over 150 mm.) of some individuals from the Sunda Islands or

Table 20. Geographic variation in size and certain body proportions of *Rana macrodon*[1]

Log$_{10}$ snout-vent length

	No.	Mean ± SE		Range	
Luzon	27	1.9098±0.0138	(= 81.25 mm.)	1.7657-2.0531	(=58.3-113.0 mm.)
Visayan ...	21	1.8595±0.0140	(= 72.36 mm.)	1.7210-1.9425	(=52.6- 87.6 mm.)
Mindanao..	50	1.9326±0.0129	(= 85.63 mm.)	1.7042-2.1000	(=50.6-125.9 mm.)
Calamian..	49	1.8079±0.0073	(= 64.25 mm.)	1.7093-1.8993	(=51.2- 79.3 mm.)
Borneo	22	2.0402±0.0305	(=109.70 mm.)	1.8837-2.0976	(=76.5-125.2 mm.)

	Difference of means	*t*	*n*	P
Luzon-Visayan	0.0503	2.528	46	0.02
Luzon-Calamian	0.1019	7.176	74	<0.001
Visayan-Mindanao ..	0.0731	3.308	69	0.003
Visayan-Calamian ..	0.0516	3.559	68	<0.001
Mindanao-Calamian .	0.1247	8.313	97	<0.001
Mindanao-Borneo	0.1076	3.843	70	<0.001
Calamian-Borneo	0.2323	10.144	69	<0.001

Tymponum diameter/snout-vent

	No.	Mean ± SE	Range
Luzon	14	0.049±0.002	0.038-0.060
Visayan	20	0.058±0.001	0.049-0.074
Mindanao	50	0.051±0.001	0.034-0.068
Calamian	47	0.064±0.001	0.051-0.077

	Difference of means	*t*	*n*	P
Luzon-Visayan	0.009	3.896	32	<0.001
Luzon-Calamian	0.015	7.886	61	<0.001
Visayan-Mindanao ..	0.007	3.906	68	<0.001
Visayan-Calamian ..	0.006	3.647	65	<0.001
Mindanao-Calamian .	0.013	9.863	95	<0.001

Lower leg/snout-vent

	No.	Mean ± SE	Range
Luzon	27	0.481±0.003	0.440-0.518
Visayan	21	0.513±0.003	0.493-0.542
Mindanao	50	0.505±0.003	0.463-0.540
Calamian	47	0.529±0.003	0.467-0.571

	Difference of means	*t*	*n*	P
Luzon-Visayan	0.032	7.202	46	<0.001
Luzon-Calamian	0.048	10.098	80	<0.001
Visayan-Mindanao ..	0.008	1.737	69	0.09
Visayan-Calamian ..	0.016	3.245	74	0.004
Mindanao-Calamian .	0.024	6.024	95	<0.001

[1] Data for both sexes combined.

the mainland. Furthermore, the observed differences between successive Philippine samples are statistically significant (for summary of size data see Table 20). Also exhibiting extensive geographic variation are the ratios of head width to snout-vent, eye-tympanum distance to snout-vent (see Tables 18 and 21), tympanum diameter to snout-vent, and lower leg length to snout-vent (see Table 20). No sex dimorphism exists in the tympanum diameter and lower leg ratios or in size (with the single exception noted, p. 279); consequently, data for both sexes are lumped. The low values of P in Table 20 indicate the significance of the inter-sample differences in every instance but that of the lower leg ratio difference of the Visayan-Mindanao pair. In the analyses of the head width and eye-tympanum ratios, the sexes are considered separately. Most of the significant inter-island differences (Table 21) are found in the males; all but the differences between the Visayan-Calamian and Mindanao-Borneo pairs are significant in the case of the eye-tympanum ratio and all but the differences between the Visayan, Mindanao, and Calamian samples in the case of the head width ratio. (For differences between sets of samples in characters discussed in this section see Table 22.)

In view of the geographic variation noted, four subspecies of *macrodon* should be recognized in the Philippine Islands. They are as follows:

Rana macrodon acanthi Taylor

Rana macrodon blythii Boulenger, 1920, Rec. Ind. Mus., **20**: 43 (part)—southeastern Asia, Borneo, Philippine Islands.

Rana acanthi Taylor, 1923, Phil. Jour. Sci., **22**: 523, pl. 2, fig. 1—Busuanga Island.

Material examined.—Busuanga, 36 (CNHM); Culion, 39 (CNHM); Palawan, 18 (4 CAS; 11 CNHM; 3 MCZ); Balabac, 9 (CNHM).

Diagnosis.—A small form of *macrodon* (probably not in excess of 90 mm. snout to vent); males with vocal sacs; a dark W-shaped mark usually visible on back; posterior part of abdomen without dark spots; tubercles present on anterior half of back (9/10 of adults), tubercles generally elongate; center strip of ventral surface of lower leg usually without spots (5/6 of adults).

Remarks.—Considering the wide area from which Boulenger (1920) selected specimens for the variety *blythii*, it obviously is not equivalent to *m. acanthi*.

Table 21. Significance of inter-island differences in body proportions in *Rana macrodon*[1]

	Males				Females			
	Difference of means	*t*	*n*	P	Difference of means	*t*	*n*	P
				Eye-tympanum/snout-vent				
Luzon—Visayan	0.019	2.478	26	0.02	0.007	1.426	17	0.18
Luzon—Calamian	0.025	4.738	36	<0.001	0.014	5.133	33	<0.001
Visayan—Mindanao	0.013	2.340	36	0.03	0.002	0.474	31	0.64
Visayan—Calamian	0.006	1.780	34	0.09	0.007	1.865	30	0.07
Mindanao—Calamian	0.019	5.027	46	<0.001	0.005	2.084	47	0.04
Mindanao—Borneo	0.004	0.591	31	0.56	0.001	0.346	36	0.71
Calamian—Borneo	0.023	6.133	29	<0.001	0.004	1.646	35	0.11
				Head width/snout-vent				
Luzon—Visayan	0.030	3.591	26	0.002	0.018	2.557	18	0.02
Luzon—Calamian	0.024	4.304	37	<0.001	0.013	2.515	34	0.02
Visayan—Mindanao	0.009	1.577	36	0.17	0.008	1.363	31	0.19
Visayan—Calamian	0.006	1.345	35	0.19	0.005	0.911	30	0.37
Mindanao—Calamian	0.003	0.766	47	0.45	0.003	0.739	47	0.46
Mindanao—Borneo	0.024	4.013	32	<0.001	0.000	—	--	—
Calamian—Borneo	0.027	6.547	31	<0.001	0.003	0.650	36	0.51

[1] Means and ranges of ratios given in Table 18.

Range.—Busuanga (Dimaniang, Singay); Culion (San Pedro, Siuk); Palawan (Brooke's Point, Puerto Princesa); Balabac (Balabac).

Rana macrodon magna Stejneger

Rana magna Stejneger, 1909, Smiths. Misc. Coll., **52:** 437 (part)—Mount Apo, Mindanao; Boulenger, 1920, Rec. Ind. Mus., **20:** 45 (part); Taylor, 1923, Phil. Jour. Sci., **22:** 522 (part).

Rana macrodon Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 24 (part); 1920, Rec. Ind. Mus., **20:** 40 (part); Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 121 (part).

Rana macrodon blythii Boulenger, 1920, Rec. Ind. Mus., **20:** 43 (part)—southeastern Asia, Borneo, Philippine Islands.

Rana modesta Roux, 1918, Rev. Suisse Zool., **26:** 412.

Rana modesta magna Smith, 1927, Proc. Zool. Soc. London, **1927:** 211.

Material examined.—Basilan, 1 (USNM); Mindanao, 88 (60 CNHM; 28 USNM).

Diagnosis.—A moderate-sized form of *macrodon* (frequently in excess of 100 mm. and occasionally over 120 mm. snout to vent); males with vocal sacs; no dark W-shaped mark on back; posterior part of abdomen with dark spots (2/3 of adults); anterior half of back usually without tubercles (2/3 of adults), tubercles round when present; center strip of ventral surface of lower leg with dark spots (7/8 of adults).

Range.—Basilan. Mindanao: Bukidnon Province (near Agusan, Misamis Oriental Province); Cotabato Province (Burungkôt near Upi, Conel, Parang); Davao Province (Caburan, Calian, Maco near Tagum, Madaum, Malita, Mati, Mount McKinley, Tagum, Todaya on Mount Apo); City of Zamboanga (Zamboanga).

Rana macrodon macrocephala subsp. nov.

Rana macrodon Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 24 (part); Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 121 (part).

Rana magna Stejneger, 1909, Smiths. Misc. Coll., **52:** 437 (part); Boulenger, 1920, Rec. Ind. Mus., **20:** 45 (part); Taylor, 1920, Phil. Jour. Sci., **16:** 243, pl. 2, fig. 2; 1923, op. cit., **22:** 522 (part).

Material examined.—Luzon, 28 (2 CM; 6 CNHM; 12 MCZ; 5 UMMZ; 3 USNM); Mindoro, 3 (USNM).

Diagnosis.—A moderate-sized form of *macrodon* (frequently in excess of 100 mm.; probably reaches same size as *macrodon magna*); males with vocal sacs; no dark W-shaped mark on back; posterior part of abdomen with dark spots in some individuals (2/9 of adults);

Table 22. Summary of geographic variation in *Rana macrodon*

+, significant difference; o, no significant difference; -, no information

Character	Luzon–Visayan	Luzon–Calamian	Visayan–Mindanao	Visayan–Calamian	Mindanao–Calamian	Mindanao–Borneo	Calamian–Borneo
Vocal sacs	o	o	o	o	o	+	+
Light vertebral marking	o	+	o	+	+	+	+
W mark on back	o	+	o	+	+	+	o
Spotting on abdomen	o	+	+	o	+	+	o
Spotting on lower leg	+	+	+	o	+	+	o
Tubercles on back	o	o	+	+	+	+	+
Size	+	+	+	+	+	+	+
Tympanum diameter[1]	+	+	+	+	+	-	-
Lower leg length[1]	+	+	o	+	+	-	-
Eye-tympanum distance[1]	+ (♂)	+ (♂, ♀)	+ (♂)	o	+ (♂, ♀)	o	+ (♂)
Head width[1]	+ (♂, ♀)	+ (♂, ♀)	o	o	o	+ (♂)	+ (♂)

[1] Ratio to snout-vent length.

anterior half of back usually with round tubercles (9/10 of adults); center strip of ventral surface of lower leg with dark spots (4/5 of adults).

Type.—Chicago Natural History Museum no. 40519. Sampaloc, Tayabas Province, Luzon. Adult male, collected June–August, 1940, by Albert W. Herre.

Description of type.—Body heavy; head slightly broader than long; snout rounded; bony mandibular processes large; tympanum one-half diameter of eye, distance from eye roughly equal to diameter of tympanum; first finger longer than second, equal to fourth; hind limb heavy; lower leg less than one-half body length. Skin of back, sides, and dorsal surfaces of legs with white spinules and scattered tubercles; posterior part of upper eyelid with small tubercles; ventral regions smooth. Color (in alcohol) of dorsal surfaces brownish black; ventral surfaces cream with indistinct mottling on chin and throat and dark spots on latero-ventral margins of legs. Otherwise as in description of the species.

Measurements of type.—Snout-vent 93.8 mm.; head width 37.8; tip of snout to posterior border of tympanum 36.9; tympanum to eye 4.5; tympanum width 4.7; lower leg 43.8.

Notes on paratypes.—The following Luzon specimens are designated as paratypes: CM 3555–56 (Montalban); CNHM 40518 (Sampaloc), 51280–83 (Mount Data); MCZ 14159, 14165, 14168, 14170–74 plus four unnumbered (all from Baguio); UMMZ 65417 (5; Baguio); USNM 39963 (Lagonoy Gulf), 39968 (Antipolo), 57841 (Antipolo). (For comments on variation in these see above.)

Remarks.—Not enough adults from Mindoro have been examined to permit satisfactory subspecific allocation. Their listing under *macrocephala* is provisional. Similarly, Taylor's Polillo specimens have not been seen and they are also tentatively included here.

Range.—Luzon: Bataan Province (Taylor, 1923); City of Baguio (Baguio); Laguna Province (Taylor, 1923); Mountain Province (Mount Data); Rizal Province (Antipolo, Montalban); Tayabas Province (Sampaloc); Lagonoy Gulf. Mindoro (Mount Halcon). Polillo (Taylor, 1920).

Rana macrodon visayanus subsp. nov.

Rana macrodon Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 24 (part); Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 121 (part).

Rana macrodon blythii Boulenger, 1920, Rec. Ind. Mus., **20:** 43 (part).

Rana magna Boulenger, Rec. Ind. Mus., **20:** 45 (part); Taylor, 1923, Phil. Jour. Sci., **22:** 522 (part).

Material examined.—Panay, 7 (USNM); Bohol, 4 (MCZ); Negros, 10 (CNHM); Leyte, 6 (1 MCZ; 5 USNM); Siquijor, 5 (CNHM).

Diagnosis.—A small form of *macrodon* (probably not in excess of 90 mm.); males with vocal sacs; no dark W-shaped mark on back; posterior part of abdomen without dark spots (21/22 of specimens); elongate and round tubercles present on anterior half of back (4/5); center strip of ventral surface of lower leg usually without spots (9/10).

Type.—Chicago Natural History Museum no. 61636. Adult male. Collected on Siquijor Island, by D. S. Rabor, in December, 1949.

Description of type.—Body moderately heavy; head as long as broad; snout obtusely pointed; mandibular processes moderately developed. Skin of back with both elongate and round tubercles; several long dermal ridges in dorso-lateral region; webbing as in species description except that flap of skin on inner edge of first toe is poorly developed.

Color (in alcohol) brown above with indistinct black markings; ventral surfaces uniform cream with faint dark marbling on throat. Otherwise as in description of the species.

Measurements of type.—Snout-vent 80.1 mm.; head width 30.4; tip of snout to posterior border of tympanum 31.1; tympanum to eye 5.5; tympanum width 4.1; lower leg 39.8.

Notes on paratypes.—The following are designated as paratypes: CNHM 54101–104 (Luzuriaga, Negros), 61633–35 and 61637 (Siquijor); MCZ 14152 (Cabalian, Leyte), 23167–70 (Bohol); USNM 78072–78 (Iloilo, Panay), 121597–98 (Tarragona, Leyte). (For comments on variation in these see preceding discussion of geographic variation.)

Range.—Panay (Iloilo). Bohol. Negros: Negros Oriental (Amio, Lake Balinsasayo, Luzuriaga, Pagyabunan near Bais). Leyte (Cabalian, Ormoc [Boettger, 1899], Tarragona). Siquijor. Dinagat (Boulenger, 1882).

Rana microdisca Boettger

Taxonomic notes.—The Philippine frogs of this species have been considered by most authors to belong to two distinct species. The first of these, *leytensis*, included those specimens from the Philippine Islands south of Mindoro and Luzon with the exception of Palawan. Boulenger (1920) and van Kampen (1923) placed *leytensis* in the synonymy of *microdisca* (type locality Java). According to both of these authors, *microdisca* is a frog without vocal sacs. Mertens (1929a) pointed out that vocal sacs are present in the Philippine material and in specimens from Borneo and Celebes. Using the presence of these structures as a diagnostic character, he defined *leytensis* as a subspecies of *microdisca* and included specimens from Borneo in it. Mertens described a third subspecies, *dammermani*, including one specimen from Celebes and many from the Lesser Sundas.

The second nominal form, *palavanensis*, has been recorded from Palawan, Borneo, and Celebes. Boulenger (1920) distinguished *palavanensis* from *microdisca* (*sensu latu*) on the basis of the presence of vocal sacs and absence of bony mandibular processes in males of the former. But the vocal sacs do not serve to separate Palawan males from *microdisca leytensis*. The length of the mandibular processes in males of *m. leytensis* from Leyte varies with body length and/or age (Taylor, 1923). The difference in the processes, therefore, is closely associated with the differences in the body length attained (see p. 298). Accordingly, on Borneo and Celebes there may be no distinction possible between specimens identified as *microdisca* and *palavanensis*. This view is strengthened by the apparent identity of so-called "*palavanensis*" tadpoles from Celebes (Smith, 1927) and those of *microdisca* from Flores and Java (Mertens, 1930).

Examination of material from the Philippine Islands and Borneo reveals a dichotomy of the populations based upon the development of flaps of skin along the first and fifth toes and upon the condition of the skin of the back (see below). The specimens from Borneo and Palawan fall into one category, those from the remainder of the Philippines into the other. The similarities between these two groups are so extensive that they can not be treated as distinct species. This opinion is substantiated by a comparison of the boundaries between "good" species of East Indian *Rana*. On the other hand, not to call them separate subspecies would be to ignore the constant minor differences that do exist. The name *microdisca palavanensis* (type locality Palawan) must apply to those from Palawan and Borneo and *m. leytensis* (type locality Leyte) to the other group.

The Celebes population (or populations) requires a separate discussion. Specimens that I examined are readily divisible into two forms or groups distinguished by differences in size and in the development of skin folds and webbing on the feet. These two groups of specimens combine the diagnostic characters of *m. leytensis* and *m. palavanensis* in such a fashion that it is difficult to assign them to either subspecies. With some hesitation Mertens (1929a) had placed the one poorly preserved individual he had from Celebes in *m. dammermani*, but comparison of the present Celebes material with Mertens' (1930) data on *dammermani* indicates considerable difference in snout-vent lengths. It is apparent that additional study is needed to clarify the position of the Celebes frogs (see also p. 298).

The relation of *Rana woodworthi* Taylor to *microdisca* must also be discussed. The former apparently replaces *microdisca* on Luzon and Polillo. *R. woodworthi* is a somewhat larger frog and is also distinguished from *microdisca leytensis* by its completely webbed feet. Otherwise the two species are very similar. Perhaps *woodworthi* should be considered a subspecies of *microdisca*. However, on the basis of present knowledge *woodworthi* may be just as closely related to *macrodon*. The solution of this problem must wait until large collections are made on Mindoro and until the larvae of the forms involved are known.

Diagnosis.—Small to medium-sized frogs with round expanded digit tips lacking a horizontal circummarginal groove; toes with extensive webbing, but second and third toes never broadly webbed to disk on inner sides (fig. 53); a ridge or flap of skin on outer side of fifth metatarsal; only one metatarsal tubercle; usually without a continuous dorso-lateral fold; a pair of small bony projections at anterior end of mandible noticeable in males only.

In the Philippines the extent of the web serves to separate *microdisca* from small specimens of *macrodon* and *woodworthi*, the only forms with which it may be confused.

Description.—Body generalized raniform, neither stocky nor elongate; head as long as broad; snout rounded or obtusely pointed; tympanum distinct, one-half to two-thirds diameter of eye; dorsolateral fold narrow, continuous or interrupted; supratympanic fold from eye to arm present.

First finger longer than second, equal to or longer than fourth; third finger long, equal to twice the length of the palm; tips of fingers and toes slightly dilated into rounded disks; no circummarginal groove between dorsal and ventral surfaces of disks; dorsal surface of disks with a longitudinal groove; second and third fingers usually with a very narrow fringe of skin on inner sides. Toes three-fourths to almost completely webbed (fig. 53); fourth toe broadly webbed at least to middle subarticular tubercle but never beyond last tubercle; a fringe of skin on outer edge of fifth toe and inner edge of first; fringe continued along corresponding metatarsals in most populations; a prominent elongate inner but no outer metatarsal tubercle.

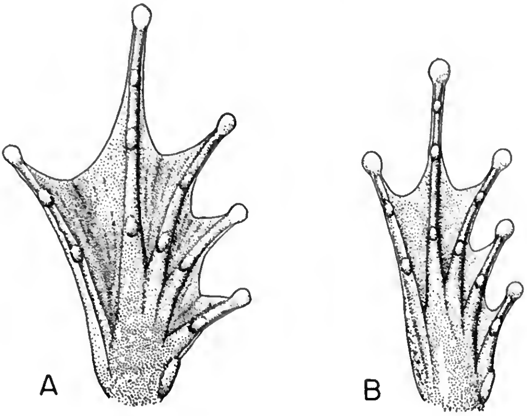


FIG. 53. Feet of (A) *Rana microdisca leytensis* (× 2.5) and (B) *R. m. palavanensis* (× 3).

An inverted V-shaped tubercle between shoulders; remainder of back usually with round or elongate tubercles, white spinules usually present posteriorly; gular region smooth; abdomen smooth, occasionally rugose posteriorly.

Color (in alcohol) of back and sides chestnut brown or slate, some individuals with broad dorso-lateral light lines; interorbital bar and tubercle between shoulders distinctly darker than remainder of dorsum; a dark temporal spot bordered above by supratympanic fold and occupying upper half of tympanum; limbs with dark cross-bars; venter cream, immaculate or variously mottled with dark brown.

Secondary sex characters.—The males of *microdisca*, with the exception of the typical subspecies, have paired, internal vocal sacs located at the sides of the throat. The sacs extend beyond the posterior edge of the subhyoideus muscle. The round openings of the vocal sacs are situated at the corners of the mouth. A pair of bony projections is developed at the front of the mandible in males.

Table 23. Sex dimorphism in snout-vent lengths in *Rana microdisca leytensis*

	Females			Males		
Samples	No.	Mean±SE	Range	No.	Mean±SE	Range
Samar	7	40.77±1.04	38.5-46.2	5	37.78±0.80	36.6-39.0
	Difference = 2.99; *t* = 2.119; P = 0.06					
Leyte	18	37.34±0.98	32.1-44.5	7	35.37±0.55	33.4-38.0
	Difference = 1.97; *t* = 1.173; P = 0.26					
Mindanao:						
Davao	13	44.47±0.98	39.8-50.1	17	40.66±0.87	33.4-46.3
	Difference = 3.81; *t* = 2.902; P = 0.009					
Cotabato	11	43.97±1.02	39.0-49.8	8	38.26±1.47	33.6-45.1
	Difference = 5.71; *t* = 3.297; P = 0.007					
Zamboanga	12	50.54±1.10	43.1-57.6	12	44.33±0.78	40.1-48.6
	Difference = 6.21; *t* = 4.624; P = <0.001					
Sulu	6	38.68±1.94	34.1-44.6	8	38.34±1.75	34.2-44.8
	Difference = 0.34; *t* = 0.13; P = 0.9					

The relation between the size of these processes and body length has been referred to above.

Very little sexual dimorphism in size and in body proportions was observed. Only in the Mindanao populations were statistically significant differences in size between adult males and females found. (For pertinent data see Table 23.)

Ecological notes.—Rana microdisca remains almost invariably in the immediate vicinity of water. Field notes of the Philippine Zoological Expedition agree with the published statements of Taylor (1920) and Mertens (1930). Only six specimens were found by members of the expedition away from the vicinity of water as compared to 53 found in or near water.

This species does not exhibit a clear preference for a particular type of aquatic habitat. Taylor, for instance, says that it is "usually" found near streams, indicating flowing water. Mertens states that he encountered *microdisca* in large numbers in mountain creeks, ditches and flooded rice fields on Lombok; these habitats include a range from swiftly moving water to standing water. Of the previously mentioned 53 specimens captured in the vicinity of water on Mindanao, 34 were collected near or in "streams," which I interpret as flowing water, and 19 in or near standing water (pools, swamps, and ponds). Too much emphasis must not be placed on the greater numbers of specimens from flowing water, as the period spent at such localities by members of the expedition was three times that spent at localities yielding specimens from standing water.

There is not much agreement between published accounts and expedition field notes in the matter of altitudinal distribution. Mertens, for example, states that he did not find *m. microdisca* or *m. dammermani* below 1,000 meters on Java, Lombok, or Flores. Dunn (1928) collected larvae at 400 meters and many adults at 1,190 meters on Lombok. These specimens were identified by Dunn as *modesta*. Mertens (1929a) changed this identification to *microdisca dammermani*. After examination of the specimens, I concur in Mertens' opinion. Six specimens from Negros (CNHM 61524–29) were taken at an altitude of 915 meters. The specimens collected on Mindanao by the expedition had the following altitudinal distributions: Below 30 meters, 42; 30–60 meters, 24; 300–600 meters, 1; over 600 meters, 6. One individual was captured at 840 meters on Mount McKinley.

Inter-island variation.—As indicated above, the populations of *microdisca* present in the Philippines and Borneo are divisible into two subspecies. The outer side of the fifth toe and the inner side of the first together with the corresponding metatarsals bear dermal folds developed to different degrees. Specimens from Leyte, showing maximum development of these structures, have distinct flaps of skin along the entire length of the fifth toe and metatarsal and the first toe and its metatarsal. These flaps can be moved easily by the touch of a forceps. Similar development is found in the populations of Mindanao, Basilan, Negros, Samar, and the Sulu Islands, with a slight reduction in the flap in the Sulu frogs. By contrast, Palawan and Bornean specimens have only a ridge or line along the fifth toe and metatarsal. A fold or ridge is present on the first toe of these, but only a line on the first metatarsal.

This split in the populations coincides with geographic variation in the skin of the back. All populations are characterized by narrow, continuous or interrupted dorso-lateral folds, and an inverted V-shaped ridge between the shoulders is almost invariably present. Between the dorso-lateral folds there may be elongate ridges or round tubercles; these are not found in the frogs from Palawan and Borneo, but are characteristic of those from the other Philippine Islands.

Table 24. Geographic variation in size and body proportions in *Rana microdisca leytensis* and *m. palavanensis*[1]

Snout-vent length

Sample[1]	Sex	No.	Mean±SE	Range
Basilan ...	♂	11	42.96±1.00	37.7-49.6
Negros	♂	4	38.75	32.7-46.8
Palawan ..	♀	5	31.02±0.98	28.2-33.5
Borneo	♀	7	34.96±1.12	31.2-39.4

Samples	Sex	Difference of means	*t*	*n*	P
Samar–Leyte	♀	3.43	2.044	23	0.05
	♂	2.41	2.564	10	0.03
Leyte–Davao	♀	7.13	5.004	29	<0.001
	♂	5.29	3.738	22	0.001
Leyte-Cotabato	♀	6.63	4.529	28	<0.001
Leyte –Zamboanga	♀	13.20	8.811	28	<0.001
	♂	8.96	8.043	17	<0.001
Zamboanga–Cotabato	♀	6.57	4.368	21	<0.001
	♂	6.07	3.970	18	<0.001
Basilan–Sulu	♂	4.62	2.442	14	0.03
Sulu–Zamboanga	♀	11.86	5.751	16	<0.001
	♂	5.99	3.659	15	0.005
Borneo–Cotabato	♀	9.01	5.706	16	<0.001
Palawan–Borneo	♀	3.94	2.463	10	0.04
Zamboanga–Davao	♀	6.07	4.149	23	<0.001
	♂	3.67	2.991	27	0.008

[1] Only those differences approaching statistical significance are listed. Means, standard errors, and ranges of samples from Samar, Leyte, Mindanao, and the Sulu Islands are given in Table 23.

An additional support of the dichotomy of populations is provided by the ventral coloration. The ground color of the gular and pectoral regions is cream, frequently covered by dark brown spots or marbling. The dark markings are not found in the Palawan and Bornean populations whereas they are present on the throat of almost all individuals of the other populations.

Individuals of *m. leytensis* usually have dark mottling on the abdomen. The distribution of this character in the samples of *leytensis* is as follows:

	Mottling present	Mottling absent		Mottling present	Mottling absent
Negros..........	6	0	Mindanao........	86	4
Samar...........	5	7	Basilan...........	14	0
Leyte...........	15	14	Sulu Islands.......	8	0

Geographic variation is also evident in the extent of webbing. The maximum development of the web is found in the Mindanao and Basilan populations (fig. 53, A), in which the first and second toes are webbed to the disks on the outer sides and the fifth toe to

Table 24. Geographic variation in size and body proportions in *Rana microdisca leytensis* and *m. palavanensis (continued)*

Head width/snout-vent

Sample	No.	Mean±SE	Range
Samar	12	0.357±0.005	0.333-0.384
Leyte	24	0.348±0.003	0.324-0.369
Mindanao:			
Davao	28	0.354±0.003	0.323-0.389
Cotabato	18	0.355±0.003	0.320-0.374
Zamboanga	25	0.358±0.003	0.340-0.392
Negros	4	0.377	0.358-0.403
Basilan	11	0.372±0.004	0.342-0.394
Sulu	11	0.371±0.004	0.353-0.403
Palawan	5	0.364±0.003	0.355-0.372
Borneo	7	0.391±0.004	0.372-0.407

Samples	Difference of means	*t*	*n*	P
Leyte—Zamboanga	0.010	2.628	47	0.01
Zamboanga—Basilan	0.014	2.784	34	0.01
Zamboanga—Sulu	0.013	2.532	34	0.02
Zamboanga—Borneo	0.033	5.717	30	<0.001
Sulu—Borneo	0.020	3.141	16	0.009
Palawan—Borneo	0.027	4.782	10	<0.001

Lower leg/snout-vent

Sample	No.	Mean±SE	Range
Samar	11	0.479±0.004	0.448-0.497
Leyte	25	0.503±0.005	0.456-0.540
Mindanao:			
Davao	30	0.488±0.004	0.440-0.540
Cotabato	19	0.473±0.005	0.439-0.521
Zamboanga	25	0.494±0.004	0.467-0.521
Negros	5	0.500±0.011	0.477-0.529
Basilan	11	0.495±0.007	0.451-0.537
Sulu	11	0.513±0.008	0.461-0.549
Palawan	5	0.605±0.010	0.579-0.640
Borneo	7	0.601±0.007	0.577-0.638

Samples	Difference of means	*t*	*n*	P
Leyte—Samar	0.024	2.978	34	0.007
Leyte—Davao	0.015	2.361	53	0.02
Leyte—Cotabato	0.030	4.187	42	<0.001
Davao—Cotabato	0.015	2.374	47	0.02
Cotabato—Zamboanga	0.021	3.817	42	<0.001
Zamboanga—Sulu	0.019	2.605	34	0.01
Zamboanga—Borneo	0.107	15.39	30	<0.001
Sulu—Borneo	0.088	7.732	16	<0.001

the disk on the inner side. The other extreme is shown by the Palawan form (fig. 53, B), in which the first and second toes are webbed to a point between the subarticular tubercle and the disk. The web between the fourth and fifth toes of this form is correspondingly reduced. The Leyte and Sulu Island populations lie between these two extremes, with the former approaching the Mindanao population and the latter the Palawan.

Size and some body proportions also exhibit geographic variation. Three samples were available from Mindanao, one each from eastern Davao Province, Cotabato Province, and the Zamboanga peninsula. Statistically significant differences exist between the Zamboanga and Cotabato samples in snout-vent length and the ratio of lower leg to snout-vent; the Davao sample differs from the Zamboanga in size and from the Cotabato sample in the ratio of lower leg to snout-vent (Table 24). Because of these intra-island differences, the Mindanao samples were compared individually with samples from adjacent islands (see Table 24). The largest snout-vent lengths are found among specimens from Basilan and Mindanao and the smallest among specimens from Palawan and Borneo (*palavanensis*). Though, in general, the subspecies *leytensis* attains a greater length than *palavanensis*, there is variation within *leytensis*, and some of its populations (Leyte, Sulu Islands) approach those of the latter (see Tables 23 and 24).

In relative head width the same pattern is observed; in general, the two subspecies differ (head width ratio larger in *palavanensis*) although populations within each subspecies vary and some approach populations of the other subspecies. The two subspecies are still more distinct in the higher ratio of lower leg to snout-vent in *palavanensis*. Intra-subspecific variation is found in this character also, but the gap between subspecies is relatively great (see Table 24).

More detailed information concerning the Celebes groups or "varieties" is appended here. The small "variety" consists of two series, eleven specimens from Djikoro and twenty from "South Celebes." The ten adult females (with enlarged and pigmented eggs) vary from 27.7 to 32.4 mm. snout to vent and the fourteen adult males (with vocal sac openings) from 23.5 to 29.5 mm. The large "variety" consists of nine specimens from scattered localities. Only two of the females contain enlarged eggs; these individuals are 43.3 and 44.6 mm. snout to vent. The other five females measure from 35.9 to 41.7 mm. Two males with vocal sacs measure 34.4 and 42.8 mm. The first and fifth toes and associated metatarsals bear distinct flaps of skin in the small group but not in the large. The fifth toe is webbed to a point between the distal subarticular tubercle and the terminal disk in the large group, but only as far as the subarticular tubercle in the small. Both groups are heavily pigmented ventrally.

The Philippine subspecies (see ranges in fig. 98) of *microdisca* now recognized are as follows:

Rana microdisca palavanensis Boulenger

Rana palavanensis Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 85—Palawan; 1920, Rec. Ind. Mus., **20**: 59 (part); Taylor, 1920, Phil. Jour. Sci., **16**: 242; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 182 (part); Smith, 1927, Proc. Zool. Soc. London, **1927**: 209 (part).

Material examined.—Palawan, 7 (2 BM, types of *palavanensis;* 2 EHT; 3 MCZ); Borneo, 9 (5 BM; 4 MCZ).

Diagnosis.—Males with vocal sacs; dorso-lateral fold usually continuous; mid-dorsum without ridges or tubercles except for Λ-shaped one between arms; venter immaculate; fifth and first metatarsals without flaps of skin, at most a low ridge.

Range.—Palawan (Iwahig, Thumb Peak). Borneo.

Rana microdisca leytensis Boettger

?Hylarana mindanensis Girard, 1853, Proc. Acad. Nat. Sci. Phila., **6**: 423—Caldera, Mindanao; 1858, U. S. Expl. Exp., Herpetology, p. 52.

Rana leytensis Boettger, 1893, Zool. Anz., **16**: 365—Leyte; Boulenger, 1897, Proc. Zool. Soc. London, **1897**: 229; Taylor, 1920, Phil. Jour. Sci., **16**: 246, pl. 2, fig. 1; 1923, op. cit., **22**: 525.

Rana microdisca (part) Boulenger, 1920, Rec. Ind. Mus., **20**: 57; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 180.

Rana microdisca leytensis Mertens, 1929, Zool. Anz., **86**: 67.

Material examined.—Leyte, 35 (CNHM); Samar, 10 (CNHM); Negros, 6 (CNHM); Mindanao, 121 (20 CM; 96 CNHM; 5 USNM); Basilan, 14 (MCZ); Jolo, 11 (2 CNHM; 9 MCZ); Tawi Tawi, 4 (3 BM; 1 CM).

Diagnosis.—Males with vocal sacs; dorso-lateral fold usually interrupted; mid-dorsum with numerous elongate ridges or tubercles; dark spots present posterior to pectoral region on venter (except in some individuals from Leyte); distinct flaps of skin along free edges of first and fifth toes and corresponding metatarsals.

Remarks.—The status of *Hylarana mindanensis* Girard, known from only two specimens, has been in doubt almost since the time of the original description. The whereabouts of the types are unknown, so that identification of the form must depend on Girard's descriptions. From the more complete description (Girard, 1858; reprinted in Taylor, 1920) one may conclude safely that Girard had two young individuals of some species of *Rana*. The presence of only one metatarsal tubercle and of a membranous fringe along the outer edge of the fifth toe restricts the possible identification to *R. cancrivora*, *R. macrodon*, and *R. microdisca*. The first of these can be eliminated by Girard's statement that the swellings at the tips of the toes are larger than the subarticular tubercles. Girard also stated that the web, although nearly reaching the disks, was deeply excised between the toes. This leads me to believe that *mindanensis* is to be identified with *microdisca* rather than with *macrodon* (see figs. 51 and 53).

Range.—Leyte (Carigara, Inayupan near Abuyog, Tacloban). Samar (Catarman). Negros: Negros Oriental (Lake Balinsasayo). Mindanao: Agusan Province (Bunawan); Cotabato Province (Bugasan, Buayan, Parang, Upi); Davao Province (Caburan, Malita, Mati, Mount McKinley, Tagum); City of Zamboanga (San Ramon). Basilan (Abungabung). Sulu Archipelago: Bongao (Taylor, 1920); Jolo; Papahag (Taylor, 1920); Tawi Tawi.

The collections of the Carnegie Museum contain four specimens (CM 3391–94) bearing the locality datum "Polillo Island." These were collected by J. Canonizado and were obtained by the Carnegie Museum through E. H. Taylor, who had some doubt about the authenticity of the locality (personal communication). Taylor himself made an extensive collection on Polillo but did not obtain any specimens of *leytensis*, which is very common wherever it is known to occur. When it is considered that *leytensis* is not known from Mindoro or Luzon, the Polillo record seems extremely dubious.

Rana parva Taylor

Rana parva Taylor, 1920, Phil. Jour. Sci., **16**: 241, pl. 3, fig. 4—Bunawan, Agusan, Mindanao.

Material examined.—Mindanao, 7 (3 AMNH; 2 CM; 2 CNHM).

Taxonomic notes.—The relations of *parva* with other southeastern Asiatic species of the genus are very obscure. In some ways it resembles *microdisca*, particularly *m. palavanensis*. This similarity is seen in the groove on the dorsal surface of digit tips, in habitus, in size, and in the Λ-shaped mark on the back between the arms. But these similarities may not be significant, as only the first character is not widespread in the genus. Furthermore, the small web of *parva* suggests that it is less intimately connected with water than is *microdisca*. There is even some reason to believe that *parva* may lay its eggs on land. This possibility is discussed below.

Some of the characters of *parva* suggest convergence towards *Cornufer;* for example, the very small web, distinctly enlarged toe disks, and large eggs recall species of *Cornufer*. However, the degree of separation of the outer metatarsals, the absence of supernumerary tubercles on hand and foot, and the absence of circummarginal grooves on the toe disks of *parva* all indicate that, although it may be an ecological equivalent of *Cornufer*, it has little phylogenetic relation to the latter.

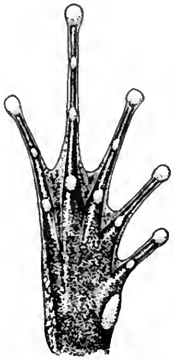


FIG. 54. Foot of *Rana parva;* × 3.

Diagnosis.—A small frog, body length of adult females around 30 mm.; tips of digits slightly expanded, without horizontal groove; feet with greatly reduced web; broad web extending only short distance beyond proximal tubercle of fourth toe (fig. 54); skin of back smooth; no dorso-lateral fold; back pale brown (in alcohol) or reddish brown (in life) contrasting sharply with the darker sides.

Description.—Body moderately stout; head slightly longer than broad; snout obtusely pointed or rounded; tympanum distinct, two-thirds diameter of orbit; no dorso-lateral fold; a weak supratympanic fold. First finger equal to or slightly longer than second and fourth; third finger less than twice length of palm; tips of fingers rounded, a trifle wider than last phalanges; a very narrow fringe of skin along inner side of second and third fingers. Hind limb moderately long; very small web reaching as a broad sheet only just beyond subarticular tubercle of first and second toes and just beyond proximal subarticular tubercle of third, fourth, and fifth toes; web extending as a narrow fringe to disks of all toes; a small oval inner but no outer metatarsal tubercle; no flap of skin on outer side of fifth metatarsal (fig. 54). Skin on back smooth or shagreened; usually a few light pustules on upper eyelid; skin of gular and abdominal regions smooth.

Color (in alcohol) pale brown dorsally with a narrow darker interorbital bar and usually a dark inverted V between the arms; dark brown of lores and sides sharply set off from lighter back and top of head along the dorso-lateral regions and canthi; lips dark brown, usually with a few small white spots; throat cream or cinnamon; belly cream, immaculate; posterior half of ventral surface of thigh cinnamon; dorsal surface of hind limbs reddish brown or slate brown with darker crossbars. According to Taylor the back is reddish brown in life.

Secondary sex characters.—Taylor's original description does not give any indication of sexual dimorphism. I have seen only female adults.

Ecological notes.—Ecological observations of *parva* are practically non-existent. The small web indicates that it is not a strictly aquatic frog in the sense that *macrodon* and *microdisca* are. There are indications that the breeding behavior of *parva* may differ markedly from these aquatic species. Two female *parva* (CNHM 50269–70, body lengths 27 and 31 mm., respectively) appear to be in breeding condition. The oviducts and ovaries are greatly enlarged. The right ovary of the small female contains only eleven enlarged, pigmented eggs, that of the larger female only eight, even though in both cases the ovaries occupy much of the abdominal cavity. In both specimens there are numerous undeveloped ova. The diameters of the enlarged eggs measure about 2 mm., some being slightly larger and others smaller. Contrasting with this situation, an adult female *microdisca leytensis* (CNHM 50075, body length 44 mm.) has slightly more than fifty fully grown eggs on the right side, including twenty gelatinous capsules, as well as many undeveloped ova. Of the encapsuled ova none exceeds 2 mm., the majority measuring between 1.5 and 1.8 mm. The enlargement of the eggs and the decrease in their number in *parva* may reflect a deviation from the usual *Rana* pattern of many small eggs deposited in water. The life history of *Rana parva* accordingly affords an attractive field problem.

Apparently *parva* is a mountain species. The type series was collected in the low mountains near Bunawan, Mindanao (Taylor, 1920). The two specimens in Chicago Natural History Museum were caught at 760 meters and 1,300 meters. The American Museum specimens were collected along the Padada River, which drains the southern end of the mountain range containing Mount Apo.

Range.—Mindanao: Agusan Province (Bunawan); Davao Province (Mainit and Todaya on Mount Apo, Padada River).

Rana micrixalus Taylor

Rana micrixalus Taylor, 1923, Phil. Jour. Sci., **22**: 526, pl. 2, figs. 2 and 3—Abungabung, Basilan Island.

Material examined.—Basilan, 2 (1 CAS, paratype; 1 MCZ, paratype).

Diagnosis.—A small frog (female with eggs 30 mm. snout to vent), without a horizontal groove around the expanded toe tips; web not extending beyond level of second subarticular tubercle of fourth toe; a broad dorso-lateral fold (fig. 46, A); first finger longer than second.

Description.—Body slightly stocky; head as broad as long; snout blunt, rounded; tympanum distinct, two-thirds diameter of eye; dorso-lateral fold present, broad; supratympanic fold from eye to insertion of arm.

Fingers not noticeably expanded at tips; first finger longer than second and fourth; third finger approximately one and one-half times length of palm; second and third fingers with a narrow fringe of skin on inner side. Tips of toes distinctly expanded into disks lacking a circummarginal horizontal groove, but having a dorsal groove; toes about half webbed, web reaching disk of first toe, last joint of second and penultimate joint of third on the outer side, penultimate joint of fifth, and second subarticular tubercle of fourth; no fringe of skin along outside of fifth toe; an elongate inner metatarsal tubercle, but no outer one.

Skin of back shagreened or granular with pustules on upper eyelid and round tubercles posteriorly; an inverted V-shaped dermal ridge between the arms on the back; ventral surfaces smooth; tibia with several tubercles dorsally.

Color of dorsal surfaces purplish brown in life (Taylor, 1923), brown in alcohol; throat and belly cream to flesh, variously marked with dusky or purple color; limbs with dark crossbars.

Range.—Basilan (Abungabung). Mindanao: City of Zamboanga (Pasonanca [Taylor, 1923]).

Rana everetti Boulenger

Taxonomic notes.—Certain characters indicate that the Philippine frogs, *R. everetti* Boulenger and *luzonensis* Boulenger, are very closely related, and, as the concept is applied in this report, must be treated as subspecies. Among these characters are: a granulate belly, among Philippine *Rana* found only in this species; extremely large digital disks; shape and length of the nuptial pad; absence of vocal sacs; and presence of large infra-anal tubercles. In many respects *everetti* is very similar to *R. chalconota* of the East Indies, the notable differences appearing in the secondary sex characters. Males of *chalconota* have vocal sacs; the nuptial pad of *chalconota* does not extend to the last phalanx as in *everetti*. Additional study may indicate the advisability of placing these two forms in one wide-ranging species.

A number of names have been applied to this group of Philippine frogs. It was first described from Zamboanga, Mindanao, by Boulenger (1882) and was redescribed from eastern Mindanao by Stejneger (1905) as *mearnsi*. These two type descriptions agree in most details. They differ in statements as to the length of the first and second fingers (according to Boulenger the first equaled the second; according to Stejneger the first was shorter) and the length of the adpressed hind leg. The last of these characters is subject not only to individual variation but also to differences in mode of measurement; consequently it is of little use in distinguishing obviously related frogs. I have examined the type and topotypes of *everetti* and the type of *mearnsi* and find no important difference between the two nominate forms. The difference in finger lengths referred to must be considered as individual variation. *Rana dubita*, described by Taylor (1920) from a single specimen from Mindanao, is probably also a synonym of *everetti*. Except for the statement that the skin of the belly is smooth, the description of *dubita* might be that of a juvenile *everetti*.

The Luzon population has been named even more frequently. Boulenger described the Luzon frog as *luzonensis* in 1896. Taylor (1920) established a second species, *guerreroi*, but later placed it in the synonymy of *luzonensis* (1922b). Taylor also described *igorota* from Balbalan in northern Luzon and *tafti* from southwestern Luzon. He distinguished *igorota* from *luzonensis* on the basis of four characters: (1) the shorter hind limb; (2) the less flattened snout; (3) narrower interorbital distance; (4) coloration and marking. The first three characters are subject to considerable individual variation. Comparison of three paratypes of *igorota* and a series of *luzonensis*, the latter identified by Taylor and now in the collection of the Museum of Comparative Zoology, demonstrates that no separation of two forms can be made on the basis of these characters. Furthermore, an analysis of the color notes in Taylor's descriptions does not bear out his contention that *igorota* differs from *luzonensis* in this respect. Accordingly, I consider *igorota* a synonym of *luzonensis*.

After examining the types of *luzonensis* and *tafti* Taylor, I am unable to support recognition of two forms from Luzon. The type of *tafti* has two small tubercles on the head and is unique in this respect. This fact, however, is of no taxonomic importance in the light of the over-all resemblance of *tafti* to *luzonensis*. Taylor (1922b) himself stated that *tafti* was related to *mearnsi*, which is conspecific with *luzonensis*.

The granulate belly and elongate infra-anal tubercles noted in the original description of *Rana merrilli* Taylor (1922a) suggest its relationship to this group. Examination of the type of *merrilli* confirms this suggestion.

Diagnosis.—A medium-sized frog; outer fingers (fig. 33, B) expanded into large disks with groove separating dorsal and ventral surfaces; disks of outer fingers approximately twice width of penultimate phalanges; first finger shorter than second, in some individuals equal to second; outer fingers with fringe of skin; toes completely webbed (see fig. 55); a thin dorso-lateral fold; no dorso-lateral light line; posterior part of abdomen coarsely granular; males without vocal sacs or humeral glands; a nuptial pad on first finger (see fig. 56).

Description.—Body slender (males) to moderately stocky (females); head longer than broad, depressed; snout obtusely pointed, projecting beyond lower jaw; tympanum distinct and large, two-thirds of or equal to diameter of eye; a thin distinct dorso-lateral fold from eye to groin; a skin fold behind tympanum from dorso-lateral fold to insertion of arm.

First finger shorter than second, rarely equal to second; third and fourth fingers very long, third twice the length of palm; tips of fingers expanded into rather truncate disks; tip of first finger scarcely expanded; disk of second not as wide as disks of third and fourth; disks of third and fourth twice width of penultimate phalanges; dorsal and ventral surfaces of disks separated by a groove; second, third, and fourth fingers with a distinct fringe of skin on outer and inner sides. Hind leg moderately long; disks of toes equal to that of second finger or slightly smaller; toes broadly webbed to disk on outer side of first, second, and third toes, to disk on inner side of fifth and to distal subarticular tubercle of fourth toe; web only slightly excised; a slight flap of skin on outer side of fifth toe but not along fifth metatarsal; two metatarsal tubercles, an oval inner and a small round outer one.

Skin of back and head smooth or with small spinules; upper eyelid rugose posteriorly in many specimens; gular and pectoral regions smooth; posterior half of abdomen and medio-ventral surface of thighs coarsely granular; in some populations two large tubercles present below anus.

Color (in alcohol) variable; dorsal surfaces brown to light grayish brown or slate, frequently with scattered indistinct darker spots; legs usually with bars, the bars varying in width and number; ventral surfaces cream, with varying suffusion of brown on gular and pectoral regions; ventral surfaces of hind limb variously spotted with brown.

Secondary sex characters.—The males of this species have nuptial pads on the first fingers (fig. 56) but have no vocal sacs or humeral glands. There are some differences between the sexes in size and body proportions (see Table 25). The females are larger than the males and have relatively broader heads (head length/head width). In the Mindanao frogs there is sexual dimorphism in the size of the tympanum relative to snout-vent length, the males of the sample having a significantly larger tympanum. The tympanum of the Luzon males appears to be slightly larger than that of the females, but the difference does not approach a statistically significant level.

Ecological notes.—Recorded habitat notes (Taylor, 1920, 1922a, 1922b) associate *everetti* with woodland streams. Field notes of the Philippine Zoological Expedition agree with the published data. These frogs are usually found in and about moving water; for example, Taylor speaks of "mountain streams" and "brooks" and the field notes of the expedition refer to "creeks." These remarks hold, to the best of my knowledge, for all specimens of *luzonensis*. The typical form on Mindanao, however, has been collected about "pools" (Taylor, 1922a; notes of the Philippine Expedition) and "dry stream beds" (Philippine Expedition) as well as "mountain streams" (Taylor, 1920). It is possible that the association with "pools" and "dry stream beds" may have been due to dryness of the season. The depressed body, the long fingers bearing large disks, the granulated belly, and the extensive webbing of the feet would seem to adapt this frog to swimming and to clinging to rocks in strong currents.

The vertical distribution of *everetti* is extensive. On Mindanao most of the specimens recorded were taken near sea level or in low hills. Taylor collected his specimen from Negros at an elevation of 915 meters on Canlaon Volcano; two Negros specimens in Chicago Natural History Museum are from 915 and 305 meters. All the Luzon specimens reported on here were collected in mountainous areas; the Mount Data specimens (CNHM 51289–91) came from an elevation of 2,135 meters.

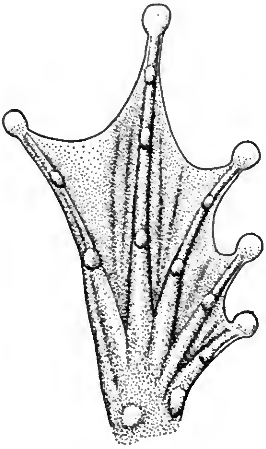


FIG. 55. Foot of *Rana e. everetti;* × 1.2.

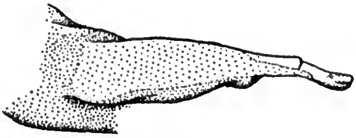


FIG. 56. Mesial view of first finger of *Rana e. everetti*, showing extent of nuptial pad; × 3.

Inter-island variation.—The three samples examined differ in the nature of the skin on the dorsal surfaces, in the frequency and type of tubercles below the anus, in body length, and in some body proportions. The specimens from Leyte are characterized by light spinules on the dorsal surfaces. The spinules are most dense on the upper eyelid, in the temporal region, along the dorso-lateral fold, and on the dorsal surfaces of the limbs. Only five of the twenty-nine individuals in this series lack the small spines. These five are young, none exceeding 45 mm. snout to vent; the next larger specimen is 54 mm. long. The spinules have not been observed in any other population of *everetti.*

Table 25. Comparison of males and females of *Rana everetti*

	Sex	No.	Mean±SE	Range	Difference of means	*t*	*n*	P
				Snout-vent				
Luzon........	♀	5	60.72±2.39	53.2-66.2	11.45	5.696	18	<0.001
	♂	15	49.27±0.87	43.7-55.5				
Mindanao....	♀	7	87.23±1.37	80.5-90.5	14.61	6.120	15	<0.001
	♂	10	72.62±1.74	62.8-78.7				
Leyte........	♀	3	84.20	81.0-88.9	25.04	-----	---	------
	♂	20	59.16±0.70	43.0-64.4				
				Head length/head width				
Luzon........	♂	13	1.205±0.020	1.029-1.274	0.152	4.028	16	0.001
	♀	5	1.053±0.033	0.959-1.158				
Mindanao....	♂	10	1.127±0.010	1.074-1.182	0.093	5.386	15	<0.001
	♀	7	1.034±0.014	0.993-1.081				
Leyte........	♂	20	1.198±0.013	1.087-1.309	0.084	-----	--	------
	♀	3	1.114	1.083-1.138				
				Tympanum diameter/snout-vent				
Luzon........	♂	14	0.069±0.002	0.049-0.079	0.007	1.314	17	0.21
	♀	5	0.062±0.005	0.057-0.068				
Mindanao....	♂	10	0.084±0.001	0.078-0.090	0.015	6.550	15	<0.001
	♀	7	0.069±0.002	0.062-0.075				
Leyte........	♂	20	0.079±0.001	0.069-0.092	0.020	-----	--	------
	♀	3	0.059	0.057-0.061				

A pair of enlarged white tubercles below the anus is conspicuous in all nineteen of the Mindanao specimens and in all but three of those from Leyte. In the latter group the white patches are broken up into a linear series of large granules in all but two. Only rarely are the white tubercles broken up in Mindanao frogs. In the Luzon series only eight of twenty-three specimens have slightly enlarged tubercles arranged in a line below the vent. However, these tubercles or granules are not much larger and are only slightly lighter than the surrounding granules of the posterior surface of the thigh. Testing the frequency of tubercles in the Luzon sample against that of both the others by means of a 2 × 2 contingency table indicates that the differences observed are statistically significant (against Leyte: chi square=14.724, P=<0.001; against Mindanao: chi square=16.539, P=<0.001; Yates' correction used). The one specimen from Polillo seen (the type of *merrilli*) resembles Mindanao specimens in this character.

In Table 26 are summarized the differences between the three samples in size and body proportions. Only males are employed because too few females are available. In each sample there are several specimens considerably smaller in body length than the remainder. In order to use a more homogeneous sample and to

Table 26. Geographic variation in size and body proportions in males of *Rana everetti*

Snout-vent[1]

	Difference of means	t	n	P
Luzon–Mindanao....	23.35	13.201	23	<0.001
Luzon–Leyte........	9.89	8.942	33	<0.001
Leyte–Mindanao....	13.46	8.578	28	<0.001

Tympanum diameter/snout-vent[1]

	Difference of means	t	n	P
Luzon–Mindanao....	0.015	4.841	22	<0.001
Luzon–Leyte........	0.010	3.768	32	<0.001
Leyte–Mindanao....	0.005	2.131	28	0.04

Head length/head width[1]

	Difference of means	t	n	P
Luzon–Mindanao....	0.078	3.213	21	0.007
Luzon–Leyte........	0.007	0.312	31	0.75
Leyte–Mindanao....	0.071	3.628	28	0.001

Head width/snout-vent

	No.	Mean±SE	Range
Luzon.................	15	0.291±0.004	0.270-0.328
Leyte..................	20	0.301±0.002	0.284-0.317
Mindanao.............	10	0.322±0.003	0.299-0.332

	Difference of means	t	n	P
Luzon–Mindanao....	0.031	5.281	23	<0.001
Luzon–Leyte........	0.010	2.268	33	0.03
Leyte–Mindanao....	0.021	5.402	28	<0.001

[1] Means given in Table 25.

reduce as far as possible the effects of growth on the statistics, I have not included in Table 26 or in the following discussion one male (35.0, next larger 43.7 mm.) from Luzon, 4 males (43.0 to 44.9, next larger 53.8 mm.) from Leyte, and one male (51.0 mm., next larger 62.8) from Mindanao.

It will be noted that each population differs from the others in snout-vent length. The same holds true in the case of the ratios of tympanum to snout-vent and of head width to snout-vent, although statistically the difference is at the border line of significance in the first ratio for the pair Leyte-Mindanao and in the head width ratio for the pair Leyte-Luzon. The Mindanao males have relatively broader heads and differ from the others in the ratio of head length to head width.

In view of the differences observed, the populations of this species are divided into the following subspecies:

Rana everetti everetti Boulenger

Rana everetti Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 72, pl. 6—Zamboanga, Mindanao; 1920, Rec. Ind. Mus., **20**: 210; Fischer, 1885, Jahrb. Hamburg Wiss. Anst., **2**: 80; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 121; Taylor, 1920, Phil. Jour. Sci., **16**: 262, pl. 6, figs. 1, 1*a*, 1*b*; 1922, op. cit., **21**: 166.

Rana mearnsi Stejneger, 1905, Proc. U. S. Nat. Mus., **28**: 343—Baganga River, East Coast Range Mountains, Mindanao; Boulenger, 1920, Rec. Ind. Mus., **20**: 209; Taylor, 1920, Phil. Jour. Sci., **16**: 251, pl. 4, fig. 4, text fig. 2.

Rana dubita Taylor, 1920, Phil. Jour. Sci., **16**: 267—Bunawan, Agusan, Mindanao.

Material examined.—Mindanao, 26 (1 BM, type of *everetti;* 1 CAS; 4 CM; 13 CNHM; 6 MCZ; 1 USNM, type of *mearnsi*).

Diagnosis.—This subspecies of *everetti* is distinguished by its large size (adult females in excess of 80 mm.; males often exceeding 70 mm.), by the almost constant appearance of two large white tubercles below the anus, by the relatively broader head, and by the large tympanum that in males is usually equal to the eye in diameter. There are no spiny excrescences.

Remarks.—Taylor (1920) states that only one of three specimens from Bunawan, Mindanao, has the white patches below the vent. The three Leyte individuals lacking the white tubercles are young; all of the adults possess the white areas. This suggests that the character is acquired with maturity. Taylor does not give the size of his Bunawan specimens; however, their age may explain the absence of the large tubercles.

So far only three specimens of *everetti* are known from Negros, one collected on Canlaon Volcano (EHT 855) and two in or near Lake Balinsasayo (CNHM 61530–31). None of these has spiny excrescences on the back, thus differing from the Leyte population. Taylor (1920) assigned his specimen to *mearnsi,* but I do not think that these individuals can be identified with *e. everetti.* In size and body proportions they differ markedly from the Mindanao form, having narrower heads and smaller tympana and being smaller in size. With so few specimens at hand the significance of quantitative differences is uncertain. The Negros specimens cannot be placed in any of the defined subspecies with any reasonable degree of assurance.

Range.—Mindanao: Agusan Province (Bunawan); Cotabato Province (Saub, Tatayan); Davao Province (Caburan, Calian); City of Zamboanga (Zamboanga).

Rana everetti albotuberculata subsp. nov.

Type.—Museum of Comparative Zoology no. 23190, from Cabalian, Leyte. Adult male collected by E. H. Taylor, December, 1922.

Diagnosis.—A form of *everetti* with medium-sized males (average near 59 mm. in body length) and large females (average near 84 mm.); spiny excrescences scattered over dorsal surfaces; a pair of white glandular areas below anus, each area usually broken into several large granules; crossbars of hind limbs obscure or absent; tympanum of males approximately equal to eye in diameter.

Description of type.—Head longer than broad; snout obtusely pointed, projecting beyond lower jaw; canthus rostralis sharp; lores concave; tympanum slightly less than diameter of eye; light spinules concentrated on upper eyelid, canthal border, upper lip, median borders of dorso-lateral folds, the sides, upper arm, and two proximal segments of hind limb; each of white areas below vent divided into three large granules.

Color (in alcohol) of dorsal regions slate; crossbars of leg obscured; ventral surfaces cream with scattered brown spots on throat, thigh, and tibia. A nuptial pad on first finger. Other characters as in species description.

Paratypes.—Thirty topotypical specimens from the collections of the Museum of Comparative Zoology (MCZ 23188–91 and duplicates) (for individual variations see p. 307).

Range.—Leyte (Cabalian).

Rana everetti luzonensis Boulenger

Rana luzonensis Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**: 401—Lepauto (=Lepanto), Luzon; 1902, Rec. Ind. Mus., **20**: 208; Taylor, 1920, Phil. Jour. Sci., **16**: 254; 1922, op. cit., **21**: 259.

Rana guerreroi Taylor, 1902, Phil. Jour. Sci., **16**: 255—Baguio, City of Baguio, Luzon.

Rana merrilli Taylor, 1922, Phil. Jour. Sci., **21**: 164—Burdeos, Polillo Island.

Rana igorota Taylor, 1922, Phil. Jour. Sci., **21**: 260—Balbalan, Kalinga Subprovince, northern Luzon.

Rana tafti Taylor, 1922, Phil. Jour. Sci., **21**: 265—between Famy, Laguna Province, and Infanta, Tayabas Province, Luzon.

Material examined.—Luzon, 40 (4 BM, types of *luzonensis;* 8 CAS, including type of *tafti;* 2 CNHM; 20 MCZ, including paratypes of *igorota;* 5 UMMZ; 1 USNM); Polillo, 1 (CAS, type of *merrilli*).

Diagnosis.—A small form of *everetti* (males below 60 mm., females below 75 mm. in body length); the tubercles below the anus evident in about one-third of the individuals, not conspicuously lighter than surrounding areas; no spinules on dorsal surfaces; tympanum rarely larger than two-thirds of diameter of eye.

Remarks.—*Rana merrilli* Taylor is tentatively placed in this form on geographic grounds. In the character of the infra-anal tubercles the type of *merrilli* does not resemble *e. luzonensis.* In the absence of a series of the Polillo frog, no accurate statement can be made as to its relations.

Range.—Luzon: Abra Province (Lepanto); City of Baguio (Baguio); Laguna Province (near Famy, Mount Maquiling); Mountain Province (Balbalan, Bontoc, Mount Data). Polillo (Burdeos).

Rana signata Günther

Taxonomic notes.—At least four subspecies of *signata* may be distinguished. These are:

Rana signata signata Günther—Borneo, Sumatra, Malay Peninsula.
Rana signata similis Günther—Luzon, Polillo, Mindoro.
Rana signata moellendorffi Boettger—Palawan, Busuanga, Culion.
Rana signata grandocula Taylor—Mindanao, Basilan.

There has been considerable disagreement as to the relationship of these forms. In his catalogue Boulenger (1882) considered *signata* and *similis* to be distinct species; later (1920) he decided that the two forms were conspecific and placed *similis* in the synonymy of *signata.* He maintained Boettger's designation of *moellendorffi* as a separate species, although recognizing a relationship to *signata.* Boulenger at the same time described a new species, *picturata,* from Borneo and related it to *signata* and *glandulosa.* Van Kampen (1923) placed *moellendorffi, similis,* and *picturata* in the synonymy of *signata* without commenting on the existence of geographic races.

Consistent with his treatment of other groups of related forms, Taylor (1920, 1922b, 1923) considered *similis* and *moellendorffi* to be specifically distinct from each other and from *signata.* Taylor (1920, p. 273) apparently thought that the males of *signata* lacked the humeral gland (see below) for he distinguished *similis* from the former on the basis of the presence or absence of the gland. The relationship of this group of frogs was further confused by Taylor, since he named the Mindanao population twice (1920). The first name, *philippinensis*, was based on a single female individual supposedly distinguished by an opposed first finger. Beyond the statement that the character of the first finger marked *philippinensis* off from all other Philippine forms of the genus *Rana*, Taylor did not compare or relate his new form to any other. I have examined the type in the Carnegie Museum and do not find that the first finger is "opposed" to the others. In all significant characters the type does not differ from *signata*. *Rana grandocula*, the second name applied to the Mindanao form by Taylor, was based on several specimens, including males. In all important respects (color pattern, secondary sex characters, habitus) the type series shows its relationship to *signata*. Taylor indicated that *grandocula* was related to *similis*, but his failure to compare it with *signata* or even *philippinensis* is inexplicable. The name *grandocula* is used for the Mindanao form because, unlike *philippinensis*, it was based on several individuals of both sexes.

Rana yakani Taylor (1922b) was described on the basis of a large number of specimens from Basilan and several from Zamboanga, Mindanao. The original description is misleading. Taylor does not refer to the humeral gland—one of the distinctive features of this group of frogs—in the males he collected. He does indicate that the type, a female, lacks the gland, but as no female *Rana* from the East Indies is known to have such a structure this information is useless. Furthermore, the only species to which Taylor compares *yakani* is *Rana erythraea*, which *yakani* does not resemble as much as it does other Philippine forms that Taylor himself had previously described. I have examined fourteen paratypes of *yakani* from Basilan. Except for minor differences in color and in the nuptial pad (see below), these are essentially identical with *signata* from Mindanao. Certainly the distinction between Basilan specimens and those from Mindanao is much less marked than the differences separating the Calamian, Mindanao, and Luzon forms. Consequently, I do not think that *yakani* can be retained as a separate form.

Recognition of the subspecies rests upon differences in coloration, shape of the nuptial pad, size, and body proportions. Unfortunately for the convenience of the taxonomist, these characters (see below) may vary not only between subspecies but also show some tendency to vary within subspecies. For example, the color pattern exhibits considerable variation within the Bornean population of *s. signata;* indeed all of the patterns of the other subspecies may be found in Borneo. Yet there is no difficulty in distinguishing between a specimen from Mindanao and one from Luzon or Busuanga. Similarly, although it is evident that *grandocula* is the largest form, *moellendorffi* the smallest, and the others intermediate, there are also statistically significant size differences within subspecies. Apparently the species consists of populations that, though not sharply demarcated from one another, can be definitely grouped into recognizable subspecies.

Diagnosis.—Small to medium-sized frogs; digit tips with groove separating dorsal and ventral surfaces; digit tips slightly enlarged; less than twice the width of the penultimate phalanges; first finger longer than second; two metatarsal tubercles; dorso-lateral light lines present, interrupted or obscured by markings of mid-dorsum; hind limbs with crossbars; belly smooth; males with humeral glands, nuptial pads, and internal vocal sacs.

Description.—Body slender, except in large females; head longer than broad, depressed; snout obtusely pointed, tympanum distinct, one-half to two-thirds diameter of eye; dorso-lateral glandular fold present but not prominent; no supratympanic fold.

First finger longer than second; third finger more than twice length of palm; tips of fingers distinctly expanded but pads not twice width of penultimate phalanges; pads with a groove separating dorsal and ventral surfaces; fingers without a distinct fringe of skin (fig. 57, A). Hind leg slender; tips of toes dilated as fingers and with groove (fig. 57, B); webbing variable: on outer side of first toe web generally reaches midway between subarticular tubercle and disk, outer side of second and third toes usually webbed to disk, fourth toe broadly webbed to middle subarticular tubercle, fifth toe usually webbed to disk; excising of web variable (for example, web between second and third toes may be excised to level of proximal subarticular tubercle of third toe or may not be excised at all); two metatarsal tubercles, an oval inner and a round outer one; no flap of skin on outer side of fifth toe.

Skin of back smooth to granular; ventral surfaces, except that of thigh, smooth.

Color (in alcohol) of back, sides and head, light brown to dark chocolate; back and sides uniform or with lighter or darker spots; a light stripe on dorso-lateral region extending forward along edge of upper eyelid and canthus rostralis to tip of snout; stripe continuous or interrupted, varying in width from 1.5 mm. to a thin line; limbs with dark crossbars and spots; a dark spot on ventral side at insertion of arm; ventral surfaces uniform cream or with a suffusion of small dark dots; light markings of back and legs yellow, green, or red in life.

Secondary sex characters.—Males have paired internal subgular vocal sacs. The nuptial pad, present on the first finger only, does not extend beyond the subarticular tubercle and has a constriction on the median side (fig. 57, A). The males also have a small, subcircular gland in the skin of the upper arm.

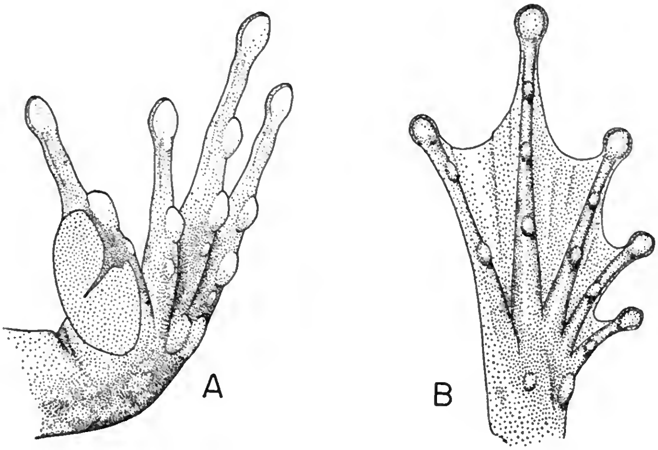


FIG. 57. *Rana signata.* A, medio-ventral view of hand (× 4); B, ventral view of foot (× 2.7).

The females are larger than the males; the latter have somewhat narrower head proportions and relatively larger tympana (see Table 27).

Ecological notes.—These frogs are found in and around wooded streams. According to my field observations in North Borneo, males calling along banks of streams are usually within two inches of the water's surface. Although *signata* generally remains on the ground, occasional individuals may get into the lower arboreal strata. Thus, Taylor (1920) observed *moellendorffi* in vines and the Philippine Zoological Expedition caught a specimen of *signata* 3 meters above the ground in a tree.

Table 27. Comparison of males and females of *Rana signata* from various Philippine Islands and Borneo

Snout-vent length

	Males			**Females**						
	No.	**Mean±SE**	**Range**	**No.**	**Mean±SE**	**Range**	**Difference of means**	***t***	***n***	**P**
Polillo.........	15	38.99±0.48	35.7-42.4	6	49.07±1.57	45.4-54.7	10.08	8.235	19	<0.001
Mindanao......	25	45.53±0.62	40.2-51.0	25	67.25±0.76	56.9-74.6	21.72	22.2	48	<0.001
Calamian[1]	5	34.18±1.01	31.2-36.4	2	51.20	51.0-51.4	17.02	—	—	—
Palawan.......	7	39.09±0.95	36.2-44.2	2	49.35	49.0-49.7	10.26	—	—	—
Borneo.........	15	42.35±1.02	35.0-46.8	5	62.32	50.6-68.7	19.97	7.734	18	<0.001
Basilan........	10	41.90±0.66	37.4-44.1	—	—	—	—	—	—	—
Luzon..........	12	41.44±0.69	36.5-44.4	—	—	—	—	—	—	—

Head length/head width

	No.	**Mean±SE**	**Range**	**No.**	**Mean±SE**	**Range**	**Difference of means**	***t***	***n***	**P**
Polillo.........	14	1.253±0.014	1.208-1.383	4	1.195	1.156-1.293	0.058	—	—	—
Mindanao......	24	1.255±0.009	1.164-1.338	25	1.134±0.009	1.008-1.216	0.121	9.831	47	<0.001
Calamian......	5	1.190±0.014	1.145-1.217	2	1.095	1.073-1.116	0.095	—	—	—
Palawan.......	6	1.172±0.013	1.128-1.241	2	1.097	1.079-1.115	0.075	—	—	—
Basilan........	10	1.247±0.013	1.179-1.297	—	—	—	—	—	—	—
Luzon..........	12	1.220±0.009	1.167-1.255	—	—	—	—	—	—	—
Borneo.........	5	1.182±0.030	1.105-1.280	—	—	—	—	—	—	—

Analysis of variance[2]

Source of variance	Mean of squares	Degrees of freedom
Within sexes..............	2008	6
Between sexes...........	15225	1

F (1,6) = 7.58; P = 0.04

Table 27. Comparison of males and females of ***Rana signata*** from various Philippine Islands and Borneo *(continued)*

Tympanum/snout-vent

	Males			Females						
	No.	Mean±SE	Range	No.	Mean±SE	Range	Difference of means	*t*	*n*	P
Polillo.........	15	0.078±0.002	0.066-0.095	4	0.074	0.073-0.075	0.004	------	---	-------
Mindanao......	25	0.077±0.002	0.055-0.095	25	0.065±0.001	0.052-0.076	0.012	5.286	48	<0.001
Calamian......	5	0.074±0.002	0.069-0.080	2	0.066	0.064-0.067	0.008	------	---	-------
Palawan.......	7	0.073±0.007	0.052-0.109	2	0.069	0.068-0.069	0.004	------	---	-------
Basilan........	10	0.083±0.002	0.073-0.090	---	------	------------	------	------	---	-------
Luzon..........	12	0.074±0.002	0.062-0.082	---	------	------------	------	------	---	-------
Borneo.........	5	0.068±0.003	0.060-0.076	---	------	------------	------	------	---	-------

Analysis of variance[2]

Source of variance	Mean of squares	Degrees of freedom
Within sexes.............	11	6
Between sexes...........	98	1

F (1,6) = 8.91; P = 0.03

[1] The Calamian "sample" consists of specimens from Busuanga and Culion. The individuals from these two islands are so similar that lumping probably does not affect statistical analysis.

[2] The three samples lacking females are not included in this analysis.

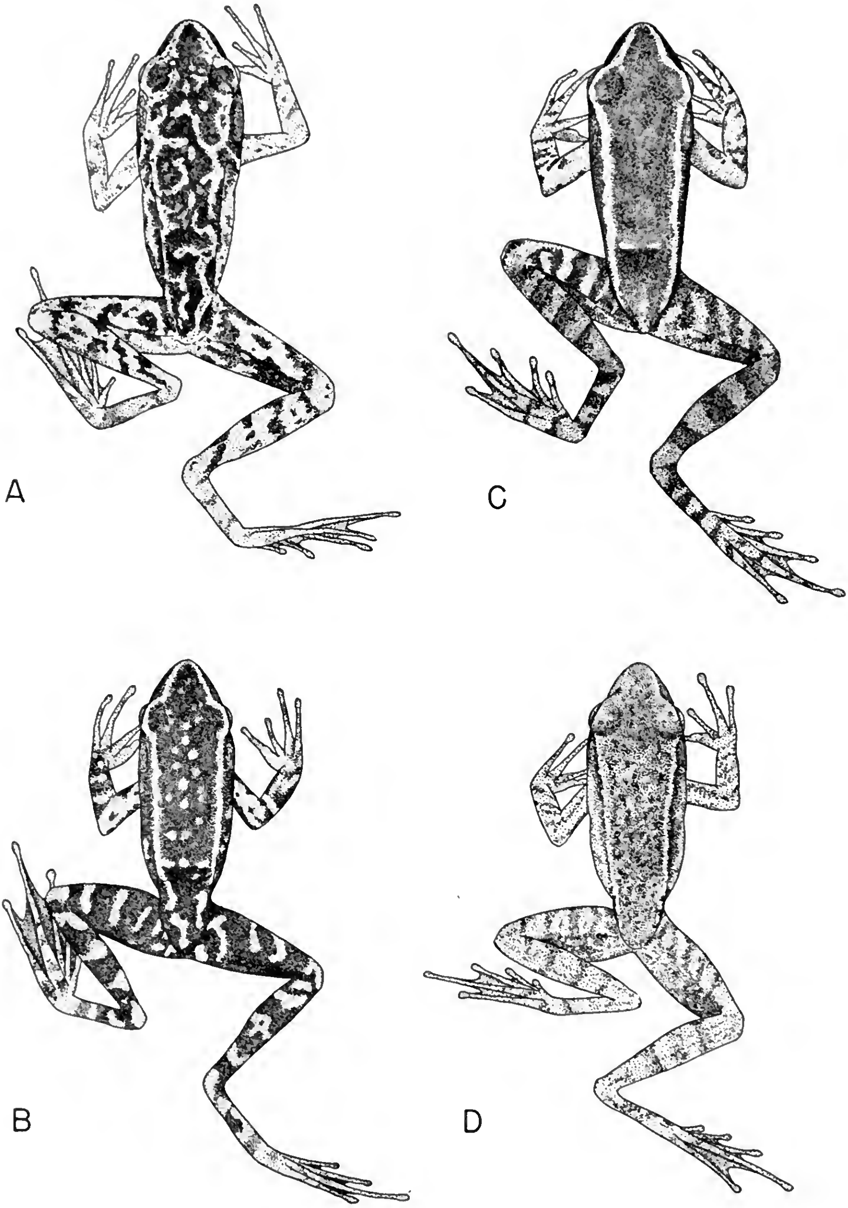


FIG. 58. A, *Rana signata moellendorffi* (× 1.1); B, *R. s. signata* (× 0.9); C, *R. s. similis* (× 1); D, *R. s. grandocula* (× 0.9).

A moderate altitudinal range is shown by *signata*. Specimens were collected from sea level to 855 meters on Palawan by members of the Philippine Expedition.

Inter-island variation.—The coloration of this species is highly variable. Basically, it consists of a light line or stripe (usually yellow in life) beginning at the tip of the snout, passing caudad along the canthus and the edge of the upper eyelid, and extending for a varying distance towards the vent in the dorso-lateral region. The lores, top of the head, back, and sides are dark brown or black with or without yellow spots. Of the Philippine material studied there is relatively little intra-island variation; the population of each island is seemingly characterized by a particular coloration type. The specimens from Luzon (*signata similis*), for example, have broad (ca. 1.5 mm.), light stripes continuous from snout to vent and sharply defined; there are no yellow spots on the back or head, these areas being an almost uniform tone of dark brown (fig. 58, C). The frogs from Polillo and Mindoro have the same type of coloration.

On Busuanga, Culion, and Palawan a different pattern is found. *Rana signata moellendorffi* from these islands has large irregular yellow (cream in alcohol) spots on the back and sides. There are almost equal amounts of black and yellow. The irregular masses of color may extend across the dorso-lateral area so that the broad dorso-lateral stripe is sometimes interrupted in several places. Usually the line is discernible to the vent (fig. 58, A).

A third variant occurs on Mindanao. Specimens from there have very thin dorso-lateral light lines, uninterrupted from snout to vent. Occasionally the head is of such a light color that the stripe is not clearly defined along the canthi. The light line is bordered laterally by a dark line; the median border is not sharply demarcated. There are no yellow spots on the sides or back, but these areas are mottled with lighter and darker brown (fig. 58, D). This pattern is also found in specimens from Basilan.

No single coloration type is characteristic on Borneo (type locality of *signata* Günther, *obsoleta* Mocquard, and *picturata* Boulenger). The dorso-lateral light stripes may be thin (ca. 0.5 mm.) or broad (1.5 mm.) (fig. 58, B); they may be continuous from snout to vent (11 out of 25 specimens), continuous from snout to sacral region (2), interrupted at several points by black areas from back or sides (5), or distinct only on the canthus and upper eyelid (7). The yellow of the back may take the form of large irregular patches as

Table 28. Geographic variation in size and some body proportions in *Rana signata*[1]

	Sex	Difference of means	*t*	*n*	P
Snout-vent length					
Luzon—Polillo	♂	2.45	2.991	25	0.008
Luzon—Mindanao	♂	4.09	4.042	35	< 0.001
Luzon—Palawan	♂	2.35	2.026	17	0.06
Luzon—Calamian	♂	7.26	5.761	15	< 0.001
Polillo—Mindanao	♂	6.54	7.423	38	< 0.001
Mindanao—Basilan	♂	3.63	3.392	33	0.003
Mindanao—Borneo	♂	3.18	2.814	38	0.009
Mindanao—Palawan	♂	6.44	5.070	30	< 0.001
Basilan—Palawan	♂	2.81	2.509	15	0.03
Palawan—Borneo	♂	3.26	1.964	20	0.07
Palawan—Calamian	♂	4.91	3.482	10	0.008
Mindanao—Borneo	♀	4.93	2.231	28	0.04
Mindanao—Polillo	♀	18.18	10.5	29	< 0.001
Head length/head width					
Luzon—Polillo	♂	0.033	1.970	24	0.06
Luzon—Mindanao	♂	0.035	2.594	34	0.015
Luzon—Palawan	♂	0.048	3.186	16	0.008
Mindanao—Borneo	♂	0.073	3.163	27	0.007
Mindanao—Palawan	♂	0.083	4.446	28	< 0.001
Basilan—Palawan	♂	0.075	3.841	14	0.004
Basilan—Borneo	♂	0.065	2.338	13	0.04
Tympanum/snout-vent					
Mindanao—Borneo	♂	0.009	2.000	28	0.055
Basilan—Borneo	♂	0.015	4.775	13	< 0.001

[1] Only those inter-island differences approaching statistical significance are listed. Means and ranges are given in Table 27.

in *moellendorffi* (15 specimens), small round dots (2), or a wavy vertebral line; six specimens have no yellow (or cream) on the back, but are mottled with different shades of brown as is the Mindanao form. The various stripe types are combined at random with the various types of mid-dorsal coloration.

Although the general characteristics of the nuptial pad are the same throughout this species, there are certain minor distinctions to be made between populations. In the Leyte and Luzon males the latero-proximal limit of the pad is at the junction of the first and second fingers, the median edge of the pad coinciding with the dorso-median edge of the first finger. In Bornean males the latero-proximal limit of the pad does not quite reach the juncture of the two fingers. Also, the dorso-proximal border is more transverse than in the preceding, resulting in a more attenuated medio-proximal portion.

Table 29. Comparison of subspecies of *Rana signata*. Only males were used.

Snout-vent length

Form	No.	Mean±SE	Range
signata............	15	42.35±1.02	35.0-46.8
grandocula........	35	44.49±0.55	37.4-51.0
similis.............	33	40.19±0.44	35.7-44.4
moellendorffi.....	12	37.04±0.98	31.2-44.2

Form	Difference of means	*t*	*n*	P
signata–grandocula..........	2.14	1.981	48	0.055
signata–moellendorffi.......	5.31	3.662	25	0.002
grandocula–moellendorffi..	7.45	6.772	45	<0.001
grandocula–similis..........	4.30	6.056	66	<0.001
similis–moellendorffi.......	3.15	3.387	43	0.003

Head length/head width

Form	No.	Mean±SE	Range
signata............	5	1.182±0.030	1.105-1.280
grandocula.......	34	1.253±0.007	1.164-1.338
similis............	32	1.230±0.009	1.110-1.383
moellendorffi....	11	1.180±0.009	1.128-1.241

Form	Difference of means	*t*	*n*	P
signata–grandocula..........	0.071	3.276	37	0.004
signata–moellendorffi.......	0.002	<1.0	14	-------
grandocula–moellendorffi..	0.073	5.268	43	<0.001
grandocula–similis..........	0.023	2.044	64	0.05
similis–moellendorffi.......	0.050	3.062	41	0.006

Composition of samples: *R. s. grandocula:* Mindanao 25, Basilan 10. *R. s. signata:* Borneo 15. *R. s. moellendorffi:* Palawan 7, Busuanga 2, Culion 3. *R. s. similis:* Polillo 15, Luzon 12, Mindoro 3, Leyte 3.

Generally the males of Mindanao and Polillo resemble those from Luzon in this respect, whereas males from Mindoro, Palawan, Busuanga, and Culion resemble those from Borneo. In males from Basilan the constriction of the nuptial pad is complete, resulting in a divided structure. The divided pad has been observed in seven out of ten males from Basilan, two out of four from Mindoro, two of fifteen from Luzon, two of twenty-four from Mindanao, one of seven from Palawan, two of five from the Calamian Islands, and two of fourteen from Borneo.

The populations also differ in size and some body proportions (see Tables 27 and 28). In most cases not enough females were available, so that comparison of populations is almost limited to males. Only those differences approaching statistical significance are listed in Table 28.

As noted, three subspecies of *signata* occur in the Philippines. When the data for all populations of a subspecies are lumped and a comparison of subspecies is made on the basis of these data, the results (Table 29) support the division of forms based on coloration, body proportions, and nuptial pad shape.

Rana signata grandocula Taylor

Rana grandocula Taylor, 1920, Phil. Jour. Sci., **16**: 274, pl. 7, fig. 2—Bunawan, Agusan Province, Mindanao.

Rana philippinensis Taylor, 1920, Phil. Jour. Sci., **16**: 266—Mindanao.

Rana yakani Taylor, 1922, Phil. Jour. Sci., **21**: 262, pl. 1, fig. 1, pl. 2, fig. 1—Abungabung, Basilan.

Material examined.—Mindanao, 92 (45 CNHM; 5 CM, including type of *philippinensis* and 4 paratypes of *grandocula;* 6 MCZ; 2 UMMZ; 34 USNM); Basilan, 14 (11 MCZ; 3 UMMZ; all paratypes of *yakani*); Bohol, 1 (MCZ).

Diagnosis.—A large form of *signata* (body length of males about 45 mm., females 67 mm.); dorso-lateral light lines narrow (less than 1 mm.) with indistinct median border; mid-dorsum usually light with irregular mottling of darker pigment; light line on upper eyelid and canthus rostralis indistinct (fig. 58, D).

Remarks.—There is a great deal of variation in the nature of the skin in this form. Most of the individuals examined have shagreened skin, although the full range from smooth to coarsely granular skin is found.

The specimen (female) from Bohol resembles others from Mindanao. The skin of the back is slightly more granular than in most Mindanao females. However, the coloration and large size (74 mm.) clearly indicate relationship to *signata grandocula.*

Range.—Bohol. Mindanao: Agusan Province (Bunawan); Cotabato Province (Burungkôt near Upi, Tatayan); Davao Province (Badiang near Tagabuli, Baganga River, Caburan, Mount McKinley, Maco and Sitio Taglawig near Tagum, Todaya on Mount Apo); City of Zamboanga (Caldera). Basilan (Abungabung, Maluso, Port Holland).

Rana signata similis Günther

Polypedates similis Günther, 1873, Proc. Zool. Soc. London, **1873**: 171—Laguna del Bay, Luzon.

Rana similis Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 72; Taylor, 1920, Phil. Jour. Sci., **16**: 271, pl. 4, fig. 5; 1922, Phil. Agriculturist, **11**: 129.

Rana signata Boulenger, 1920, Rec. Ind. Mus., **20**: 177.

Material examined.—Polillo, 41 (40 CAS; 1 MCZ); Luzon, 20 (16 CAS; 4 CM); Mindoro, 4 (MCZ): Leyte, 6 (MCZ).

Diagnosis.—A medium- to small-sized form of *signata* (body length of males about 40 mm.). Distinguished by the broad (over 1 mm.) dorso-lateral stripe with distinct margins. Mid-dorsum usually uniform dark brown. Light line prominent on upper eyelid and canthus rostralis (fig. 58, C). Skin smooth to shagreened, never granular as in some specimens of *s. moellendorffi* and *s. signata.*

Remarks.—The inclusion of the Leyte population in this form is done with hesitation. In the collections of the Museum of Comparative Zoology there are two groups of specimens with the locality "Cabalian, Leyte." Both groups were purchased from E. H. Taylor, the collector. The first series (MCZ 14217–22 = EHT 2297–98, 2300–03) resembles specimens from Luzon. The second series (MCZ 23181–85 plus duplicates = EHT 276–77, 280, 997, 1363–4, 2281) resembles specimens from Mindanao. Checking these field numbers against the cards (in possession of the Museum of Comparative Zoology) on which Taylor listed his material indicates that the locality data for the second series are doubtful because some of the field numbers are listed from two islands and others not at all. The locality information for the first group (*similis*-like) appears to be correct. If both series do indeed come from Cabalian, the Leyte population must be considered as intermediate between *similis* and *grandocula.*

Range.—Polillo. Luzon: Bataan Province (Taylor, 1920); Laguna Province (Los Baños, Mount Maquiling); Laguna del Bay (Günther, 1873). Mindoro. Leyte (Cabalian).

Rana signata moellendorffi Boettger

Rana moellendorffi Boettger, 1893, Zool. Anz., **16**: 363—Culion; Boulenger, 1920, Rec. Ind. Mus., **20**: 180; Taylor, 1920, Phil. Jour. Sci., **16**: 270, pl. 1, fig. 4.

Rana signata van Kampen, 1923, Amph. Indo-Austr. Arch., p. 226.

Material examined.—Culion, 12 (CNHM); Busuanga, 2 (CNHM); Palawan, 11 (1 BM; 2 CAS; 5 CNHM; 3 UMMZ).

Diagnosis.—A small form of *signata* (body length of males about 37 mm., females 50 mm.); distinguished from other forms by the irregular light markings of the mid-dorsum; dorso-lateral light line obscured by mid-dorsal pattern; light line distinct on upper eyelid and canthus rostralis (fig. 58, A); skin shagreened to coarsely granular.

Range.—Busuanga (Dimaniang). Culion (San Pedro). Palawan (Brooke's Point, Lapulapu near Iwahig, Puerto Princesa, Tigoplan River near Brooke's Point).

Rana melanomenta Taylor

Rana melanomenta Taylor, 1920, Phil. Jour. Sci., **16**: 268—Papahag Island, Sulu Islands.

Material examined.—None.

Taxonomic remarks.—Taylor states that *melanomenta* is closely related to *similis* (=*signata similis*), *grandocula* (=*signata grandocula*), and *glandulosa.* As he points out, it differs from these in not having a humeral gland. In the dorsal color and the external vocal sacs, it resembles *glandulosa* more than *signata.*

The following is adapted from the original description:

Description.—A small frog (type 35 mm. snout to vent); snout rounded; tympanum distinct, three-fifths diameter of orbit; no dorso-lateral fold; fingers with small disks with a horizontal, circummarginal groove; first finger longer than second; web does not reach disk of any toe except as a narrow fringe; two metatarsal tubercles.

Color in life lavender brown above with a few small dark spots; sides of head and tympanum black; throat black, sometimes with small white spots; belly dusky; limbs with crossbars; no dorso-lateral light lines.

Secondary sex characters.—Males with nuptial pad on first finger, and paired, subgular, external vocal sacs. No humeral gland.

Ecological notes.—The type series was collected near forest pools.

Range.—This species is known only from Papahag Island in the Sulu Archipelago.

Rana erythraea Schlegel

Hyla erythraea Schlegel, 1837, Abbild. Amph., p. 27, pl. 9, fig. 3—Java.

Rana erythraea Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 65, text fig.; 1920, Rec. Ind. Mus., **20**: 152; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 121; Taylor, 1920, Phil. Jour. Sci., **16**: 249, pl. 1, fig. 2, text fig. 1; 1922, op. cit., **21**: 264; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 222; Mertens, 1934, Arch. Hydrobiol., **12**, Suppl. (Trop. Binnengew.), **4**: 684.

Hylorana erythraea Fischer, 1885, Jahrb. Hamburg Wiss. Anst., **2**: 80.

Material examined.—Tablas, 10 (MCZ); Sibuyan, 4 (CAS); Panay, 57(7 CNHM; 50 USNM); Negros, 88 (43 CAS; 44 CNHM; 1 USNM); Java, 11 (USNM); Borneo, 6 (2 BM; 4 MCZ); Siam, 4 (CNHM); Sumatra, 1 (BM); Great Natuna, 2 (BM); Nias, 3 (BM).

Diagnosis.—Small (male) to moderately large (female) frogs with distinctly expanded digit tips; disks with a circummarginal horizontal groove; a ridge of skin along the fifth metatarsal but no fold; two metatarsal tubercles; a broad cream dorso-lateral stripe from eye to leg; leg with a longitudinal pattern of dark dots or lines alternating with light lines; no crossbars on leg (fig. 47).

Description.—Body elongate; head longer than broad; snout obtusely pointed; tympanum distinct, four-fifths to slightly larger than diameter of eye; dorso-lateral fold broad, prominent; no supratympanic fold.

Fingers long with a horizontal groove around terminal disks; first finger longer than second; third almost twice the length of the palm; a distinct fringe of skin on inner side of second and third fingers; a tubercle on each metacarpal. Foot very long, longer than tibia; web reaching disk on outer side of first, second, and third toes and on inner side of fifth; fourth toe webbed to distal tubercle; an oval inner and usually a smaller round outer metatarsal tubercle; a fringe of skin along outer side of fifth toe and inner side of first.

Skin of back smooth or shagreened (with exceptions noted below); skin of throat and belly smooth except in males.

Color of back and sides in life olive to yellow-green, in alcohol olive-brown or slate; broad light (cream or yellow) stripe on dorsolateral fold, stripe running between eyelid and groin; except for white lip, head colored as back; ventral surfaces cream; dorsal surfaces of legs olive-brown with dark markings arranged longitudinally in lines; no crossbars.

Secondary sex characters.—According to Boulenger (1920) and van Kampen (1923), males of *erythraea* have vocal sacs. I have examined adult males from the Philippines, Borneo, Great Natuna, Sumatra, and Nias; none has vocal sacs. Mr. C. M. Bogert of the American Museum of Natural History very kindly examined two adult males from Java for me, and he reports that these also lack vocal sacs.

A nuptial pad is present on the first finger in males. The pad extends from the wrist to the level of the subarticular tubercle on the medio-dorsal surface of the finger.

Other structures found only in the males are clear white asperities occurring on the chin and on the back. Individual variation in this character is evident; in some males the spinules are distributed over the entire back, in others on the posterior part only. The asperities are present in all adult males from the Philippine Islands and, according to Mr. Bogert, in the two Javanese males.

Finally, sexual dimorphism in size and some body proportions may be pointed out. Only the Negros sample could be used for this purpose, as the others were either too small or consisted of poorly preserved material. The data (Table 30) show that the females are much larger than the males, but that the head length and the diameter of the tympanum, both relative to snout-vent length, are greater in the males.

Ecological notes.—This species is invariably found in the vicinity of water. Reports in the literature (Boulenger, 1920; Taylor, 1920; Mertens, 1934) associate *erythraea* with ponds, rice fields, and other aquatic habitats with little or no current. A series of sixteen specimens from Dumaguete, Negros, was collected along a river bank; twelve specimens were taken along a creek near Lake Balinsasayo, Negros. This suggests that the Philippine populations have a slightly wider habitat range, relative to current, than those on the Sunda Islands and the Malay Peninsula. The long legs, extremely large feet, and extensive webbing are of obvious use in swimming and undoubtedly are of equal importance in the known ability (Boulenger, 1912; Mertens, 1929b) of *erythraea* to skitter over the water.

Boulenger credits *erythraea* with a limited altitudinal distribution at low elevations. However, Mertens (1934), although noting a greater abundance in the low altitudes, states that *erythraea* does occasionally get into the mountains, at least in Sumatra and Java. It is perhaps significant that the usual habitat of the species, standing water, is found in the mountains in those islands in the form of terraced rice fields. On Negros *erythraea* is found from sea level (Dumaguete) to 915 meters (Lake Balinsasayo).

Inter-island variation.—The samples examined show little intraspecific variation. Taylor (1922b) states that the Philippine populations are characterized by the presence of a small outer metatarsal tubercle, thus differing from continental populations, which, according to Taylor, lack the tubercle. But three of four Siamese specimens examined in this study have an outer tubercle and occasional Philippine specimens do not.

Table 30. Comparison of adult males (25) and females (22) of *Rana erythraea* from Negros

Snout-vent length

Sex	**Mean±SE**	**Range**	**Difference of means**	*t*	**P**
Females	71.28±0.66	66.0-76.1	29.24	29.53	<0.001
Males	42.04±0.73	36.6-48.5			
		Tympanum diameter/snout-vent			
Males	0.100±0.002	0.09-0.13	0.027	11.416	<0.001
Females	0.073±0.001	0.05-0.08			
		Head length/snout-vent			
Males	0.405±0.003	0.387-0.439	0.036	7.620	<0.001
Females	0.369±0.004	0.352-0.389			

Some geographic variation is evident in size. Again the lack of material restricts comparison. Eight adult females from Java range in size from 65.7 to 71.8 mm. (mean=68.76±0.62 mm.). This is somewhat smaller than the length of the Negros females (mean 71.28±0.66 mm.; see Table 30). Comparison of these two means gives the following results: t=2.495; P=0.02. Six adult males from Tablas range in length from 31.5 to 42.8 mm., mean=38.98±1.81 mm. This is not significantly different from the mean of Negros males, 42.04±0.73 mm.; t of the difference equals 1.770 and P equals 0.09.

Range.—Tablas Island. Sibuyan Island. Panay: Capiz Province (Estancia); Iloilo Province (Ajuy, Iloilo, Pototan). Negros: Negros Occidental Province (Hinigaran [Taylor, 1920]); Negros Oriental Province (Dumaguete, Lake Balinsasayo, Pagyabunan, Mabaha). Mindanao (Fischer, 1885). The species also occurs in Celebes, Borneo, Java, Sumatra, and the peninsula of southeastern Asia.

The only record of *erythraea* from Mindanao dates from 1885. The extensive collecting of E. H. Taylor and the Philippine Expedition in suitable habitats on Mindanao failed to locate any specimens. Since this species is very abundant in areas where it exists, one would expect recent collectors to have discovered it if it did occur on Mindanao. In view of this failure, the present existence of *erythraea* on Mindanao must be doubted.

In all likelihood the gap in the distribution between Borneo and Panay is a real one and one that is difficult to explain. Certainly suitable habitats are available on both Palawan and Mindanao. Also the local abundance of *erythraea* testifies to its biological success.

Annandale (*in* Boulenger, 1920) says it is "particularly abundant" in the Malay Peninsula. Taylor (1920) refers to "incredible numbers" on Negros. An expedition sent by the United States Navy collected over 200 at Iloilo, Panay, in three days. Consequently, if a former continuous range has become disjunct as a result of local extinction, the cause would seem to lie in the biotic environment. But a comparison of the ranid faunas of Palawan, Mindanao, Borneo, and Negros indicates that the explanation for the absence of *erythraea* from Mindanao and Palawan is not to be found in the biota. Both of the last islands have what amounts to reduced Bornean ranid faunas. If *erythraea* cannot compete with a group of aquatic ranas on Mindanao, how can one explain its ability to do so on Borneo? Or, if a predator is responsible for its absence on Mindanao, why does not the same predator affect other aquatic ranas in the same adverse fashion?

Apparently a different explanation is necessary. The random pattern of distribution of *erythraea* within the Philippines is suggestive of waif dispersal (see p. 484).

Rana sanguinea Boettger

Rana sanguinea Boettger, 1893, Zool. Anz., **16:** 364—Culion; Taylor, 1920, Phil. Jour. Sci., **16:** 259, pl. 5, fig. 2; 1922, op. cit., **21:** 264.

Rana varians Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14:** 86—Palawan.

Rana papua van Kampen, 1923, Amph. Indo-Austr. Arch., p. 201.

Material examined.—Palawan, 13 (7 BM, types of *varians* Boulenger; 3 CNHM; 3 USNM); Culion, 4 (2 CNHM; 2 MCZ); Busuanga, 2 (CAS); Celebes (*papua*), 13 (9 MCZ; 1 UMMZ; 3 USNM).

Taxonomic notes.—This frog is obviously a member of the *Rana papua* wood-frog group (van Kampen, 1923). The range of the frogs of this group (see fig. 94) is disjunct. The largest gap occurs between Celebes and Palawan. Other breaks are present between Ceram and Celebes and between Wetar and Flores in the Lesser Sunda Islands. Some of these gaps may be due to inadequate collecting. This may very well be the explanation for the last two. The islands between Celebes and Ceram and those separating Flores and Wetar have not been well explored. Extensive collections have been made on Borneo, particularly in Sarawak and British North Borneo, in the type of habitat favored by *papua.* The recent Philippine Expedition failed to find a representative of the *papua* group on Mindanao although, again, the proper type of habitat was thoroughly examined. The size and habits of this group are such as to make it one of the conspicuous Salientia. In view of these factors the lack of records from Borneo and Mindanao probably reflects an actual absence of the *papua* group from these islands. Two possible explanations for the observed distribution are available: (1) The present range may be a contracted and fragmented one, assuming that Borneo and/or Mindanao once contained populations that have become extinct; (2) the population on Palawan and the Calamians may represent the result of accidental dispersal. More than 800 kilometers separate Celebes from Palawan. Aside from the obstacle of distance, this hypothesis assumes that the frogs could have been transported between these two points without establishing populations on the large intermediate land masses. This portion of the distribution certainly does not resemble a theoretical dispersal pattern based on waifing. The possibility of a land bridge is hardly worthy of consideration, for the only conceivable bridge is through Borneo. Consequently, the explanation assuming extinction is the most probable.

The Philippine population can be distinguished from Moluccan *papua* by several characters. In the series from Celebes (13) available to me the dark spot or bar on the ventral surface of the upper arm is farther distad than in *sanguinea;* also, the pectoral spot is more lateral in the Celebes series, being at the insertion of the arm. Another pigmentation difference involves the dark spots on the sides, found in all but one of the *sanguinea* series. None of the specimens from Celebes has these spots. The color of the exceptional *sanguinea* has faded in the preservative so that I can not say with certainty that it lacks the spots. A third character distinguishing *sanguinea* is the absence of vocal sacs, which are present in the males of the remainder of the *papua* group.

I consider *sanguinea* a full species rather than a subspecies of *papua*. It appears safe to assume that the distance separating *sanguinea* from the nearest population of *papua* (on Celebes) is great enough to rule out continued dispersal between the two and, hence, the exchange of genes.

Diagnosis.—A slender, long-legged frog; small (males) to medium-sized (females); digit tips with horizontal groove separating dorsal and ventral surfaces; digit tips slightly enlarged, less than twice the width of penultimate phalanges; first finger longer than second; two metatarsal tubercles; distinct dorso-lateral fold; no dorso-lateral light line; a sharply defined dark mask over lores and temporal region; hind limbs with crossbars; belly smooth; males without humeral gland or vocal sacs; males with nuptial pad on first finger (see fig. 48).

Description.—Body slender, legs long; head longer than broad; snout long, obtusely pointed, projecting beyond lower jaw; tympanum distinct, two-thirds to equal to diameter of eye; dorso-lateral fold present, thin; no supratympanic fold.

First finger longer than second; third finger about twice length of palm; tips of digits expanded to slightly wider than penultimate phalanges; pads with horizontal groove separating dorsal and ventral surfaces; fingers without a fringe of skin. Hind leg long; web to disk on outer side of first, second, and third toes, to disk on inner side of fifth toe, and to distal subarticular tubercle of fourth toe; web shallowly excised; an oval inner metatarsal tubercle and a smaller round outer one; no flap of skin on outer side of fifth toe and metatarsal.

Skin of back with small granules; sides and ventral surfaces smooth; medio-ventral surface of thigh granular.

Color (in alcohol) of back and top of head pale brown to reddish chocolate; upper lip and lower half of lores lighter, usually cream; a very dark brown sub-rhomboid spot with one corner just dorsad of arm insertion extending over tympanum and upper half of lores; lower lip marked with dark brown; sides darker than back, fading to cream ventrally and with scattered dark spots; gular region cream with light suffusion of brown; pectoral and abdominal regions cream; a pair of brown spots in pectoral region near mid-line; limbs same ground color as back, with darker crossbars; a dark stripe frequently along outer posterior margin of arm; a conspicuous dark bar on medio-ventral part of upper arm.

Secondary sex characters.—Boulenger (1894a), in describing *varians* (=*sanguinea*) from Palawan, stated that the males had internal vocal sacs. However, neither Dr. H. W. Parker of the British Museum nor I can find vocal sac openings in Boulenger's types. Vocal sacs have not been observed in other adult males from Palawan, Busuanga, and Culion. A nuptial pad with only a slight lateral constriction is present on the first finger of males; the pad extends distally as far as the level of the subarticular tubercle. There are no humeral glands.

The sexes differ markedly in size and slightly in relative head widths. Pertinent data are given in Table 31.

Ecological notes.—Little information is available on the preferred habitat of *sanguinea*. Other members of the *Rana papua* group are

Table 31. Sexual differences in *Rana sanguinea*

Sex	No.	Mean±SE	Range	Difference of means	*t*	*n*	P
Snout-vent length							
Females	8	65.7±2.34	53.3-73.1	28.0	10.159	14	<0.001
Males	8	37.7±1.45	32.4-43.4				
Head width/snout-vent							
Females	8	0.316±0.003	0.307-0.328	0.020	3.123	14	0.009
Males	8	0.296±0.006	0.272-0.316				

found in the vicinity of water in forested regions, and presumably the same is true of *sanguinea.* All but one of the specimens collected by the Philippine Expedition were captured near streams or pools. The altitudinal range of *sanguinea* as indicated by the specimens examined is from sea level to 760 meters.

Inter-island variation.—Not enough specimens were examined to comment on intraspecific variation.

Range.—Palawan (Lapulapu near Iwahig, Pancol, Puerto Princesa, Tigoplan near Brooke's Point). Culion (Mahupa, San Pedro). Busuanga.

Rana nicobariensis nicobariensis Stoliczka

Hylorana Nicobariensis Stoliczka, 1870, Jour. Asiatic Soc. Bengal, **39**: 150, pl. 9, fig. 2—Nicobar Islands.

Rana nicobariensis Boulenger, 1885, Ann. Mag. Nat. Hist., (5), **16**: 389; 1891, op. cit., (6), **8**: 291; 1912, Fauna Malay Pen., Rept. Batr., p. 240; 1920, Rec. Ind. Mus., **20**: 162; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 224.

Rana chalconota (part) van Kampen, 1923, Amph. Indo-Austr. Arch., p. 217.

Rana sanchezi Taylor, 1920, Phil. Jour. Sci., **16**: 256—northern Palawan.

Rana suluensis Taylor, 1920, Phil. Jour. Sci., **16**: 264—Tawi-Tawi Island, Sulu Archipelago; 1922, op. cit., **21**: 258, pl. 1, fig. 2.

Material examined.—Palawan, 1 (CAS); Sulu Islands, 3 (2 CAS; 1 MCZ, paratype of *suluensis*); Borneo, 3 (2 CNHM; 1 USNM); Nias, 5 (MCZ); Sumatra, 1 (USNM); Mentawei Island, 34 (RM).

Taxonomic notes.—The relations of the Philippine frogs of this species have not been set forth with any degree of clarity. The original descriptions of *sanchezi* and *suluensis* are confusing, since Taylor compared his specimens only with *sanguinea, everetti,* and *chalconota,* to which they are not closely related. The only noteworthy difference between the single *sanchezi* and the three *suluensis* specimens I have seen is the difference in the size of the finger pads. As pointed out by Taylor the disks of *sanchezi* are slightly larger and more truncate than those of specimens from the Sulu Archipelago.

The slender habitus, elongate snout, large tympanum, and strongly granular dorsal surface are indicative of the close relation between *nicobariensis* and the two forms described by Taylor. I have been unable to find any characters that would serve to separate *suluensis* from *nicobariensis*. It may be necessary, after a comparison based on larger samples, to distinguish *sanchezi* from *nicobariensis* as a subspecies. However, until such a comparison is possible, *sanchezi* should be made a strict synonym of *nicobariensis*. Van Kampen tentatively placed *sanchezi* in the synonymy of *chalconota*. However, it differs from the latter in having a smooth belly, much smaller finger disks, and a much more elongate snout.

Mertens (1927) has re-established the form, *nicobariensis javanicus* Horst, including in it specimens from Java and Bali. Pending additional material from the Philippines, *sanchezi* and *suluensis* are placed in the typical subspecies.

Diagnosis.—A slender, medium-sized frog (35–50 mm.) with elongate snout; skin of back strongly granular with scattered large tubercles; dorso-lateral folds present, usually very prominent; first finger equal to or longer than second; tips of digits expanded into disks with a circummarginal groove.

This species may be confused with individuals of *signata* in which the light lines are not obvious on the edge of the eyelid and in which the skin is strongly granular, but the narrow, elongate head and scattered dorsal tubercles of *nicobariensis* should permit distinction of all individuals of these two species.

Description.—Body slender; head much longer than broad; snout elongate, obtusely pointed; tympanum distinct, three-fourths to one times diameter of eye; a conspicuously raised and narrow dorsolateral fold almost always present (type of *suluensis* Taylor with folds); no dermal fold from eye to arm insertion.

Tips of fingers and toes expanded; disks less than twice diameter of penultimate phalanges, with circummarginal grooves; first finger usually longer than, though occasionally same length as, second; third finger over twice length of palm; fingers with fringe of skin. Hind limbs slender, long; web usually reaching subarticular tubercle on outer side of first and second toes; web to distal tubercle on outer side of third toe, somewhat farther on fifth toe; fourth toe webbed only to middle subarticular tubercle; a small oval inner metatarsal tubercle and a smaller round outer one; no flap of skin along fifth metatarsal.

Skin of head and back strongly granular, with a few distinct tubercles irregularly scattered; sides with scattered tubercles; ventral surfaces smooth.

Color (in alcohol) brown above, uniform or marked with a darker reticulation or spots; lores and temporal region dark brown, gradually fading posterior to tympanum; lips cream or white; ventral surfaces cream or white, uniform or with a few indistinct spots; legs with dark crossbars.

Secondary sex characters.—The males have paired internal vocal sacs located at the sides of the throat. The round openings are situated near the corners of the mouth. Males also have a nuptial pad extending from the base of the first finger to the level of the subarticular tubercle. Distally it occupies the dorsal and median surfaces of the finger, but near the base of the finger it is limited to the median surface. The humeral glands are well developed, being elongate and extending almost the entire length of the upper arm.

The females are larger than the males. Sex dimorphism in snout-vent length observed in the Mentawei sample is as follows:

	No.	Mean±SE mm.	Range mm.
Females	9	49.81±0.64	46.7–52.4
Males	25	40.29±0.52	35.7–46.2

Difference of means=9.52; t=10.03; P=<0.001

Ecological notes.—Taylor (1920) found specimens in leaf litter away from water and others (1922b) along a small stream. Mertens (1930) discovered specimens in the grass of coffee groves. In North Borneo *nicobariensis* is associated with man. It is common in drainage ditches beside roads and along small streams in large clearings and cultivated areas.

Rana nicobariensis has been collected only at low elevations in the Philippine Islands. In other parts of its range it is distributed up to 1,400 meters (van Kampen, 1923).

Range.—Palawan. Sulu Archipelago: Jolo; Tawi Tawi. This species is also found from Bali to the Malay Peninsula and Borneo.

Staurois Cope

According to Noble and succeeding authors the primary distinguishing character of *Staurois* is the specialization of the larvae.

The large abdominal sucker and modified mouth parts fit the larvae for a life in strong currents and thus effect a change of adaptive zone from the genus *Rana*. This is the kind of generic difference referred to above (p. 195).

Unfortunately, present identification of *Staurois* tadpoles leaves something to be desired. The Chinese forms are relatively well known (Liu, 1950). Among the Indo-Malayan species only the larvae of *whiteheadi* Boulenger and *cavitympanum* Boulenger can be said to be identified. Boulenger (1893) had a metamorphosing larva of the latter with erupted forelimbs and larval mouth parts; the color pattern illustrated in Boulenger's plate very closely resembles that of the figured adult. According to his statement, Boulenger had all stages of development of another *Staurois* tadpole that he assigned to *whiteheadi*. Two *Staurois* larvae from Java have been identified as *jerboa* Günther. Boulenger's opinion (1893) was based on the fully webbed toes and large digital disks of the tadpole; van Kampen (1907), while tentatively assigning Boulenger's larva to *hosii* Boulenger, identified the second one as *jerboa* because adults of the latter occurred in the same stream. Mocquard (1890) described a *Staurois* tadpole from Mount Kina Balu; he suggested that it was the larva of *Ixalus nubilus* Mocquard (=*Staurois natator* Günther). He adduced as evidence the agreement in details of the fore and hind limbs with those of adult *nubilus*. Examination of these details (as given in Mocquard's description)—toes fully webbed, outer metatarsals separated, one metatarsal tubercle, first and second fingers of equal length—indicates that the larva could as readily be identified as *hosii*. Of interest is the fact that as yet no *Staurois* tadpole has been found in the Philippine Islands, though numerous adults of *natator* have been collected.

Excluding *natator* Günther, *guttatus* Günther, and *tuberilinguis* Boulenger, adults of the species that have been assigned to *Staurois* (Noble, 1931; Liu, 1950) usually have an extra subarticular tubercle at the base of the third and fourth fingers, long fingers, and non-forked omosterna; in short, most of the characters of adult *Hylarana*. The three excepted forms differ only in lacking the extra supernumerary tubercle on the fingers. This difference, in our present state of ignorance, seems trivial. But the additional fact that the larvae of these species are not known makes their current generic designation questionable. No change in the status of *natator* is made, although the possibility that it is a *Micrixalus* should not be ignored.

Staurois natator Günther

Ixalus natator Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 75, pl. 4, fig. C—Philippines.

Staurois natator Cope, 1865, Nat. Hist. Rev., **1865**: 117; Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 87; 1918, op. cit., (9), **1**: 374; Taylor, 1920, Phil. Jour. Sci., **16**: 277, pl. 4, figs. 2 and 2a; 1922, op. cit., **21**: 269.

Ixalus guttatus Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 76, pl. 4, fig. D—Borneo.

Staurois guttatus Cope, 1865, Nat. Hist. Rev., **1865**: 117; Boulenger, 1918, Ann. Mag. Nat. Hist., (9), **1**: 374; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 235.

Rana guttata Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 87.

Rana natatrix Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 71.

Ixalus nubilus Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **2**: 153, pl. 11, fig. 3—Palawan.

Staurois nubilus Boulenger, 1918, Ann. Mag. Nat. Hist., (9), **1**: 374; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 236.

Material examined.—Mindanao, 244 (235 CNHM; 6 AMNH; 3 USNM); Leyte, 35 (16 CNHM; 19 MCZ); Samar, 4 (BM); Busuanga, 5 (CNHM); Palawan, 44 (4 CNHM; 13 MCZ; 15 UMMZ; 12 USNM); Basilan, 10 (4 MCZ; 6 USNM); Borneo, 28 (9 BM, including type of *guttatus* Günther; 18 MCZ; 1 UMMZ).

Taxonomic notes.—After some vacillation Boulenger (1918) decided that *guttatus* Günther was specifically distinct from *natator*, the sole difference being the presence of vomerine teeth in the former and their absence in the latter. Both of these species, according to Boulenger, differed from *nubilus*, as the last had a papilla on the tongue.

Although it is true that the Bornean individuals (*guttatus*) differ from the Philippine ones in the presence of vomerine teeth, to consider them distinct species despite their agreement in almost every other point is to ignore the essential identity of the populations. The two groups may, however, be separated as subspecies, the vomerine teeth illustrating the geographic variation of the two.

Taylor (1920) points out that some but not all Palawan specimens have the tongue papilla. The *natator* lacking the papilla differ in no other respect from those with the papilla. Consequently, it is not possible to distinguish two taxonomic groups on Palawan.

The exact type locality of *natator* has been in doubt. Günther (1858) stated merely that his specimens came from the "Philippines." However, his description of the dorsal color of the type series suggests a restriction. The types were characterized as "uniform

Table 32. Sex dimorphism of two characters in *Staurois natator*

Snout-vent length

	Females			Males		
	No.	**Mean±SE**	**Range**	**No.**	**Mean±SE**	**Range**
Samar..............	1	45.0	-------	3	31.93	29.4-36.5
Leyte..............	12	46.08±0.48	43.3-48.5	23	34.18±0.77	29.8-40.8
Mindanao[1]........	24	45.12±0.44	41.0-50.2	25	40.32±0.56	29.8-43.7
Basilan	4	41.45	40.3-42.8	---	-------	-------
Busuanga.........	2	41.80	41.1-42.5	2	33.55	33.1-34.0
Palawan	17	42.24±0.61	37.3-46.6	12	31.20±0.39	29.4-33.3
Borneo	4	53.00	50.8-54.6	5	34.04±0.69	31.4-35.3

Analysis of variance

Source	**Sum of squares**	**Degrees of freedom**	**Mean of squares**
Between sexes......	373.52	1	373.52
Within sexes.........	147.68	11	13.43
Total	521.20	12	

F (1,11) = 27.82; P = <0.01

Table 32. Sex dimorphism of two characters in *Staurois natator (continued)*

Lower leg/snout-vent

	Females			Males		
	No.	**Mean±SE**	**Range**	**No.**	**Mean±SE**	**Range**
Samar..............	---	-------	-------	3	0.628	0.615-0.650
Leyte..............	12	0.582±0.007	0.538-0.628	23	0.598±0.004	0.546-0.634
Mindanao[1]........	23	0.563±0.004	0.532-0.596	24	0.599±0.004	0.560-0.632
Basilan...........	4	0.584	0.556-0.600	--	-------	-------
Palawan..........	16	0.566±0.008	0.527-0.620	12	0.597±0.006	0.557-0.631
Borneo............	4	0.574	0.549-0.594	5	0.606±0.007	0.589-0.630

Analysis of variance

Source	Sum of squares	Degrees of freedom	Mean of squares
Between sexes......	2527	1	2527
Within sexes.........	1027	8	128
Total................	3554	9	

F (1,8) = 19.74; P = < 0.01

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[1] Specimens from Mount Apo only

brown" and "greyish brown with rounded bluish-white spots." These particular patterns are not found in samples from Palawan and Busuanga but are relatively common among specimens from Mindanao and Leyte. Hence I believe that Günther's types came from one of the last two islands.

Diagnosis.—A medium-sized frog; tips of all digits strongly dilated into large disks which have a deep horizontal groove around the edge (fig. 59); toes completely webbed; two metatarsal tubercles; no vomerine teeth; skin of back densely set with small tubercles.

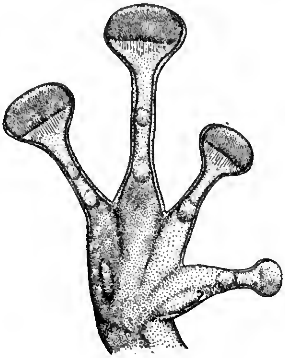

FIG. 59. Hand of *Staurois natator;* × 3.

Description.—Body elongate; head longer than broad; upper jaw projecting; snout narrow, blunt or obtusely pointed; tympanum distinct, one-third to one-half diameter of eye.

Tips of digits dilated into large disks with a horizontal circummarginal groove; ventral surface of pad with distinct transverse border proximally; longitudinal striae proximal to pad; first finger shorter than second; third finger almost twice as long as palm; fringe of skin usually evident on outer side of first finger and on both sides of others; no supernumerary tubercles on hand (fig. 59). Legs slender, long; web complete, reaching disks of all toes; small oval inner metatarsal tubercle (not equal to distance between subarticular tubercle and pad of first toe) and smaller round outer one; subarticular tubercles prominent, round.

Skin above coarsely granular, the granules or tubercles closely set and usually of one size; occasionally intermixed with large tubercles; sides with larger tubercles; chin and throat smooth; belly rugose; no dorso-lateral fold; no fold above tympanum.

Color above in life olive or bronze green (in alcohol grayish brown) with dark spots; some individuals uniformly dark; others

Table 33. Sex dimorphism in head width and tympanum diameter in *Staurois natator*

	Sex	No.	Mean±SE	Range	Difference of means	t	n	P
				Head width/snout-vent				
Leyte........	♂	23	0.287±0.002	0.268-0.307	0.012	3.063	33	0.007
	♀	12	0.275±0.003	0.264-0.289				
Mindanao[1]..	♂	25	0.283±0.002	0.265-0.308	0.010	4.021	46	<0.001
	♀	23	0.273±0.002	0.255-0.289				
Palawan....	♂	11	0.314±0.004	0.299-0.336	0.013	2.413	24	0.03
	♀	15	0.301±0.004	0.280-0.319				
				Tympanum diameter/snout-vent				
Leyte........	♂	22	0.052±0.001	0.043-0.067	0.007	3.528	32	0.002
	♀	12	0.045±0.001	0.036-0.052				
Mindanao[1]..	♂	25	0.044±0.001	0.031-0.052	0.005	3.225	46	0.004
	♀	23	0.039±0.001	0.028-0.048				
Palawan....	♂	11	0.055±0.002	0.044-0.065	0.011	4.632	23	<0.001
	♀	14	0.044±0.001	0.038-0.051				

[1] Specimens from Mount Apo only.

dark with white spots; ventral surfaces immaculate white or cream; legs with crossbars.

Secondary sex characters.—The first finger in males is swollen and covered dorsally with a cream-colored nuptial pad from the base to the level of the subarticular tubercle. The vocal sacs are paired and subgular; the elliptical openings are situated in the floor of the mouth near the angle of the jaws.

The males are slightly smaller than the females, but have relatively longer legs, wider heads, and larger tympana (see Tables 32 and 33).

Ecological notes.—Taylor (1920) observed that *natator* was always found in the immediate vicinity of forest streams, frequently perched on rocks in mid-stream. The field notes of the Philippine Expedition confirm these observations. The known altitudinal range of *natator* extends from sea level to 1,310 meters.

Inter-island variation.—Geographic variation in the character of the vomerine teeth has been commented on above (see p. 335).

Before considering inter-island variation in size and body proportions, some comment on intra-island variation is in order. Specimens of *natator* were available from three widely separated areas on Mindanao (Zamboanga City, Upi, and Mount Apo) and two on Leyte (Carigara and Cabalian).

Table 34. Geographic variation in size and body proportions of *Staurois natator*[1]

Snout-vent

		Females			Males	
Samples	**No.**	**Mean±SE**	**Range**	**No.**	**Mean±SE**	**Range**
Mindanao:						
Mount Apo..	24	45.12±0.44	41.0-50.2	25	40.32±0.56	29.8-43.7
Upi..........	---	------	------	5	42.76±1.93	36.8-47.8
Zamboanga.	6	43.98±0.64	41.7-45.8	4	35.33	29.6-42.4

Samples	Sex	Difference of means	*t*	*n*	P
Leyte—Mount Apo..............	♀	0.96	1.344	34	0.19
	♂	6.14	6.534	46	<0.001
Leyte—Upi......................	♂	8.58	4.585	26	<0.001
Leyte—Zamboanga.............	♀	2.10	2.573	16	0.02
Mount Apo—Upi.................	♂	2.44	1.624	28	0.12
Mount Apo—Zamboanga........	♀	1.14	1.201	28	0.24
Palawan—Zamboanga	♀	1.74	1.573	21	0.14
Palawan—Mount Apo	♀	2.88	3.903	39	0.001
	♂	9.12	10.630	35	<0.001
Palawan—Borneo	♂	2.84	3.771	15	0.004
Borneo—Mount Apo	♂	6.28	4.812	28	<0.001

Head width/snout-vent

Samples	No.	Mean±SE	Range	No.	Mean±SE	Range
Mindanao:						
Mount Apo..	23	0.273±0.002	0.255-0.289	25	0.283±0.002	0.265-0.308
Upi..........	---	------	------	5	0.293±0.006	0.280-0.309
Zamboanga.	6	0.292±0.002	0.285-0.301	4	0.301	0.286-0.311
Borneo	4	0.268	0.260-0.276	5	0.271±0.003	0.261-0.279

Samples	Sex	Difference of means	*t*	*n*	P
Leyte—Mount Apo..............	♀	0.002	0.631	33	0.53
	♂	0.004	1.458	46	0.16
Leyte—Upi......................	♂	0.006	1.083	26	0.29
Leyte—Zamboanga.............	♀	0.017	4.232	16	<0.001
Mount Apo—Upi.................	♂	0.010	2.329	28	0.03
Mount Apo—Zamboanga........	♀	0.019	4.820	27	<0.001
Palawan—Zamboanga	♀	0.009	1.493	19	0.15
Palawan—Mount Apo	♀	0.028	7.505	36	<0.001
	♂	0.031	8.630	34	<0.001
Palawan—Borneo...............	♂	0.043	6.561	14	<0.001
Borneo—Mount Apo	♂	0.012	3.098	28	0.007

Table 34. Geographic variation in size and body proportions of *Staurois natator*[1] *(continued)*

Tympanum diameter/snout-vent

	Females			Males		
Samples	No.	Mean±SE	Range	No.	Mean±SE	Range
Mindanao:						
Mount Apo..	23	0.039±0.001	0.028-0.048	25	0.044±0.001	0.031-0.052
Upi..........	---	------	------	5	0.044±0.001	0.041-0.046
Zamboanga.	6	0.042±0.001	0.038-0.047	4	0.057	0.050-0.064

Samples	Sex	Difference of means	t	n	P
Leyte—Mount Apo..............	♀	0.006	3.123	33	0.007
	♂	0.008	4.520	45	<0.001
Leyte—Upi.......................	♂	0.008	2.798	25	0.01
Leyte—Zamboanga.............	♀	0.003	1.488	16	0.16
Mount Apo—Zamboanga........	♀	0.003	1.108	27	0.28
Palawan—Zamboanga	♀	0.002	0.929	18	0.36
Palawan—Mount Apo	♀	0.005	2.693	35	0.01
	♂	0.011	4.921	34	<0.001

Lower leg/snout-vent

Samples	No.	Mean±SE	Range	No.	Mean±SE	Range
Mindanao:						
Mount Apo..	23	0.563±0.004	0.532.0.596	24	0.599±0.004	0.560-0.632
Upi..........	---	------	------	5	0.606±0.011	0.571-0.629
Zamboanga.	6	0.593±0.008	0.570-0.618	4	0.605	0.599-0.608

Samples	Sex	Difference of means	t	n	P
Leyte—Mount Apo..............	♀	0.019	2.595	33	0.02
	♂	0.001	0.185	45	----
Leyte—Upi.......................	♂	0.008	0.816	26	0.42
Leyte—Zamboanga.............	♀	0.011	0.916	16	0.37
Mount Apo—Upi.................	♂	0.007	0.743	27	0.43
Mount Apo—Zamboanga........	♀	0.030	3.710	27	0.001
Palawan—Zamboanga	♀	0.027	1.942	20	0.08
Palawan—Mount Apo	♀	0.004	0.506	37	0.62
	♂	0.002	0.303	34	0.76
Palawan—Borneo	♂	0.009	0.891	15	0.39
Borneo—Mount Apo	♂	0.007	0.804	27	0.43

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[1] Only those means, standard errors, and observed ranges not listed in Tables 32 and 33 are given.

Mount Apo, located on the east side of the central mass of Mindanao, is approximately 125 kilometers due east of Upi, which is in Cotabato Province near the eastern shore of the Moro Gulf. The City of Zamboanga is about 200 kilometers west of Upi. Carigara and Cabalian are on opposite ends of Leyte, about 125 kilometers apart.

In size and the three body proportions tested (ratios of head width to snout-vent, lower leg to snout-vent, tympanum diameter to snout-vent) no statistically significant differences separate the two Leyte samples. Hence I have treated them as one sample. The three Mindanao samples do not exhibit similar homogeneity. The Mount Apo and Upi samples are less distinct from each other than either is from the Zamboanga sample in these four characters. In fact, in most instances the Mount Apo sample is less different from the Leyte sample than from the Zamboanga specimens (see means, Table 34). Unfortunately the Upi and Zamboanga samples are small and, therefore, statistical tests of differences were restricted to the males of the former and the females of the latter. The Mount Apo specimens are statistically distinct from the Upi males in the head width ratio only and from the Zamboanga females in head width and lower leg ratios (see Table 34).

Because of these differences the three Mindanao samples were compared individually with samples from other islands. Statistical analysis of the differences between samples in snout-vent length and the three ratios, presented in Table 34, yields the following results: Males from Leyte differ significantly from those of both Mount Apo and Upi in size and relative width of tympanum. Statistically significant differences distinguish females of Leyte and Mount Apo in relative lower leg length and tympanum width, and females of Leyte and Zamboanga in size and relative head width. Males from Borneo differ significantly in size and relative head width from those of both Palawan and Mount Apo. Both sexes from the last two samples differ significantly in size and relative head width and tympanum diameter.

Variation in pigmentation also occurs. Females from Leyte, Samar, and Mindanao are usually darker in color than those from Busuanga, Palawan, and Borneo. In the last three populations the common dorsal coloration consists of dark spots (about a centimeter in diameter) set in lighter reticulation (gray or light brown in alcohol, olive or bronze green in life). The backs of females from Leyte and Mindanao are most often an almost uniform dark color with only a slight indication of the lighter hue, which is considerably reduced in extent. Only a few individuals have the pattern typical of Palawan specimens.

The males are generally colored as the females, the only exception being spots (bluish-white in alcohol; greenish-white [?] in life) that appear on the backs of males from Mindanao and Leyte. These spots are distinguishable both by their color and by their isolation (from each other) from the light reticulation of males from Busuanga and Palawan. The observed frequency of this character in the males of the various samples is as follows:

	Spots present	Spots absent
Leyte:		
Carigara	9	1
Cabalian	6	7
Mindanao:		
Upi	0	5
Mount Apo	22	78
Zamboanga	1	3
Palawan	0	13

The observed difference between the Leyte samples is not significant; chi square obtained from a 2 × 2 contingency table equals 3.052 and P=0.09. Intra-island differences of the Mindanao samples are not statistically significant. Upon lumping the data for each island and applying a chi square test to the whole, the inter-island differences appear to be significant (chi square=24.172; $n=2$; P=0.001). Statistically significant levels are also reached if the islands are compared two at a time in the Leyte-Mindanao (chi square=15.943; P=0.001) and Leyte-Palawan sets (chi square= 11.974; P=0.001) but the differences are not significant in the case of the Mindanao-Palawan pair (chi square=2.382; P=0.13).

There is also a slight difference in the skin external to the vocal sacs. In males from Leyte and Mindanao this skin seems to be more modified than in those from Busuanga and Palawan. But the difference is not great, and it would be extremely difficult to tell from which of the two groups a particular male came on this basis.

Range.—Leyte (Cabalian, Carigara, Ormoc [Boettger, 1899]). Samar. Dinagat (Boulenger, 1882). Mindanao: Agusan Province (Bunawan); Cotabato Province (Burungkôt near Upi); Davao Province (Badiang near Tagabuli, Baganga River, Mainit and Todaya on Mount Apo, Mount McKinley, Padada River); City of Zamboanga (Zamboanga); Zamboanga Province (Dapitan). Basilan.

Busuanga (Dimaniang). Culion (Taylor, 1920). Palawan (Brooke's Point, Iwahig, Kabalnecan near Brooke's Point, Malinao River, Mauyon near Babuyan, Puerto Princesa, Thumb Peak). Known also from Borneo.

Micrixalus Boulenger

Micrixalus mariae[1] sp. nov.

Type.—Chicago Natural History Museum no. 51360. Male collected on the south slope of Mount Balabag, Mantalingajan Range, Palawan, at 850 meters, May 13, 1947, by Mr. Floyd Werner.

Diagnosis.—A small frog with depressed head and rounded snout (fig. 60); digit tips expanded into large, rounded disks with circum-marginal grooves (fig. 61); fingers rather short, third finger being only slightly longer than palm; no supernumerary tubercles on hand.

Description of type.—Habitus stocky; head broad, width at level of tympanum greater than distance from posterior edge of tympanum to tip of snout; head depressed; canthus rostralis rounded; lores concave, oblique; snout rounded, short; length of eye equal to its distance from tip of snout; tympanum visible though rim hidden by skin, slightly less than one-half diameter of eye; vomerine teeth present; omosternum forked at base; nasals separated from each other and from fronto-parietals.

Tips of digits dilated into large round disks; disks of fingers and toes roughly equal, that of third finger twice width of penultimate phalanx; pad clearly differentiated from ventral surface of digits; a deep horizontal groove around edge of disk, the part ventral to groove projecting a considerable distance beyond dorsal portion; ventrally with a transverse line marking proximal limit of swollen pad; terminal phalanges T-shaped; first finger shorter than second, which is only slightly shorter than fourth; third finger only slightly longer than palm; no supernumerary subarticular tubercles, third and fourth fingers bearing two and first and second one tubercle.

Legs stout, relatively short; web reaching disks on outer side of first, second and third toes and on inner side of fifth, and falling just short of disk on inner side of second and third and on both

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[1] I name this species for my wife, Mary Inger, whose constant aid was so important to this paper.

sides of fourth toe; narrow fringe of skin along free edges of first and fifth toes; subarticular tubercles large, elongate; inner metatarsal tubercle flat but large, length greater than distance from distal edge of subarticular tubercle to tip of first toe; no outer metatarsal tubercle; outer metatarsals separated for two-thirds their lengths.

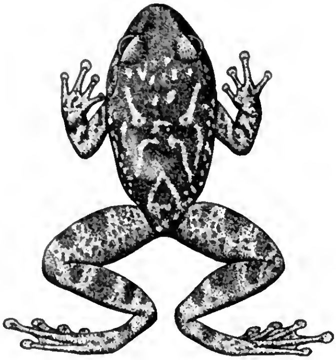

FIG. 60. *Micrixalus mariae* sp. nov.; × 0.9.

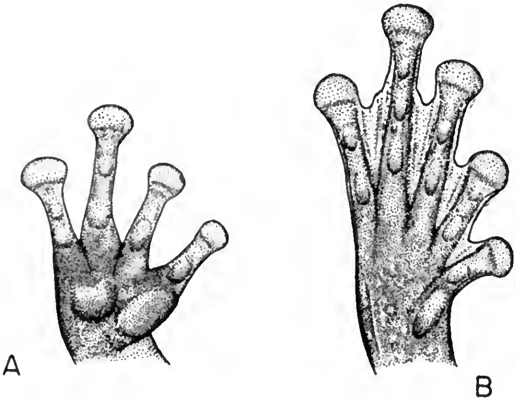

FIG. 61. Hand (A) and foot (B) of *Micrixalus mariae* sp. nov.; × 2.7.

Skin of all dorsal surfaces coarsely shagreened; chest and belly strongly rugose, gular region less so but not smooth; tubercles present laterally; no dorso-lateral fold; a weak supratympanic fold from eye to insertion of arm.

Color (in alcohol) of dorsal surfaces dark purple with scattered irregular light markings; gular region gray with white spots; chest and belly white with gray reticulation; legs with dark crossbars dorsally, ventrally white with brownish marbling.

Measurements of type.—Snout to vent 33.1 mm.; head width 14.4; head length (from posterior border of tympanum to snout) 13.2; lower leg 16.5.

Paratypes.—One additional specimen, a male (CNHM 51359; 32.3 mm. snout to vent) collected at the same time, agrees with the type in almost all details.

Secondary sex characters.—Both specimens have finely granulated nuptial pads on the medio-dorsal surface of the first finger. Vocal sacs are absent.

Remarks.—The possession of broad specialized digit tips (a groove separating dorsal and ventral surfaces) immediately sets *mariae* off from the species grouped by Boulenger (1920) in the subgenus *Rana* (genus *Rana* of Noble, 1931) but not from *Hylarana, Staurois, Micrixalus* (the last three as defined by Noble), or *Cornufer.*

The partial fusion of outer metatarsals in *mariae* recalls *Cornufer,* but in no species of the latter are they separated to the extent seen in *mariae.* Other distinctions are to be found in the web, in the tubercles of the finger, in the shape of the terminal disks of the digits, and in the secondary sex characters. The web of *mariae* is much more extensive than in any species of *Cornufer.* Every form of the latter has at least one supernumerary tubercle at the base of the lateral fingers (figs. 63 and 64); in *mariae* these tubercles are lacking. In those species of *Cornufer* with relatively large disks at the digit tips, the disks are truncate, whereas in *mariae* they are round. The males of *Cornufer* uniformly possess median subgular vocal sacs; *mariae,* on the other hand, lacks vocal sacs. As noted above, the omosternum of *mariae* is forked at the base; in this respect it agrees with species of *Cornufer. Cornufer* has obviously become adapted for life away from water (see p. 348). The extensive web of *mariae* sets it apart ecologically from *Cornufer.*

All East Indian *Hylarana* have three subarticular tubercles on the third and fourth fingers. By contrast, *mariae* has only two. The fingers of most species of *Hylarana* are long relative to the palm, the third finger usually being one and one-half to more than two times as long as the palm. In *mariae* the fingers are short; the third finger is only slightly longer than the palm. The outer metatarsals of *Hylarana* are widely separated by the web and usually are separated for their entire lengths. In *mariae,* however, the metatarsals are only narrowly separated and for only two-thirds of their lengths. The omosternum of *Hylarana* is usually unforked, though in some species it has a slight notch (Boulenger, 1920). The omosternum of *mariae* is deeply forked.

The relations of *mariae* to the genus *Staurois* are not clear. As the larva of *mariae* is unknown the critical element of a comparison with this genus is missing. Most adults of *Staurois* agree with *Hylarana* in the points discussed in the preceding paragraph. Consequently *mariae* differs from adults of the former as it differs from *Hylarana*. This is not true if *mariae* is compared with *Staurois natator*. But it has been noted above (p. 335) that the generic status of *natator* is questionable.

Significant similarity to other groups of species, however, is not seen until *mariae* is compared with *Micrixalus*. *M. torrentis* Smith (type examined), for example, has no supernumerary tubercle at the base of the fingers, its outer metatarsals are separated for most of their lengths, the feet are extensively webbed (to disks of toes), the disks of fingers and toes are large, rounded, and equipped with circummarginal grooves. *Micrixalus saxicolus* Jerdon (type examined), *M. baluensis* (=*Cornufer baluensis* Boulenger; type examined), and *M. herrei* Myers in the main agree with *mariae* in these characters although the web of *baluensis* does not reach the toe disks and the metatarsals of *herrei* are not separated as much as in the other species. The omosternum of *torrentis* is not forked (Smith, 1923); that of *mariae* and of *baluensis* is. I have no information on the other species. These species also differ in the development of secondary sex characters. *M. herrei* and *saxicolus*, for instance, have paired vocal sacs and a nuptial pad. Only the latter is found in *mariae*, whereas neither structure is present in *torrentis*. Males of *baluensis* are unknown. Finally, *mariae* is the only species of this group possessing vomerine teeth. Despite the constant appearance of "no vomerine teeth" in the diagnoses of *Micrixalus*, the distinction between *mariae* and other species of the genus in this character strikes me as relatively unimportant. There is sufficient evidence for the unreliability of this character in other groups to warrant great circumspection in its application.

It is clear from the foregoing that the relationship of *mariae* to various groups of Ranidae is subject to many doubts. Nevertheless, it definitely belongs with those genera grouped by Noble in the Cornuferinae. The morphology of *mariae* is evidence that a wide ecological gap separates it from *Cornufer*. Without additional information no such comment can be made with reference to *Hylarana*, *Staurois*, or *Micrixalus*. With these limitations in mind, I suggest that *mariae* belongs in the genus *Micrixalus*.

In the above paragraphs *Cornufer baluensis* Boulenger has been referred to the genus *Micrixalus*. The extensive webbing, absence of supernumerary metacarpal tubercles, separation of the outer metatarsals, and round shape of the digital disks so distinguish *baluensis* from *Cornufer* as defined below that it cannot be left in that genus.

Range.—Palawan (Mount Balabag).

Cornufer Tschudi

The separation of *Cornufer* (and/or *Platymantis*) from *Rana* has depended on the reduced webbing of the former, its forked omosternum, and the fusion of the outer metatarsals. Some species of *Rana* (for example, *glandulosa*) have a small web, no greater than is found in some species of *Cornufer* (for example, *guentheri*). The forked omosternum is of dubious diagnostic value as it also appears in some species of *Rana* (for example, *cancrivora*), although not in those species (*Hylarana*) that are the assumed precursors of *Cornufer* (Noble, 1931). Furthermore, the extent of the fusion of outer metatarsals varies both in *Rana* and *Cornufer* although the fusion is much more common and more extensive in the latter. This gradation of characters from some species of *Rana* to some species of *Cornufer* (including *Platymantis*) does not detract from the fact that the species of the latter have a number of common characteristics: the forked omosternum, the reduced webbing, the fused metatarsals, supernumerary tubercles on the metacarpals, and, almost always, a median subgular vocal sac. There is another and perhaps more significant difference between *Rana* and *Cornufer*. All species of *Rana* (including *Hylarana*), so far as known, lay large numbers of relatively small, pigmented eggs in water; none are known to deposit ova on land; and none are known to skip the free-swimming tadpole stage in development. On the other hand, what little is known indicates that all species of *Cornufer* deposit large, non-pigmented eggs (see Table 35), probably out of water. The few larvae that are known do not pass through a free-swimming stage; the characters of the eggs suggest that none do.

This change in the life cycle is paralleled by the morphology of the adult. Both the fused metatarsals and the rudimentary web are modifications from the common *Rana* morphotype and would be non-adaptive in a form that spent much time in water, but these changes do not hinder life on the forest floor. Thus, both the modified life cycle and modified foot morphology point to an important shift in adaptive zone away from the typical life of a *Rana*.

Table 35. Comparison of egg size and pigmentation in some species of *Cornufer* and *Rana*

Species	Size of female	Size of egg[1]	Pigment of egg[2]
Cornufer:	mm.	mm.	mm.
corrugatus	41	3.3	0
papuensis	53	3.3	0
guentheri	43	2.2	0
meyeri	43	3.0	0
pelewensis	45	3.0	0
vitianus	70	3.3	0
solomonis[3]	71	3.4	0
hazelae[4]	23	3-3.5	0
Rana:[5]			
microdisca leytensis	44	1.7	+
signata signata	70	2.0	+
erythraea	75	1.5	+
cancrivora cancrivora	79	1.4	+
everetti everetti	88	1.6	+

[1] The egg size represents the average of two measurements on each of two diameters of the largest egg visible laterally in the right ovary. In all species a number of the ova approached in size the one finally selected for measurement.

[2] + indicates that one hemisphere is black and the other light (usually cream). 0 indicates that both hemispheres are light (usually cream).

[3] Van Kampen (1923) gives 5 mm. as diameter of ripe egg.

[4] Data from Taylor (1922b).

[5] Very large species of *Rana* with proportionately larger eggs might have been cited here. It is significant, however, that in these species also the eggs are pigmented.

Boulenger (1918) was of the opinion, concurred in by Noble, that *Cornufer* and *Platymantis* should be separated, the forms with large disks to be assigned to the former and those with small disks to the latter. At the same time Boulenger pointed out that the large disks or pads of *Cornufer*, in this limited sense, were provided ventrally with a transverse groove essentially continuous with the distal, horseshoe-shaped groove. This supposed difference between the two genera reflects only differences in the specialization of the pads such as occur within other genera.

Noble and Jaeckle (1928) have shown that the stages in the development of a specialized pad include: (1) a slight swelling of the tip of the digit; (2) a movement inwards of mucous glands; and (3) a modification of the superficial epidermis. These authors show that in the Ranidae, as well as in some other groups, the progressive specialization of the epidermis of the pad is marked by the appearance of a horseshoe-shaped groove around the end of the digit, delimiting the region of differentiated epidermis both laterally and distally.

Noble and Jaeckle illustrate these stages with a series of American ranids: *Rana pipiens, R. sylvatica,* and *R. warschewitschi.* The same can be done with Indo-Australian *Rana,* which also exhibit one additional stage. In *Rana everetti* (and several other species) there is a faint transverse groove at the proximal border of the pad, so that the area of modified epidermis has become completely delimited.

This picture of progressive differentiation of the pad in *Rana* is precisely what is indicated by the difference between *Platymantis* and *Cornufer.* But inasmuch as the distinction of the two groups is based on one character and can not as yet be associated with an ecological difference, two genera should not be recognized.

1a. Tips of fingers slightly expanded into small round disks (fig. 63)..........2
1b. Tips of fingers expanded into large truncate disks (fig. 64, A)............3
2a. Back set with longitudinal ridges, at least two of which exceed one-third the body length (fig. 62, A)........................*Cornufer corrugatus*
2b. Back set with longitudinal ridges that do not exceed one-third the body length (fig. 62, B)....................................*Cornufer meyeri*
3a. A prominent backwardly directed dermal "horn" on upper eyelid. *Cornufer cornutus*
3b. No such process...4
4a. Distinct areolations at groin (fig. 62, C)..............*Cornufer subterrestris*
4b. Without areolations...5
5a. First toe (measured from distal edge of inner metatarsal tubercle) more than twice the length of inner metatarsal tubercle............*Cornufer guentheri*
5b. First toe less than twice the length of inner metatarsal tubercle...........6
6a. Snout acutely pointed (fig. 65, C, D)..................*Cornufer polillensis*
6b. Snout obtusely pointed or rounded (fig. 65, A, B).........*Cornufer hazelae*

Cornufer corrugatus Duméril

Hylodes corrugatus Duméril, 1853, Ann. Sci. Nat., (3), **19:** 176—Java (in error).

Platymantis corrugata Peters, 1873, Monatsber. Acad. Wiss. Berlin, **1873:** 611; Boulenger, 1918, Ann. Mag. Nat. Hist., (9), **1:** 373.

Cornufer corrugatus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 110 (part); Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 123; Taylor, 1920, Phil.

Jour. Sci., **16:** 314, pl. 4, figs. 3, 3*a*, and 3*b*, text fig. 5; 1922, op. cit., **21:** 269.

Platymantis corrugatus corrugatus Loveridge, 1948, Bull. Mus. Comp. Zool., **101:** 406.

Platymantis plicifera Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 95, pl. 8, fig. B—Philippines; 1877, Proc. Zool. Soc. London, **1877:** 132.

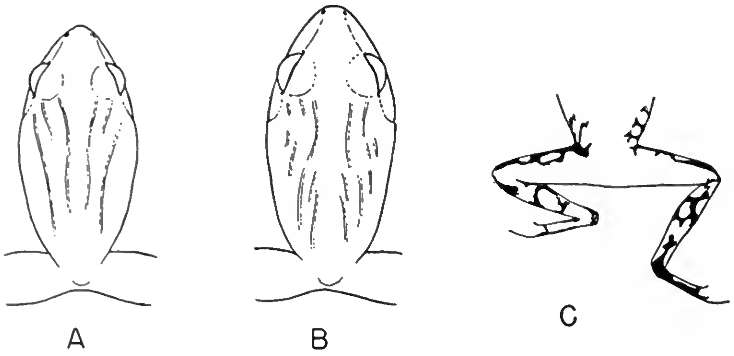

FIG. 62. A, *Cornufer corrugatus* (× 1.3); B, *C. meyeri* (× 1); C, *C. subterrestris* (× 2).

Material examined.—Luzon, 13 (2 BM, types of *plicifera* Günther; 2 CAS; 1 CM; 8 MCZ); Mindoro, 1 (USNM); Negros, 12 (2 CNHM; 5 CM; 5 MCZ); Leyte, 2 (CAS); Mindanao, 27 (20 CNHM; 7 CM); "Java?," 1 (MHNP, type of *corrugatus*).

Taxonomic notes.—Some confusion concerning this species has been occasioned by the erroneous type locality given *corrugatus* by Duméril. The only specimens identified as *Cornufer* (or *Platymantis*) supposedly from Java are the types of *C. dorsalis* Duméril and *C. corrugatus* Duméril, this despite the fact that Java is better known, herpetologically, than most parts of the world. It has been suggested by Peters (1873) that the type of *corrugatus* came from the Philippines inasmuch as the Müller collection, of which Duméril's types were a part, contained only Philippine species. After an examination of the type of *corrugatus*, the type series of *plicifera* (definitely from the Philippines) and various Philippine and Papuan specimens identified as *corrugatus* or *plicifera*, there can be no doubt that Duméril's type originated in the Philippines. Nor can the Philippine and Papuan specimens be placed in the same species without stretching the species concept to the breaking point.

Loveridge (1948) also believes that the type of *corrugatus* came from the Philippines, but his argument is defective. His line of reasoning is as follows: Philippine specimens have broader heads than Papuan individuals assigned to *corrugatus;* Duméril wrote that the type had a broad head; therefore, it is more likely that the questionable specimen came from the Philippines than from New Guinea. The defect in all this is that Duméril did not say that *corrugatus* had a broad head. He merely noted (p. 176) that the vomerine tooth rows of *corrugatus* were longer than those of "Hylode . . . a large tête," which is described by Duméril in the same paper (p. 178) as *Hylodes* (=*Eleutherodactylus*) *laticeps.*

As noted above, the Papuan frogs are specifically distinct from the Philippine *corrugatus* but are related to *meyeri* Günther. Consequently, the trinomial proposed by Loveridge (1948) can not be used.

Diagnosis.—A medium-sized *Cornufer* (females up to 50 mm., males to 35 mm.); tips of fingers round, slightly dilated; without circummarginal grooves; back with long ridges, most of which are over one-third of the trunk length, a narrow dorso-lateral fold commencing just above the tympanum and extending the length of the body (fig. 62, A) being the most conspicuous; ventral surface coarsely granular in both sexes behind the level of the arms; males with granular throats; usually with many small supernumerary tubercles (fig. 34) on soles of feet; males with paired subgular vocal sacs.

Description.—Habitus stocky; head broader than long; snout obtusely pointed; tympanum oval with vertical axis longest, horizontal axis one-half to two-thirds diameter of eye; tongue with papilla; a strong supratympanic fold from eye to arm; skin of back set with granules and longitudinal folds; folds regularly placed and over one-third the length of the trunk (fig. 62, A); skin of venter posterior to axilla coarsely granular; throats of males granular.

Tips of fingers scarcely dilated, without horizontal grooves; first finger longer than second; a large supernumerary tubercle on each metacarpal. Tips of toes distinctly swollen into round disks larger than those of fingers; toe disks with circummarginal grooves; third toe longer than fifth; web reaching base of proximal subarticular tubercle of first and second toes, center of tubercle of third toe, and beyond tubercle of fifth toe; two metatarsal tubercles; many small supernumerary tubercles on sole of foot.

Color (in alcohol) of dorsal surfaces cinnamon, lavender or brownish gray; a dark interorbital bar; a very dark loreal mask or streak continued behind eye below supratympanic fold, and in some individuals completely covering tympanum; usually two or four black spots across anterior part of back; inner surface of tarsus and sole of foot black or dark brown, otherwise limbs colored as back and with crossbars; abdomen usually immaculate cream, occasionally suffused or spotted with brown; throat of female usually cream, occasionally with brown suffusion; throat of male dark.

Secondary sex characters.—As in many species of the genus, the males of *corrugatus* have coarsely granular throats, the granules tipped with light spinules. This is in sharp contrast with the smooth gular region of the female. The throat is always darker than the chest in males but only occasionally so in females. Unlike many other species of *Cornufer*, male *corrugatus* have paired subgular vocal sacs. The skin covering the vocal sacs is not modified; that is, not stretched and wrinkled as in the external type of vocal sac. The males do not have enlarged arms, nuptial pads, or humeral glands.

Female *corrugatus* are larger than the males. Only twelve of the males examined and sufficiently well preserved to be measured were mature, judging by the presence of the secondary sex characters. These varied in snout-vent length from 28.5 to 34.8 mm. with a mean of 31.97±0.60 mm. All females over 33.6 mm., the smallest containing enlarged ova or enlarged and convoluted oviducts, were considered mature. There were ten of these in the sample, ranging from 36.3 to 50.2 mm. with a mean of 41.44±1.24 mm.

Ecological notes.—According to Taylor (1922c) *corrugatus* is a woodland form rarely found in the vicinity of water. This statement is borne out by field notes of the Philippine Expedition. All thirteen frogs collected on Mindanao for which there are habitat notes were captured in forests away from the immediate vicinity of water. Most of the Mindanao specimens were found in the mountains: three between sea level and 30 meters, one at 460 meters, and fourteen between 850 and 1,070 meters. Taylor collected *corrugatus* at elevations exceeding 940 meters on Mount Maquiling, Luzon.

Inter-island variation.—Some geographic variation is to be noted in coloration. As stated above, the number of black spots across the anterior part of the back varies; there may be none or as many as six, with four and two the most common numbers. These black spots occur in symmetrical pairs, each individual spot being centered on a longitudinal fold. The variation in specimens taken from north to south in the Philippines is as follows:

Number of spots	0	2	4	6	Mean/Individual
Locality:					
Luzon	2	5	1	0	1.75
Mindoro	2	0	0	0	0
Leyte	0	2	1	0	2.67
Negros	1	0	6	0	3.43
Mindanao	2	4	6	1	2.92

Only unfaded specimens are included in the table. No other variation of consequence was observed.

Range.—Polillo (Taylor, 1922b). Luzon: Laguna Province (Los Baños, Mount Maquiling). Mindoro (San José, Mount Halcon). Negros: Negros Oriental Province (Bais, Canlaon Volcano, Dumaguete, Inubungan near Tolong). Leyte (Inayupan near Abuyog). Mindanao: Agusan Province (Bunawan); Cotabato Province (Burungkôt near Upi); Davao Province (Mount McKinley, Todaya on Mount Apo, Sitio Taglawig near Tagum). Taylor (1920) states erroneously that Boettger (1886) reported a specimen from Tablas. The species may very well occur on Tablas but a valid record from there has yet to be made.

Cornufer meyeri Günther

?Halophila jagori Peters, 1863, Monatsber. Akad. Wiss. Berlin, **1863:** 456—Samar.

Platymantis meyeri Günther, 1873, Proc. Zool. Soc. London, **1873:** 171—Laguna del Bay, Luzon; 1879, op. cit., **1879:** 79; Boulenger, 1918, Ann. Mag. Nat. Hist., (9), **1:** 372.

Cornufer meyeri Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 109, pl. 11, fig. 4; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 124; Taylor, 1920, Phil. Jour. Sci., **16:** 311, pl. 8, fig. 3.

Cornufer laticeps Taylor, 1920, Phil. Jour. Sci., **16:** 317, pl. 3, fig. 1—Bunawan, Agusan, Mindanao.

Material examined.—Luzon, 58 (3 BM; 27 CAS; 7 CM; 3 CNHM; 17 MCZ; 1 USNM); Polillo, 13 (7 MCZ; 5 UMMZ; 1 USNM); Lubang, 6 (CM); Tablas, 10 (5 MCZ; 5 UMMZ); Mindoro, 1 (MCZ); Negros, 39 (CM); Leyte, 2 (1 CAS; 1 MCZ); Mindanao, 22 (4 CM, type and 3 paratypes of *laticeps* Taylor; 18 CNHM); Basilan, 1 (MCZ). Many of these were in such poor condition that measurement was impossible and morphological study seriously handicapped.

Taxonomic notes.—I tentatively identify *Halophila jagori* Peters with *meyeri.* The juvenile type, poorly preserved according to

Peters, is the only specimen of the genus known from Samar. The original description does not give a clear picture of *jagori*. Nevertheless, some conclusions can be drawn from Peters' description. His statement that the body has granular and distinct longitudinal folds allies *jagori* with either *meyeri* or *corrugatus*. The color notes —dark brown above; below whitish, sprinkled with dark brown on the throat; lips with brown spots—seem to limit the possibilities to *meyeri*. Peters does not, for example, mention dark lores or dark spots in a row across the back, both characters typical of *corrugatus*.

Specimens from Agusan, Mindanao, were regarded by Taylor as a distinct species, *laticeps*. After comparison of specimens from Mindanao, including the type series of *laticeps*, with those of other islands, I am forced to conclude that the Mindanao population cannot be separated from the others even as a subspecies. There are some minor differences (see below), but these are not sufficient to warrant subspecific recognition.

Taylor's comparison of *laticeps* with other forms is misleading, and, unfortunately, typical of his handling of such matters. Instead of comparing it with the obviously related *meyeri*, of which specimens were at hand, he contrasts *laticeps* with *jagori*, a form he could only have conjectured about. In fact, he states (1920, p. 314) that he had seen no specimens he could refer to *jagori*. Also, he states his belief that the type of *jagori* was immature. In view of these two statements, it is surprising to find Taylor (1920, p. 318) saying that *laticeps* differs from Peters' species "in being larger in size, and in having greater ruggedness of skin . . . ." Obviously there could have been no basis for the comparison of size. Furthermore, it is extremely difficult to understand how he arrived at the conclusion that *laticeps* had a rougher skin, because his reasonably accurate translation of Peters' description of *jagori* includes the statement that the "body is covered with granular and distinct longitudinal folds."

The relations of *meyeri* are not with other Philippine *Cornufer* but instead seem to be with non-Philippine species. Yet it is difficult to relate *meyeri* to these other species, largely because the taxonomy of the genus has never been worked out adequately. Another disturbing factor is the variation within *meyeri*. I can only mention several forms resembling *meyeri* with no assurance of being able to point out the correct relationship.

The three forms most similar to *meyeri* are *C. papuensis* Meyer (New Guinea), *C. rubristriatus* Barbour (Waigeu Island), and *C.*

pelewensis Peters (Palau Islands). These are approximately the size of *meyeri* (females between 30 and 50 mm., males somewhat smaller) and agree with it in the nature of the skin on the back (set with fine granules and short longitudinal folds). Except for the Mindanao populations, *meyeri* is characterized by horizontal grooves around the finger tips. Such grooves apparently are found in almost all individuals of *papuensis* (15/18 of those examined) and in about half of the individuals of *pelewensis* (11/19 of those seen). The three specimens of *rubristriatus* examined lacked the grooves. About one-third of the Mindanao sample have the grooves on the fingers. Supernumerary tubercles are present on the metatarsals of *papuensis, pelewensis,* and *rubristriatus* as well as in half of the Mindanao sample of *meyeri.* I saw no other specimens of *meyeri* with these supernumerary tubercles. All adult males of *meyeri* have a median subgular vocal sac, in agreement with the three non-Philippine species. But in another secondary sex character the correspondence is not at all good. The males of the three non-Philippine forms have small white or clear asperities on the chin. I have observed these in only 8 out of 44 males of *meyeri*—2 from Mindanao, 4 from Luzon, and one each from Lubang and Basilan.

FIG. 63. Hand of *Cornufer meyeri;* × 5.

These non-Philippine forms and *meyeri* may belong to one widespread species. However, it is wiser to consider them all distinct species until a thorough study of the whole genus has been made.

Diagnosis.—A medium-sized *Cornufer* (adult females 30–45 mm., males smaller); tips of fingers round (fig. 63), disk of first finger not noticeably smaller than those of other fingers; tips of fingers with or without horizontal grooves; skin of back granular, with irregular longitudinal ridges, none of which are over one-third the distance between eye and vent; males with median vocal sac.

Description.—Body moderately stocky; head broader than long; snout rounded; tympanum a distinct oval, horizontal diameter shortest and equal to one-third to one-half diameter of eye; tongue with large papilla, occasionally papilla retracted and indistinct; a strong supratympanic fold from eye to arm; skin of back granular with irregular longitudinal folds; none of folds equal to one-third the distance between eye and vent; skin of abdomen granular on posterior half only or smooth; skin of throat in females smooth (for males see below).

Tips of fingers slightly swollen into round disks with or without horizontal circummarginal grooves (see below); pads without a transverse groove proximally; first finger longer than or equal to second; a large supernumerary tubercle on each metacarpal. Tips of toes with distinct round pads invariably with circummarginal groove; toe pads without transverse proximal groove; third toe longer than fifth; web variable, reaching to base or center of proximal subarticular tubercle on first and second toes, reaching to center of or beyond proximal subarticular tubercle on third and fifth toes; two prominent metatarsal tubercles, an oval inner and a round outer; usually without numerous small supernumerary tubercles on metatarsals (see below).

Color extremely variable; most often dark brown or purple above (in alcohol) with a few black spots usually on larger tubercles or longitudinal ridges; occasional individuals with a posteriorly directed elongate triangular salmon area mid-dorsally, or with a thin light vertebral line, or with a pair of light dorso-lateral stripes; lips with dark bars; chin and throat suffused with light brown; abdomen cream or white, immaculate; limbs with dark crossbars.

Secondary sex characters.—The males have a median subgular vocal sac. This is at variance with the findings of Liu (1935), who lists *meyeri* as one of the species with paired subgular vocal sacs. My conclusion is based both upon dissection and upon the results of inflating the vocal sac through a tube inserted in one of the vocal sac openings. It should also be pointed out that a median vocal sac is characteristic of *C. nova-britannae, pelewensis, rubristriatus, weberi, solomonis,* and *papuensis,* with some of which *meyeri* has been compared above. The skin covering the vocal sac is slightly modified in some individuals and not in others, but possibly this variation merely reflects the differences in activity of the males just prior to preservation. The small round openings to the sacs are located at the corners of the mouth.

Although both sexes have small brown spots on the chin and throat, the skin at the sides of the throats of the larger males is conspicuously darker. As stated above, only 8 males of the 44 examined have small clusters of asperities on the chin. In no other respect do these eight differ from the other males. The males do not have nuptial pads or humeral glands.

Table 36. Sexual dimorphism in size of *Cornufer meyeri*

	Females			Males		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Luzon	11	34.42±1.14	27.0-38.5	8	25.85±0.67	21.7-28.2
Polillo	5	34.88±1.97	29.0-40.6	1	27.0	---
Tablas	4	32.03	26.5-36.9	1	23.2	---
Lubang	---	---	---	3	26.67	23.7-30.3
Negros	6	30.48±1.67	25.5-35.3	6	25.92±1.05	21.5-29.0
Mindanao	5	35.84±1.94	30.7-42.4	4	26.48	24.8-29.4

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes	162.1205	1	162.1205
Within sexes	30.0168	9	3.3352
Total	192.1373	10	

F (1,9) = 48.61; P= < 0.01

As in many other species of frogs the females are larger than the males. That the differences observed (see Table 36) are statistically significant is shown by the results of the analysis of variance included in the table. No sex dimorphism involving body proportions was observed.

Ecological notes.—In common with other members of the genus, *meyeri* is not strictly bound to water, as are most species of Ranidae. Taylor (1920) states that he usually found *meyeri* on the forest floor away from the immediate vicinity of water, at least on Negros, Luzon, Mindoro, and Lubang. On Mindanao Taylor collected this species (*laticeps* Taylor) in the immediate vicinity of water, usually under logs or leaves. Of the eighteen collected on Mindanao by the Philippine Expedition, seven were found in water, one on the edge of a stream, eight on the forest floor away from water, and two above ground in pandanus. The breeding habits presumed from the type of egg (see p. 349) and the greatly reduced web are other indications of relative freedom from water.

Very little in the way of a quantitative analysis of the altitudinal distribution can be attempted here. Of the Mindanao series referred to above, four came from elevations between 760 and 915 meters, the remainder from below 30 meters. Taylor's field notes indicate that he captured this species at 915 meters on Mount Maquiling.

Inter-island variation.—The most prominent of the characters showing geographic variation are the grooves on the finger tips and the supernumerary tubercles of the metatarsals. The finger tip grooves were present in all the material examined from Luzon, Tablas, Polillo, Lubang, Mindoro, Negros, and Leyte, but in only 9 of 21 individuals from Mindanao. The supernumerary tubercles of the foot were found in only 9 specimens, all from Mindanao. There is an indication of association between the presence of grooves on the finger tips and absence of the supernumerary tubercles of the foot in the Mindanao sample. The observed data are as follows:

	Supernumerary tubercles of the foot		
	Present	Absent	Total
Grooves on finger tips:			
Present	1	8	9
Absent	8	4	12
Total	9	12	21

Using Yates' correction for small samples, chi square of this contingency table is 4.411. With one degree of freedom P equals 0.04. This apparent dichotomy of the sample receives no support from any other characters. It should be noted that the type series of *laticeps* is like specimens of *meyeri* from the northern islands in these characters; that is, grooves are present on the finger tips and there are no supernumerary tubercles on the feet.

No statistically significant geographic variation was observed in body proportions or size. Observed variation in size of mature individuals may be seen in Table 36.

Range.—Polillo. Luzon: Laguna Province (Mount Maquiling, Los Baños); Laguna del Bay (Günther, 1873). Lubang. Mindoro (Carayrayan at base of Mount Halcon). Tablas. Negros: Negros Oriental (Bais, Canlaon Volcano, Lake Balinsasayo). Leyte (Cabalian). Dinagat (Günther, 1879). Mindanao: Agusan Province (Bunawan); Cotabato Province (Conel, Saub, San Teodoro); Davao Province (Badiang near Santa Cruz, Caburan, Calian, Malalag, Mount Pantod near Santa Cruz, Mount McKinley, Sitio Taglawig near Tagum). Basilan (Port Holland).

Samar, the type locality of *jagori* Peters, should undoubtedly be included in the range of *meyeri*. Because of the spotty collecting on Panay, Cebu, and Bohol, the occurrence of *meyeri* on those islands remains in doubt.

Cornufer cornutus Taylor

Cornufer cornutus Taylor, 1922, Phil. Jour. Sci., **21**: 175—Balbalan, Mountain Province, Luzon.

Material examined.—Luzon, 1 (CAS, type).

Diagnosis.—The type of *cornutus* is distinguished from all other Philippine *Cornufer* with truncate finger disks by the prominent outwardly directed dermal projection on the upper eyelid.

Description.—Body tapering to groin; tympanum distinct, about one-half diameter of eye; vomerine teeth present; a supratympanic fold from eye to axilla; skin of back granular, with short longitudinal ridges; throat smooth.

Tips of fingers dilated into broad truncate disks with horizontal circummarginal grooves but without transverse grooves at proximal edge of pads; first finger shorter than second; a supernumerary tubercle on each metacarpal. Tips of toes dilated into round disks, these smaller than the disks of fingers; two metatarsal tubercles; no supernumerary tubercles on foot.

Color in life (according to original description) dark brown above with light lines laterally; head light brown; groin yellow. In alcohol there is a dark stripe under the canthus and one under the supratympanic fold; there are no areolations in the groin.

Range.—Known only from the type locality on Luzon.

Cornufer subterrestris Taylor

Cornufer subterrestris Taylor, 1922, Phil. Jour. Sci., **21**: 274—Mountain Trail, Mountain Province, Luzon.

Cornufer montanus Taylor, 1922, Phil. Jour. Sci., **21**: 272, pl. 4, fig. 4—Mount Banahao, Laguna Province, Luzon.

Material examined.—Luzon, 4 (2 CAS, types of *subterrestris* and *montanus;* 2 MCZ).

Taxonomic notes.—Taylor (1922b) fails to compare *subterrestris* with *montanus*. Analysis of his original descriptions indicates only two uncertain distinctions.

Cornufer montanus, according to Taylor, has vomerine teeth, whereas these are lacking in *subterrestris*. The presence or absence of vomerine teeth is a notoriously unreliable taxonomic character. Even within the genus *Cornufer* there is at least one species (*hazelae*) in which the vomerine teeth may be present or absent. My own examination of the type of *montanus* did not detect vomerine teeth, but this failure may be the result of inadequate optical equipment available at the time. The two specimens (MCZ) that Taylor identified as *subterrestris* have no vomerine teeth.

The only other distinction that may be adduced from the original descriptions concerns the granulation of the ventral surfaces. *Cornufer montanus* was said to have "strongly granular" throat and belly, whereas *subterrestris* was said to have a smooth throat and an "indistinctly granular" belly. However, examination of the types reveals that both have coarsely granular skin covering the belly. Furthermore, the throat of the *subterrestris* type is finely granular. The other two specimens (MCZ) are coarsely granular over the entire ventral surface of the body.

The two types are almost identical. Noteworthy is the fact that only the four specimens listed above, of all the Philippine *Cornufer* examined for this study, have yellow and brown areolations in the groin and on the legs (fig. 62, C). There is no choice but to place *montanus* in the synonymy of *subterrestris*.

Diagnosis.—Size small (probably only rarely, if ever, over 30 mm.); finger tips (except first) dilated into broad truncate disks having horizontal circummarginal grooves only; belly granular; no supernumerary tubercles on the foot; groin with conspicuous areolations (fig. 62, C); no dermal "horn"; males with a median internal subgular vocal sac.

Description.—Body short, neither stocky nor elongate; head broader than long; snout rounded; tympanum distinct, one-third to three-fifths diameter of eyes; vomerine teeth present or absent; tongue with a papilla anteriorly; a supratympanic fold from eye to axilla; skin of back with or without irregularly scattered tubercles; no longitudinal folds; skin of abdomen granular.

Tips of fingers (except first) broadly dilated into truncate disks with horizontal circummarginal but no transverse proximal grooves; first finger shorter than second; a supernumerary tubercle on each metacarpal. Tips of toes dilated into truncate disks with grooves similar to those of fingers; disk of fourth toe subequal to that of third finger; disks of other toes smaller; web reaching only to base of proximal subarticular tubercles as broad sheet; web extending along greater part of toes as a fringe; third toe longer than fifth;

two metatarsal tubercles, inner oval, outer round; no supernumerary tubercles on sole of foot.

Color (in alcohol) dark to light brown above with various markings; a dark interorbital bar; venter cream with or without brown markings on throat and chest; conspicuous brown and yellow areolations in groin and on ventral surface of legs; areolations may also be present on anterior and posterior faces of thigh.

Secondary sex characters.—The secondary sex characters of *subterrestris* are common to most of the species of *Cornufer*. As noted above, the male has a median internal subgular vocal sac with round openings placed near the corners of the mouth. The throat of the male bears sharp-tipped granules; by contrast the throat of the female is smooth. Nuptial pads are absent. The males mature at a small size. Two specimens (MCZ 14387–88) measuring only 20.0 and 22.5 mm., snout to vent, have vocal sacs and granular throats.

Ecological notes.—All the known specimens of *subterrestris* have been taken in the mountains of Luzon. The type was collected on the bank of a small mountain stream in the northern highlands, the Museum of Comparative Zoology specimens at an elevation over 2,100 meters on Mount Santo Tomas, and the type of *montanus* on Mount Banahao.

Range.—Luzon: Mountain Province (Mount Santo Tomas); Laguna Province (Mount Banahao).

Cornufer guentheri Boulenger

Cornufer guentheri Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 108, pl. 11, fig. 3—Dinagat Island; 1918, Ann. Mag. Nat. Hist., (9), **1**: 373; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 124; Taylor, 1920, Phil. Jour. Sci., **16**: 308, pl. 8, figs. 1 and 1*a*, text fig. 3; Noble, 1927, Ann. New York Acad. Sci., **30**: 108, fig. 28, A, B, and D.

Cornufer worcesteri Stejneger, 1905, Proc. U. S. Nat. Mus., **28**: 345—Mindanao.

Material examined.—Dinagat, 1 (BM, type of *guentheri*); Luzon, 3 (MCZ); Polillo, 4 (1 BM; 3 MCZ); Leyte, 1 (CAS); Mindanao, 8 (3 CNHM; 2 CM; 2 MCZ; I USNM, type of *worcesteri* Stejneger); "Philippine Islands," 2 (CM).

Taxonomic notes.—As in the case of *C. meyeri*, *guentheri* is more closely related to a Papuan species, *guppyi* Boulenger, than to any of the other Philippine species. *Cornufer guentheri* and *guppyi* both have transverse grooves that form the proximal border of the terminal digital disks. The grooves are present on toes as well as fingers.

The enlarged disks of the toes are another character common to *guentheri* and *guppyi*. The two forms differ considerably in size, *guppyi* reaching 100 mm. and *guentheri* less than 50 mm., and *guentheri* has a far less coarsely granular ventral surface than *guppyi;* indeed some individuals of *guentheri* have completely smooth venters.

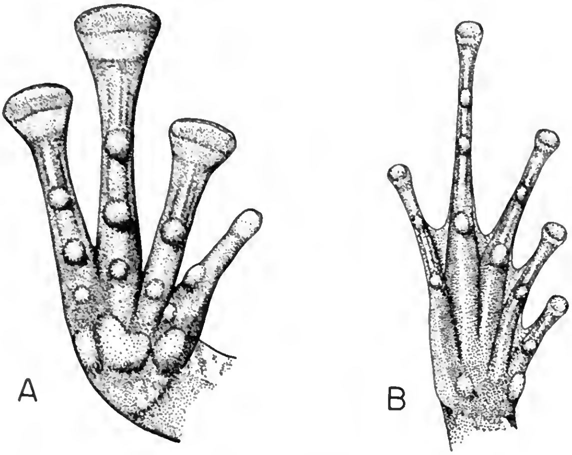

FIG. 64. *Cornufer guentheri.* A, hand (× 3.7); B, foot (× 2.5).

Cornufer worcesteri Stejneger must be placed in the synonymy of *guentheri.* Examination of the type of *worcesteri* indicates no basis for the maintenance of two species. Taylor (1920) expressed some doubt of the distinctness of *worcesteri,* pointing out that only the absence of a lingual papilla in the type prevented his considering the two forms as identical. The papilla is evident in most individuals I have examined but is hidden in a few. Accidents of preservation may account for the varying appearance of this structure. In no other significant respect do the individuals without papillas differ from the rest.

Diagnosis.—Size moderate, females up to 45 mm., males somewhat smaller; finger tips with broad truncate disks (fig. 64, A), with horizontal circummarginal and transverse proximal grooves; granulation of the ventral surface variable (see below); no supernumerary tubercles on the foot; no dermal "horn"; no areolations at the groin; first toe, measured from distal edge of inner metatarsal tubercle, more than twice as long as tubercle.

Description.—Head wider than body; body tapering slightly to groin; head as broad as or broader than long; snout obtusely pointed or rounded; tympanum distinct, one-third to one-half diameter of eye; tongue with a papilla anteriorly, occasionally with the papilla retracted and indistinct; vomerine teeth present; a supratympanic fold from eye to axilla; skin of back with a few scattered tubercles or smooth, occasionally a pair of short longitudinal folds; skin of throat smooth; abdomen granular posterior to chest, granular only caudally, or entirely smooth.

Tips of fingers broadened into truncate disks having horizontal circummarginal and transverse proximal grooves; first finger shorter than second; a supernumerary tubercle on each metacarpal. Tips of toes with disks similar to those of fingers in shape and with same grooves; disks of toes smaller than those of fingers; web variable (see below); third toe longer than fifth; two metatarsal tubercles, inner elongate, outer round; no supernumerary tubercles on the foot (fig. 64, B).

Color variable; back (in alcohol) brown with irregular small black spots, or with a pair of light dorso-lateral stripes, or with a light mid-dorsal line, or with a median lavender band; gular region cream densely powdered with brown; chest and belly cream, uniform or with a few brown spots; limbs crossbarred.

Secondary sex characters.—The males have median subgular internal vocal sacs with round openings near the corners of the mouth. The throat is smooth in both sexes. There is some reason to believe that the females attain a larger body length than the males, but the extent of the difference is unknown. At any rate, the data available are as follows (presence of vocal sacs signified by "v," presence of enlarged eggs by "e"):

Males	Females
mm.	mm.
21.0	22.4
24.0 (v)	25.8
34.0 (v)	26.3
35.7 (v)	27.2
37.2 (v)	35.6
	36.8
	37.5
	42.6 (e)
	43.5 (e)

Ecological notes.—Fragmentary evidence indicates that *guentheri* is a forest-inhabiting species. Specimens collected by Taylor (1920) at Bunawan, Mindanao, were found under bark in forest away from the vicinity of water. Three specimens were collected by the Philippine Expedition in original dipterocarp forest, one of them on a log over a stream, a second on the ground, and the third adhering to a tree trunk. The altitudinal distribution of *guentheri* is unknown. The Mindanao specimens cited above are from elevations very close to sea level.

Inter-island variation.—The only noteworthy variation observed involves the webbing of the foot. The minimum extent of web, which is typical of the Mindanao sample, is as follows: to base or center of the proximal subarticular tubercles of first, second, and third toes; to just below the base of the proximal tubercle of the fourth toe; and to slightly beyond the proximal tubercle of the fifth toe. With the exception of the fifth toe, the points of reference are on the outer sides of the toes. In webbing, the Leyte specimen agrees with the Mindanao series. In the three Luzon specimens the web extends to the center of the subarticular tubercle of the first toe, to the distal edge of the tubercle of the second toe, to a point midway between the tubercles of the third toe, to the distal edge of the proximal tubercle of the fourth toe, and to the base of the distal tubercle of the fifth toe. Three of four Polillo specimens have slightly more extensive webs than do those from Luzon. The fourth individual from Polillo has only slightly more web than described for the Mindanao sample.

Head shape also varies slightly. In the Luzon and Polillo frogs the snout is round, whereas in those from Mindanao and Leyte it is obtusely pointed.

Although the geographic variation described points to two recognizable populations of *guentheri,* I do not think it wise to establish subspecies in this case without examination of more material.

Range.—Polillo Island. Luzon: Laguna Province (Mount Maquiling). Leyte: Cabalian. Mindanao: Agusan Province (Bunawan), Cotabato Province (Saub), Davao Province (Tagum). Dinagat Island. Probably *guentheri* will be discovered on Samar.

Cornufer polillensis Taylor

Philautus polillensis Taylor, 1922, Phil. Jour. Sci., **21:** 171—southern end of Polillo Island.

Rhacophorus polillensis Ahl, 1931, Das Tierreich, Lief. 55, p. 107.

Material examined.—Polillo, 6 (4 MCZ, paratypes; 2 CAS).

Taxonomic notes.—It is difficult to determine the basis of Taylor's allocation of this species to the family Rhacophoridae. With some hesitation Taylor placed it in the genus *Philautus* rather than in

Rhacophorus because of the "character of the digits" (Taylor, 1922a); just which character Taylor unfortunately did not say.

As a matter of fact, a character of the digits is reason for placing it in a different family: there are no intercalary cartilages. Other features of *polillensis*, such as the forked omosternum, the fused outer metatarsals, the reduced web, the metacarpal tubercles, and the shape of the finger disks, furnish the basis for my generic allocation.

Apparently Ahl shifted *polillensis* to *Rhacophorus* because of the presence of vomerine teeth. It is not possible to determine whether Ahl had seen a specimen of *polillensis* or had based his account solely on Taylor's description. The failure to indicate what material he had examined is a general criticism to be made of Ahl's report (1931).

Diagnosis.—Size small, males with vocal sacs 20.3 (MCZ 14470) and 22.6 mm. (CAS 62251) snout to vent; tips of fingers broadly dilated into truncate disks with horizontal circummarginal grooves; no longitudinal ridges on the back; belly with coarse granules; no supernumerary tubercles on the foot; no areolations on the groin; a low papilla on the upper eyelid; snout acutely pointed (fig. 65, C, D).

Description.—Body tapering to groin; head longer than broad; snout acutely pointed; tympanum visible, one-third diameter of eye; vomerine teeth usually present; tongue with a papilla anteriorly; a supratympanic fold from eye to axilla; skin of back smooth with a few small scattered tubercles, no longitudinal ridges; skin of belly coarsely granular; for skin of throat see *Secondary sex characters.*

Tips of fingers dilated into broad truncate disks with horizontal circummarginal grooves, without transverse groove at proximal border of pad; first finger shorter than second; a supernumerary tubercle on each metacarpal. Tips of toes dilated, the disks smaller than those of fingers; web reaching center of proximal subarticular tubercle on first, second, and fourth toes, distal edge of tubercle on third, and between subarticular tubercles on fifth toe; web extending to disk of fourth toe as a narrow fringe; third toe slightly longer than fifth; first toe, measured from distal edge of inner metatarsal tubercle, less than twice the length of the tubercle; two metatarsal tubercles, the outer one not distinct; without supernumerary tubercles on the foot.

Color in life (Taylor, 1922a) cream with fine brown dots dorsally; a faint indication of two dark lines on the back; ventrally cream, immaculate or with brown spots on the throat and belly; usually a brown line extending forward from the eyes on the lores and a second running backward from the eye through the tympanum.

Secondary sex characters.—As in many species of *Cornufer*, the males of *polillensis* have median internal subgular vocal sacs with round openings at the corners of the mouth. Also, the males have granular throats and chests; in the females these areas are smooth. The males are without nuptial pads.

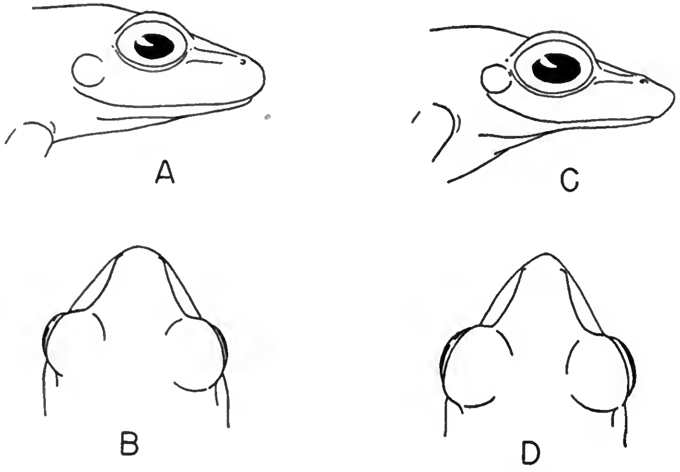

FIG. 65. Heads of *Cornufer hazelae* (A, B) and *C. polillensis* (C, D); × 3.

Range.—Known only from the type locality on Polillo.

Cornufer hazelae Taylor

Philautus hazelae Taylor, 1920, Phil. Jour. Sci., **16**: 298, pl. 3, fig. 2—Canlaon Volcano, Negros; Ahl, 1931, Das Tierreich, Leif. 55, p. 67.

Cornufer rivularis Taylor, 1922, Phil. Jour. Sci., **21**: 270, pl. 4, fig. 3—Balbalan, Mountain Province, Luzon.

Material examined.—Negros, 11 paratypes (10 CM; 1 CNHM); Luzon, 3 (2 CAS, type and topotype of *rivularis;* 1 MCZ, paratype of *rivularis*).

Taxonomic notes.—An examination of the digits of *hazelae* reveals that no intercalary cartilages are present. This, of course, necessitates removing the species from the Rhacophoridae. Other characters of *hazelae,* such as the presence of maxillary teeth, the forked omosternum, the fusion of outer metatarsal, the reduced web, the metacarpal tubercles, and the shape of the finger disks, indicate that it belongs in the genus *Cornufer*. It is not possible to determine why Ahl (1931) followed Taylor's designation.

The type and topotype specimens of *rivularis* are identical with *hazelae* in habitus, granulation of the belly, shape of finger disks, size of toes, and secondary sex characters—in short, in so many respects that one is forced to conclude that they constitute a single species. Not enough material is available to determine the extent of geographic variation.

Cornufer hazelae shows extensive similarity to *C. polillensis*. The only consistent difference I can find is in the shape of the snout (see fig. 65). In *polillensis* the snout is acutely pointed and long; in *hazelae* it is shorter and obtusely pointed or round. There are some, though doubtfully reliable, indications that *polillensis* is smaller, the measurements of the type (sex unknown) and two mature male paratypes being 27 (Taylor, 1922a), 22.6, and 20.3 mm. These compare with my own observation of a range from 27.8 to 31.4 mm. (mean 25.9) for the mature paratypes, both males and females of *hazelae* and *rivularis* combined. It is with considerable hesitation that I maintain Taylor's separation of *polillensis* and *hazelae.*

Both *hazelae* and *polillensis* seem to be closely related to the Luzon forms, *cornutus* and *subterrestris*. These, considered as a group, are set apart somewhat both from *guentheri* and the Papuan forms, such as *guppyi* and *unicolor*, on the one hand, and from the forms without large disks, such as *meyeri* and *solomonis*, on the other. Surprisingly, the group of northern Philippine species shows many points of similarity to the Papuan *Batrachylodes vertebralis* Boulenger, which probably is a *Cornufer*.

Diagnosis.—Size moderate, males probably not in excess of 30 mm., females somewhat larger; finger tips dilated into broad truncate disks with horizontal circummarginal but without transverse proximal grooves; no longitudinal folds on the back; belly coarsely granular; no supernumerary tubercles on the foot; no prominent "horn" on the eyelid; no areolations at groin; first toe, measured from distal edge of inner metatarsal tubercle, less than twice length of tubercle; snout not acutely pointed (fig. 65, A, B).

Description.—Body moderately stocky; head as broad as or broader than long; snout obtusely pointed or rounded; tympanum distinct, one-fourth to one-half diameter of eye; vomerine teeth present or absent, sometimes present on one side but not on the other; papilla on tongue anteriorly; a supratympanic fold from eye to arm; skin of back smooth, occasionally with several small tubercles; one or two low papillae on upper eyelid; skin of chest slightly wrinkled to granular; throat variable.

Tips of fingers broadened into truncate disks, with horizontal circummarginal grooves distally and laterally, without transverse proximal grooves; first finger shorter than second; a supernumerary tubercle on each metacarpal. Toes dilated at tips; disks smaller than those of fingers; web reaching only to center of proximal tubercles of first and second toes, to center or distal edge of proximal tubercles of third and fifth toes, and to base or center of proximal tubercle of fourth toe; third toe longer than fifth; first toe, measured from distal edge of inner metatarsal tubercle, less than twice length of tubercle; two metatarsal tubercles, outer frequently obscured; no supernumerary tubercles on foot.

Color variable, dorsally ground color cream densely speckled with dark brown, dark brown uniform or with light mid-dorsal stripe, or gray brown with several dark lines; ventrally cream, uniform or with varying amounts of dark brown on throat and abdomen; limbs almost invariably with dark crossbars dorsally.

Secondary sex characters.—Beyond the presence of median internal vocal sacs in males, the extent of sexual dimorphism is not clear. The males have a more rugose throat than the females, but the difference is not as sharp as in, for example, *corrugatus*. In two of the mature males examined the skin of the throat was weakly pitted or shagreened, in six the throat was wrinkled, and in a single male definitely granular. Only two females were examined; in one the throat was shagreened and in the other slightly wrinkled. There also appears to be a difference in body lengths. The males with vocal sacs varied from 21.8 to 26.0 mm. snout to vent, whereas the two female paratypes measured 31.0 and 31.4 mm. The type, also a female, measured 34 mm. (Taylor, 1920).

Ecological notes.—Cornufer hazelae, together with *C. cornutus* and *C. subterrestris*, constitutes a group of small montane species that seemingly are the ecological equivalents in the northern Philippines of *Oreophryne* (Mindanao, Celebes, the Moluccas, and New Guinea). The type series of *hazelae* was collected by Taylor on Canlaon Volcano, the known Luzon material near 1,000 meters, and one specimen from Panay at 1,000 meters (Taylor, 1920). Taylor collected the Canlaon material in the leaf axils of abaca.

Range.—Negros: Oriental Province (Mount Canlaon). Luzon: Mountain Province (Balbalan). Panay: Antigue Province (Culasi [Taylor, 1920]).

RHACOPHORIDAE

Rhacophorus Kuhl and van Hasselt

1a. Web between third and fourth fingers extending beyond distal subarticular tubercles (fig. 66)........*R. pardalis*
1b. Web between outer fingers not extending beyond distal subarticular tubercles........2
2a. A transverse, light-tipped dermal appendage below anus (fig. 67). *R. appendiculatus*
2b. No such transverse dermal appendage below anus........3
3a. Skin adhering to or ossified with fronto-parietals; females usually over 65 mm........*R. leucomystax*
3b. Skin not adhering to fronto-parietals; all individuals under 65 mm........4
4a. Two conspicuous light tubercles above the anus........*R. hecticus*
4b. No such tubercles........5
5a. A row of light tubercles along posterior surface of tarsus (fig. 71)..*R. everetti*
5b. No such tubercles on tarsus........6
6a. Lateral edge of lower arm with a light line formed by a low ridge of skin or row of tubercles........*R. leucomystax*
6b. Lateral edge of lower arm without light line; no row of tubercles or ridge of skin........7
7a. Outer edge of fifth toe with a crenulated fringe of skin........*R. surdus*
7b. Fringe of skin along fifth toe with smooth edge or absent........8
8a. Fingers distinctly webbed at base (fig. 68)........*R. lissobrachius* sp. nov.
8b. Fingers without web (fig. 69)........*R. emembranatus* sp. nov.

Rhacophorus pardalis pardalis Günther

Rhacophorus pardalis Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 83, pl. 6, fig. D—Philippines; Boulenger, 1882, op. cit., p. 91; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 123; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 263; Ahl, 1931, Das Tierreich, Lief. 55, p. 160, figs. 95–96.

Rhacophorus pardalis pardalis Wolf, 1936, Bull. Raffles Mus., no. 12, p. 204.

Polypedates pardalis Taylor, 1920, Phil. Jour. Sci., **16**: 281, pl. 4, fig. 1, pl. 6, figs. 2 and 2a; 1922, op. cit., **21**: 275.

Rhacophorus rizali Boettger, 1899, Abh. Ber. Mus. Dresden, **1898–1899**, no. 1, p. 1—Dapitan, Mindanao.

Material examined.—Luzon, 1 (MCZ); Polillo, 1 (MCZ); Bohol, 2 (MCZ); Mindanao, 5 (2 CNHM, 2 CM, 1 USNM); Basilan, 1 (MCZ); Borneo, 12 (CNHM).

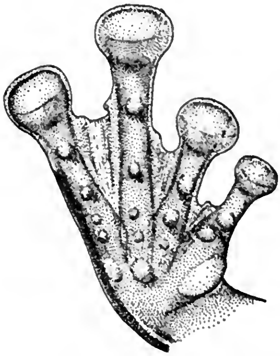

FIG. 66. Hand of *Rhacophorus pardalis;* × 2.6.

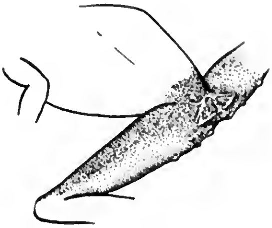

FIG. 67. Infra-anal dermal appendages of *Rhacophorus appendiculatus;* × 1.5.

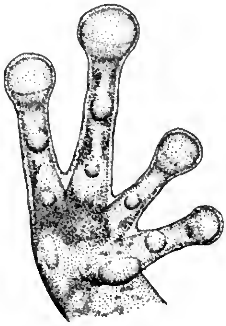

FIG. 68. Hand of *Rhacophorus lissobrachius* sp. nov.; × 2.7.

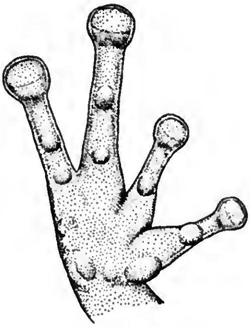

FIG. 69. Hand of *Rhacophorus emembranatus* sp. nov.; × 2.7.

Taxonomic notes.—Wolf recognizes the following as distinct subspecies of *pardalis: rhyssocephalus* Wolf (Sangihe Island), *pulchellus* Werner (Borneo and Sumatra), *robinsoni* Boulenger (Malay Peninsula), *annamensis* Smith (Indo-China), and *pardalis* Günther (Philippines). The distinctions between *pardalis pardalis* and *pardalis pulchellus* are, according to Wolf, body proportions and reduction of the cutaneous flap of the vent in *pulchellus.* Wolf had seen only one specimen from Borneo and one from Sumatra. The body proportions in question are length of leg, interorbital distance, and head width; these are all subject to variation, the range of which Wolf could not have determined from two specimens. As for the cutaneous development around the anus, there is variation within the sample from Mindanao available to me, indicating that this distinction between *pulchellus* and *pardalis* must be subjected to statistical analysis before it is accepted. In the absence of adequate material from Borneo I am obliged to consider *pulchellus* subspecifically identical with *pardalis.*

Of the two remaining subspecies, two, *robinsoni* and *annamensis,* had not been examined by Wolf. I suggest that the relations of these forms (known from only two and one specimen respectively) are still in doubt. Perhaps these should not be recognized as subspecies of *pardalis.* However, *rhyssocephalus* Wolf is apparently correctly designated as a distinct subspecies of *pardalis.*

Diagnosis.—A large-sized species of *Rhacophorus,* females over 65 mm., males occasionally over 50 mm.; fingers extensively webbed, outer fingers webbed beyond distal subarticular tubercle (fig. 66); a horseshoe-shaped or transverse flap of skin usually present over vent; a second dermal fold below vent, this frequently confluent with first flap; a smooth-edged fold of skin from elbow to pad of fourth finger and a similar one from heel to pad of fifth toe; skin of head free from skull; the fold below the anus continuous from one thigh to the other, thus differing from the dermal development found in *appendiculatus.*

Description.—Body tapering abruptly behind shoulders except in gravid females; head a little broader than long; skin of head not involved in ossification of skull; snout rounded or obtusely pointed, projecting slightly; vomerine teeth present; tympanum visible, one-half to two-thirds diameter of eye; a curved supratympanic fold from eye to arm; no dorso-lateral fold.

Fingers with well-developed web; web extending beyond distal subarticular tubercles between second and third and between third and fourth fingers, occasionally reaching disks; web reaching distal edge of subarticular tubercles between first and second fingers (fig. 66); first finger shorter than second; tips of fingers with very large pads, that of third finger wider than tympanum; pads circumscribed by grooves. All toes, including fourth, webbed to disks; occasionally web not quite reaching pad of fifth toe; disks of toes smaller than those of fingers but with same grooves; a small oval inner metatarsal tubercle but no outer one.

Skin smooth or somewhat shagreened dorsally; gular and pectoral regions smooth; venter behind pectoral girdle coarsely granular. Skin around the vent variously modified; the dorsal lip of the anus horseshoe-shaped or transversely elongated; the skin below the opening forming a transverse fold usually continuous from one thigh to the other and usually continuous with the dorsal fold. A prominent non-serrated dermal fold from the elbow to the pad of the fourth finger; another from the heel to the pad of the fifth toe.

Color variable; dorsum (in alcohol) brown or purplish, uniform or with a dark cruciform mark or with small light spots; ventrally uniform white or cream; limbs with or without dark crossbars.

Secondary sex characters.—According to Liu (1935) males of *pardalis* have a median subgular internal vocal sac with round openings at the corners of the mouth. Dissections of Philippine specimens confirm this statement. A nuptial pad is present on the mediodorsal portion of the first finger in males. The nuptial asperities usually run along the median edge of the finger from the base of the disk to the articulation of the basal phalanx and metacarpal. At this point the nuptial pad spreads over the dorsal surface of the finger, then contracts to continue along the median border. In some males the pad does not extend distad beyond the articulation of metacarpal and phalanx.

Although there is only meager statistical evidence, the females are apparently larger than the males. Of the specimens examined, four females range from 52 to 66 mm., snout to vent (mean 58.4 mm.); five males, all with vocal sacs and nuptial pads, vary from 43.3 mm. to 50.8 mm. (mean 45.6 mm.).

Ecological notes.—Taylor (1922b) observed *pardalis* breeding on Basilan. The species attaches a yellow foam nest to plants overhanging still water or deposits the mass on the banks. In North Borneo *pardalis* is common both within and at the edges of lowland forests. The altitudinal range as determined from specimens examined is from sea level to about 600 meters.

Range.—Luzon: Mountain Province (Kalinga Subprovince). Polillo. Bohol. Negros: Negros Oriental (Pagyabunan). Mindanao: Agusan Province (Bunawan, between Gibong and Simulao rivers [Taylor, 1920]); Cotabato Province (Talayan); Davao Province (Sitio Taglawig near Maco); Zamboanga Province (Dapitan [Boettger, 1899]). Dinagat (Boettger, 1886). Basilan (Wolf, 1936). Palawan (van Kampen, 1923).

I consider the Palawan record doubtful. Palawan was first included in the range by van Kampen, who had seen no specimens from there. Neither Ahl (1931) nor Wolf (1936) examined material from Palawan but both apparently included it in the range on the strength of van Kampen's report. The species may occur on Palawan but a reliable report is lacking.

Outside the Philippine Islands *p. pardalis* is known from Borneo and Sumatra (Wolf, 1936).

Rhacophorus appendiculatus appendiculatus Günther

Polypedates appendiculatus Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 79—Philippine Islands; Taylor, 1920, Phil. Jour. Sci., **16**: 280, pl. 8, fig. 2; 1922, op. cit., **21**: 278.

Rhacophorus appendiculatus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 86, pl. 8, fig. 4; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 122; 1895, Abh. Ber. Mus. Dresden, **1894–95**, no. 7, p. 2; Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat., (3), **2**: 150; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 255.

Rhacophorus appendiculatus appendiculatus Wolf, 1936, Bull. Raffles Mus., no. 12, p. 161.

Rhacophorus phyllopygus Werner, 1900, Zool. Jahrb. (Syst.), **13**: 494, pl. 32, fig. 5—Sumatra.

Rhacophorus chaseni Smith, 1924, Proc. Zool. Soc. London, **1924**: 226, pl. 1, fig. 1—Teku River, Malay Peninsula.

Rhacophorus appendiculatus chaseni Smith, 1930, Bull. Raffles Mus., no. 3, p. 113.

Material examined.—Mindanao, 19 (14 CM; 4 CNHM; 1 USNM); Basilan, 7 (MCZ); Borneo, 17 (CNHM).

Taxonomic notes.—Wolf (1936) recognized two subspecies of *appendiculatus*, one in Indo-China and Burma (*a. verrucosus*) and a second occupying the southern part of the Malay Peninsula, Sumatra, Mentawei Island, Borneo, and the Philippines (*a. appendiculatus*). This arrangement can be accepted only provisionally. Very little is known of the populations of the Malay Peninsula and Sumatra, as only a few specimens are now present in collections. Smith (1930) differentiates the Bornean and Malayan specimens (*a. chaseni*) from those of the Philippines on the basis of the greater development of the dermal fringes. Although I can confirm this difference (Bornean vis-à-vis Philippine specimens), I do not think it alone is sufficient grounds for subspecific recognition.

Diagnosis.—A small species of *Rhacophorus*, males only rarely exceeding 35 mm., females 5 to 10 mm. larger; skin of head not involved in ossification of skull; fingers with a rudimentary web in each interdigital space; web never reaching distal subarticular tubercles; a transverse, white-tipped fringe of skin below anus (fig. 67); a denticulate fringe of skin along lower arm and tarsus.

Description.—Head longer than broad (except in specimens with the snout damaged); skin of frontal region not involved in cranial ossification; snout acutely pointed, with projecting tip (in undamaged specimens); vomerine teeth present; tympanum visible, one-half diameter of eye; supratympanic fold from eye to insertion of arm, slightly curved; no dorso-lateral fold.

Fingers with a distinct web; web in all three interdigital spaces reaching distal subarticular tubercle as a fringe only; first finger shorter than second, which is slightly shorter than fourth; disks of fingers well developed, that of third finger equal to tympanum; each pad completely circumscribed by a groove ventrally. Foot about two-thirds webbed; web reaching distal level of subarticular tubercle of first toe, midway between pad and subarticular tubercle on outer edge of second toe, proximal edge of pad on outer side of third and on inner side of fifth, and distal subarticular tubercle of fourth; pads of toes only slightly smaller than those of fingers and with the same grooves; an oval inner metatarsal tubercle but no outer one.

Skin of dorsal surfaces shagreened; skin of gular region granular in males, smooth in females; entire abdominal region with coarse granules; conspicuous dermal appendages on lower jaw; a denticulate fringe of skin extending along outer edge of fourth finger and posterior edge of lower arm to elbow; another similar fringe from tibiotarsal joint to disk of fifth toe; a white-tipped, ruffled dermal flap a few millimeters in length below anus.

Color (in alcohol) dorsally grayish brown, uniform or with dark interorbital chevron; ventral surfaces cream or white, immaculate except for occasional brown mottling on chin; limbs with or without dark crossbars.

Secondary sex characters.—Males have a nuptial pad developed on medio-dorsal portion of first finger only. The males also have a median internal subgular vocal sac with openings near the corners of the mouth. As indicated in the description above, the sexes also differ in the skin of the gular region, that of males being granular, that of females smooth.

Sexual dimorphism is apparent in size. Only nine females from the Philippines were examined. These vary in snout-vent length from 27.4 to 42.4 mm., including three below 30 mm. and the remainder above 35 mm. The three smallest may be immature. The mean length of those above 35 mm. is 38.90±0.86 mm. The Philippine males examined ranged from 26.5 to 35.3 mm. The nine with vocal sacs and nuptial pads varied from 30.4 to 35.3 mm., centering about a mean of 32.50±0.58 mm. The differences between these means is statistically significant: $t=6.432$; $P=<0.001$.

Ecological notes.—Taylor (1920) reports finding *appendiculatus* in large caladiums (Araceae) in cut-over forests and along rivers. Two specimens of Chicago Natural History Museum were collected in original dipterocarp forest. The altitudinal range of the Philippine form is unknown. The two just mentioned were captured near sea level. Smith (1930) collected *appendiculatus chaseni* at 1,500 meters.

Inter-island variation.—Reference to variation over the range has been made in the taxonomic notes.

Range.—Polillo (Taylor, 1922b). Dinagat (Boettger, 1886). Mindanao: Agusan Province (Bunawan); Cotabato Province; Davao Province (Sitio Taglawig near Maco); Zamboanga Province (Dapitan [Boettger, 1899]). Basilan (Port Holland). Culion (Boettger, 1895).

Outside the Philippine Islands *a. appendiculatus* is known from the southern part of the Malay Peninsula, Sumatra, the Mentawei Islands, and Borneo (Wolf, 1936).

The Culion record is based on specimens in the Moellendorff collection. The localities Culion and Samar were confused in that collection. Because of this unfortunate circumstance, Taylor (1922b) has reservations about the occurrence of this species on Culion. Although scepticism of this particular record is justifiable, the presence of *appendiculatus* on Culion is not inconsistent with the known close relationship of the fauna of the Calamian Islands to that of Borneo.

The Polillo record is surprising in view of the large gap in known distribution it reveals. Taylor's description of the Polillo specimen leaves little doubt as to its identity.

Rhacophorus leucomystax Boie

Taxonomic notes.—Many authors have credited this species to Kuhl *in* Gravenhorst. However, Gravenhorst made it quite clear that *leucomystax* was another of the new species collected on Java by Kuhl but described by Boie in manuscript (see p. 267).

See pages 380 ff.

Diagnosis.—A large form of *Rhacophorus*, males up to 65 mm. in body length, females occasionally over 80 mm., skin of head adhering to and ossified with fronto-parietals in all individuals exceeding 45 mm. (with the possible exception of those from Jolo); first, second, and third fingers with a rudiment of web (fig. 70); usually not even a rudiment between third and fourth fingers; no dermal excrescences around anus other than the common salientian granules on posterior surfaces of thigh; a row of very weak tubercles on outer edge of lower arm; none on tarsus.

FIG. 70. Hand of *Rhacophorus leucomystax;* × 1.7.

Description.—Habitus moderately elongate; head as broad as long (females) or slightly longer than broad (males); skin of frontal region involved in fronto-parietal ossification; snout obtusely pointed, projecting; vomerine teeth present; tympanum visible, two-thirds to three-fourths diameter of eye; a narrow skin fold from posterior corner of eye forming dorsal border of tympanum and continuing to just beyond axilla or to mid-point of body.

Fingers with a rudimentary web usually discernible only between first and second and between second and third fingers; first finger shorter than second, which is much shorter than fourth; finger pads large, with horseshoe-shaped distal groove and proximal transverse groove (fig. 70); pad of third finger two-thirds to three-fourths horizontal diameter of tympanum. Foot extensively webbed; web narrowly misses reaching pads on outer sides of first, second, and third toes; fourth toe broadly webbed to between two distal subarticular tubercles; toe pads smaller than pad of third finger, but with similar grooves; an oval inner metatarsal tubercle; a small round outer metatarsal tubercle present or absent.

Skin above smooth or slightly shagreened; gular region smooth to granular; entire abdomen behind arms with very large granules; no conspicuous dermal appendages.

The color (in life) is changeable; the ground color may change from light yellow to dark purplish brown; the range of the dorsal pattern is from immaculate through spotted to striped; the ventral coloration is cream, immaculate or with brown mottling on throat.

Secondary sex characters.—The males of this species have nuptial pads on the first two fingers. The pad extends distally only as far as the distal edge of the subarticular tubercle on the first finger. On the second it appears as a small circle on the dorsal surface at the base of the finger. A median, internal, subgular vocal sac with round or oval openings at the corners of the mouth is found in the males of most populations (see *Inter-island variation*).

A series of twelve adult males (over 40 mm. snout to vent) taken in the vicinity of San José, Mindoro, sheds light on the question of seasonal variation in these characters. According to the collector, Dr. W. H. Stickel, the region about San José is subject to pronounced wet and dry seasons, the former commencing in April and the latter in December. The specimens were collected between December 23, 1944, and January 25, 1945. Both dates of capture and the condition of gonads and oviducts of the five large females in the sample (ovaries without enlarged eggs; oviducts small) indicate that the series was not collected during, immediately before, or immediately after the breeding season. Ten of the males had neither vocal sacs nor nuptial pads; the remaining two had both. Thus it appears that both vocal sacs and nuptial pads undergo regression or disappear between breeding periods.

As has been noted by other authors, sex dimorphism in size is marked. Table 37 summarizes data on Philippine specimens. The sexes also differ in the ratio of head width to snout-vent length (see Table 37). The analyses of variance of both the ratio and the snout-vent length indicate clearly the statistical significance of these differences between the sexes.

Ecological notes.—*Rhacophorus leucomystax* is one of the commonest frogs in the Orient. Despite its adaptations for arboreal life (intercalary cartilage, large digital pads, granulations of belly) it is far from being restricted to living above ground. Mertens (1930), for example, found *leucomystax* as often on the ground as in bushes and trees. Stickel's field notes concerning this species on Mindoro are illuminating and typical; in part they read: "These frogs seem to be omnipresent, by day hiding in grass, *Alocasia* axils, crevices in houses and boxes, either on the ground or far

Table 37. Sex dimorphism in snout-vent lengths of adult *Rhacophorus leucomystax* from various Philippine Islands

Snout-vent lengths

	Females			Males		
	No.	Mean ±SE	Range	No.	Mean ±SE	Range
Luzon	12	61.78±7.90	48.0-75.0	25	46.42±0.70	35.4-52.4
Mindoro	7	62.03±2.80	53.7-76.8	13	44.88±0.97	35.4-49.2
Negros	4	60.13	53.0-68.4	1	35.7	---
Mactan	9	61.28±1.99	50.5-66.9	7	49.01±0.97	45.8-53.0
Leyte	2	74.65	73.9-75.4	8	53.70±1.63	48.4-65.3
Mindanao	18	73.27±1.06	63.0-79.8	25	47.52±0.55	41.2-52.3
Palawan	3	63.90	62.0-66.2	25	43.55±0.39	40.0-46.5
Jolo	1	62.1	---	1	37.1	---

Analysis of variance[1]

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes	1383.70	1	1383.70
Within sexes	386.71	12	32.22
Total	1770.41	13	

F (1,12) = 42.94; P = < 0.01

Head width/snout-vent

	Females			Males		
	No.	Mean ±SE	Range	No.	Mean ±SE	Range
Luzon	15	0.335±0.003	0.317-0.352	25	0.321±0.003	0.293-0.353
Mindoro	7	0.340±0.007	0.323-0.376	13	0.317±0.003	0.298-0.331
Mactan	9	0.352±0.007	0.328-0.384	7	0.315±0.004	0.304-0.333
Leyte	2	0.337	0.329-0.345	8	0.328±0.004	0.311-0.349
Mindanao	18	0.321±0.004	0.294-0.360	25	0.315±0.002	0.294-0.346
Palawan	3	0.337	0.327-0.344	25	0.318±0.002	0.297-0.344

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between sexes	972	1	972.0
Within sexes	616	10	61.6
Total	1588	11	

F (1,10) = 15.78; P = < 0.01

[1] Does not include Jolo specimens.

above it. At night they hop about everywhere, on the ground, onto tables, tree trunks and even onto people sitting in the dark."

Altitudinal range in the Philippines as determined by specimens at my disposal is from sea level to 915 meters. Mertens (1930) records the species up to 1,200 meters in the Lesser Sundas.

The foamy egg masses are usually suspended on low branches of trees and shrubs overhanging pools into which the tadpoles eventually fall. According to the field notes of Mr. S. B. Horowitz the egg masses may be deposited in holes in the banks of pools.

Inter-island variation.—In *leucomystax* the extent to which the skin is involved in cranial ossification varies individually and geographically. No skin is so involved in Chinese specimens (Stejneger, 1925). At the other extreme, found in other parts of the range, the skin covering the canthal portion of the nasals, the fronto-parietals, and the supratympanic portion of the squamosal is ossified with the skull. The progress of this ossification in Philippine specimens is as follows: the skin is entirely free in newly transformed individuals (ca. 20 mm. snout to vent); from 40 to 45 mm. the skin of the interorbital region is usually ossified; from 45 to 55 mm. the skin of the temporal region is adherent to the squamosal but does not exhibit the rugosities typical of the final stages; from 55 to 65 mm. the rugosities appear in the temporal region and the skin of the canthi becomes adherent; over 70 mm. the rugosities are usually present in all three regions. Too few specimens in the size class 20–40 mm. were available to determine when ossification sets in. Pope (1931) also noticed an association between size and ossification of the skin in material from Hainan. Inasmuch as males rarely exceed 55 mm. snout to vent (only four out of 190 examined), that sex is a poor indicator of local differentiation in this character.

Of the Philippine material examined, three adult females (62–66 mm.) from Palawan, one from Dumaran (66 mm.) and one from Jolo (62 mm.) have the ossification confined to the skin of the fronto-parietal region. This is in agreement with observations on specimens from northeast Borneo (nine females, 68–85 mm. snout to vent). On the other hand, females of the same size range from Luzon, Mindoro, Negros, Cebu, Leyte, and Mindanao exhibit the maximum extent of ossification described above. No female from Panay was available; on geographic grounds one presumes the population of that area would agree with that of Mindoro and Negros. Outside the Philippines, large females from Mount Kinabalu, North Borneo, have the maximum ossification (three females seen; 64–71 mm.), in contrast with those already mentioned from northeast Borneo (regions about Labuk Bay, Sandakan Harbour, and Dewhurst Bay). In the small (two to four large females) samples seen from Java, Sumatra, Malay Peninsula, and Thailand, the maximum ossification is found.

Rhacophorus leucomystax also exhibits geographic variation in the presence or absence of vocal sacs. The distribution of these

Table 38. Geographic variation of snout-vent length in Philippine sample of *Rhacophorus leucomystax*[1]

	Sex	Difference of means	*t*	*n*	P
Luzon–Mindoro	♀	0.25	0.023	17	---
	♂	1.54	1.287	36	0.20
Luzon–Leyte	♂	7.28	3.352	19	0.005
Leyte–Mactan	♂	4.69	2.384	13	0.04
Leyte–Mindanao	♂	6.18	4.664	31	< 0.001
Mindoro–Palawan . . .	♂	1.33	1.523	36	0.14
Mindanao–Mactan . . .	♀	11.99	5.889	25	< 0.001
	♂	1.49	1.287	30	0.20
Mindanao–Palawan . .	♂	3.97	5.917	48	< 0.001
Borneo–Mindanao . . .	♀	1.76	1.009	26	0.32
	♂	3.42	4.065	47	< 0.001
Borneo–Palawan . . .	♂	7.39	9.983	47	< 0.001

[1] Means and standard errors are given in Table 37, with the exception of the data for the "northeast" Bornean sample, which are as follows:

Males (24): mean ± SE = 50.94 ± 0.64 mm.; range = 44.5 - 57.4.
Females (10): mean ± SE = 75.03 ± 1.34 mm.; range = 68.5 - 84.6.

structures parallels that of maximum ossification of the skin on the head. Vocal sacs are found in males from Luzon, Mindoro, Panay, Negros, Leyte, and Mindanao in the Philippines and from Mount Kinabalu (nine males), Sumatra (one specimen), the Malay Peninsula (eleven specimens), and Thailand (two specimens). Males from Palawan (twenty-five) and Jolo (one) lack vocal sacs, though they all possessed nuptial pads. Only three of the thirty-seven males from northeast Borneo (as defined above to include samples from Labuk Bay, Sandakan Harbour, and Dewhurst Bay) with nuptial pads had vocal sacs.

An outer metatarsal tubercle may be present or absent. Because of the obscuring effects of various preservation treatments, I cannot be sure that the variation in this character is geographic. None of 32 individuals from Palawan has a visible outer tubercle whereas all of 29 specimens from Mindoro have a prominent one. The tubercle is present in some and absent in other Mindanao individuals, being invariably absent in those specimens that are somewhat dried. Fourteen uniformly well-preserved specimens from Abra Province, Luzon, have a prominent outer metatarsal tubercle, but only half of 22 from Rizal Province (not as well preserved) show the character. It is obvious that inter-island variation in the tubercle can only be studied from fresh and/or uniformly well-preserved material. My examination of heterogenous samples gives the following results, in addition to those already mentioned: With the tubercle: Leyte, 12 of 13; Negros, 8 of 9; Panay, one; Cebu, one. Without the tubercle: Jolo, 3; Dumaran, one. Of the Bornean specimens, half lacked any sign of an outer tubercle and half had a weak tubercle.

Finally, geographic variation in snout-vent length was observed. Males of the Palawan sample, which differs from the other Philippine samples in characters already mentioned, have the smallest mean snout-vent length of any sample containing more than one male. The size difference between the Palawan males and those of the other Philippine series is statistically significant in every case except that of the Palawan-Mindoro comparison. The Mindoro males, with the next smallest snout-vent mean, differ statistically from all other samples except the Luzon and, of course, Palawan. Other inter-island comparisons are presented in Table 38.

In the Philippine Islands the following two subspecies of *leucomystax* are recognizable (ranges in fig. 85):

Rhacophorus leucomystax quadrilineatus Boie

Hyla leucomystax Boie *in* Gravenhorst, 1829, Delic. Mus. Vrat., Fasc. 1, p. 26—Java.

Hyla quadrilineatus Boie *in* Wiegmann, 1835, Nova Acta Acad. Leop., **17**, pt. 1, p. 260, pl. 22, fig. 1—Manila, Luzon (as restricted by Wolf, 1936).

Polypedates leucomystax (part) Taylor, 1920, Phil. Jour. Sci., **16**: 288, pl. 2, fig. 4; 1923, Phil. Agriculturist, **11**: 129; Villadolid and Rosario, 1930, op. cit., **18**: 483.

Rhacophorus leucomystax van Kampen, 1923, Amph. Indo-Austr. Arch., p. 246 (part).

Rhacophorus leucomystax sexvirgata van Kampen, 1923, Amph. Indo-Austr. Arch., p. 249 (part).

Rhacophorus leucomystax leucomystax Wolf, 1936, Bull. Raffles Mus., no. 12, p. 178 (part).

Polypedates rugosus Duméril and Bibron, 1841, Erp. Gén., **8**: 520—Java and Manila (part).

Rhacophorus maculatus Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 122 (part).

Material examined.—Luzon, 62 (29 CM; 18 CNHM; 15 UMMZ); Mindoro, 34 (27 CNHM; 6 MCZ; 1 USNM); Leyte, 13 (1 CM; 10 CNHM; 2 USNM); Cebu, 1 (MCZ); Negros, 14 (8 CM; 1 CNHM; 5 USNM); Panay, 1 (CNHM); Mindanao, 113 (108 CNHM; 5 USNM); Basilan, 1 (CNHM); Mactan, 22 (CM).

Diagnosis.—A large form (females up to 80 mm., snout to vent) of *Rhacophorus;* females over 60 mm. with skin of head involved in ossification of fronto-parietals and squamosals; those over 70 mm.

with skin over nasals so involved; males with nuptial pads on first and second fingers, and median, internal vocal sacs.

Range.—Luzon: Abra Province (Licuan); City of Baguio (Baguio); Bataan Province (Mariveles); Laguna Province (Los Baños); City of Manila (Manila); Mountain Province (Balbalan, Nayom); Nueva Vizcaya Province (Bayombong); Pampanga Province (Dau); Pangasinan Province (Umingan); Rizal Province (Antipolo, Fort McKinley, Las Piñas, Novaliches). Mindoro (Calapan). Cebu. Mactan. Leyte (Carigara, Inayupan, Tacloban, Tarragona). Samar (Taylor, 1920). Negros: Negros Occidental Province (Himamaylan, Hinigaran, Saravia, Victorias); Negros Oriental Province (Pagyabunan near Bais, Pamoat near Amio). Panay: Iloilo Province (Ajuy). Mindanao: Agusan Province (Bunawan); Cotabato Province (Barak, Cotabato City, Parang); Davao Province (Caburan, Calian, Maco and Madaum near Tagum, Mount McKinley, Sitio Taglawig near Tagum, Todaya on Mount Apo); Misamis Occidental Province (Bonifacio); Misamis Oriental Province (Agusan, Cagayan); City of Zamboanga (Zamboanga); Zamboanga Province (Bucong near Pagadian, Katipunan). Basilan.

Rhacophorus leucomystax linki Taylor

Polypedates linki Taylor, 1922, Phil. Jour. Sci., **21**: 276, pl. 3, fig. 2—Jolo, Jolo Island.

Rhacophorus leucomystax linki Wolf, 1936, Bull. Raffles Mus., no. 12, p. 181.

Rhacophorus maculatus Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat., (3), **2**: 149.

Rhacophorus macrotis Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 87.

Polypedates macrotis Taylor, 1920, Phil. Jour. Sci., **16**: 285.

Polypedates leucomystax Taylor, Phil. Jour. Sci., **16**: 288 (part).

Rhacophorus leucomystax van Kampen, 1923, Amph. Indo-Austr. Arch., p. 246 (part).

Rhacophorus leucomystax sexvirgata van Kampen, 1923, Amph. Indo-Austr. Arch., p. 249 (part).

Material examined.—Dumaran, 1 (MCZ); Palawan, 32 (31 MCZ; 1 USNM); Jolo, 3 (MCZ, paratypes of *linki*).

Diagnosis.—Same as preceding form, except that males lack vocal sacs and largest females are without the canthal and supratympanic skin ossification.

Remarks.—*Polypedates linki* from Jolo Island was distinguished by Taylor from *leucomystax* by the shorter legs, the narrower interorbital space, the color and markings, and the freedom of the interorbital skin from ossification. It has been stated above that a large female paratype of *linki* exhibits ossification of the skin over the fronto-parietals. Van Kampen (1923) and Villadolid and Rosario (1930) have indicated that a given individual of *leucomystax* may assume a striped, spotted, or immaculate pattern as well as different ground colors at different times. The color pattern cannot be used in taxonomic investigations until careful study of the capacity for color change is made. There may be differences in leg length and interorbital space between the Jolo population and others. Not enough material was available from Jolo to test this possibility. However, even should such investigation show differences in body proportions, the Jolo population could be recognized only as a subspecies of *leucomystax* by this reviewer. Wolf (1936) considered *linki* to be a subspecies of *leucomystax* but restricted the form to Jolo.

The relations of *linki* to the Bornean populations cannot be determined with the material at hand. It has been shown above that specimens from the northeast coast of Borneo (Labuk Bay south to Dewhurst Bay) agree with *linki* in the absence of vocal sacs and the limited amount of dermal ossification. The Kinabalu sample, on the other hand, differs in both of these characters.

Range.—Calamians (Taylor, 1920). Palawan (Brooke's Point, Iwahig). Dumaran (Dumaran). Sulu Archipelago (Jolo Island).

Rhacophorus hecticus Peters

Polypedates hecticus Peters, 1863, Monatsber. Akad. Wiss. Berlin, **1863:** 457—Loquilocum, Samar; Taylor, 1920, Phil. Jour. Sci., **16:** 286.

Rhacophorus hecticus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 18; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 122; Ahl, 1931, Das Tierreich, Lief. 55, p. 117; Wolf, 1936, Bull. Raffles Mus., no. 12, p. 184.

Material examined.—None.

Taxonomic notes.—This species (known from a single specimen) is considered by Wolf (1936) to be closely related to *leucomystax linki*. However, the coloration and the dorso-lateral fold described by Peters are very distinctive. The diagnosis and description that follow are syntheses of the original description and the comments of Wolf, who examined the type.

Diagnosis.—A medium-sized *Rhacophorus*, body length of males about 50 mm.; skin of head free from ossification of skull; fingers webbed at base only; two conspicuous light tubercles above anus;

a fringe of skin on the arm and one on the foot from the heel to the pad of the fifth toe.

Description.—Body slender (according to Peters, resembling *Staurois natator*); head longer than broad; skin of head apparently free of skull; snout rounded, projecting; vomerine teeth present; tympanum distinct, two-thirds diameter of eye. Type, according to Peters, with a thin skin fold from eye to leg; this fold is not mentioned by Wolf. Fingers webbed at base only; first shorter than second; presumably pads of fingers with grooves, as in other species of *Rhacophorus*. Disks of toes smaller than those of fingers; toes three-fourths webbed; last two phalanges of fourth toe free; two metatarsal tubercles. Skin of back granular; belly smooth.

Color (in preservative) blue-gray above; dorso-lateral fold white, bordered by black; upper lip white; under side white; limbs brown, with indistinct spots.

The type is a male lacking vocal sacs (Peters, 1863).

Range.—Known only from the type locality on Samar.

Rhacophorus everetti Boulenger

Rhacophorus everetti Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 87—Palawan; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 251; Ahl, 1931, Das Tierreich, Lief. 55, p. 119.

Polypedates everetti Taylor, 1920, Phil. Jour. Sci., **16**: 287.

Rhacophorus buergeri everetti Wolf, 1936, Bull. Raffles Mus., no. 12, p. 170.

Material examined.—Palawan, 11 (9 CNHM; 2 MCZ).

Taxonomic notes.—Objections to the classification of Wolf (1936) appear under *R. surdus* (p. 388). It is conceivable that there is a close relationship between *everetti* and the Sunda Islands forms, *hosi* (Borneo), *depressus* (Java), and *modestus* (Sumatra), as suggested by Wolf. However, in the absence of comparative material, I prefer, temporarily at least, to consider *everetti* a distinct species. Wolf also speculates on the possibility of synonymizing *surdus* and *everetti*. Comparison of the present sample of *everetti* with the original description of *surdus* seems to eliminate such a possibility. In addition to the differences evident from the diagnoses here presented, the colorations of the two forms have nothing in common.

Diagnosis.—Small species of *Rhacophorus*, male about 34 mm., female 43 mm. snout to vent; fingers with a small web at the base; from three to a dozen large white conical tubercles below anus (fig. 71, C); tubercles not arranged in definite rows; a series of similar asperities along lateral edge of forearm and tarsus (fig. 71, A, B); these tubercles arranged in a single column on each limb; skin of head free of skull.

Description.—Body short, tapering from the head; head broader than long; skin of frontal region not involved in fronto-parietal ossification; snout obtusely pointed, projecting; vomerine teeth present in two short oblique rows; tympanum visible, less than one-half diameter of eye; supratympanic fold from eye to axilla present, somewhat curved; no dorso-lateral fold.

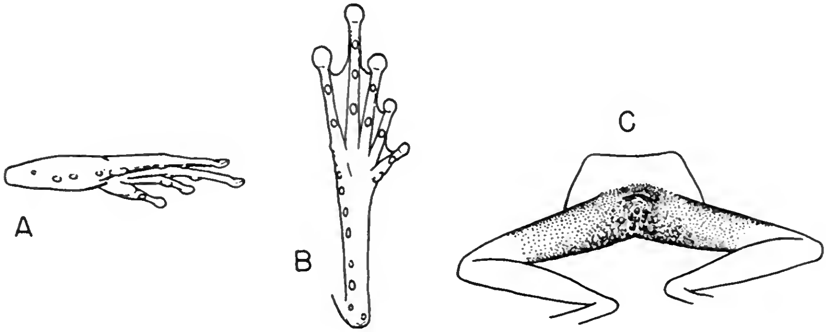

FIG. 71. *Rhacophorus everetti.* A, lateral view of lower arm (× 1.7); B, ventral view of foot and tarsal region (× 1.7); C, anal region (× 1.3).

Fingers with a rudiment of web in each inter-digital space; web not extending beyond distal subarticular tubercles; first finger shorter than second; disks of fingers completely circumscribed ventrally by grooves; disk of third finger as large as or larger than tympanum. Toes extensively webbed; first toe generally webbed to a point just distad of the subarticular tubercle; second and third toes webbed beyond distal subarticular tubercle on outer sides, web sometimes reaching toe pad; fifth toe similarly webbed on inner side; fourth toe webbed to middle subarticular tubercle; disks of toes smaller than those of fingers; an oval inner but no outer metatarsal tubercle. Skin of back shagreened; entire ventrum coarsely granular; lateral edge of lower arm and tarsus with conical tubercles (see *Diagnosis*); area below anus with similar tubercles (see *Diagnosis*).

Color (in alcohol) light brown to cinnamon above with dark brown or black spots forming an inter-orbital bar and an hourglass figure on the back; ventral surfaces cream or white; dorsally limbs with same ground color as back, with dark crossbars; posterior surface of thigh uniform cinnamon or grayish brown.

Secondary sex characters.—The males have a median, internal, subgular vocal sac. Nuptial pads are present on the medio-dorsal edge of the first finger. The asperities do not extend beyond the level of the subarticular tubercle. Sexual dimorphism is also evident in size, the females being larger. Seven males range from 29.6 to 35.2 mm. in body length (mean 33.5); two females measure 41.4 and 44.3 mm.

Ecological notes.—Little is known of the ecology of this arboreal species. The specimens reported on here were collected at altitudes between 230 and 850 meters. One pair was captured while copulating on a shrub on the bank of a stream. Noble (1927) was of the opinion that *everetti* did not make a froth nest, as do most other species of *Rhacophorus*. This belief was based upon the fact that dissection of a 42 mm. female disclosed non-pigmented eggs 2.5 mm. in diameter. The large size attained by the eggs is confirmed by dissection of the two Chicago Natural History Museum females.

Range.—Palawan (Mount Balabag, Thumb Peak, Tigoplan River near Brooke's Point).

Rhacophorus surdus Peters

Polypedates surdus Peters, 1863, Monatsber. Akad. Wiss. Berlin, **1863**: 459—Luzon; Taylor, 1920, Phil. Jour. Sci., **16**: 291.

Rhacophorus surdus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 79; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 122; Ahl, 1931, Das Tierreich, Lief. 55, p. 188.

Rhacophorus buergeri surdus Wolf, 1936, Bull. Raffles Mus., no. 12, p. 169.

Material examined.—Luzon, 20 (MCZ).

Taxonomic notes.—*Rhacophorus surdus* is one of those species whose status was indeterminate for many years, having been known from a unique type since 1863. In 1922 E. H. Taylor collected a series of over twenty rhacophorids (MCZ 23280–89) on Mount Maquiling, Luzon, but did not record them in publication. These agree remarkably well with Peters' original description. In the Mount Maquiling specimens the disks of the toes are slightly smaller than those of the third fingers whereas in the type of *surdus* the disks of the toes are reputed to be larger. This constitutes the only point of disagreement with the original description.

Wolf (1936) considered *surdus* to be a subspecies of *buergeri*. In addition to populations of tree frogs from Japan, the Riukiu

Islands, and Formosa, Wolf included in the species *buergeri* frogs from Hainan, northern Indo-China (Tonkin), Sumatra, Java, Borneo, Palawan (*everetti*), and Luzon. With the exception of the Tonkin population, Wolf designated no related forms on the adjacent eastern Asiatic mainland. The relating of the populations of Formosa, the Riukius, and Japan is a reasonable and perhaps correct procedure, since these islands form a natural faunal unit, with a closely knit geologic history (Inger, 1947). Borneo, Sumatra, Java, and Palawan also form a faunal and geographic unit. However, in the absence of related intervening continental forms, the combining into one species of these two groups of populations, even with a somewhat intermediate population on Luzon, seems to me to be unwarranted. The failure of Wolf to designate such continental relatives may only reflect our general ignorance of the fauna of eastern and southeastern Asia. Yet this lack of knowledge, if it is that, is another reason for *not* lumping the Sunda Islands' forms with *buergeri*.

Several other criticisms of Wolf's arrangement can be made. Of the twelve forms he listed under *buergeri* Wolf did not see any specimens of three and only a single specimen (the type) of each of two others.

In the case of *surdus*, of which he saw the only specimen known at that time, one of the conspicuous characters Wolf considers typical of his *buergeri* complex is absent, namely, tubercles on the lateral edges of the lower arm and tarsus. Peters did not refer to any dermal excrescences on the type specimen. In his own discussion of *surdus*, Wolf does not mention these structures either. Tarsal tubercles are absent in all of the Mount Maquiling specimens. Approximately one-fourth of them have a single small tubercle near the wrist on the lower arm.

Diagnosis.—A small species of *Rhacophorus*, adult males 23 to 28 mm., females 5 to 10 mm. larger; skin of head not involved in ossification of skull; fingers free or with a rudiment of web; no conspicuous folds or tubercles in neighborhood of anus; no fringe of skin or row of tubercles along lateral edges of tarsus and lower arm; no light line along edge of lower arm.

Description.—Body tapering gradually from temporal region to groin; head at tympanum broader than long; skin of head not involved in ossification of skull; snout subacuminate or rounded, projecting; vomerine teeth present in approximately three-fourths of individuals; tympanum indistinct posteriorly, about one-third diameter of eye; a supratympanic fold present; no dorso-lateral fold.

Fingers free or with a rudiment of web; first finger shorter than second; disks of fingers completely circumscribed by a horizontal groove; disk of third finger slightly larger than tympanum. Toes, except fourth, webbed to beyond the distal subarticular tubercles; fourth webbed to penultimate subarticular tubercle; a weak, but distinct crenulated fringe of skin on outer margin of fifth toe; disks of toes smaller than disk of third finger; an oval inner, but no outer metatarsal tubercle.

Skin usually smooth above with tubercles on eyelids and a pair on anterior part of back, occasionally several pairs of faint ridges on back; hind limbs with or without small tubercles dorsally; throat weakly corrugated or coarsely granular; chest and belly coarsely granular; outer edge of lower arm and lower leg without fringe of skin, row of tubercles, or light line.

Color variable; above (in alcohol) gray brown to dark reddish brown ground color, uniform or with darker markings; markings of dorsum varying from an oblique stripe running between sacrum and groin to diverse cruciform patterns; a dark interorbital bar; an oblique light line below eye; under side cream with varying amounts of brown speckling, throat occasionally solid brown; limbs with dark crossbars; posterior face of thigh with large cinnamon blotches dotted with fine white specks.

Secondary sex characters.—Males have a median, internal, subgular vocal sac. The nuptial pads are large and cover parts of the first two fingers. On the dorsal surface of the first finger, the pad extends from the base of the finger to a point just proximal to the scansorial disk. The pad also covers the medial surface of the first finger, giving the finger a greatly thickened appearance when viewed from below. On the second finger the pad is limited to the mediodorsal surface from the penultimate phalanx to the base of the finger. Under magnification the nuptial pad appears to consist of a number of small yellow lumps that, upon sectioning, prove to be acinous glands. There are no epidermal spines on the pad, making *surdus* unique among the Philippine *Rhacophorus*.

The single female examined had the throat slightly wrinkled, whereas in each of the males this region was coarsely granular.

Range.—Known only from Luzon. The Mount Maquiling record suggests that *surdus* may be limited to high elevations.

Rhacophorus lissobrachius[1] sp. nov.

Type.—Chicago Natural History Museum no. 50683. Female with large eggs collected on the east slope of Mount McKinley, Davao Province, Mindanao, altitude 1,340 meters, September 24, 1946, by Harry Hoogstraal.

Diagnosis.—A small species of *Rhacophorus*, web between third and fourth fingers reaching level of penultimate subarticular tubercle on third finger (fig. 68); no conspicuous folds or tubercles in anal region; outer edge of forearm and lower leg without fringe of skin, row of tubercles, or light line; a weak but distinct, movable fringe of skin on outer edge of fourth finger.

Description of type.—Body tapering slightly from temporal region to groin (fig. 72); head at tympanum broader than long; snout rounded, not projecting, longer than horizontal diameter of eye; interorbital space one and one-half times width of upper eyelid; canthus rostralis angular; lores concave and sloping; vomerine teeth in oblique groups at medio-anterior corners of choanae; tympanum distinct, about one-half diameter of eye; supratympanic fold present; no dorso-lateral fold. Skin of head not involved in ossification of skull; shagreened above with several small tubercles on upper eyelid and occipital region; gular region rugose; chest and abdomen coarsely granular.

Fingers with large round disks; disks completely circumscribed by groove; disk of third finger largest; those of third and fourth fingers larger than tympanum; web between third and fourth fingers reaching about to the level of penultimate subarticular tubercle of third finger; distinct rudiments of web between other fingers; all fingers with distinct fringe of skin to disks; fringe on lateral edge of fourth finger uneven. Disks of toes slightly smaller than those of lateral fingers; toes except first and fourth webbed to between distal subarticular tubercles and disks; first toe webbed to subarticular tubercle, fourth to center tubercle; outer edge of fifth toe with distinct smooth-edged fringe of skin; metatarsals with small supernumerary tubercles; inner metatarsal tubercle oval; no outer metatarsal tubercle.

Color (in alcohol) dark brown above with indistinct darker spots anteriorly; upper lip barred with darker color; vertical white bar below posterior half of eye, not reaching mouth; lower sides with

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[1] Named *lissobrachius* because of the smooth-edged forearm.

equal areas of white and brown; lower surfaces of body and limbs cream with brown spots, limbs with least amount of cream and abdomen with least amount of brown; three dark crossbars on dorsal surface of thigh, two on lower leg; posterior surface of thigh cinnamon brown, with large white blotches in proximal third and uniform in distal two-thirds.

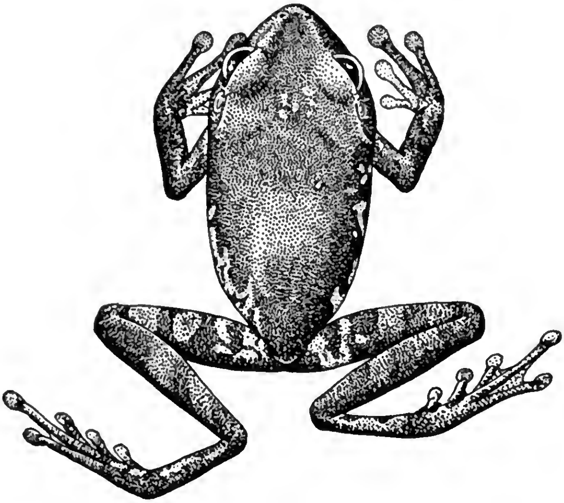

FIG. 72. *Rhacophorus lissobrachius* sp. nov.; × 1.3.

The eggs are uniform cream in color and measure approximately 3 mm. in diameter exclusive of the gelatinous envelope.

Measurements of type.—Snout to vent 38.2 mm.; head width 16.0 mm.; head length (from posterior rim of tympanum) 13.3 mm.; lower leg 20.7 mm.

Paratypes.—None.

Remarks.—One adult female (44.7 mm. snout to vent, with large eggs) in the British Museum (B.M. 1911.1.30.40) from an elevation of 1,200 meters on Mount Penrissen, Sarawak, may belong to this species. In general appearance it is strikingly like *lissobrachius.* However, the Penrissen specimen does differ slightly from *lissobrachius* in extent of webbing, shape of snout, and coloration of belly. The web between the third and fourth fingers reaches a level midway between the subarticular tubercles of the third finger. The webbing of the toes comes closer to the disks than in *lissobrachius.* The snout of the Penrissen specimen is more broadly rounded. There are only faint traces of brown on the dirty cream belly instead of bold brown spots.

Both of these specimens resemble *R. surdus* Peters and *hosi* Boulenger. From the former they differ in the following ways: snout not projecting, webbing of fingers and toes more extensive (see descriptions, p. 388 and above), posterior surface of thighs with larger areas of brown. They do not differ markedly from *surdus* in habitus. It is in precisely this character that the type of *lissobrachius* and the Penrissen specimen differ from the type of *hosi* (examined at British Museum) most strikingly. *Rhacophorus hosi* is a much slimmer and longer-legged form. The head of *hosi*, for instance, is narrower than in the present species; the interorbital area is equal in width to the upper eyelid in *hosi* but is much wider than the eyelid in *lissobrachius* and in the Penrissen specimen. Other distinctions between these two specimens and the type of *hosi* involve the webbing of the fingers (less extensive in *hosi*) and the relative size of tympanum and finger disks (tympanum greater than disks of lateral fingers in *hosi*, disks larger in *lissobrachius* and the Penrissen specimen).

Range.—Mindanao: Davao Province (Mount McKinley).

Rhacophorus emembranatus[1] sp. nov.

Type.—Chicago Natural History Museum no. 50684. Female with large eggs collected on the east slope of Mount McKinley, Davao Province, Mindanao, altitude 950 meters, August 21, 1946, by Donald Heyneman and Harry Hoogstraal.

Diagnosis.—A small *Rhacophorus*, adult female 40 mm. snout to vent; fingers without web even at base (fig. 69); weak fringe of skin along outer edge of fourth finger not movable with forceps; no distinctive folds or tubercles in anal region; outer edges of forearm and lower leg without fringe of skin or row of tubercles; no light line along outer edge of forearm.

Description of type.—Body tapering from temporal region to groin; head at tympanum broader than long; snout obtusely pointed, not projecting; interorbital space one and one-third width of upper eyelid; canthus rostralis obtuse; lores weakly concave and sloping; vomerine teeth present on left side only, teeth in oblique row

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[1] Specific name refers to the absence of web between the fingers.

touching medio-anterior corner of choana; tympanum faintly visible, one-fourth diameter of eye; supratympanic fold present. Skin of head free from skull; skin shagreened above with one small tubercle on upper eyelid; gular region rugose; chest and abdomen coarsely granular.

Fingers without rudiment of web; third finger with weak lateral fringe to disk; fringe on outer side of fourth weak, smooth-edged, not movable; disks completely circumscribed by horizontal grooves; disk of third finger much larger than tympanum. First toe webbed to base of subarticular tubercle; second, third, and fifth toes webbed to distal edge of outer subarticular tubercle; fourth toe webbed to base of penultimate tubercle; lateral edge of fifth toe with weak smooth fringe; disks of toes smaller than those of lateral fingers; an oval inner, but no outer metatarsal tubercle; no supernumerary tubercles on foot.

Color (in alcohol) slate speckled with black dorsally; five small cream spots in frontal region; upper lip cream; below uniformly cream; dorsal surfaces of limbs with dark crossbars; ventral surfaces of legs gray; posterior surface of thigh uniformly speckled with fine dark dots, a cinnamon suffusion distally.

Measurements of type.—Snout to vent 40.1 mm.; head width 16.3 mm.; head length (from posterior rim of tympanum) 14.5 mm.; lower leg 23.6 mm.

The eggs are uniformly cream-colored.

Remarks.—Like *Rhacophorus lissobrachius* this specimen resembles *surdus* Peters and the *Rhacophorus buergeri* group (*sensu* Wolf, 1936) in general. Nevertheless it cannot be identified with any of the forms described by Wolf. It is distinguished from both *surdus* and *lissobrachius* by differences in coloration, webbing, and size of tympanum. These and other differences are brought out by a comparison of descriptions.

Range.—Mindanao: Davao Province (Mount McKinley).

Philautus Gistel

The distinction of *Philautus* from *Rhacophorus* is arbitrary and therefore unsatisfactory. Boulenger (1882) maintained *Philautus* on the basis of the presence (*Rhacophorus*) or absence (*Philautus*) of vomerine teeth. Subsequent authors, among them van Kampen (1923), Smith (1930), and Wolf (1936), have questioned the validity of this distinction, pointing out that the vomerine teeth are sometimes variable in appearance and development within species of this large group of rhacophorids. These authors, however, have refrained from putting the genus *Philautus* into the synonymy of *Rhacophorus*, preferring to wait until an intensive study of *Philautus* is made. Thus, both faunal works such as van Kampen's and taxonomic revisions such as Wolf's, though distinguishing *Philautus* from *Rhacophorus* on the basis of the vomerine teeth, recognize as *Rhacophorus* some species that lack vomerine teeth (for example, *edentulus* Müller). It is obvious that only an intensive study of *Philautus* will end this confusion.

An investigation of the sort needed is beyond the scope of this report. However, it may be worth while to note that of the Philippine *Philautus*, of which adult males were examined, the nuptial pads of *longicrus*, *schmackeri*, *williamsi*, *acutirostris*, *Philautus* sp. of Mindanao, and *Philautus* sp. of Palawan are not set with fine spines, whereas of the *Rhacophorus* (*leucomystax*, *pardalis*, *surdus*, *everetti*, and *appendiculatus*) in all but one (*surdus*) such spinules are present. The spinules are also present in the pads of *Philautus spinosus*.

There are additional problems connected with species of *Philautus*. Preserved specimens that have been determined as *Philautus* present difficulties in the further identification to species. One of the problems consists of determining the population limits. A series from a relatively restricted area may exhibit unusually extensive variation in such characters as coloration and tuberculation of the skin, at the same time showing much similarity to populations from other regions. Occasionally it is difficult to determine whether a sample includes individuals of one, two, or three species. Obviously, considerable field observation by the research worker is a necessary condition for satisfactory delimitation of the species in such cases. My own lack of field experience in the Philippines has been a handicap at many points in this study, but nowhere has it been as evident to me as in dealing with *Philautus*. Consequently the conclusions as to relationships presented below should be considered tentative and regarded with scepticism.

Not the least of the problems in working with *Philautus* is the state of the literature. The descriptions are not at all satisfactory. It is often impossible to distinguish between several species by the use of published descriptions (see Smith, 1930, p. 115), a difficulty that is probably the result of insufficient field observation combined with the variability within and the similarity between species.

So far as the Philippine species of *Philautus* are concerned, the relationships among them seem to be as follows: *Philautus spinosus* Taylor and *P. bimaculatus* Peters are set off from each other and from the other species, the former by virtue of its cranial crests and peculiar dermal asperities, the latter by the shape of its head, its color pattern, and its webbed fingers.

The other forms—*williamsi* Taylor, *schmackeri* Boettger, *longicrus* Boulenger, *acutirostris* Peters, *leitensis* Boulenger, *alticola* Ahl, *Philautus* sp. of Palawan, and *Philautus* sp. of Mindanao—constitute a complex of similar species that may eventually be found to belong to one or two widely distributed species. Most of them have extensive brown areas on the medio-ventral surfaces of the lower leg, a wide variety of dorsal patterns, small supernumerary tubercles on the metatarsals, the same amount of webbing between the toes, and measure less than 23 mm. snout to vent.

Philautus acutirostris Peters

Ixalus acutirostris Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**: 32—eastern Mindanao; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 99; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 123.

Philautus acutirostris Stejneger, 1905, Proc. U. S. Nat. Mus., **28**: 347; Taylor, 1920, Phil. Jour. Sci., **16**: 304; Ahl, 1931, Das Tierreich, Lief. 55, p. 96.

Philautus woodi Stejneger, 1905, Proc. U. S. Nat. Mus., **28**: 346—Mount Apo, Mindanao; Taylor, 1920, Phil. Jour. Sci., **16**: 296; Ahl, 1931, Das Tierreich, Lief. 55, p. 66.

Philautus basilanensis Taylor, 1922, Phil. Jour. Sci., **21**: 169, pl. 1, figs. 1, 2—Abungabung, Basilan; Ahl, 1931, Das Tierreich, Lief. 55, p. 81.

Material examined.—Basilan, 2 (MCZ, paratypes of *basilanensis* Taylor); Mindanao, 26 (23 CNHM; 3 USNM, including type of *woodi* Stejneger).

Taxonomic notes.—The original description of *acutirostris* Peters gives only one useful diagnostic character: an acuminate snout. The failure to mention a web between the outer fingers of *acutirostris* coupled with a sentence devoted to such structure in the original description of *bimaculatus*, which appeared on the same page of Peters' report (1867), suggests that the type of *acutirostris* lacked webbing on the fingers.

Stejneger's description of *woodi* does not provide any basis for the separation of this nominal form from *acutirostris*. Although Stejneger does state that both the throat and the belly of his type are coarsely granular, whereas Peters refers only to the belly, I judge this difference to be sexual rather than specific (see *Secondary sex characters*). Another presumed difference involves the skin. According to Peters, *acutirostris* has small scattered granules on the eyelids and body, but according to Stejneger (1905), *woodi* lacks these protuberances. I have examined Stejneger's type (USNM 34781) and can attest that there is a papilla on each eyelid and a pair of raised prominences between the eyes. Furthermore, a series of 14 specimens collected on Mount McKinley, Mindanao, by the Philippine Expedition, exhibits considerable variation in the roughness of the dorsal surface, so that this difference between the two type descriptions does not have much significance. The fact that both types originated in eastern Mindanao further strengthens my belief that the two forms are identical.

Philautus basilanensis was said by Taylor (1922a) to be related to *woodi* and to be distinguished from the latter by the arrangement of its tubercles and its more extensive web. In the light of the Mount McKinley sample, the first difference is individual, not specific. Examination of paratypes of *basilanensis* (MCZ 14467–68) fails to bear out Taylor in the matter of the webbing distinction. I am unable to distinguish between the paratypes of *basilanensis* and Mount McKinley specimens identified here as *acutirostris*. This similarity, plus the close faunal relationship of Basilan and Mindanao, constitute my reasons for placing *basilanensis* in the synonymy of *acutirostris*.

Diagnosis.—A medium-sized *Philautus;* fingers free; no cranial crests; only rarely with vomerine teeth (one out of 28 examined); third and fifth toes webbed to outer edge of distal subarticular tubercles or slightly beyond; an indistinct fringe of skin occasionally present on outer margin of fifth toe; small supernumerary metatarsal tubercles present; never with cruciform pattern dorsally; medioventral surface of lower leg with an extensive brown area; males with oval nuptial pad on first finger only.

Description.—Size moderate (adult female ca. 25 mm., adult male 23 mm., snout to vent); body widest at temporal region, tapering to groin; snout acutely or (less commonly) obtusely pointed, in some individuals drawn out slightly, in all cases projecting, longer than orbit; distance between nostrils greater than distance to snout, equal to distance to orbit, nostril one and one-third to one and one-half times as far from eye as from tip of snout; usually without vomerine teeth (present in only one out of 28 examined); canthus rostralis distinct, lores concave and sloping; interorbital space wider than upper eyelid; tympanum indistinct, one-third to one-half diameter of orbit; supratympanic fold present.

Fingers free, without rudiment of web; disks of fingers completely circumscribed by a groove; disk of first finger two-thirds as wide as that of second finger, and less than twice width of penultimate phalanx; pad of third finger largest, twice width of penultimate phalanx, and a trifle larger than tympanum; palm of hand rugose with obscure supernumerary metacarpal tubercles. Disks of toes smaller than disk of third finger; first toe united to second to center of subarticular tubercle, a rudiment of web; second toe webbed to distal edge of or slightly beyond subarticular tubercle; third and fifth toes webbed to distal edge of or slightly beyond outer subarticular tubercle; fourth toe webbed to basal subarticular tubercle; with or without a weak fringe of skin on outer edge of fifth toe; only two large subarticular tubercles on fourth toe; an elongate inner but no outer metatarsal tubercle; many small supernumerary metatarsal tubercles.

Skin shagreened above; papillae on upper eyelid; usually two prominences between eyes; back with a few scattered tubercles or short ridges; lateral edge of forearm with three to five white tubercles; dorsal surface of limbs with small asperities; belly and ventral surface of thigh coarsely granular. There is much variation in the development of dorsal rugosities.

Color variable. There appear to be two basic dorsal patterns. One consists of an extremely fine reticulation in which the lighter hue predominates, resulting in a green or pinkish gray tone. The other pattern consists of a few obscure dark spots scattered irregularly on a brown or slate ground color. The throat and belly are cream marked with brown, with a wide range of variations in the amount of brown. The anterior and posterior faces of the thigh and the medio-ventral surface of the lower leg are brown peppered with fine light dots; the dorsal surfaces of the legs are crossbarred.

Secondary sex characters.—The males of *acutirostris*, as here defined, have median, internal, subgular vocal sacs with round openings. Nuptial pads are present on the dorsal surfaces of the first finger in the males. These oval pads, which extend from a point opposite the subarticular tubercle proximally two-thirds of the distance to the base of the finger, lack horny spines.

Only two females were available. In these the skin of the throat was weakly rugose or smooth, contrasting with the coarsely granular throat in all of the males. In this respect this form agrees with

Philautus sp. of Mindanao. The insufficient number of females prohibits any conclusions as to sex dimorphism in size.

Ecological notes.—Approximately half of the twenty specimens collected by the Philippine Expedition were found on trees and shrubs, the remainder on the ground. All of them were captured in wooded areas.

The altitudinal distribution of *acutirostris* is extensive. Of the twenty-six individuals for which I have data, seven are from near sea level (less than 30 meters), two from 610–900 meters, ten from 915–1,190 meters, five from 1,200–1,500 meters, and two from elevations over 1,500 meters. The highest record is that of a specimen taken at 1,830 meters on Mount Apo.

Range.—Mindanao: Cotabato Province (Saub); Davao Province (Mount Apo, Mainit, Mount McKinley, Parang, Tagum). Basilan.

Philautus alticola Ahl

Philautus montanus Taylor, 1920, Phil. Jour. Sci., **16**: 305, pl. 3, fig. 5—Mount Bongao, Bongao Island, Sulu Archipelago.

Philautus alticola Ahl, 1931, Das Tierreich, Lief. 55, p. 95—substitute name.

Material examined.—None.

Taxonomic notes.—Although Taylor (1920) suggests that *alticola* is related to *vittiger* Boulenger of Java, the general nature of the original descriptions of other East Indian *Philautus* makes *alticola* appear just as similar to *petersi* Boulenger of Borneo, *leitensis,* and *acutirostris.* At present nothing can be said about the relationships of this form with any degree of assurance.

The diagnosis and description below are adapted from Taylor.

Diagnosis.—A large-sized *Philautus* (type 39 mm. snout to vent); fingers webbed at base (webbed to base of proximal subarticular tubercles between third and fourth fingers?); no cranial crests; no vomerine teeth; toes two-thirds webbed; no fringe of skin along outer edge of fifth toe; no dorsal cruciform pattern.

Description.—Body tapering very little from temporal region to groin; head longer than broad; snout obtusely pointed, longer than eye; nostril two and one-half times as far from eye as from tip of snout; no vomerine teeth; canthus rostralis rounded, lores concave and sloping; interorbital space wider than upper eyelid, tympanum a little more than one-half diameter of eye; a weak supratympanic fold.

Fingers webbed at base (to proximal subarticular tubercles?); disks well developed, equal to two-thirds diameter of tympanum;

an indistinct fringe of skin along outer edge of fourth finger and lower arm. Toes two-thirds webbed, web reaching base of disk on outer side of second toe; no fringe of skin along outer margin of fifth toe; an inner but no outer metatarsal tubercle.

Skin smooth above; gular region smooth; posterior portion of abdomen coarsely granular.

Color (in life) lavender gray above with numerous small yellow dots; a cream spot below and behind eye; dark spots along sides; throat and belly cream or white with dusky spots; under side of limbs powdered with brown; dorsal surfaces of limbs crossbarred; a light-edged, dark anal spot.

Range.—Sulu Archipelago: Bongao. The only specimen known is the type, collected at 700 meters.

Philautus bimaculatus Peters

Leptomantis bimaculata Peters, 1867, Monatsber. Akad. Wiss. Berlin, **1867**: 32—Upper Agusan Valley, Mindanao.

Philautus bimaculatus Stejneger, 1905, Proc. U. S. Nat. Mus., **28**: 347; Taylor, 1920, Phil. Jour. Sci., **16**: 305; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 269; Smith, 1930, Bull. Raffles Mus., no. 3, p. 117, fig. 8.

Ixalus bimaculatus Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 106; 1898, Proc. Zool. Soc. London, **1898**: 475; Boettger, 1899, Abh. Ber. Mus. Dresden, **1898–1899**, no. 1, p. 3.

Philautus zamboangensis Taylor, 1922, Phil. Jour. Sci., **21**: 173, pl. 1, fig. 7—near Pasonanca, Zamboanga, Mindanao.

Material examined.—Mindanao, 1 (CNHM).

Taxonomic notes.—*Philautus zamboangensis* was considered by Taylor (1922a) to be closely related to *bimaculatus* but to differ from the latter in six points. The first of these concerned the shape of the vocal sac openings. Peters (1867) described those of *bimaculatus* as being small, whereas in *zamboangensis* the openings were elongate slits. Smith (1930), after examining the type of *bimaculatus* as well as specimens from Borneo, Siam, and the Malay Peninsula, wrote that the vocal sac openings are large slits, so that this distinction no longer holds.

Taylor's second point was that, according to Peters, *bimaculatus* had strong tubercles on the lower jaw, these being absent in *zamboangensis*. Smith's account does not mention any tubercles on the lower jaw or throat of either the type or any of the other specimens he had examined, although the characteristics of the skin are discussed; moreover, Smith's figure (of a specimen from the Malay

Peninsula) does not exhibit such tubercles. Thus, even if the type of *bimaculatus* did have the tubercles, the most that could be said about them is that they are variable in appearance, and certainly with only one specimen at hand Taylor could come to no certain conclusion.

A third point made by Taylor was that *zamboangensis* had prominent subarticular tubercles on the foot, but *bimaculatus*, again according to Peters, did not. The adjective "subarticular" is commonly restricted to those tubercles present on the ventral surfaces of the digits. As Peters did not refer to the digits only but, instead, commented only on the smoothness of the soles of the feet ("Fusssohlen"), there is no basis for the distinction made by Taylor.

Two of the remaining points cited by Taylor involve characters that exhibit sufficient variation in other species of *Philautus* to account for differences between the two types. These are the amount of webbing on the foot and the distance between the nostrils. The final distinction offered by Taylor, the difference in the length of the forelimb, appears to be wholly unfounded, for Peters did not mention this character at all.

Any conclusion arrived at here is of course subject to the serious criticism that neither type specimen was examined. Nevertheless, given the fact of the comprehensive agreement of the two original descriptions and the negative evidence of no significant differences, *zamboangensis* Taylor should be identified with *bimaculatus* Peters.

The diagnosis and description that follow combine the descriptions of Peters, Taylor, and Smith with the characters of the one specimen seen.

Diagnosis.—A medium- to large-sized species of *Philautus*, adult males 28 to 34 mm. snout to vent; web between third and fourth fingers reaching distal subarticular tubercles; no cranial crests; no vomerine teeth; third and fifth toes webbed to a point midway between distal subarticular tubercle and scansorial disk; a weak fringe of skin along outer edge of fifth toe; metatarsals smooth, without cruciform dorsal pattern.

Description.—Body widest at temporal region, tapering to groin; snout obtusely pointed or truncate, equal to or slightly longer than eye; distance between nostrils greater than distance to tip of snout, equal to or greater than distance between nostril and eye; no vomerine teeth; canthus rostralis distinct; interorbital space equal to or greater than width of upper eyelid; tympanum partially hidden, one-third to one-half diameter of eye; supratympanic fold present.

Fingers webbed; a rudiment of web between first and second fingers; web reaching basal subarticular tubercles between second and third and distal subarticular tubercles between third and fourth fingers; disks of fingers completely circumscribed by a horizontal groove; disk of third finger largest, larger than tympanum. Disks of toes smaller than those of fingers; web extending beyond subarticular tubercles of all toes except the fourth; fourth toe webbed to middle subarticular tubercle or somewhat beyond; three sub-equal subarticular tubercles on fourth toe; metatarsals smooth, no supernumerary tubercles; an oval inner but no outer metatarsal tubercle.

Skin smooth above; chin and throat with faint wrinkles; abdomen finely granular.

Color (in alcohol) grayish white to violet brown, with dark dots or short bars scattered over back; a dark interorbital bar; a light cream spot below and behind eye; under side cream or yellow; limbs with dark crossbars dorsally.

Secondary sex characters.—Vocal sacs are present in the males; however, the type of sac is unknown. The openings are elongate slits at the sides of the floor of the mouth.

Ecological notes.—The two Philippine specimens for which data are available were collected in low vegetation between 305 and 455 meters above sea level.

Range.—Mindanao: Agusan Province (Peters, 1867); Cotabato Province (Upi near Burungkôt); Zamboanga Province (Dapitan [Boettger, 1899]; Pasonanca [Taylor, 1922a]). Outside of the Philippine Islands *bimaculatus* has been recorded from Borneo and peninsular Thailand (Smith, 1930).

Philautus leitensis Boulenger

Ixalus leitensis Boulenger, 1897, Ann. Mag. Nat. Hist., (6), **19**: 107—Leyte.

Philautus leitensis Stejneger, 1905, Proc. U. S. Nat. Mus., **28**: 347; Taylor, 1920, Phil. Jour. Sci., **16**: 301, pl. 1, fig. 3; Ahl, 1931, Das Tierreich, Lief. 55, p. 82.

Material examined.—Leyte, 1 (BM, type).

Taxonomic notes.—A comparison of the diagnosis and description presented below with those of *acutirostris*, *schmackeri*, and *longicrus* indicates that *leitensis* is closely related to them. The two known specimens of *leitensis* lack the cruciform pattern found in the last two forms.

Taylor's specimen from Biliran Island differs somewhat from the type. The latter has a granular throat, the Biliran specimen a smooth one; this difference may be sexual (see *acutirostris*, p. 397). The Biliran specimen has indistinct tubercles along the outer edge of the foot; these are absent in the type. The type measures 19.5 mm. snout to vent; it does not have either vocal sac openings or nuptial pads, but its sex is not definitely known. The Biliran specimen, likewise of unknown sex, is 26 mm. long.

Diagnosis.—A medium-sized *Philautus;* fingers free; no cranial crests; outer edge of fifth toe crenulate or not; small supernumerary metatarsal tubercles present; medio-ventral surface of lower leg with an extensive brown area.

Description.—Body tapering from sacral region to groin; snout obtusely pointed, not projecting; nostril nearer to tip of snout than to eye; no vomerine teeth; canthus rostralis distinct, lores concave; interorbital space wider than upper eyelid; tympanum indistinct; supratympanic fold present.

Fingers free; disks of fingers larger than those of toes; toes, except fourth, webbed to distal subarticular tubercles; supernumerary metatarsal tubercles present; an inner but no outer metatarsal tubercle.

Skin shagreened above; gular region smooth or coarsely granular; abdomen coarsely granular; a row of tubercles along outer edge of forearm.

Color (in preservative) yellow or reddish brown with scattered dark spots; limbs with crossbars or dots dorsally; throat and belly cream or white; groin, anterior and posterior faces of thigh and medio-ventral surface of lower leg brown.

Range.—Leyte. Biliran (Taylor, 1920).

Philautus longicrus Boulenger

Ixalus longicrus Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 88—Palawan.

Philautus longicrus Taylor, 1920, Phil. Jour. Sci., **16**: 303; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 272; Smith, 1925, Sarawak Mus. Jour., **3**, pt. 1, p. 36.

Material examined.—Palawan, 21 (3 BM, types; 13 CNHM; 5 MCZ); Balabac, 1 (BM).

Taxonomic notes.—The specimens I have identified as *longicrus* agree well with the types in the British Museum. These specimens (types included) resemble the types of *petersi* Boulenger (type locality Borneo). The following distinctions were noted; the head of *petersi* is relatively broader and shorter; the snout of *petersi* usually bears a dermal projection not found in *longicrus;* the skin along the outer edge of the fifth metatarsal is crenulated in *petersi* but not in *longicrus.* The relations of *longicrus* to other Philippine species of *Philautus* are discussed above (pp. 393 and 412).

Diagnosis.—A moderate-sized *Philautus;* fingers free; no cranial crests; no vomerine teeth; third and fifth toes webbed to center or basal edge of distal subarticular tubercles; no fringe of skin along outer margin of fifth toe; small supernumerary metatarsal tubercles present; some modification of a cruciform pattern present on back; medio-ventral surface of lower leg with an extensive brown area; males with round nuptial pad on first finger.

Description.—Size moderate (adult male 18–23 mm., adult female 23–29 mm., snout to vent); body tapering only slightly behind head; head wider at tympanum than long; snout obtusely pointed, projecting very little, equal to orbit; distance between nostrils greater than distance to snout, equal to or somewhat greater than distance from eye; nostril closer to tip of snout than to eye or equidistant between them; vomerine teeth absent; canthus rostralis distinct, lores concave and sloping; interorbital space equal to or wider than upper eyelid; tympanum obscure, about one-third diameter of eye; a supratympanic fold present.

Fingers free; terminal disks of fingers completely circumscribed by a horizontal groove; disk of first finger only half width of that of second finger and very little wider than penultimate phalanx; pad of third finger twice width of penultimate phalanx and a little larger than tympanum; distinct small supernumerary metacarpal tubercles. Disks of toes smaller than disk of third finger; first toe webbed to center or distal edge of subarticular tubercle, second toe to distal edge of subarticular tubercle, third and fifth toes to center or proximal edge of distal subarticular tubercle, and fourth toe to base of proximal subarticular tubercle; a very weak fringe represented by a row of small white tubercles on outer edge of fifth toe; only two large, subequal, subarticular tubercles on fourth toe and metatarsal; an elongate inner but no outer metatarsal tubercle; small supernumerary metatarsal tubercles present.

Skin shagreened above; head and back with tubercles and ridges; upper eyelid with papillae; limbs with tubercles dorsally; throat smooth in juveniles, weakly granular in adults; chest and belly coarsely granulate.

Color (in alcohol) above variable; ground color gray-blue, light gray-brown or dark brown with variously modified dark cruciform patterns; lips barred; a dark temporal spot bordered by the eye, the corner of the mouth, and the supratympanic fold; temporal spot occasionally split by a light line; under side cream or white variously marked with brown, especially on the throat; legs crossbarred dorsally; anterior and posterior surfaces of thigh cinnamon brown with fine light dots; medio-ventral surface of calf similarly colored.

Secondary sex characters.—Males have median, internal subgular vocal sacs with round openings. The nuptial pad is a small, round, glandular swelling lacking fine spines. The pad occupies the middle third (or somewhat less) of the dorsal surface of the first finger only and does not extend distally beyond the level of the subarticular tubercle.

There is apparently some sex dimorphism in size. Unfortunately, the number of mature individuals in the sample examined is too small to warrant statistical analysis. The two females measure 28.9 and 23.4 mm., snout to vent, the latter specimen containing large ova. The five males with developed nuptial pads and vocal sacs ranged from 18.0 to 22.4 mm. in body length.

Ecological notes.—With the exception of the types, for which the altitudinal data are unknown, all specimens of *longicrus* collected so far have been found at high altitudes. Palawan specimens were collected by Taylor at 1,220 meters and by the Philippine Expedition at 1,550 meters. All of the latter group were found on stunted shrubs and on the ground in a mossy forest. Specimens have been reported from 915 meters on Mount Poi, Borneo (Smith, 1925b).

Range.—Palawan (Mount Balabag in the Mantalingajan Range; Thumb Peak). Balabac. Also recorded from Borneo (Smith, 1925b).

Philautus schmackeri Boettger

Ixalus schmackeri Boettger, 1892, Kat. Batr. Mus. Senck. Naturf. Ges., p. 17—Mount Halcon, Mindoro; Boulenger, 1894, Ann. Mag. Nat. Hist., (6), **14**: 88.

Philautus schmackeri Taylor, 1920, Phil. Jour. Sci., **16**: 302.

Ixalus mindorensis Boulenger, 1897, Ann. Mag. Nat. Hist., (6), **19**: 107—Mount Dulangan, Mindoro.

Philautus mindorensis Taylor, 1920, Phil. Jour. Sci., **16**: 303.

Material examined.—Mindoro, 31 (4 BM, types of *mindorensis;* 1 CAS, cotype of *mindorensis;* 25 CNHM; 1 USNM).

Taxonomic notes.—Comparison of the original descriptions of the two species of *Philautus* described from Mindoro, *schmackeri* Boettger and *mindorensis* Boulenger, reveals only minor differences: the nostril in *schmackeri* is much nearer the tip of the snout than the eye but in *mindorensis* only slightly nearer; the tympanum is one-fourth the diameter of the eye in the one, and one-third to two-fifths in the other; the toes are one-half webbed as opposed to one-third webbed; toe disks are distinctly larger than the tympanum in one and as large as or slightly smaller than the tympanum in the other; the tibio-tarsal articulation reaches beyond the snout in *schmackeri* and to the nostril or snout in *mindorensis*.

Sufficient individual variation in the size of the tympanum, the amount of webbing, the relative size of the toe disks, and the length of the leg is evident within a series collected around San José, Mindoro, to account for these differences. Furthermore, most of these characters are subject not only to individual variation of the frogs but also to variation in the methods of measurement and to ambiguities in the word choice of the authors. Such extraneous sources of variation apply to the position of the nostril, the amount of webbing, and the length of the leg and could account for the differences in these characters.

In the absence of reliable differences between the original description of *schmackeri* and the types of *mindorensis*, I must consider the latter a synonym. (For comments on relations with other forms see p. 393.)

Diagnosis.—A small species of *Philautus;* no cranial crests; fingers free, no vomerine teeth; third and fifth toes webbed to outer edge of distal subarticular tubercles; a distinct fringe of skin along outer margin of fifth toe; small supernumerary metatarsal tubercles usually present; some modification of a dark cruciform pattern usually present dorsally; medio-ventral surface of lower leg with extensive brown area; males with oval nuptial pad, equal in length to one-third of first finger.

Description.—Size small (adult female ca. 22 mm., adult male ca. 20 mm., snout to vent); body rather stocky, tapering between sacral region and groin; head at tympanum as wide as long; snout subacuminate or obtusely pointed, projecting, longer than orbit; distance between nostrils greater than their distance from tip of snout and from eye, nostril from one and one-half to two times as far from eye as from tip of snout; vomerine teeth absent; canthus rostralis distinct, lores concave and sloping only slightly; interorbital space wider than upper eyelid; front rim of tympanum distinct, posterior hidden, tympanum one-fourth to two-fifths diameter of eye; a supratympanic fold present.

Fingers free; disks of fingers completely circumscribed by a horizontal groove; disk of first finger smallest, only slightly wider than penultimate phalanx; disk of third finger largest, about twice width of penultimate phalanx, equal to or slightly wider than tympanum; palm of hand rugose. Disks of toes smaller than disk of third finger; first toe not separated from second by webbing; second, third, and fifth toes webbed to distal edge of outer subarticular tubercles; fourth toe webbed to base of penultimate subarticular tubercle; a weak fringe of skin on outer edge of fifth toe; fourth toe with three subarticular tubercles, the basal one smaller than the outer two; an elongate inner but no outer metatarsal tubercle; small supernumerary metatarsal tubercles present.

Skin above smooth or shagreened; all individuals with tubercles on eyelid and in interorbital space; some specimens with small tubercles on back and dorsal surface of limbs; no dermal ridges on back; chest and belly coarsely granular; throat less coarsely granulated or merely wrinkled.

Color (in alcohol) above grayish to dark reddish brown usually with some modification of a cruciform pattern on the back. The pattern may consist of two short, curved dorso-lateral stripes, an open cruciform mark, or a solid, dark hourglass. Ventral surfaces cream with various admixtures of brown, occasionally throat almost solid brown; limbs with crossbars dorsally, occasionally obscure; anterior and posterior faces of thigh and medio-ventral surface of lower leg cinnamon brown sprinkled with small light dots; groin yellow in life.

Secondary sex characters.—The males have median, internal, subgular vocal sacs. Climatic conditions at the time of capture of the San José specimens (see also p. 378), as well as the absence of large eggs in the females, indicate that this sample was collected out of the breeding season. This fact suggests an explanation for the observation that only one male from San José had round vocal sac openings in the center of raised areas of oval epithelium, the condition characteristic of breeding males of many species of *Rana* and *Rhacophorus*. All other males of this sample have slit-like openings; these are not surrounded by raised epithelium. Probably the vocal sac openings appear crater-like only during the breeding season or shortly thereafter. One male from the type series of *mindorensis* has crater-like round openings; a second has short slit-like openings.

The nuptial pads of the males are oval glandular swellings occupying the middle third of the dorsal surface of the first finger only. The distal margin of the pad reaches the level of the distal edge of the subarticular tubercle. Spinules are not present on the nuptial pads of the males.

There appears to be some sexual dimorphism in the color of the throat, the males tending to be darker in this region than the females. The only individuals (two) with solid brown throats were males. Furthermore, about one-fourth of the females had almost no brown in the gular region, being much lighter than any of the males. This difference between the sexes needs additional observation, especially on individuals collected during the breeding season.

Ecological notes.—The excellent field notes of Dr. W. H. Stickel state that the San José specimens were collected in the leaf axils of the trunk taro (*Alocasia*) in a swampy forest. If the identification of this series as *schmackeri* is correct, then a wide altitudinal distribution is indicated for this species. San José is near sea level, whereas the type localities of *schmackeri* and *mindorensis* are in the mountains, the latter at 1,520 meters.

Range.—Mindoro (San José, Mount Halcon, Mount Dulangan).

Philautus spinosus Taylor

Hazelia spinosa Taylor, 1920, Phil. Jour. Sci., **16**: 292, pl. 7, fig. 1—Bunawan, Agusan Province, Mindanao.

Philautus spinosus Ahl, 1931, Das Tierreich, Lief. 55, p. 75.

Rhacophorus leprosus spinosus Wolf, 1936, Bull. Raffles Mus., no. 12, p. 156.

Material examined.—Mindanao, 1 (CM, type); Basilan, 1 (CAS).

Taxonomic notes.—The only character in Taylor's (1920) diagnosis of the genus *Hazelia* that sets it off from *Philautus* is the presence of bony cranial ridges. Within the genus *Rhacophorus* at least three species, *acanthostomus* Werner, *georgi* Roux, and *otilophus* Boulenger, have been discovered to have bony excrescences on the head, yet the definition of the genus has not been altered. Consequently, to maintain a monotypic genus in the Rhacophoridae on such slim grounds hardly seems warranted.

Wolf (1936) makes *spinosus* a subspecies of *Rhacophorus leprosus* Müller. According to Wolf's views *leprosus* includes populations that may be characterized by the presence or by the absence of vomerine teeth, by the extensive development or by the absence of web between the fingers, and by the presence or by the absence of cranial ridges. In all of the populations the individuals have many tubercles scattered over the dorsal surface.

The typical subspecies, occurring in Sumatra and the lower Malay Peninsula, has vomerine teeth but no cranial ridges, thus contrasting with *spinosus* (or *leprosus spinosus*, as Wolf would have it). Two of Wolf's subspecies, *leprosus phrynoderma* Ahl of Assam and *l. moloch* Annandale of Burma, agree with *spinosus* in lacking vomerine teeth; however, one, *phrynoderma*, is distinct in the possession of very extensive webbing between the fingers. Wolf suggests that the other, *moloch*, resembles *spinosus* in having cranial ridges, but in *spinosus* the ridges are bony, and in *moloch* they are formed by rows of tubercles. Wolf's last subspecies, *l. corticalus* of Tonkin, differs from *spinosus* in the possession of vomerine teeth and in the absence of cranial ridges. The fact that the skin of the head in *spinosus* is involved with the cranial ossification further sets this form apart from the other forms in Wolf's *leprosus*. It should also be noted that there are other species of rhacophorids (*Philautus asper* Boulenger and *P. pictus* Peters) that have as much in common with *spinosus* as does *Rhacophorus leprosus*. Accordingly, I conclude that not only is Wolf's definition of the species *leprosus* based upon unjustifiable lumping, but also that there is no reason for his relating *spinosus* to *leprosus*.

To maintain consistency within this report it is necessary to place *spinosus* in the genus *Philautus*. Yet *spinosus*, by virtue of the ossifications of the head, appears to be more closely related to certain species of *Rhacophorus* than to other species of *Philautus*. Also, in the possession of a nuptial pad bearing small spines, *spinosus* more nearly resembles *Rhacophorus* than *Philautus*. This is another instance of the difficulties arising from the uncertain status of *Philautus*.

Diagnosis.—A large, elongate-bodied species of *Philautus;* adult female 41 mm. snout to vent, adult male 35 mm.; fingers free; distinguished from all other Philippine species of *Philautus* by the cranial crests and wartlike tubercles scattered over the dorsal surfaces; the head superficially bufonid-like; males without vocal sacs.

Description.—Body tapering from temporal region; head at tympanum as broad as long; snout obtusely pointed, longer than eye, nostrils almost at tip of snout, no vomerine teeth; a pair of prominent crests running from the canthi between the eyes to the occipital region; tympanum distinct, four-fifths diameter of eye; supratympanic fold present as an inconspicuous bony ridge.

Fingers without web; disks of fingers completely circumscribed by a horizontal groove; disk of third finger largest, smaller than tympanum, twice width of penultimate phalanx. Disks of toes smaller than disk of third finger; first and second toes webbed to center or distal edge of subarticular tubercle; third and fifth toes webbed to base of outer subarticular tubercles; fourth toe webbed about to proximal subarticular tubercle; two metatarsal tubercles, the outer poorly differentiated.

Skin with prominent spinose tubercles on all dorsal surfaces, especially dense on eyelid; skin of head involved in cranial ossification; throat weakly rugose with small spiny granules; belly with larger spiny granules.

Color in life (after Taylor, 1920) brown above, anteriorly darker with varying number of yellow spots; under side yellow or orange.

Secondary sex characters.—The nuptial pad of the single male is on the dorsal surface of the first finger and extends on to the median face of the digit. The pad begins at the base of the finger and ends opposite the subarticular tubercle. Unlike the males of most Philippine species of *Philautus*, this individual lacks vocal sacs. The presence of the nuptial pad indicates that the specimen is mature; therefore it appears that this species is without vocal sacs.

Range.—Mindanao: Agusan Province (Bunawan). Basilan (Abungabung).

Philautus williamsi Taylor

Philautus williamsi Taylor, 1922, Phil. Jour. Sci., **21**: 167, pl. 1, figs. 3–6—southern Polillo; Ahl, 1931, Das Tierreich, Lief. 55, p. 101.

Material examined.—Polillo, 2 (1 CAS; 1 MCZ, paratype).

Taxonomic notes.—Philautus williamsi most nearly resembles *schmackeri* of Mindoro. On the basis of the inadequate material examined, *williamsi* seems to differ from *schmackeri* in the extent of webbing, the coloration, and the size of the nuptial pad.

Diagnosis.—A small species of *Philautus* (males 21–22 mm.); fingers free; no crests on head; no vomerine teeth; third and fifth toes webbed beyond distal subarticular tubercles; no fringe of skin along outer margin of fifth toe; sole of foot wrinkled; no supernumerary metatarsal tubercles; with or without a dark cruciform pattern on the back; medio-ventral surface of lower leg without extensive brown area; nuptial pad of male elongate, covering one-half of dorsal surface of first finger.

Description.—Body tapering from sacral region to groin; head at tympanum broader than long, equal to width of anterior half of trunk; snout obtusely pointed, slightly longer than eye; distance between nostrils greater than distance between nostril and tip of snout, slightly less than distance between nostril and eye; nostril one and one-half times as far from eye as from tip of snout; interorbital space equal to or wider than upper eyelid; no vomerine teeth; tympanum with indistinct posterior rim, about one-third diameter of eye; a supratympanic fold present.

Fingers with rudiment of web; disks of fingers completely circumscribed by a horizontal groove; disk of first finger only very little wider than penultimate phalanx; pad of third finger largest, twice width of penultimate phalanx, and equal to tympanum. Disks of toes smaller than disk of third finger; toes, except fourth, webbed beyond distal subarticular tubercles; fourth toe webbed to penultimate tubercle; fourth toe with only two subequal, large, subarticular tubercles; with or without a weak crenulated fringe of skin on outer edge of fifth toe; a long inner but no outer metatarsal tubercle; sole of foot wrinkled, the wrinkles perhaps representing supernumerary metatarsal tubercles.

Skin mostly smooth above, with tubercles on the upper eyelids; variation in number and distribution of tubercles on head and back (Taylor, 1922a); throat slightly corrugated; chest and belly coarsely granular.

Color above yellowish brown in life (Taylor, 1922a), reddish brown in alcohol; back with or without varying cruciform patterns; under side cream, peppered with fine brown spots; limbs with dark crossbars; posterior face of thigh with a large interrupted area of cinnamon brown finely dotted with cream; no brown area on medioventral surface of lower leg.

Secondary sex characters.—Contrary to Taylor's statement, males of *williamsi* (at least the one paratype seen) do have a median, internal, subgular vocal sac. The nuptial pad, situated on the dorsal surface of the first finger, extends from the level of the distal edge of the subarticular tubercle to the base of the finger.

Range.—Polillo. Luzon: Tayabas Province (Mauban [Taylor, 1922a]).

Philautus sp. of Mindanao

Material examined.—Mindanao, 4 (2 CNHM; 2 MCZ).

Taxonomic notes.—The primary difference between this series of specimens and those I have identified as *acutirostris* is the presence of a dark cruciform pattern in these and its absence in *acutirostris*. This is a feeble distinction when one considers the variation in coloration of *acutirostris*. Field observations may indicate that this form is not separable from *acutirostris*.

Diagnosis.—Same as *acutirostris* except that cruciform dorsal pattern is present.

Description.—Size moderate (adult female 28 mm., adult male 21 mm., snout to vent); body widest at temporal region, tapering slightly to groin; head at tympanum wider than long; snout pointed, projecting, longer than orbit; distance between nostrils greater than distance to snout, equal to or slightly less than distance to orbit, nostril one and one-third to one and two-thirds times as far from eye as from tip of snout; no vomerine teeth; canthus rostralis distinct, lores concave and sloping; interorbital space wider than upper eyelid; tympanum indistinct, one-third to two-fifths diameter of orbit; supratympanic fold present.

Fingers free, without rudiment of web; disks of fingers completely circumscribed by a horizontal groove; disk of first finger two-thirds as wide as that of second finger and about one and one-half times width of penultimate phalanx; pad of third finger as large as or a trifle larger than tympanum, twice width of penultimate phalanx; palm of hand lumpy, with indications of supernumerary metacarpal tubercles. Disk of fourth toe as large as disk of third finger; pads of other toes smaller; first toe with web to base or center of subarticular tubercle; second toe webbed to distal edge of subarticular tubercle or beyond; third and fifth toes webbed to distal edge of outer subarticular tubercle or slightly beyond; web reaching or just failing to reach basal edge of proximal subarticular tubercle of fourth toe; no fringe on outer edge of fifth toe; only two large subarticular tubercles on fourth toe; many small supernumerary metatarsal tubercles; an elongate inner but no outer metatarsal tubercle.

Skin above shagreened; eyelid with one large and several small papillae; two prominences between eyes; two to four short irregular ridges on back; dorsal surfaces of limbs with small weak tubercles; lateral edge of forearm with three to five white tubercles; belly and ventral surface of thighs with coarse granules (for gular region see *Secondary sex characters*).

Color (in alcohol) above light grayish brown, brown, or rufous with a dark interorbital bar and a variously modified cruciform pattern on the back; limbs with crossbars dorsally; below cream or white, immaculate or with varying amounts of brown mottling; anterior and posterior surfaces of thigh and medio-ventral surface of lower leg brown with small light dots.

Secondary sex characters.—The two males of this form seen are characterized by very coarse granulation of throat and chest. In the two females this region is only faintly wrinkled. The males are also distinguished by median internal subgular vocal sacs with round openings at the corners of the mouth. Nuptial pads are not evident in these males.

Ecological notes.—As is true of several of the Philippine forms of *Philautus,* the present one has a wide altitudinal distribution. Two of the four specimens were collected at sea level, another at 945 meters, and the fourth at 1,860 meters.

Range.—Mindanao: Cotabato Province (Saub); Davao Province (Mount Apo, Mount McKinley).

Philautus sp., of Palawan

Material examined.—Palawan, 6 (CNHM).

Taxonomic notes.—This form is apparently similar to *jacobsoni* van Kampen of Java, and to *petersi* Boulenger of Borneo. It differs from *longicrus* Boulenger of Palawan in the coloration and in the tuberculation of the feet and hands (see *Description,* below, and p. 403).

Diagnosis.—A small species of *Philautus;* fingers free; no cranial crests; no vomerine teeth; third and fifth toes webbed to outer edge of distal subarticular tubercles; no fringe of skin along outer margin of fifth toe; no supernumerary metatarsal tubercles; some modification of a dark cruciform pattern present dorsally; medio-ventral surface of lower leg without an extensive brown area; males with round nuptial pad on first finger only.

Description.—Size small (snout to vent of six adult males 18.0–20.9 mm.); body tapering only slightly behind head; head at tympanum wider than long; snout pointed, projecting, equal to orbit; distance between nostrils greater than distance from snout and from eye, nostril about one and one-third times as far from eye as from snout; vomerine teeth absent; canthus rostralis distinct, lores concave and sloping; interorbital space wider than upper eyelid; tympanum obscure, one-fourth to two-fifths diameter of orbit; a supratympanic fold present.

Fingers free, without rudiment of web; terminal pads or disks of fingers completely circumscribed by horizontal groove; pad of first finger at most two-thirds as wide as that of second finger and only slightly wider than penultimate phalanx; pad of third finger larger than tympanum and twice width of penultimate phalanx; palm of hand relatively smooth, without conspicuous supernumerary metacarpal tubercles. Disks of toes smaller than disk of third finger; first toe webbed to center of subarticular tubercle, second toe to distal edge of subarticular tubercle or slightly beyond, outer side of third and inner side of fifth toe to distal edge of outer subarticular tubercle, and fourth toe to basal edge of proximal tubercle; no fringe on outer edge of fifth toe; only two large subarticular tubercles visible on fourth toe and metatarsal; sole of foot smooth, without small supernumerary metatarsal tubercles (see *longicrus*, p. 403); an elongate inner but no outer metatarsal tubercle.

Skin of head rough with small round prominences and short ridges; upper eyelid with numerous papillae; back shagreened, with faint tubercles scattered irregularly; throat, chest, and belly very coarsely granulated.

Color (in alcohol) above light gray-brown with lighter and darker spots giving a pebbly appearance; superimposed on this ground color is a darker gray pattern varying from straight or oblique dorso-lateral stripes posteriorly to modified cruciform markings; with or without an interorbital bar; sides of head and body and ventral surfaces of legs cream, uniformly and lightly sprinkled with small dark dots; under side white or cream with sparser sprinkling of fine dark dots; limbs with crossbars dorsally; posterior face of thigh with cinnamon brown area dotted with white, a smaller and somewhat paler area of the same colors on anterior face of thigh; no such area on lower leg.

Secondary sex characters.—All of the six specimens examined are males. The vocal sac is median subgular internal with round openings situated at the corners of the mouth. The nuptial pad is a small round swelling on the first finger. This structure is limited almost completely to the dorsal surface, commencing at about the level of the center of the palmar tubercle and not extending distally beyond the level of the subarticular tubercle.

Ecological notes.—Five specimens were collected at 850 meters and a sixth at 1,220 meters.

Range.—Palawan (Mount Balabag in the Mantalingajan Range).

MICROHYLIDAE

Chaperina fusca Mocquard

Chaperina fusca Mocquard, 1892, Le Naturaliste, (2), **6**: 35—Sintang, Borneo; Mem. Soc. Zool. France, **5**: 194, pl. 7, figs. 2, 2b; Smith, 1931, Bull. Raffles Mus., no. 5, 21; Parker, 1934, Monogr. Microhylidae, p. 103, figs. 41, 42.

Sphenophryne fusca Nieden, 1926, Das Tierreich, Lief. 49, p. 45 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 109 (part); Smith, 1930, Bull. Raffles Mus., no. 3, p. 125.

Microhyla leucostigma Boulenger, 1899, Ann. Mag. Nat. Hist., (7), **3**: 275, pl. 12, fig. 1—Larut, Perak; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 156.

Sphenophryne leucostigma Smith, 1925, Jour. Sarawak Mus., **3**, pt. 1, p. 17.

Chaperina beyeri Taylor, 1920, Phil. Jour. Sci., **16**: 333, pl. 3, fig. 3—between Agusan and Simulao rivers, Mindanao.

Sphenophryne beyeri van Kampen, 1923, Amph. Indo-Austr. Arch., p. 110.

Nectophryne picturata Smith, 1921, Jour. Fed. Malay States Mus., **10**: 198, pl. 2, fig. 2—Mount Dulit, Borneo; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 72.

Material examined.—Mindanao, 6 (1 CNHM; 5 CM; paratypes of *beyeri* Taylor); Palawan, 2 (1 CNHM; 1 MCZ); Borneo, 2 (UMMZ).

Taxonomic notes.—In the original description of *Chaperina beyeri*, Taylor distinguished it from *fusca* on the basis of the presence of the dermal spine on the heel and the absence of a tympanum in *beyeri*. Specimens of *fusca* from all parts of its range, including the Philippines, have the dermal spine. The tympanum is obscured by the skin to a greater or lesser degree, but this variation is individual and not geographic. Although large series may indicate geographic variation in some characters, the Philippine populations are certainly not to be placed in a distinct species; over-all similarity is too great.

Diagnosis.—A small microhylid; dark brown or black above; below cream or yellow with a bold reticulation; a delicate but distinct dermal projection at the elbow and heel.

Description.—Habitus stout; head broader than long; snout rounded or truncate; canthus rostralis indistinct, lores concave; tympanum obscured or completely hidden; interorbital space much wider than upper eyelid. Skin smooth above and below; a conspicuous small dermal projection at elbow and heel.

Fingers dilated at ends into round disks, that of third finger about one and two-thirds width of penultimate phalanx; a horizontal circummarginal groove separating dorsal and ventral surfaces of disks of outer two or three fingers; first finger much shorter than others; no supernumerary metacarpal tubercles. Tips of toes dilated into disks larger than those of fingers; a horizontal circummarginal groove on each toe disk; toes webbed at base only; first and second toes not webbed beyond subarticular tubercle; third and fourth toes not webbed beyond proximal tubercle; fifth toe webbed to center of proximal tubercle or slightly beyond; a weak, oval inner metatarsal tubercle; no outer metatarsal tubercle.

Color (in alcohol) dark brown or black above, uniform or with small cream dots or with obscure dark markings; dorsal surface of limbs somewhat lighter than back, uniform, with dark crossbands or with small cream dots; ventral surfaces of body and limbs cream, with bold brown network; gular region may have more brown than abdomen.

Secondary sex characters.—Taylor (1920) found no vocal sacs in the males of the type series of *beyeri*. This is at variance with Parker's (1934) statement that males of *fusca* had subgular vocal sacs. Examination of a male paratype of *beyeri* (CM 3314) substantiates Parker and eliminates one of the distinctions between *beyeri* and *fusca*. I do not find nuptial pads on the fingers of the male.

The smallest female (20.5 mm.) observed to contain large pigmented eggs is larger than the single adult male (17.5 mm.) examined. The other females ranged in size up to 25.4 mm. Sexual dimorphism in size remains to be established.

Ecological notes.—Taylor (1920) collected specimens under rocks, along a dry stream bed, and in a wet hole in a tree trunk. Another specimen (CNHM 51461) was found in leaf litter of a mountain forest. Judging both from the ecological observations and from its reduced webbing, *fusca*, like many other microhylids, is an inhabitant of the forest floor.

Most of the localities from which *fusca* has been taken are at moderate elevations. On the Malay Peninsula it has been found at 1,065 to 1,220 meters in the Perak Hills (Parker, 1934), on Borneo at 1,005 meters (Smith, 1931), on Palawan at 850 to 1,220 meters, and on Mindanao in the low mountains (Taylor, 1920). Several Bornean localities mentioned by Parker are near sea level.

Range.—Mindanao: Agusan Province (between Agusan and Simulao rivers). Palawan (Mount Balabag in the Mantalingajan Range, Thumb Peak). Sulu Archipelago (Jolo Island).

Known also from the Malay Peninsula and Borneo (Parker, 1934).

Kalophrynus pleurostigma pleurostigma Tschudi[1]

Kalophrynus pleurostigma Tschudi, 1838, Mem. Soc. Sci. Neuchatel, **2**: 86—Sumatra; Noble, 1927, Ann. New York Acad. Sci., **30**: 114, fig. 30.

Kalophrynus pleurostigma pleurostigma Parker, 1934, Monogr. Microhylidae, p. 97, figs. 39, 40.

Calophrynus pleurostigma Peters, 1871, Monatsber. Akad. Wiss. Berlin, **1871**: 579; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 102, fig. 12 (part).

Calophrynus acutirostris Boettger, 1897, Zool. Anz., **20**: 165—Culion or Samar.

Kalophrynus acutirostris Stejneger, 1908, Proc. U. S. Nat. Mus., **33**: 576; Taylor, 1920, Phil. Jour. Sci., **16**: 331.

Kalophrynus stellatus Stejneger, Proc. U. S. Nat. Mus., **33**: 575—Basilan; Taylor, 1920, Phil. Jour. Sci., **16**: 329, pl. 9, fig. 2.

Material examined.—Leyte, 4 (2 CNHM; 1 MCZ; 1 USNM); Mindanao, 42 (CNHM); Basilan, 11 (10 UMMZ; 1 USNM, type of *stellatus*).

Diagnosis.—A conspicuous black, usually light-edged ocellus on the back near each groin (absent in only a few individuals); skin coarsely granular; inner metatarsal tubercle oval, but not compressed as in species of *Kaloula;* the fourth finger very short, not as long as the first; tympanum distinct and large; snout projecting and usually pointed; dark mark on the back a distinct cross with the arms of the pattern converging shortly behind the occiput (fig. 73), never with a *Kaloula*-like pattern (see fig. 77); males with nuptial pads.

Description.—A medium-sized microhylid; habitus stout, the body widest in the sacral region; head broader than long; snout overhanging lower jaw; snout usually pointed, sometimes with a "nose"-like projection, or rounded; canthus rostralis distinct, rounded; tympanum distinct, two-thirds to five-sixths diameter of eye. Skin granular dorsally and ventrally (see also *Secondary sex characters*). Entire back and area behind supratympanic fold set with large, presumably mucous epidermal glands. These glands cause the skin to be unusually thick.

Fingers with slightly swollen rounded tips, only a trifle wider than penultimate phalanges; fourth finger shorter than first and second; subarticular tubercles pronounced; a large supernumerary tubercle at base of each finger. Tips of toes similar to those of fingers; webbing shows individual and sexual variation (see below); a round or oval inner metatarsal tubercle, not compressed; a small round outer metatarsal tubercle present or absent.

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[1] For a complete synonymy of this species see Parker (1934).

Color (in alcohol) gray, brown, or reddish above, bordered on the sides by an oblique blackish or brownish band that continues forward on to lores. Usually a dark pattern on the back consisting of two stripes, each running from one eyelid across the back to the opposite groin, the stripes intersecting shortly behind the occiput. In some individuals the stripes are broken up into a series of spots; in others this pattern is lacking. Almost all individuals have a dark ocellus, usually light-edged, on the back near each groin. These ocelli are part of the dorsal stripes or rows of spots in those specimens with the pattern, but even in those the ocelli are conspicuous. Only four of the 57 specimens examined lacked the ocellus. A single crossbar on the thigh and one on the lower leg, these continuous when the leg is flexed; abdomen cream-colored, uniform, lightly spotted with white or suffused with the dorsal ground color on the chest.

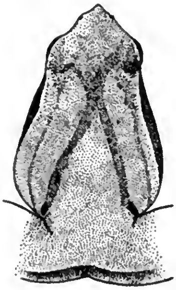

FIG. 73. Dorsal color pattern of *Kalophrynus pleurostigma;* × 0.9.

Secondary sex characters.—The adult males of *Kalophrynus pleurostigma* are immediately distinguishable from those of *Kaloula* by the presence of nuptial pads. These pads extend from the base to the tip on the medio-dorsal surfaces of the first three fingers. The present study confirms Liu's (1935) observations that males of *pleurostigma* have median subgular internal vocal sacs provided with elongate, slit-like openings in the floor of the mouth. In approximately half of the males, the gular skin is blackish. In the rest of the males and in all females the throat is light gray or pinkish.

Parker (1934) states that specimens often have numerous small horny spines on the dorsal surfaces. This variation can be more specifically defined as sex dimorphism. Every one of the 36 adult males examined had white spinules uniformly and densely distributed

Table 39. Sexual dimorphism in extent of webbing in *Kalophrynus pleurostigma pleurostigma*

	Sex	Base of tubercle	Center of tubercle	Distal edge of tubercle	Between tubercle and swollen tip	Base of swollen tip	Total
First Toe							
Mindanao . .	♂	---	---	---	15	9	24
Basilan . . .	♂	---	---	1	5	1	7
Mindanao . .	♀	---	---	4	6	---	10
Basilan . . .	♀	---	---	1	2	---	3
Second Toe							
Mindanao . .	♂	---	---	1	17	6	24
Basilan . . .	♂	---	---	---	7	---	7
Mindanao . .	♀	---	1	5	4	---	10
Basilan . . .	♀	---	---	---	3	---	3
Third Toe							
Mindanao . .	♂	1	---	11	11	1	24
Basilan . . .	♂	1	2	3	1	---	7
Mindanao . .	♀	6	4	---	---	---	10
Basilan . . .	♀	---	2	1	---	---	3
Fifth Toe							
Mindanao . .	♂	---	---	---	4	20	24
Basilan . . .	♂	---	---	---	3	4	7
Mindanao . .	♀	---	2	6	2	---	10
Basilan . . .	♀	---	2	---	1	---	3

over all of the dorsal surfaces of the body and legs, and on the sides of the head. None of the 18 females examined showed this character.

Another secondary sex character is to be found in the extent of webbing on the feet. Parker states that the toes are one-third to three-fourths webbed, that the variation is correlated roughly with size, and that in large males the toes are almost completely webbed. Examination of Philippine material bears out Parker's contention of much individual variation. There is definitely sex dimorphism in the extent of the web, and this dimorphism is not limited to the largest males on the one hand and small females on the other. Table 39 presents the observed distribution of webbing in the Mindanao and Basilan samples. Except in the case of the fifth toe, the table deals with the extent of webbing on the outer sides of the toes. Although there is some overlapping between males and females, it is evident that the former have the more extensive webs. This is particularly clear in the case of the fifth toe. Although I find no evidence for a correlation between size and extent of web, it may be that there is a spurt in the growth of the web in males coincident with the achievement of sexual maturity.

The extent of web in Philippine *pleurostigma* may be summarized as follows: In males, the first and second toes are webbed to between the center of the penultimate phalanx and the base of the swollen tip of the toe; the web may reach only to the base or center of the distal subarticular tubercle of the third toe but usually reaches the distal edge of the tubercle or the middle of the penultimate phalanx; the fourth toe is usually webbed to the distal edge of the middle subarticular tubercle or slightly beyond; the fifth toe is usually webbed to the tip of the toe, though in a few individuals the web reaches only to the center of the penultimate phalanx. In females, the web extends to the distal edge of the subarticular tubercle or slightly beyond on the first and second toes; on the third toe the web reaches the base or the distal edge of the outer tubercle; the fourth toe is usually webbed to the base of the middle tubercle; on the fifth toe the edge of the web varies from the center of the outer tubercle to the center of the penultimate phalanx.

Finally, sex dimorphism is evident in snout-to-vent length. The females attain a larger size than the males. The pertinent data for the two samples examined are summarized below:

	Sex	*No.*	*Mean ± SE*	*Range*
Mindanao	♀	10	45.04±1.49	37.0–52.5
Mindanao	♂	25	39.61±0.53	35.0–45.0
Basilan	♀	3	45.43	44.8–46.3
Basilan	♂	7	38.27±0.90	36.1–42.8

The differences between the sexes in both samples is of the same magnitude. The significance of the differences was tested only for the Mindanao sample: $t=4.309$, $P=<0.001$.

Ecological notes.—*Kalophrynus pleurostigma* is a common species of the forest floor, according to Taylor (1920) and the field notes of the Philippine Expedition. Of 22 specimens collected at sea level by the members of the expedition, 17 were found under leaves and rocks; the others were hopping in a dry stream bed. Shallow temporary pools of rain water are selected as breeding sites by this species. On Mount McKinley *pleurostigma* was observed breeding in rain-filled road ruts.

The altitudinal distribution is extensive. Mindanao specimens were taken from sea level to 1,005 meters by the Philippine Expedition. Smith (1931) reports the species from over 915 meters on Mount Kinabalu, Borneo.

Inter-island variation.—As samples with more than two individuals were available only from Basilan and Mindanao, discussion must be limited to these series. Some differences can be observed between the two populations (see Table 39). The Mindanao males appear to have slightly more extensive webbing than those from Basilan. However, statistical analysis with the use of contingency tables reveals that the difference is not statistically significant. Similarly, the apparent difference in body lengths of the males (see *Secondary sex characters*) is not statistically significant, *t* being equal to 1.230 and P to 0.23.

Range.—Leyte (Cabalian, Carigara, Tacloban, Tarragona). Siargao Island (Dapa [Peters, 1871]). Mindanao: Agusan Province (Bunawan); Davao Province (Caburan, Calian, Madaum, Mount McKinley). Basilan (Port Holland).

The type locality of *K. acutirostris* Boettger was given as Culion or Samar. On the basis of the presence of *pleurostigma* on Leyte and the nearness of Samar to it, it is highly probable that Boettger's specimen came from Samar. No reliable reports of *pleurostigma* in the western islands exist, further strengthening the choice of Samar.

The range also includes Sumatra, Borneo, Natuna Islands, and part of the Malay Peninsula (Parker, 1934).

Kaloula Gray

The Philippine forms of this genus arrange themselves into two groups, one with a small supernumerary tubercle on each metacarpal (fig. 75) and the other without. The affinities of the latter group are so obviously with the East Indian *K. baleata* that I have no hesitation in placing them in the same species. In addition to the absence of the supernumerary tubercles, this relationship is evident in the presence of yellow or red[1] in the axilla and on the thigh, in the absence of stratified coloration on the posterior face of the thigh (fig. 74), in the absence of a belly gland (see p. 429) in the males, in the similarity of the sexes in the extent of webbing, and in the broadly expanded digit tips.

The other group, the one possessing supernumerary metacarpal tubercles, is further characterized by the development of the belly gland in the males, by the absence of yellow in the axilla and on the thigh (fig. 74), and by the presence of a crossbar on the lower leg continuous with the one on the thigh when the leg is flexed. This group contains three species, *conjuncta*, *picta*, and *rigida*.

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[1] Mertens (1930) describes the color as brick-red in most living specimens of *baleata* except those from Bali, in which these areas were yellow. The color was always yellow on the preserved material I have seen.

The presence of dilated finger tips in both *baleata* and *conjuncta* could be interpreted as suggesting a relationship between them as opposed to the grouping of *conjuncta, picta,* and *rigida,* because the last two lack the digital dilations. However, the degree of expansion of the finger tips varies greatly in *conjuncta.* That fact, plus the overwhelming evidence of other characters, seems to eliminate the possibility of a close *conjuncta-baleata* relationship.

Some of the characters found in *Kaloula* not only indicate the relationships of the species but also afford a clue to the sequence of their dispersal into the Philippine Islands. With two exceptions the males of all species of the genus have belly glands. It therefore seems likely that the basic stock from which the present species are derived had this secondary sex character. The populations grouped in the species *conjuncta, picta,* and *rigida* have the belly gland. The ranges of these three species do not include Palawan, Borneo, or Celebes. The only species of *Kaloula,* so far as is known to me,[1] without this structure are *baleata* and *pulchra.* Their ranges are interposed between the *conjuncta-picta-rigida* group and the remaining species. It would appear that the *baleata* populations are the latest arrivals in the Philippine Islands and that the *conjuncta-picta-rigida* populations are derived from an older stock that may have given rise later to *baleata.*

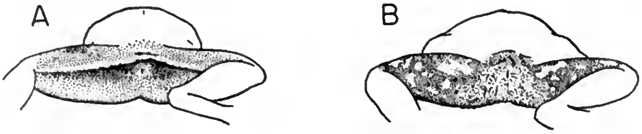

FIG. 74. Coloration of rear of thighs in *Kaloula conjuncta* (A) and *K. baleata* (B); × 1.5.

These conclusions are not based solely on the presence or absence of the belly gland. When the populations of closely related forms are broken up into insular sub-populations, independent yet parallel local differentiation certainly falls in the realm of probability, but it is highly improbable that several such insular sub-populations will undergo parallel and independent evolution in four characters. The populations of *baleata* have in common four characters (see above) that distinguish them from the *conjuncta-picta-rigida* group.

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[1] One species, *mediolineata,* was not examined. The literature does not indicate whether or not *mediolineata* has a belly gland. Information on this point is not crucial to the discussion.

It is not likely that this situation arose as the result of chance after the populations arrived in their present homes. Considering the compact range of the populations here called *baleata*, their parallel evolution could conceivably be the result of selective factors operative on certain islands. This suggestion, however, is weakened to the breaking point, because *conjuncta, picta, rigida,* and *baleata* all occur on Luzon and it thus becomes necessary to postulate selective forces that would operate only on *baleata*. As yet no ecological differences between *baleata* and *conjuncta* are known.

One-half of the ten species of *Kaloula* exhibit sexual dimorphism in the extent of the web, the male having the more extensive membrane. Three of these, *rugifera, macroptica,* and *verrucosa* are found in China, and two, *conjuncta* and *rigida,* in the Philippines. The five species—*pulchra, baleata, mediolineata, borealis,* and *picta*—not showing this type of dimorphism are scattered over the generic range. The distribution of this character suggests that if it was characteristic of the basal stock of *Kaloula* it has been lost several times. On the other hand, if the basal stock of *Kaloula* did not have this particular sex dimorphism, it arose at least twice, once in the Chinese forms and once in the Philippine forms. The relations of *picta, conjuncta, and rigida* have some bearing at this point. In the final section of this report (p. 500) reasons will be advanced for considering the *conjuncta-rigida* stock (or stocks) to be the first member (or members) of the genus in the Philippines, *picta* being a later arrival. If this is true, then sex dimorphism of the web, shown by *conjuncta* and *rigida,* appears to be the original condition, and its absence in *picta* a later development in the genus. The absence of this character in *baleata* favors this conclusion.

An entirely different distribution is shown by a particular pattern of the posterior surface of the thigh. In most species this area is mottled in an irregular fashion. In *conjuncta, picta,* and *rigida,* the posterior surface of the thigh most often has two strata of olive gray, an upper lighter zone and a lower darker one. The definition between the two is sharp. All individuals of *conjuncta* have this stratified pattern from the anus to the lower leg. In both *picta* and *rigida,* however, this pattern is found in only two-thirds of the individuals; furthermore, the dark zone reaches the anus in only 45 per cent of those specimens with this pattern. The occurrence of the pattern only in these three species lends support to the idea that they are derived from a single stock.

The three Chinese forms, *rugifera, macroptica,* and *verrucosa,* have in common a secondary sex character unique among frogs—

the males have pustules with bony cores on the tips of the fingers (Parker, 1934, figs. 35 and 36; Liu, 1950). Their agreement in the three secondary sex characters, including one restricted to them, suggests a common origin for them. The proximity of their ranges is additional support for this suggestion.

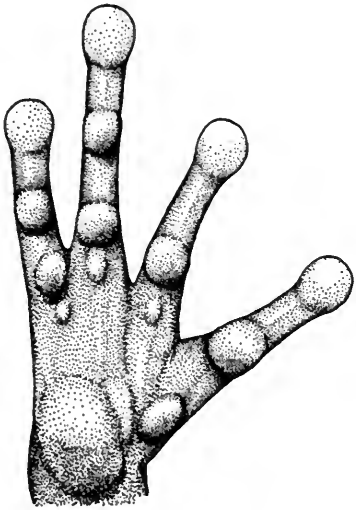

FIG. 75. Hand of *Kaloula rigida;* × 7.

1a. A supernumerary tubercle at the base of each finger (fig. 75)............. 2
1b. No such tubercles.. *Kaloula baleata*

2a. Inner metatarsal tubercle equal to or longer than first toe..... *Kaloula picta*
2b. Inner metatarsal tubercle less than length of first toe.................... 3

3a. Digit tips rounded, never wider than penultimate phalanges.. *Kaloula rigida*
3b. Digit tips truncate, usually much wider than penultimate phalanges. *Kaloula conjuncta*

The following descriptive notes apply to all the Philippine forms of the genus: Small or moderate-sized frogs, 25–60 mm. snout to vent; habitus stout; head broader than long; snout short; canthus rostralis distinct, usually rounded; tympanum usually hidden by skin, one-half to three-fourths diameter of eye; supratympanic fold present; transverse occipital fold evident in most large individuals; skin of back thick, densely set with large mucous glands; skin variable in texture; webbing of foot variable; two metatarsal tubercles, the inner one well developed and compressed; belly cream, uniform or variously mottled with brown.

Kaloula baleata Müller

Taxonomic notes.—For comments on the characteristics of this species and its relations to other Philippine forms see preceding pages.

Comparison of the populations included in this species indicates that the one from Luzon should be separated as a subspecies, differing in a number of details from the typical form but obviously closely allied to it.

Diagnosis.—Finger tips much wider than penultimate segments; no metacarpal tubercles at base of fingers; outer metatarsal tubercle without a sharp edge; inner tubercle less than length of first toe; coloration of posterior surface of thigh mottled, never stratified (fig. 74); yellow or red spots or bars usually present in axilla and on thigh.

Descriptive notes.—Skin above smooth or with scattered pustules, ventrally smooth or granular. Fingers moderate in length; third finger equal to distance from its base to proximal edge of outer palmar tubercle. Toes slightly dilated at tips; web reaching little beyond subarticular tubercles of first and second toes; third and fifth toes webbed to base or center of distal tubercles; two or three subarticular tubercles on fourth toe; outer metatarsal tubercle separated from inner by width of former or slightly less (at least in Philippine specimens).

Color (in preservative) brown or purplish dorsally with darker spots or, more rarely, a mid-dorsal pattern similar to that of *picta* (see fig. 77); lower leg usually without a crossbar, although dark spots are often present.

Secondary sex characters.—Sex dimorphism is not as highly developed in *baleata* as in the other Philippine species. Males of *baleata* do have dark and strongly granular gular skin and median, internal, subgular vocal sacs, as do the males of *conjuncta*, *rigida*, and *picta;* but the males of *baleata* lack belly glands and do not have more extensive webbing on the foot than the females.

Observed differences between the sexes in size are not statistically significant. The small samples available for this study yield inconclusive information (see Table 40).

Ecological notes.—The habits of *baleata* coincide to a great extent with those of other species of the genus. Except during the breeding period it is a retiring animal, being found usually under stones and loose bark, in rotting logs (Taylor, 1922a) and in burrows which it

Table 40. Comparison of snout-vent lengths in males and females of *Kaloula baleata*

	Males			Females		
	No.	Mean±SE	Range	No.	Mean±SE	Range
Luzon	2	29.60	26.4-32.8	7	35.51±1.21	28.7-38.3
Palawan . . .	9	44.48±0.78	41.5-48.7	6	42.95±0.77	40.2-45.8
Borneo	4	58.68	54.6-60.6	2	66.25	66.0-66.5
Celebes . . .	5	52.28±1.30	48.4-56.3	3	49.30	45.8-53.8
Java	1	50.0	---	2	48.70	46.9-50.5

apparently digs (Mertens, 1930). In its habit of inflating itself when handled, *baleata* resembles *K. pulchra, rugifera,* and *macroptica* (Mertens, 1930; Liu, 1950).

As yet, *baleata, conjuncta,* and *rugifera* (Liu, 1950) are the only species of *Kaloula* that are known to climb trees. Mertens (1930) observed two specimens of *baleata* in trees at a height of about two meters, the first of these on Java and the second on Sumbawa. Members of the Philippine Expedition found one individual on Palawan in a tree hole at a height of two meters.

Mertens states that *baleata,* at least in the Lesser Sundas, is eurytopic, occurring about human habitations, in grasslands, and in forests. The species has an extensive altitudinal distribution. It is found from sea level to 1,525 meters (Parker, 1934).

Inter-island variation.—Geographic variation is evident in a number of characters, among them size. Specimens from Java, Borneo, and the Lesser Sunda Islands appear to be much larger than those from Palawan and Luzon. The last population has the smallest snout-vent length (see Table 40). The following analysis of variance is based on the means of Table 40 (except for the data of the small Javan sample, which is omitted):

Source of variance	Sum of squares	Degrees of freedom	Mean of squares
Between islands.	944.796	3	314.932
Within islands.	51.727	4	12.932
Total.	996.523	7	

F (3,4)=24.35; P=<0.01

Clearly the samples are not homogeneous with respect to size. The difference between the females from Luzon and Palawan is statistically significant ($t=4.973$; $n=11$; $P=<0.001$).

The terminal segment of the fingers is broadly dilated in *baleata.* However, the relative width of the disk is not the same in all populations. This difference is reflected in the width of the terminal phalanx supporting the disk. The Luzon population has the largest disk, relative to snout-vent length, the width of the phalanx equaling about 5 per cent of snout-vent length. In the Palawan, Bornean, and Javanese material at hand, the width of the phalanx is about 3.5 per cent of the length.

A difference in the shape of the phalanx is associated with the difference in its size. In the Luzon population the end is concave; in the other samples the end is straight, with a few irregularities (fig. 76).

Additional distinctions exist between the Luzon populations and the others in coloration. There seems to be a general reduction in the red (or yellow) spots in the Luzon form; for example, the spots commonly found in the groin of *baleata* are usually absent in Luzon specimens. The inguinal spots appeared in only one of the ten specimens examined, but only one specimen from Palawan and none from Java, Borneo, and Celebes lacked inguinal spots. There is also a slight diminution in the amount of red (or yellow) on the posterior surface of the thigh; usually, though not always, the red of that region is in the form of vertical bars or relatively large spots in specimens from Java, Borneo, and Palawan, but in those from Luzon it is usually in the form of small spots (6 specimens out of 10) rather than bars or larger spots (2:10) and may even be absent (2:10). The amount of red or yellow in the axilla is much the same in all specimens examined.

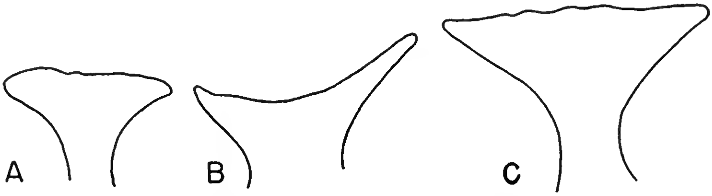

FIG. 76. Shape of terminal phalanges in *Kaloula baleata*. Specimens from (A) Palawan, (B) Luzon, (C) Borneo. All greatly enlarged.

Finally, the Luzon population is distinguished from the others in the number of subarticular tubercles on the fourth toe. When each foot is considered as a separate unit, the fraction of each sample with three tubercles is as follows: Luzon 1:20, Palawan 50:54, Borneo 12:12, Java 12:14, Celebes 20:20.

These differences between the Luzon population and the others constitute sufficient grounds for recognizing the former as a distinct subspecies.

The forms of *baleata,* then, are as follows:

Kaloula baleata baleata Müller[1]

Bombinator baleatus Müller, 1836, Verh. Genootsch. Batavia, **16:** 96—Krawang, Java.

Kaloula baleata Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 122; Taylor, 1920, Phil. Jour. Sci., **16:** 324, fig. 7 (part); van Kampen, 1923, Amph. Indo-Austr. Arch., p. 148, fig. 21 (part); Mertens, 1930, Abh. Senck. Naturf. Ges., **42:** 235 (part); Parker, 1934, Monogr. Microhylidae, p. 88 (part).

Callula baleata Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 169, fig. (part); Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 124 (part).

Material examined.—Palawan, 19 (2 CNHM; 17 MCZ); Borneo, 6 (BM); Java, 7 (3 AMNH; 4 MCZ); Celebes, 10 (8 BM; 1 EHT; 1 USNM).

Diagnosis.—Size relatively large, no adults under 35 mm.; usually three subarticular tubercles on fourth toe; red or yellow spots in the groin.

Range.—Palawan (Brooke's Point, Puerto Princesa). Outside the Philippine Islands the range includes the Malay Peninsula, Nias, Sumatra, Java, Borneo, Komodo, Sumbawa, Sumba, Lombok, Bali, Flores, and Celebes.

Kaloula baleata kalingensis Taylor

Callula baleata (part) Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 169, fig.; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886:** 124.

Kaloula baleata (part) Barbour, 1912, Mem. Mus. Comp. Zool., **44:** 72; Taylor, 1920, Phil. Jour. Sci., **16:** 324, fig. 7; van Kampen, 1923, Amph. Indo-Austr. Arch., p. 148, fig. 21; Mertens, 1930, Abh. Senck. Naturf. Ges., **42:** 235; Parker, 1934, Monogr. Microhylidae, p. 88.

Kaloula kalingensis Taylor, 1922, Phil. Jour. Sci., **21:** 178, pl. 3, figs. 1–2—Balbalan, Mountain Province, Luzon; Parker, 1934, Monogr. Microhylidae, p. 84.

Material examined.—Luzon, 10 (2 BM; 1 CAS, topotype; 1 EHT; 6 MCZ, one paratype).

Diagnosis.—Distinguished from typical form by the small size (rarely, if ever, over 40 mm.), by the presence of only two subarticular tubercles on the fourth toe, and by the absence (except in occasional individuals) of yellow or red in the groin.

Range.—Luzon: Laguna de Bay; Laguna Province (Mount Maquiling); Mountain Province (Balbalan).

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[1] For a complete synonymy see Parker (1934).

There has been disagreement as to the status of the Laguna de Bay specimens. Taylor (1920) doubted the locality, but Parker (1934) pointed out that there was no reason for such doubt. After an examination of the specimens, I agree with Parker. The shape of the distal phalanges corresponds to that of the topotypes of *kalingensis* and is thereby sharply distinguished from the shape in *b. baleata*. Furthermore, the number of subarticular tubercles on the fourth toe, the size of head and body, and, in one individual, the coloration of the groin, agree with *b. kalingensis* rather than with the typical form.

Kaloula picta Duméril and Bibron

Plectropus pictus Duméril and Bibron, 1841, Erp. Gén., 8: 737—Manila, Luzon; Bibron, 1842, *in* Eydoux and Souleyet, Voy. Bonite, Rept., p. 152, pl. 9, figs. 3–4; Peters, 1863, Monatsber. Akad. Wiss. Berlin, **1863**: 455.

Kaloula picta Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 123 (part); Taylor, 1920, Phil. Jour. Sci., **16**: 322, pl. 9, fig. 4, text fig. 6; 1922, Phil. Agriculturist, **11**: 130; Parker, 1934, Monogr. Microhylidae, p. 79; Cendaña and Fermin, 1940, Phil. Agriculturist, **28**: 626, pl. 1, text fig. 1.

Callula picta Günther, 1864, Rept. Brit. India, p. 436; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 168; Boettger, 1892, Kat. Batr. Senck. Mus., p. 23; Nieden, 1926, Das Tierreich, Lief. 49, p. 26.

Material examined.—Luzon, 97 (13 AMNH; 63 CAS; 12 CNHM; 9 UMMZ); Polillo, 4 (CAS); Mindoro, 10 (CNHM); Leyte, 43 (42 CNHM; 1 CM); Mactan, 8 (CM); Mindanao, 14 (CNHM); Cuyo, 113 (CNHM).

Taxonomic notes.—See pages 420 ff.

Diagnosis.—Digit tips not wider than penultimate segment of digits; tips rounded; a small metacarpal tubercle present at base of each finger; both metatarsal tubercles strongly developed and with sharp edges; inner metatarsal tubercle equal to or longer than first toe; pattern of posterior surface of thigh usually consisting of two horizontal layers of gray sharply demarked (as in fig. 74, A), the darker stratum rarely reaching the anus; no yellow or red spots in axilla or on thigh.

Descriptive notes.—Skin above smooth except for a few irregularly scattered tubercles, smooth ventrally except in adult males (see below); a narrow glandular ridge from hind corner of eye to groin, variable in length and not clearly visible in poorly preserved material.

Fingers long and slender; fourth finger usually not reaching beyond outer subarticular tubercle of third; distance from base of third finger to proximal edge of outer palmar tubercle much less than length of finger, generally not longer than distance from base of finger to outer subarticular tubercle. Web of foot not extensive; first and second toes usually webbed to a point slightly beyond subarticular tubercle; web usually not reaching base of outer subarticular tubercle of third toe; web not reaching middle tubercle of fourth toe; fifth toe webbed to distal tubercle; three subequal tubercles on fourth toe; metatarsal tubercles closely approximated, never separated by as much as width of outer one.

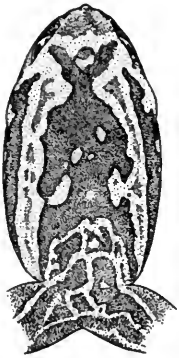

FIG. 77. Dorsal pattern of *Kaloula picta;* × 0.9.

Color in life olive, olive-brown to dull red above (Taylor, 1920); in alcohol brown to violet-gray; a dark mid-dorsal pattern (fig. 77), variable (see below); area beneath lateral glandular fold dark as mid-dorsal pattern; limbs with same ground color as back; leg with single dark crossbar on thigh and lower leg, the bars continuous when leg is flexed; posterior surface of thigh usually as noted in *Diagnosis;* more rarely, thigh uniform behind.

Secondary sex characters.—Kaloula picta exhibits sex dimorphism in coloration of the throat in common with other species of the genus. Taylor (1920) states that the skin of the gular region of adult males is green in life and slate in alcohol. Cendaña and Fermin (1940), on the other hand, report the usual color to be black with a greenish drab overcast. The preserved males I have examined have black throats. In females this area is cream-colored, uniform or variously mottled with black.

Another secondary sex character common to the males of most forms of *Kaloula,* including *picta,* is the development of a "belly gland," which is an aggregation of one-celled epidermal glands distributed on the ventral surface of the body between the pectoral region and the thighs. The margin of the area containing these glands is usually easily seen with the naked eye. In males of *picta* the belly gland occupies between one-half and five-sixths of the area of the abdomen. The gland apparently functions as an aid in amplexus (see below).

There is also sex dimorphism in size. The larger size of the females was first pointed out by Cendaña and Fermin for their large sample from Los Baños, Luzon. Of the present samples of sufficient size to warrant statistical analysis, only the one from Manila failed to show a statistically significant difference in the snout-vent lengths of the sexes, although in this series the mean of the females was the larger (for comparison of body lengths see Table 41).

The males of *picta* are further distinguished from the females by the presence of a vocal sac. This has been described by Liu (1935) as median, subgular, external. The openings are slit-like and placed just inside the mandible.

There is no sexual dimorphism in the extent of webbing.

Ecological notes.—A good account of the ecology of *picta* is contained in Cendaña and Fermin. Briefly, their observations, carried out at Los Baños, Luzon, are as follows: The adult is terrestrial and essentially nocturnal, hiding by day under stones, logs or other debris, or in burrows. The food, as determined from 100 frogs collected every month for a year, is about 53 per cent insects by volume, with ants, termites, and Dermaptera contributing the largest number of individuals to the diet.

Females with mature eggs are to be found every month of the year and egg masses every month but March, April, and the early part of May, the driest period of the year at Los Baños. The peak of the breeding season falls between July and October, coinciding with the heaviest rainfall. The coincidence between the weather and the breeding cycles is to be expected, as the authors point out, for *picta* always oviposits in pools of rain water, at least in the vicinity of Los Baños.

According to Cendaña and Fermin, *picta* exhibits the common anuran breeding behavior pattern, in which the males precede the females to the breeding sites and initiate a breeding chorus. In oviposition a pair floats at the surface for several hours, the male stuck to the female by a "gelatinous" substance secreted by the

Table 41. Comparison of snout-vent measurements in males and females of *Kaloula picta*

Sample	Sex	No.	Mean±SE	Range	t[1]	P
Luzon: Los Baños[2]	♀	450	42.22±0.11	35.0-54.5	18.2	< 0.001
	♂	353	39.63±0.09	32.8-51.0		
Luzon: Manila	♀	18	40.70±0.78	35.0-47.0	1.064	0.30
	♂	25	39.71±0.56	36.0-46.0		
Leyte	♀	14	45.76±0.90	38.7-49.5	3.012	0.006
	♂	25	42.58±0.61	35.9-48.7		
Cuyo	♀	25	49.22±0.50	44.4-56.5	9.449	< 0.001
	♂	25	43.73±0.29	41.0-46.2		
Mindanao	♀	1	44.6		---	---
	♂	9	40.39±0.30	39.5-41.7		
Mactan	♀	2	41.25	38.5-44.0	---	---
	♂	3	37.8	37.1-38.4		

[1] Student's t test was applied in all cases except for the Los Baños sample in which diff./SE_d was used.

[2] Data for Los Baños sample from Cendaña and Fermin (1940). A check computation based on their frequency distributions, which group the data in 1 mm. classes, yields means of (♀) 42.67±0.16 and (♂) 40.67±0.13 and a diff./SE_d of 12.5. Thus the *relations* of the means and the significance of their difference remain unchanged.

male's belly gland. Amplexus is axillary. The number of eggs laid by twenty individual females varied from 812 to 4,029, with a mean of 2,250±161.25.

Cendaña and Fermin state that the hind limbs are used for burrowing, the toes loosening and pushing the soil particles, but doubt attaches to the last part of this statement. The toes of *picta* are not modified in any way—they are not particularly long or strong, they are not expanded at the tip, they are not provided with a thick or complete web; in short, the toes give no indication of being adapted to digging. However, *picta* is provided with two extremely well-developed metatarsal tubercles. These blade-like structures form an almost continuous raised surface at the tarsal-metatarsal articulation very similar to the digging apparatus of the burrowing American salientians, *Bufo cognatus* and the various species of *Scaphiopus*. Any extension of the leg or, if burrowing in *picta* resembles that of *Scaphiopus*, any sideways movement of the rear of the body with the legs flexed would push the metatarsal tubercle against the substrate. Thus it is far more likely that the metatarsal tubercles are employed in both loosening and pushing the soil than that the toes serve these functions.

Table 42. Geographic variation in snout-vent length of *Kaloula picta*[1]

	Males			Females		
Samples	Difference of means	$\text{Diff./SE}_{\text{diff.}}$	P	Difference of means	$\text{Diff./SE}_{\text{diff.}}$	P
Luzon: Los Baños, Manila	0.08	0.14	0.98	1.52	1.941	0.052
Luzon (Los Baños)–Leyte	2.95	4.79	<0.001	3.54	3.91	<0.001
Luzon (Los Baños)–Mindanao . .	0.76	2.508	0.012	---	---	---
Luzon (Los Baños)–Cuyo	4.10	13.53	<0.001	7.00	13.56	<0.001

	Difference of means	t	n	P	Difference of means	t	n	P
Luzon (Manila)–Leyte	2.87	3.478	48	0.001	5.06	4.526	30	<0.001
Luzon (Manila)–Mindanao	0.68	0.710	32	0.48	---	---	---	---
Luzon (Manila)–Cuyo	4.02	6.411	48	<0.001	8.52	9.404	41	<0.001
Leyte–Mindanao	2.19	2.114	32	0.04	---	---	---	---
Leyte–Cuyo	1.15	1.704	48	0.09	3.46	3.669	37	<0.001
Cuyo Mindanao	3.34	6.497	32	<0.001	---	---	---	---

[1] Means and standard errors listed in Table 41.

The observations of Dr. W. H. Stickel (personal communication) on *picta* in the vicinity of Carigara, Leyte, supplement and corroborate some of the findings of Cendaña and Fermin. Stickel found large singing aggregations in wet rice fields. The call, according to Stickel, is "ack-ack" or "quack-quack"; Cendaña and Fermin describe it as "cokak-okak." Stickel also notes that *picta* is covered with an extremely persistent slime that "clung to the hands, at least in spots, for three days despite much washing." This slime is secreted by the skin glands covering the back in both sexes and the belly of the male.

In their report, Cendaña and Fermin make no mention of the habitat or altitudinal distribution of *picta*. From available literature and field notes *picta* appears to be restricted to grasslands, cultivated areas, and areas about human habitations. None of the localities from which it is known is more than 150 meters above sea level.

Inter-island variation.—The characters showing variation of this type are size and coloration. Of the populations for which adequate data are available, the one on Luzon has the smallest snout-vent average and that of Cuyo the largest. Conclusions based on statistics are that the Cuyo population is significantly larger than either the Luzon or Mindanao populations; the Leyte population is also larger than the last two; there is a significant difference between the males of Leyte and those of Cuyo but not between the females; the Mindanao males are significantly larger than those from Los Baños, Luzon, but not so when compared with the males of Manila (for data and statistical analysis see Tables 41 and 42).

In this report the population or populations of any given island are all too frequently represented by a sample from one locality. This situation does not allow for testing the difference between intra-island and inter-island variation. In the present instance, adequate samples from two localities on Luzon, Los Baños and Manila, were available, thus providing some check on intra-island differences. The large size of local populations of *picta* on Luzon (Taylor, 1920; K. P. Schmidt, personal communication), the nearness of Manila and Los Baños, and the absence of any barriers to dispersal between these localities combine to make local differentiation of these populations unlikely. A comparison of these two samples is given at the head of Table 42. It will be noted that there is no difference between the males of the two localities; however, in the females the difference approaches a statistically significant level.

Inter-island differentiation was observed in minor points of coloration. On the anterior face of the thigh of some individuals there is a dark band that continues over the knee. In other individuals this band is absent. The dark crossbar on the lower leg also varies. In some specimens the bar runs completely across the dorsal surface of the leg; in others either it does not extend all the way across the leg or it is broken up into spots. A dark spot may or may not be present at the tibio-tarsal joint. Lastly, as noted above (*Descriptive notes*), coloration of the posterior surface of the thigh may or may not be stratified into light and dark areas. There is an additional breakdown of the stratified category into a type in which the well-defined strata are continuous from behind the knee to the vent, and a type in which the lower, dark stratum does not reach the vent. The four largest samples were compared two at a time for each of the four characters. Observed frequencies and the results of the comparisons are presented in Table 43. The Cuyo sample shows the greatest degree of differentiation in these characters and the Mindanao sample the least.

The matter of intra-island variation in these characters may also be considered here. The Luzon sample of Table 43 consists of material from four localities: Nayom in Batangas Province, San Fernando in Pampanga Province, Los Baños in Laguna, and Manila. Chi square values based on contingency tables reveal no significant intra-island differences in these Luzon samples in coloration (for data see Table 44).

The geographic variation observed does not permit easy recognition of subspecies. Each population seems to differ from every

Table 43. Geographic variation in coloration of *Kaloula picta*

	Anterior thigh band over knee			Crossbar of lower leg		
	Present	Absent	Total	Complete	Incomplete	Total
Polillo	3 (75.0%)	1	4	0	4	4
Luzon	11 (28.9%)	27	38	19 (48.7%)	20	39
Mindoro	3 (60.0%)	2	5	4 (80.0%)	1	5
Leyte.	11 (28.2%)	28	39	7 (18.0%)	32	39
Mindanao . . .	11 (100%)	0	11	7 (63.6%)	4	11
Cuyo	45 (90.0%)	5	50	36 (72.0%)	14	50

	Diff.(%)±SE[1]	Diff./SE	P	Diff.(%)±SE[1]	Diff./SE	P
Luzon–Leyte	0.7±10.3	0.07	0.95	30.7±10.8	2.86	0.004
Leyte–Mindanao . . .	71.8±17.0	4.23	< 0.001	45.6±15.4	2.96	0.003
Luzon–Mindanao . .	71.1±17.3	4.11	< 0.001	14.9±17.1	0.871	0.38
Leyte–Cuyo.	61.8±13.1	4.71	< 0.001	54.0±10.7	5.04	< 0.001
Mindanao–Cuyo . . .	10.0± 9.1	1.096	0.27	8.4±15.2	0.553	0.58
Luzon–Cuyo	61.1±10.3	5.93	< 0.001	23.3±10.4	2.24	0.03

	Spot at tibio-tarsal joint			Posterior surface of thigh			
				Uniform or mottled	Stratified: Dark stratum		
	Present	Absent	Total		Complete	Incomplete	Total
Polillo	0	4	4	3	0	1	4
Luzon	5 (12.8%)	34	39	20	3	16	39
Mindoro	0	5	5	1	3	1	5
Leyte.	3 (7.7%)	36	39	19	0	20	39
Mindanao . . .	1 (9.1%)	10	11	0	7	4	11
Cuyo	26 (52.0%)	24	50	8	25	15	48

	Diff.(%)±SE[1]	Diff./SE	P	Chi square[2]	n	P
Luzon–Leyte	5.1± 6.9	0.731	0.46	3.49	2	0.17
Leyte–Mindanao . . .	1.4± 9.3	0.150	0.88	30.56	2	< 0.001
Luzon–Mindanao. . .	3.7±11.1	0.332	0.74	19.10	2	< 0.001
Mindanao–Cuyo . . .	42.9±16.6	2.59	0.01	2.11	2	0.33
Leyte–Cuyo.	44.3±10.1	4.40	< 0.001	29.61	2	< 0.001
Luzon–Cuyo	39.2±10.2	3.84	< 0.001	21.65	2	< 0.001

[1] The following test was carried out for each pair of samples:

	Present	Absent	Total
Luzon	11	27	38
Cuyo	45	5	50
Total	56	32	88

Difference (%) = 61.1

$$\text{SE difference} = \sqrt{\left(\frac{56}{88}\right)\left(\frac{32}{88}\right)\left(\frac{1}{38}+\frac{1}{50}\right)} = 10.3\%$$

Probability value (P) of ratio diff./SE obtained from table of areas of normal curve.

[2] Chi square obtained from contingency tables based on observed frequencies.

Table 44. Intra-island variation in coloration of *Kaloula picta* from Luzon

	Anterior thigh band over knee			Crossbar of lower leg		
	Present	Absent	Total	Complete	Incomplete	Total
San Fernando . . .	2	9	11	5	6	11
Manila.	8	9	17	9	9	18
Nayom	0	4	4	3	1	4
Los Baños	1	5	6	2	4	6
Total	11	27	38	19	20	39
	Chi square = 5.51; n = 3; P = 0.15			Chi square = 1.82; n = 3: P = 0.62		

	Spot at tibio-tarsal joint			Posterior surface of thigh			
	Present	Absent	Total	Uniform or mottled	Stratified; dark stratum: complete	incomplete	Total
San Fernando . . .	1	10	11	5	0	6	11
Manila	2	16	18	12	1	5	18
Nayom	2	2	4	0	1	3	4
Los Baños	0	6	6	3	1	2	6
Total	5	34	39	20	3	16	39
	Chi square = 6.24; n = 3; P = 0.10			Chi square = 8.67; n = 6; P = 0.19			

other in several characters. But the differentiation varies in extent from population to population as well as from character to character. In situations of this sort, especially when the characters showing variation are limited, it is perhaps wise to describe inter-island differences without formally naming subspecies.

Range.—Luzon: Abra Province (Bangued); Bataan Province (Mariveles); Batangas Province (Nayom); Cavite Province (Bacoor); Laguna Province (Los Baños); City of Manila; Pampanga Province (Dau, San Fernando); Rizal Province (Pasig [Cendaña and Fermin, 1940]). Polillo. Mindoro (San José, Calapan [Boettger, 1892]). Mactan. Leyte (Dulag, Carigara, Tacloban). Cuyo. Mindanao: City of Davao; Davao Province (Caburan); City of Zamboanga. Negros (Boulenger, 1882).

Taylor (1920) received three specimens supposedly from Dumaran Island, but had doubts as to the authenticity of the locality. Dumaran is but eight kilometers off the northeast coast of Palawan, from which *picta* has not been recorded.

The presence of *picta* on Mactan, lying one kilometer off Cebu, suggests that it will also be found on Cebu. The latter is practically unexplored herpetologically.

Though the identification of the specimen has been confirmed through the courtesy of Mr. J. C. Battersby of the British Museum, the Negros record of Boulenger is open to doubt. *Kaloula picta* is usually abundant wherever it occurs. It therefore seems strange that none of the recent collections made on Negros, collections containing many specimens of *K. conjuncta,* include *picta.*

Kaloula rigida Taylor

Kaloula rigida Taylor, 1922, Phil. Jour. Sci., **21**: 176, pl. 3, figs. 5–6—Balbalan, Mountain Province, Luzon; Parker, 1934, Monogr. Microhylidae, p. 79.

Material examined.—Luzon, 42 (paratypes) (2 AMNH; 15 CAS; 2 EHT; 18 MCZ; 5 UMMZ).

Taxonomic notes.—See pages 420–422.

Diagnosis.—Digit tips scarcely wider than penultimate phalanges (fig. 75), the tips rounded; a small metacarpal tubercle present at base of each finger; outer metatarsal tubercle round and without a sharp edge; inner tubercle less than length of first toe; posterior surface of thigh uniform, mottled, or with two contrasting layers of olive gray; no yellow or red spots in axilla or on thigh.

Descriptive notes.—Skin above smooth or shagreened, smooth ventrally except in males (see *Secondary sex characters*); a feeble, short ridge commencing behind eye. The skin of the back is even thicker than it is in most species of *Kaloula,* measuring almost 1 mm. in a specimen of 40 mm. snout to vent, or about twice as thick as in *picta* of comparable size.

Fingers not quite as long as in *picta;* distance from base of third finger to proximal edge of outer palmar tubercle less than length of finger, but longer than distance from base of finger to outer subarticular tubercle. Tips of toes resembling those of finger; web reaching subarticular tubercles of first and second toes, the base of distal tubercle of third and fifth toes of females; slightly more extensive in males (see below); usually three subarticular tubercles on fourth toe, occasionally two; the two metatarsal tubercles separated by more than the length of the outer one.

Color above reddish brown to purple in life (Taylor, 1922a), olive in alcohol; a mid-dorsal pattern similar to that of *picta* often present; most specimens with small black spots irregularly arranged around border of dorsal pattern; lores, tympanic region, and sides as dark as mid-dorsal pattern; limbs same ground color as back; a dark crossbar on lower leg continuous with one on thigh when leg is flexed; a dark longitudinal bar on anterior surface of thigh, usually passing over knee.

Secondary sex characters.—Differences between the sexes are evident in size, extent of webbing, glandular development, and coloration of throat. The snout-vent length of 21 adult females varied from 41.8 to 55.0 mm., the mean being 47.78±0.78 mm. The corresponding statistics of 16 adult males are: range 34.2 to 43.8 mm. and mean 39.40±0.69 mm. The difference between the two means (8.38) is significant, t being equal to 7.760 and P less than 0.001.

Parker (1934) states that the males have more extensive webs than the females. He writes that the membrane between the third and fourth toes does not extend beyond the proximal tubercle of the third toe in females, whereas in males it reaches the distal tubercle. Actually there is some overlap between the distributions observed in the two sexes, as may be seen below. In Table 45 the distal tubercle of the third toe is used as the point of reference.

Table 45. Level Reached by Web between Third and Fourth Toes of *Kaloula rigida*

	Proximal to base of tubercle	Base of tubercle	Center of tubercle	Distal edge of tubercle or beyond
Females..	16	5	0	0
Males....	2	5	4	5

A contingency test based on these data gives: chi square=19.58; $n=3$; P=<0.001. The sexual difference is statistically significant.

A belly gland (see p. 429) occupies from two-thirds to six-sevenths of the ventrum between the pectoral girdle and the vent, in males only.

The males have black or dark brown throats contrasting with the lighter coloration of this region in females. The males are further distinguished by the presence of median, internal, subgular vocal sacs. There are no nuptial pads.

Ecological notes.—*Kaloula rigida* is similar to a number of members of the genus, including *picta*, in selecting shallow, temporary pools for breeding, in burrowing (Taylor, 1922a), and in feeding largely on ants and termites.

K. rigida has been collected only in the mountainous region of northern Luzon. Apparently it is limited to elevations above the observed upper limit (150 meters) of *picta*.

Range.—Luzon: City of Baguio (Baguio); Mountain Province (Balbalan, Bontoc).

Kaloula conjuncta Peters

Taxonomic notes.—See pages 420–422.

Diagnosis.—Finger tips usually much wider than penultimate phalanges; tips always truncate; a small metacarpal tubercle present

Table 46. A comparison of extent of web along outer side of third toe in males and females of *Kaloula conjuncta*

	Sex	Proximal to tubercle[1]	Center of tubercle	Distal edge of tubercle	Between tubercle and disk	Disk	Total
Polillo	♂	---	---	---	2	---	2
	♀	---	1	2	---	---	3
Negros	♂	---	---	1	---	24	25
	♀	2	3	---	---	---	5
Mindanao . . .	♂	---	---	---	---	7	7
	♀	---	1	2	---	---	3
Leyte	♂	---	---	2	1	---	3

[1] Distal tubercle.

Table 47. A comparison of snout-vent lengths in males and females of *Kaloula conjuncta*

	Sex	No.	Mean±SE	Range
Polillo	♂	2	28.80	28.6-29.0
	♀	3	30.97	28.8-33.6
Negros	♂	25	34.17±0.90	30.4-36.5
	♀	5	43.00±0.68	41.1-45.1
Difference of means = 8.83; t = 12.51; n = 28; P = < 0.001				
Mindanao	♂	7	37.33±1.52	32.6-42.0
	♀	3	43.00	39.1-47.2
Leyte	♂	3	42.97	41.9-44.4
Mindoro	♀	1	40.4	---

at base of each finger; outer metatarsal tubercle usually round and without a sharp edge; inner tubercle not as long as first toe; coloration of posterior surface of thigh consisting of two horizontal layers of lighter and darker gray, the two zones sharply demarcated by a light line and both extending to anus (fig. 74); no yellow or red spots in axilla or on thigh.

Descriptive notes.—Skin above smooth or with scattered small tubercles; skin of belly smooth, rugose, or granular; gular region variable (see *Secondary sex characters*); an oblique row of small tubercles from posterior corner of eye towards groin.

Fingers moderate in length; third finger greater than, equal to, or less than distance from its base to proximal edge of outer palmar tubercle. Tips of toes dilated into round disks which are smaller than those of fingers; web varying with sex (see below); two or three subarticular tubercles on fourth toe; outer metatarsal tubercle usually separated from inner by more than the width of the former (see *Inter-island variation*).

Color (in alcohol) grayish brown above with a dark mid-dorsal pattern similar to *picta* (fig. 77), the pattern obscured in darker individuals or broken up into small spots posteriorly; sides below row of tubercles as dark as mid-dorsal pattern; a dark crossbar on the lower leg continuous with one on the thigh when the leg is flexed.

Secondary sex characters.—In common with the males of most species of the genus, those of *conjuncta* have median subgular external vocal sacs (Liu, 1935), with slit-like openings at the sides of the mouth. The gular skin of the males is black and drawn into folds. In the females, although this region may be dark, it always has at least some light spots. The males of *conjuncta* have well-developed belly glands. The skin of the abdomen occupied by these glands varies from two-thirds to the entire area between the vocal sac and thighs.

In common with *K. rugifera, macroptica,* and *rigida, conjuncta* exhibits sex dimorphism in the extent of webbing of the foot, the web being more extensive in males. Table 46 compares males and females in this character.

Finally, the females appear to be larger than the males. Only one sample was large enough to permit statistical analysis (see Table 47).

Ecological notes.—*Kaloula conjuncta* exhibits the general habits of all kaloulas. It is usually secretive, except during the breeding season.

As in the case of the other species, *conjuncta* burrows—it is frequently found in earth about the roots of commercially grown plants (Taylor, 1920). It is active at night and utilizes shallow water for breeding sites. Surprisingly enough, *conjuncta* is also arboreal. Taylor found specimens in the leaf axils of pandanus. Most of the individuals collected by the Philippine Expedition were obtained after dark.

According to Taylor the breeding aggregations are enormous and the calling males of such aggregations may be heard for over a mile. He says that the males adhere to the females by virtue of a slimy secretion of the belly. It is true that the males have belly glands, but it might be a mistake to overlook the part played by the female in this copulatory adjustment, for both sexes have very well-developed mucous glands on the back.

Little information is available on the habitat of *conjuncta*. Taylor states that individuals came from "all parts of the forest" to breeding sites in the Mindanao swamps. There is no other record of specimens collected in forests, although the species probably occurs there. The Mindanao specimens collected by the Philippine Expedition came from swamps, wet areas in coconut groves, and open grass-lands. One specimen was taken in a small stream. The ability to withstand the relatively xeric conditions of the grass-lands probably depends on the burrowing habit and the thick, mucous skin. Still, shallow water, such as the swamps Taylor mentions, and ponds, are utilized for breeding sites. *Kaloula conjuncta* is apparently most common in the lowlands. Only five specimens examined by me came from more than 150 meters above sea level. The maximum elevation was 770 meters, on the island of Negros.

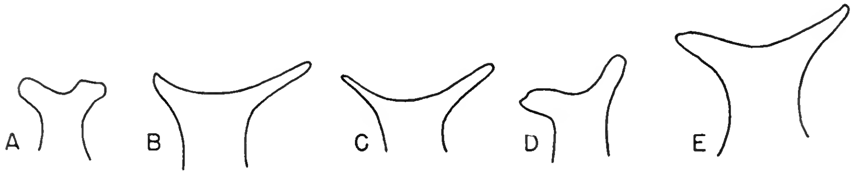

FIG. 78. Geographic variation in terminal phalanges of *Kaloula conjuncta*. Specimens from (A) Leyte, (B) Polillo, (C) Mindoro, (D) Negros, (E) Mindanao. All magnified to same extent.

Inter-island variation.—Geographic variation in this species is marked in the width of the finger tips. In order of decreasing width, the island populations fall into the following sequences: Mindanao, Polillo and Mindoro, Negros, and Leyte. The widths of the terminal phalanges relative to the body length agree with this sequence, and differences in the shape of these phalanges are correlated with the difference in width. In figure 78 it may be seen that the terminal phalanges of the Mindoro, Polillo, and Mindanao forms are only shallowly concave and have long-drawn-out tips. By contrast the Leyte and Negros forms are characterized by deeply concave phalanges with relatively short, truncated tips.

Inter-island variation is also evident in the number of subarticular tubercles on the fourth toe. For most of the populations, two is the characteristic number, but apparently three is characteristic of the Leyte form (see Table 48).

Table 48. Number of Subarticular Tubercles on Fourth Toe in Various Samples of *Kaloula conjuncta*

Numbers refer to feet

	No. of tubercles	
	2	*3*
Polillo	10	0
Mindoro	2	0
Leyte	0	6
Negros	54	5
Mindanao	17	5

The belly gland is another character in which inter-island variation was found. Despite the difficulty of delimiting its area, there can be no doubt that the most extensive belly gland occurred in the Negros sample. Distinctions between the other populations are difficult and uncertain.

Still another character showing inter-island variation is the extent of webbing. Table 46 shows that the males from Leyte had less webbing than males from other islands. Although the table indicates only the extent of webbing along the third toe, the differences were not limited to this point. In the Leyte males the fifth toes were not webbed to the disk, whereas this was almost invariably the case in males from Mindanao and Negros. The two males from Polillo seem to have less webbing than those from Negros and Mindanao. However, the difference was not so marked. One of these had the fifth toe webbed to the disk, the other webbed to the point between the outer tubercle and the disk.

Finally, there seemed to be some differences between samples in snout-vent length. It is difficult to make a statistical analysis of this character because of the few specimens available from some of the islands, but some generalizations seem to be justified. The comments are based solely on adults. The Polillo specimens are much smaller than any of the others. The Leyte males are considerably larger than the same sex of other islands. Apparently the Mindanao males are larger than those from Negros; applying Student's t test to the difference between these two samples, a t value of 3.372 is obtained, corresponding to a probability of 0.004. On the basis of these inter-island variations, I propose the following subspecies:

Kaloula conjuncta conjuncta Peters

Hylaedactylus (*Holonectes*) *conjunctus* Peters, 1863, Monatsber. Akad. Wiss. Berlin, **1863**: 455—Luzon; Steindachner, 1864, Verh. Zool. Bot. Ges. Wien, **14**: 256, pl. 11, fig. 5, *a–d*.

Kaloula conjuncta (part) Taylor, 1920, Phil. Jour. Sci., **16**: 325, text fig. 8; Parker, 1934, Monogr. Microhylidae, p. 89.

Callula conjuncta Cope, 1867, Jour. Acad. Nat. Sci. Phila., (2), **6**: 192; Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 168; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886**: 124 (part); 1892, Kat. Batr. Samm. Senck. Naturf. Ges., p. 23 (part); Nieden, 1926, Das Tierreich, Lief. 49, p. 26.

Material examined.—Polillo, 5 (3 CAS; 2 MCZ); Mindoro, 1 (CNHM).

Diagnosis.—Tips of fingers almost twice as wide as penultimate phalanges; terminal phalanges of fingers shallowly concave; two subarticular tubercles on fourth toe; a small form, males mature at 28 mm. (or possibly less), females at 30 mm. (or less); males with glandular skin occupying approximately three-fourths of area between vocal sac and thighs; web not reaching disk of third toe.

Range.—Luzon (Peters, 1863) (Manila [Steindachner, 1864]). Polillo (Burdeos). Mindoro (San José).

Remarks.—This form is rather poorly defined. It is possible that Polillo specimens are distinguished by their small size from those of Luzon and Mindoro. More specimens from Mindoro and topotypes must be examined before the limits of this subspecies can be satisfactorily determined.

It is strange that only two authentic records are available from Luzon. These are the type and a specimen from Manila (Steindachner, 1864). Taylor (1920) examined a specimen in the collections of the Philippine Bureau of Science that reputedly was from Manila and measured 68 mm. snout to vent. This record is open to suspicion primarily because of the large size. The snout-vent length is 12 mm. larger than any Philippine *Kaloula* recorded and is almost 20 mm. longer than the largest *conjuncta*. Either the locality or the identification may be incorrect.

Kaloula conjuncta negrosensis Taylor

Kaloula conjuncta (part) Taylor, 1920, Phil. Jour. Sci., **16**: 325, text fig. 8; Parker, 1934, Monogr. Microhylidae, p. 89.

Kaloula negrosensis Taylor, 1922, Phil. Jour. Sci., **21**: 180, pl. 3, figs. 3–4—Hinigaran, Negros Occidental, Negros.

Material examined.—Negros, 34 (1 CAS; 29 CNHM; 4 MCZ).

Diagnosis.—Tips of fingers about one and one-third times width of penultimate phalanges; terminal phalanges deeply concave; usually (11:12 of specimens seen) two subarticular tubercles on fourth toe; medium-sized, mature males averaging around 35 mm. snout to vent, females larger; males with glandular skin covering five-sixths to all of area between vocal sac and thighs; web of mature males reaching disk on outer side of third toe.

Range.—Negros: Negros Occidental (Himamaylan, Hinigaran); Negros Oriental (Dumaguete, Luzuriaga). Guimaras Island (Taylor, 1920).

Geographical considerations are the grounds for placing the Guimaras specimen in this subspecies. I have not examined the specimen.

The presence of *conjuncta* on Guimaras suggests that it will also be found on Panay inasmuch as only one mile separates the two islands.

Kaloula conjuncta stickeli[1] subsp. nov.

Type.—No. 60786 Chicago Natural History Museum, from Carigara, Leyte, Philippine Islands. Adult male, collected by Dr. William H. Stickel, November 20, 1944.

Diagnosis.—Tips of fingers truncate, only slightly wider than penultimate phalanges; terminal phalanges deeply concave; three subarticular tubercles on fourth toe; adult males moderately large for this species, about 42 mm. snout to vent; males with glandular skin occupying two-thirds to three-fourths of area between vocal sac and thighs; web not reaching disk of third toe.

Description of type.—Tympanum covered but visible, about two-thirds diameter of eye; no occipital fold; supratympanic fold and lateral row of tubercles present; small tubercles scattered over dorsal surface, concentrated near vent and occiput; tips of fingers truncate, only slightly wider than penultimate phalanges; tips of toes expanded into round disks that are smaller than those of fingers; three subarticular tubercles on fourth toe; web reaching disks on outer side of first and second toes, though excised; outer side of third toe webbed to a point between distal tubercle and disk; inner side of fifth toe webbed as third; fourth toe webbed to middle tubercle; belly gland occupying two-thirds of abdominal skin; dorsal surface grayish brown with a complete dark *picta*-like pattern; a dark lateral area bounded by the supratympanic fold and the lateral row of glandules; ventral surface a dirty cream; throat dark, becoming lighter caudally. Otherwise as in species description (p. 423).

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[1] It is a pleasure to name this form after the collector, Dr. Stickel, who, though realizing the distinctive nature of this material, kindly permitted its description to be included in this report.

From snout to vent 42.6 mm., lower leg 16.4 mm.

Paratypes.—CNHM 60787 and 60788, both with same data as the type. They agree in all essential details with the type except that the web does not extend beyond the distal subarticular tubercle on the outer side of the third toe.

Remarks.—These specimens were collected at night in an inundated grassy area. According to the collector's field notes the water was from 15 to 30 centimeters deep and the grass 15 centimeters high. The specimens were taken in the midst of a chorus of *K. picta*.

Range.—Known only from the type locality, Carigara, Leyte.

Kaloula conjuncta meridionalis subsp. nov.

Kaloula conjuncta (part) Taylor, 1920, Phil. Jour. Sci., **16**: 325, pl. 9, fig. 1, text fig. 8; Parker, 1934, Monogr. Microhylidae, p. 89.

Type.—No. 50754 Chicago Natural History Museum, from Madaum, Tagum Municipality, Davao Province, Mindanao, Philippine Islands. Adult male, collected by Mr. Harry Hoogstraal, October 15, 1946.

Diagnosis.—Tips of fingers one and two-thirds to twice as wide as penultimate phalanges; terminal phalanges shallowly concave; usually (five-sixths of specimens seen) two subarticular tubercles on fourth toe; moderate to large-sized, adult males frequently over 40 mm., females over 45 mm. snout to vent; males with glandular skin covering two-thirds to four-fifths of area between vocal sac and thighs; web in males reaching disks of third and fifth toes.

Description of type.—Tympanum covered, about one-half diameter of eye; no occipital fold; supratympanic fold and oblique row of tubercles present; disk of third finger approximately one and two-thirds times width of penultimate phalanx, other disks smaller; tips of toes expanded into round disks, smaller than those of fingers; two subarticular tubercles on fourth toe; all toes except fourth webbed to disks, fourth toe to distal subarticular tubercle; dorsal surface gray; *picta*-like dark pattern distinct and complete; sides below row of tubercles dark gray; ventral surfaces grayish-brown with cream reticulation; throat black.

From snout to vent 33.0 mm., lower leg 13.0 mm.

Paratypes.—The following Mindanao specimens are designated as paratypes: CNHM 22521–22 (Bunawan), 50748–51 (Maco), 50752 (Sitio Taglawig), 50753 (Madaum), 50755 (Sputon); EHT

F717 (Saub). The variation among these is documented in Tables 46–48.

Remarks.—In addition to the above specimens, one immature individual from Bubuan Island in the Sulu Archipelago was examined. Its characters agree with those of the type series.

Range.—Mindanao: Agusan Province (Bunawan); Cotabato Province (Saub, Sputon near Dadiangas); Davao Province (Maco, Madaum, Sitio Taglawig near Maco—all in Tagum Municipality). Sulu Archipelago: Bubuan Island (in Tapiantana group).

Oreophryne annulata Stejneger

Phrynixalus annulatus Stejneger, 1908, Proc. U. S. Nat. Mus., **33**: 573—Davao, Mindanao; Taylor, 1920, Phil. Jour. Sci., **16**: 336.

Oreophryne annulata Parker, 1934, Monogr. Microhylidae, p. 167.

Chaperina visaya Taylor, 1920, Phil. Jour. Sci., **16**: 335, pl. 9, fig. 3—Biliran Island.

Material examined.—Mindanao, 32 (30 CNHM; 2 USNM, including type of *annulatus*).

Taxonomic notes.—In a group as poorly known as *Oreophryne,* it is perhaps not wise to propose relationships between nominate forms. Nevertheless, a glance at the distribution of the members of this genus (fig. 93) makes it difficult to refrain from suggesting that the Philippine species is related either to a species from Celebes or to the one found in the Moluccas.

Actually, comparison of *annulata* with *celebensis* (range: Celebes), *variabilis* (range: Celebes), and *moluccensis* (range: Halmaheira, Batjan, Ternate) reveals but little differentiation. Using Parker's (1934) summary of the genus, it is found that *annulata* differs from *moluccensis* only in the matters of webbing and the relative lengths of the third and fifth toes. In *annulata* there is no web at all; in *moluccensis* the toes are webbed at the base ("one-third" webbed). In *annulata* the fifth toe is longer than the third; in *moluccensis* they are equal in length.

Again according to Parker, *celebensis* and *variabilis* both differ from *annulata* in having the third and fifth toes equal and in the possession of "long" fingers; the fingers are said to be "short" in *annulata.* Comparison of the available series of *annulata* with a paratype of each of the other two species confirms the difference in relative lengths of third and fifth toes. But laying off the length of the third finger along the snout (employing dividers) indicates that the length of this finger at least does not differ in the three forms.

The fact that the fingers of *annulata* are thicker than those of *celebensis* and *variabilis* gives the impression that they are also shorter. Parker also suggests differences in the lengths of the legs of the three forms, but the method of measurement—extending the leg forward along the body—is subject to too many extraneous sources of error to warrant consideration of the minor differences.

Parker states (p. 161) that the males of *celebensis* lack vocal sacs. This would distinguish *celebensis* from the other two forms, but the male paratype of *celebensis* at my disposal (MCZ 26091 from the Boclawa Mountains, Celebes) has a median subgular vocal sac.

Diagnosis.—A small microhylid (see p. 447) with well-developed disks on fingers and toes; no dermal projections at heel and elbow; ventral pattern not a bold reticulum; no web on feet; subarticular tubercles at most only faintly visible.

Description.—Habitus stocky, trunk about the same width as head; head broader than long; snout rounded or obtusely pointed, length equal to diameter of eye; canthus rostralis rounded; tympanum visible, occasionally hidden by skin, two-fifths to three-fifths diameter of eye; interorbital space wider than upper eyelid. Skin above smooth with a few irregularly distributed small tubercles; supratympanic fold from eye to arm obscure or absent; some individuals with several faint longitudinal ridges on the back; gular region smooth; belly weakly granulate.

Tips of fingers dilated into broad disks; disks with horizontal circummarginal grooves; disk of third finger approximately twice width of penultimate phalanx and as large as or larger than tympanum; first finger shorter than second, which is longer than fourth. Tips of toes dilated into disks smaller than disk of third finger; toes without web; fifth toe longer than third; a poorly developed, elongate inner metatarsal tubercle; no outer metatarsal tubercle; subarticular tubercles of toes barely visible or absent.

Color variable; above (in alcohol) brown, usually with a dark H- or W-shaped mark; a dark crossbar between the eyes; posterior portion of back and dorsal surfaces of hind legs pink in some individuals; under surfaces brown or gray, with fine dots of cream, yellow, or even blue (according to field notes of Philippine Expedition); under side of forelegs, ventral and lateral surfaces of hind legs, and lower lip lemon yellow in some specimens (again, according to notes of Philippine Expedition), mottled in others.

Secondary sex characters.—Parker (1934) states that male *annulata* have vocal sacs. Three males examined in the course of this study vary from 17.2 to 18.2 mm., snout to vent. Only the smallest has a vocal sac, of the median subgular internal type. The males do not have nuptial pads.

There appears to be a difference in size between males and females. The data available on adults are summarized below:

	No.	Mean±SE	Range
Females..........	6	20.77±0.39	19.0–21.7
Males............	3	17.60	17.2–18.2

Ecological notes.—*Oreophryne annulata,* in common with the other species of the genus, is found in humid forests and has secretive habits. Of the thirty specimens collected by the Philippine Expedition, all but one was found in original forest; the exceptional individual was from second growth forest. Only one specimen was discovered hopping on the ground. The rest were found in moss growing on logs or trees, under bark, or in leaf axils.

The eggs of *annulata* are laid in small clusters. Three such clutches, found in moss covering tree trunks on Mount McKinley by the Philippine Expedition, contain three, eight, and nine eggs, respectively. The eggs vary from 3 to 4 mm. in diameter; including the capsules, they measure about 6 mm. The larvae do not go through a free-swimming tadpole stage, but instead undergo metamorphosis within the egg capsule. The larvae of one Mount McKinley clutch were reared through to hatching in the field.

The altitudinal distribution of *annulata* cannot be given with certainty. All of the specimens discussed in the previous paragraph are from elevations between 1,830 and 2,040 meters. Specimens were collected by Taylor (Parker, 1934) along the Cotabato coast of Mindanao, but, although these elevations are certain to be lower than the preceding, the exact altitudes are unknown.

Range.—Biliran Island (Taylor, 1920). Mindanao: Cotabato Province (between Milbuk and Saub, between Milbuk and Santo Cotabato [Parker, 1934]); Davao Province (Baclayan and Meran on Mount Apo, east slope of Mount McKinley); City of Davao (Davao).

The last locality, although it is the type locality, is open to doubt. Davao is only a few meters above sea level. This constitutes the only sea level record for the genus *Oreophryne* and obviously requires verification. The Cotabato localities cited are along the coast, but the presence of mountains fringing the coast at these points introduces the probability of higher altitudes for the specimens in question. Taylor collected specimens on Biliran, so the species may also be found in the mountains of Leyte.

THE ZOOGEOGRAPHY OF THE PHILIPPINE AMPHIBIA

INTRODUCTION

The zoogeographic relations of the Philippine Amphibia were discussed by Taylor (1928). Since that time Parker's taxonomic revision of the important family Microhylidae (1934), faunal works on neighboring areas (van Kampen, 1923; Mertens, 1930), additional collecting, and important contributions to the geology of the Indo-Australian archipelago (Umbgrove, 1938; van Bemmelen, 1949) have made a revision of Taylor's essay essential.

The historically important Wallace's Line was originally drawn east of Borneo and south of the Sulu Islands and Mindanao. Thus, all of the Philippine archipelago was considered by Wallace to lie in one faunal region. Huxley (1868) modified Wallace's Line to include only the Balabac-Palawan-Calamians chain in the same faunal region as Borneo; Huxley's paper concerned itself primarily with birds and mammals. This division of the Philippines into two major faunal regions has been maintained by Dickerson and others (1928), who refer the Palawan group of islands to the Oriental Region and the remainder of the archipelago to "Wallacea," a faunal region intermediate between the Oriental and Papuan regions. This monograph is comprehensive, relative to the organisms discussed, and even draws in the plants. In discussing the distribution of reptiles and amphibians, Taylor (*in* Dickerson and others) not only supports the dichotomy of the Philippines but also suggests the existence of four Philippine subregions east of the modified Wallace's Line.

The status of Wallace's Line and of the controversy that has arisen over it is reviewed by Mayr (1944a), who also presents data drawn from the distribution of various groups of animals. Mayr concludes, in agreement with many earlier authors, that the entire Philippine archipelago belongs in the Oriental Region. Delacour and Mayr (1946) also agree that the Palawan group is biologically more closely related to Borneo than to the rest of the Philippines, and they refer the Balabac-Palawan-Calamians chain to the Malaysian and the remaining islands to the Philippine subregions of the Oriental Region. Delacour and Mayr deal only with birds and recognize, for birds at least, two provinces within the Philippines subregion.

GEOLOGIC STRUCTURE AND HISTORY OF THE PHILIPPINE ISLANDS[1]

The Philippine Islands consist of two tectogenic arcs and related structures. The older of these down-bucklings of the earth's crust, according to Hess, runs from Palawan through the Calamians, Mindoro, and western Luzon. Van Bemmelen views this curve, which he calls the Luzon Arc, as a double structure composed of a western portion, coinciding with Hess's description, and another portion passing from northeastern Luzon through Ticao, the northwestern tip of Leyte, Bohol, the Zamboanga Peninsula of Mindanao, and the Sulu Archipelago. The two authors are agreed that the arc extends southward into North Borneo and northward into Formosa, where it connects with a similar arc passing through the Riukius and Japan. It is presumed that the trench(es), which is the topographic expression of a tectogene, disappeared in the neighborhood of the Philippines when isostatic balance was achieved. During this process, the area was deformed and uplifted, resulting in the Cordillera Central, the Sierra Madre, and the Zambales Mountains of Luzon and the mountain ridges of Mindoro, Palawan, the Zamboanga Peninsula, and North Borneo. Hess tentatively suggests a mid-Mesozoic origin for the Luzon Arc; van Bemmelen merely notes it as pre-Tertiary.

Both authors agree that the second tectogene is younger. This structure, the Samar Arc of van Bemmelen, extends from southeastern Luzon along the east coasts of Samar and Mindanao. This tectogene is still evident as the deep Mindanao Trench. The land on the inside border of the trough was folded and uplifted, but the resultant mountains in Samar and Mindanao are not as high as those of the Luzon Arc. The volcanism accompanying these orogenic movements is evident over most of southeastern Luzon. South of Mindanao the Samar Arc is continuous with the East Celebes–Timor geosyncline (Umbgrove, 1938).

Between the two arms of the Luzon Arc lies the area named by Willis the Central Plateau. This includes the islands of Panay, Negros, Cebu, and Siquijor. A high ridge of basement complex rocks forms the western boundary of Panay and the crest of the

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[1] This section is based upon the work of Dickerson (1924), Faustino (1927), Willis (1937), Hess (1948), King and McKee (1949), Umbgrove (1938, 1942), and van Bemmelen (1949).

ridge of Cebu. A volcanic belt extends north and south, the length of Negros. Except for these areas, the islands of the Central Plateau are covered with sedimentary deposits.

Central Mindanao forms still another unit. It is composed of three volcanic uplands divided by the lowlands of the Agusan Valley, the Pulangi River, and the Cotabato marshes.

The geologic history of the Philippines is at present a highly speculative matter. The distribution of the various types of rocks and fossiliferous deposits is not known in sufficient detail to permit more than tentative suggestions. Correlation of Philippine strata with those of other parts of the world is uncertain. In any case the Philippine island arcs appear to be younger than the continental areas of Asia and Australia.

In broad outline, the Cenozoic history of the Philippine archipelago has been one of horizontal compression and uplift (Eocene?, continuing into Oligocene), subsidence and submergence (Lower Miocene), horizontal compression and uplift (Upper Miocene), planation and subsidence (Pliocene), and land rejuvenation and uplift (Quaternary). Volcanism and faulting have been extensive and not limited to any single period. The evidence for the various stages in this cycle is not uniformly good or uniformly distributed over the islands. It is geologically unlikely that any single process would occur over the entire archipelago at any one time.

Dickerson and van Bemmelen were of the opinion that the Eocene or possibly early Oligocene was a period of land emergence. The evidence now at hand indicates that the Malay Peninsula–west Borneo area—the Sunda Shelf—was a region of uplands in the Eocene (Umbgrove, 1942). The genetic relationship of the Luzon Arc to that area suggests that western and northern Luzon, Mindoro, the Calamians, Palawan, and the Zamboanga Peninsula may also have been exposed during this era. Depending on the amount of uplift, varying proportions of the Luzon-Palawan chain may have been connected to Borneo at this time. At least it is highly probable that these islands were early Tertiary uplands and that ocean distances separating them must have been reduced (fig. 79). Palawan was isolated from Borneo by late Eocene; Umbgrove indicates that shallow seas had transgressed northern Borneo.

A forked submarine ridge, which with few exceptions does not go above the two-hundred meter isobath, extends south of Mindanao. The western branch (the Sangihe–Minahasa ridge of van Bemmelen) joins the northern arm of Celebes and is indicated by the Sangihe

FIG. 79. Probable Cretaceous-Eocene land masses. Modified from Umbgrove, 1938.

and Sarangani Islands, between which the ridge dips below the thousand-meter isobath. The eastern branch (Talaud–Maju ridge of van Bemmelen) runs into the eastern arm of Celebes but has a subsidiary branch pointing towards the Moluccas. Evidence is available that the north peninsula of Celebes was probably emergent in the Eocene (Umbgrove, 1938). There are also indications of late Cretaceous and early Eocene uplands in western New Guinea, the Moluccas, and the Talaud Islands. Hess dates the eastern Philippine tectogene from the Cretaceous, whereas van Bemmelen places its origin in the Oligocene. Umbgrove has shown that such an area has a strong tendency to rise in the period following the downbuckling. Consequently, if Hess's date is correct, it is possible that land uplift and emergence occurred coincidentally in the Samar Arc and Celebes. This would have made possible at least the reduction of existing water gaps between successive islands in the Celebes–Mindanao ridge, and made a Mindanao–Molucca–Papua relationship more intimate. On the other hand, if van Bemmelen's dating is correct, these Eocene associations could not have existed. The existence of an elongate eastern island connecting southeastern Luzon with Mindanao in the Eocene hinges on the same question.

Dickerson postulated from biotic evidence that Luzon and Formosa formed a single land mass in the early Tertiary. He adduced very little geologic evidence for this idea, and later geologists have not followed him. Distributional data of amphibians do not support Dickerson.

Subsidence of the land in the Lower Miocene (fig. 80) was widespread not only in the Philippines but also in adjacent areas of the East Indies. Luzon was divided into several parts by shallow seas. The Calamians, most of Palawan, Bohol, Cebu, Samar, and Negros were covered by Miocene seas. Central Panay, the eastern lowlands of Mindoro, and the east coast, Agusan Valley, and Cotabato lowlands of Mindanao are covered by Lower Miocene marine deposits.

The Upper Miocene period of folding and uplift affected the Luzon Arc, the Samar Arc, and the Celebes–Timor geosyncline. Upland areas of the Philippines may have included the elongate eastern island from southeastern Luzon to eastern Mindanao. No conclusive geologic evidence for this suggestion, first advanced by Dickerson, exists; nevertheless, this area does form a structural unit and would tend to rise up as a unit although not necessarily uniformly along its length. The height to which the area rose would determine whether a continuous strip of land or merely a chain of islands was exposed. Umbgrove and van Bemmelen cite evidence of intensive folding in eastern Celebes. Indication of Miocene uplift in western New Guinea is available but has not been satisfactorily correlated with that of Celebes. As yet there are no indications of Upper Miocene land in northern Celebes, the Moluccas, or the

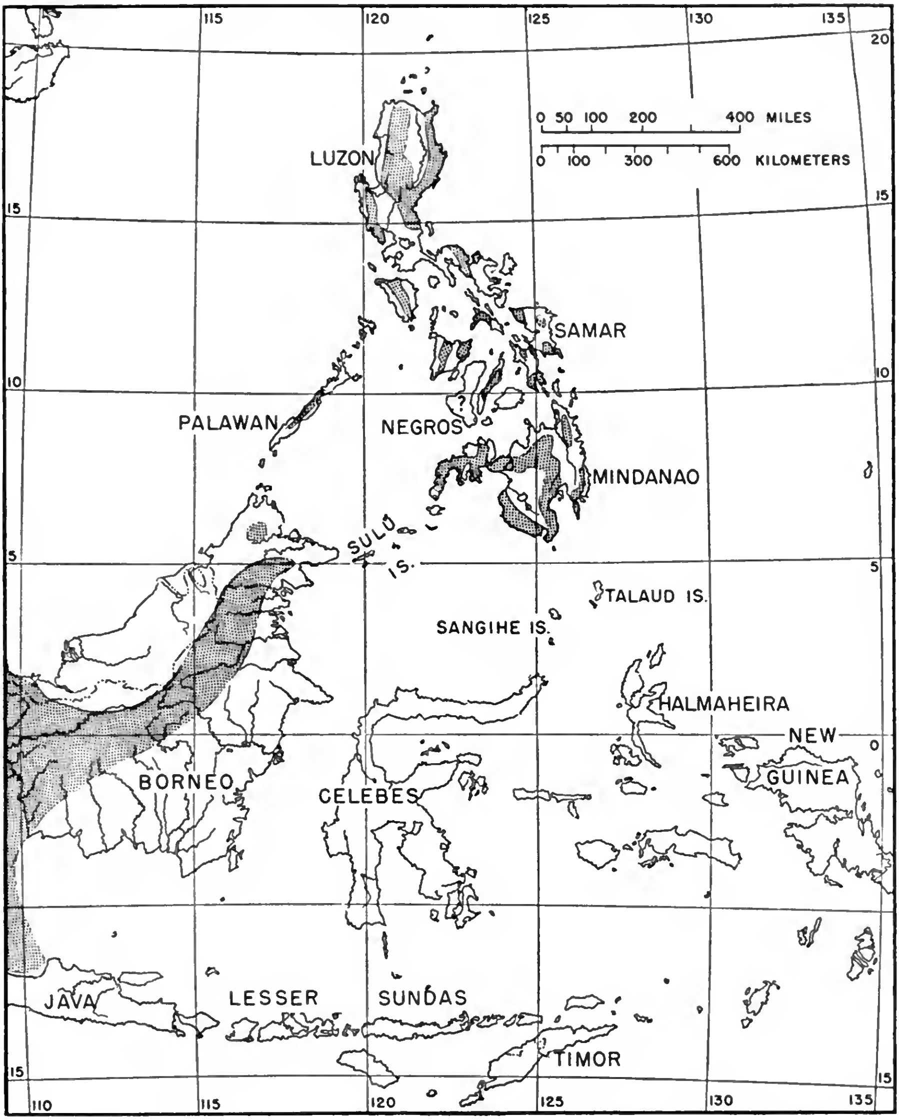

FIG. 80. Probable Lower Miocene land areas. Modified from Umbgrove, 1938.

Talaud Islands. Therefore, Celebes–Mindanao and Mindanao–Molucca–Papua connections of this period are uncertain, although the tectonics were favorable.

Other Upper Miocene lands in the Philippines probably included northern and western Luzon and the axial ridges of Mindoro, Panay, Cebu, and Palawan. Land connections of the western Philippines to Borneo and the Sunda Shelf in the Upper Miocene are uncertain.

Pliocene land areas of the Philippines are also doubtful. Willis cites the axial ridge of Mindoro and the west coast range of Panay as probable uplands of this time. Umbgrove and van Bemmelen disagree sharply on the Pliocene history of Borneo and Celebes, the former suggesting that they were largely emergent and the latter that they were covered by shallow seas.

Quaternary land masses were expanded as the result of two phenomena. During the glaciations of the Pleistocene, when the level of the oceans was lowered, large areas of the Philippines that had been covered by the sea were exposed. The amount of lowering of sea level has been the subject of controversy, but Umbgrove (1929) states that in this part of the world 100 meters is the approximate maximal lowering; Kuenen (1950) suggests 90 meters as the correct figure. The drowned courses of Pleistocene rivers in the Sunda Shelf supply the basic date for these estimates. If a continuous tongue of land did not extend north from Borneo and include Balabac, Palawan, and the Calamian Islands (all of which lie on a shallow platform nowhere more than 100 meters deep), certainly the over-water distances between successive islands must have been greatly reduced. This extension of land may have reached Mindoro and Luzon. At present, the straits separating Mindoro and Luzon and Mindoro and the Calamians exceed 300 meters in depth. If these depths are pre-Pleistocene in age, Sundaland (the lower Malay Peninsula, Sumatra, Borneo, and Java) did not extend into Mindoro and Luzon. But Umbgrove and van Bemmelen agree that the most recent geologic past of the East Indies was characterized by block faulting in many places, with parts of sea basins dropping and adjacent areas rising. This is the second phenomenon pointing to the existence of larger Pleistocene land areas. Van Bemmelen explicitly refers to such events in the Luzon Arc. Thus, the deep straits may be recent in origin, in which case a continuous Pleistocene isthmus ran from Sundaland to Luzon. At the same time a Zamboanga–Sulu Islands connection with Borneo becomes likely, if the same contingencies applied to the straits in-

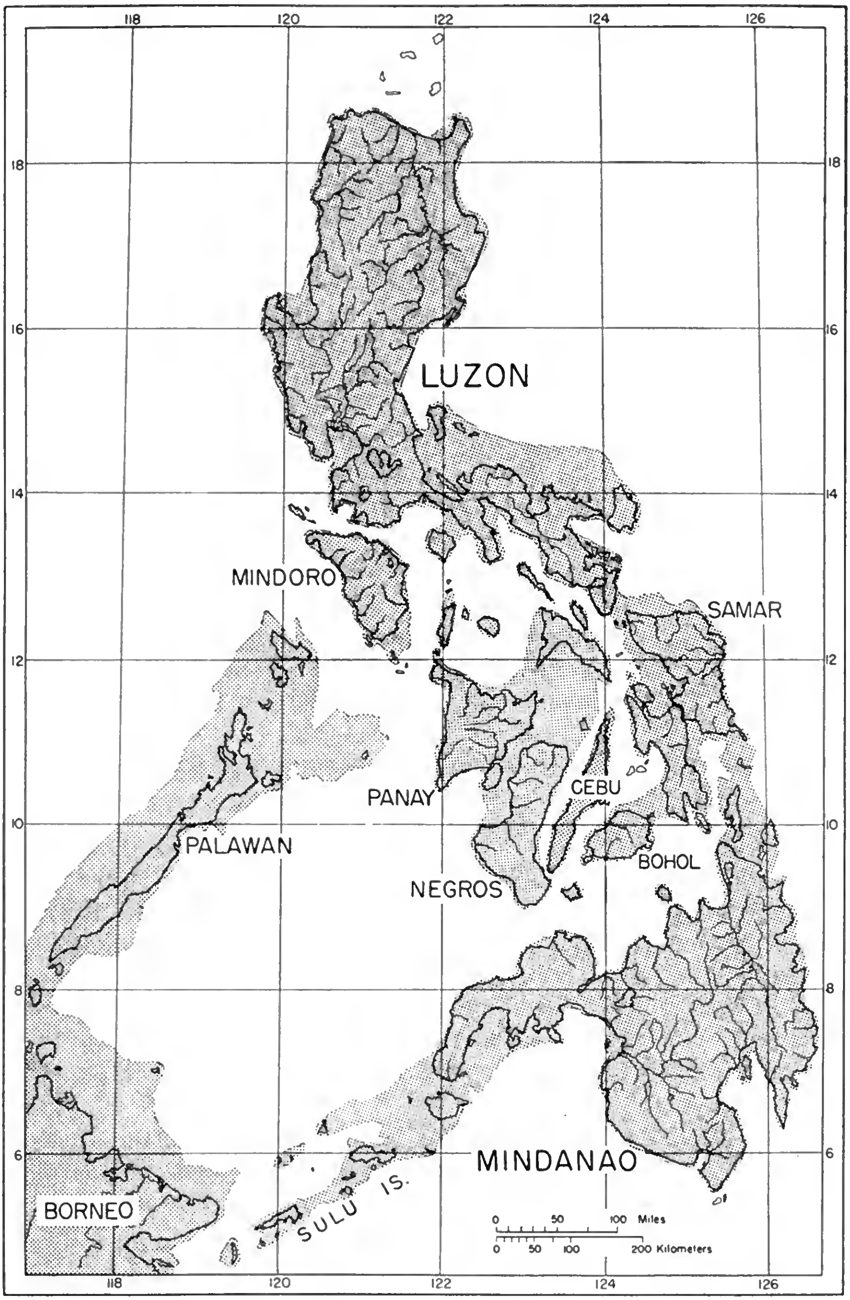

FIG. 81. Probable Pleistocene land areas at maximum regression of sea.

tervening between Tawi Tawi and Sibutu and the latter and Borneo. A regression of the sea of the magnitude indicated by Umbgrove would establish land connections along the Samar Arc from southeastern Luzon to Mindanao. In the interior of the archipelago the shallow seas separating Panay, Negros, Masbate, and Ticao are everywhere less than 100 meters deep; this becomes another probable intermittent Pleistocene land mass, a large Visayan island. This may have been connected with southeastern Luzon—and thus with the elongate island of the Samar Arc—if the present depth of the Ticao Strait is the result of recent faulting. Attention is called to the Philippine Fault Zone passing through this area. Cebu and Bohol are currently separated from each other and from the large Visayan block by straits exceeding 200 meters in depth. Both of these islands show clear evidence of being elevated recently as blocks so that the ages of the straits are not critical. These recent movements make Pleistocene connections of Cebu and Bohol with the large Visayan mass and with the elongate island of the Samar Arc improbable.

The Pleistocene regression of the sea was probably not sufficient to effect a connection between Mindanao and areas to the south and east, although over-water distance between successive islands in the two ridges must have been reduced. Probable maximum land areas during the Pleistocene are shown in figure 81.

COMPOSITION OF THE FAUNA

With a single exception all of the seven families[1] to which the Philippine amphibians belong are found in the Oriental Region. The exceptional family, the Discoglossidae, represented in the Philippines by one species, is distributed through the Palaearctic Region, its southeasternmost representative (otherwise) being *Bombina orientalis* of Yunnan. Three of the families, the Discoglossidae, the Bufonidae, and the Rhacophoridae, have no representatives in the Papuan region.

All except three of the sixteen genera found in the Philippines occur in the Malaysian subregion. Of the three, one (*Barbourula*) is endemic to the Philippines, and the others (*Oreophryne* and *Cornufer*) are distributed in the Philippines and the Papuan region.

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[1] The presence of the Hylidae in the Philippines is currently based upon a single specimen (see p. 247). Pending confirmation of this record, the Hylidae are excluded from these zoogeographic considerations.

Fifty-six Philippine species are recognized in this report. On the basis of origin and/or affinities, they may be classified as follows:

A. Non-endemic species distributed from Sundaland to Papua, probably of western origin: *Rana macrodon.* This species is considered to be of western or Sundaland origin because of its more general distribution in the west.

B. Non-endemic western species: *Ichthyophis monochrous, Megophrys hasselti, M. monticola, Bufo biporcatus, Rana limnocharis, R. cancrivora, R. microdisca, R. erythraea, R. signata, R. nicobariensis, Staurois natator, Ooeidozyga laevis, Philautus bimaculatus, P. longicrus, Rhacophorus appendiculatus, R. leucomystax, R. pardalis, Chaperina fusca, Kalophrynus pleurostigma, Kaloula baleata.* All of the species in this category inhabit Borneo as well as the Philippines, though only one, *Staurois natator,* is so limited. The remainder are also known from the Malay Peninsula, with the exceptions of *Bufo biporcatus* and *Rhacophorus pardalis,* and Sumatra, with the exceptions of *Chaperina fusca* and *Philautus bimaculatus.* Only five species, *Rana signata, Philautus bimaculatus, Rhacophorus appendiculatus, R. pardalis,* and *Chaperina fusca,* are not recorded from Java. Six species have been found in Celebes: *Rana cancrivora, R. microdisca, R. erythraea, Ooeidozyga laevis, Rhacophorus leucomystax,* and *Kaloula baleata.* None of these species occurs east of Celebes and the Lesser Sundas.

C. Endemic species of western affinity: *Ansonia muelleri, Pelophryne brevipes, P. albotaeniata, Rana everetti, R. woodworthi, R. melanomenta, Micrixalus mariae, Ooeidozyga diminutiva, Philautus acutirostris, P. alticola, P. leitensis, P. schmackeri, P. williamsi, P. spinosus, Rhacophorus everetti, R. hecticus, R. surdus, R. lissobrachius, R. emembranatus, Kaloula conjuncta, K. picta, K. rigida.* These species are clearly allied to Sundaland and/or southeastern Asiatic stocks. In some cases the particular species to which a member of this category is most clearly related is unknown. Nevertheless, with the exception of *Rana* the genera to which these species belong are not found east of Celebes and the Lesser Sundas but all are represented in Borneo and southeastern Asia. Thus over 75 per cent of the Philippine amphibians (the 43 species of categories A, B, and C out of a total of 56) have Oriental affinities and at least this part of the Philippine fauna falls within Mayr's (1944a) definition of the Oriental Region.

D. Endemic species of Papuan affinity: *Rana sanguinea, Cornufer cornutus, C. corrugatus, C. guentheri, C. hazelae, C. meyeri, C.*

polillensis, C. subterrestris, Oreophryne annulata. These forms are clearly allied to Papuan stocks. As in the previous group, some of the species of *Cornufer* can not be associated with particular species in other regions, but the genus is confined to the Philippines and the Papuan areas. That no species is distributed in the Philippines and Papua and only in those areas signifies a long separation between them.

E. Endemic species of Palaearctic affinity: *Barbourula busuangensis* (see comments above).

F. Endemic species of unknown affinity: *Rana micrixalus, R. parva.* The latter may be related to *microdisca* and hence be of Malaysian affinity. The known range of *Rana micrixalus*—Basilan and the Zamboanga Peninsula—suggests Malaysian relations.

G. Neotropical species: *Bufo marinus.* The recent widespread dispersal of this species by man is well known.

RELIABILITY OF DISTRIBUTIONAL DATA

In this discussion I have arbitrarily defined the range of a species as including those islands on which the species occurs. Probably no species inhabits all parts of any island, but our present state of ignorance does not permit the refinement of range to signify only those areas that are in fact occupied.

An obvious factor entering into an evaluation of known range is collecting effort. This factor includes not only man-days but also the special interests of the collectors. On the average, one expects a herpetologist to collect more frogs in a given time than, say, a mammalogist. The following tabulation, covering the larger islands, illustrates some effects of collecting effort.

	No. of collectors[1]	No. of species recorded	Rank of island in area
Luzon	9 (T)	21	1
Mindanao	6 (T, P)	33	2
Leyte	5 (T)	16	8
Negros	5 (T)	15	4
Palawan	4 (T, P)	21	5
Mindoro	4	12	7
Panay	4	7	6
Samar	2	8	3
Cebu	1	2	9
Bohol	1	3	10
Basilan	2 (T)	16	12
Polillo	1 (T)	15	18

[1] Based on literature records and specimens examined by myself. T=Taylor; P=Philippine Zoological Expedition.

FIG. 82. Range of *Bufo biporcatus*.

Note especially the great discrepancy in number of species between Samar and Leyte and between Cebu or Bohol and Polillo.

Ecological, geographical, and geological factors are also involved in range evaluation. There is little reason to expect a tropical rainforest species to be found where that biotope does not exist. This introduces the geographic factor of areal extent, which may influence the survival of species on very small islands by limiting the variety of habitats. On such small areas the population size of a species may be reduced below a minimum necessary to prevent almost automatic ecological or genetic catastrophes. One such ecological catastrophe is the failure to encounter mates during the breeding season. Fixation of deleterious alleles by means of gene drift is an example of genetic catastrophe. All other things being equal, we anticipate the occurrence of a species on an island intervening between two others from which the animal is known. When geologic evidence exists for relatively recent land connections among these three islands, the probability of the species' occurrence on the middle island is increased; but, if the middle island is very small, the influence of area may be preponderant. The absence of records of a species from a small island should, therefore, be discounted, unless there has been repeated effort by specialists to obtain it.

In some instances the known range can be safely said to coincide with actual range. *Bufo biporcatus* (fig. 82) provides one of the best illustrations. Its range, from Borneo to the Calamians, is continuous. The islands to the north have been moderately well collected without revealing the presence of *biporcatus*. Moreover, five other Bornean species found on Palawan are unknown from Mindoro and Luzon. Because of the intensive collecting to which various parts of Mindanao have been subjected, it is almost a certainty that *biporcatus* does not occur there. We can not be sure about the Sulu Islands.

In other cases, parts of the known range limits are probably reliable, whereas others are not. Consider, as examples, the ranges of *Staurois natator* (fig. 83) and *Megophrys monticola* (fig. 84) in the eastern Philippines. Does their apparent absence from Luzon reflect the facts? The following considerations lead to an affirmative answer. The distributions are continuous—ignoring, momentarily, the gap in the Sulus—from Borneo through Samar and Leyte. Collecting effort has been greatest in Luzon and nearly the poorest in Samar (see table, p. 458). Furthermore, the collecting on Luzon has covered suitable habitats for both species. The negative evi-

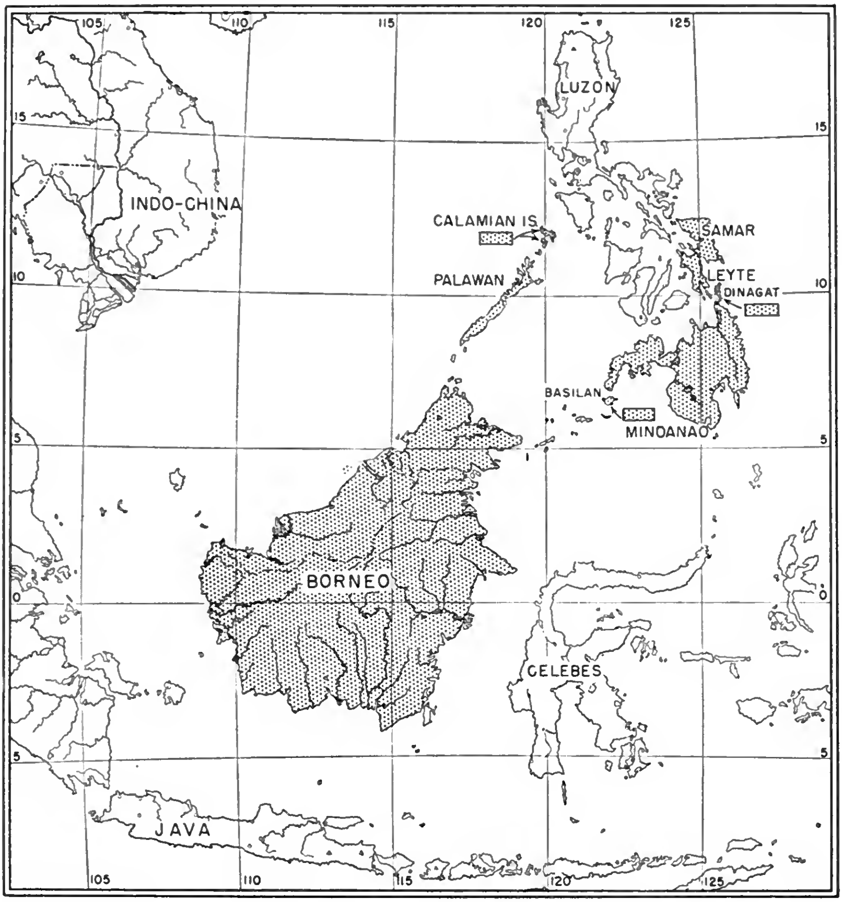

FIG. 83. Range of *Staurois natator*.

dence on the Sulu gaps does not appear to be reliable, but a decision must be held in abeyance. The proper habitats exist at least on Jolo and Tawi Tawi. There is good evidence that in the Pleistocene a continuous strip of land ran from Mindanao through the Sulus and, possibly, on to Borneo. The Sulus were, therefore, probably accessible to Pleistocene populations of the northeast and west. Also pertinent is the fact that no extensive field work has been carried on in the Sulus. On the other hand, the islands are small and this smallness may have operated against the continued existence of part of the Pleistocene fauna.

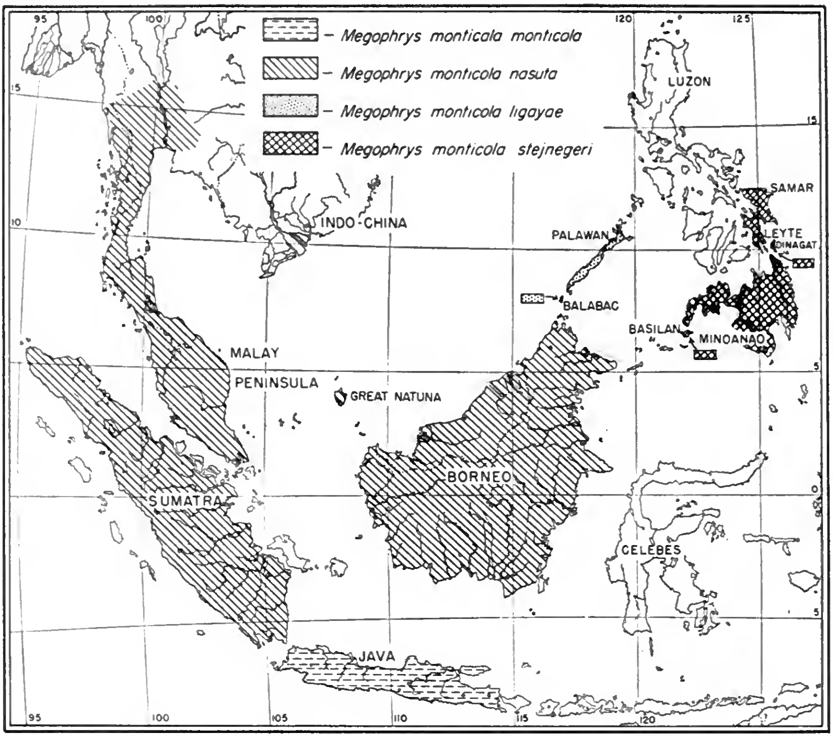

FIG. 84. Range of *Megophrys monticola.*

Finally, some gaps in known ranges are so obviously inconsistent with other information that the areas in question may safely be included in the species distribution. An example of this situation is provided by *Rhacophorus leucomystax* (fig. 85). This species, almost universally distributed in the Philippines but not yet recorded from Bohol, undoubtedly occurs there, for the habitat of *leucomystax* occurs on Bohol; the association of *leucomystax* with man increases the likelihood of waif dispersal if over-land migration is ruled out by geologic history; amphibians do occur on Bohol. However, two of the most widely distributed Philippine species other than *leucomystax* (*Rana cancrivora* and *Ooeidozyga laevis*) have not been reported from Bohol.

An obviously incomplete list of the amphibians currently known from each of the Philippine Islands will be found at the end of this report. Appended to it are those species whose discovery may be safely predicted, as in the case of *Rhacophorus leucomystax.*

FIG. 85. Range of *Rhacophorus leucomystax*. Full extent of distribution in north and west not shown.

In the following discussion, therefore, it will be assumed that the fauna of any given island is composed of those species definitely recorded plus those almost certainly occurring.

FAUNAL DIVISION OF THE PHILIPPINE ISLANDS

Faunal Relations of the Philippine Islands

Among the Malaysian genera of Philippine amphibians, there is a diminution in numbers northward in the Palawan–Luzon Arc and northeastward in the Sulu—Zamboanga and Samar arcs. The greatest reduction occurs between Borneo and the Philippines. Thirteen Bornean genera fail to reach either Palawan or Mindanao.[1] Two of the 13, *Kalophrynus* and *Ansonia*, reach Mindanao but not Palawan; two others, *Micrixalus* and *Bufo*, reach the latter but not Mindanao. Between Palawan and the Calamians three additional genera, *Pelophryne*, *Chaperina*, and *Micrixalus*, drop out. The genera *Bufo*[2] and *Staurois* do not occur north of the Calamians. *Megophrys* reaches Mindoro but not Luzon. In the eastern Philippines *Chaperina*, *Ansonia*, and *Pelophryne* do not occur north of Mindanao. *Megophrys*, *Staurois*, and *Kalophrynus* continue up the Samar Arc but do not reach Luzon. The same genera are not found west of Leyte (west of the Samar Arc) in the Visayan Islands.

Of the two Papuan genera, *Cornufer* is distributed throughout the archipelago, with the exception of the Sulu Islands and the Palawan–Calamians chain. *Oreophryne* is known only from Mindanao and from Biliran, which lies two kilometers off the north end of Leyte.

The distribution of the species is roughly parallel to that of the genera. The following comments ignore *Rana micrixalus* and *R. parva*, which are of unknown affinity, and *Bufo marinus*. The basic relationship shown by the distribution of the species is a decrease in the proportion of Malaysian or Bornean elements with increase in the distance from Borneo. Conversely, the proportion of Papuan elements increases with distance from Borneo. These trends are brought out in figure 86.

In actual numbers, Palawan and Mindanao with 16 have the greatest number of Bornean species. None of the islands to the north has more than 9. But, in terms of the proportions of the faunas composed of Bornean species, Mindanao (49 per cent) is surpassed by all save Polillo (47 per cent) and Luzon (38 per cent). Considering non-endemics occurring in Borneo together with those endemics derived from Bornean stocks (second percentage), the proportion of the faunas composed of Bornean elements decreases steadily along the Palawan–Luzon Arc and the combined Sulu–Samar arcs. There are a few exceptions (the Calamians and Samar) but these do not alter the general picture. The change in proportion of Papuan elements naturally takes the reverse course. *Rana san-*

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[1] I consider these large islands rather than those intervening between them and Borneo (Balabac and Sulu Islands) because Palawan and Mindanao have been more thoroughly collected and because the effects of small area may be of foremost significance on Balabac and the Sulus.

[2] The recently introduced *Bufo marinus* is not considered in these paragraphs.

guinea is the only Papuan element occurring on Palawan and the Calamians. Because it almost certainly did not enter the Philippines from Papua (see p. 329), perhaps it should be omitted from consideration here.

The faunal relation of islands is determined not only by the origin of faunal elements but also by the correspondence of the species present. The faunal similarity between islands is here determined to be the ratio of species held in common by two islands to the number of species in the smaller of the two faunas. For example, Mindanao and Leyte are known to have 15 species in common; Leyte has a total fauna of 16; therefore, the measure of their faunal similarity is 15/16 or 94 per cent. On the whole, faunal similarity decreases with distance, especially if there are intervening islands. These relationships are brought out in figure 87.

When the geographic distribution of Philippine lizards and snakes[1] is compared with that of the amphibians, an over-all similarity is immediately recognizable. The fauna consists primarily of genera occurring on Borneo and other parts of Malaysia. For example, 21 of the 27 genera of Philippine lizards and 24 of the 31 genera of snakes are known to occur on Borneo and other parts of Malaysia. Three genera of lizards and five of snakes are endemic to the Philippines. One genus of lizards (*Perochirus*) occurs only on Mindanao and in Polynesia. Two others are known, outside the Philippines, from the eastern part of the Indo-Australian archipelago: *Hydrosaurus*, Celebes to New Guinea; *Otosaurus*,[2] Celebes and New Guinea. One genus of snakes, *Stegonotus*, has a similar distribution; outside the Philippines it occurs in the Moluccas, Ceram, and New Guinea. Another genus of snakes, *Hemibungarus*, is restricted to the Philippines, India, southern China, Formosa, and the Riukiu Islands.

As in the case of the amphibians, the number of Malaysian genera diminishes with increasing distance from Borneo in the Palawan–Luzon and Sulu–Mindanao–Samar arcs. Of the 32 genera of lizards known from Borneo, only 16 have been collected on Palawan. Because the reptilian fauna of the Calamian Islands is

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[1] The distribution of the reptiles is based on Taylor's work (1922d, 1922e, 1928). Except for the modifications presented by de Haas (1950), Taylor's taxonomic arrangements are accepted. The distribution and taxonomy of the Indo-Australian forms have been taken from de Haas and de Rooij (1915). The sea snakes, Hydrophiidae, are not considered.

[2] The subgenera of *Lygosoma* as given by de Rooij are treated as genera in this discussion.

so poorly known, it is not certain which of the Palawan genera fail to reach them. However, the genus *Lygosoma* (*sens. str.*) is not found north of the Calamians.

In the eastern islands, 19 Bornean genera are known to occur on Mindanao. This total does not include three, *Hemiphyllodactylus*, *Lygosoma*, and *Riopa*, found in Palawan. *Hemiphyllodactylus* and *Riopa* occur in the Sulu Islands. *Lygosoma* has not been reported from the eastern islands. Seven of the 19 have not been collected on Palawan: *Ptychozoon*, *Gonyocephalus*, *Emoia*, *Leiolopisma*, *Tropidophorus*, *Siaphos*, and *Dibamus*. *Ptychozoon* reaches the end of its Philippine range in Mindanao. North of Mindanao *Dibamus* has been found only on Negros and *Emoia* only on Dinagat and Cebu. *Gonyocephalus*, *Siaphos*, *Tropidophorus*, and *Leiolopisma* continue northward into Luzon. Both genera with Papuan affinities, *Otosaurus* and *Hydrosaurus*, apparently occur from Mindoro and Luzon through the eastern islands to Mindanao. This parallels the distributions of the Papuan genera of frogs, *Oreophryne* and *Cornufer* (see p. 464). None of the endemic genera has been collected on Palawan or the Calamian Islands.

A similar phenomenon is exhibited by the snakes: 24 of the 44 Bornean genera reach the Philippines. Of this number only one, *Pseudorhabdion*, is not known from Palawan. Five genera (*Xenopeltis*, *Sibynophis*, *Dryocalamus*, *Liopeltis*, and *Haplopeltura*) are not found north of the Calamian Islands. *Sibynophis* is the only Palawan genus not reported from the eastern Philippines. *Liopeltis* and *Xenopeltis* apparently reach their limits of distribution in the Sulu Islands. *Dryocalamus* has been collected on Basilan but not to the north. *Haplopeltura* reaches the limits of its range in Mindanao.

The only genus with Papuan affinities, *Stegonotus*, is found in the eastern islands only, from Luzon to Mindanao. The endemic genera of snakes are not yet recorded from Palawan or the Calamians.

The ranges of the non-endemic species of lizards and snakes recognized by Taylor exhibit the same phenomenon observed in the

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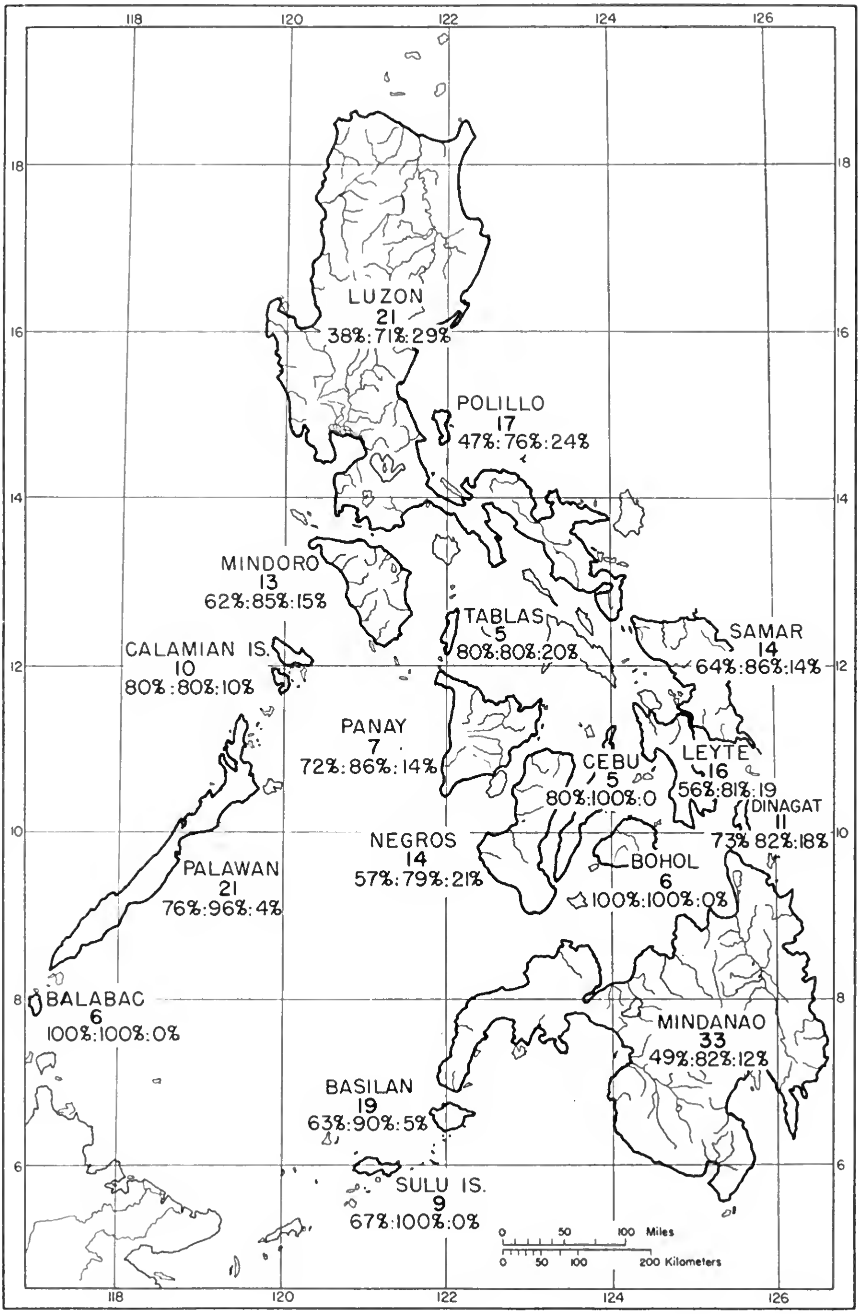
FIG. 86. Composition of amphibian faunas of individual islands with respect to origins. The number in bold-faced type below each island name represents the total number of species present. In the second tier of numbers, the first equals the percentage of Bornean species (species *now* found in Borneo) in the fauna. The second is equal to the preceding percentage plus that of the Philippine endemics clearly of Bornean derivation. The third number equals the percentage of species with definite Papuan relations.


118
120
122
124
126
18
16
14
12
10
8
6
LUZON
21
38%:71%:29%
POLILLO
17
47%:76%:24%
MINDORO
13
62%:85%:15%
TABLAS
5
80%:80%:20%
SAMAR
14
64%:86%:14%
CALAMIAN IS.
10
80%:80%:10%
PANAY
7
72%:86%:14%
CEBU
5
80%:100%:0
LEYTE
16
56%:81%:19
DINAGAT
11
73% 82%:18%
NEGROS
14
57%:79%:21%
BOHOL
6
100%:100%:0%
PALAWAN
21
76%:96%:4%
BALABAC
6
100%:100%:0%
MINDANAO
33
49%:82%:12%
BASILAN
19
63%:90%:5%
SULU IS.
9
67%:100%:0%
0
50
100
Miles
0
50
100
200 Kilometers

genera of reptiles and amphibians and in the non-endemic species of amphibians; that is, with increasing distance from Borneo, the number of Bornean species decreases. Among the lizards 14 Bornean forms are known from Palawan, 10 from Mindoro, 9 from Luzon, 11 from Negros, and 15 from Mindanao. The numbers for Bornean species of snakes are 22 on Palawan, 12 on Luzon, 13 on Negros, and 15 on Mindanao. Available information is not sufficient to warrant inclusion of other islands.

Because of the great differences in the taxonomic approaches of Taylor and myself (see discussion, p. 201), a more detailed comparison of the reptiles and amphibians is not feasible. It may be noted here that Taylor recognized 89 species of Philippine amphibians whereas only 56 are considered as full species in this review. Despite the incompleteness of the comparison, the similarity between the faunal relations of the lizards and snakes on the one hand and the amphibians on the other is clear.

Faunal Divisions of the Philippine Islands

Pelseneer (as quoted by Mayr, 1944a), in discussing the boundary between the Oriental and Papuan Regions, stressed the fact that a zoogeographic border is a zone in which there is some mixing of faunas. But he also stated that there is a line in such a zone on one side of which one fauna predominates, whereas on the other the second has the lead. Mayr supports this conception and places the entire Philippine archipelago in the Oriental Region, since much less than 50 per cent of the fauna have Papuan affinities, thus differing sharply with Dickerson and his co-authors (1928; see above, p. 448). Inasmuch as over 70 per cent of the species on every Philippine island show Oriental relations, the amphibians certainly bear out Mayr's position.

So far as the amphibians and reptiles are concerned, the Palawan–Calamians chain is distinguished from the rest of the Philippine Islands primarily by the absence of Papuan genera. It is worth repeating that the amphibian genus *Cornufer* is found throughout the Philippine archipelago exclusive of the Palawan–Calamians chain. This is also true of the saurian genera *Otosaurus* and *Hydrosaurus*. The Papaun genera *Oreophryne* and *Stegonotus* are of more limited distribution in the eastern Philippines. Thus, the Palawan–Calamians chain has an almost purely Bornean fauna. The only non-Bornean elements are, at least among the amphibians, relicts.

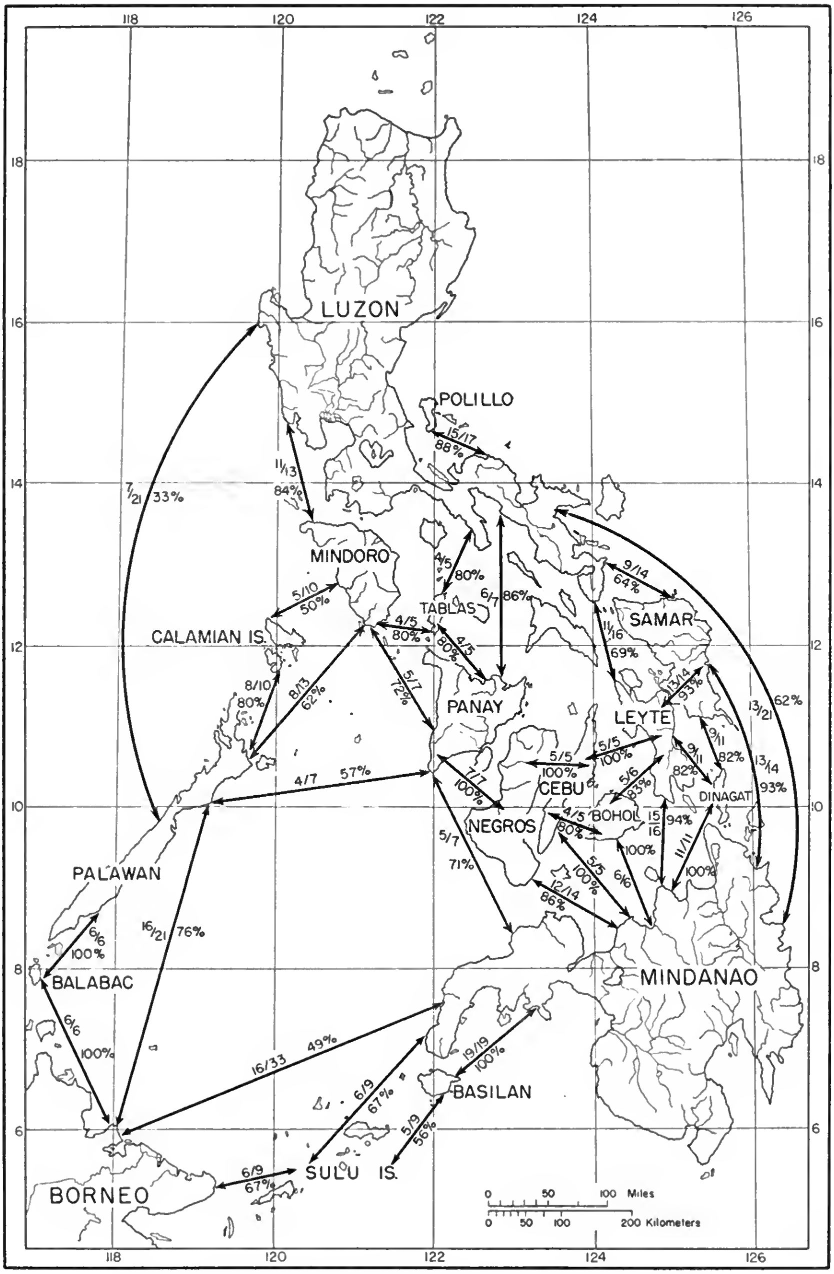


FIG. 87. Faunal similarity of the various islands (see p. 465).

Delacour and Mayr (1946) approach the position of Dickerson and his co-authors (1928) by placing the Palawan–Calamians chain in the Malaysian subregion of the Oriental Region and the remainder of the archipelago in a separate Philippine subregion. This report confirms such a division. But, because the faunal distinction between Palawan and the eastern Philippines is sometimes over-emphasized, it seems advisable to indicate some of the difficulties of this division. Only information concerning amphibians, lizards, and snakes is drawn upon.

If the absence of distinctly Papuan genera is adopted as the criterion, the Sulu Islands should be grouped with Palawan and Borneo as opposed to Mindanao. But as many (6) of the Sulu species of amphibians occur in Mindanao as in Borneo or Palawan. Fourteen genera of Sulu lizards occur in Mindanao and in Borneo; only 12 occur in Palawan. Nine of the genera of Sulu snakes are known from Mindanao and 11 from Borneo and Palawan. Also pertinent is the fact that as many Bornean genera and species of amphibians are present in Mindanao as in Palawan. There is a higher proportion of Malaysian elements among the Amphibia of Basilan and Mindanao than among those of the Calamians.

The subregions within the Philippines proposed by Taylor (1928) on the basis of amphibians and reptiles are difficult to maintain. Taylor divides Mindanao into three faunal zones: the Zamboanga Peninsula, which he groups with Basilan and the Sulu Islands; south-central Mindanao; and eastern Mindanao, which he brackets with Leyte, Samar, Dinagat, and Biliran. Based on the list of species of amphibians, the measure of faunal similarity (as computed above, p. 465) between the Zamboanga Peninsula and south-central Mindanao is 92 per cent (22/24), between the latter and eastern Mindanao 100 per cent (24/24), and between the Zamboanga Peninsula and eastern Mindanao 88 per cent (21/24). All but one of the species found on Leyte occur in eastern and central Mindanao; all but three occur in the Zamboanga subdivision. Obviously these divisions of Mindanao rest upon the feeblest of faunal differences.

The remaining islands, which fall into Taylor's fourth subdivision, also present problems of delimitation. For example, Negros shows the same degree of faunal similarity (86 per cent) to Luzon, with which it was associated by Taylor, as to Mindanao, from which Taylor separated it. However, Negros has less faunal similarity to Leyte (79 per cent). As figure 87 indicates, Luzon shows less affinity to Leyte and Samar than to Negros and still less to Mindanao. Is this subdivision to be maintained in the face of the intermediacy of Negros?

Delacour and Mayr (1946) recognized two Philippine faunal provinces: an eastern one, including Luzon, Samar, Leyte, Mindanao, and Basilan; and a central province, including the western Visayas. In addition they recognize Mindoro and the Sulu Islands as transitional districts. It is clear from the preceding paragraphs and figure 87 that the amphibians do not fit this pattern.

The principal difficulty in defining faunal divisions is concisely stated by Mayr (1944a) as the problem of dividing arbitrarily any continuous set of values somewhere between the extremes. This is precisely the objection to the faunal subdivisions of the Philippines. The search for such divisions is at best a digression from the standpoint of the data presented here, for it fails to emphasize the nature of the alteration of the fauna. That change is described simply as a gradual diminution of the Malaysian element and a corresponding increase in the Papuan element with increasing distance from Borneo, the principal source of the fauna (see below). In my opinion the distribution of the amphibians and, possibly, the lizards and snakes permits only one faunal division: that between the Balabac–Palawan–Calamian chain and the rest of the archipelago. Even this division is in a measure arbitrary.

DISPERSAL OF THE PHILIPPINE AMPHIBIA

Ecological Aspects of Dispersal

All hypotheses of animal dispersal must be tested against the ecological requirements of the individual species involved. Given sufficient time a population will spread through any space until an ecological barrier is met. An extensive analysis of the barriers to dispersal, which are more generally described as filter zones by Simpson, is presented by Hesse, Allee, and Schmidt (1951). I shall review only the ecological distribution of the Philippine Amphibia and the factors limiting their dispersal.

The Philippine Amphibia are distributed from sea level to an altitude of more than 2,100 meters. Many species are associated with aquatic situations—with standing water (in ponds, flooded fields, leaf axils, water-filled holes in trees, etc.) as well as with torrents (mountain streams). Some are subterranean and some arboreal. Almost all are limited to humid niches. Given these varied situations the most common limiting factors are salt water, the gradient of the substrate, humidity, and the distribution of forest. Almost without exception amphibians cannot tolerate salt water. An exception among the Philippine species is the ubiquitous *Rana cancrivora* (see p. 263).

Land surfaces with a steep gradient and, therefore, a rapid run-off of surface water restrict dispersal of species requiring slowly moving or standing water. Except for high altitude lakes, which are few, upland drainages have moderate to rapid currents, even where the topography is flat, so that moderately high elevations also reduce the dispersal of this group of species. But the movement of species adapted to more or less strong current will be restricted in low-lying flat areas. These differences are reflected in the altitudinal distribution of the two ecological groups. Table 49, which presents the altitudinal distribution of specimens collected by the Philippine Expedition on Mindanao and Palawan, illustrates this point. The more limited the current tolerance, the more intense the altitudinal restriction. *Staurois natator* and *Ansonia muelleri,* which are found only in the swiftest streams, are examples of extreme altitudinal restriction.

Mertens' observations (1934) on Sumatran and Javan amphibians support these relationships. He notes that *Ooeidozyga laevis, Rana limnocharis, R. erythraea,* and *Rhacophorus leucomystax,* which pass their larval stages in standing water, are typically inhabitants of lowlands but may be found in high lakes—for example, Lake Toba, Sumatra, 906 meters above sea level. Mertens records species associated with strong currents—for example, *Staurois jerboa* and *Rana kuhli*—from high altitudes only.

In this connection the activities of man have resulted in significant extensions of ranges by providing suitable artificial habitats. The shallow, warm, flooded fields in the hill rice culture of southeastern Asia have been of pronounced importance, although the ditches and wells of all types of human communities cannot be ignored. *Rana limnocharis* has followed man up the mountains in Fukien Province, China (Pope, 1931), and the Sunda Islands (Mertens, 1934). As noted elsewhere (p. 271) this may explain the presence of *limnocharis* at an elevation of 600 meters on Luzon.

Humidity and forest vegetation as limiting factors are closely related but not identical. Because of the respiratory function of the skin, most amphibians require high relative humidity. The tropical rain forest originally found over most of the Philippines (Merrill, 1926) is noted for its high humidity and to this extent is

Table 49. Altitudinal distribution of specimens collected by Philippine Expedition on Mindanao and Palawan[1]

	Total	0-300 M.	300-600 M.	600-900 M.	900 M.+
Species associated[2] with standing or slowly moving water					
Bufo biporcatus	63	63	---	---	---
Kaloula picta	4	4	---	---	---
K. conjuncta	8	8	---	---	---
Kalophrynus pleurostigma	40	22	---	5(12%)	13(33%)
Ooeidozyga laevis	34	23	1(3%)	10(29%)	---
Rana cancrivora	40	40	---	---	---
R. limnocharis	127	127	---	---	---
Rhacophorus leucomystax	113	92	1(1%)	17(15%)	3(3%)
Total	429	379(88%)	2(0.5%)	32(7%)	16(4%)
Species associated[2] with moderate to strong currents					
Rana macrodon	76	44	9(12%)	23(30%)	---
R. microdisca	73	66	1(2%)	6(8%)	---
R. sanguinea	3	2	---	1(33%)	---
R. signata	49	12	18(37%)	19(39%)	---
R. everetti	13	13	---	---	---
Staurois natator	233	2	17(7%)	212(91%)	2(1%)
Ansonia muelleri	132	---	3(2%)	118(90%)	11(8%)
Total	579	139(25%)	48(8%)	379(65%)	13(2%)

[1] The only islands on which field work was conducted at various elevations.

[2] Association as used here indicates a necessary relationship at some time during life cycle.

an ideal amphibian habitat. With the advent of human culture and the partial destruction of the forests, the newly developed open areas (grasslands, open cultivated fields, and centers of human habitation) form obstacles to the continued dispersal of some species requiring high humidity. We may deal here only with the species that are not fully aquatic, for, obviously, by remaining in water courses the aquatic species can satisfy their moisture requirements in any floral association. At present only six species—*Bufo biporcatus, Rana limnocharis, Kaloula baleata, K. conjuncta, K. picta,* and *K. rigida*—are known to occur in the open, non-forested areas away from bodies of water. *Bufo biporcatus,* as is true of almost all species of *Bufo,* has a thick skin protecting it from desiccation. Luts (1948) comments on the possibility that neotropical species of *Bufo* are not dependent on cutaneous respiration. The fossorial habit of species of *Kaloula* may explain their ability to invade open areas. Presumably of additional significance are their thick, glandular skins. *Rana limnocharis* is not as independent of bodies of water as the other five species of the genus, but it is known to move into grassy areas away from water in the Lesser Sundas (Mertens, 1930). The morphology permitting this behavior is uncertain, but the many longitudinal glands on the back may be important. Without exception these six species have been found in forests, either original or secondary. Because of the relative youth of the large open areas, their historical significance in the dispersal of the fauna is limited to the few species tolerant of relatively dry regions.

Seventeen non-aquatic, terrestrial species of Philippine Salientia have not been collected outside the forest. Of these, *Pelophryne albotaeniata, P. brevipes, Cornufer hazelae, C. subterrestris,* and *Oreophryne annulata* are known only from the montane mossy forest in which the relative humidity approximates 100 per cent most of the time.[1] If moisture relations are critical in the distribution and dispersal of these species, their movements through the lowlands would be restricted by the reduction in relative humidity (see below). But for the remaining twelve terrestrial species of the forest, it is improbable that differences in humidity have been limiting factors in their dispersal in the past. This assumes the existence of a humid, ubiquitous forest. Merrill (1926) expresses the opinion, based on fossil plant remains, that the present forest existed practically unbroken at least as early as the Pliocene.

Recording hygrometers in dipterocarp forest between 300 and 740 meters on Mount Maquiling, Luzon, yield mean annual relative humidities of 88 to 90 per cent. In essentially identical forest at elevations between sea level and 100 meters in North Borneo, the average relative humidity was 81 per cent.[2]

As the forested areas diminish, moisture requirements may become the limiting factor in the dispersal of species such as *Megophrys hasselti, Cornufer meyeri, Chaperina fusca,* and *Kalophrynus pleurostigma,* which have not yet spread throughout the archipelago.

For the preceding species the vegetation itself is of significance only in that it affects other circumstances of the environment. But in the case of the arboreal genera *Philautus* and *Rhacophorus* the nature of the vegetation has an obvious and direct effect. As noted above, the great likelihood of a widespread forest cover in the past makes it improbable that the dispersal of these species, prior to the advent of man, was limited by the distribution of the forest. Since the impact of man on the vegetation, the absence of forest over large areas can seriously limit expansion of ranges. Nevertheless, one species, *Rhacophorus leucomystax,* has become so

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[1] Except where stated otherwise, humidity data of forest taken from Brown (1919).

[2] Average based on twenty-five readings made in daylight hours during the relatively dry month of June, 1950, by Mr. D. Dwight Davis and myself. Observed range=71–86 per cent.

well adjusted to the activities of man that the distribution of forest is unimportant. This species is even found in houses.

Finally, the distribution of the fauna itself may seriously limit dispersal of some species. Montane forms may be unable to meet the competition of more advanced lowland species and thus be prevented from spreading from one suitable habitat to another, not because of the physical conditions of intervening lowlands, but because of the presence of certain competitors. The presence of particular predators is probably also involved.

Man is of primary importance in this connection and not alone for montane species. Taylor (1923) remarks upon the human predation on *Rana macrodon*. Man has also affected the biotic environment through the introduction of domesticated animals. These may be predators (for example, dogs and cats) or competitors for food and/or breeding sites (for example, *Bufo marinus*).

Modes of Dispersal

The modes of dispersal fall into two types: (1) movement through a continuous, ecologically satisfactory space, and (2) saltatory movement from one such environment to another through or across barriers of varying effectiveness, which are referred to as filter zones. The first type of dispersal is easy to understand. Barring chance, only time is needed to accomplish dispersal over extensive regions. However, dispersal through or across filter zones presents serious problems. Because of the hazards involved, the probability of an individual's surviving the passage across a filter zone is small. Such movement is referred to as accidental dispersal or waifing, because of its chance nature. The character of the filter zone conditions the degree of difficulty of transition.

Accidental dispersal has been discussed at some length by Hesse, Allee, and Schmidt (1951), Darlington (1938), and Mayr (1944b). In view of the facts that the Philippine Amphibia originated primarily to the southwest and secondarily to the south and southeast and that there is no evidence for movement of species from the Philippines to one of these areas, an agent of dispersal to have been effective must have provided for greater (if not exclusive) movement from the southwest and southeast to the north than the reverse.

Another critical consideration is the distance between successive habitats. The importance of this factor has been brought out by Darlington (1938), who shows that if the probability of successful crossing of a gap m units in width is x, then the probability of success in crossing a gap of n units is approximately $(x)^{n/m}$. In terms of the Philippines, if the chance for successful crossing of the channel between Mindanao and Basilan (18 kilometers) is 1/1000, the chance of successful crossing of the strait between Mindanao and Negros (45 kilometers) is $(1/1000)^{45/18}$ or roughly 1/30,000,000. This relationship increases the likelihood of successful "island hopping" (dispersal along chains of islands) during the periods of land emergence (Upper Miocene and Pleistocene), when the widths of ocean straits were reduced.

Man may deliberately transport animals for their economic value. It is doubtful that any of the Philippine amphibians have been carried about as food, but it is certain that at least one species, *Bufo marinus,* has been introduced because of its usefulness in insect control. However, if man has played a role in the dispersal of the Philippine Amphibia, he has probably done so unintentionally in the majority of cases. The most likely manner in which man has transported amphibians is in connection with commerce. Amphibians concealed in a stalk of bananas or among baled leaves and branches of other plants or those happening to take refuge in small boats may be carried distances far exceeding those within the power of individual locomotion. Many of the channels between islands are sufficiently narrow to be crossed by boats in a short period so that waifs might not be exposed to mildly xeric conditions beyond their endurance.

Man as an agent of dispersal has been selective with regard to direction of movement. Prior to the last five hundred years, all of the human invasions of the Philippines have come from Sundaland. This does not imply that there have been no individual movements from the Philippines to, say, Borneo; but, because the great preponderance of human movement has been directed towards the Philippines, man is much more likely to have carried animals into, rather than out of, the Philippines.

Wading birds may have effected the dispersal of some amphibians by transporting eggs. Conceivably strands of eggs may become tangled in the birds' toes, or a few eggs may be involved in mud which in turn adheres to the birds' feet. Subsequent flight by the birds would move the eggs beyond the capacity of amphibian locomotion. It might be thought that the accompanying exposure to desiccation in the air would preclude this mode of passive dispersal. But experiments by Lebedinsky and Menzel (1919) demonstrate that the eggs of *Bufo bufo* are able to withstand exposure to air for nineteen hours with 78 per cent survival. The great blue heron (*Ardea*) of North America is known to achieve speeds of 40 kilometers per hour (Cooke, 1933). Although similar data for the various species of herons and egrets of the western Pacific are not available, it is reasonable to assume that the speeds of several Malaysian species will at least equal 20 kilometers per hour. At that rate one of these wading birds, which wander a great deal, could cross the strait between Samar and Luzon (21 kilometers) in an hour or the one between Mindanao and Dinagat in twenty minutes. These intervals probably lie within the tolerance to air of many aquatic amphibian eggs. Transportation by birds over longer distances rests not only upon the speed of the birds but also upon the limit of sustained flight. With regard to the selectivity of movement, this mode of waif dispersal has an important deficiency. These wading birds are as likely to move southward as northward. On the other hand, through the possibility of involving several individuals at a time, dispersal by birds has a relatively good chance of establishing a species in a new area.

Interest in storm winds as agents of animal dispersal has been stimulated by Darlington (1938). The rather common waterspouts accompanying cyclonic storms over water attest to the lifting power of these winds and demonstrate the possibilities for dispersal of amphibian eggs, larvae, and adults. Gudger (1921) lists many authentic cases of rains of fishes that were due to cyclonic winds. The tolerance of aquatic amphibian eggs to air has been referred to above. But in addition to sucking amphibians up out of water, typhoons may also distribute non-aquatic species by transporting pieces of vegetation in which amphibians may be resting. Tree limbs with small hollows and pitcher plants (*Nepenthes*) common in Malaysia are examples of such resting niches.

Typhoons (referred to as hurricanes in the western hemisphere) are common in the Philippines. During one 22-year period (1880–1901), the mean annual frequency of these violent cyclonic storms was 21 (Algué, 1904). The average rate of progression of typhoons in the Philippines is about 19 kilometers per hour, but occasional "fast" typhoons may travel as much as 32 (Deppermann, 1939). The counterclockwise rotational velocity of winds within the typhoons, however, is much greater; Selga (1931) reports that the winds frequently exceed 100 kilometers per hour and on rare occasions attain speeds of more than 150. Unfortunately, no estimates of the diameters of the Philippine typhoons are given. Darlington refers to diameters in excess of 300 kilometers in West Indian storms. Assuming now a diameter of 100 kilometers and a rotational velocity of 100 kilometers per hour, a typhoon moving west between Mindanao and Leyte could carry objects from Mindanao to Dinagat (6.5 kilometers) in approximately four minutes, from Dinagat to Leyte (30 kilometers) in twenty minutes, and from Mindanao to Leyte (60 kilometers) in forty minutes. Mountain ranges do not constitute obstacles, as the typhoons are known to pass over mountains without appreciable loss of strength (Deppermann, 1939).

The majority of the Philippine typhoons occur north of the center of Leyte, but the entire archipelago has been affected by one or more typhoons since 1880, the beginning of regular, continuous meteorological observations in the Philippines (Algué, 1904; Claxton, 1932). These storms generally move west, northwest, or north, although occasional typhoons have aberrant courses (Deppermann, 1939). Philippine typhoons originate most often over the Pacific Ocean, although a few build up in the Sulu Sea. During the interval 1880–1930, no typhoons were recorded over Borneo or Celebes (Claxton, 1932), which lie largely in the belt of the equatorial doldrums.

Because of the direction and distribution of contemporary typhoons, they appear to be of greatest importance in dispersal northwestward along the Samar Arc and the western Visayas. If, as Darlington suggests, during the relatively uniform pre-Pleistocene climate the cyclonic paths were less regular than now, waifs might then have been brought into the Philippines from the areas to the south.

Of the agents of accidental dispersal overseas, floating rafts of vegetation carried to the sea by rivers are probably the least satisfactory for amphibians. Salt spray breaking over such a raft would have a serious detrimental effect on the waifs, unless the raft included trees that protruded far enough out of the water to offer protection. Non-arboreal species would be at a distinct disadvantage in this situation. Another drawback of the raft is the slow speed at which it would move once it reached the sea. Unless the river flood headed the raft across a narrow channel towards a neighboring island, the raft would move with the speed of the ocean current plus the amount added by parallel prevailing winds once it left the field of force of the flood. In the South China Sea and adjacent areas, the ocean currents have a velocity of 1.9 kilometers per hour (one nautical mile per hour). The longer the duration of such a voyage the greater the hazards from the instability of the raft, salt spray, and prolonged exposure to desiccation. However, certain factors, by adding to the likelihood of raft formation, increase the probability of raft dispersal into the Philippines. The entire Malaysian region is noted for its extremely heavy falls of rain. Rivers frequently rise more than three meters in a matter of a few hours after these downpours, and the resultant floods tear away large masses of vegetation that float out to sea. In addition to these products of floods, masses of floating plants, such as the recently introduced water hyacinth (*Eichornia*), drift down streams, touch the banks at intervals, and finally reach the sea.

Ocean currents at present run northeastward along the west and east coasts of Borneo, northward in the passage between Celebes and the Moluccas and northwestward along the north coast of New Guinea. Currents in Philippine waters have a northward trend. The mid-year prevailing winds follow the direction of the ocean currents; the prevailing winds of January blow southeastward. The ocean currents have a velocity of 1.9 kilometers per hour, so that a raft starting from the mouth of either the Segama or Kinabatangan rivers in northeastern Borneo could cover the distance—approximately 225 kilometers—to Jolo in the Sulu Islands in five days. During the middle of the year, favorable winds could reduce the time.

Not all animals are able to utilize the various means of accidental dispersal to the same extent. Flying forms are more susceptible to dispersal by wind than are terrestrial forms and these much more so than burrowers. Forms with hard, impervious integuments can withstand the rigors of a raft voyage better than thin-skinned ones. Analogous variation in vagility exists within groups. Among the biological characters upon which these intrinsic differences depend is population size. Obviously, if the chance of an individual's crossing a gap between suitable habitats is one in a thousand, a population of ten thousand is more likely to send out a successful emigrant than one of one thousand, all other conditions being equal, and a population of millions of individuals may capitalize on even a very remote chance.

Habitat preferences also affect the prospects for waifing. A species living at low altitudes has a greater chance of jumping a sea channel than one confined to mossy forests. This applies to dispersal by man for the following reasons: The lowlands support more people; people living on the coasts are often seafarers, whereas those inhabiting mountains usually are not; human commerce would probably deposit a waif in the lowlands of a neighboring island, a habitat unfavorable for a montane species. It is not only in terms of human transportation, however, that the lowland form has the advantage. Consider also transportation by storm winds. In the Philippines the total land area 600 meters or more above sea level is much less than the area below that altitude. Consequently, the chances are that a wind-borne object, if deposited on land at all, will fall on land with an elevation of less than 600 meters, again operating against the high altitude species. Transportation on rafts across ocean straits is unlikely for montane forms for obvious reasons.

If we compare the ranges of the montane forms with those of other species, we find that none of the most widely distributed species (the fourth category of the arrangement on p. 498) is more abundant above 600 meters than below. On the other hand, nine of the seventeen endemics occurring on only one island and its dependent islets (first category, p. 498) are confined to such high elevations. Two non-endemics, *Megophrys monticola* and *Philautus longicrus*, are apparently limited to high altitudes; one other, *Staurois natator*, is much more abundant at high than at low elevations. None of these is found throughout the Philippine Islands. One of the causes for the limitation of horizontal range in these high altitude forms is undoubtedly low vagility (including the low capacity for waif dispersal), although the operation of other factors, such as the length of time each has been in the Philippines and the reduced ability of endemics to meet competing forms successfully, is granted.

In certain situations arboreal species are distinctly more vagile than burrowing or terrestrial forms. Many arboreal frogs use holes in tree branches as resting niches. On a raft of vegetation these species would stand a better chance of avoiding salt spray than terrestrial forms because they are adapted to climbing, and because their normal behavior patterns would give them an advantage in seeking out and utilizing elevated holes and crevices.

Breeding habits may also have differential effects on accidental dispersal. The number of eggs per clutch and the site of deposition are particularly important. Clutch size is related to this mode of dispersal in the same manner as population size. Although little is known of clutch size in the Philippine Amphibia, we may note the association between extent of range and number of eggs per ovary in *Bufo biporcatus*, *Ansonia muelleri*, and *Pelophryne albotaeniata*. The first species, with a range covering a large part of the East Indies (fig. 82), has a clutch size of over two thousand (p. 241); *A. muelleri*, known only from Mindanao, has a clutch size under two hundred (p. 241); *P. albotaeniata*, limited to Palawan, deposits less than twenty-five eggs at a time (p. 236). *Rana parva* and *R. microdisca* (p. 302) present a parallel case. As in the case of altitudinal range other factors are probably involved in these examples; yet, by improving the chances for successful colonization, increase in clutch size increases vagility.

The site of egg deposition will partially determine which mode of dispersal is most probable. It is not likely that frog spawn normally deposited in small rain pools in the forest will be transported by wading birds. However, eggs laid in flooded fields are at least exposed to this means of dispersal. The latter site also increases the likelihood of dispersal by means of typhoons, for the eggs deposited in the forest pools will be protected somewhat from the force of the winds by the overhanging trees. Because the situation most often utilized by species breeding in moderate or swift currents is the forest areas, eggs of these species naturally have the same diminished susceptibility to wind distribution as those laid in forest rain pools. What is true of the eggs also holds for the larvae. Of the Philippine species with aquatic larvae, fourteen breed only in forested situations,[1] whereas eleven frequently breed in open areas (flooded fields, ditches along fields and roads, wells, etc.). Only three of the fourteen forest breeders are among the most widely distributed species (fourth category, p. 498); by contrast seven of the open country breeders are so distributed.

Certain species of frogs have aerial nesting sites. The eggs are usually attached to vegetation. This situation predisposes them for wind dispersal, although the opportunities do not seem to be uniform throughout the group.

The foamy egg masses of *Rhacophorus* are attached to herbaceous plants or the branches of low trees growing beside stagnant pools or slow-moving streams. The surface of the gelatinous mass dries into a crust protecting the developing eggs from desiccation. In three to five days the mass is either broken up by rain or by the activity of the hatched larvae. The larvae then fall into the water, in which they complete their development. Two of the Philippine species, *R. leucomystax* and *R. pardalis*, are known to breed in clearings, at the edge of forests, or in other open situations. These habits expose the spawn to distribution by typhoons. The endemic species of *Rhacophorus* are not found out of the forest and apparently breed only within its confines. The ranges of the endemic species

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[1] An assumption based on the known distribution of adults.

are restricted, whereas *leucomystax* occurs throughout the archipelago and *pardalis* from Luzon to Mindanao.

Species of *Oreophryne* often deposit eggs in moss growing on trees. Parker (1934) records a clutch of *Oreophryne* eggs laid in a hollow tuber of an epiphyte (*Hydnophyton*). Conceivably storm winds could tear either egg site from its support and carry the eggs long distances. A light, hollow, aerial tuber is particularly subject to such transportation.

Finally, morphology modifies the probabilities for waif dispersal. Darlington (1938) emphasizes the relation of size to wind dispersal, pointing out that small animals are affected by air currents to a greater extent than large ones because of the higher ratio of surface to weight among the former. One presumes that small amphibians would also have an advantage over large ones in the event of raft transportation by being better able to retire into crevices and holes, thus avoiding some of the dangers of the journey. The same capacity is of conceivable advantage in accidental dispersal by man, for small size would tend to protect the amphibian from the eyes of young predatory boys.

Yet the most widely distributed non-endemics include the largest Philippine amphibians. The most widely distributed endemics, though smaller than the corresponding group of non-endemics, are nevertheless larger than the rest of the endemic species.[1] Thus despite the postulated advantage of small size, its influence in the Philippine fauna is probably less than that of other factors.

In the ratio of surface to weight, an increase is effected by the development of webs and various dermal structures as well as by decrease in size. *Rhacophorus pardalis,* for example, attains almost the same body length as *R. leucomystax* (females of the latter average 5–10 mm. larger) but has much more surface area, its fingers and toes being much more extensively webbed (see descriptions, pp. 372 and 377). Also, *pardalis* has large folds of skin along the lower arm and lower leg; corresponding structures are absent in *leucomystax.* Although the increase in surface area is of primary importance in the arboreal habits of *pardalis,* it is easy to visualize the significance of these developments to wind dispersal. The fact that *leucomystax*

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[1] I have established arbitrary size values for the purposes of this comparison: snout-vent length under 25 mm. is assigned a value of 1, snout-vent length 25–45 mm. a value of 2, snout-vent 45–65 mm. a value of 3, and over 65 mm. a value of 4. On this basis the wide-ranging endemics have an average value of 2.4, the remainder of the endemics an average of 2.0. The wide-ranging non-endemics have an average size value of 3.7, the rest of the non-endemics an average of 2.5.

is more widely distributed than *pardalis* indicates not the lack of importance of surface area to dispersal, but rather the greater importance of other factors—especially the association with man.

The envelopment of the amphibian egg in several sheaths of gelatinous material protects the egg from desiccation and mechanical shock. Both functions are of clear importance in waif dispersal whether by winds or by wading birds. Some characteristics of the *Rhacophorus* foam nest have already been mentioned (p. 481) in this connection.

Several instances of waif dispersal of Philippine Amphibia are either certain or of high probability. *Bufo marinus* was deliberately introduced into the Philippines by man in 1934 and is being spread through the islands in the same manner. The presence of *Oreophryne annulata* is probably to be traced back to waif dispersal. Like all members of the genus, *annulata* is restricted to high altitudes. As Mayr (1944b) has emphasized, the ecology of discontinuously distributed, montane species practically precludes the possibility of extensive dispersal through a continuously favorable space. If it is to account for the present distribution of *Oreophryne,* this type of dispersal implies the existence of geographically continuous, though not necessarily synchronous, mountain ridges exceeding 750 meters in elevation,[1] running the length of New Guinea, and connecting New Guinea, the Moluccas, Celebes, the Lesser Sundas, and Mindanao. This implication receives no support from geologic history or the present topography in these regions. Therefore, some mode of waif dispersal must have been utilized. Distribution by man, by rafts of vegetation or by birds can be eliminated. The first two would carry *Oreophryne* through and deposit it in lowlands, which would militate against successful introduction. The eggs of *Oreophryne* are deposited (p. 447) in places not usually visited by the kinds of birds most likely to be the agents of dispersal. Only wind dispersal remains and we can list several items favorable to this mode of dispersal. First of all, the species of *Oreophryne* are very small (*annulata,* for example, rarely reaches 25 mm. snout to vent). The site of egg deposition exposes the ova to wind transportation. It is important to note that the cloud forest is composed of stunted vegetation and as a consequence does not check the force of wind as would the dense stand of large trees typical of lowland forests. Thus available evidence suggests that *Oreophryne annulata* (or

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[1] Approximate lower altitude of cloud forest, which *Oreophryne* typically inhabits.

rather, its ancestral stock) reached the Philippines by means of wind dispersal over a Celebesian or Moluccan–Talaud route (see p. 492).

Somewhat less convincing is the explanation of how *Rana erythraea* entered the Philippines. Present knowledge of its range indicates that a large gap exists between its Philippine populations, reliably recorded from Negros, Panay, Sibuyan, and Tablas, and the nearest extra-Philippine population on Borneo. A report of a single specimen of *erythraea* from Mindanao was made by Fischer in 1885. In view of the facts that Mindanao is one of the best collected islands and Panay one of the poorest, and that *erythraea* is exceedingly abundant wherever it is known to occur, the Mindanao record must be doubted, pending confirmation. If, as seems likely now, the range is disjunct, the present distribution is to be explained on the basis of introduction by man. There are good reasons for ruling out the explanation of local extinction. Nor is there the faintest evidence of a land bridge from Borneo direct to Panay or Negros. Waif dispersal is, consequently, the most plausible explanation. Because of the distance between Borneo and Negros or Panay, transportation by man is the most probable mode of dispersal. It should be noted that *erythraea* is commonly found about cultivated fields. Conceivably it could have been carried with agricultural products by the seafaring people of the Sulu Sea.

Dispersal by man as an explanation of the distribution of *Rana cancrivora, R. limnocharis, Ooeidozyga laevis,* and *Rhacophorus leucomystax* is distinctly possible. These species are almost never found in the primary forest; on the contrary, they occur in large numbers in areas disturbed and occupied by man; they are almost universally distributed not only in the Philippines, but also in all of western Malaysia; they exhibit little differentiation into subspecies. The last two facts taken together suggest rapid and recent dispersal. The second demonstrates their tolerance of conditions created by man and the frequency with which they come in contact with man. The first fact reduces the possibility of waif dispersal on rafts of vegetation.

While not wishing to minimize the importance of overland dispersal through a continuous and suitable environment, I think it important to keep in mind both the necessity in some cases and the possibility in others of a saltatory mode of dispersal.

Dispersal routes

The tectogenic arcs described in the discussion of geologic structure and history (pp. 449ff.) are the most likely routes of dispersal into the Philippines. On the north the western arc passes from northern Luzon into Formosa and thence into the mainland of China, with which Formosa has had direct communication from time to time. To the south the western arc connects with North Borneo, a part of Sundaland which in turn has been intimately connected with southeastern Asia during most of the Cenozoic. The minor arc through the Zamboanga Peninsula and the Sulu Islands also intersects Borneo.

FIG. 88. Range of *Rana limnocharis*. Full extent of distribution to north and west not shown.

The connections of the eastern arc are not definite, but south of eastern Mindanao it is continuous with the East Celebes-Timor tectogenic Arc. The eastern flank of the latter is formed by the Papuan or Sahul Shelf. The Moluccas and the Talaud Islands form intermediate steps between Papua and the Philippines. An alternative route from the Philippines to Papua may have passed through the Sangihe Islands to Celebes, thence eastward across the Banggai and Soela Islands to the Moluccas and New Guinea.

Dispersal routes within the Philippines are partially defined by these tectogenic arcs. The western curve includes Balabac, Palawan, the Calamians, northwestern Mindoro, and western and northern Luzon. An eastern branch of this route points towards the Cuyo Islands, which lie on the same submarine shelf as Palawan and the Calamians. The Sulu-Zamboanga Arc gives access to central and eastern Mindanao; thence the route to the north passes through Dinagat, Leyte, Samar, and southeastern Luzon. The possibilities for dispersal into the central group of islands are far more complex. Bohol and Cebu might have been colonized from western Leyte. Negros, Panay, and Masbate are on a single shallow submarine shelf that is closest to the eastern arc at Masbate and southern Negros. The latter could have received its fauna from Mindanao or Cebu, and Masbate from northwestern Leyte or southeastern Luzon.

The evidence for the entry of the Philippine fauna by these various dispersal routes is not uniformly good. The Formosa-Luzon relationship can be eliminated at once. Only two species, *Rana limnocharis* (fig. 88) and *Rhacophorus leucomystax* (fig. 85), are common to Formosa and the Philippines. Both are represented on Formosa and Luzon by different subspecies and both are widely distributed in southeastern Asia and Sundaland. Alternative avenues of immigration to the Philippines are, therefore, just as likely for these species: via Borneo, or directly from southeastern Asia (Indo-Chinese peninsula), when the South China Sea retreated. The preponderance of evidence from other species of amphibians is in support of a Bornean route. Consequently, this would be the preferred explanation of the dispersal of *limnocharis* and *leucomystax* into the Philippines, quite aside from the negative evidence of a comparison of the Formosan and Philippine faunas in general.

Direct dispersal from southeastern Asia to the Philippines is a remote possibility. To be explained only on the basis of this route, the range of a Philippine species must include Asia and some portion

FIG. 89. Range of *Ooeidozyga laevis.*

of the western arc of the Philippines; it must exclude Borneo. If Mindanao is included, so must be the entire archipelago. Any other condition[1] would introduce the possibility of a Bornean route. No Philippine species satisfies these requirements. *Barbourula busuangensis* (range Busuanga) comes closest. In this case we are obliged to deal with related species. The distribution of the Discoglossidae —one species in the Philippines, one in southwest China, and six in the north temperate zone—indicates that *Barbourula* is a relict. Darlington (1948) summarized the evidence for the tropical origin of all families of Salientia and rightly terms a distribution such as that of the Discoglossidae peripheral and characteristic of a receding

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[1] All species with definite Papuan affinities are excluded, of course, from consideration at this point.

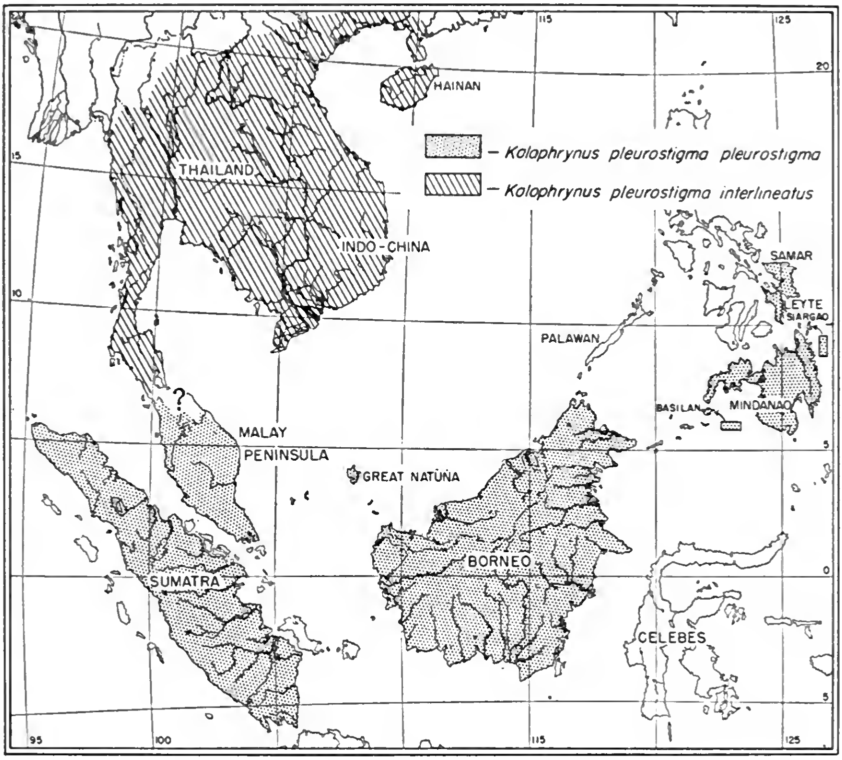

FIG. 90. Range of *Kalophrynus pleurostigma.*

group. Assuming that *Barbourula* is now a relict, one concludes that it moved into the Philippines when the family was common in the Old World tropics. This would not exclude a Bornean dispersal route.

The ranges of *Rana cancrivora* and *Ooeidozyga laevis* (fig. 89), including all of southeastern Asia, might be interpreted in the light of direct mainland–Philippines dispersal; but they can also be interpreted as supporting the Bornean route. The range of *Kalophrynus pleurostigma* (fig. 90), although it embraces the Indo-Chinese peninsula, can not be explained on the basis of direct dispersal from the mainland, for it is inconceivable that such dispersal would skip the western Philippines. Evidence for the Bornean dispersal route is as conclusive as is usually possible to obtain in zoogeography. First of all, the geologic evidence is favorable. We can be certain that, during the Pleistocene, water gaps between Borneo and the Palawan

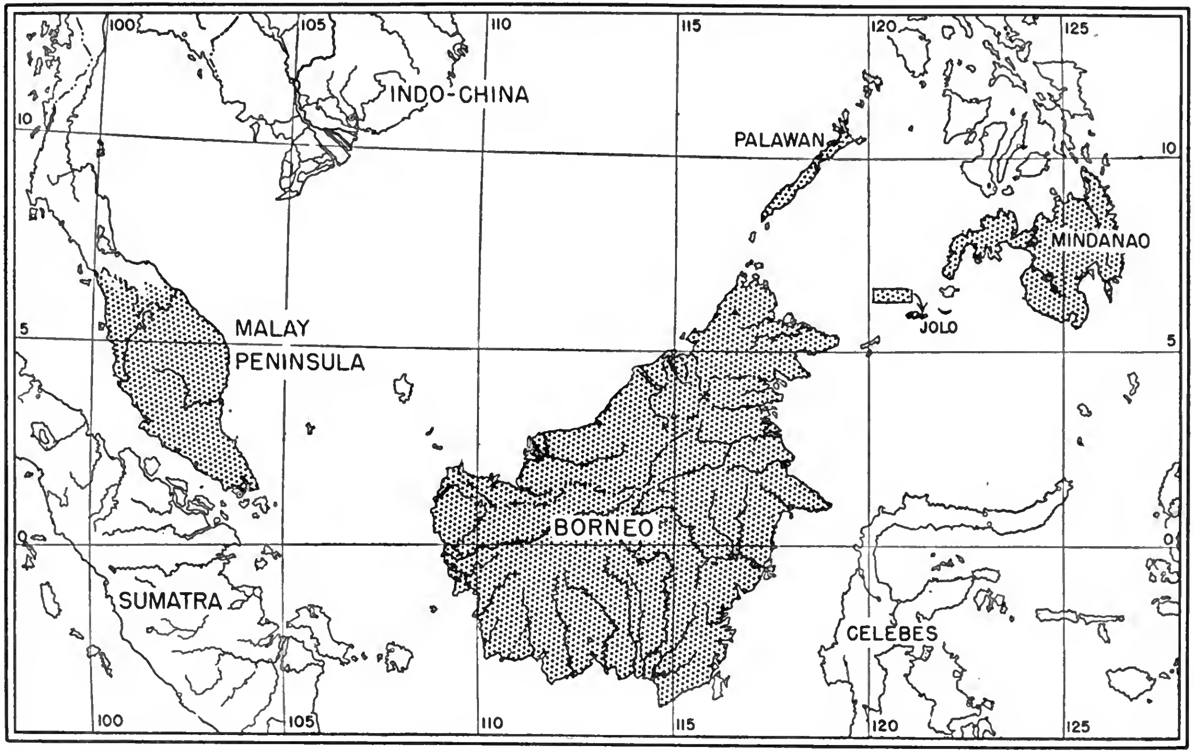

FIG. 91. Range of *Chaperina fusca*.

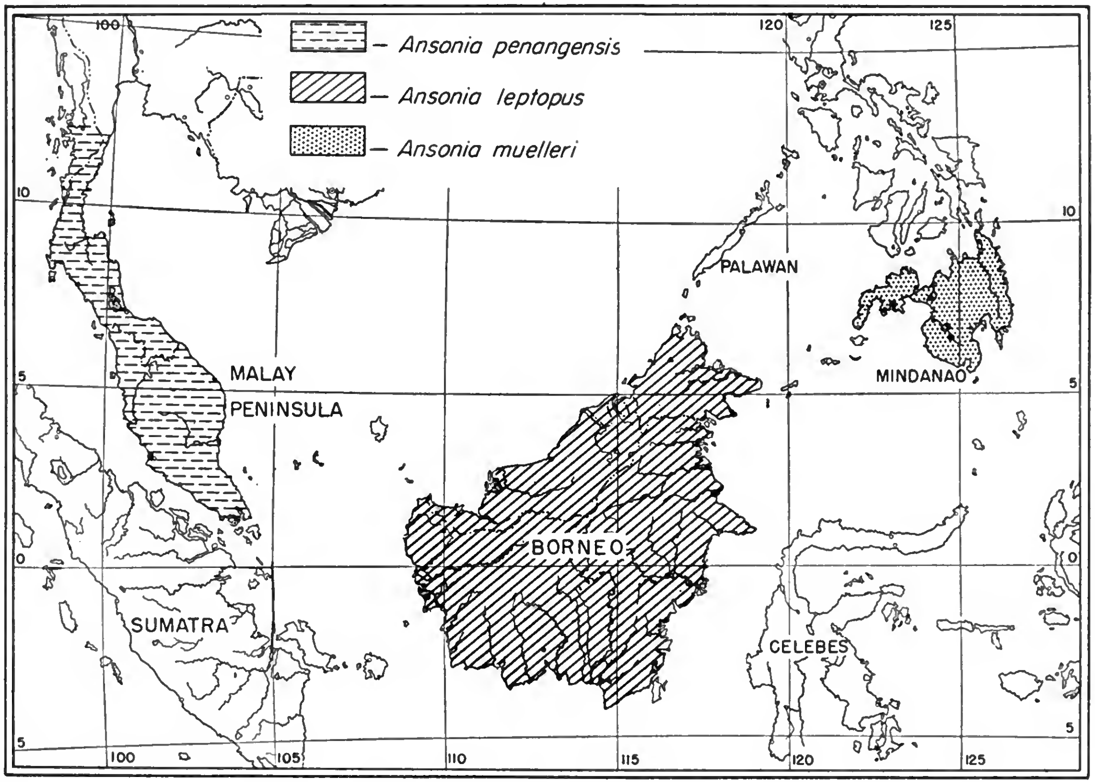

FIG. 92. Range of the genus *Ansonia*.

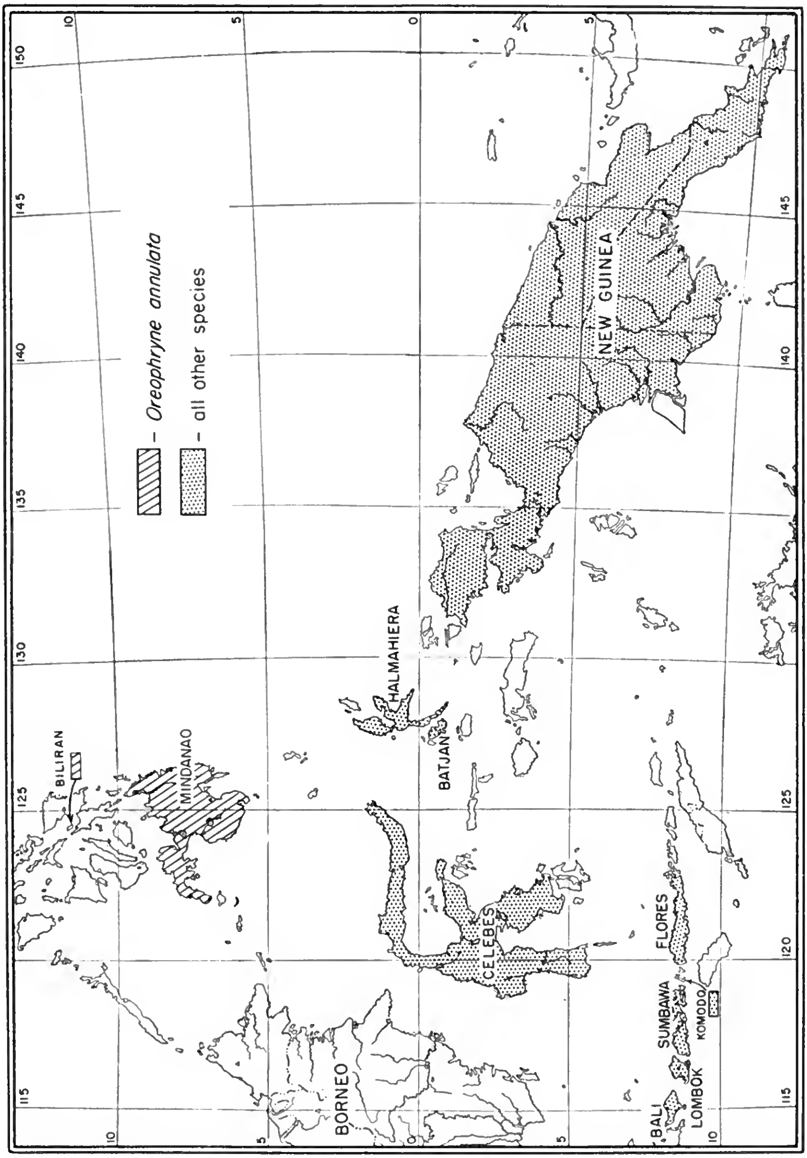

FIG. 93. Range of the genus *Oreophryne*.

Arc on the west and the Sulu Arc on the east were greatly reduced or completely eliminated. Secondly, the known ranges of certain Philippine species can only be understood on the basis of immigration via Borneo. These are species that are presently found on the Malay Peninsula, Borneo, and Mindanao. They are not known from Celebes. They do not occur throughout the Philippines although their ranges may include Palawan, Leyte, and Samar. Examples of such species, in addition to *Kalophrynus pleurostigma* (fig. 90), include *Megophrys monticola* (fig. 84), *M. hasselti,* and *Chaperina fusca* (fig. 91). *Staurois natator* (fig. 83), occurring only in the Philippines and Borneo, also substantiates the Bornean avenue. The distribution of the genus *Ansonia* (fig. 92) is further evidence. Finally, we may note that 43 of the 56 species of Philippine Amphibia —77 per cent—either occur on Borneo or are represented there by a close ally. These ranges indicate that both the Palawan and Sulu–Zamboanga arcs have served as routes into the Philippines.

The evidence for a Celebesian route is weak. Geographic and geologic considerations eliminate all possibilities save a Celebes–Mindanao relationship. Five species, *Rana cancrivora, R. macrodon, R. microdisca, Ooeidozyga laevis,* and *Rhacophorus leucomystax,* are common to Celebes and Mindanao. Inasmuch as all five are also found on Borneo, they do not support a Celebesian route. The distribution of the genus *Oreophryne* (fig. 93) is suggestive of this route. But a Moluccan–Talaud route will serve as well to explain this distribution. The *Rana papua* group (fig. 94) connects Celebes with the Philippines. Here, however, the Philippine representative, *sanguinea,* is widely separated from Celebes and presents a typical relict range. I suggest that the *Rana papua* group was once widely distributed in the western part of the Indo-Australian Archipelago and has contracted its range in the face of competition, leaving an isolated population in the Palawan–Calamians chain. If this suggestion is correct, the Philippine population undoubtedly traversed the Bornean invasion route. Thus we are left without any clear-cut amphibian evidence for a Celebes–Philippines dispersal route.

As noted above, a Moluccan–Talaud avenue between New Guinea and the Philippines may account for the range of *Oreophryne.* The distribution of the genus *Cornufer* (fig. 95) is indicative of the same route. This case, at present, constitutes more definite evidence for the Moluccan–Talaud avenue than the Celebesian. *Cornufer* is not now known from Celebes. It may also be conceived of as another peripheral group driven out of Sundaland by more advanced

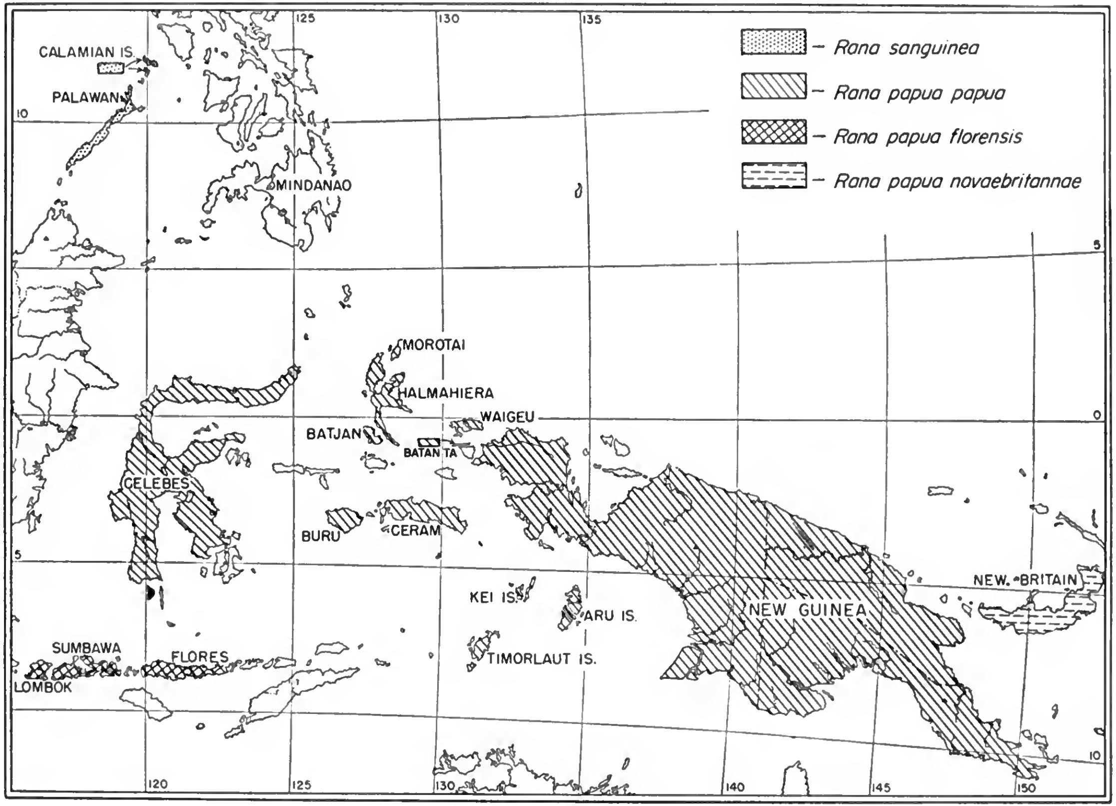

FIG. 94. Range of the *Rana papua* group.

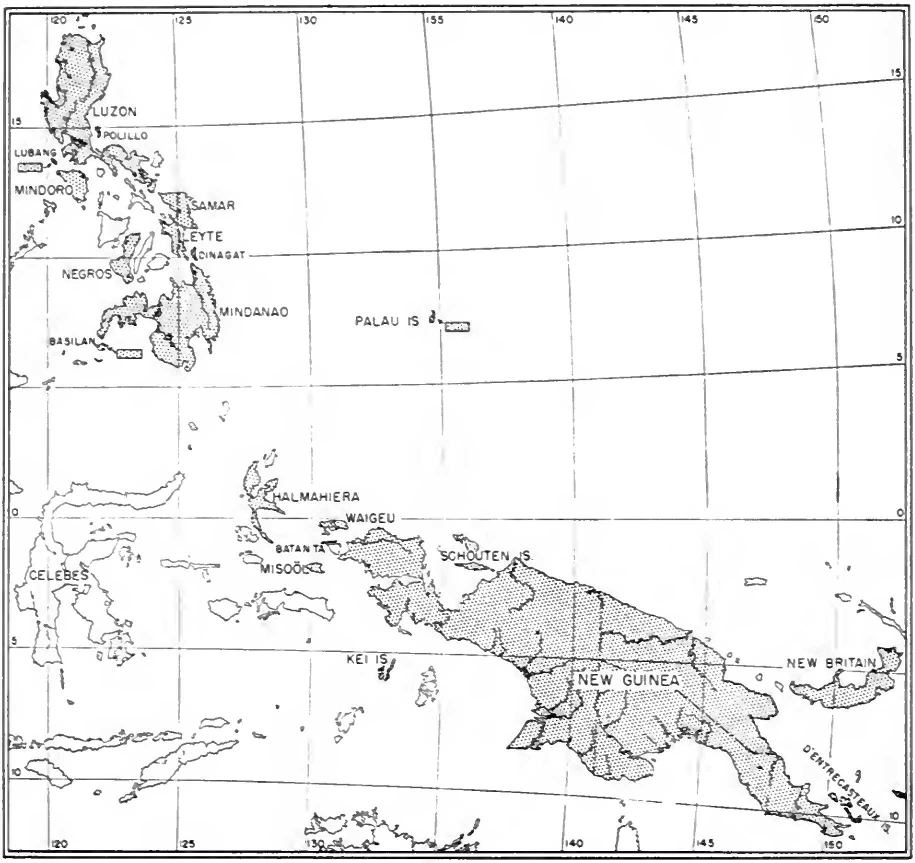

FIG. 95. Distribution of the genus *Cornufer.*

competitors. According to this hypothesis, members of the genus may have entered the Philippines and the Papuan region independently, in which case *Cornufer* offers no evidence of a Philippine–Papuan dispersal route. The development of many species at each end of the generic range speaks for this interpretation. However, the similarity of the Philippine species, *meyeri* and *guentheri,* to Papuan forms is suggestive of a Philippine–Papuan route for these two species.

Some doubt is cast on the relict nature of *Cornufer* by its apparent absence from Celebes. A group of species retreating eastward in the face of competing Malaysian forms is likely to leave representative populations in Celebes. This may be a consequence of the impoverished fauna of the latter (Celebes, 22 species of amphibians; Borneo, 80 species) as well as its geographic position. *Rana papua* is an example of a species that apparently has retreated eastward and now has populations on Celebes and in Papua. *Rana modesta* may be another example.

Cornufer can not be represented as a primitive ranid. The specialization of its breeding behavior would remove its larvae from competition with almost all other amphibians. The habitat of the adults of many *Cornufer* would remove them from competition with the non-aquatic rhacophorids (arboreal) and many microhylids (fossorial). On the whole, the evidence against the relict nature of *Cornufer*—its absence from Celebes, its specializations, the relationships of some Philippine and Papuan species, and the continuity of the generic range—outweigh the evidence for such a proposal.

In the preceding discussion I have implied that all dispersal took place *into* the Philippines, that none of the Bornean species, for example, moved there from the Philippines. The Philippine archipelago constitutes a peripheral area with respect to the Asiatic mainland. Peripheral insular areas are characterized by faunas that are unbalanced relative to and smaller than faunas of equivalent areas of adjacent mainland (Hesse, Allee, and Schmidt, 1951). In the present case, the Philippines, with a land area of 296,000 square kilometers, contains 56 species of amphibians as compared to 80 species known from the Malay Peninsula (Smith, 1930), which is less than 230,000 square kilometers in extent. The following comparison of the amphibian faunas of these two areas demonstrates the incompleteness of the Philippine fauna.

Genus	Malay Peninsula	Philippine Islands
Discoglossidae		
Barbourula	......	present
Pelobatidae		
Megophrys	present	present
Bufonidae		
Pelophryne	present	present
Pedostibes	present	......
Bufo	present	present
Ansonia	present	present
Cacophryne	present	......
Pseudobufo	present	......
Ranidae		
Ooeidozyga	present	present
Rana	present	present
Staurois	present	present
Micrixalus	present	present
Cornufer	......	present

Genus	Malay Peninsula	Philippine Islands
Rhacophoridae		
Rhacophorus	present	present
Philautus	present	present
Microhylidae		
Caluella	present	......
Phrynella	present	......
Metaphrynella	present	......
Kalophrynus	present	present
Chaperina	present	present
Microhyla	present	......
Oreophryne	......	present
Kaloula	present	present
Caeciliidae		
Ichthyophis	present	present

Seven of the 21 genera occurring in the Malay Peninsula are not found in the Philippines; of the 17 genera in the Philippines only three do not occur in the Malay Peninsula and two of those, *Cornufer* and *Oreophryne*, are obviously of Papuan relations. Similarly, of the 23 genera known from Borneo, nine are absent from the Philippines; but only the same three Philippine genera are absent from Borneo. It is probably safe to conclude that the direction of dispersal has been *into* the Philippines along the Bornean invasion routes.

Considering the Papuan elements of the fauna, only one species of *Oreophryne* occurs in the Philippines as opposed to three in Celebes, one in the Moluccas, and five in New Guinea. Because of their habits and small size, all the species of this genus may not yet have been discovered, but on the basis of present knowledge New Guinea appears to be the center of speciation and dispersal for *Oreophryne*. Supporting this hypothesis is the fact that of the remaining 22 species in the subfamily Sphenophryninae, of which *Oreophryne* is part, 20 are known only from New Guinea. The distribution of most of the species and the limited range within the Philippines are clear indications that in this case dispersal has been *into* the Philippines.

Cornufer (including *Platymantis* of authors) presents a much more difficult case. Six species are known from Luzon, and three from Leyte, Samar, Negros, and Mindanao. One is reported from the Moluccas (*papuensis* Meyer), five from New Guinea (*beauforti* van Kampen, *cheesmanae* Parker, *papuensis* Meyer, *punctatus* Peters and Doria, and *unicolor* Tschudi), and five from the Solomons (*guppyi* Boulenger, *myersi* Brown, *neckeri* Brown and Myers, *solomonis* Boulenger, and *weberi* Schmidt).

This situation suggests two speciation centers—one in the northern Philippines and one in Papua—but does not solve the question of direction of dispersal between the two areas. During most of the Mesozoic and Tertiary the Papuan region was a relatively stable continental area isolated from Sundaland (Umbgrove, 1938). Such circumstances are favorable for the development of new groups of animals. A comparable period does not seem to have existed in the Philippines. Among the Amphibia two large groups, the family Microhylidae and the genus *Hyla*, have undergone striking speciation in New Guinea, whereas no comparable phenomenon has occurred in the Philippines. Arguing from analogy, therefore, it seems more likely that the genus *Cornufer* also arose in Papua. If so, then dispersal in this case also has been directed into the Philippines.

Rana sanguinea is irrelevant to the discussion at this point since dispersal of the *Rana papua* group probably did not take place directly between the Philippines and Papua.

ORDER AND TIME OF ENTRY

Although the order in which the elements of a fauna entered a region is a highly speculative matter, an approach resembling that of a stratigrapher may sometimes be illuminating. Peripheral areas like the Philippines are particularly suited to such methods. This approach utilizes differences in the ranges of individual species and their related stocks.

It has been noted elsewhere (Inger, 1947) that endemic species of peripheral regions are probably older colonizers than the non-endemics. The Philippine fauna is unbalanced relative to and smaller than that of its principal region of origin (see p. 495). These differences have the effect of reducing the competition to which the fauna will be subjected. The usual consequence of such a reduction in selective pressures (to which competition is to be equated) is that, on the whole, the longer an insular form is isolated the less able it is to expand its range in the face of invaders from the center of dispersal or even to maintain its range. This argument carried to its penultimate phase results in restriction of distribution to a single island. The final phase, of course, is extinction.

With regard to extent of range, both endemics[1] and non-endemics

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[1] Because of the uncertain taxonomy, endemic species of *Philautus* are not included in this discussion.

can be divided into four categories. In order of increasing magnitude the ranges are as follows:

	Endemic species	*Non-Endemic species*
1.	One island and dependent islets; examples: Mindanao and Basilan, Luzon and Polillo.	Minute penetration; examples: Borneo to Palawan and/or Sulus
2.	Short chain; examples: Palawan-Calamians Mindanao-Sulus Mindanao-Biliran	Minor penetration; examples: Borneo-Palawan-Mindanao, or Calamians may be included.
3.	Moderate range; examples: Luzon-Negros Luzon-Mindanao	Moderate penetration; examples: Borneo-Palawan-Luzon *or* Borneo-Sulus-Mindanao-Leyte (and/or Samar).
4.	All island groups but Palawan-Calamians chain.	Complete penetration: Borneo-Palawan-Luzon-Leyte-Mindanao; may include western Visayas.

Although the divisions are not strictly equivalent, the comparisons are useful. The endemic ranges have the following distribution: 64 per cent (of total of 28 species) in the first category, 11 per cent in the second, 7 per cent in the third, and 18 per cent in the last. The corresponding distribution of the non-endemic ranges is 16, 16, 31, and 37 (of total of nineteen[1] species). The observed differences between endemics and non-endemics would be expected on the basis of the hypothesis just outlined.

In an archipelago a period of land submergence might provide a terminal population of a widespread species with geographic isolation, which is necessary for development of genetic isolation. Consequently, there is the danger of confusing this situation with that resulting from the continued retreat of an old stock into a peripheral position if only the distribution of the species in question is used. In some instances the two types can be distinguished on the basis of the distribution of related species.

Examples of both types occur on Luzon. *Rana woodworthi* is found only on Luzon and Polillo at moderate elevations and in localities where it is exposed to the competition of the wide-ranging *Rana macrodon*. It has been stated above (p. 292) that *woodworthi* is related to *macrodon, modesta,* and *microdisca;* the exact relationship is at present unknown. The range of *woodworthi* is thus connected

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[1] *Rhacophorus appendiculatus*, *Rana erythraea*, and *Bufo marinus* have not been included in this tabulation. The large gap between Dinagat and Polillo in the range of *appendiculatus* prevents its disposition in the above classification. As yet it is not possible to determine whether the observed gap is real or apparent. The ranges of *Rana erythraea* and *Bufo marinus* do not fit into the categories but are discussed elsewhere.

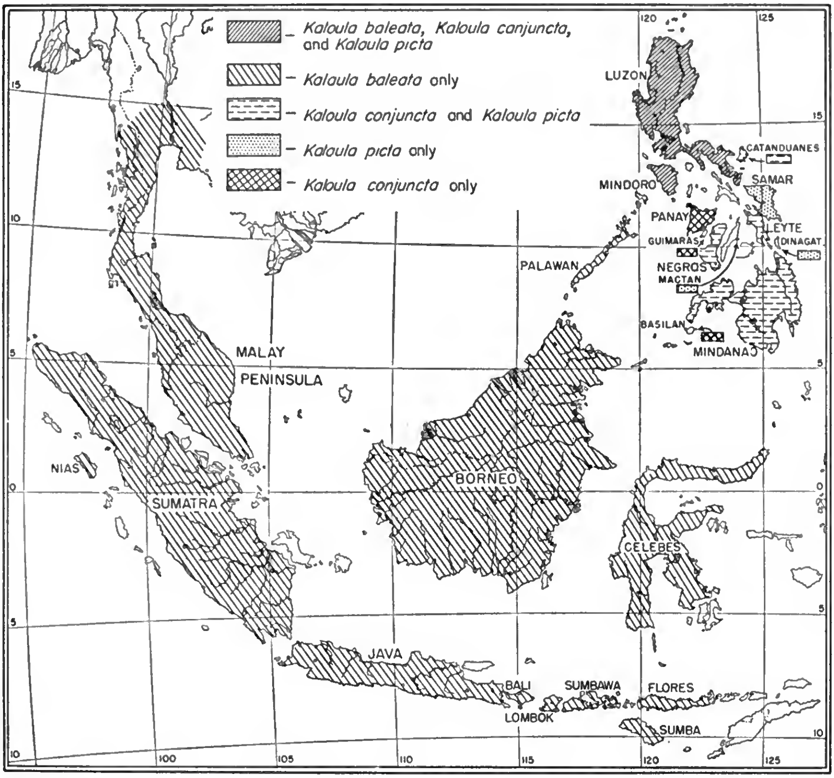

FIG. 96. Ranges of *Kaloula baleata, K. conjuncta,* and *K. picta.*

by those of other related species to the group's center of dispersal in Sundaland. This circumstance, plus the fact that the habitat is not isolated, suggests that *woodworthi* does not represent an old wave of immigration.

A contrasting situation is provided by *Cornufer cornutus.* This species is known only from the mountains of northern Luzon. Its nearest relatives, *C. hazelae, subterrestris,* and *polillensis,* are also known only from moderately high elevations on Negros, Luzon, and Polillo. The group does not seem to be closely related to any other Philippine or Papuan species. The absence of related stocks along the most likely dispersal route to the south (the Samar Arc) and the special isolation of the montane habitat of this group lead to the supposition that the restriction of *cornutus* to Luzon is a result of long residence in the archipelago.

Summarizing the arguments presented by these two examples, an endemic species (or the stock from which it is derived) restricted to one or a few islands and separated from related stocks by great distances—in other words, a relict—must be considered an older resident rather than a non-relict.

On this basis *Barbourula busuangensis*, *Rana sanguinea*, and the *Cornufer cornutus–hazelae* group (or the corresponding ancestral stocks) are probably earlier invaders of the Philippines than such forms as *Micrixalus mariae* (range, Palawan; nearest relative *M. baluensis* in Borneo), *Ansonia muelleri* (range, Mindanao; nearest relative *A. leptopus* in Borneo), or *Rana everetti* (range, Mindanao to Luzon; nearest relative *R. chalconota* in Borneo and Celebes).

An order of entry for the non-relict endemics can be suggested in only a few cases. There is weak evidence that *Kaloula conjuncta* is an older resident than *picta* (fig. 96). The former has broken up into four subspecies whereas such populational distinctions have not developed in *picta*. If rates of evolution of the two species are roughly equivalent, *conjuncta* must be adjudged the older. *K. rigida* is limited to northern Luzon. It has been shown elsewhere (p. 420) that *rigida* is related to *conjuncta* and *picta*. Therefore, either *rigida* is a remnant of a stock older than *conjuncta* or *picta* or it is a species derived in situ from one of them, most likely from *conjuncta*. No information will permit a choice between these alternatives, so that the position of *rigida* in the order of entry of these species is indeterminate.

As noted above, the *cornutus–hazelae* group of *Cornufer* is not closely related to any other known members of the genus. The other Philippine *Cornufer* (*C. meyeri*, *C. corrugatus*, and *C. guentheri*) are obviously related to extant Papuan species. This difference between the two groups of species argues for a more recent connection between the last three species and the proposed Papuan center of origin. The ranges support this suggestion, for the *cornutus–hazelae* group is confined to Luzon and Polillo (with the exception of the *hazelae* population on Negros), whereas *meyeri*, *corrugatus*, and *guentheri* are distributed from Mindanao to Luzon.

For the most part the endemics can not be placed in an order of entry. Part of the difficulty here is lack of detailed knowledge concerning the ancestral stocks. It has been tentatively suggested above that *Rhacophorus surdus* (range, Luzon), *R. lissobrachius* (range, Mindanao), *R. emembranatus* (range, Mindanao) and *R. hosi* (range, Borneo) are inter-related. But the nature of the relationship

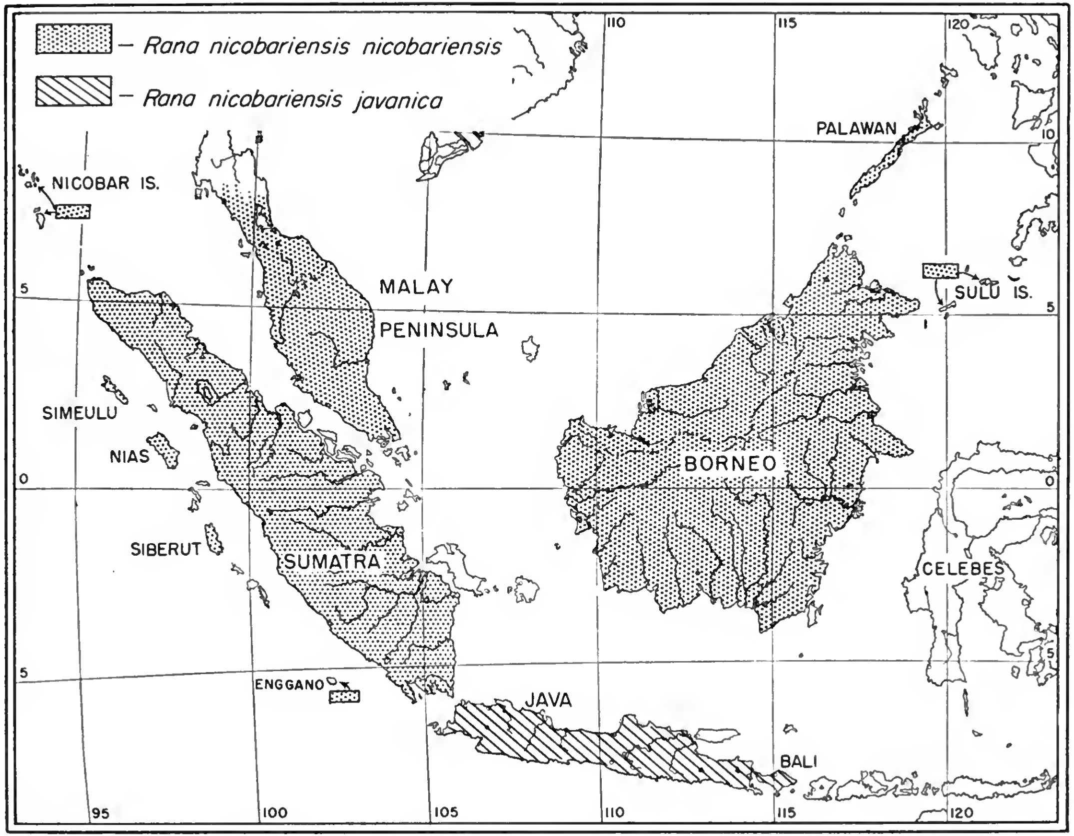

FIG. 97. Range of *Rana nicobariensis*.

is unknown, nor is the relationship of this group to other *Rhacophorus* clear. The Philippine species may be derived from one stock or several stocks. Only in the latter circumstance could there be a difference in time of entry.

The non-endemic species that have barely penetrated the Philippine archipelago are probably the most recent ones to have entered. This is a consequence of the fact that dispersal is not an instantaneous process. All other things being equal, the greater the time available the greater the opportunities for extensive dispersal.

A comparison of the ranges of *Rana nicobariensis* (fig. 97) and *Rana limnocharis* (fig. 88) is pertinent here. Both species have apparently moved into the Philippines from Borneo (evidence for *limnocharis* on p. 486). Both species are abundant in similar situations in lowland Borneo—streams and ponds in cultivated areas and in the immediate vicinity of human habitation. This is also the habitat of *limnocharis* in the Philippines. Ecological information for Philippine *nicobariensis* is not available, but presumably it would have the same habitat preferences as on Borneo. Therefore, the range differences can not be attributed to the absence of the habitat. Nor can they be explained by differential vagility, as both species occur in large numbers, both are closely associated with man and his activities, and both utilize the same type of breeding site, all of which might be factors in waif dispersal. Competition with other amphibians can also be ruled out. All of the Philippine non-endemics associated with man occur side by side with *nicobariensis* on Borneo; indeed, some of them (*Rana cancrivora, Kaloula baleata, Bufo biporcatus,* and *Ooeidozyga laevis,* according to my own observations) are often found in the same ditch with *nicobariensis.* The only endemic species associated with man but not with *nicobariensis* are *Kaloula conjuncta, K. picta,* and *K. rigida.* They are replaced on Borneo by an ecological equivalent, *K. baleata,* which, as just noted, is found with *nicobariensis.* Predation, too, can be ignored, for most of the predators (primarily snakes) occurring in the Philippines are represented on Borneo either by conspecific populations or by closely related species. The best explanation for the differences in extent of range of *limnocharis* and *nicobariensis* is the duration of opportunity for dispersal that has been available to each.

By analogous arguments *nicobariensis* is probably a more recent immigrant than all of the non-endemics of the second, third, and fourth categories on page 498. This statement may be made despite differences in ecology. The necessary requirements of these comparisons are that the habitat of the less widespread species be present in unoccupied areas and that the less widespread species be as vagile as the more widespread. These conditions are satisfied in the comparisons of *nicobariensis* with other non-endemics.

Bufo biporcatus, with approximately the same range (fig. 82) as *nicobariensis,* has probably been in the Philippines for an equivalent length of time, although the fact that the Philippine populations are subspecifically distinct from the Bornean suggests that *biporcatus* may be a slightly older resident.

The species of the second and third categories (p. 498) are not as easy to deal with as the preceding. *Chaperina fusca* is a small, forest species. Its habitat and size combine to increase the difficulty with which it may be collected. The limitations of its range (fig. 91) may be apparent and the result of inadequate collecting rather than real. The only safe statement is that *Chaperina* entered the Philippines before *Bufo biporcatus* and *Rana nicobariensis.*

Megophrys hasselti has a greater range than *Chaperina* and approximately the same as that of *M. monticola* (figs. 84, 91). Both species of *Megophrys* inhabit the forest floor and have similar life cycles. However, *monticola* is limited to moderate or high elevations (over 400 meters) whereas *hasselti* occurs from sea level to over 1,500 meters. Since lowlands provide a barrier to the continuous over-land migration of montane forms, *monticola* should require more time to move from island to island than *hasselti.* Waif dispersal is not likely to have played a significant role in this case; neither species has characteristics predisposing it to accidental dispersal. If waif dispersal can be ignored, *monticola* must be adjudged the older Philippine inhabitant.

Following much the same line of reasoning, I can safely state that *Kalophrynus pleurostigma* (fig. 90), *Staurois natator* (fig. 83) and *Rana microdisca* (fig. 98) probably entered the Philippines after *M. monticola. Megophrys hasselti* can not be placed in sequence with these; nor is it safe to distinguish the first and last immigrants from among *S. natator, R. microdisca,* and *K. pleurostigma.* Their Philippine ranges are almost identical. Even though Palawan is not included in the distribution of *K. pleurostigma,* this difference may be due to chance. *Rana microdisca* has reached Negros but not the Calamians; the converse is true of *Staurois natator.* Differences in vagility may be responsible for the similarity of the ranges. Yet no conspicuous biological distinctions suggesting differential vagility are known except that *pleurostigma* seems to be less abundant than the others. The fact that only *R. microdisca* has distinct subspecies in the Philippines and Borneo may be indicative of longer residence in the Mindanao–Samar chain. But here ignorance of the relative rates of evolution reduces the value of speculation.

Kaloula baleata (fig. 96) is probably an earlier immigrant than *Bufo biporcatus* and *Rana nicobariensis*. It cannot be related to the other non-endemic species.

The last group of non-endemics includes the most widely distributed species. The group is not homogeneous. Two, *Rana signata* and *R. macrodon*, occur only in forests, secondary as well as primary, and are not associated with man. A third species, *Rhacophorus pardalis*, is most abundant within forests but is sometimes found in thickets at the edge of man-made clearings. Finally, *Rana cancrivora, R. limnocharis, Ooeidozyga laevis*, and *Rhacophorus leucomystax* are associated with the activities of man, occurring in cultivated fields (rubber plantations, rice fields, etc.) and in the immediate vicinity of human habitation. Because of the increased possibilities for waif dispersal occasioned by the association with man, the last four probably have greater vagility than the other three and hence are probably more recent immigrants. Some corroboration of this is given by the more extensive local differentiation exhibited by *Rana macrodon* and *R. signata*. Four Philippine subspecies are recognizable in *macrodon* and three in *signata;* none is identical with the corresponding Bornean population. By contrast, the Philippine populations of *R. cancrivora* are distinguishable neither from one another nor from the Bornean; the same is true of *Ooeidozyga laevis*. The Philippine populations of *Rana limnocharis* constitute one subspecies distinct from that of Borneo. Two Philippine subspecies of *Rhacophorus leucomystax* are known, one of which is represented on Borneo. Not enough specimens have been collected to determine whether subspeciation of *Rhacophorus pardalis* has occurred in the Philippines. On the basis of the evidence at hand, *Rana macrodon* and *R. signata* probably have been in the Philippines longer than *R. cancrivora, R. limnocharis, Ooeidozyga laevis*, and *Rhacophorus leucomystax*.

Both *Rana macrodon* and *R. signata* are probably earlier invaders than *R. microdisca* and *Staurois natator*. All four species are inhabitants of the forest floor and forest streams; all have aquatic free-swimming larvae; all are abundant, though *macrodon* seems to be the most common; all occur on Borneo. The foregoing facts do

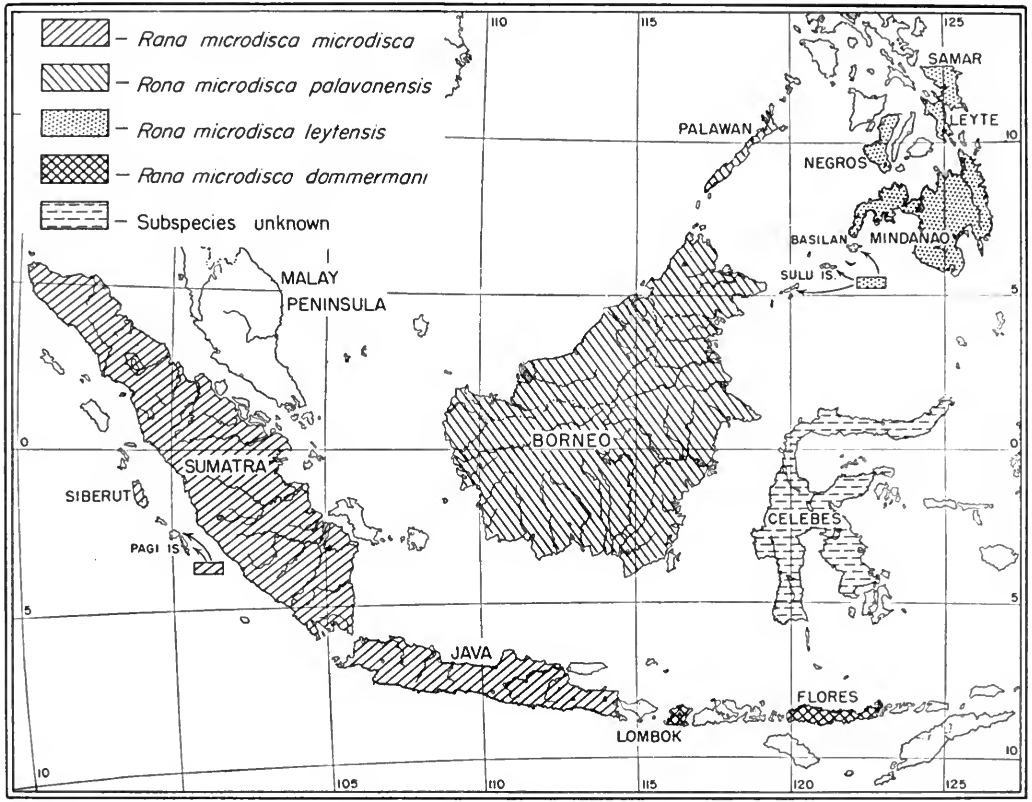

FIG. 98. Range of *Rana microdisca*.

not suggest differences in vagility. As adults *macrodon* should be the least susceptible to waif dispersal because of its large size, but it is the most widely distributed. The evidence of local differentiation supports the conclusion based on extent of range. The subspecies of *macrodon* and *signata* have been noted above; *microdisca* has two subspecies in the Philippines, one of which occurs on Borneo; as yet no subspecies of *Staurois natator* are recognized.

Differences in the extent of range of *Staurois natator* and *Rana microdisca* on the one hand and *Rana limnocharis, Rana cancrivora, Ooeidozyga laevis,* and *Rhacophorus leucomystax* on the other may be explained on the basis of differential vagility. By virtue of its association with man the latter group is much more likely to be distributed as waifs and probably has entered the Philippines no earlier and possibly even later than *S. natator* and *R. microdisca.*

It has been suggested above (p. 484) that *Rana erythraea* was carried into the Philippines by man. If this is true *erythraea* is one of the latest arrivals in the Philippines. The presence of *Bufo marinus* in the Philippines is definitely known to be the result of deliberate introduction by man within the last twenty years. This is the most recent addition to the Philippine amphibian fauna.

The integration of endemic and non-endemic species is difficult. It has been stated that the endemics generally include the older residents. Yet this may not be true in all cases. For example, *Rana everetti* is found throughout the archipelago with the exception of the Palawan–Calamian chain and the Sulu Islands, but it can not be said to have entered the Philippines earlier than the widespread non-endemic species, *R. signata.* The difficulty arises in this instance because of the presence of a close ally of *everetti* (*R. chalconota*) in Borneo. Additional study may show that *everetti* and *chalconota* are forms of the same species, in which case *everetti* and *signata,* for example, would have similar ranges. Yet *everetti* undoubtedly entered the Philippines prior to all of the non-endemic species that are not found from Mindanao to Luzon and probably before those widespread non-endemics that are associated with man.

The species of *Kaloula* (fig. 96) provide the only clear instance of integration of endemics and non-endemics. The range of *K. baleata* in the Philippines is limited to the Palawan–Luzon Arc and is interposed between that of the other Philippine species and the rest of the genus. By contrast, *K. picta* and *conjuncta* occur throughout the Philippines except on the Palawan–Calamian chain. The ranges of *picta* and *conjuncta* thus coincide with that of *baleata*

Table 50. A tentative relative time table of invasions of the Philippine Islands

Bufo marinus						
Rana nicobariensis		Rana erythraea		Bufo biporcatus		
Rana limnocharis Rana cancrivora Ooeidozyga laevis Rhacophorus leucomystax	Staurois natator Rana microdisca Kalophrynus pleurostigma	Chaperina fusca	Megophrys hasselti	Kaloula baleata	Cornufer meyeri Cornufer corrugatus Cornufer guentheri	
Rana signata	Rana everetti		Megophrys monticola	Kaloula conjuncta Kaloula picta	Cornufer hazelae Cornufer polillensis Cornufer subterrestris Cornufer cornutus	
Rana macrodon						
Rana sanguinea						Barbourula busuangensis

Newest elements are at the top. Vertical lines separate groups within which the order of entry may be approximated. Horizontal lines separate hypothetical invasions. Thus each block of species is presumed to have arrived prior to the ones above it. Within horizontal bands the vertical lines separate groups that can not be related to one another in the time sequence with reasonable assurance.

only on Luzon and, probably, Mindoro. These relations indicate that *picta* and *conjuncta* have had more time than *baleata* in which to spread through the Philippines. The difference in ranges of *picta* and *baleata* is not explicable on the basis of routes of dispersal. *Kaloula picta* occurs on Cuyo Island, an outlier of the submarine shelf on which Palawan is situated; Cuyo was probably accessible to Palawan over land during the Pleistocene (fig. 81). Therefore it seems likely that *picta* used the Palawan route also.

Nor is there reason to believe that differential vagility accounts for the range differences. Breeding habits and sites are uniform in these species. *K. baleata,* unlike *picta,* occasionally is found in trees; this trait should increase the possibilities of waif dispersal by winds. But *baleata* has the lesser range in the Philippines. Thus the available evidence leads to the conclusion that *conjuncta* and *picta* arrived in the Philippines before *baleata.*

The conclusions of the preceding section are summarized in Table 50.

The actual dating of the arrival of various stocks in the Philippines can only be tentatively suggested. Much more geologic information is needed to place speculations of this sort on a firm footing. Briefly, the geologic periods during which the relation of the Philippine archipelago with surrounding areas was most intimate were the Eocene and Pleistocene. Evidence for equally close associations in the Upper Miocene is weaker.

Among the Malaysian stocks, Philippine populations of *Rana nicobariensis* and *Bufo biporcatus* may date from the latest Pleistocene or post-Pleistocene. *Chaperina fusca, Kalophrynus pleurostigma, Kaloula baleata, Staurois natator,* and *Rana macrodon* were probably early Pleistocene arrivals in the Philippines. It has been estimated above that *Rana limnocharis, R. cancrivora, Rhacophorus leucomystax,* and *Ooeidozyga laevis* arrived in the Philippines prior to *Rana nicobariensis* but after *R. macrodon;* this would place their entry in the mid-Pleistocene.

The wide geographic separation from their most closely related congeners and their endemism indicate a much earlier arrival date for the stock(s) giving rise to *Kaloula conjuncta, picta,* and *rigida.* They were probably pre-Pleistocene, and, until the Pliocene history is better known, may be considered as Miocene invaders. The endemic *Rana woodworthi* is probably of equal age. The relict nature of *Rana sanguinea* is indicative of antiquity and it, too, may have been a Miocene arrival. *Barbourula busuangensis* appears to be a still older resident. We have already noted its primitive phyletic position and the absence of the family (otherwise) from the tropics. With the meagre evidence available it is impossible to decide between a Miocene or pre-Miocene date for *Barbourula.*

The fact that all Philippine amphibians with Papuan affinities are specifically distinct from the related species in the Moluccas and New Guinea whereas many Philippine forms are conspecific with Malaysian species in Borneo argues for very early Pleistocene or pre-Pleistocene arrival dates for Papuan stocks. It is not likely that all of the Papuan species would have significantly lower rates of evolution than half of the Bornean elements (all of the non-endemics). The difference in the degree of biological isolation of the *Cornufer cornutus–hazelae* and *C. meyeri–corrugatus* groups from their respective non-Philippine congeners suggests a much earlier date of entry for the former. If *meyeri* and *corrugatus* are Pliocene or Miocene in the Philippines, the date of entry of the *cornutus–hazelae* group is pushed back into the early Tertiary. *Oreophryne annulata* probably entered the Philippines at approximately the same time as *Cornufer meyeri* and *corrugatus.*

SUMMARY

The Amphibia of the Philippine Islands are largely endemic species of Malaysian affinities. Of the fifty-six species 61 per cent are endemic to the Philippine archipelago. For the sake of comparison it may be noted that 39 per cent of Borneo's eighty species are endemic. Forty-three Philippine species are clearly of Malaysian, nine of Papuan, one of Palaearctic, and two of unknown relations. One species has been introduced recently from the neotropics.

The gradual diminution of Malaysian and the concomitant increase of Papuan elements with increasing distance from Borneo makes difficult the definition of faunal divisions. Nevertheless, the Balabac–Palawan–Calamian chain may be set off from the remainder of the archipelago by virtue of the absence of Papuan genera. One species of the Palawan chain, *Rana sanguinea,* appears to have Papuan affinities; however, there is no evidence that *sanguinea* dispersed into the Philippines from the Papuan region. Further division of the Philippines based on the distribution of amphibians is inadvisable. The distributions of the genera of lizards and snakes confirm these conclusions.

Present specific distributions and geological data lead to the definition of two major routes of dispersal and one minor one. It is

evident that the bulk of the amphibian fauna entered the Philippines from Borneo by way of the Palawan group or by way of the Sulu Islands and Mindanao. Apparently dispersal of Papuan stocks into the Philippines has taken place along a Papuan–Moluccas–Talaud route.

It is not assumed that every species of amphibian found its way into the Philippines by means of gradual dispersal over land bridges. On the contrary there exists definite indication of saltatory or waif dispersal. It is known, for example, that *Bufo marinus* was deliberately introduced into the Philippines by man. *Oreophryne annulata* probably entered the archipelago through some mode of waif dispersal. But whether any given species has spread into the Philippines gradually over land bridges or by jumping water gaps, the dispersal routes outlined are the most probable, for it is along these lines that the geological evidence indicates that water gaps between successive islands were narrowest.

Utilizing the extent of range and the relationships among species, it is possible to formulate a tentative order in which the fauna entered the Philippine Islands. Probably the relict *Barbourula busuangensis* has been in the Philippines longer than any other species. *Rana sanguinea* is also a relict and represents an early invasion. Various non-relict endemics represent subsequent though still early waves of immigration. More recent invasions are indicated by non-endemic species such as *Staurois natator* and *Kaloula baleata*. The ranges of *Rana nicobariensis* and *Bufo biporcatus* suggest that they are very recent arrivals. The complete tentative order is given in Table 50.

Appendix: FAUNAL LISTS[1]

BALABAC

Megophrys monticola ligayae
Bufo biporcatus philippinicus
Rana macrodon acanthi
Ooeidozyga laevis laevis
Philautus longicrus
(*Rhacophorus leucomystax linki*)

BASILAN

Megophrys hasselti
Megophrys monticola stejnegeri
Pelophryne brevipes
Rana micrixalus
Rana microdisca leytensis
Rana macrodon magna
Rana cancrivora cancrivora
Rana signata grandocula
Staurois natator
Cornufer meyeri
Rhacophorus appendiculatus appendiculatus
Rhacophorus leucomystax quadrilineatus
Philautus spinosus
Philautus acutirostris
Kalophrynus pleurostigma pleurostigma
Ichthyophis monochrous
(*Ooeidozyga laevis laevis*)
(*Ooeidozyga diminutiva*)
(*Kaloula conjuncta*)

BILIRAN

Philautus leitensis
Oreophryne annulata

BOHOL

Rana macrodon visayanus
Rana signata grandocula
Rhacophorus pardalis pardalis
(*Rana cancrivora cancrivora*)
(*Ooeidozyga laevis laevis*)
(*Rhacophorus leucomystax quadrilineatus*)

BUSUANGA

Barbourula busuangensis
Bufo biporcatus philippinicus
Rana sanguinea
Rana macrodon acanthi
Rana cancrivora cancrivora
Rana signata moellendorffi
Ooeidozyga laevis laevis
Staurois natator
(*Rhacophorus leucomystax linki*)

CAMAGUIN

Rana cancrivora cancrivora

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[1] The species in parentheses have not as yet been recorded from the islands under which they are listed, but, as explained (p. 462), it is highly probable that they occur as indicated.

CEBU

Rana cancrivora cancrivora
Rhacophorus leucomystax quadrilineatus
(*Rana macrodon visayanus*)
(*Ooeidozyga laevis laevis*)
(*Kaloula picta*)

CULION

Bufo biporcatus philippinicus
Rana sanguinea
Rana macrodon acanthi
Rana cancrivora cancrivora
Rana signata moellendorffi
Ooeidozyga laevis laevis
Staurois natator
Rhacophorus appendiculatus appendiculatus
(*Rhacophorus leucomystax linki*)

CUYO

Rana cancrivora cancrivora
Kaloula picta

DINAGAT

Megophrys monticola stejnegeri
Rana macrodon visayanus
Ooeidozgya laevis laevis
Staurois natator
Cornufer guentheri
Cornufer meyeri
Rhacophorus appendiculatus appendiculatus
Rhacophorus pardalis pardalis
(*Rana cancrivora cancrivora*)
(*Rhacophorus leucomystax quadrilineatus*)
(*Kaloula picta*)

DUMARAN

Bufo biporcatus philippinicus
Rhacophorus leucomystax linki

GUIMARAS

Kaloula conjuncta negrosensis

LEYTE

Megophrys monticola stejnegeri
Rana microdisca leytensis
Rana everetti albotuberculata
Rana macrodon visayanus
Rana cancrivora cancrivora
Rana signata similis
Ooeidozyga laevis laevis
Staurois natator
Cornufer guentheri
Cornufer meyeri
Cornufer corrugatus
Rhacophorus leucomystax quadrilineatus
Philautus leitensis
Kalophrynus pleurostigma pleurostigma
Kaloula picta
Kaloula conjuncta stickeli

LUBANG

Rana cancrivora cancrivora
Cornufer meyeri

LUZON

Bufo marinus
Rana everetti luzonensis
Rana limnocharis vittigera
Rana woodworthi
Rana macrodon macrocephala
Rana signata similis
Rana cancrivora cancrivora
Ooeidozyga laevis laevis
Cornufer guentheri
Cornufer hazelae
Cornufer meyeri
Cornufer corrugatus
Cornufer subterrestris
Cornufer cornutus
Rhacophorus pardalis pardalis
Rhacophorus surdus
Rhacophorus leucomystax quadrilineatus
Philautus williamsi
Kaloula rigida
Kaloula picta
Kaloula conjuncta conjuncta
Kaloula baleata kalingensis

MACTAN

Rana cancrivora cancrivora
Rhacophorus leucomystax quadrilineatus
Kaloula picta

MINDANAO

Megophrys hasselti
Megophrys monticola stejnegeri
Pelophryne brevipes
Ansonia muelleri
Rana everetti everetti
Rana limnocharis vittigera
Rana micrixalus
Rana parva
Rana microdisca leytensis
Rana macrodon magna
Rana cancrivora cancrivora
Rana signata grandocula
Ooeidozyga diminutiva
Ooeidozyga laevis laevis
Staurois natator
Cornufer guentheri
Cornufer meyeri
Cornufer corrugatus
Rhacophorus appendiculatus appendiculatus
Rhacophorus pardalis pardalis
Rhacophorus leucomystax quadrilineatus
Rhacophorus emembranatus
Rhacophorus lissobrachius
Philautus spinosus
Philautus acutirostris
Philautus bimaculatus
Philautus sp.
Oreophryne annulata
Chaperina fusca
Kalophrynus pleurostigma pleurostigma
Kaloula picta
Kaloula conjuncta meridionalis
Ichthyophis monochrous

MINDORO

Megophrys hasselti
Rana limnocharis vittigera
Rana macrodon macrocephala
Rana cancrivora cancrivora
Rana signata similis
Ooeidozyga laevis laevis
Cornufer meyeri
Cornufer corrugatus
Rhacophorus leucomystax quadrilineatus
Philautus schmackeri
Kaloula picta
Kaloula conjuncta conjuncta
(*Kaloula baleata*)

NEGROS

Bufo marinus
Rana limnocharis vittigera
Rana everetti everetti
Rana erythraea
Rana microdisca leytensis
Rana macrodon visayanus
Rana cancrivora cancrivora
Ooeidozyga laevis laevis
Cornufer hazelae
Cornufer meyeri
Cornufer corrugatus
Rhacophorus pardalis pardalis
Rhacophorus leucomystax quadrilineatus
Kaloula picta
Kaloula conjuncta negrosensis

PALAWAN

Megophrys hasselti
Megophrys monticola ligayae
Pelophryne albotaeniata
Bufo biporcatus philippinicus
Rana nicobariensis nicobariensis
Rana limnocharis vittigera
Rana sanguinea
Rana microdisca palavanensis
Rana macrodon acanthi
Rana cancrivora cancrivora
Rana signata moellendorffi
Ooeidozyga laevis laevis
Micrixalus mariae
Staurois natator
Rhacophorus everetti
Rhacophorus leucomystax linki
Philautus longicrus
Philautus sp.
Chaperina fusca
Kaloula baleata baleata
Ichthyophis monochrous

PANAY

Bufo marinus
Rana erythraea
Rana macrodon visayanus
Rana cancrivora cancrivora
Ooeidozyga laevis laevis
Cornufer hazelae
Rhacophorus leucomystax quadrilineatus
(*Kaloula conjuncta negrosensis*)

POLILLO

Rana everetti luzonensis
Rana limnocharis vittigera
Rana woodworthi
Rana macrodon macrocephala
Rana signata similis
Ooeidozyga laevis laevis
Cornufer meyeri
Cornufer polillensis
Cornufer guentheri
Cornufer corrugatus
Rhacophorus appendiculatus appendiculatus
Rhacophorus pardalis pardalis
Philautus williamsi
Kaloula picta
Kaloula conjuncta conjuncta
(*Rana cancrivora cancrivora*)
(*Rhacophorus leucomystax quadrilineatus*)

SAMAR

Megophrys monticola stejnegeri
Rana microdisca leytensis
Rana cancrivora cancrivora
Ooeidozyga laevis laevis
Staurois natator
Cornufer meyeri
Rhacophorus hecticus
Rhacophorus leucomystax quadrilineatus
Kalophrynus pleurostigma pleurostigma
(*Rana everetti*)
(*Rana macrodon visayanus*)
(*Rana signata*)
(*Cornufer guentheri*)
(*Kaloula picta*)

SIARGAO

Kalophrynus pleurostigma pleurostigma

SIBUYAN

Rana erythraea

SIQUIJOR

Rana macrodon visayanus
Rana cancrivora cancrivora
Ooeidozyga laevis laevis

SULU ARCHIPELAGO

Rana nicobariensis nicobariensis
Rana melanomenta
Rana microdisca leytensis
Ooeidozyga diminutiva
Rhacophorus leucomystax linki
Philautus alticola
Chaperina fusca
(*Rana cancrivora cancrivora*)
(*Ooeidozyga laevis laevis*)

TABLAS

Rana erythraea
Rana cancrivora cancrivora
Cornufer meyeri
(*Rhacophorus leucomystax quadrilineatus*)
(*Ooeidozyga laevis laevis*)

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Principal taxonomic discussion indicated by **bold-faced** type.

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